



Dissociations of conscious and unconscious perception in TMS-induced blindsight

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ABSTRACT

As with some patients with primary visual cortex (V1) damage, transcranial magnetic stimulation (TMS) over V1 reliably induces blindsight, whereby observers can correctly discriminate the attributes of visual stimuli despite being unable to detect them. This TMS-induced blindsight has been demonstrated to reflect a form of unconscious vision that relies upon different neural pathways than with conscious vision. However, the timing of the neural processes mediating TMS-induced blindsight has been unclear, especially when considering suggestions that TMS interferes with feedback processes to V1 that mediate conscious visual perception. To better elucidate the neural mechanisms that give rise to blindsight, we tested TMS-induced blindsight for the orientation of visual stimuli across a range of stimulus onset asynchronies (SOAs) to assess how different latencies of visual cortex disruption, relative to a visual stimulus, affect detection rates and forced-choice discrimination accuracy. At all TMS latencies, including at SOAs with substantial visual suppression from TMS, discrimination performance was significantly above-chance, demonstrating the consistency of TMS-induced blindsight. Crucially, we observed two windows of maximum visual suppression from TMS at SOAs between 65 and 105 ms, but consistent above-chance discrimination performance accuracy across these windows. However, at longer SOAs, detection and discrimination covaried, suggesting a dependency of discrimination performance on detection only when detection rates exceed threshold levels of normal vision. Taken together, these results indicate that unconscious discrimination occurs independently of detection, including at TMS intervals that optimally interfere with conscious visual perception. They further suggest that forced-choice discrimination is less dependent on feedback processes to V1 than visual awareness and that TMS-induced blindsight is not the same as near-threshold vision.

1. Introduction

Despite sustained interest and research over several decades, the neural mechanisms associated with conscious and unconscious visual perception remain poorly understood. A fundamental unanswered question is whether these different forms of visual perception follow the same time course of visual processing. Several lines of evidence suggest that conscious vision occurs at later feedback stages of neural processing. For example, the importance of feedback to V1 for visual perception is evident from several studies in non-human primates that show distinct late neural responses that correspond with perceptual report (Hupé et al., 1998; Lamme and Roelfsema, 2000; Super et al., 2001). Additionally, responses of V1 neurons are considerably modulated by contextual information that is processed outside of their receptive fields, suggesting input from horizontal connections and feedback from higher cortical areas (Allman et al., 1985; Gilbert and Li,

2013; Ito and Gilbert, 1999; Kapadia et al., 1995; Knierim and Van Essen, 1992; Rossi et al., 1996).

In humans, feedback processing for visual awareness is supported by several lines of evidence, including studies using visual masking, in which perception of a target stimulus is reduced when followed by a mask. One proposed mechanism for visual masking is that the subsequent mask interferes with feedback processes to V1 that are responsible for rendering the preceding target stimulus conscious (Ro et al., 2003; Enns, 2004; Enns and Di Lollo, 2000; Tapia and Beck, 2014). Furthermore, in trials in which a mask causes suppression of the target, disrupting early visual cortex (EVC) approximately 100 milliseconds (ms) after the mask with transcranial magnetic stimulation (TMS), a non-invasive brain stimulation technique that creates a transient virtual cortical lesion, causes recovery of the target's visibility and suppression of the mask (Amassian et al., 1993; Ro et al., 2003). Such unmasking of the target stimulus and masking of the mask suggests that

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feedback to visual cortex is a critical mechanism for visual awareness (Di Lollo et al., 2000; Fahrenfort et al., 2007; Lamme, 2001; Lamme et al., 2000) and that feedback compares the results of higher-order cortical processing with the earlier stages of processing to improve the detail of visual percepts (Hochstein and Ahissar, 2002).

In comparison to conscious visual perception, our knowledge of the neural basis of unconscious forms of vision is more limited. Investigations of blindsight, a neurological disorder characterized by visual discrimination without conscious perception after damage to V1 (Weiskrantz, 2009; Weiskrantz et al., 1974), have suggested both subcortical (Dodds et al., 2002; Pöppel et al., 1973; Rafal et al., 1990) as well as cortical (Fendrich et al., 1992; Schmid et al., 2010) mechanisms for unconscious vision. As with blindsight patients, TMS over V1 at approximately 100 ms after visual stimulus onset reliably causes blindsight behavior, whereby normal observers can correctly discriminate the attributes of visual stimuli despite their inability to detect them (Allen et al., 2014; Boyer et al., 2005; Christensen et al., 2008; Jolij and Lamme, 2005; Railo et al., 2012; Ro, 2008; Ro et al., 2004). The later time window of disruption that produces TMS-induced blindsight may suggest that unconscious vision relies on earlier feedforward stages of visual processing in V1, such that disrupting later feedback activity will affect only visual awareness (Lamme, 2001; Lamme et al., 2000). Alternatively, TMS-induced blindsight may occur as a result of visual processing in pathways that bypass V1, leading to the prediction that TMS over V1 at time intervals that correspond with feedforward processing should also cause TMS-induced blindsight.

In order to assess whether feedforward geniculostriate activity through EVC or whether processing in extrastriate pathways that bypass V1 causes the unconscious discriminations observed in TMS-induced blindsight, a systematic investigation of the time course of the effect is required. That is, although the functional contribution of EVC to visual processing for visual awareness across time has been investigated (Amassian et al., 1993; Corthout et al., 2001, 2000, 1999; de Graaf et al., 2014; Kammer et al., 2005), no such chronometric analysis has been conducted for unconscious discrimination in blindsight. We hypothesized that if unconscious vision in blindsight is independent of EVC activity, unconscious discrimination should dissociate from conscious perception in both early and late time windows in which visual detection is suppressed by TMS. Alternatively, if above-chance discrimination without awareness in blindsight is dependent on the feedforward sweep of EVC activity, detection and discrimination should dissociate only in a late time window corresponding to feedback activity to EVC. To test these hypotheses, we disrupted EVC activity with TMS across a range of SOAs from 55 to 155 ms in 10 ms increments and measured detection and forced-choice discrimination for the orientation of visual stimuli. Based on previous studies demonstrating alternative visual pathways supporting blindsight, we predicted that discrimination performance can be independent of EVC activity and that disrupting EVC with TMS would have little to no effect on above-chance orientation discrimination across SOAs. However, if discrimination is dependent on feedforward EVC activity, disrupting EVC with TMS should disrupt both detection and discrimination during the time window corresponding to the feedforward sweep, but disrupt only detection during the feedback window.

2. Methods

2.1. Subjects

Seventeen adults with normal or corrected-to-normal vision were recruited for this experiment and gave written informed consent prior to participating. One participant was excluded from analysis because visual suppression could not be attained with a TMS strength that was comfortable. Therefore, the final number of subjects was 16 (6 female; median age = 26.5). All subjects were recruited from the undergraduate and graduate student populations at the City University of

New York and from the New York City area. All subjects were monetarily compensated for their participation. TMS was administered following all safety guidelines (Rossi et al., 2009), and this study was approved by the Institutional Review Board of the City University of New York.

2.2. Stimuli and procedure

The stimuli were presented on a Dell Trinitron cathode ray tube monitor that was set at a 100 Hz vertical synchronization rate and connected to an ATI Radeon Graphics card on a Dell Optiplex 755 computer. All stimuli, TMS triggers, and response collection were controlled using custom software written in Visual C++ with Microsoft DirectX libraries. The stimuli consisted of individual horizontal or vertical lines. At a viewing distance of 57 cm, the lines were either $0.3^\circ \times 0.05^\circ$ (horizontal lines) or $0.05^\circ \times 0.3^\circ$ (vertical lines) of visual angle and were positioned 0.25° to the right of the fixation square, which was $0.25^\circ \times 0.25^\circ$ in size. Stimuli were dark gray with a luminance of 12.98 candelas per square meter (cd/m^2) and presented on a light gray background with a luminance of $24.61 \text{ cd}/\text{m}^2$. Hence, the Weber contrast of the visual stimuli was 0.896. For each trial, a line would appear on the screen for 10 ms and would be followed by a single TMS pulse at varying SOAs. The SOA between the visual stimulus and TMS ranged from 55 to 155 ms in steps of 10 ms and was randomized across trials.

In order to ensure that participants could accurately discriminate line orientation without TMS, a familiarization and a practice block were run before any TMS was introduced. For the familiarization block, subjects simply advanced through 22 trials, carefully viewing the stimuli without any required responses. For the subsequent practice block, we recorded orientation discrimination performance on 22 trials to ensure line discrimination performance accuracy of at least 80%. All subjects were able to accurately perform the line discrimination without any TMS.

For TMS, we used a Cadwell MES-10 polyphasic stimulator with a maximum output of 2.2 T and a circular coil that was 9 cm in diameter, a coil configuration that is far more effective in producing visual suppression compared to focal figure-eight coils (Kastner et al., 1998). In order to determine the optimal site and intensity for TMS-induced visual suppression, we employed the following visual cortex localization procedures. First, the base of the TMS coil was placed 2 cm above and 1 cm to the left of the subject'sinion and stimulation intensity was set to 50% (1.1 T). For each trial, a square identical in color and size to the fixation appeared for 10 ms followed by a TMS pulse that was delivered 100 ms after the visual stimulus onset. The square's location on the screen was identical to the location of the line stimuli used for the orientation discrimination task. Subjects reported after each trial whether or not they saw the square. The coil position and TMS intensity were adjusted incrementally until the subject reported not seeing the stimulus on at least three out of five trials. The optimal location on the head was then marked for stimulation throughout the experiment. For the first six participants, TMS intensity was set at 10% of maximum stimulator output above the suppression threshold; for the remaining subjects, the intensity was set at 110% of the suppression threshold intensity. To allow subjects to adapt to the stronger stimulation intensity, participants ran one practice block with TMS at this intensity before beginning the experiment. The average stimulation intensity used for this experiment was 68.7%, with a range of 50–85%.

For each trial of the experiment, participants first reported whether or not they saw the line. They then reported the orientation as horizontal or vertical and, importantly, were instructed to guess if they did not know. Finally, subjects provided a confidence rating on their orientation discrimination response (not very, somewhat, or very). Twelve blocks of 22 trials were run for each session, yielding 24 total trials for each of the 11 SOAs. The suppression curve for each participant was derived from the percentage of trials in which the subject

reported seeing the line orientation at each SOA.

2.3. Data analysis

All analyses were conducted using custom R scripts. For the detection data, we first performed a regression analysis to determine the polynomial curve of best fit. We then statistically compared the line detection rates at different SOAs of interest based on the regression analysis using one-tailed paired *t*-tests. An additional post-hoc analysis realigned the detection rate data to each subject's first suppression maximum to compensate for potentially different maximum visual suppression times between subjects. To assess for dissociations between detection rates and discrimination performance, we compared line detection and forced-choice orientation discrimination as a function of SOA using a two-way analysis of variance (ANOVA) with response type (detection vs. discrimination) and SOA (55–155 in 10 ms steps) as the two within-subject factors. We also compared confidence ratings with detection and discrimination performance by conducting two separate two-way ANOVAs with response (confidence vs. detection and confidence vs. discrimination) and SOA (55–155 in 10 ms steps) as the within-subject factors. To determine whether unconscious forced-choice discrimination was above-chance, we computed the proportion of trials in which participants correctly guessed the orientation when they had reported not detecting the stimulus and compared this proportion to a chance value of 0.5 at each SOA using false-discovery rate (FDR) corrected one-tailed *t*-tests.

3. Results

To assess how visual cortex disruption at varying latencies affects conscious and unconscious perception, we applied TMS over EVC at different SOAs to induce visual suppression. The two principal dependent measures were stimulus detection rate and forced-choice orientation discrimination accuracy. We also measured orientation discrimination confidence to assess whether metacognitive judgments about performance reflected conscious and/or unconscious perception (Fig. 1).

Stimulus detection rates and discrimination performance accuracy as a function of SOA are shown in Fig. 2 whereas confidence ratings as a function of SOA are shown in Fig. 3. Although the magnitude of TMS suppression was similar to the U-shaped function found in previous studies (e.g., Amassian et al., 1989; Corthout et al., 2001, 2000, 1999; Kammer et al., 2005; Ro et al., 2003), with lower detection rates at intermediate SOAs framed by higher detection rates at shorter and longer SOAs, there are two notable exceptions. First, we ran a regression analysis and found that the best fit occurred for a fourth-degree quartic model ($R^2 = 0.9665$, adjusted $R^2 = 0.9441$), in comparison to a linear model ($R^2 = 0.6623$, adjusted $R^2 = 0.6248$), a quadratic model ($R^2 = 0.888$, adjusted $R^2 = 0.86$) or a cubic model ($R^2 = 0.9504$, adjusted $R^2 = 0.9291$). As quartic polynomial functions are characterized as W-shaped functions, this suggests that suppression was maximal in two time windows, the first between 65 and 75 ms, and the second between 95 and 105 ms. In order to statistically confirm that these two time windows are distinct, we used post-hoc one-tailed paired *t*-tests to compare detection rates within each of these time windows with the detection rate in the condition (SOA of 85 ms) separating the two windows. There were significant differences in detection rates between SOAs of 75 ms and 85 ms ($t_{15} = -1.7679$, $p = 0.0487$) and between SOAs of 85 ms and 95 ms ($t_{15} = 2.0749$, $p = 0.0278$). These results further indicate that there is a distinct increase in detection rates in between the two time windows associated with maximal visual suppression.

Although the significant quartic function provides some justification for conducting posthoc one-tailed *t*-tests, these differences would only be marginally significant if two-tailed *t*-tests were applied. These borderline differences may be because the SOA at which TMS causes

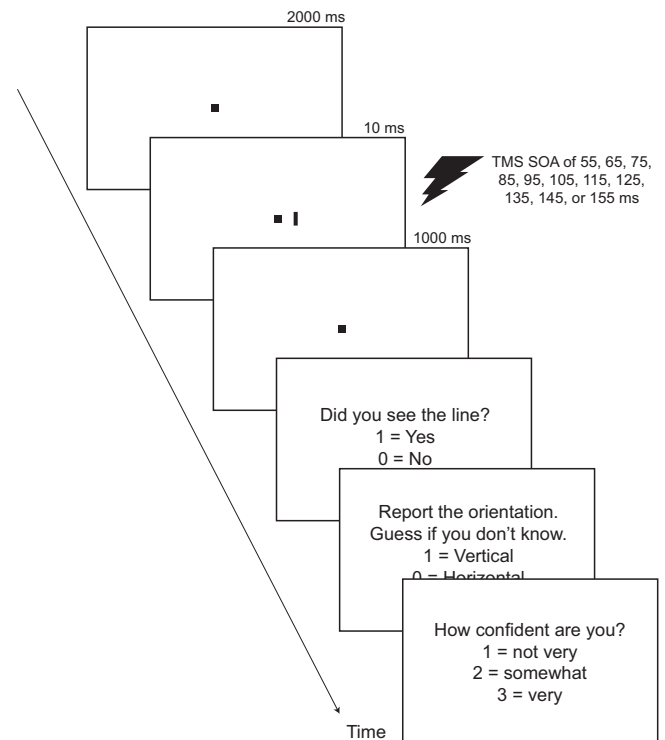


Fig. 1. A schematic of the sequence of events on a typical trial. A horizontal or vertical line was presented to the right of a central fixation square while processing in early visual cortex was disrupted with TMS at stimulus onset asynchronies ranging from 55 to 155 ms post-stimulus. Subjects were asked to first report whether or not they had seen the line, to then report (or guess in trials in which they did not detect the line) the orientation of the line, and finally to report their confidence in their orientation discrimination.

maximal visual suppression is not the same across subjects, causing the changes in detection rates across SOAs to be less clearly defined when averaged across subjects. As an additional post-hoc analysis of the effect, we located the SOA at which each subject experienced maximal suppression and aligned data to this condition. We then used one-tailed paired *t*-tests and found significant differences between detection rates at this SOA of peak suppression with the detection rate at the subsequent SOA ($t_{15} = -4.5305$, $p < 0.001$) and also this subsequent SOA with the following SOA ($t_{15} = 2.6132$, $p < 0.001$). These results demonstrate that when each subject's time window of peak suppression is aligned, this window of maximal suppression is followed by a significant increase in detection rate, and subsequently by a significant decrease in detection rate. This further suggests the existence of two windows of maximal suppression, with latencies that vary across subjects.

The second way that our data differs from previous TMS visual suppression curves is in the magnitude of suppression at earlier SOAs, which was greater than in previous studies. These differences are likely the result of using a larger and more effective stimulating coil, a finer temporal resolution of SOAs, a larger number of subjects compared to previous studies (Amassian et al., 1989; Corthout et al., 1999), and smaller, more briefly presented stimuli.

Importantly, forced-choice orientation discrimination accuracy as a function of SOA dissociated from detection performance across the two maximum suppression windows (Fig. 2). To confirm this dissociation, we tested the effect of task (detection vs. forced-choice orientation discrimination) and SOA on performance using a two-way, within-subjects ANOVA. There was a significant interaction between task and SOA ($F_{(10,150)} = 11.71$, $p < 0.001$), indicating that TMS at specific SOAs altered performance differently depending on the task. Despite participants frequently reporting that they had not detected the visual

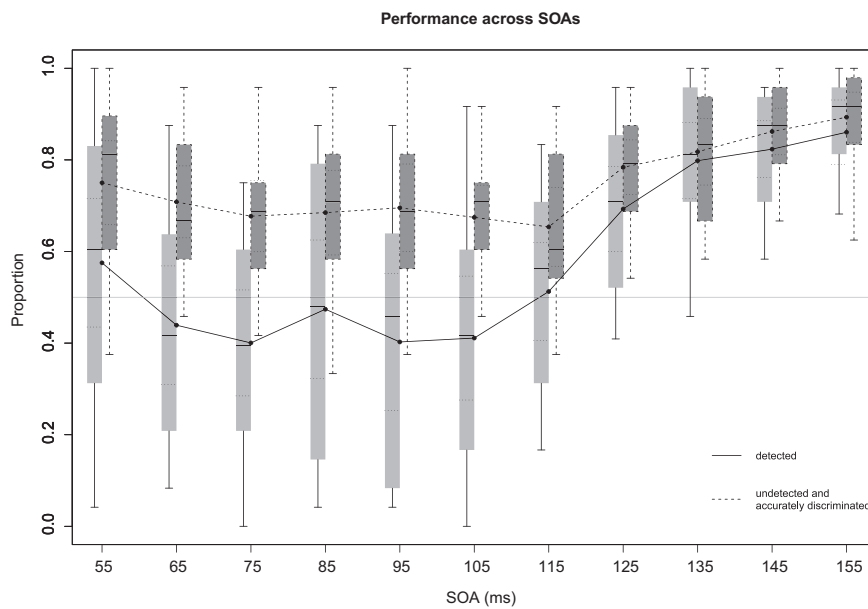


Fig. 2. Line detection rates (solid line) and orientation discrimination performance (dashed line) as a function of SOA. The solid gray horizontal line depicts the chance level for the forced-choice discrimination. Solid light gray Tukey box plots represent the quartiles and the median of the detection rate at each SOA. Dashed dark gray Tukey box plots represent the quartiles and the median of orientation discrimination performance at each SOA. The whiskers of the box plots represent data within 1.5 times the interquartile range whereas the dotted horizontal lines on all box plots represent 95% confidence intervals.

stimulus, orientation accuracy was significantly above-chance for all SOAs (i.e., discrimination accuracy was significantly different from 0.5; mean = 0.74, SD = 0.17, $t_{15} \geq 3.36$, $p \leq 0.0043$). These results show that despite disruption of EVC with TMS that suppressed visual awareness, the orientation of visual stimuli was still processed. Multiple FDR-corrected paired t-tests indicated that there were significant differences in performance between the detection and discrimination performance tasks when TMS was administered at SOAs of 55, 65, 75, 85, 95, 105, 115 and 125 ms ($p \leq 0.022$), but not for TMS at SOAs of 135, 145 or 155 ms ($p \geq 0.368$). This indicates that detection performance was more susceptible to TMS in these time windows compared to unconscious discrimination performance. These results show that disruption of EVC activity with TMS in a time window between 55 and 125 ms caused a loss of visual awareness only, without an accompanying decrease in visual discrimination accuracy.

We also compared confidence ratings with detection and discrimination performance using two separate two-way ANOVAs. Confidence ratings interacted with detection and discrimination

performance across SOAs ($F_{(10,150)} = 3.33$, $p < 0.001$ for detection and $F_{(10,150)} = 8.54$, $p < 0.001$ for discrimination).

4. Discussion

The aim of this study was to gain insight into the neural basis of unconscious visual perception by systematically comparing how the latency of EVC disruption may differentially affect detection and unconscious discrimination performance. When EVC activity was disrupted by TMS, it caused a loss of visual awareness in a window of 65–75 ms and in a second window of 95–105 ms. In both of these windows, unconscious orientation discrimination performance was significantly above-chance. In fact, unconscious orientation discrimination was above-chance for all SOAs. The significant interaction between task (detection vs. discrimination) and SOA demonstrates that in a time window of 55 to 125 ms, unconscious discrimination performance dissociated from detection performance as a result of TMS. This interaction was further corroborated by statistically significant

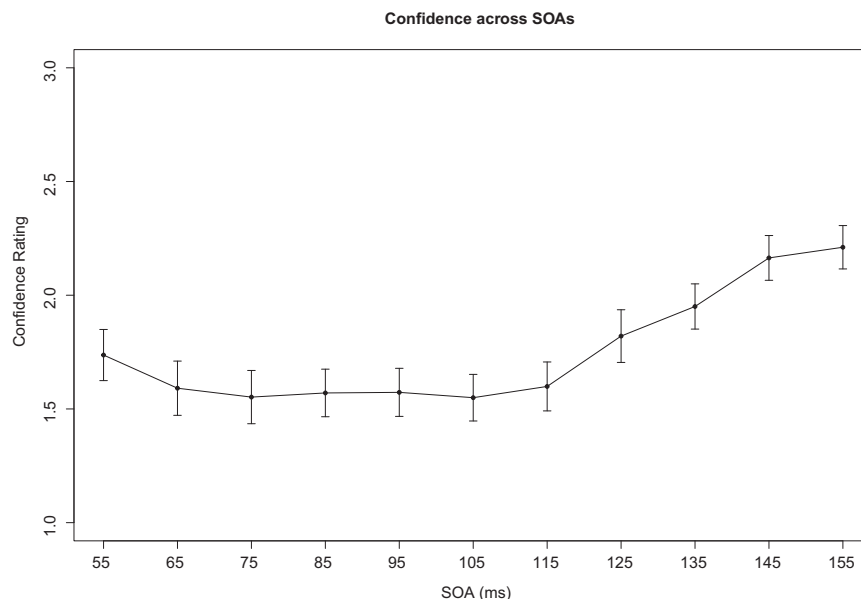


Fig. 3. Confidence ratings for the orientation discrimination as a function of SOA. Error bars represent the within-subjects standard error of the mean.

differences between detection and discrimination performance within the two times windows of maximum visual suppression. Thus, these results show that unconscious discrimination is less vulnerable to an interruption of EVC activity compared to detection. These dissociations were time-specific, however, and detection and discrimination performances covaried for SOAs longer than 125 ms. Finally, although there were significant differences between detection and discrimination responses at certain SOAs, confidence ratings interacted with both detection and discrimination responses across SOAs, suggesting that these introspective reports may reflect a hybrid of conscious and unconscious perceptions or may not adequately reflect performance in some other way (e.g., Peters et al., 2017).

Importantly, the current results replicate and extend previous findings demonstrating TMS-induced blindsight (Allen et al., 2014; Boyer et al., 2005; Christensen et al., 2008; Koivisto et al., 2017; Railo et al., 2012; Ro, 2008; Ro et al., 2004). Unlike studies that have failed to demonstrate TMS-induced blindsight, either because suboptimal experimental designs and TMS parameters were used (Lloyd et al., 2013; see Peters et al., 2016 for further discussion) or there was an insufficient number of trials to adequately measure absolute TMS-induced blindsight (Peters et al., 2017), we show that TMS-induced blindsight is very systematic, robust, and reliable. Furthermore, the timecourse of the TMS-induced blindsight and visual suppression are consistent with several well-established properties of neural processing in the visual system.

The later 95–105 ms time window, in which TMS over V1 caused a maximal attenuation in detection rates, replicates the results of the seminal study that first demonstrated the effects of TMS over EVC (Amassian et al., 1989). Furthermore, the dissociation between detection and unconscious discrimination performance in this time window corresponds to the TMS-induced blindsight effect that is reliably observed at ~ 100 ms (Allen et al., 2014; Boyer et al., 2005; Jolij and Lamme, 2005; Ro, 2008; Ro et al., 2004). This relatively late time window is thought to reflect the incidence of feedback activity in V1 that is necessary for visual awareness (Lamme, 2001; Lamme and Roelfsema, 2000; Ro et al., 2003; Tapia and Beck, 2014). The dissociation between detection and discrimination performance at this latency demonstrates that orientation discrimination performance is less vulnerable to disruption of EVC and that EVC activity in this later time period is not necessary for this type of unconscious vision. This result in and of itself is consistent with proposals that the earlier, feedforward sweep of activity in V1 may be sufficient for simple unconscious visual discrimination tasks (Lamme, 2001; Lamme et al., 2000).

However, we also observed another time window, from 65 to 75 ms, in which TMS over V1 caused a dissociation between detection and unconscious discrimination. This window may reflect the incidence of feedforward activity in V1. Indeed, electrophysiological studies in humans show that visual information from the retina reaches V1 within 40–70 ms after stimulus onset (Di Russo et al., 2001; Jeffreys and Axford, 1972; Kelly et al., 2008; Vanni et al., 2001; Wilson et al., 1983). This early V1 activity suggests that the EVC is necessary for conscious visual perception at multiple, distinct intervals during visual processing (de Graaf et al., 2011; Pascual-Leone and Walsh, 2001; Silvanto, 2005). Although this early time window is likely to predominantly correspond to feedforward activity in V1, it may also reflect the incidence of feedback activity occurring through rapid horizontal connections (Angelucci et al., 2017). Nonetheless, the observation of an earlier window in which detection and unconscious discrimination dissociate is problematic for the hypothesis that posits feedforward V1 activity as sufficient for unconscious orientation perception. Given that unconscious discrimination performance was significantly above-chance when EVC was disrupted at early latencies after visual stimulus onset, this further suggests that unconscious discrimination relies on a distinct processing pathway that bypasses V1 altogether.

Some candidate mechanisms for unconscious vision are the

geniculoextrastriate pathways that project from the retina to the lateral geniculate nucleus (LGN) and then directly to extrastriate regions including areas MT, V2, and V4 (Ajina and Bridge, 2018; Allen et al., 2014; Boyer et al., 2005; Bullier and Kennedy, 1983; Fries, 1981; Railo et al., 2012; Sanchez-Lopez et al., 2017; Sincich et al., 2004; Stoerig and Cowey, 1989; Yukie and Iwai, 1981). Relatively recent and compelling evidence for a role of these pathways in blindsight come from studies in non-human primates with V1 lesions, which show LGN-driven responses in extrastriate cortex to a visual stimulus presented in an affected region of the visual field (Schmid et al., 2009). Furthermore, a study of a group of patients with V1 damage found that patients with blindsight had an intact geniculolateral pathway projecting to area MT, whereas these pathways were impaired or not measurable in patients without blindsight (Ajina et al., 2015). Another candidate pathway that may be involved with unconscious processing in blindsight is the retinotectal pathway that projects from the superior colliculus (SC) to extrastriate cortex (Koller and Rafal, 2018; Koller et al., 2018; Le et al., 2017; Mundinano et al., 2017; Perenin and Jeannerod, 1975; Pöppel et al., 1973; Weiskrantz et al., 1974). Ablations of the SC abolish visually-guided behavior that occurs despite damage to striate cortex (Kato et al., 2011; Mohler and Wurtz, 1977; Solomon et al., 1981), as well as affecting extrastriate cortex responsiveness to visual stimuli (Bruce et al., 1986; Rodman et al., 1990). Although the present study cannot determine which subcortical pathway underlies the observed unconscious discrimination, the retinotectal pathway is less likely to be involved as the SC cannot effectively discriminate orientation (Ro and Rafal, 2006; Robinson and McClurkin, 1989).

Another potential mechanism for unconscious discriminations in blindsight may be processing of information by the contralesional intact hemisphere. In particular, one study showed that the intact hemisphere was recruited for unconscious visuospatial functions via corticocortical connections after damage to early visual cortex in blindsight patient G.Y. (Celegghin et al., 2017). That study suggests that ipsilesional extrastriate regions may receive retinal input that, via the pulvinar, bypasses V1 and transfers it to the posterior parietal cortex and premotor regions of the intact hemisphere through the corpus callosum. However, the existence of blindsight in patients with bilateral V1 damage (Ajina and Bridge, 2018; Mundinano et al., 2017) challenges a critical role for pathways involving the unaffected hemisphere in blindsight since both hemispheres are damaged. Similarly, in the present study, due to the use of a large circular, non-focal TMS coil, stimulation is likely to have disrupted V1 bilaterally, such that unconscious discrimination probably could not rely on processing in a less affected hemisphere, as in patients with bilateral V1 damage. However, this does not preclude the potential importance of processing in the intact hemisphere for blindsight occurring after unilateral V1 damage. Future studies should aim to assess the contribution of contralateral geniculolateral and extrastriate pathways, as well as ipsilateral pathways to blindsight, as a function of stimulus and task type.

The claim that unconscious discrimination performance relies on an alternative, likely geniculolateral, pathway bypassing V1 may at first seem at odds with a study that found that unconscious visual performance not only relies on the feedforward sweep of V1 activity but also on feedback activity to V1 (Koivisto et al., 2010, but see Persuh and Ro, 2013). However, the different and necessarily longer stimulus durations used to present motion stimuli and the different latencies of TMS over V1 in the study by Koivisto et al. complicate any comparisons between their study and the current one. In fact, the use of motion stimuli and the observation that unconscious motion perception relies on both feedforward and feedback activity in V1 may be related to the complex nature of visual motion perception. In contrast, unconscious orientation discrimination, which may be a simpler visual computation than motion discrimination, may not depend at all on feedforward and feedback processing in V1. Our finding of above-chance unconscious orientation performance in both feedforward and feedback intervals of V1 strongly implicate parallel visual processing pathways that

bypass V1. Future studies should directly compare to what extent unconscious discrimination performance relies on different latencies of V1 disruption depending on the visual task.

The present results provide strong evidence against unconvincing proposals that claim that some types of blindsight may result from near-threshold vision (Balsdon and Azzopardi, 2015; Lloyd et al., 2013). According to this hypothesis, rather than unconscious perception, a response bias that drives subjects to report visual awareness less frequently, despite some awareness of the visual stimuli, explains above-chance discrimination performance. If unconscious discriminations were merely a product of near-threshold vision, however, one should expect similar dissociations between unconscious discrimination performance and conscious detection rates across different kinds of conditions, such as with different TMS SOAs. However, our results demonstrate dissociations between detection and unconscious discrimination across different rates of detection, suggesting that conscious and unconscious vision rely upon independent visual pathways and different neural mechanisms. Additionally, if a shift in response bias caused the dissociation of detection and unconscious discrimination, it is unclear why this effect would be restricted to only two time windows, as observed in this study. It is unlikely that TMS would cause a non-perceptual effect like response bias only at specific latencies of EVC disruption. Therefore, these near-threshold accounts for unconscious vision are not adequate for explaining the current data (other inadequacies of these near-threshold accounts of unconscious vision are detailed in Peters et al., 2016).

Another potential but unlikely explanation for our data is that the TMS may have induced blinks that systematically affected detection rates, which a sham or a control TMS condition could rule out. We did not perform a sham control because of several issues that make such controls suboptimal (see Bolognini and Ro, 2010 for further discussion). For example, tilting a standard TMS coil away from the head does not adequately control for the tactile sensations of the TMS. Alternatively, using a cortical “control” site, such as the vertex, may affect task performance or introduce confounds in other ways (e.g., see Webster and Ro, 2017, which shows that phosphenes can be perceived even after vertex TMS, likely from current spread into the retina or visual cortex). Furthermore, in both types of control conditions, the intensity of the auditory “click” artifact is not the same as with TMS over visual cortex, which may affect blinking rates. Although we cannot rule out that subjects were not blinking on some of the trials of this experiment, they were instructed to blink in between trials and not during or directly after a TMS pulse. As such, it is unlikely that these results may have been due to blinks, especially since discrimination performance was significantly above-chance in all conditions. Nonetheless, future studies that control for blinks or record them directly will be necessary to rule out this possibility.

Finally, research on the neural mechanisms of TMS has shown that the facilitatory and/or suppressive effects of TMS depend on an interaction between output intensity and the ongoing neural state (Pascual-Leone et al., 1998). In the present study, we used a TMS intensity that was higher than each subject's suppression threshold, and this intensity was maintained across all conditions. Therefore, our study design minimizes the confound of different TMS intensities affecting cortical function in different ways. Moreover, according to our claim that blindsight is not dependent on EVC activity, altering EVC excitability by varying TMS intensities should not affect unconscious discrimination performance. However, if a study were to find that a lower intensity of TMS can induce suppression and also cause an increase in unconscious discrimination performance, it would suggest that EVC is in fact involved in blindsight. Future research should seek to address this interesting question.

In conclusion, this study examined the role of EVC disruption on conscious and unconscious vision across a range of temporal processing intervals. The results demonstrate that visual awareness and unconscious visual discrimination do not always covary but rather

dissociate within two distinct time windows.¹ Therefore, conscious and unconscious vision likely rely upon distinct neural mechanisms, and these differences cannot be easily accounted for by near-threshold accounts of unconscious perception. One highly plausible alternative pathway for unconscious orientation discrimination performance is the geniculostriate pathway from the LGN to V4, which has been shown to exist anatomically and contains the appropriate neural architecture for orientation perception. Given that there was an early as well as a late temporal interval during which detection rates dissociated from discrimination performance, and that detection and discrimination performance was similar once detection rates exceeded threshold levels of performance, the present results provide new evidence that TMS-induced blindsight occurs independently of striate activity. Further research will be required to confirm the role of V4 in unconscious orientation discrimination and its potential contributions to other types of unconscious visual perception.

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¹ Although we have attributed the two functionally relevant windows of visual cortex activity for detection to feedforward and feedback processing, it has been suggested that multiple feedforward-feedback loops operate in visual cortex within the first 200 ms of visual processing (Foxy and Simpson, 2002). These two windows may therefore reflect some overlap between feedforward and feedback activity in V1, such that it is the ratio of feedforward to feedback activity that is higher in our earlier time window and lower in our later time window.

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