VISUAL INFORMATION PROCESSING IN THE ABSENCE OF AWARENESS

by

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Abstract

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Several popular theories of consciousness propose that conscious representations entail deeper or more complex forms of information processing. We question this view and show that unconscious perception is more powerful than previously thought. In the first set of experiments we explore brightness perception, one of the most fundamental aspects of vision. We show, using a combination of metacontrast masking and priming, that the simultaneous brightness contrast (SBC) illusion occurs without awareness. These results demonstrate that our visual systems account for stimulus context in brightness perception for stimuli that we are unaware of. Our results further suggest that SBC occurs early during visual processing, likely within the initial feedforward sweep. We then extend these observations and demonstrate that activation of complex stimulus-response mappings also occurs unconsciously, when stimulus processing times are adequate. One of the key claims these results support is that some of the apparent differences between unconscious and conscious vision are due to differences in information processing times, as opposed to consciousness. We also show, using transcranial magnetic stimulation (TMS), that unconscious shape priming requires primary visual cortex at specific temporal phases of processing. Because the later temporal phase of processing suppression has been proposed to interfere with feedback activity, our results further suggest that feedback is also essential for unconscious processing and may not necessarily be a signature of conscious vision. Together our results demonstrate that complex visual information can also be represented unconsciously, and suggest that conscious and unconscious vision use similar neural pathways and processes.

Dedication

To my parents, Marija and Franc Persuh.

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Chapter 1

General Introduction

One of the most challenging topics in neuroscience concerns the nature of consciousness[1] (Crick & Koch, 2003). Whereas consciousness has been explored in all sensory modalities, it is the visual consciousness that is best understood mostly because our knowledge of the visual system is most advanced (Crick & Koch, 1990). Most experimental approaches are oriented towards examining the types of information that can be processed in the absence of awareness. The hope is that these answers will provide a clue for understanding the function of consciousness. Another important problem concerns the differences between neural activities that give rise to consciousness, also known as the neural correlates of consciousness (NCC) (Crick & Koch, 2003), and those that do not. Several proposals argue for a fundamental difference between these two types of processing. According to the duplex theory of vision (Milner & Goodale, 1995), it is the dorsal stream that supports vision for action; processing along this pathway remains outside awareness. Processing along the ventral stream, allows vision for perception, and gives rise to conscious experience. Similarly, some have proposed that processing that remains unconscious extracts only basic physical aspects of our environment (e.g., wavelength); and processing subserving conscious vision is necessary for perception of (e.g., color) (Breitmeyer, Ro, & Singhal, 2004). In Chapter 2 we examine the role of consciousness in the perception of context-induced brightness and show that such information is available even when stimuli are invisible. We extend these findings in Chapter 3, where we demonstrate that activation of complex stimulus response (SR) mappings proceeds in the absence of awareness but only for sufficient processing times. We further show in Chapter 4 that primary visual cortex (V1) and recurrent processing are necessary for unconscious shape processing. Together these experiments reveal that processing in the absence of awareness is much more powerful than previously

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[1] Throughout the text the terms consciousness and awareness are used interchangeably and refer to the subjective experience or visibility of stimuli.

expected and that the same neural structures and pathways support both conscious and unconscious perception.

Processing of simple stimulus features in the absence of awareness

The visibility of a stimulus can be manipulated by adjusting its properties such as contrast or duration. However, visual masking (Breitmeyer & Öğmen, 2006) is the method of choice for most studies of awareness. In metacontrast masking (Kahneman, 1968) the visibility of a first stimulus is reduced or eliminated by the presentation of a second stimulus, a mask, which follows the first stimulus at an optimal, experimentally determined stimulus onset asynchrony (SOA). In this type of masking, the first stimulus fits inside the contours of the second stimulus but the two stimuli do not spatially overlap. To investigate the processing of the first stimulus, masking is usually combined with response priming. In priming, a presentation of one stimulus, the prime, affects the processing of another stimulus, the target. Depending on experimental parameters, the prime can facilitate or interfere with target processing. In an illustrative example, Klotz and Wolfe (Klotz & Wolff, 1995) investigated unconscious priming with metacontrast masking by presenting circular, diamond or square shaped primes for a short duration. Following the prime, a second stimulus, a diamond or square-shaped metacontrast mask, was presented at an optimal SOA. The mask, which rendered the prime invisible, also served as a target to which participants made speeded responses. Prime and mask combinations were categorized according to response compatibility. Primes and masks were congruent if they were assigned to identical responses, incongruent if they called for different responses or neutral if the prime carried no information about the response. Reaction times were fastest for congruent trials and slowest for incongruent trials. This experiment demonstrated that shape can be processed without awareness and that it can activate motor responses. Visibility of primes was tested in a separate forced-choice discrimination experiment, in which participants showed no better than chance performance. The authors proposed that unaware primes directly activated corresponding responses, as suggested by the direct parameter specification theory (Neumann, 1990). Using similar metacontrast masking procedures, several investigators have demonstrated processing without awareness for simple stimulus features like color (Breitmeyer, Öğmen, & Chen, 2004; Breitmeyer, Ro, Öğmen, & Todd, 2007; Breitmeyer, Ro, & Singhal, 2004; Schmidt, 2002) and shape (Breitmeyer, Öğmen, et al., 2004; Klotz & Wolff, 1995; Ro, Singhal, Breitmeyer, & Garcia, 2009).

Research on patients with damage to occipital or parietal cortex has provided converging evidence for processing without awareness. Blindsight patients, who have lesions in the primary visual cortex, demonstrate above chance performance on forced-choice discrimination tasks, although they claim no awareness for stimuli presented in the visual field corresponding to the scotoma (Weiskrantz, 1986). These patients can discriminate between locations, motion and wavelengths (Stoerig & Cowey, 1997; Weiskrantz, 1986, 1996). Damage to the parietal cortex (mostly in the right hemisphere) in some patients results in hemispatial neglect, an inability to see stimuli on the contralesional side; however, evidence suggests that these stimuli are processed without awareness and can affect patients' motor responses (Driver & Mattingley, 1998; Rafal, 1994).

Although experiments using visual masking and studies with patients demonstrate a significant processing of information without awareness, several investigators have suggested a fundamental distinction between processing that remains outside of awareness and processing that allows conscious perception. Some have proposed that visual control of action and perceptual processes involve two separate visual pathways: the dorsal stream culminating in posterior parietal cortex is involved in unconscious sensorimotor transformations, while the ventral stream terminating in the inferotemporal cortex is associated with conscious perception of objects (Milner & Goodale, 1995). Others have argued that visual information outside of awareness is represented at an earlier, stimulus dependent level of encoding (e.g., wavelength) and visual information giving rise to awareness at the percept level (e.g., color) (Breitmeyer et al., 2007; Breitmeyer, Ro, & Singhal, 2004).

In Chapter 2 we describe experiments that employ unconscious priming using metacontrast masking to address this putative distinction. Brightness, one of the most fundamental visual features, refers to the subjective experience of the surface luminance. It has been known for a long time that there is no simple relationship between the luminance and the brightness of an object. The fact that the brightness of an object depends on the context has been explored in a number of brightness illusions (Palmer, 1999; Purves, Williams, Nundy, & Lotto, 2004). A classical example is simultaneous brightness contrast (SBC), where one perceives a neutral gray object as darker/brighter when presented on a more/less luminant background. In Chapter 2 we ask whether our visual system is able to process the SBC illusion and thus account for the stimulus context in the absence of awareness.

Limits of processing in the absence of awareness

Although there is now substantial evidence for processing of simple stimulus features such as brightness and color in the absence of awareness, demonstrations of more complex processing such as the processing of semantic information, are more limited. Two important studies (Dehaene et al., 1998; Greenwald, Draine, & Abrams, 1996) provided some convincing evidence for unconscious semantic priming, however skeptics soon pointed out that priming effects were likely due to learned stimulus-response (SR) associations (Damian, 2001). This critique was based on the direct motor specification hypothesis (Neumann & Klotz, 1994), which proposes that stimuli are directly mapped to their responses without the need for semantic processing. Damian (2001) has shown that only subliminal primes included in the target set give rise to significant priming. In interpreting these results, Damian suggested that responding to target stimuli establishes direct mapping between target and response; thus when the same stimuli are presented as primes they automatically activate the response. However, another study used a set of primes that were never presented as targets and demonstrated semantic priming (Naccache & Dehaene, 2001). Subsequent studies have confirmed semantic priming for novel stimuli in the absence of perceptual awareness (Greenwald, Abrams, Naccache, & Dehaene, 2003; Reynvoet, Gevers, & Caessens, 2005).

Kunde and colleagues (Kunde, Kiesel, & Hoffmann, 2003) have proposed that subliminal primes owe their effect not to semantic processing or practiced SR associations but to pre-specified action triggers. In the first step, participants select relevant stimulus categories that fit specific motor responses. Then, during the task, the incoming stimulus is matched to a pre-specified action trigger. Others have insisted that some experimental evidence cannot be adequately explained by the action trigger account and argue that for certain tasks subliminal semantic processing occurs (Reynvoet et al., 2005). Thus, the issue of subliminal semantic priming in masking paradigms remains unresolved and intensely debated (Kunde, Kiesel, & Hoffmann, 2005; Van Opstal, Reynvoet, & Verguts, 2005a, 2005b).

Are there any cognitive processes that are in the exclusive domain of consciousness? More complex and flexible behavior, based on higher cognitive functions, such as response inhibition, task-switching or conflict resolution, is generally thought to require consciousness. Several leading theories of awareness postulate a global workspace framework (Baars, 1988, 2002; Dehaene & Naccache, 2001) and argue for a major role of the prefrontal cortex (PFC) in consciousness. In the global workspace model, different brain regions process information in parallel. This modular processing is unconscious; however, information can become conscious if the active modules that represent that information receive top-down attentional amplification. The PFC is vital for the mobilization of separate modules into the active global network, and therefore the coherent activity that gives rise to conscious experience.

Inhibitory control is an example of a higher cognitive function which depends substantially on the prefrontal cortex (PFC) (Casey et al., 1997; Konishi et al., 1999; Picton et al., 2007), and is believed to require awareness. If PFC activity is indeed associated with awareness, then inhibitory control, which requires PFC, might not be possible for unconscious stimuli. Tsushima and colleagues (Tsushima, Sasaki, & Watanabe, 2006) have shown that task irrelevant unconscious motion is not subject to inhibitory control by PFC. However, abundant evidence from the metacontrast masking paradigm combined with a Go/No-Go task suggests inhibitory control by PFC for unconscious stimuli (Cohen, van Gaal, Ridderinkhof, & Lamme, 2009; van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008). Other studies contrasting conscious and unconscious vision in tasks that required higher cognitive functions such as sequential modulation of congruency effects (Ansorge, Fuchs, Khalid, & Kunde, 2011; Kunde, 2003; but see van Gaal, Lamme, & Ridderinkhof, 2010), context-specific prime-congruency effects (Heinemann, Kunde, & Kiesel, 2009), conflict detection in 2-choice flanker task (Scheffers & Coles, 2000) or saccade-error awareness (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001) suggest a special role of awareness. However, recent findings also suggest unconscious triggering of task-set preparation (Lau & Passingham, 2007; Reuss, Kiesel, Kunde, & Hommel, 2011; Wokke, van Gaal, Scholte, Ridderinkhof, & Lamme, 2011) or conflict detection (Ursu, Clark, Aizenstein, Stenger, & Carter, 2009). The issue of whether the operations that monitor and control cognitive processes occur outside awareness is currently a subject of intense debate (Desender & Van den Bussche, 2012; Eimer & Schlaghecken, 2003; Kunde, Reuss, & Kiesel, 2012; Mayr, 2004; van Gaal, de Lange, & Cohen, 2012; van Gaal & Lamme, 2011).

Complex stimulus-response mapping requires consciousness

A well-known example of cognitive flexibility, which is generally thought to require consciousness, is the learning and execution of new arbitrary SR associations. These capabilities include assigning different stimuli to the same responses, which is a form of categorical learning. Flexible rule learning, as well as skills for learning arbitrary SR mappings and their execution, rely on intact frontal lobes, specifically the PFC and the premotor cortex (Fuster, 2001; Petrides, 1985, 1990). Similar evidence has been obtained in non-human primates (Gaffan & Harrison, 1988, 1989; Halsband & Passingham, 1982; Petrides, 1982). The PFC represents new SR associations and biases response selection for particular stimulus presentations (Miller & Cohen, 2001; Murray, Bussey, & Wise, 2000).

With practice, execution of novel arbitrary mappings becomes faster, more efficient and automatic. There is extensive evidence in the literature that the neural structures for controlled processes are distinct from those involved in automatic processing. With the acquisition of automaticity, the contribution of cortical structures is reduced, while the role of subcortical structures, especially the basal ganglia, is increased (Debaere, Wenderoth, Sunaert, Van Hecke, & Swinnen, 2004; Seitz & Roland, 1992). Once automatic execution of arbitrary mappings is achieved, conscious control might not be necessary, which would be consistent with significant reduction in the activity of the frontal cortical structures. An alternative hypothesis, however suggests that basal ganglia play a dominant role in the initial stages of learning (Bar-Gad, Morris, & Bergman, 2003; Houk & Wise, 1995). For example, one recent study has revealed rapid changes in learning related activity in striatum compared to more gradual changes in the prefrontal cortex (Pasupathy & Miller, 2005). The classical view will thus likely need a substantive revision as accumulating evidence suggests significant contributions of subcortical structures to initial learning (Ashby, Turner, & Horvitz, 2010).

Some evidence suggests that complex SR mappings require awareness (Ro et al., 2009). Such a suggestion seems plausible considering the well documented role of the PFC in complex cognitive tasks as well as the proposed role of the PFC in controlling access to consciousness. Is complex SR mapping possible exclusively in the domain of consciousness? In Chapter 3 we describe a set of experiments in which we dissociated prime processing requirements from visual awareness and examined the activation of complex SR mappings in the absence of awareness.

Visual pathways mediating unconscious shape priming

If unconscious and conscious perceptionare fundamentally different they might depend on separate neural pathways and mechanisms. Much is known about the neuroanatomical details of different visual pathways. In the geniculo-striate pathway, visual information is relayed from the retina via the lateral geniculate nucleus of thalamus (LGN) to the primary (striate) visual cortex (V1). From V1, fibers project to extrastriate visual areas (Felleman & Van Essen, 1991). Although the geniculo-striate pathway is the most important visual pathway in humans, other pathways have been documented, which do not involve the primary visual cortex. For example, some fibers from the LGN bypass V1 and directly project to the extrastriate areas (Sincich, Park, Wohlgemuth, & Horton, 2004). In addition a large number of fibers project from the superior colliculus to the pulvinar of the thalamus and terminating in the extrastriate visual cortex

(Poppel, Held, & Frost, 1973). While the neuroanatomy of different visual pathways is well characterized, much less is known about their contributions to conscious and unconscious visual perception.

In Chapter 4 we present an experiment that investigated whether early visual cortex (V1/V2) and recurrent processing are necessary for shape processing in the absence of awareness. A large body of evidence suggests an important role of V1 in awareness. For example, an elegant functional MRI study has demonstrated that activity in V1 correlates with conscious visual perception (Ress & Heeger, 2003). Converging evidence is provided by studies on blindsight patients with lesions in V1, who demonstrate accurate performance on discrimination tasks, even though they claim no awareness of the stimuli presented in the blind field (Weiskrantz, 1986). Although critics sometimes point out that blindsight may be a result of neural plasticity that develops in time after the lesion to V1, similar effects have been demonstrated in non-clinical populations. In neurologically normal people, transient lesions can be induced using transcranial magnetic stimulation (TMS). In TMS, a brief electromagnetic pulse from a metallic coil placed on the subject’s scalp, temporarily disrupts cortical activity. In one of the earliest TMS studies Amassian and colleagues (Amassian et al., 1989) applied TMS pulses over the occipital cortex of participants performing a letter discrimination task. In this experiment the TMS pulse completely eliminated letter visibility. TMS is therefore a suitable experimental approach to consciousness, since cortical disruption is only transient. Using transcranial magnetic stimulation (TMS) of V1/V2, Boyer and colleagues demonstrated unconscious processing of color and orientation in neurologically normal individuals and suggested that residual visual processing can occur without V1/V2, possibly through the geniculo-extrastriate pathway (Boyer, Harrison, & Ro, 2005). These studies suggest that processing outside awareness proceeds through alternative pathways, bypassing V1/V2.

Others have proposed that the fundamental distinction between processing outside of awareness and processing that gives rise to awareness is not in specificity of visual pathways but instead relies upon two separate modes of information processing. According to these views unconscious perception is supported by the initial feedforward sweep, whereas conscious perception requires feedback or recurrent processing stages (Di Lollo, Enns, & Rensink, 2000; Lamme & Roelfsema, 2000; Lamme, 2001).

In Chapter 4 we adopted the priming paradigm developed in Chapter 3. To suppress the visibility of shape primes we used TMS to disrupt neural activity in V1/V2 at varying temporal intervals. These experiments revealed the contributions of V1/V2 and recurrent processing to unconscious shape priming.

Chapter 2

Context-dependent brightness priming occurs without visual awareness

Abstract

It has long been known that the human visual system accounts for stimulus context in brightness perception. Whether such context-dependent brightness processing occurs for stimuli that we are unaware of, however, has not been established. We therefore assessed whether brightness processing occurs in the absence of visual awareness, and whether different stimulus contexts influence brightness processing, by measuring unconscious priming with metacontrast masking. To induce context-dependent brightness differences, a middle-gray priming disk was presented on either a darker or brighter background to induce a simultaneous brightness contrast. When the middle-gray disk was presented on a darker (or brighter) background, such that it could be consciously perceived as brighter (or darker), reaction times were significantly faster to a bright (or dark) annulus than to a dark (or bright) annulus. We further show that context-dependent brightness priming does not correlate with visibility using objective measure of awareness (Experiment 1) and that context-dependent brightness priming, but not stimulus-dependent/context-independent brightness priming, occurs as strongly for stimuli below the subjective threshold for visual awareness as for those above it (Experiment 2). These results suggest that simultaneous brightness contrast occurs at very early levels of visual input and is not influenced by conscious perception.

Introduction

Because of capacity limitations, our visual systems must continuously extract relevant from irrelevant information from our environments to successfully guide behavior. As a result, it is a common notion that we only process and consciously experience a small fraction of visual information at any given time. Compelling evidence now suggests, however, that significant amounts of information can be unconsciously processed to very extensive levels of representations. For example, several studies have demonstrated that an unconscious prime can modulate responses to a subsequent shape (Neumann & Klotz, 1994; Klotz & Wolff, 1995; Klotz & Neumann, 1999; Ro et al., 2009), color (Schmidt, 2002; Breitmeyer, Ro, & Singhal, 2004), and even semantic information (Dehaene et al., 1998).

A series of studies from our laboratory has further suggested that unconscious visual information may be represented differently from consciously perceived visual information (Breitmeyer et al., 2007; Breitmeyer, Ro, & Singhal, 2004). Using a metacontrast masking procedure (Breitmeyer & Öğmen, 2000, 2006), in which a prime stimulus was rendered invisible by using a spatially adjacent but non-overlapping mask, we demonstrated a dissociation between unconscious and conscious priming. Specifically, we showed that white primes, which were consciously perceived as a bluish-white color but physically composed of mostly green light on a CRT monitor, produced priming effects resembling green primes when unconsciously presented. These results suggest that priming from unconscious visual stimuli is based on raw, physical features (wavelength), while priming from consciously processed stimuli is percept-dependent.

In the current study, we examined whether such a distinction between conscious and unconscious levels of representation might be demonstrated for another visual property, namely brightness. The perception of brightness, arguably the most basic aspect of vision, is produced not only by stimulus luminance (i.e., the physical intensity of the light stimulus), but also by the luminance of other objects in the scene. For example, a gray object on a dark background is perceived brighter than the same gray object on a bright background, an extremely robust and extensively studied phenomenon referred to as simultaneous brightness contrast (SBC). Typically, SBC involves awareness in that it is the subjective perceptual experience of a surface property. However, whether SBC stimuli can be unconsciously processed and produce priming effects similar to those that are consciously perceived remains heretofore unknown. We therefore assessed whether SBC occurs in the absence of awareness or whether only purely luminance-based brightness processing without any influences from stimulus context (i.e., the brightness of the background) occurs unconsciously.

In addition to assessing whether SBC occurs both consciously and unconsciously, we also indirectly assessed the level at which SBC might be occurring. One of the most common explanations of SBC suggests that illusory brightness is a result of early encoding that is based on lateral interactions between cells at the earliest input levels of the visual system (i.e., the retina). However, examples incompatible with this explanation have been constructed (Cornsweet, 1970; Gilchrist, 1977; Adelson, 1993), and some evidence also suggests the involvement of higher order processes that are dependent on experience (Williams, McCoy, & Purves, 1998a, 1998b). Because we manipulated the brightness and visibility of the prime stimulus and evaluated its effects on a trailing metacontrast mask that was either congruent or incongruent in brightness, our experimental design allowed us to distinguish between two different explanations for SBC:

1) If SBC occurs only with awareness of the stimuli, then priming from unaware stimuli should be based only on physical properties of the primes (i.e., luminance), whereas priming

from visible stimuli should reflect context-dependent levels of processing. Such results would be more in agreement with higher level explanations of SBC in that context-dependent effects would only occur with visual awareness.

2) On the other hand, if SBC is coded at early levels of visual processing prior to presumably later, context-dependent perceptual effects, then we should expect similar priming effects from both visible and invisible stimuli. Such results would be more consistent with low level theories of SBC that do not presuppose influences from higher level perceptual processes that may require visual awareness.

We also used both objective and subjective measures of awareness because of a long standing debate regarding the optimal ways for measuring awareness (Eriksen, 1960; Holender, 1986; Merikle, Smilek, & Eastwood, 2001; Hannula, Simons, & Cohen, 2005; Schmidt & Vorberg, 2006; Wiens, 2007). An objective criterion, based on the ability to discriminate stimuli, is problematic because it requires accepting the null-hypothesis (e.g., chance-level performance). Additionally, it can underestimate unconscious perception; in many circumstances human observers can discriminate above chance while claiming no subjective experience (e.g., as in blindsight, in which patients with visual cortex damage can discriminate visual information without awareness). Because of these shortcomings, many authors emphasize subjective reports (Merikle et al., 2001; Dehaene & Changeux, 2011). Although subjective reports might be influenced by response biases, they better capture the nature of subjective experience, which is what motivates consciousness research in the first place. Our findings reported here therefore rely primarily on subjective measure of awareness, although we provide converging evidence using objective measures. The results from two experiments, which used these different measures for assessing visual awareness, both show that SBC can be processed unconsciously, and they suggest that this illusion occurs at early levels of visual encoding.

Experiment 1

Using metacontrast masking we tested whether context-dependent brightness priming requires awareness. In the SBC conditions, a middle-gray priming disk was briefly presented on either a darker or brighter background to induce a context-dependent brightness of the disk via SBC. To assess whether luminance-dependent (non-SBC) brightness processing also occurs without awareness, a dark or bright priming disk was presented on a middle-gray background (constant context). We manipulated the visibility of the prime stimuli by using two different prime-mask intervals: one that ensures optimal masking (low visibility) and one for non-optimal masking (high visibility).

Method

Participants

Twenty-two subjects (11 female), between the ages of 18 and 36 (M= 20.6 years), were recruited from the undergraduate subject pool of The City College of the City University of New York. All observers had normal or corrected to normal vision and participated after informed consent.

Stimuli and Apparatus

Two 16” CRT monitors (Sony Model G220) with a refresh rate of 100 Hz were used for testing. All stimuli were presented at the center of the monitor and consisted of a fixation cross measuring 0.1^{o} of visual angle, disks with a diameter of 0.53^{o} of visual angle, and annulus masks with an inner diameter of 0.53^{o} and outer diameter of 1.06^{o}. The masks also served as the targets in this experiment. The remaining 20% of the trials were catch trials in which no disk and only the mask was presented. To generate the stimuli, we used three levels of luminance (dark = 4.0

cd/m^2; middle-gray = 11.1 cd/m^2; bright = 18.8 cd/m^2 for one monitor and dark = 5.4 cd/m^2; middle-gray = 13.2 cd/m^2; bright = 21.4 cd/m^2 for the other monitor). For the non-SBC conditions, a bright or dark disk was presented on a middle-gray background. The disk was followed by a dark or bright annulus, also presented on a middle-gray background (Fig.1, left). The four combinations of disks and annuli formed two categories: congruent (a dark or bright disk followed by a dark or bright annulus, respectively) and incongruent (a dark or bright disk followed by a bright or dark annulus, respectively). Note that for the congruent conditions, the disks and masks were identical in luminance and appearance, and this is what we refer to as the non-SBC conditions. Note, however, that non-SBC does not imply that the perception of disk brightness is independent of the background, but rather that the background luminance was always the same and disk brightness was manipulated by changing the actual luminance of the disks.

For the SBC conditions, middle-gray disks that were intermediate in luminance between the bright and dark masks were presented on a bright or dark background followed by a bright or dark annulus presented on the middle-gray background (Fig. 1, right). Although the luminance of the middle-gray disk was the same on either background, the middle-gray disk on the dark background was perceived as bright, whereas the middle-gray disk on the bright background was perceived as dark. The four disk/annulus combinations formed two categories: congruent (middle-gray disk on a dark/bright background followed by a bright/dark annulus on a middle-gray background) and incongruent (middle-gray disk on a dark/bright background followed by a dark/bright annulus).

Procedures

Subjects were seated in a dimly lit, sound attenuated chamber. Chin rests were used to minimize head movements and to fix the eye-to-monitor viewing distance at 57 cm. Each trial started with the presentation of the fixation cross for 1000 ms (Fig. 1). On 80% of the trials, the disk was then presented for 10 ms and the annulus mask (target) for 20 ms at a stimulus onset asynchrony (SOA) of either 40 or 140 ms. These SOAs were chosen based on previous research and pilot experiments that showed that subjects were unaware of the disks at the short SOA (low visibility) and aware of the disks at the long SOA (high visibility). The order of presentation of the two SOAs was randomized within each block. On the 20% of catch trials, no disk was presented, but the mask was presented at the same intervals within the trials as the disk present trials. The subjects participated in two phases of the experiment, which together lasted approximately 45 minutes. In the first phase, subjects completed five blocks of 90 trials, each with short rest periods between blocks. On each trial, subjects reported whether the mask was bright or dark by pressing one of two response buttons on the mouse as quickly as possible. In the second phase, which was conducted to objectively determine prime visibility, subjects completed five blocks of 90 trials each in which they were asked to report the brightness of the priming disks (dark/bright) by pressing one of two response buttons on a mouse. They were encouraged to guess if necessary. The presentation order of the different disks and annuli combinations was randomized within each block. The response assignments were counterbalanced between the subjects, with half of the subjects using the left mouse button to indicate a bright stimulus and the right mouse button to indicate a dark stimulus and the other half of the subjects using the left mouse button to indicate a dark stimulus and the right mouse button to indicate a bright stimulus.

Results and Discussion

Whereas prime and mask stimuli were presented on the same background in the non-SBC conditions, this was not the case for the SBC conditions. To induce SBC, a middle-gray disk was presented on either a dark or bright background and was followed by a dark or bright mask on a middle-gray background. Catch trials were identical except that no disk was presented. In this design, the background alone, which was different from the background on which the masks were presented, could potentially prime responses to the masks. For example, if a middle-gray disk was presented on a bright background, the bright background alone could potentially prime a response to a bright mask. The opposite direction of priming could also be possible; for a middle-gray disk presented on a bright background, the transition to the darker (middle-gray) background of the mask could prime the response to a dark mask. In order to account for any potential effects of the background, we subtracted reaction times (RTs) to the background alone (i.e., catch) trials from RTs to the corresponding disk-present trials using the same backgrounds. Even though the disks in the non-SBC conditions were always presented on the middle-gray background, we nonetheless subtracted RTs on the middle-gray background catch trials from the non-catch trials before all statistical analyses to balance out any biases that this subtraction procedure may have introduced. A complete analysis with uncorrected RTs resulted in the same pattern of results.

Table 1 shows the mean RTs for correct trials and error rates as a function of disk brightness, prime-mask SOA and trial type. Corrected RTs were analyzed in a three-way ANOVA with disk brightness (SBC or non-SBC), SOA (40 or 140 ms) and congruency (congruent or incongruent) as the within-subjects factors. The ANOVA revealed a significant main effect of congruency [$F(1, 21) = 192.67$, $MSE = 1353.67$, $p < .001$], with significantly faster RTs for the congruent as compared to the incongruent trials. Although the main effects of disk brightness and SOA and the disk brightness x SOA interaction were not significant, there was a significant SOA x congruency two-way interaction [$F(1, 21) = 136.39$, $MSE = 717.28$, $p < .001$]. This interaction is illustrated in Figure 2, showing that priming was much stronger at the 140 ms SOA for both the SBC and non-SBC disks. This effect of SOA is very likely due to priming effects being larger with longer SOAs, which allow for more extensive prime processing. There was also a significant three-way interaction [$F(1,21) = 6.62$, $MSE = 500.76$, $p = .018$].

Additional two-way ANOVAs (disk brightness x congruency) were conducted for each SOA separately. The main effect of congruency was significant at the 40 ms (i.e., unconscious) SOA [$F(1, 21) = 38.39$, $MSE = 510.20$, $p < .001$], indicating that both the SBC and non-SBC disks affected RTs to the brightness of the annulus masks. Importantly, significant priming was measured in the SBC conditions (33.4 ms), suggesting that SBC occurs without awareness. The main effect of disk brightness and the disk brightness x congruency two-way interaction were not significant at the 40 ms SOA. At the 140 ms SOA, however, both the main effect of congruency [$F(1, 21) = 217.24$, $MSE = 1560.75$, $p < .001$] and the disk brightness x congruency two-way interaction were significant [$F(1,21) = 5.08$, $MSE = 821.74$, $p = .035$]. This interaction was a result of stronger congruency effects for the non-SBC disks as compared to the SBC disks. Thus, when visibility of the primes was high, the non-SBC disks showed stronger priming effects than the SBC disks; however, when prime visibility was low, the priming effects for SBC disks and non-SBC disks were comparable.

The overall error rates were low, except for the incongruent conditions with high prime visibility, which is likely due to the long SOA (140 ms) allowing for more extensive prime processing and incorrect response activation. Because error rates were lower for congruent as compared to incongruent conditions, our main RT data were not influenced by speed accuracy tradeoffs.

In the objective awareness task, accuracy of prime discrimination at the long, 140 ms SOA was high for both non-SBC (76.87%) and SBC disks (77.92%). At the 40 ms SOA, accuracy was low for both non-SBC (59.16%) and SBC disks (64.37%), but above chance levels [non-SBC disks: $t(21) = 4.24$, $p < .001$; SBC disks: $t(21) = 6.23$, $p < .001$]. Although participants in a pilot experiment reported not being aware of the brightness of the disks at the short SOAs, they were able to guess the brightness of the disks at above chance levels in the current experiment, perhaps unconsciously.

To further explore whether the magnitude of the priming effects was dependent on visual awareness, we performed a correlation analysis between priming and visibility at the 40 ms SOA. For each subject we calculated the magnitude of priming for both non-SBC and SBC disks and the corresponding prime discrimination accuracy. A significant positive correlation would demonstrate that priming increases with prime visibility and would suggest that the priming effects at the 40 ms SOA were a result of conscious prime processing. However, we found that priming was unrelated to the magnitude of visibility for both non-SBC [$r = .2$, $p = .38$] and SBC disks [$r = .29$, $p = .19$]. Our analyses thus show a dissociation between priming effects and awareness.

The results from this first experiment suggest that SBC can occur without awareness. Furthermore, the equivalent magnitudes of priming for the non-SBC and SBC disks at the short SOA, but larger priming effects for the non-SBC disks as compared to the SBC disks at the long SOA suggest a potential dissociation between unconscious and conscious representations of brightness. However, there were several complicating factors in this experiment that make these conclusions tentative. First, some subjects may have been aware of some of the disks at the short SOA, as indicated by the slightly, yet still significant above chance performance levels in the prime discrimination task. Although the correlation analysis that we performed addresses this complication, it might still be the case that even for subjects with overall chance levels of discrimination, there may have still been a few trials on which the subjects were aware of the brightness of the disk. These few aware trials alone could have contributed to the “unconscious” priming effects at the short SOA. Second, awareness was confounded with SOA, which may have allowed for more extensive disk processing at the longer SOA, regardless of visual awareness. This longer processing time likely contributed to the larger priming effects at the longer as compared to the shorter SOA, especially for the non-SBC disks. Because our results in Experiment 1 were based on objective awareness measures, with subjects performing above chance, albeit most likely without awareness in the prime discrimination task, we tested whether SBC can occur without awareness using subjective awareness reports in the second experiment.

Experiment 2

In Experiment 2, we used only one intermediate level SOA so that approximately half of the disks were perceived. Subjects reported on every trial after the speeded response to the mask whether they perceived the brightness of the disk. This procedure allowed us to examine brightness priming from non-SBC and SBC disks under both aware and unaware states that are based on differential subjective reports but under identical stimulus presentation conditions.

Method

Participants

Twenty-two subjects (12 female), between the ages of 18 and 33 (M=20.1 years), were recruited from the undergraduate subject pool of The City College of the City University of New York. All observers had normal or corrected to normal vision and participated after informed consent.

Stimuli and Apparatus

The stimuli were identical to those used in Experiment 1, but the timing parameters were modified. On the non-catch trials, the disks, presented for 10 ms as in the first experiment, were followed by the annulus masks at a constant 60 ms SOA. The mask was then presented for 20 ms. This SOA setting was determined based on a pilot experiment that resulted in subjects being unaware of the disks on approximately 50% of the trials.

Procedures

Subjects participated in one 45 minute session in which they were seated in a dimly lit, sound attenuated chamber. Chin rests were used to minimize head movements and to fix the eye-to-monitor viewing distance at 57 cm. On each trial, the subjects first reported the brightness (dark/bright) of the mask by pressing one of two mouse buttons as quickly as possible and then reported (yes/no) whether they were able to perceive the brightness (dark/bright) of the disks (i.e., a trial-by-trial subjective report procedure was used in this experiment). This procedure allowed us to separate aware from unaware trials under identical stimulus conditions. At the beginning of the experimental session, subjects received a block of 30 practice trials. Each subject then completed nine experimental blocks of 60 trials, for a total of 540 trials, with short rest periods between each block. The presentation order of the different disks and mask annuli combinations was randomized within each block. The button response assignments for both the brightness and the subjective reports were completely counterbalanced between the subjects.

Results and Discussion

Subjects were aware of the brightness of the disk on 57% of the trials (SD = 16%). The mean RTs for correct trials and error rates as a function of disk brightness, awareness and trial type are shown in Table 2. We first corrected for any effects of the background by using the same background subtraction procedure for the RTs described for Experiment 1. The data were then analyzed in a three-way ANOVA with disk brightness (non-SBC or SBC), awareness (aware or unaware) and congruency (congruent or incongruent) as the three within-subject factors. The priming effects were consistent with the data from the first experiment (Fig. 3). There was a significant main effect of congruency [*F*(1, 21) = 15.11, *MSE* = 3973.16, *p* = .001], as well as a marginally significant awareness x congruency two-way interaction [*F*(1, 21) = 3.45, *MSE* = 441.74, *p* = .078], with slightly stronger priming in the aware condition. There was also a marginally significant disk brightness x awareness x congruency three-way interaction [*F*(1, 21) = 3.81, *MSE* = 712.71, *p* = .064]. None of the other main effects or interactions approached significance.

The disk brightness x awareness x congruency three-way interaction was primarily driven by differences in the magnitude of priming as a function of awareness for the non-SBC and SBC disks. Follow-up two-way ANOVAs were conducted separately for the non-SBC and SBC disk trials, with awareness and congruency as the two within subject factors. The awareness x congruency two-way interaction for non-SBC disks was significant [*F*(1, 21) = 6.80, *MSE* = 610.73, *p* = .016], with larger congruency effects for the aware as compared to the unaware conditions. In contrast, however, this was not the case for the SBC disks, in which the priming effects were identical regardless of whether subjects were aware or not of the disks [*F*(1, 21) = 0.16, *MSE* = 543.71, *p* = .695].

To assess whether the magnitude of the priming effects differed depending on the disk brightness condition (non-SBC vs. SBC), two additional two-way ANOVAs were conducted separately for the aware and unaware trials. For the aware conditions, although the non-SBC disks produced numerically larger priming effects than the SBC disks, as in Experiment 1, the congruency x brightness type two-way interaction was not significant [*F*(1, 21) = 1.04, *MSE* = 728.74, *p* = .32]. In the unaware trial conditions, however, the congruency x disk brightness two–way interaction approached significance [*F*(1, 21) = 3.22, *MSE* = 664.41, *p* = .087], with stronger priming effects for the SBC disks as compared to the non-SBC disks.

These results, in conjunction with those from Experiment 1, demonstrate that priming occurs for SBC disks under conditions of unawareness. They further show that SBC is processed to the same extent, regardless of whether subjects are aware of the stimuli, but that awareness increases the magnitude of priming for brightness differences that do not depend on SBC. Thus, unconscious priming from SBC disks is at least comparable to, if not stronger, than priming for non-SBC disks.

General discussion

In two experiments, we tested whether simultaneous brightness contrast occurs without awareness. The results from the first experiment, in which visibility of the primes was manipulated by using different prime-mask SOAs, showed that under conditions of low visibility, brightness priming effects were comparable for both non-SBC and SBC disks. We also demonstrated that priming effects do not correlate with discrimination accuracy. To circumvent the various problems associated with objective measures of awareness, including the possibility that awareness on some trials was driving the priming effects in Experiment 1, we used a subjective measure of awareness in the second experiment. Participants reported whether they were aware of the brightness of the disk on each trial. Similar to the first experiment, the same magnitude of brightness priming from SBC disks occurred regardless of whether subjects were aware or not of the disks, and was at least comparable, if not stronger, to those for non-SBC disks under the unaware conditions. The second experiment also controlled for confounding effects of different prime processing times by having one fixed SOA. The results from these two experiments together show that SBC occurs without awareness, that unconscious SBC priming is as strong as conscious SBC priming and suggest that priming from invisible primes may be stronger for SBC disks than for non-SBC disks.

In addition to shedding some light on the differences between conscious and unconscious visual representations, our results may also be informative regarding the mechanisms underlying SBC, for which there are several competing hypotheses. Some hypotheses attempt to explain SBC in terms of lower level processing, whereas others posit higher level, complex computations. One still predominant hypothesis, offering a low level account, is championed by Mach (Mach, 1886) and Hering (Hering, 1874) and is based on lateral interactions early in the retina. This hypothesis suggests that a target embedded in a region of higher luminance will be perceived as darker than the same target embedded in a region of a lower luminance because the surround of the on-ganglion cells located at the edge of the target will be inhibited more in a region with higher luminance compared to the same target in a region with lower luminance. However several illusions have been constructed that challenge this account. For example, in White’s illusion (Fig. 4, (White, 1979), a target surrounded by a region of predominantly higher luminance looks brighter than an identical target embedded in a region of lower luminance.

(Note that this is the opposite of SBC, in which targets appear dim when presented on a dark as opposed to a bright background.) The multi-scale spatial filtering theory (Blakeslee & McCourt, 2004), which is another low-level account, offers an explanation for these phenomena based on responses in V1, using a set of filters, which resemble receptive fields in early visual cortex. In contrast to these low-level accounts of SBC, a different perspective is embodied by a set of hypotheses that suggest the involvement of higher level processes, such as inferred illumination (von Helmholtz, 1867) or local and global anchoring of lightness values (Gilchrist et al., 1999). Our results are consistent with accounts that are based on fast lateral processes occurring in V1 or as early as in the retina in that they demonstrate that SBC occurs without awareness and very rapidly (i.e., at the short SOAs and with the very brief presentation durations used in these experiments). Given these fast processing times, extensive computations, inferences, and anchoring (i.e., extraction of higher-order scene information) seem unlikely to play a role in the unconscious SBC effects measured in these experiments. However, our results do not allow us to exclude the possibility that more subtle aspects of brightness perception do require some higher level processes.

On a related note, it is possible that only simple brightness illusions such as SBC are coded unconsciously and early during visual processing. Fast, more local, intra-areal computations performed during the initial feedforward stages of processing (Lamme & Roelfsema, 2000; Ro, Breitmeyer, Burton, Singhal, & Lane, 2003) might be sufficient for unconscious representations of simple brightness illusions. However, more complex brightness illusions that combine objects from more extended regions of visual space may require inter-areal computations, which likely require lateral and feedback connections and multiple iterative loops between different visual areas. Future research using different and more complicated brightness illusions will be necessary to more precisely assess which aspects of brightness perception rely upon higher-level processing mechanisms and whether longer processing times and conscious vision is necessary to process them.

In the current study, we sought to show unconscious SBC using both an objective (Experiment 1) and a subjective (Experiment 2) measure. Although some argue that assessing awareness with objective criteria is a more optimal, conservative approach, it requires that exclusivity (it should be sensitive to conscious information only) and exhaustiveness (a measure should be exhaustive for all conscious information) assumptions are met (Reingold & Merikle, 1988). These assumptions are highly problematic because it is not possible to demonstrate conclusively that any measure will meet them. As a consequence, objective criteria have a tendency to overestimate conscious perception. Another drawback is that it requires researchers to prove a true null sensitivity, which is an impossible feat. On the other hand, subjective measures of awareness tap directly into phenomenal experience. Importantly, in some paradigms and experimental designs, as in the one used in the second experiment, subjects report on stimulus visibility on every trial, allowing for separation of trials with identical stimuli parameters but with different conscious experiences. The downside of subjective reports is that they can be contaminated with response biases. It is important to note however, that objective and subjective measures are generally in strong agreement (Del Cul, Dehaene, & Leboyer, 2006; Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009), as in our two experiments, and although objective measures are more conservative, when all factors are taken into account, subjective reports provide a better measure of awareness (Merikle et al., 2001; Dehaene & Changeux, 2011).

If unconscious information is represented at more basic, lower levels and conscious information is percept-dependent, as our previous results suggest (Breitmeyer, Ro, & Singhal, 2004), one would expect little to no unconscious priming for SBC compared to non-SBC disks at the short SOA, when prime visibility was low. However, the current results showed priming effects for the SBC disks that were the same regardless of whether subjects were aware or not of the disks and priming effects at least as large as those for the non-SBC disks in the unaware conditions. On the other hand, in the aware conditions we measured larger priming effects for the non-SBC (significantly in Experiment 1, but only numerically in Experiment 2) as compared to the SBC conditions. Because the SBC disks were not as dark or bright as the dark and bright disks on middle-gray backgrounds, these results further suggest that priming in the aware conditions may have been percept-dependent and that some visual information may be represented differently when we are conscious of them.

In summary, we demonstrate in two experiments that used different parameters and measures of awareness that SBC occurs without awareness. Our results further suggest that unconscious visual representations differ from conscious ones and that SBC occurs early during visual processing, most likely within the initial feedforward sweep of visual information processing.

Table 1

Mean RTs (in milliseconds) and error rates (in percentages) as a function of disk brightness, SOA and trial type in Experiment 1. Standard errors of the mean for RTs are shown in parentheses.

	Disk brightness							
	Non-SBC				SBC			
	SOA				SOA			
	40		140		40		140	
Disk trial type	RT	Errors	RT	Errors	RT	Errors	RT	Errors
Congruent	453 (11)	4.7	397 (11)	3.6	466 (14)	4.5	417 (14)	4.0
Incongruent	479 (11)	8.3	535 (15)	27.2	507 (11)	9.4	543 (13)	24.5
Catch trial type								
Middle-gray	473 (13)	5.1	464 (13)	5.8	n/a	n/a	n/a	n/a
Congruent	n/a	n/a	n/a	n/a	486 (14)	3.8	476 (11)	4.5
Incongruent	n/a	n/a	n/a	n/a	494 (14)	5.6	491 (14)	6.8

Table 2

Mean RTs (in milliseconds) and error rates (in percentages) as a function of disk brightness, awareness and trial type in Experiment 2. Standard errors of the mean for RTs are shown in parentheses.

	Disk brightness							
	Non-SBC				SBC			
	Unaware		Aware		Unaware		Aware	
Disk trial type	RT	Errors	RT	Errors	RT	Errors	RT	Errors
Congruent	579 (34)	4.1	567 (37)	2.2	590 (34)	4.4	594 (34)	3.0
Incongruent	600 (27)	11.2	616 (31)	5.6	645 (29)	10.9	645 (30)	8.9
Catch trial type								
Middle-gray	583 (34)	2.9	n/a	n/a	n/a	n/a	n/a	n/a
Congruent	n/a	n/a	n/a	n/a	597 (31)	2.8	n/a	n/a
Incongruent	n/a	n/a	n/a	n/a	611 (34)	4.3	n/a	n/a

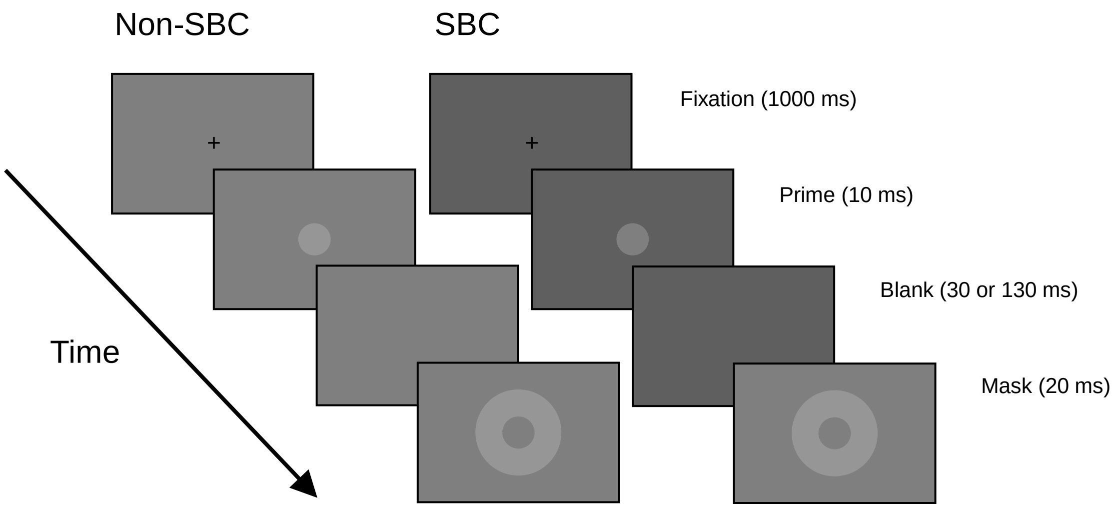


Figure 1. Schematic showing examples of congruent trials with non-SBC or SBC disks in Experiment 1. Note that the disk in the SBC condition is the same middle-gray used as the background in the non-SBC conditions, but appears brighter because it is presented on a darker background.

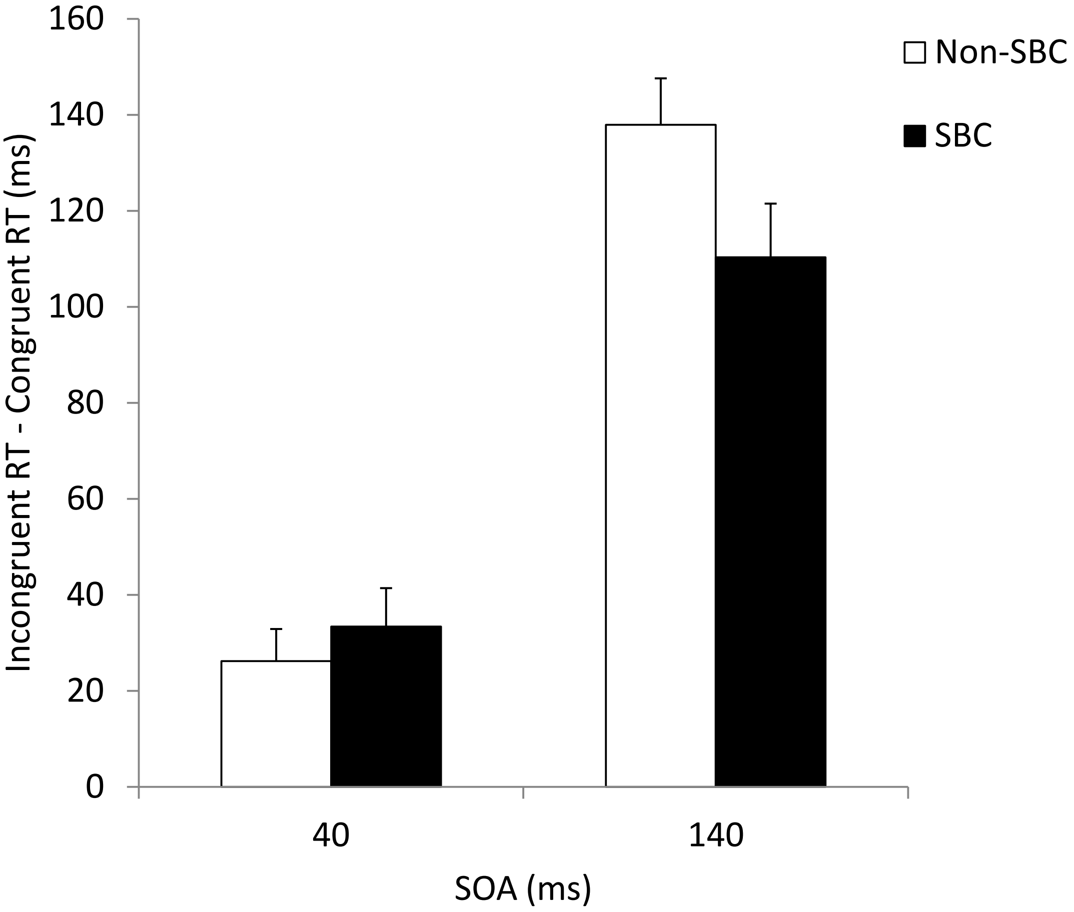


Figure 2. The priming effects (incongruent minus congruent RTs) measured for non-SBC and SBC disks as a function of SOA in Experiment 1. Bars indicate 1 standard error of mean.

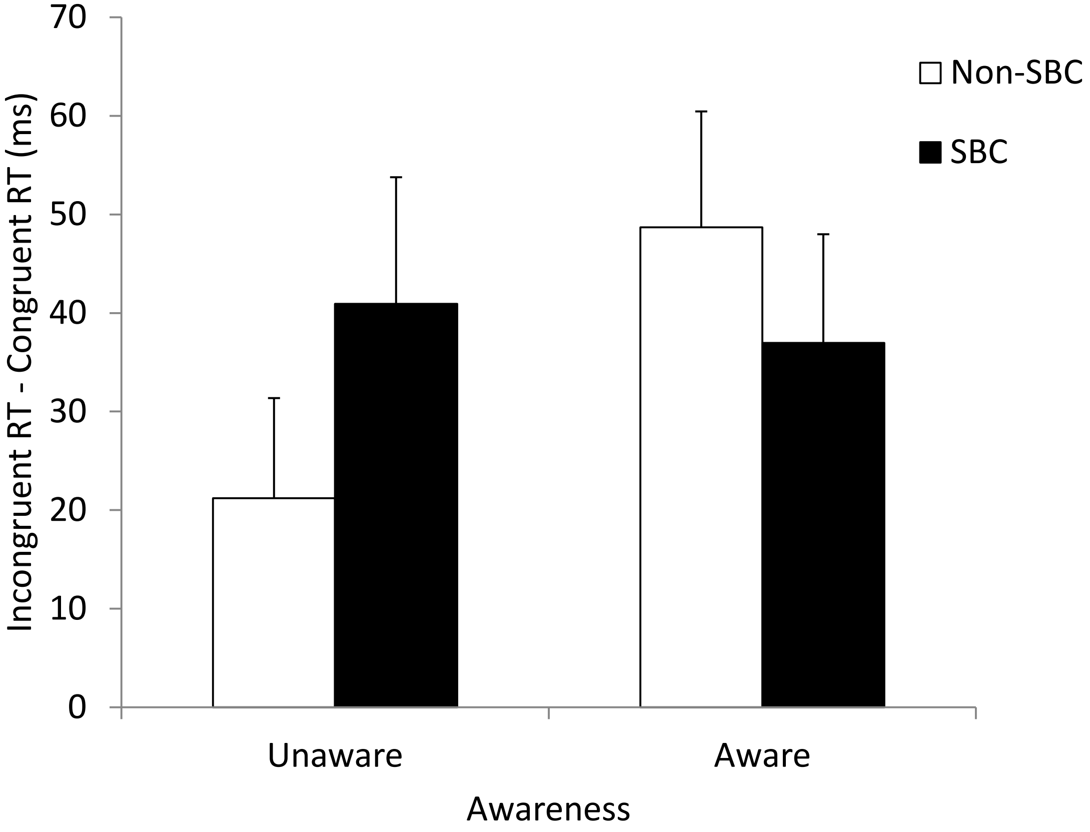


Figure 3. The priming effects (incongruent minus congruent RTs) measured for non-SBC and SBC disks as a function of disk awareness in Experiment 2. Bars indicate 1 standard error of mean.

Figure 4. White’s illusion. Even though the gray segments falling on the black bars (left half) are identical to those falling in between the black bars (right half), the gray segments on the left appear brighter than those on the right.

Chapter 3

Complex stimulus-response priming without visual awareness

Abstract

Conscious representations are generally thought to entail deeper or more complex forms of information processing than unconscious ones. Although several priming studies support this claim, other studies show processing of complex information in the absence of awareness. In the current study we provide evidence that such discrepancies might be due to the specific constraints imposed on prime processing as opposed to consciousness of the prime per se. In two experiments, we disentangled the role of awareness from prime processing time in a priming task with complex stimulus response (SR) mappings, where physically different stimuli are mapped to the same response. Primes were rendered invisible using metacontrast masks, which also served as the targets. When the primes were physically different than the targets, they were either response congruent or response incongruent. In the first experiment, we used a subjective measure of awareness and multiple prime-mask intervals. We found that reaction times were faster for physically different stimuli when they were mapped to the same response, but only when the prime to target temporal intervals were sufficiently long. In the second experiment, we confirmed these results using an objective measure of awareness. Forced-choice prime discrimination showed that participants were unaware of the primes. These results provide strong evidence for unconscious priming with complex SR mappings and demonstrate the importance of allowing for sufficient prime processing in the absence of perceptual awareness.

Introduction

Conscious representations are generally thought to be a result of deeper, more complex or superior information processing as compared to unconscious representations. For example, the global workspace theory (Baars, 1988, 2005; Dehaene & Naccache, 2001), higher order theory (Lau & Rosenthal, 2011), and information integration theory (Tononi, 2004) are amongst some of the theories of consciousness that implicitly or explicitly suggest that conscious processes are represented in deeper or more complex ways than unconscious ones.

Recent studies have provided some compelling evidence for processing of simple stimulus features that are not consciously experienced; however, whether more complex forms of information are processed in the absence of perceptual awareness, remains controversial. For example, using various masking procedures to test whether simple stimulus features are processed when those features are presented below the threshold of awareness, several investigators have demonstrated processing for color (Breitmeyer et al., 2007; Breitmeyer, Ro, & Singhal, 2004; Schmidt, 2002) and shape (Eimer & Schlaghecken, 1998; Klotz & Wolff, 1995; Neumann & Klotz, 1994; Ro et al., 2009) in normal subjects. Studies on patients with damage to occipital or parietal cortex provide further evidence for processing in the absence of perceptual awareness. Blindsight patients, who have lesions in the primary visual cortex, can discriminate between locations, motion, shapes and wavelengths (Stoerig & Cowey, 1997; Weiskrantz, 1986, 1996), although they claim no awareness for stimuli presented in the blind field (Weiskrantz, 1986). Furthermore, neglect patients, with damage to the temporo-parietal junction, have an inability to consciously report stimuli on the contralesional side but nonetheless encode figure-ground segregation (Driver, Baylis, & Rafal, 1992), perceive geometrical illusions (Daini, Angelelli, Antonucci, Cappa, & Vallar, 2002; Mattingley, Bradshaw, & Bradshaw, 1995; Ro &

Rafal, 1996), and even process semantic information (D'Esposito, McGlinchey-Berroth, Alexander, Verfaellie, & Milberg, 1993; Làdavas, Paladini, & Cubelli, 1993).

Although some studies in normal subjects have shown unconscious semantic priming, which is thought to represent more complex and extensive levels of information processing (Abrams, Klinger, & Greenwald, 2002; Dehaene et al., 1998; Greenwald et al., 1996; Klinger, Burton, & Pitts, 2000; Marcel, 1983a, 1983b), other studies suggest that these semantic priming effects may be based more on automatic spreading of activation or stimulus-response associations than more complex or extensive levels of information processing (Damian, 2001; Kiefer & Brendel, 2006; Kiefer, 2002). Such evidence indicates that semantic priming requires awareness.

Several other studies suggest that consciousness is necessary for sequential modulation of congruency effects (Ansorge et al., 2011; Kunde, 2003), conflict detection in 2-choice flanker task (Scheffers & Coles, 2000), saccade-error awareness (Nieuwenhuis et al., 2001), and inhibitory control (Tsushima et al., 2006). However, a number of studies show that some high-level computations can be performed unconsciously. For example, evidence exists for unconscious processing of numeric stimuli assigned to shared response mappings (Naccache, Blandin, & Dehaene, 2002), unconscious cognitive control (Lau & Passingham, 2007; van Gaal et al., 2008) and unconscious complex decision making (Bargh & Ferguson, 2000; Dijksterhuis, Bos, Nordgren, & van Baaren, 2006; Ferguson & Bargh, 2004). Consequently, the simple distinction of conscious and unconscious representations in terms of the complexity of processing remains intensely debated (Desender & Van den Bussche, 2012; Eimer & Schlaghecken, 2003; Kunde et al., 2005, 2012; Kunde, 2003; Mayr, 2004; van Gaal et al., 2012; van Gaal & Lamme, 2011; Van Opstal et al., 2005a, 2005b).

Instead of reflecting differences between conscious and unconscious representations, these discrepancies between different studies may rather be a consequence of stimulus presentation factors, unique to each specific manipulation of visual awareness. For example, many studies control awareness by manipulating stimulus timing, and timing manipulations are often arbitrary and differ greatly between studies. Notably, in studies of masked priming, unaware conditions often use short prime durations and brief delays between primes and masks whereas aware conditions are created using longer intervals as well as longer prime presentations. With this confound, it becomes unclear whether demonstrated differences in processing between primes that are consciously experienced and those that are not are due to prime awareness or due to differences in the prime processing duration.

In the current study, we disentangled the prime processing requirements from prime awareness for one well-known example of cognitive flexibility, which is generally thought to require consciousness: the execution of complex stimulus-response (SR) mappings, in which physically different stimuli map to the same response. One recent study suggests that complex SR mappings require awareness (Ro et al., 2009). In that unconscious priming study, two physically different stimuli were mapped to the same or to different responses. Primes were rendered invisible with metacontrast masks, which were also the targets. The results showed no reaction time differences for physically dissimilar primes and masks even though they mapped to the same or to a different response. Reaction times decreased only when primes and masks were of identical shapes. Those results suggested that priming without awareness is based on early stimulus-dependent levels of processing and that more abstract forms of response mapping require awareness. Here, we demonstrate that priming with complex SR mappings can occur for stimuli that are not consciously experienced but only when sufficient time is allowed for prime processing prior to target/mask presentation.

Experiment 1

Ro et al. (Ro et al., 2009) used a single optimal prime-mask SOA of 40 ms and a subjective measure of awareness in which participants reported on each trial whether they were aware of the prime. We reasoned that the lack of priming might have been due to insufficient prime processing time prior to subsequent target stimulus presentation rather than awareness per se. We sought to dissociate prime processing requirements from visual awareness by collecting unaware trials using a subjective measure of awareness at multiple SOAs, including the 40 ms SOA.

Method

Participants

Twenty-one subjects were tested. Two subjects had insufficient number of unaware trials (less than 10 unaware trials for certain conditions). The data from the remaining 19 subjects (11 female), between the ages of 18 and 24 (M = 19.3 years) were analyzed. Subjects were recruited from the undergraduate subject pool of The City College of the City University of New York. All observers had normal or corrected to normal vision and participated after informed consent.

Stimuli and Apparatus

Two 17” CRT monitors (Sony Model G220), set at a 100 Hz refresh rate, were used for testing. Four semicircles (oriented up, down, left or right) were used as primes (Figure 1). Primes were black (luminance = 0 cd/m^2), and were presented centrally on a uniform gray background (luminance of 10.65 cd/m^2 for one monitor and 13.34 cd/m^2 for the other) (Figure 2). The primes, subtending 0.5^o, preceded one of four randomly chosen semicircular masks each subtending 1.5^o of visual angle. Each trial started with the presentation of a fixation cross for 500 ms, followed by a blank interval of 300 ms. Next, a prime stimulus was displayed for 10 ms, followed by a mask displayed for 30 ms at either a 40, 60 or 80 ms stimulus onset asynchrony (SOA). The first SOA (40 ms) was identical to the value used previously, which showed identity but no evidence of response priming (Ro et al., 2009). The intertrial interval (ITI) was 1 s.

Semicircle masks oriented left and right required left and right button presses. Masks oriented up or down required left or right button presses for half of the participants. The mappings were reversed for the second half of the participants. Note that in this design the masks also served as the targets. Prime-mask combinations, displayed in Figure 1, created three main conditions of interest: 1) physically congruent, response congruent (PcRc), where prime and mask are physically similar 2) physically incongruent, response congruent, (PiRc) where physically different primes and masks share the same response, and 3) physically congruent, response incongruent (PiRi), where physically different primes and masks require different responses. Within the complete set of 16 prime (4) and mask (4) pairings, PcRc condition represented 25% (4 pairings) of the trials, PcRc condition comprised another 25% of the trials (4 pairings), and the remaining 8 pairings (50%) were PiRc trials.

Procedures

Participants were seated in a dimly lit, sound attenuated room, 57 cm away from the monitor. They completed a total of 672 trials that were broken down into 14 experimental blocks of 48 trials each with short breaks in between each block. On each trial, participants made a speeded response to the mask and then reported whether they had perceived the shape of the prime. This procedure allowed us to separate trials based on a subjective measure of awareness.

Results and Discussion

Trials with reaction times faster than 150 ms or slower than 2000 ms were excluded from analysis. This procedure removed 1.9% of trials. Participants were unaware of 89.8% (SD = 8.4), 76.6% (SD = 17.7) and 62.1% (SD = 27.8) of trials for the 40, 60 and 80 ms SOA, respectively. Only unaware trials were analyzed. Reaction times for correct trials were analyzed in a two-way ANOVA with congruency (PcRc, PiRc, PiRi) and SOA (40, 60, and 80 ms) as within-subject factors. The ANOVA revealed a significant main effect of congruency [$F(2,36) = 24.67$, $p < .001$], SOA [$F(2,36) = 4.28$, $p = .021$], as well as a significant SOA x congruency interaction [$F(4,72) = 2.78$, $p = .033$]. This interaction reflects stronger priming effects for longer SOAs (Figure 3A).

We conducted additional one-way ANOVAs for each SOA. For the 40 ms SOA, the congruency effect was significant [$F(2,36) = 8.05$, $p = .001$]. Reaction times for the PcRc condition were the fastest. Fisher's protected t-tests (Seaman, Levin, & Serlin, 1991) showed significant differences between the PcRc and PiRi conditions [$t(18) = 4.57$, $p < .001$], as well as between the PcRc and PiRc conditions [$t(18) = 3.50$, $p = .003$]. The comparison between the PiRc and PiRi conditions was not significant [$t(18) = 0.792$, $p = .438$], consistent with the results of Ro et al. (Ro et al., 2009). For the 60 ms SOA, there was again a significant effect of congruency, [$F(2,36) = 15.59$, $p < .001$]. Like for the 40 ms SOA condition, paired-samples t-tests for the 60 ms conditions revealed a significant difference between the PcRc and PiRi conditions [$t(18) = 5.58$, $p < .001$] and between the PcRc and PiRc conditions [$t(18) = 3.19$, $p = .005$]. Importantly, and unlike the 40 ms SOA condition, there was a significant difference between the PiRc and PiRi conditions [$t(18) = 2.41$, $p = .027$]. The results for the 80 ms SOA condition showed an overall congruency effect [$F(2,36) = 9.37$, $p = .001$], as well as significant differences between the PcRc and PiRi conditions [*t*(18) = 3.95, *p* = .001], and between the PiRc and PiRi conditions [*t*(18) = 3.24, *p* = .005]. The difference between the PcRc and PiRc conditions did not reach significance [*t*(18) = 1.72, *p* = .102].

An ANOVA on accuracy revealed only a main effect of congruency [*F*(2,36) = 7.79, *p* = .002]. Overall, participants made more errors in the PiRi condition (Figure 3B). Separate Fisher's protected t-tests showed that the difference between the PiRc and PiRi conditions was significant at 40 ms SOA, [*t*(18) = 2.51, *p* = 0.022] and 60 ms SOA [*t*(18) = 3.84, *p* = 0.001].

These results demonstrate that priming with complex SR mappings occurs with invisible shape primes; however, the magnitude of the priming critically depends on the amount of prime processing duration prior to the presentation of the mask. This experiment thus establishes a dissociation between awareness and prime processing per se and also resolves the discrepancy with the results of the previous study (Ro et al., 2009).

Experiment 2

The main aim of the first experiment was to demonstrate unconscious priming effects for complex SR mappings using a paradigm comparable to the previous study that used a single optimal masking SOA and subjective measure of awareness. The results of Experiment 1 demonstrate that activation of complex mappings occurs in the absence of awareness of primes but requires adequate processing time. In Experiment 2, we sought to assess the temporal boundary for measuring unconscious identity and response priming and to confirm this effect using an objective measure of awareness. Neutral primes were also included to analyze the nature of priming effects (facilitation vs. inhibition).

Method

Participants

Thirty-two subjects were recruited from the undergraduate subject pool of The City College of the City University of New York. One subject was excluded because his target discrimination was not above chance for one condition. Data from thirty-one subjects (15 female), between the ages of 18 and 30 (M= 20.9 years), were included in the analysis. All observers had normal or corrected to normal vision and participated after informed consent.

Stimuli and Apparatus

The stimuli and apparatus were similar to those in Experiment 1. We modified the design of the first experiment in several respects. Six stimuli were used as primes: four semicircles (oriented up, down, left or right) and two neutral stimuli: two opposite quarters of the circle across a diagonal (Figure 1). Each trial started with the presentation of a fixation cross for 500 ms, followed by a blank interval of 300 ms. Next, a prime stimulus was displayed for 10 ms, followed by a mask at either a 50 ms or 90 ms stimulus onset asynchrony (SOA). The intertrial interval (ITI) was 1 s. These masking conditions produced two types of trials, aware (SOA = 90 ms) and unaware (SOA = 50 ms). We selected these SOAs based on preliminary testing. Because the results from Experiment 1 showed unconscious activation of complex SR mappings for 60 but not for 40 ms SOA, we increased the SOA from 40 to 50 ms; this modification allowed for a slightly longer prime processing time, while keeping forced-choice discrimination at chance. The 90 ms SOA was included to assess whether larger priming effects could be measured with longer prime processing durations prior to the presentation of the mask and to keep subjects motivated during the forced-choice discrimination task with some visible primes.

Prime-mask combinations, displayed in Figure 1, created four conditions: PcRc, PiRc, PiRi (see Methods for Experiment 1) and neutral (N), where prime is physically different from the mask and it has no assigned response. Within the complete set of 24 prime (6) x mask (4) pairings, PcRc and PiRc conditions occurred on 16.7% (4 pairings) of the trials each, while PiRi and N categories were twice as frequent (33.3% or 8 pairings of each).

Procedures

Participants were seated in a dimly lit, sound attenuated room, 57 cm away from the monitor. They first completed 10 experimental blocks of 48 trials each, with short breaks in between. On each trial in the main experiment, participants made speeded responses to the masks. After the main part of the experiment, participants performed a prime discrimination task to objectively assess levels of prime awareness. The prime discrimination task used a design that was identical to the main experiment, except that it consisted of 5 blocks of 48 trials. Participants were instructed to respond to the shape of the prime and to respond as accurately as possible, to guess if unsure, and to take as much time as needed.

Results and Discussion

In Experiment 2 we employed an objective measure of awareness. Participants were not aware of the primes at the 50 ms SOA; their accuracy on the prime discrimination task was 51.57%, which is no better than chance [$t(30) = 1.51$, $p = .142$]. They were, however, able to discriminate primes above chance at 90 ms SOA [$t(30) = 4.27$, $p < .001$] with an average accuracy of 57.46%.

Trials with reaction times faster than 150 ms or slower than 2000 ms were excluded from analysis. This procedure removed 0.95% of trials. Reaction times for correct trials were analyzed in a two-way ANOVA with congruency (PcRc, PiRc, PiRi, and N) and SOA (50 or 90 ms) as the within-subject factors. The main effect of congruency [$F(3,90) = 68.03$, $p < .001$] and the congruency x SOA interaction [$F(3,90) = 12.44$, $p < .001$] were significant. When primes were visible (SOA = 90 ms) priming effects were stronger (Figure 4A).

To clarify the interaction effect, we conducted, for each SOA, a separate one-way ANOVA followed by paired sample t-tests performed with Hochberg's Bonferroni method (Hochberg, 1988). The ANOVA for the 50 ms SOA revealed a significant effect of congruency [$F(3,90) = 20.58$, $p < .001$]. The PcRc condition produced faster RTs than the PiRc condition, which in turn was faster than the PiRi condition. Paired-sample t-tests showed that all pairwise comparisons were significant (all *p*s < .05) except for the comparison between the PiRc and the N conditions [$t(30) = 0.299$, $p = .767$]. The pattern of results was similar for the 90 ms SOA. There was a significant effect of congruency [$F(3,90) = 55.71$, $p < .001$]. All paired t-tests were significant (all *p*s < .01), except for the PiRc and N comparison [$t(30) = 0.563$, $p = .578$].

The error analysis showed a similar pattern (Figure 4B). A two-way ANOVA revealed a significant main effect of congruency [$F(3,90) = 19.90$, $p < .001$] as well as significant congruency x SOA interaction [$F(3,90) = 3.49$, $p = .019$]. Across both SOAs, the PcRc conditions produced the fewest errors, followed by the PiRc and then the PiRi conditions. Additional one-way ANOVAs were conducted for each SOA. The ANOVA for the 50 ms SOA revealed a significant congruency effect, [$F(3,90) = 12.20$, $p < .001$]. Paired t-tests revealed significant differences for all comparisons (all *p*s < .05), except for the PcRc vs. PiRc comparison [$t(30) = 0.494$, $p = .625$]. The effect of congruency was also highly significant for the 90 ms SOA, [$F(3,90) = 14.72$, $p < .001$]. Paired t-tests revealed significant RT differences for all pairwise comparisons (all *p*s < .05) except for the PcRc and PiRc [$t(30) = 0.805$, $p = .427$],the PiRc and N [$t(30) = 1.302$, $p = .406$] and the PcRc and N comparisons [$t(30) = 1.891$, $p = .204$].

These results demonstrate that even when objective measures of awareness are employed, it is clear that priming with complex SR mappings occurs with invisible shapes. Although participants were unaware of the primes at 50 ms SOA, they showed significant RT differences between PiRc and PiRi categories. Because primes and masks were physically different in these two categories, priming must have occurred at some stage beyond perceptual analysis. Second, the presentation of prime 50 ms prior to the presentation of a mask is sufficient for unconscious response-congruent priming to be measured. Finally, the inclusion of neutral primes revealed that priming is due to both facilitatory and inhibitory components; however, PiRc and N did not differ in reaction times.

General discussion

There is a long standing contention in the consciousness literature; some are proposing processing of only basic features in the absence of perceptual awareness, while others argue for extensive unconscious processing of even semantic information (Kouider & Dehaene, 2007). In this study we addressed these perplexing discrepancies using a well-known example of cognitive flexibility that is generally thought to require consciousness: the execution of new, complex SR associations. A previous study (Ro et al., 2009) reported unconscious priming only for simple SR mappings. We hypothesized that more complex or abstract forms of SR mappings likely require longer processing times than simpler forms but not necessarily perceptual awareness. In two experiments we manipulated the processing duration of primes while keeping them below the threshold of awareness.

The pattern of results from Experiment 1 confirmed our supposition. Priming for both simple and complex SR mappings increased with longer SOAs. At 40 ms SOA, there was no priming for complex SR mappings, which is consistent with the results of Ro et al. (Ro et al., 2009). However, priming effects became significant at the 60 and 80 ms SOAs. The error analysis was consistent with the reaction time data. Participants made more errors in the PiRi condition compared to the PcRc and PiRc conditions. Our results clearly establish a dissociation between the contributions of prime processing duration and prime awareness per se in the activation of complex SR mappings.

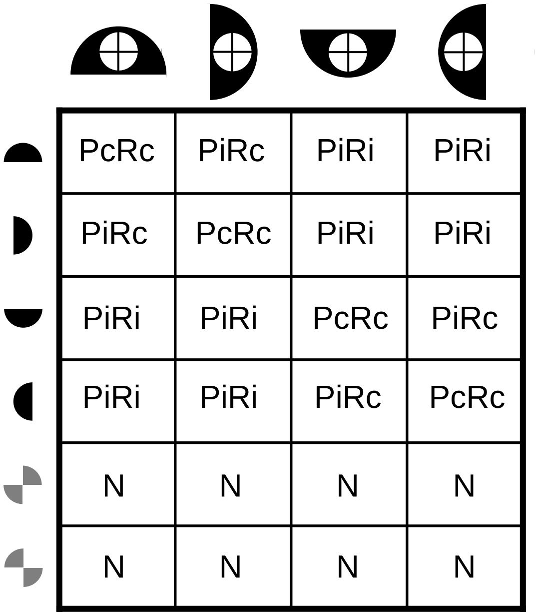
In the second experiment, we used two different SOAs and an objective measure of awareness. For the unaware condition, we used a short SOA of 50 ms. This SOA was selected because the results from Experiment 1 demonstrated that priming occurs for 60 but not for 40 ms SOA. Reaction time and accuracy for physically different stimuli depended on whether they mapped onto the same or to a different response, with faster RTs for physically different primes that shared the same response as the target masks. We observed this type of priming with complex SR mappings at the 50 ms SOA condition in Experiment 2 but not in the 40 ms SOA of Experiment 1, suggesting that unconscious response priming requires the primes to be presented for at least around 50 ms before a mask. It has been demonstrated previously that metacontrast mask interferes only with the conscious perception of primes and leaves motor activation unaffected (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003a). Although prime-related and target (mask) – related motor activations are thus independent (Klotz, Heumann, Ansorge, & Neumann, 2007), primes are likely unable to sufficiently activate more complex motor responses when SOAs are too brief.

One could argue that because PiRi trials were twice as frequent as the other conditions, participants may have rapidly learned this irregularity, which thereby caused a decrease in reaction times for the incongruent trials. Although this effect would go in the opposite direction and actually reduce priming effects, it could explain results for 40 ms SOA in the first experiment, where we found no differences between PiRc and PiRi trials. However, although PiRi trials were twice as frequent as the other trial types, both the PcRc and PiRc trials required the same types of responses. Thus, left and right button presses were equally likely after each prime stimulus, making such a strategy of preparing for the incongruent trials not viable.

The results of this study offer an important insight into the long standing debate about which types of information can be processed in the absence of perceptual awareness. Because more complex forms of information processing likely require longer processing times, this can directly interfere with the requirements necessary for making primes invisible, namely brief prime presentation times and short prime-mask intervals. The current findings highlight the necessity to disentangle prime processing from prime awareness for each type of stimulus by parametrically manipulating prime processing duration before the necessity for perceptual awareness can be established.

The aware vs. unaware dichotomy usually confounds stimulus processing times with subjective conscious experience. It is well established that response priming with simple SR mappings can occur outside awareness (Eimer & Schlaghecken, 1998; Neumann & Klotz, 1994). It has also been shown previously that such unconscious priming effects can increase with longer SOAs (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). However, in other paradigms, priming effects can reverse with longer SOAs (Eimer & Schlaghecken, 1998). We are thus not suggesting that longer SOAs (or processing times) will always result in better performance. The exact processing requirements need to be determined for each case individually.

In this study we demonstrate that longer processing times of primes prior to the presentation of masks allow for activation of unconscious priming with complex SR mappings, which was previously thought to depend on awareness. These results suggest that assigning the role of consciousness to specific processes based on limited conditions (e.g., a single time SOA) or a single technique to interfere with stimulus processing may be very misleading and premature. It is likely that different techniques to render stimuli invisible interfere with processing at different levels of unconscious representations (Breitmeyer, Koç, Oğmen, & Ziegler, 2008). It is thus imperative that we seek converging lines of evidence before we declare that any type of processing requires awareness.



	◓	◑	◒	◐
◓	PcRc	PiRc	PiRi	PiRi
◑	PiRc	PcRc	PiRi	PiRi
◒	PiRi	PiRi	PcRc	PiRc
◐	PiRi	PiRi	PiRc	PcRc
	N	N	N	N
	N	N	N	N

Figure 1. The stimuli and prime–mask categories for Experiments 1 (black) and 2 (black and gray). Six prime stimuli are displayed in the first column; two primes are response neutral. Masks are displayed in the top row. In this example, a semi-circle oriented up requires a right button press. For half of the participants the mappings were reversed (circle oriented up maps to the left response button). PcRc – physically congruent and response congruent, PiCc – physically incongruent, response congruent, PiRi – physically incongruent, response incongruent, N – neutral. Note that categories PiRi and N are twice as frequent as categories PcRc and PiCc.

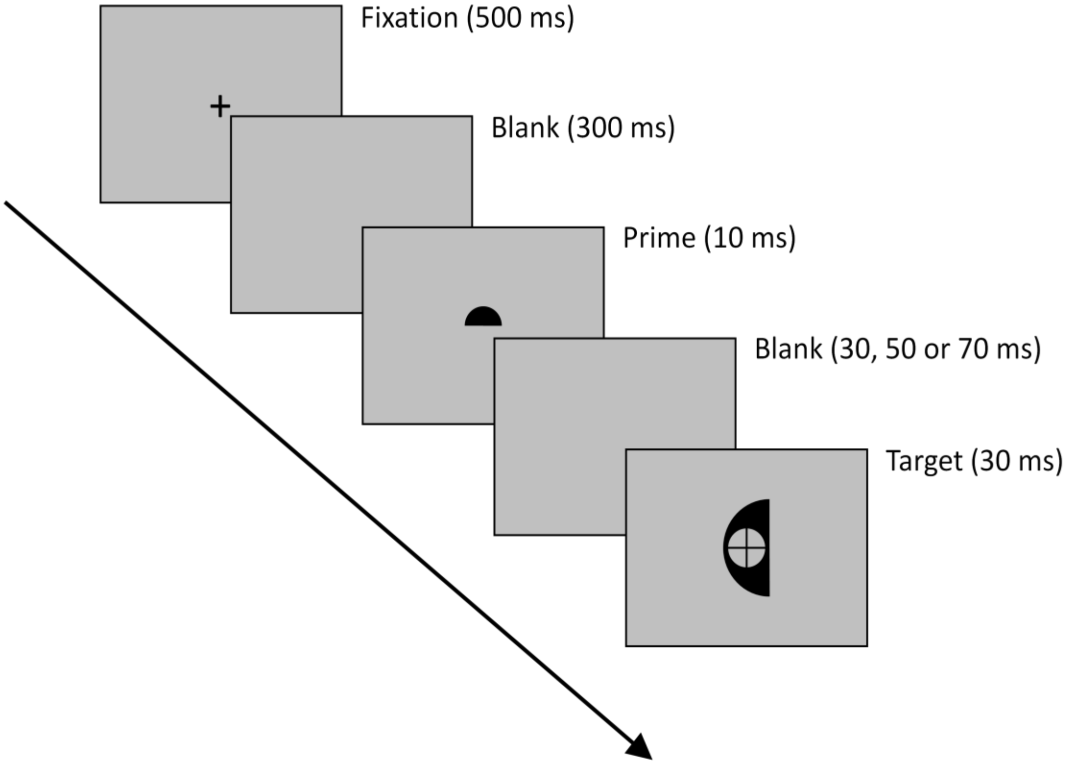
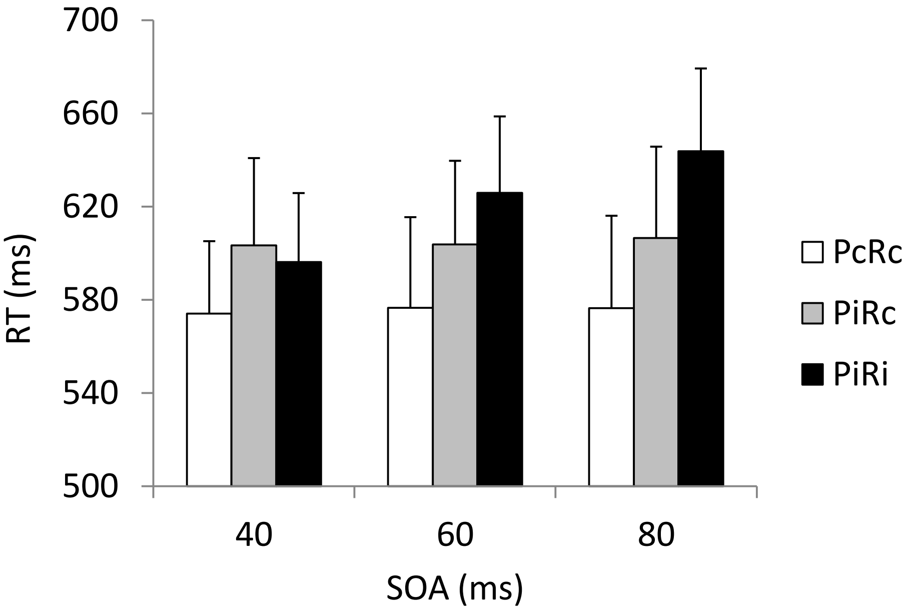


Figure 2. The temporal sequence for a typical trial in Experiment 1. Masks were either physically identical to the prime (PcRc – physically congruent and response congruent), physically different and mapped to the same response (PiCc – physically incongruent, response congruent) or physically different and mapped to the opposite response (PiRi – physically incongruent, response incongruent). In this example, assuming that semicircles oriented up required right button press, the temporal sequence represents a PiRi trial. In the prime discrimination experiment, the trial structure remained identical but participants responded to the primes.

A



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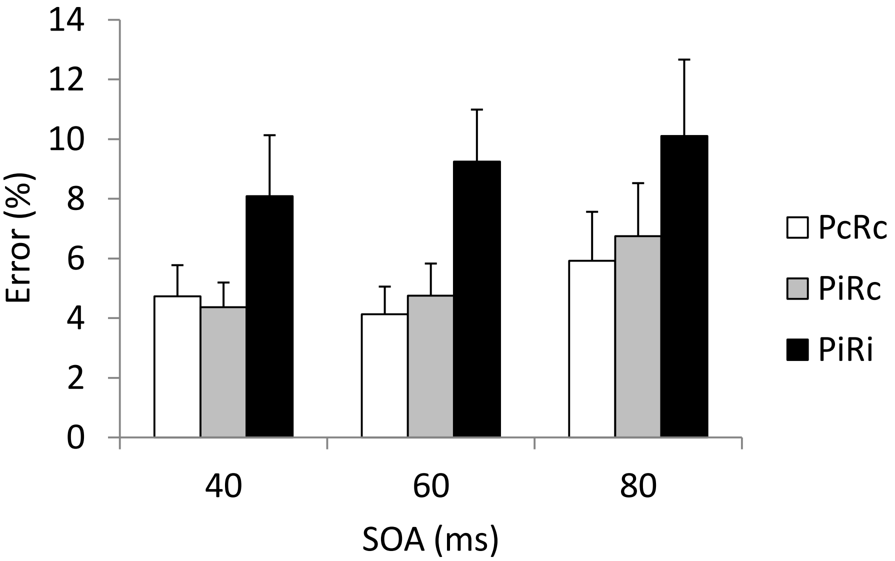

Figure 3. Reaction times (A) and errors (B) for the different prime – mask conditions as a function of SOA in Experiment 1. PcRc = physically congruent, response congruent; PiRc = physically incongruent, response congruent; PiRi = physically incongruent, response incongruent.

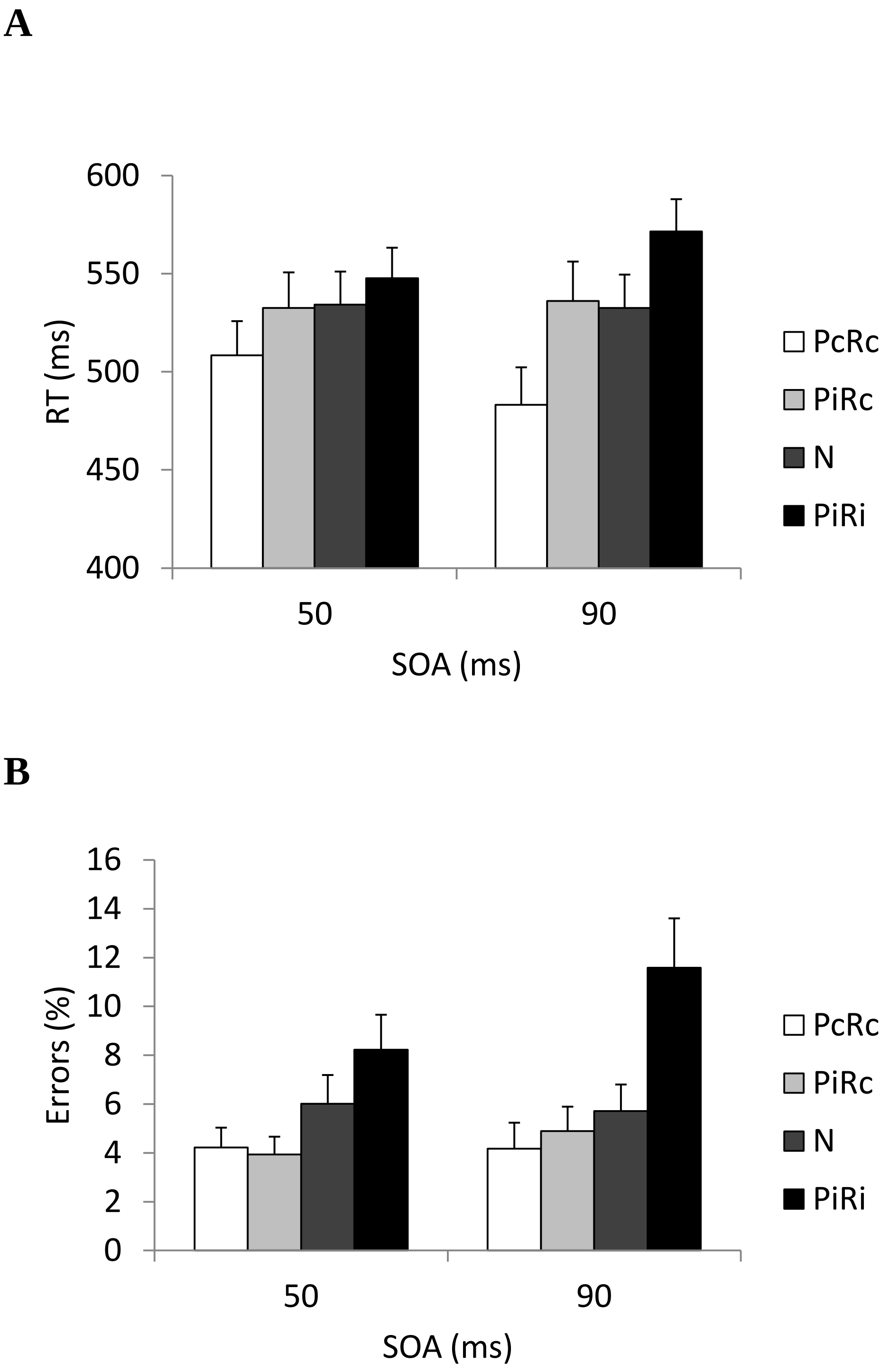

Figure 4. Reaction times (A) and errors (B) for the different prime – mask conditions as a function of SOA in Experiment 2. PcRc = physically congruent, response congruent; PiRc = physically incongruent, response congruent; PiRi = physically incongruent, response incongruent; N = neutral.

Chapter 4

Unconscious priming requires early visual cortex at specific temporal phases of processing

Abstract

Although examples of unconscious shape priming have been well documented, whether such priming requires early visual cortex (V1/V2) has not been established. In the current study, we used transcranial magnetic stimulation (TMS) of V1/V2 at varying temporal intervals to suppress the visibility of preceding shape primes while the interval between primes and targets was kept constant. Our results show that although conscious perception requires V1/V2, unconscious priming can occur without V1/V2 at an intermediate temporal interval but not at early (5 - 25 ms) or later (65 - 125 ms) stages of processing. Because the later time window of unconscious priming suppression has been proposed to interfere with feedback processing, our results further suggest that feedback processing is also essential for unconscious priming and may not necessarily be a sufficient condition for conscious vision.

Introduction

Most of us enjoy the sight of a sunny beach or a flowing river, and, upon inspection of water clarity, we might decide to go for a swim. However, visual experience is not always essential for our actions. Indeed, several lines of evidence suggest that visual awareness and behavior can be dissociated (Milner & Goodale, 1995; Neumann & Klotz, 1994; Poppel et al., 1973; Weiskrantz, 1986). Such dissociations demonstrate that our behavior is sometimes guided by the processing of visual information that we are unaware of. Although the neuroanatomy of different visual pathways is well characterized, it is unclear which visual areas, pathways, and processes are necessary for conscious visual perception and whether those same pathways and structures also process visual information that never reaches our awareness.

Several converging lines of evidence suggest that processing of visual input that we are unaware of may not involve the main retino-geniculostriate pathway, but instead proceeds through alternative visual pathways that bypass primary visual cortex (V1) (see Figure 1A). Some evidence for this position comes from studies demonstrating that cortical area V1 is required for conscious visual perception. For example, studies using binocular rivalry, where physical stimuli remain constant but perception fluctuates, have demonstrated correlations between V1 activity and conscious perception (Leopold & Logothetis, 1996; Polonsky, Blake, Braun, & Heeger, 2000; F Tong & Engel, 2001). Similarly, single-unit recordings in monkeys during a target detection task have revealed enhanced responses in V1 only for perceived targets (Lee, Yang, Romero, & Mumford, 2002; Supèr, Spekreijse, & Lamme, 2001). Converging evidence comes from functional MRI studies that show increased activity in V1 for trials on which subjects perceived (hits) or believed to have perceived the target (false alarms) (Ress, Backus, & Heeger, 2000; Ress & Heeger, 2003).

Further evidence for the critical role of V1 in visual awareness is supported by lesion and inactivation studies. Patients with damage to V1 show no awareness for stimuli presented in the affected part of the visual field (Holmes, 1918), yet they sometimes demonstrate “blindsight”, the ability to discriminate visual stimuli in the absence of awareness (Poppel et al., 1973; Weiskrantz, Warrington, Sanders, & Marshall, 1974; Weiskrantz, 1986). Importantly, such instances of blindsight have been demonstrated in neurologically healthy humans using transcranial magnetic stimulation (TMS) of V1/V2 (Boyer et al., 2005; Jolij & Lamme, 2005). For example, Boyer et al. (2005) used TMS of V1/V2 to suppress visual awareness and showed that subjects can unconsciously discriminate color and orientation. This result implicates an alternative geniculo-extrastriate pathway that bypasses V1 for unconscious visual discriminations (see also (Schmid et al., 2010). Other lesion and TMS studies of V1/V2 have reported unconscious effects of stimuli on eye and manual movements (Rafal, Smith, Krantz, Cohen, & Brennan, 1990; Ro, Shelton, Lee, & Chang, 2004; Ro, 2008), suggesting involvement of the retino-tectal pathway. Together, these studies provide evidence for the role of alternative visual pathways in unconscious visual perception.

Another non-mutually exclusive possibility is that processing of visual information that we remain unaware of requires the geniculostriate pathway, but only during the feedforward stages of processing in V1 (see Figure 1B) (Lamme & Roelfsema, 2000) and/or when there is insufficient V1 for awareness, such as a few spared islands after brain damage or TMS (Fendrich, Wessinger, & Gazzaniga, 1992). Transient inactivation of V1/V2 with TMS in healthy humans maximally suppresses visual awareness approximately 100 ms after the stimulus onset (Amassian et al., 1989). Because the initial volley of visual information reaches V1 as early as 35 ms after the stimulus offset (Lamme & Roelfsema, 2000), whereas feedback from higher exstrastriate areas (V5/MT) to V1 may take between 5 and 45 ms (Hupé et al., 2001; Pascual-Leone & Walsh, 2001), TMS has been proposed to primarily interfere with feedback or recurrent processing in V1 (Corthout, Uttl, Juan, Hallett, & Cowey, 2000; Lamme, 2006a). Similarly, single-unit recordings of neurons in V1 in non-human primates show response enhancements only at late temporal processing windows (> 100 ms) when targets are perceived (Supèr et al., 2001). Some current models thus link differences between unconscious and conscious vision to two different modes of visual processing. For example, Lamme (2001) has proposed that the bottom-up or feedforward sweep is a neural substrate for unconscious perception, whereas top-down or feedback (reentrant) processing is essential for conscious vision (see Figure 1C and 1D). Similarly, according to the reentrant theory of visual perception, conscious visual perception requires a perceptual match between hypothesis and sensory evidence, which requires not only a feedforward but also a feedback (reentrant) phase (Di Lollo et al., 2000; Enns & Di Lollo, 1997). According to these models, unconscious visual processing depends only on the feedforward sweep.

Although some have questioned the relevance of feedback to V1/V2 for visual awareness and have proposed that late activity in V1/V2 simply reflects target offset related after-discharge (Macknik & Martinez-Conde, 2007), evidence from monkey ablation and inactivation studies (Hupé et al., 1998; Lamme, Supèr, & Spekreijse, 1998; Supèr & Lamme, 2007), as well as from MEG (Boehler, Schoenfeld, Heinze, & Hopf, 2008), patient (Allen, Humphreys, Colin, & Neumann, 2009) and TMS experiments (Pascual-Leone & Walsh, 2001; Ro et al., 2003; Silvanto, Lavie, & Walsh, 2005) strongly suggest an essential role of feedback to V1/V2 for visual awareness.

In the current study we evaluated the role of V1/V2 and the role of these different visual pathways in unconscious visual processing using a sensitive unconscious shape priming measure. Shape priming has been used extensively to probe visual processing in the absence of awareness (Eimer & Schlaghecken, 1998; Neumann & Klotz, 1994; Sumner, Tsai, Yu, & Nachev, 2006). Priming occurs when one stimulus (the prime) influences the processing of a subsequently presented stimulus (the target), even when observers are unaware of the prime stimulus, which is frequently accomplished with a pattern or a metacontrast mask (Breitmeyer & Öğmen, 2006; Breitmeyer, Ro, & Singhal, 2004). The extensive evidence for priming in the absence of awareness has prompted some to suggest that priming depends on feedforward processing, whereas conscious perception depends on feedback or recurrent processing (Schmidt, Niehaus, & Nagel, 2006). The rationale is that the mask that follows the prime interferes only with recurrent processing of the prime, which influences prime visibility but not priming per se (Di Lollo et al., 2000).

In order to assess the roles of feedforward and feedback processing on conscious and unconscious vision, we capitalized on the high temporal resolution of TMS to disrupt shape priming in V1/V2 at different temporal intervals. It has been demonstrated that TMS and masking interact and both strongly interfere with visual processing (Breitmeyer, Ro, & Öğmen, 2004; Kammer, Scharnowski, & Herzog, 2003; Ro et al., 2003). Importantly, in our experimental design, the TMS pulse alone rendered primes invisible, allowing us to measure prime processing after disruption of V1/V2 that is uncontaminated by any influence from a mask or target stimulus, in contrast to other studies that combined TMS with masking (Koivisto, Henriksson, Revonsuo, & Railo, 2012). Another study reported reduced shape priming with TMS of V1/V2 (Sack, van der Mark, Schuhmann, Schwarzbach, & Goebel, 2009), but did not directly address processing in the absence of perceptual awareness. Furthermore, in that study, TMS only moderately reduced shape prime discriminability. Our design, however, allowed us to investigate prime processing without visual awareness by disrupting V1/V2 at varying temporal intervals and directly probing whether the participants were conscious of visual events.

On each trial, we presented shape primes followed by a single TMS pulse to V1/V2 at varying temporal intervals, which was in turn followed by a target. By using an optimal TMS intensity and low contrast stimuli to maximally disrupt V1/V2 to produce visual suppression, we were able to assess the contributions of V1/V2 to unconscious priming at different durations of visual processing, spanning both the feedforward and feedback stages. If unconscious shape priming depends on alternative visual pathways, TMS to V1/V2 should affect awareness of the shape prime but not reduce the priming magnitude. Alternatively, if feedforward but not recurrent processing along the geniculostriate pathway subserves unconscious priming, we should observe the effects of TMS on unconscious shape priming only during early time intervals that reflect the feedforward sweep. Another possibility is that both conscious perception and unconscious priming depend on feedback processing. In this case, TMS should eliminate awareness as well as unconscious shape priming at both early and late intervals. This third possibility would imply that both conscious shape perception and unconscious shape priming require the geniculostriate pathway and the same processing stages, but it may be that conscious perception requires stronger and more robust representations at these stages, as has been recently suggested (Balduzzi & Tononi, 2008; Schurger, Pereira, Treisman, & Cohen, 2010).

Method

Participants

Sixteen subjects were recruited from The City University of New York and participated in the study after giving informed consent. All subjects had normal or corrected to normal vision, were free of any neurological disorder, and were compensated at the rate of $15 per hour. The data from two subjects were excluded because their target discrimination accuracy was at chance for several SOAs, even though the targets were clearly visible because of their large size and appearance well after the prime and TMS on all of the trials. The data from two additional subjects were excluded because of an insufficient number of trials on which they were unaware of primes (i.e., these subjects saw the majority of the primes and had fewer than 10 trials with no prime awareness for certain SOAs, likely due to an ineffective location and/or intensity of the TMS). The data for the remaining twelve subjects (1 female) between the ages of 21 and 27 (M = 24.2 years) were included in the main analysis.

Stimuli, Apparatus, and Procedures

A Cadwell MES-10 polyphasic stimulator with two interchangeable, circular, 9 cm diameter coils was used for TMS. A PC with an Intel dual-core processor was used to trigger the TMS and for stimulus display and data acquisition. The PC was connected to a 17” CRT monitor (Sony Model G220) with a refresh rate of 100 Hz, with all stimuli presented at the center of the display. Subjects sat comfortably in a dimly lit sound attenuated chamber 57 cm away from the monitor. The distance from the monitor was maintained and head movements were minimized through the use of the chin rest.

Each experimental session started with a two step procedure for the functional localization of the visual cortex. First, four random digits were presented for 10 ms at the center of the monitor. The black digits used for the functional localization of V1/V2 had a luminance of 0 cd/ m^2, subtended 0.3º x 0.5º, and were displayed on a gray background with a luminance of 6.8 cd/ m^2. Subjects were asked to report whether they perceived the digits and to report their identity. A TMS coil was initially positioned about 2.5 cm above the inion and a magnetic pulse at 50% of maximum output intensity was delivered 95, 105 or 115 ms after the digits appeared on the screen. Coil position was adjusted and the TMS intensity increased until a stable visual suppression of the digits was achieved. In the second step, the prime semi-circles that were used in the main experiment were presented instead of digits. Minimal adjustments to coil position and TMS intensity were made until at least 3 out 5 primes were suppressed. Visual suppression was assessed with subjective reports of visibility. The position of the coil on the scalp was marked with a grease pencil and output intensity recorded. These parameters were then used for the remainder of the experiment. The mean TMS intensity was 73 % of maximum (2.2 Tesla) output.

All stimuli in the main experiment were black, had a luminance of 0 cd/ m^2 (Figure 2), and were displayed on a gray background with a luminance of 2.6 cd/m^2. Each trial started with a 500 ms presentation of a fixation cross measuring 0.25º of visual angle. A blank interval of 300 ms occurred after fixation offset. Next, a semi-circle prime (radius = 0.44º) was presented for 10 ms followed on most trials by a TMS pulse at a prime–TMS SOA of 5, 25, 45, 65, 85, 105, 125 or 145 ms. After 160 ms from the onset of the prime, a larger semi-circle target (radius = 1.07º) was presented for 50 ms. The central part of the target semi-circles was removed and the target was presented long enough after the prime to prevent masking of the primes. The cut out area had the shape of two overlapping semicircles (radius = 0.63º) and prevented the prime from being pattern masked. There was no metacontrast masking of the primes from the targets because the prime–target SOA on every trial was too long for this type of masking (160 ms) (Breitmeyer, 1984).[1] The prime and target semi-circles were oriented either left or right, were presented an equal number of times in random order, and were orthogonally manipulated. In this design, prime and target shapes were identical (congruent) on half of the trials and different (incongruent) on the other half. If prime information is processed without V1/V2 and visual awareness, then target responses on congruent trials should be faster than on incongruent trials, even on trials in which there was no awareness of the prime.

Subjects made three separate responses on each trial. First, subjects made a speeded response to the shape of the target by clicking the left mouse button for left semi-circles or the right mouse button for right semi-circles. Second, subjects were prompted by a question on the screen to report whether they were aware of the prime shape by pressing the left or right mouse button. Button response assignments for the awareness question were counterbalanced across subjects. There was no time constraint for reporting the awareness. Third, subjects were prompted by a question on the screen to make a forced-choice discrimination of the prime shape using the left or right mouse button. Again, there was no time constraint and subjects were instructed to guess if unsure of the prime or target shape. Button assignment for the prime shape was identical to the one for the target shape. Each participant completed 15 blocks of 36 trials. A total of 540 trials were comprised of 60 trials for each of the 8 SOAs and 60 trials with no TMS. The order of trials was randomized within each block.

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[1] The lack of metacontrast masking was confirmed in a separate prime discrimination control experiment with six subjects, in which targets were presented only on half of the trials. There was no statistically significant difference for prime discrimination with or without the target $t(5) = 1.307$, $p = .248$.

Data analysis

We excluded trials with reaction times (RT) that were faster or slower than 2.5 standard deviations from the mean. This procedure removed 3.7% of data. Only trials on which participants responded correctly to the targets were included in the analysis. When the assumption of sphericity was violated, we adjusted the degrees of freedom using the Greenhouse-Geisser correction (Greenhouse & Geisser, 1959). To correct for multiple comparisons, we adjusted *p* – values using Hochberg's Bonferroni method (Hochberg, 1988).

Results

Prime awareness

On trials with no TMS, an analysis of subjective reports of prime visibility (awareness) showed that the primes were highly visible (M = 95.0%, SD = 5.9%). To examine the contributions of V1/V2 to prime visibility, we measured awareness for each prime–TMS SOA separately. Most studies have consistently demonstrated a maximum amount of TMS suppression of visual processing between 60 and 120 ms after visual stimulus onset (Amassian et al., 1989; Boyer et al., 2005; Jolij & Lamme, 2005), but in some studies an additional earlier and more variable window of suppression has been reported (Corthout, Hallett, & Cowey, 2002; Corthout, Uttl, Walsh, Hallett, & Cowey, 1999; Corthout, Uttl, Ziemann, Cowey, & Hallett, 1999; Paulus, Korinth, Wischer, & Tergau, 1999). Note, however, that with high TMS intensities (>70%), such as those used in the current study, substantial visual suppression can be measured for all SOAs up to about 100 ms (Beckers & Hömberg, 1991; Kammer, Puls, Strasburger, Hill, & Wichmann, 2005). In the current study, subjects were largely unaware of the prime for SOAs up to 105 ms, with stimuli becoming more visible at the longer SOAs (Figure 3a). One-way, repeated measures

ANOVA showed a main effect of SOA, *F*(1,15) = 12.21, *p* = .002, with the degrees of freedom for this main effect adjusted using the Greenhouse-Geisser correction.

Prime discrimination

We first analyzed prime discrimination accuracy for all trials. Visual inspection of the data (Figure 3b, solid line) shows that prime discrimination rates were similar to the subjective report rates of visibility across the SOAs. On trials with no TMS, performance was high (M = 80.1%, SD = 12.8%), although lower than the reports of subjective visibility. This result was expected because we used low contrast stimuli presented briefly for 10 ms to increase the magnitude of TMS suppression and also because prime discrimination perfomance was lowered by interference from the incongruent targets. A one-way, repeated measures ANOVA showed a significant main effect of SOA, *F*(7, 77) = 6.63, *p* < 0.001, demonstrating that the magnitude of prime suppression depended on prime–TMS SOA.

Because there was less suppression for SOAs longer than 100 ms, we obtained a sufficient number of trials on which participants were unaware of the primes (at least 10, see Methods) for measuring unconscious priming without V1/V2 only when the TMS was applied between 5 and 105 ms after the prime was presented. On these trials, participants were unable to unconsciously discriminate the shape of the prime at each of these SOAs (Figure 3b, dashed line), unlike our previous studies that have shown processing of orientation and color in the absence of perceptual awareness (Boyer et al., 2005). A one-way, repeated measures ANOVA for SOAs between 5 and 105 ms showed that SOA had no effect on discrimination accuracy, *F*(2, 24) = 1.50, *p* = .243 (degrees of freedom adjusted using Greenhouse-Geisser correction). One-tailed, paired-sample t-tests confirmed that discrimination was not significantly different from chance (i.e., 50%) for all SOAs between 5 and 105 ms, 5: *t*(11) = 0.626, *p* = .271, 25: *t*(11)

= 1.198, *p* = .384, 45: *t*(11) = 1.242, *p* = .480, 65: *t*(11) = 0.986, *p* = .345, 85: *t*(11) = 2.724, *p* = .059 and 105: *t*(11) = 1.418, *p* = .459.

We considered the possibility that participants had forgotten prime shape because of the distraction caused by the TMS pulse and because prime discrimination was the third response on each trial. To test this possibility, we calculated the expected prime discrimination accuracies for the 125 and 145 ms SOAs and compared them to the accuracy rates measured in the experiment; substantial discrepancies in this comparison would suggest forgetting. Because discrimination accuracy was at 80% on no TMS trials, performance for the 125 ms SOA should be around 59% (i.e., we assumed that for the 29% of the trials on which participants reported awareness of primes at this SOA, discrimination should be around 80% accurate, which was the level of discrimination performance on the no TMS trials on which participants were aware of the primes. For the remaining 71% of the trials at this SOA on which participants reported unawareness of primes, prime discrimination should be around chance (50%), hence (80% x 29%) + (71% x 50%) = 59%), which exactly matches the measured accuracy of 59%. Similar calculations predict that for the 145 ms SOA, accuracy should be around 63% (80% x 44%) + (56% x 50%)), which is only slightly less than the actual accuracy of 66%. These analyses of discrimination performance confirm that the TMS effectively suppressed processing in V1/V2 that is necessary for conscious shape perception.

To address both the possibility of forgetting and blindsight more rigorously, we tested three subjects in an additional control experiment. On each trial there was either no TMS or TMS administered at an SOA of 105 ms, which corresponds to an optimal SOA for inducing blindsight with TMS (Boyer et al., 2005). To minimize forgetting, we eliminated responses to targets. Instead, participants first reported the shape of the prime and then its awareness.

Participants' accuracy on the no TMS trials (M = 80.7%) corresponded closely with discrimination accuracy in the main experiment. Although in this control experiment participants first reported prime shape, prime discrimination performance remained at chance on trials with TMS (M = 47.1%).

Priming

We first analyzed priming for all trials. On trials with no TMS, there were highly significant priming effects (M = 117.2 ms, SD = 22.0 ms, *t*(11) = 5.32 , *p* < .001). However, on trials with TMS, disruption of V1/V2 produced a strong effect on priming that varied with the timing of the TMS (Figure 4a and Figure 3c, solid line). Priming was completely suppressed during two time windows: an early time window (SOAs between 5 and 25 ms) and then again at a later time window (SOAs between 65 and 125 ms) with reliable priming only occurring between these two time windows (SOA 45 ms) as well as at the later SOA of 145 ms. This phasic effect of the TMS on priming was statistically confirmed by a two-way ANOVA with SOA (5, 25, 45, 65, 85, 105, 125 and 145) and congruency (congruent, incongruent) as within-subject factors. The ANOVA showed significant main effects of SOA, *F*(2, 19) = 20.02, *p* < .001 (degrees of freedom adjusted using Greenhouse-Geisser correction) and congruency, *F*(1, 11) = 8.31, *p* = .015, as well as a significant SOA x congruency interaction, *F*(3, 28), *p* = .015 (degrees of freedom adjusted using Greenhouse-Geisser correction). The main effect of SOA likely reflects a generalized TMS-induced alerting response in which participants generally respond faster with longer TMS to target intervals (Figure 4a) (Burle, Bonnet, Vidal, Possamaï, & Hasbroucq, 2002; Nickerson, 1973; Terao et al., 1997). We further examined priming effects at each SOA using one-tailed, paired samples t-tests. Priming effects were significant only for the 45 ms, *t*(11) = 4.33, *p* = .013 and 145 ms, *t*(11) = 3.68, *p* = .005 SOAs. We then separately analyzed only trials on which participants reported unawareness of the primes (SOAs 5 – 105 ms). A two-way ANOVA with SOA (5, 25, 45, 65, 85, 105) and congruency (congruent and incongruent) showed a significant main effect of SOA, $F(2, 18) = 12.77$, $p = .001$ (degrees of freedom adjusted using Greenhouse-Geisser correction) as well significant SOA x congruency interaction, $F(5, 55) = 2.99$, $p = .019$. Only priming effects at the 45 ms SOA, $t(11) = 2.92$, $p = .042$ were significant (Figure 4B and Figure 4C, dashed line). These results demonstrate that unconscious priming requires V1/V2 at both early and later temporal processing phases, but not at intermediate one.

Discussion

Whereas most researchers would agree that some information can be processed in the absence of perceptual awareness, where and how this happens, and whether this type of processing is fundamentally different from processing that leads to awareness, remains unresolved. In the current study, we investigated whether V1/V2, an area essential for conscious perception, is necessary for shape processing in the absence of perceptual awareness as measured by unconscious priming. Suppression of unconscious priming was found at two prime–TMS windows, one between 5 and 25 ms and another between 65 and 125 ms. These data show that an intact V1/V2 is required for shape processing in the absence of perceptual awareness at early and late but not intermediate phase of visual processing. Our findings suggest that unconscious visual processing in V1/V2 proceeds in distinct phases, which can be independently interrupted with single pulse TMS.

These results thus provide evidence that V1/V2 is critical for unconscious shape priming at certain temporal intervals. Although our analyses of trials on which participants were unaware of primes demonstrate significant unconscious shape priming at an intermediate phase of visual processing, which shows that V1/V2 is not essential at this intermediate stage, successful shape processing in the absence of perceptual awareness does require V1/V2 at other phases, including later ones that occur after an intermediate processing phase in which V1/V2 is unnecessary. These data therefore suggest an important role of V1/V2 in shape processing at both early and later temporal intervals. The earlier processing stage likely reflects the initial volley or feedforward input into V1/V2, without which the processing would be eliminated. The later processing stage may reflect an integration, comparison, or feedback processing stage, without which all traces of any previous shape processing without awareness would be eliminated. These results therefore indicate that alternative visual pathways that bypass V1/V2, such as the retinotectal (Ro et al., 2004; Ro, 2008) or geniculo-extrastriate pathways (Boyer et al., 2005; Schmid et al., 2010), alone are not sufficient for unconscious shape priming (Figure 1A) and that V1/V2 is necessary at specific temporal phases of processing. However, we cannot exclude the possibility that these alternative visual pathways also play some role in unconscious shape priming, especially during the intermediate processing stage.

The priming suppression function obtained in the current experiment sheds light on different temporal stages of processing in V1/V2 and provides some evidence for an early feedforward stage of processing that is important for shape priming. The earlier window of priming suppression (5 – 25 ms) in our study is consistent with a previously reported early TMS suppression of visibility (Corthout et al., 2002; Corthout, Uttl, Walsh, et al., 1999; Corthout, Uttl, Ziemann, et al., 1999). Although this early suppression might reflect the early, feedforward phase of visual processing, as has been suggested (Corthout, Uttl, Ziemann, et al., 1999), this timing may at first seem inconsistent with human EEG/MEG studies showing the earliest visual response latencies in V1/V2 around 50 ms (Baseler & Sutter, 1997; Foxe & Simpson, 2002; Vanni, Tanskanen, Seppä, Uutela, & Hari, 2001). However, because we used a high TMS intensity with a large circular coil that is optimal for producing visual suppression, it is likely that we affected V1/V2 processing long enough to influence the early initial volley of feedforward activity, as has been shown in the somatosensory system (Seyal, Masuoka, & Browne, 1992). Alternatively, early suppression might be a result of disruption of prior information processing in V1/V2 or changes in baseline activity (Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Macaluso, Eimer, Frith, & Driver, 2003). Emerging evidence suggests that each cortical area, including V1/V2, acts as an adaptive processor subject to various top-down influences (prior information) such as attention, expectation, and task requirements (Gilbert & Sigman, 2007). Cortical processing may thus occur in discrete stages as prior information and sensory evidence converge to a unified solution. Interference with prior information in V1/V2 before the arrival of sensory evidence would thus disturb subsequent cortical computations. Consistent with this proposal, recent studies have shown that microstimulation or TMS of the frontal eye fields (FEF) affects subsequent visual processing (Moore & Armstrong, 2003; Ruff et al., 2006; Taylor, Nobre, & Rushworth, 2007).

These data also provide some evidence that questions the claim that feedback processing is a sufficient condition for conscious perception. This account of conscious vision postulates the involvement of feedback stages of visual processing along the geniculostriate pathway (Lamme & Roelfsema, 2000; Lamme, 2001). If this proposal is correct, unconscious shape priming should be executed entirely through the feedforward processing stages (Figure 1B). Our results show complete suppression of unconscious shape priming not only when the TMS was applied at 5 ms or 25 ms, but also when the TMS was applied between 65 and 125 ms after the prime onset. Because this later time window of priming suppression has been proposed to interfere with feedback processing (Corthout et al., 2000; Lamme, 2006a), our results suggest that feedback processing is also essential for unconscious shape priming and may not be a sufficient condition for conscious vision (Figure 1C). In light of this new evidence, we suggest that proposals of using feedback processing as a marker and sufficient condition for conscious vision need to be reconsidered.

A recent related study also claimed that recurrent activity may be necessary for "unaware perception" (Koivisto, Mäntylä, & Silvanto, 2010). In that study, TMS applied to V1/V2 at 60 ms after the offset of a motion stimulus that was of varying durations led to a reduction in both motion visibility and forced-choice discrimination. However, their conclusion was unjustified for several reasons. First, because forced-choice discrimination may not be a sensitive measure of unconscious perception, evidence of motion direction discrimination without awareness of the motion stimulus could have been revealed using a more sensitive measure, such as priming. Furthermore, because subjects were unaware of the motion stimulus even on trials without TMS, the weak motion stimulus to begin with may have been more susceptible to the effects of TMS as compared to a clearly visible stimulus, as in our study. In the current study, we used both subjective measures of visibility as well as forced-choice discrimination to demonstrate that participants were unaware of the primes, but importantly demonstrate the effects of TMS on unconscious perception using an independent measure (i.e., priming). Thus, unlike the study by Koivisto et al. (2010), our results provide direct and conclusive evidence that processing in the absence of awareness requires both feedforward and feedback activity to early visual cortex. Another recent study by Soto et al. (Soto, Llewelyn, & Silvanto, 2012) demonstrated with a visual working memory paradigm that TMS of visual cortex may also affect color priming at a relatively long SOA (1 s), providing further evidence that late activity in V1/V2 may be necessary for both conscious and unconscious perception.

Our results show that under certain conditions, TMS of V1/V2 may interfere with awareness but not with unconscious shape priming, suggesting a dissociation between the two processes. Specifically, at the intermediate SOA between prime presentation and TMS of V1/V2, we measured significant priming in the absence of awareness. This shows that disruption of V1/V2 can sometimes eliminate awareness but not priming, which is consistent with proposals that consciousness requires more stable neuronal states (Balduzzi & Tononi, 2008; Schurger et al., 2010). Other studies have demonstrated that the same brain regions that are involved in processing information that reaches awareness are active during unconscious priming; however, the intensity of activation is much lower (Dehaene et al., 2001). These findings thus offer a plausible account for the ability of TMS to suppress visibility but not shape priming and further suggest that sufficiently stronger representations of visual information during the feedback stages are also necessary for conscious vision, not simply the existence of a feedback relay per se (see Figure 1D).

Alternative explanations that exclude differential V1/V2 states might also account for the dissociation between visual awareness and unconscious shape priming that we measured at the intermediate temporal interval. For example, information processing during the intermediate SOA could take place in other visual areas, such as through geniculo-extrastriate pathways, which then convey information to V1/V2 through feedback connections at later processing intervals (note that priming was disrupted from TMS of V1/V2 at later temporal intervals). However, because both early and late suppression eliminated unconscious shape priming, TMS of V1/V2 at early temporal intervals would also have to induce remote inhibitory effects on these other visual areas that encode shape information without V1/V2. Another alternative is that the TMS of V1/V2 was sufficient enough to eliminate activity for visual awareness, but not for shape priming, perhaps through islands of spared cortex (Fendrich et al., 1992). We believe that such alternative explanations are possible but unlikely because they are less parsimonious; TMS of V1/V2 eliminated both awareness and priming at the other SOAs.

This experiment did not show above chance shape discrimination in the absence of awareness. These results may at first seem to be inconsistent with previous studies that have demonstrated blindsight, in which patients with lesions to V1/V2 show no awareness for stimuli presented in the affected part of the visual field (Holmes, 1918), but they sometimes demonstrate the ability to locate or discriminate these stimuli (Weiskrantz, 1986). Such instances of "blindsight" have provided evidence for the involvement of alternative visual pathways and have been demonstrated in normal subjects using transcranial magnetic stimulation (TMS) of V1/V2 (Boyer et al., 2005; Jolij & Lamme, 2005). The lack of blindsight for shape in the current study sheds light on the nature of how different visual stimuli may be processed in the human brain. For example, Boyer et al. (2005) used orientation and color stimuli, which may be readily processed via geniculo-extrastriate visual pathways that project from the LGN of the thalamus to extrastriate areas (Fries, 1981; Sincich et al., 2004; Yukie & Iwai, 1981). In the current study, we eliminated both conscious perception and unconscious priming of shape, but only at specific temporal processing intervals. Blindsight studies in monkeys have repeatedly demonstrated that simple stimulus features such as luminance, color, or orientation can be discriminated without V1/V2, but that shape discrimination cannot (Humphrey, 1974). In humans, although initial experiments suggested that shape discrimination is possible in the absence of V1/V2 (Weiskrantz et al., 1974), a follow up study showed that discrimination was possible only when orientation cues were strong, with a lack of unconscious shape discrimination when orientation cues were weak or absent (Weiskrantz, 1987). Our results provide further evidence that unconscious shape discrimination is not possible without V1/V2. Note that all of the stimuli in our experiments had a vertical orientation and otherwise lacked strong orientation cues to distinguish between the shapes. Thus, unconscious shape discrimination without primary visual cortex may only occur with shapes that can be distinguished using orientation cues.

If shapes cannot be discriminated unconsciously without an intact primary visual cortex, how more complex types of information are processed in blindsight remains to be elucidated. For example, it has been suggested that emotional stimuli, including emotional faces, are processed rapidly and in the absence of awareness through subcortical routes that bypass primary visual cortex (Tamietto & de Gelder, 2010). However, new proposals are questioning this view and delegate a more important role of cortical processing for processing of emotional stimuli that we are unaware of (Pessoa & Adolphs, 2010). Further work is necessary to determine how these more complex forms such as emotion expressing faces are processed without V1/V2 and awareness.

In summary, our findings demonstrate that early visual cortex is necessary for both conscious as well as unconscious shape perception at early and later stages of visual information processing. These results also suggest that feedback processing per se is not a sufficiently defining signature of conscious vision. Rather it might be that although feedback processing may be necessary, not all types or strengths of feedback may be sufficient to generate visual awareness. Future studies focusing on the types and ways in which feedback processing may or may not give rise to visual awareness might bring us closer to the neural correlates of consciousness.

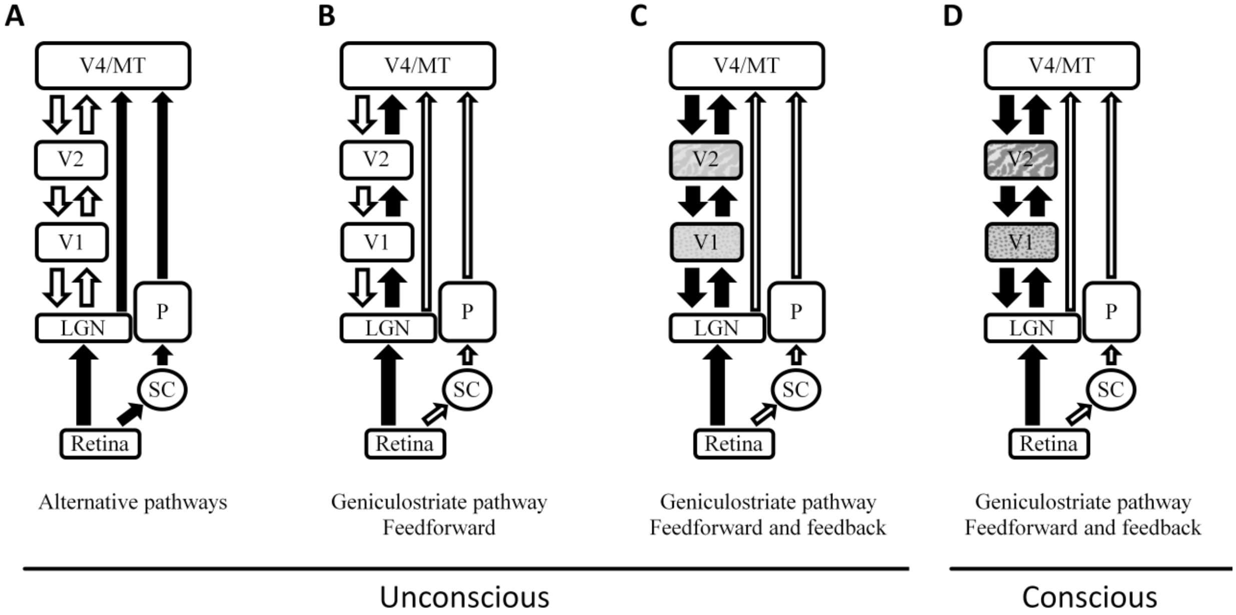


Figure 1. Three models of unconscious vision and one model of conscious vision. A schematic of the main geniculostriate and alternative visual pathways. LGN: lateral geniculate nucleus, P: pulvinar, SC: superior colliculus, V1: primary visual cortex, V2: secondary visual cortex, V4/MT: higher extrastriate visual areas. Arrows indicate feedforward and feedback connections between different cortical areas. Black filled arrows indicate the flow of visual information that supports unconscious/conscious processing. (A) Unconscious priming depends on alternative visual pathways, which bypass V1, (B) unconscious priming depends on the feedforward sweep, (C) unconscious priming requires feedforward as well as recurrent activity in V1, and (D) conscious vision requires both feedforward and feedback activity in V1, as well as sufficiently strong and/or stable representations (depicted by the higher contrast patterns in V1/V2).

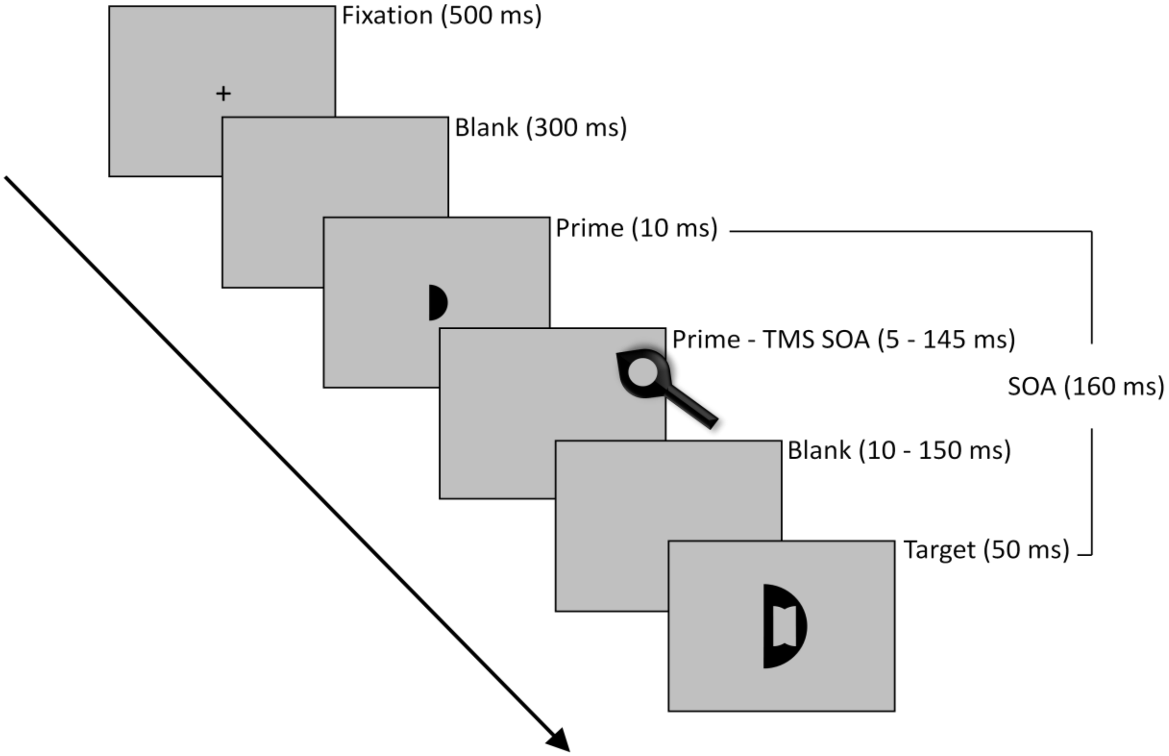


Figure 2. A schematic of the stimuli and procedures. The primes and targets were either the same (congruent, as illustrated) or different (incongruent, not shown) shapes. The prime–target SOA was constant for all trials (160 ms), whereas TMS was applied at different prime–TMS SOAs in 20 ms steps. On the baseline control trials, no TMS pulse was administered.

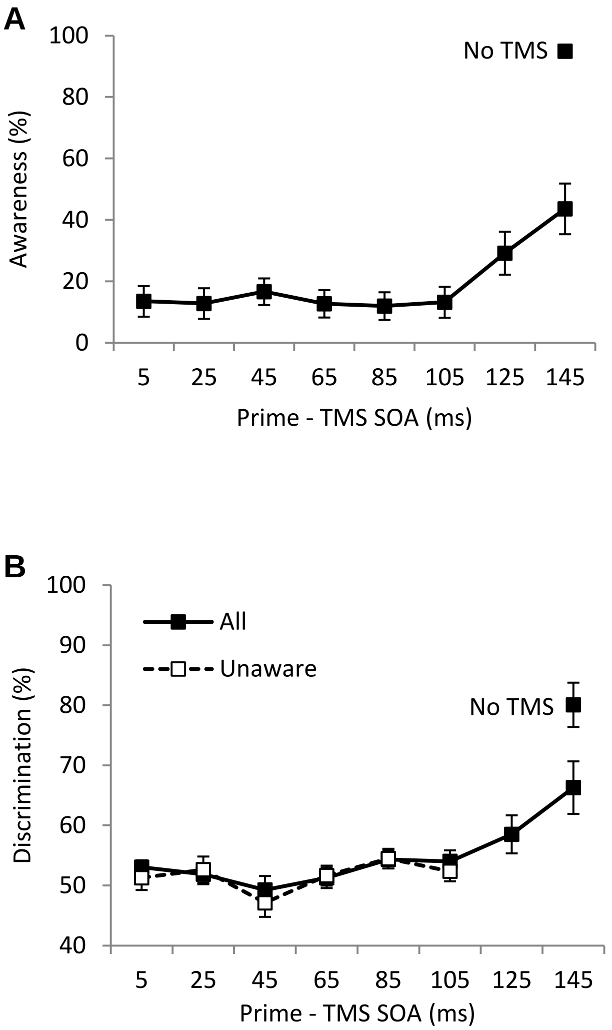
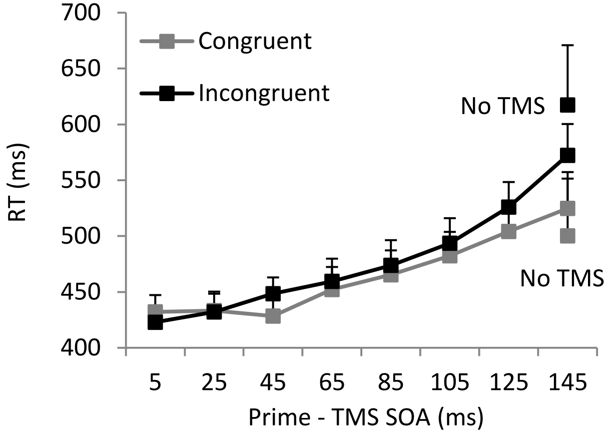


Figure 3. Prime awareness and prime discrimination performance as a function of prime–TMS SOA. (A) The mean percentage of trials on which subjects reported awareness of the prime, and (B) shape discrimination performance of the prime for all trials (solid lines) and only trials on which subjects reported unawareness of the prime (dashed lines). Error bars represent ±1 standard error of the mean (SEM).

A


700
650
600
550
500
450
400
Congruent
Incongruent
No TMS
No TMS
RT (ms)
5
25
45
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105
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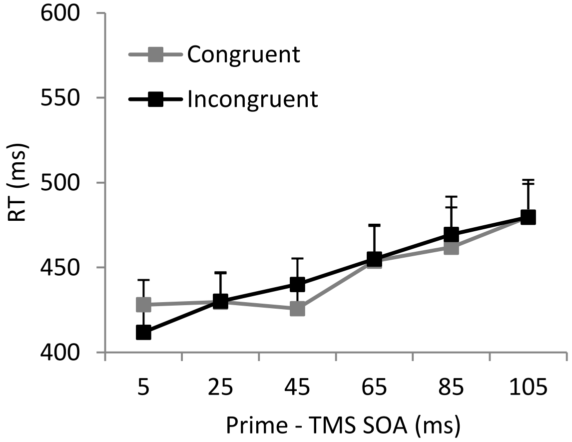
Prime - TMS SOA (ms)

B


600
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Prime - TMS SOA (ms)

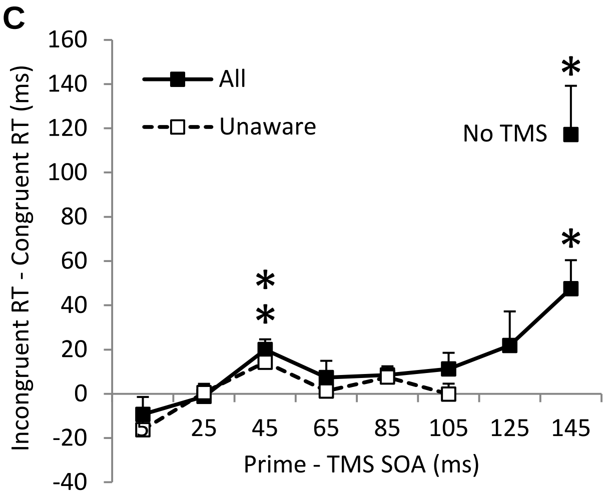

Figure 4. Overall response times and priming effects as a function of prime–TMS SOA. (A) Response times to targets for all trials, (B) response times to targets only for trials on which subjects reported unawareness of the prime, and (C) priming for all trials (solid lines) and only trials on which subjects reported unawareness of the prime (dashed lines) as a function of prime–TMS SOA. Error bars represent 1 standard error of the mean (SEM). Asterisks indicate significant priming effects.

Chapter 5

General Discussion

The main objective of this thesis was to illuminate differences between conscious and unconscious vision. In Chapter 2 we explored brightness perception, one of the most fundamental aspects of vision, and demonstrated that context-dependent brightness illusions can be represented unconsciously. Unlike higher-level theories that suggest more elaborate and complex processing more compatible with the view that processing of brightness requires awareness, our results suggest that simultaneous brightness contrast (SBC) occurs at very early levels of visual input. We further showed in Chapter 3 that even activation of complex stimulus–response (SR) mappings, previously believed to require awareness, may proceed in the absence of awareness as long as processing times for visual stimuli are sufficient. These experiments show that our visual system can process very complex information in the absence of awareness; previous demonstrations of limitations of unconscious vision might be due to insufficient processing times. In Chapter 4 we then showed that unconscious shape priming requires V1/V2, which demonstrates that such processing cannot proceed through alternative visual pathways alone. Our results also indicate that feedback to V1/V2 is important for unconscious priming and suggest that feedback activity is not a marker of conscious vision. Overall, our experiments demonstrate that complex visual information can also be represented unconsciously and that conscious and unconscious vision use similar neural pathways and processes.

Visual information processing and visual awareness

It is a common assumption that consciousness involves more elaborate and complex information processing and that processing outside awareness involves more simple and basic transformations of visual information. Indeed, several dominant theories propose that consciousness involves global processing (Dehaene, Sergent, & Changeux, 2003) or high capacity to integrate information (Tononi, 2004). An earlier but still popular duplex theory of vision postulates that vision for action is both neurally and conceptually distinct from vision for perception (Goodale & Milner, 1992; Milner & Goodale, 1995). Some of the strongest evidence for this theory comes from patients with visual form agnosia. These patients have lesions in the ventral visual stream and are unable to recognize objects; however, they show normal performance in grasping them (Milner et al., 1991). According to this theory the dorsal stream subserves vision for action, operates outside awareness and represents raw visual information undistorted from contextual effects. Vision for perception however, depends on the ventral stream and is affected by context. Similarly, it has been suggested that unconscious vision represents only raw visual information unaffected by higher level mechanisms that involve perceptual constancies which are the hallmark of conscious vision. Such dissociation was demonstrated in priming experiments where unconscious effects were shown to depend on wavelength but conscious effects on the perceived color of the prime (Breitmeyer et al., 2007; Breitmeyer, Ro, & Singhal, 2004). We tested these proposals using the perception of brightness, arguably one of the most basic aspects of vision. Brightness perception has been studied extensively by some of the early vision theorists including Helmholtz, who proposed that brightness perception depends on higher-level inferential processes that account for the context (von Helmholtz, 1867). Others have proposed different versions of higher-level mechanisms (Gilchrist et al., 1999; Williams et al., 1998a). It appears then that these views would be in line with the proposal that contextual effects on brightness require conscious vision, whereas unconscious vision might represent only the raw luminance. Our experiments however, demonstrate that simultaneous brightness contrast (SBC) occurs in the absence of awareness (Chapter 2). We also show that priming effects due to SBC occur with very brief presentation times; this result suggests that this illusion occurs early and rapidly, making the involvement of higher-level processes unlikely. This interpretation is consistent with the opposite low-level account of brightness perception (Blakeslee & McCourt, 2004) supported by studies that show very early encoding of context-dependent brightness (McCourt & Foxe, 2004).

Although our results demonstrate that SBC occurs without awareness, they are not necessarily incompatible with the current theories of consciousness. One might suggest that simple brightness illusions, such as SBC, occur without awareness but more complex illusions (e.g., Adelson illusion, http://web.mit.edu/persci/people/adelson/checkershadow_illusion.html) or processing of any complex information requires consciousness[1]. We however, favor an alternative possibility. Although it might appear that processing of simple visual attributes goes hand in hand with unconscious perception, whereas the processing of complex visual information requires consciousness, it might be that more complex visual information simply requires more elaborate and prolonged processing regardless of visual awareness. We tested this possibility by asking whether activations of more complex forms of SR mappings require awareness (Chapter 3). As we predicted, we obtained evidence for the activation of complex SR mappings in the absence of awareness but only when processing time was adequate. This result has important implications. First, it shows that equating unconscious and conscious vision with the complexity of visual information processing is misleading. Not only have we shown that complex information processing in the absence of awareness is possible, our results also indicate that in some cases simple forms of information processing might in fact require awareness. Second, previously demonstrated dissociations of conscious and unconscious vision might have been confounded with processing requirements and need to be reexamined. This realization is most directly applicable to visual masking, which is one of the most effective means of rendering

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[1] We assume that only NCC, but not the subjective experience itself are causal.

visual stimuli unconscious (Breitmeyer & Öğmen, 2006; Breitmeyer, 2007). Regardless of the type of masking (e.g., pattern, metacontrast), visibility is frequently manipulated by target - mask SOA. Shorter SOAs are critical to render stimuli invisible; however, this intervention directly influences basic processing of the prime stimulus. Clearly, any demonstrated dissociation between conscious and unconscious vision might simply be due to basic processing requirements of selected visual stimuli.

The crux of our argument is that setting up the aware versus unaware dichotomy within any experimental paradigm confounds stimulus processing with subjective conscious experience. Using multiple SOAs within a visual masking paradigm is just one example. It is well established that response priming with simple response mapping can occur outside awareness (Eimer & Schlaghecken, 1998; Neumann & Klotz, 1994). It has also been shown that such unconscious priming effects can increase with longer SOAs (Vorberg et al., 2003). This might not however, be the case in other paradigms in which priming effects can reverse with longer SOAs (Eimer & Schlaghecken, 1998). We are thus not suggesting that longer SOAs (or processing times) will always result in better performance. The exact processing requirements need to be determined for each paradigm individually. In Chapter 3 we demonstrated that longer processing times allow for activation of unconscious priming with complex SR mappings, which was previously thought to depend on awareness. We are suggesting that it is simply premature to assign the role of consciousness to specific processes based on a single time point (SOA) or a single technique to interfere with stimulus processing. Another illustrative example is crowding, one of the key limiting factors of peripheral vision. Two studies examined whether the awareness of flankers affects crowding and reported conflicting results. Gratings rendered invisible by interocular suppression (IOS) produce crowding (Ho & Cheung, 2011); however, letters rendered invisible by adaptation-induced blindness (AIB) do not (Wallis & Bex, 2011). A recent report confirmed results of these two studies by comparing two techniques using identical stimuli and suggests that crowding starts before the neural locus of IOS and after that of AIB (Shin & Tjan, 2013). It is thus likely that different techniques for rendering stimuli invisible interfere with processing at different levels of unconscious representations and there is further experimental evidence to support this notion (Breitmeyer et al., 2008; Faivre, Berthet, & Kouider, 2012). Thus, it is imperative that we seek converging lines of evidence before we declare that any type of processing requires awareness.

In fact, we need to reexamine the entire spectrum of tools and tricks to render stimuli unconscious (Kim & Blake, 2005). Let us consider some of the most popular ones. Binocular rivalry has been praised as one of the best tools in the quest to discover the neural correlates of consciousness (NCC) (Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Polonsky et al., 2000). In binocular rivalry, a different image is presented to each eye; however, the resulting visual percept is not a mixture of the two but instead fluctuates between the images. Such a setup is considered optimal because the physical stimulus remains constant, whereas the subjective visual experience changes (Kim & Blake, 2005). Any neural activity accompanying a subject's report of a change in percept should thus reflect NCC and not a change in the stimulus itself; this is the rationale behind experiments using binocular rivalry to discover the NCC. However, the insight gained from experiments on complex SR mappings (Chapter 3) reveals why such a strategy is problematic and cannot provide NCC. We suggest that when our neural system is presented with conflicting information fluctuations in interpretation will occur regardless of whether one is aware of the visual stimulus. In other words, fluctuations in subjective visual experience are downstream or independent of basic neural processing. Once more, basic visual processing is confounded with awareness. An elegant experimental support for this proposition comes from a very recent binocular rivalry study in macaque monkeys using an intrinsic signal optical imaging (Xu et al., 2012). The authors were able to demonstrate, in anesthetized monkeys, neural activity fluctuations that correlated with the presentation of two different images. When the same images were presented under binocular rivalry conditions, similar fluctuations were observed. This demonstration supports our notion that under uncertainty the brain makes a decision and that neural activity supporting such a decision is not NCC.

Another popular approach to uncovering NCC that holds stimulus constant on every trial capitalizes on the fact that stimuli presented at the threshold of visual awareness are consciously perceived only on some proportion of trials. Investigations of the underlying neuronal mechanisms have linked this interesting perceptual phenomenon to the power and phase of alpha oscillations (Berger, 1929). The phase analysis of alpha oscillations revealed that stimuli that reach awareness coincide with the opposite phase of the alpha cycle than stimuli that remain invisible (Busch, Dubois, & VanRullen, 2009; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). Yet again one can conjecture that such sampling of visual information simply reflects basic visual processing strategy. The reason why it appears that alpha phase plays a role in visual awareness (Mathewson et al., 2011; Wyart & Sergent, 2009) is similar to one used to explain visual masking. If stimuli are presented at the threshold of awareness (Figure 1), we are guaranteed that dynamics of the alpha rhythm will make some of them conscious. Future experiments could clarify the role of alpha phase. For example, one could present stimuli below the threshold of awareness and measure their effect in a priming paradigm separately for different phases of the alpha cycle. Differential priming effects under unaware conditions would unequivocally demonstrate that alpha oscillations represent basic visual processing mechanisms, independent of visual awareness.

Some have suggested that the current approaches to studying NCC confound awareness with performance and have proposed an experimental setup where performance levels are matched while awareness varies (Lau, 2008). The rationale behind this approach is that differences in neural activity with such a setup should correlate only with subjective experience. For example, Lau and Passingham (Lau & Passingham, 2006) used a metacontrast masking paradigm and presented either a square or a diamond-shaped stimuli at various SOAs. On each trial, they collected objective forced-choice measure of performance as well as subjective measure of perceptual consciousness. Capitalizing on the U-shaped metacontrast function they were able to find two SOAs where performance was matched; however, the subjective level of visual consciousness differed. The authors reasoned that activity in mid-dorsolateral prefrontal cortex (mid-DLPFC) reflected different levels of consciousness and concluded that unlike previous studies, which have confounded awareness with performance, their study allows for direct access to NCC uncontaminated by performance confound. As we explained in detail in our critique of the current approaches to NCC, it is the basic stimulus processing that is the source of confound and this confound cannot be circumvented with performance matching. Although Lau and Passingham (Lau & Passingham, 2006) matched performance for two different SOAs, differential activation of any brain region, including mid-DLPFC, could be a consequence of different stimulus processing at two SOAs regardless of the awareness levels.

If our views are correct, we have been (i) overestimating the role of consciousness and (ii) confounding neural processing with awareness. What can be done to remedy the situation? To render stimuli invisible, yet preserve the crucial aspects of visual processing, we need new, innovative ways to present our stimuli. In principle, we can answer the question of which stimuli can be processed in the absence of awareness. Contrary to earlier claims (Harris, Schwarzkopf, Song, Bahrami, & Rees, 2011), we have recently demonstrated, using a new presentation technique, an unconscious modal completion – the perception of illusory shapes in the absence of awareness of inducers, (Persuh, Emmanouil & Ro, unpublished). Addressing the second concern will be more challenging. The most pessimistic view would be to concede and admit that whereas it is possible to demonstrate unconscious perception for any stimulus, it is impossible to discover neural activity that differentiates conscious from unconscious vision because this distinction is always confounded by some kind of manipulation that affects neural processing per se. Creating a dichotomy between aware and unaware conditions within any paradigm will not work. One way to approach this difficult question would be to parametrically manipulate stimulus presentation conditions to create several levels below and above perception threshold (Figure 1). One could then compare differences in neural activity for stimuli just below and just above the threshold (levels 3 and 4 in Figure 1) with those for pairs of stimuli completely below (levels 1 vs. 2 and 2 vs. 3 in Figure 1) or completely above the threshold (levels 4 vs. 5 and 5 vs. 6 in Figure 1). This type of manipulation should be performed within different paradigms for rendering stimuli invisible (Kim & Blake, 2005); one could then use converging evidence to get at the putative NCC.

Both conscious and unconscious vision depend on the geniculo-striate pathway

One critical step towards discovering NCC is to determine whether conscious and unconscious vision depend on the same visual pathways. Several different accounts have been proposed regarding the visual pathways involved in unconscious vision. One line of reasoning supported by evidence from blindsight patients (Weiskrantz, 1986) and TMS-induced blindsight in normal subjects (Boyer et al., 2005) implicates alternative visual pathways. Another account implicates the geniculo-striate pathway but proposes that feedforward activity alone can support unconscious vision, whereas recurrent activity is important for visual awareness (Lamme & Roelfsema, 2000). We capitalized on the high temporal resolution of TMS to disrupt neural processing at specific time points after the presentation of the visual stimulus (Chapter 4). Because we eliminated unconscious shape priming at both early and late prime-TMS SOAs, we conclude that alternative pathways alone can’t support processing of shape outside of visual awareness. Although we cannot conclude that alternative pathways do not play a role, our results suggest that both conscious and unconscious vision depend on the geniculo-striate pathway. This result is compatible with the view that unconscious vision might be just as powerful as conscious vision, which is known to depend on the geniculo-striate pathway. Perhaps then it is the recurrent activity that differentiates conscious from unconscious vision, as several authors have suggested (Di Lollo et al., 2000; Lamme, 2001). Once again our results show unsuspected similarities between the unconscious and conscious vision. The second window of priming suppression coincides with the classical TMS suppression window, which is considered to mark the recurrent processing in V1 (Corthout et al., 2000; Lamme, 2006a). It thus appears that even recurrent processing is not a unique signature of conscious vision; instead it constitutes a basic visual processing mechanism. This result reiterates our view that conscious and unconscious vision are more similar than previously thought.

One might argue that evidence implicating V1 in visual awareness only shows that visual information must pass through V1 and that processing in V1 does not constitute the NCC. In that sense, asking whether conscious and unconscious vision depends on the same visual pathways cannot be answered by interfering with V1. One could even take this argument a step further and suggest that answering such a question is as trivial as asking whether eyes are important for unconscious vision. We think that such reasoning is not justified for the following reasons. First, whether activity in V1 is part of the NCC is far from being settled (Frank Tong, 2003). One theory of consciousness specifically suggests that recurrent activity in V1 is the NCC (Lamme, 2006b). This theory and other related theories (Block, 2007; Tse, Martinez-Conde, Schlegel, & Macknik, 2005; Zeki, 2003), also known as the first-order theories (Lau & Rosenthal, 2011) claim that NCC reside in the local activity of brain modules, including V1, and that loops connecting such areas with posterior parietal and prefrontal networks only afford access. Even if these theories are invalidated in future experiments, we maintain that it is still important to understand the role of the geniculo-striate pathway in unconscious vision. This pathway is the main route for visual information processing in humans and V1 serves as a “gatekeeper” to other visual cortical areas (Felleman & Van Essen, 1991). It is thus important to know whether there is a divergence between conscious and unconscious vision at this early but important stage of visual processing. This knowledge directly contributes to our understanding of differences between processing that remains outside of awareness and processing that gives rise to awareness.

In summary, our results demonstrate that complex visual information can be processed outside of awareness when stimuli are allowed to undergo sufficient processing and that conscious and unconscious vision depend on the same visual pathways. These findings show that we may be overestimating conscious vision and that apparent dissociations between conscious and unconscious vision might be only due to differences in neural processing and thus need to be revisited.

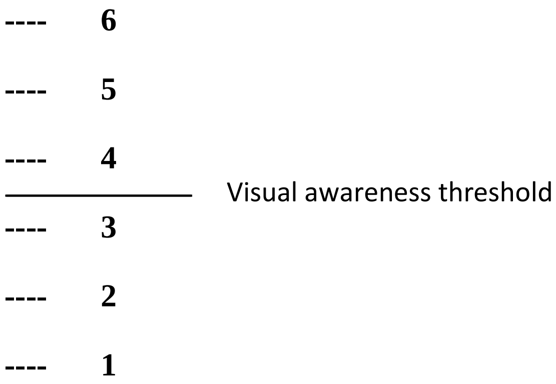

Figure 1. A diagram representing different levels of stimulus processing around the threshold of visual awareness. Different levels of stimulus processing could be achieved within any of several paradigms employed to render visual stimuli unconscious. For example, in masking, one can vary the target – mask interval or the mask strength.

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