

Unconscious Priming Requires Early Visual Cortex at Specific Temporal Phases of Processing

Marjan Persuh and Tony Ro

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 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, uncon-

scious priming can occur without V1/V2 at an intermediate temporal interval but not at early (5–25 msec) or later (65–125 msec) 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 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; Weiskrantz, 1986; Poppel, Held, & Frost, 1973). 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 (Tong & Engel, 2001; Polonsky, Blake, Braun, & Heeger, 2000; Leopold & Logothetis, 1996). 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 fMRI studies that show increased activity in V1 for trials on which participants perceived (hits) or believed to have perceived the target (false alarms; Ress & Heeger, 2003; Ress, Backus, & Heeger, 2000).

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 (Weiskrantz, 1986; Weiskrantz, Warrington, Sanders, & Marshall, 1974; Poppel et al., 1973). Importantly, such instances of blindsight have been demonstrated in neurologically healthy humans using TMS of V1/V2 (Boyer, Harrison, & Ro, 2005; Jolij & Lamme, 2005). For example, Boyer et al. (2005) used TMS of V1/V2 to suppress visual awareness and showed that participants 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 (Ro, 2008; Ro, Shelton, Lee, & Chang, 2004; Rafal, Smith, Krantz, Cohen, & Brennan, 1990), suggesting involvement of the retinotectal pathway. Together, these studies provide evidence for the role of alternative visual pathways in unconscious visual perception.

Another nonmutually 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;

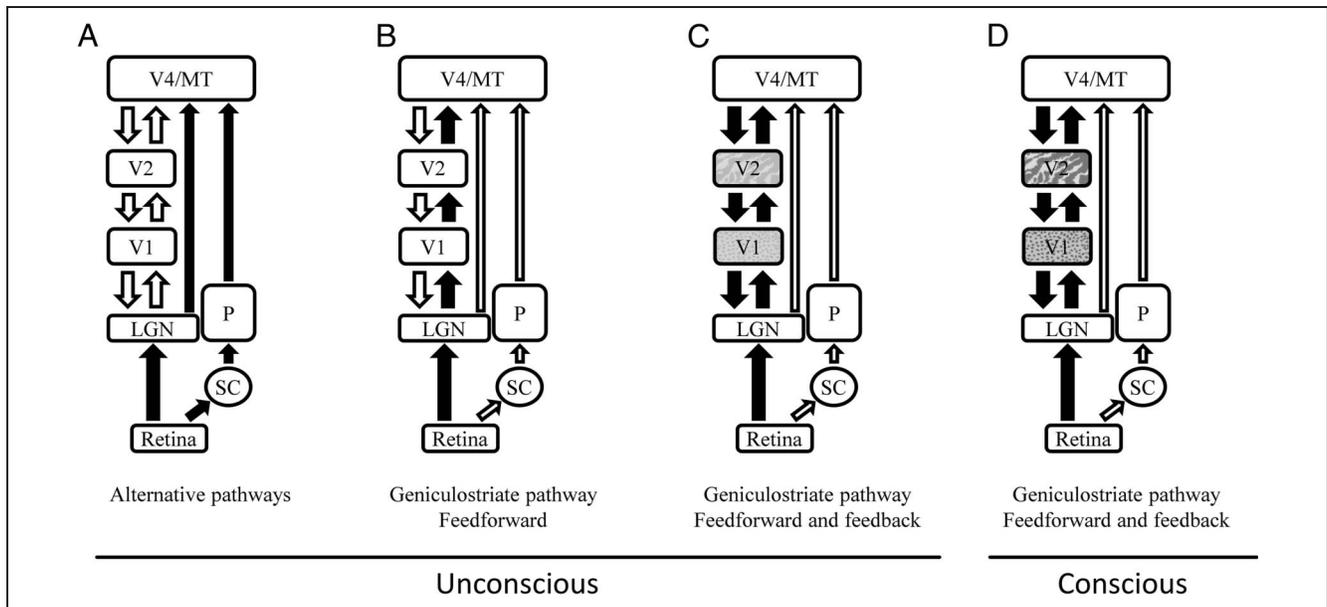


Figure 1. Three models of unconscious vision and one model of conscious vision. A schematic of the main geniculostriate and alternative visual pathways. LGN = lateral geniculate nucleus; P = pulvinar; SC = superior colliculus; V1 = primary visual cortex; V2 = secondary visual cortex; V4/MT = higher extrastriate visual areas, including the color-sensitive fourth visual area (V4) and the motion-sensitive middle temporal (MT) area. Arrows indicate feedforward and feedback connections between different cortical areas. Black filled arrows indicate the flow of visual information for the given model. (A) Unconscious priming depends on alternative visual pathways that bypass V1. (B) Unconscious priming depends on the feedforward sweep through V1. (C) Unconscious priming requires feedforward as well as recurrent activity in V1. (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).

Lamme & Roelfsema, 2000) and/or when there is insufficient V1 for awareness, such as a few spared islands after brain damage (Fendrich, Wessinger, & Gazzaniga, 1992). Transient inactivation of V1/V2 with TMS in healthy humans maximally suppresses visual awareness approximately 100 msec after the stimulus onset (Amassian et al., 1989). Because the initial volley of visual information reaches V1 as early as 35 msec after the stimulus offset (Lamme & Roelfsema, 2000), whereas feedback from higher extrastriate areas (e.g., V5/MT) to V1 may take between 5 and 45 msec (Hupé et al., 2001; Pascual-Leone & Walsh, 2001), TMS has been proposed to primarily interfere with feedback or recurrent processing in V1 (Lamme, 2006; Corthout, Uttl, Juan, Hallett, & Cowey, 2000). Similarly, single-unit recordings of V1 neurons in nonhuman primates show response enhancements only at late temporal processing windows (>100 msec) 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 1B and D). 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, Enns, & Rensink, 2000; Enns & 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 the target offset-related discharge (Macknik & Martinez-Conde, 2007), evidence from monkey ablation and inactivation studies (Supèr & Lamme, 2007; Hupé et al., 1998; Lamme, Supèr, & Spekreijse, 1998), as well as evidence from MEG (Boehler, Schoenfeld, Heinze, & Hopf, 2008), patient (Allen, Humphreys, Colin, & Neumann, 2009), and TMS experiments (Silvanto, Lavie, & Walsh, 2005; Ro, Breitmeyer, Burton, Singhal, & Lane, 2003; Pascual-Leone & Walsh, 2001), 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 (Sumner, Tsai, Yu, & Nachev, 2006; Eimer & Schlaghecken, 1998; Neumann & Klotz, 1994). 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 & Ögmen, 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).

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, & Ögmen, 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 one study 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 (see Figure 1C). 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 (Schurger, Pereira, Treisman, & Cohen, 2010; Balduzzi & Tononi, 2008).

METHODS

Participants

Sixteen participants were recruited from The City University of New York and participated in the study after giving informed consent. All participants 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 participants 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 participants were excluded because of an insufficient number of trials on which they were unaware of primes (i.e., these participants 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 12 participants (one woman) between the ages of 21 and 27 years ($M = 24.2$ 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-in. CRT monitor (Sony Model G220) with a refresh rate of 100 Hz and with all stimuli presented at the center of the display. Participants 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 msec 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 $0.3^\circ \times 0.5^\circ$, and were displayed on a gray background with a luminance of 6.8 cd/m^2 . Participants 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 msec after the digits appeared on the screen. Coil position was adjusted and the TMS intensity was increased until a stable visual suppression of the digits was achieved. In the second step, the prime semicircles 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 three of five 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 T) output.

All stimuli in the main experiment were black, had a luminance of 0 cd/m² (Figure 2), and were displayed on a gray background with a luminance of 2.6 cd/m². Each trial started with a 500-msec presentation of a fixation cross measuring 0.25° of visual angle. A blank interval of 300 msec occurred after fixation offset. Next, a semicircle prime (radius = 0.44°) was presented for 10 msec followed on most trials by a TMS pulse at a prime-TMS SOA of 5, 25, 45, 65, 85, 105, 125, or 145 msec. After 160 msec from the onset of the prime, a larger semicircle target (radius = 1.07°) was presented for 50 msec. The central part of the target semicircles 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 = 0.63°) 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 msec; Breitmeyer, 1984).¹ The prime and target semicircles 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.

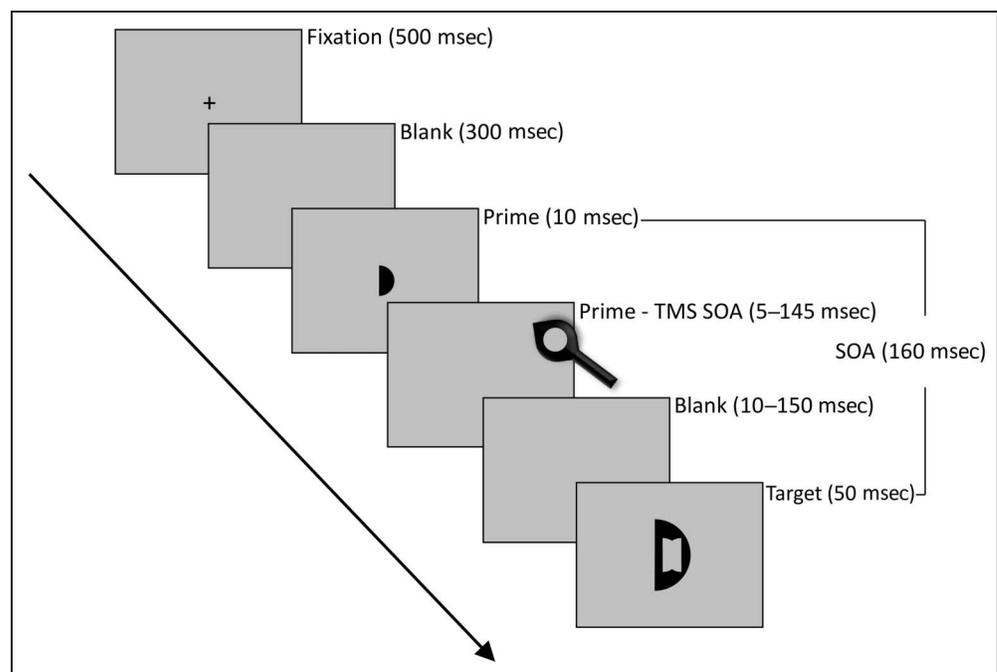
Participants made three separate responses on each trial. First, they made a speeded response to the shape

of the target by clicking the left mouse button for left semicircles or the right mouse button for right semicircles. Second, participants 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 participants. There was no time constraint for reporting the awareness. Third, participants 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 participants 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.

Data Analysis

We excluded trials with RTs 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).

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 msec), whereas TMS was applied at different prime-TMS SOAs in 20-msec steps. On the baseline control trials, no TMS pulse was administered.



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 msec after visual stimulus onset (Boyer et al., 2005; Jolij & Lamme, 2005; Amassian et al., 1989), 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 msec (Kammer, Puls, Strasburger, Hill, & Wichmann, 2005; Beckers & Hömberg, 1991). In the current study, participants were largely unaware of the prime for SOAs up to 105 msec, with stimuli becoming more visible at the longer SOAs (Figure 3A). A 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 msec to increase the magnitude of TMS suppression and also because prime discrimination performance was lowered by interference from the incongruent targets. A one-way, repeated-measures ANOVA showed a significant main effect of SOA, $F(7, 77) = 6.63$, $p < .001$, demonstrating that the magnitude of prime suppression depended on prime-TMS SOA.

Because there was less suppression for SOAs longer than 100 msec, 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 msec 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).

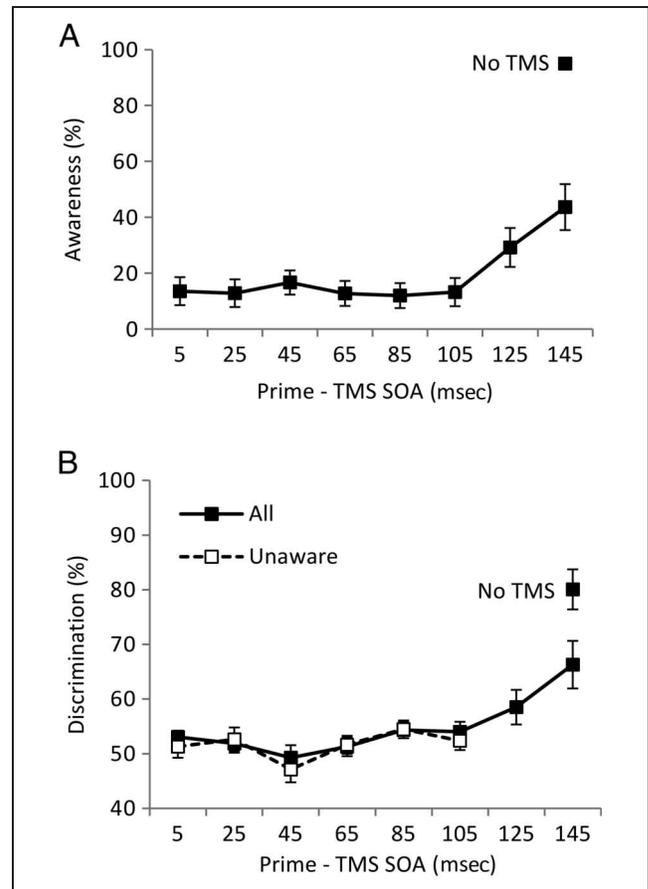


Figure 3. Prime awareness and prime discrimination performance as a function of prime-TMS SOA. (A) The mean percentage of trials on which participants reported awareness of the prime, and (B) shape discrimination performance of the prime for all trials (solid lines) and only trials on which participants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

A one-way, repeated-measures ANOVA for SOAs between 5 and 105 msec 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 msec, 5: $t(11) = 0.628$, $p = .271$; 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 rather than producing visual suppression with TMS, the participants had forgotten the prime shapes 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 msec SOAs and compared them with 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 msec 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 (see Figure 3A), 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 $(29\% \times 80\%) + (71\% \times 50\%) = 59\%$, which exactly matches the measured accuracy of 59%. Similar calculations predict that for the 145 msec SOA, accuracy should be around 63% ($(44\% \times 80\%) + (56\% \times 50\%)$), 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 further address both the possibility of forgetting and blindsight more rigorously, we tested three participants in an additional control experiment. On each trial, there was either no TMS or TMS administered at an SOA of 105 msec, 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 ($M = 117.2$ msec, $SD = 76.3$ msec, $t(11) = 5.32$, $p < .001$). 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 solid line in Figure 4C, solid line). Priming was completely suppressed during two time windows: an early time window (SOAs between 5 and 25 msec) and then again at a later time window (SOAs between 65 and 125 msec) with reliable priming only occurring between these two time windows (SOA 45 msec) as well as at the later SOA of 145 msec. 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 \times Congruency interaction, $F(3, 28) 4.42$, $p = .015$ (degrees of freedom adjusted using Greenhouse–Geisser correction). The main effect of SOA likely reflects a generalized TMS-induced alerting response in which participants respond faster with longer

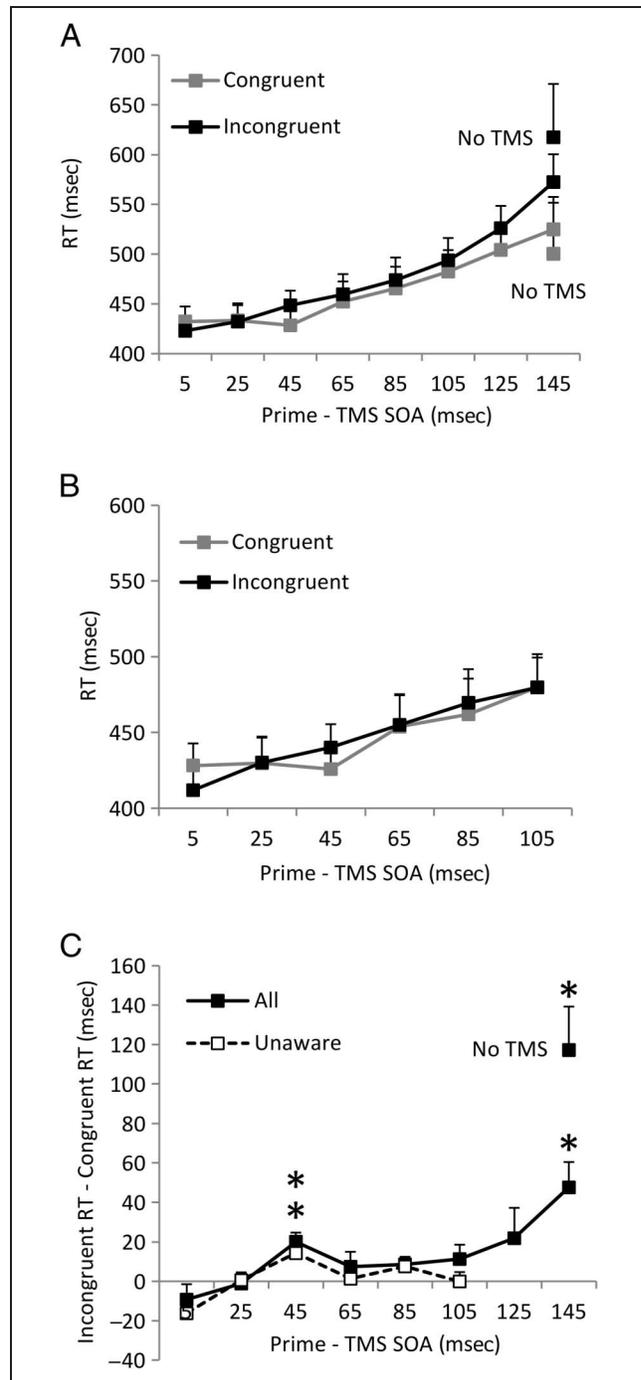


Figure 4. Overall RTs and priming effects as a function of prime-TMS SOA. (A) RTs to targets for all trials, (B) RTs to targets for trials on which participants reported unawareness of the prime, and (C) priming for all trials (solid lines) and only trials on which participants reported unawareness of the prime (dashed lines) as a function of prime-TMS SOA. Error bars represent 1 SEM. Asterisks indicate significant priming effects.

TMS-to-target intervals (Figure 4A; Burle, Bonnet, Vidal, Possamai, & Hasbroucq, 2002; Terao et al., 1997; Nickerson, 1973). We further examined priming effects at each SOA using one-tailed, paired samples t tests. Priming effects were significant only for the 45 msec, $t(11) = 4.33$, $p = .013$

and 145 msec, $t(11) = 3.68$, $p = .005$ SOAs. We then separately analyzed only trials on which participants reported unawareness of the primes (Figure 4B). 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 as a significant SOA \times Congruency interaction, $F(5, 55) = 2.99$, $p = .019$. Only priming effects at the 45 msec SOA, $t(11) = 2.92$, $p = .042$ were significant (Figure 4B and dashed line in Figure 4C). These results demonstrate that unconscious priming requires V1/V2 at both early and later temporal processing phases, but not at an intermediate one.

DISCUSSION

Although 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 msec and another between 65 and 125 msec. 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 an 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 most traces of any previous shape processing without awareness might be eliminated. These results therefore indicate that alternative visual pathways that bypass V1/V2, such as the retinotectal (Ro, 2008; Ro et al., 2004) or geniculolateral pathways (Schmid et al., 2010; Boyer et al.,

2005), 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 msec) 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 msec (Foxe & Simpson, 2002; Vanni, Tanskanen, Seppä, Uutela, & Hari, 2001; Baseler & Sutter, 1997). 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 (Macaluso, Eimer, Frith, & Driver, 2003; Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). 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 FEFs affects subsequent visual processing (Taylor, Nobre, & Rushworth, 2007; Ruff et al., 2006; Moore & Armstrong, 2003).

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, 2001; Lamme & Roelfsema, 2000). 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 or 25 msec, but also when the TMS was applied

between 65 and 125 msec after the prime onset. Because this later time window of priming suppression has been proposed to interfere with feedback processing (Lamme, 2006; Corthout et al., 2000), 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 msec 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 participants 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. 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, Llewelyn, and 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 sec), 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 (Schurger et al., 2010; Balduzzi & Tononi, 2008). 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 geniculol-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, 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 participants using 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 geniculol-extrastriate visual pathways that project from the LGN of the thalamus to extrastriate areas (Sincich, Park, Wohlgemuth, & Horton, 2004; Fries, 1981; Yuki & 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.

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Reprint requests should be sent to Marjan Persuh or Tony Ro, Department of Psychology, NAC 7/120, City College, City University of New York, 160 Convent Avenue, New York, NY 10031, or via e-mail: mpersuh@gmail.com, tro@ccny.cuny.edu.

Note

1. The lack of metacontrast masking was confirmed in a separate prime discrimination control experiment with six participants, 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, $t(5) = 1.307, p = .248$.

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