The temporal advantage for reloading vs. uploading conscious representations decays over time

Hsin-Mei Sun,1,2 Marina Inyutina,3,4 Rufin VanRullen,3,4† and Chien-Te Wu1,5,*

1School of Occupational Therapy, College of Medicine, National Taiwan University, Taipei, Taiwan; 2Department of Cognitive, Linguistic, and Psychological Sciences, Brown University, Providence, RI 02912, USA; 3Université de Toulouse, CerCo, Université Paul Sabatier, Toulouse, France; 4CNRS, UMR 5549, Faculté de Médecine de Purpan, Toulouse, France; and 5Department of Psychiatry, National Taiwan University Hospital and College of Medicine, Taipei, Taiwan

*Correspondence address. School of Occupational Therapy, College of Medicine, National Taiwan University, Taipei, Taiwan; E-mail: chientewu@ntu.edu.tw
†Rufin VanRullen - http://orcid.org/0000-0002-3611-7716

Abstract

In motion-induced blindness (MIB), a static target superimposed on a global moving pattern frequently disappears and reappears into consciousness. We previously reported an intriguing illusory temporal reversal whereby a new stimulus onset (e.g. a dot flash) presented during MIB triggers an early reappearance of the target, yet is systematically perceived as occurring after the target reappearance. This illusion implies that the unconscious target representation can be quickly reactivated, with a temporal advantage for its conscious reloading as compared to the conscious uploading of a newly presented visual stimulus. However, it remains unclear whether the temporal advantage for conscious representation reloading strengthens, decays, or remains constant over time after we lose the initial conscious access to the stimulus. To address this question, we examined the relation between the duration of MIB and the percentage of illusory temporal reversals, and we found a negative correlation between the two measures, both between and within observers. The results suggest that although the unconscious target representation retains a certain level of activation during MIB, the temporal advantage for reloading its preexisting representation into consciousness decays over time.

Key words: motion-induced blindness (MIB); illusory temporal reversal; unconscious object representation; visual awareness

Introduction

The study of visual consciousness continues to be a subject of great debate in the 21st century. For example, it is still unclear how visual information is processed with and without conscious awareness as well as whether visual stimuli can affect our behaviors to some extent when they are rendered perceptually invisible (e.g. Brogaard 2011; Kiefer et al. 2011). To tackle these questions, visual stimuli must be manipulated to create conditions that differ in conscious perception in order to compare a condition in which a stimulus is consciously perceived with a condition in which the stimulus is not consciously seen (although physically presented). A variety of methods have been proposed to manipulate visual awareness of a stimulus when studying consciousness, such as backward masking, visual crowding, binocular rivalry, bistable figures, continuous flash suppression, and so forth (for related reviews, see Blake et al. 2014; Faivre et al. 2014; Kim and Blake 2005; Kouider and Dehaene 2007). Much evidence has shown that stimuli rendered invisible can nevertheless influence subsequent visual perceptions and cognitive functions to a certain degree (Blake 1997; Ansorge et al. 2014). For example, the gaze direction in a perceptually invisible face still triggers the viewer’s attentional shifts in a backward masking task (Sato et al. 2007); a subliminal feature singleton under continuous flash suppression (Tsukaya and Koch 2005) still captures attention and enhances participants’ performance on an orientation discrimination task at the pop-out...
Here we attempt to address this question by exploiting a perceptual phenomenon called motion-induced blindness (MIB), in which a salient stationary target alternately disappears from and reappears into consciousness when superimposed on a global moving pattern, despite the fact that it is constantly present in the display (Bonneh et al. 2001). Several explanations have been proposed for the perceptual disappearance of the target during MIB, such as attentional competition between the static target and the moving background (Bonneh et al. 2001), perceptual filling-in following a boundary adaptation of the target (Hsu et al. 2006), and surface completion of the distractor (Graf et al. 2002). Recent fMRI studies have further shown that the perceptual disappearance of the MIB target is associated with a complex pattern of neural activity in various brain areas of both the ventral and dorsal visual pathways (Schölvinck and Rees 2010; Donner et al. 2008, 2013). For example, Schölvinck and Rees (2010) observed that MIB target disappearance was associated with increased activity in the low-level visual cortex (V1, V2) and area V5/MT. In contrast, Donner et al. (2008) found that MIB target disappearance was associated with decreased activity in cortical area V4 corresponding to the target but increased activity in regions of the dorsal visual pathway corresponding to the mask. Therefore, the underlying mechanisms of MIB remain unclear and require further investigation.

Recent research has utilized MIB as a powerful tool to study the nature of unconscious object representations. It has been shown that visual stimuli rendered invisible by MIB still retain a certain level of perceptual effectiveness to cause orientation-specific adaptation (Montaser-Kouharsi et al. 2004) and negative afterimages (Hofstotter et al. 2004). Furthermore, invisible objects during MIB are susceptible to perceptual grouping cues in that two initially independent stimuli tend to reenter awareness simultaneously if they are connected with a line and form a dumbbell during MIB (Mitroff and Scholl 2005). This finding also suggests that object representations can be formed and updated without conscious perception during MIB.

More recently, in a study using MIB, our group discovered an interesting temporal illusion in which the cause of a perceptual event is illusorily perceived as if occurring after the event itself (Wu et al. 2009). In that study, after participants reported the perceptual disappearance of a ring target due to MIB, a dot probe was flashed inside the ring target to trigger an early reappearance of the target (Kawabe et al. 2007). Participants then judged the perceived temporal order of the appearance of the dot probe and the reappearance of the ring target. Counterintuitively, participants reported much more frequently that they saw the ring target reappear before the dot probe, despite the fact that the flashed dot probe caused the perceptual reappearance of the ring target. Through a series of follow-up experiments, we determined that the unconscious representation of the perceptually invisible target presents a temporal advantage (estimated around 100 ms) for faster conscious access as compared to a newly presented visual event, such as the onset of the dot probe (Wu et al. 2009). That is, the time taken to reload the representation of the ring target into visual awareness is less than the time needed to upload the representation of the newly presented dot probe for conscious access. Therefore, even though the flashed dot probe terminates MIB and triggers the perceptual reappearance of the ring target, it is nevertheless perceived as occurring after the reappearance of the ring target.

However, some important questions regarding the illusory temporal reversal effect remain unanswered (Walsh 2009). For example, what are the temporal characteristics of the unconscious target representation during MIB? Specifically, how long can the unconscious MIB target maintain its temporal advantage for conscious access (i.e. perceptual reloading) relative to a novel stimulus (i.e. perceptual uploading)? To address this question, one can measure the probability of illusory temporal reversals as a function of time after MIB onset (reflecting the duration of the unconscious stage). In doing so, there are three possibilities to consider. First, if we assume that the strength of the unconscious MIB target representation is directly reflected in the strength of illusory temporal reversals, we could expect a positive relation between MIB duration and the proportion of illusory temporal reversals: it is likely that the unconscious target representation strengthens over time during MIB, allowing the MIB target to eventually recover its conscious access. The temporal advantage for perceptual reloading as compared to perceptual uploading, therefore, might also be expected to increase over time during MIB. Accordingly, there should be a positive correlation between the duration of MIB and the percentage of illusory temporal reversals: the longer the target remains perceptually invisible due to MIB, the more likely it would be perceived before the event (e.g. the onset of a dot probe) triggering its reappearance. However, this is not the only possibility, and one could even envision that the temporal advantage for perceptual reloading may have a more complex relation with the strength of the unconscious MIB target representation, and therefore, with the duration of MIB. In that case, a second possible outcome would be that when the duration of a stimulus’ unconscious state gets longer, it loses its temporal advantage for perceptual reloading back to consciousness. Consequently, there should be a negative correlation between the duration of MIB and the percentage of illusory temporal reversals: the longer the target is represented unconsciously during MIB, the less likely an illusory temporal reversal would occur. Third, it is also possible that the temporal advantage for perceptual reloading of a stimulus is unaffected by how long the stimulus stays as an unconscious representation during MIB. In that case, the target stimulus would retain the same degree of temporal advantage for perceptual reloading and there should be no correlation between the duration of MIB and the percentage of illusory temporal reversals. Distinguishing between these possibilities is of critical importance for understanding the nature of unconscious representation of a visual event. Here, we report a negative correlation between MIB duration and the occurrence of illusory temporal reversals, both between and within observers, indicating that the temporal advantage for perceptual reloading over perceptual uploading of conscious representations decays over time.

**Method**

**Participants**

Participants were thirty paid right-handed volunteers (21 females; mean age = 24.2 years). All had normal or corrected-to-normal vision and were naive to the purpose of the study. The experimental protocol was approved by the National Taiwan University Institutional Review Board (201211HS014) for the protection of human participants in research. All participants gave their informed consent prior to the experiment.

**Apparatus**

The stimuli were presented on an 18-inch CRT monitor with a refresh rate of 100 Hz and a display resolution of 1024 × 768.
pixels. Participants performed the task in a testing room with the lights off, and they viewed the stimuli at a distance of 57 cm with their head movements restrained by a chin rest. Responses for the experimental trials were collected through a computer keyboard. The experiment was programmed in MATLAB, using the Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997).

Stimuli
A static target and a central fixation were superimposed on a global moving pattern to induce MIB. The static target was a yellow ring (0.8 × 0.8") positioned 2.5° from fixation in the upper left quadrant of the display, and the global moving pattern was a grid (19° × 19°) of blue crosses (0.76° × 0.76°) rotating clockwise at a rate of 140°/s. Additionally, to trigger an early release of the ring target from MIB, a yellow dot probe (0.32" × 0.32") was briefly flashed for 50 ms inside the ring target at a certain time delay after the ring target's perceptual disappearance. During the experiment, all stimuli were presented on a black background.

Procedure and design
The entire study lasted three consecutive days, with a pretest session (200 trials) performed on Day 1 and two test sessions (225 trials each) performed on Days 2 and 3, respectively. In each trial of the pretest session, participants were required to maintain gaze on the fixation cross while paying covert attention to the peripheral target (i.e. a yellow ring). They had to press and hold an assigned key when the target disappeared from awareness, and release the key when it reappeared on the screen. The duration between key press and key release was measured as the MIB duration for that trial. After each trial, participants were offered the option to redo the trial if the target did not completely disappear, or if they had accidentally pressed the response key. Thus, for each participant, we were able to obtain a distribution of MIB durations and then extract the corresponding values of its first (PreQ25), second (PreQ50), and third (PreQ75) quartiles.

In each trial of the test session, as illustrated in Fig. 1, participants were asked to maintain their gaze on the fixation cross, pay covert attention to the peripheral target, and report the onset and offset of MIB as in the pretest session. Additionally, after the reported onset of MIB, a dot probe was flashed inside the ring target at the exact time delay corresponding to either the tested participant’s PreQ25, PreQ50, or PreQ75 value for the tested participant. Thus, there were three trial types (150 trials each) based on the probe onset delays (i.e. PreQ25, PreQ50, and PreQ75) and their presentation order was randomized within each test session. In the case when the ring target reappearance was reported before the dot probe onset, the stimulus display ended after the probe offset. At the end of each trial, participants judged the perceived temporal order between the appearance of the dot probe and the reappearance of the ring target. Participants were allowed to redo a trial if the target did not completely disappear or if they did not see the probe.

Analyses
To test whether the dot probe successfully revived the MIB target, we followed the data analytic strategy of Wu et al. (2009) and compared the similarity between the MIB duration distributions obtained from the pretest and test sessions using chi-square tests. A Pearson’s correlation analysis was subsequently performed to calculate the correlation coefficient (r) between the percentage of ring-first responses and the corresponding quartile values (i.e. probe onset times for each individual) across participants to test the relationship between the magnitude of illusory temporal reversal and the duration of MIB target disappearance. To provide a more direct evaluation of the correlation between the two measures within participants, a linear fit was performed on the chance-corrected magnitude of illusory temporal reversals of each probe onset delay condition for each participant. Based on the nature of the experimental design, the expected baseline percentages of ring-first responses were at least 25%, 50%, and 75%, respectively, for the three probe onset delay conditions. Therefore, we computed the chance-corrected magnitude of illusory temporal reversal illusion in each probe onset delay condition using the following formula: [(percentage of ring-first responses – expected percentage of ring-first responses)/(1 – expected percentage of ring-first responses)]. This ratio measures the number of illusory reversal trials relative to the number of trials in which a temporal reversal illusion could possibly have occurred. A one-sample t-test was performed to compare the 30 linear-fitted slopes to the null hypothesis of a zero slope (representing no systematic change in the corrected magnitude of illusory temporal reversal across probe onset delays). A significant nonzero slope would indicate that the temporal advantage for perceptual reloading vs. perceptual uploading changes over time.

Results
We first compared the MIB duration distribution in the pretest session with the MIB duration distributions in the three different probe onset delay conditions in the test session. As shown in Fig. 2, the MIB duration distribution was significantly shortened when a dot probe was flashed inside the ring target during MIB at an onset delay of either the tested participant’s PreQ25 [χ²(7) = 57.6, P < 0.00001], PreQ50 [χ²(7) = 37.5, P < 0.00001], or PreQ75 [χ²(7) = 19.3, P = 0.007] value, indicating that the dot probe successfully triggered an early reappearance of the ring target and thus shortened the MIB durations.

Next, for each probe onset delay condition, we ran a Pearson correlation analysis across observers to examine the association between the percentage of ring-first responses (as an index of illusory temporal reversals) and the corresponding quartile value (as an index of the duration of target disappearances due to MIB). The results showed that the percentage of ring-first responses and the corresponding quartile values correlated negatively with each other across participants (Fig. 3). Compared to participants with longer PreQ25 values, participants with shorter PreQ25 values showed more ring-first responses when judging the perceived temporal order of the ring and dot (r = -0.47, n = 30, and P = 0.009). Similarly, the percentage of ring-first responses was higher in participants showing shorter PreQ50 values than in participants showing longer PreQ50 values (r = -0.65, n = 30, and P = 0.001). Finally, participants with shorter PreQ75 values also showed more ring-first responses than participants with longer PreQ75 values (r = -0.42, n = 30, and P = 0.02). These results indicate that across participants, the unconscious target representation gradually loses its temporal advantage for perceptual reloading back to visual awareness as compared to uploading a new visual event to visual awareness.

However, this cross-participant correlation analysis does not directly examine how the temporal advantage of perceptual reloading changes over time during MIB for each participant (see “Discussion” section). To tackle this question more directly,
we further performed a within-participant analysis of how the chance-corrected magnitude of illusory temporal reversal would change as a function of probe onset delays within each participant (see “Method” section). The results showed a significant (\( P = 0.01 \)) negative average slope (mean slope of \(-45\% \pm 16\% \) per second across observers), confirming that the temporal reversal illusion is attenuated as a function of the duration of MIB within participants as well.

Our results therefore support the hypothesis that the representation of a perceptually disappeared target gradually loses its temporal advantage for perceptual reloading, leading to less reversals in the perceived temporal order of the appearance of the probe and the reappearance of the target. In contrast, when the unconscious representation of a perceptually disappeared target has little time to “age” during MIB, it retains its temporal advantage for perceptual reloading and thus leads to more reversals of the perceived temporal order between the target and probe.

**Discussion**

The main purpose of the present study was to examine the nature of the unconscious perceptual representation during MIB,
particularity how its temporal advantage for re-entering conscious perception changes over time. The results replicated our previous findings, showing that even though the presence of a dot probe triggered an early reappearance of the ring target (Kawabe et al. 2007; Wu et al. 2009), participants often reported seeing the ring reappear before the presence of the dot (Wu et al. 2009). As suggested previously, the illusory temporal order reversal between the ring and the dot probe likely results from a faster perceptual reloading of the unconscious target representation into consciousness as compared to the uploading of a newly presented visual event. In addition, we demonstrated here that the longer the target is represented unconsciously during MIB, the less likely one would experience a temporal reversal between the ring target and the dot probe.

This negative correlation between MIB duration and the occurrence of illusory temporal reversals is surprising. Considering that an object rendered invisible by MIB still produces input activation signals (by virtue of being present in the display), and can even be updated without conscious perception (e.g. Mitroff and Scholl 2005), one could expect the strength of the corresponding object representation to gradually increase over time after the initial MIB disappearance, until the suppressed object becomes consciously visible again. If the temporal advantage for reloading the object into consciousness was assumed to directly reflect the strength of this unconscious MIB target representation, then the magnitude of the temporal advantage would be expected to increase as a function of the length of MIB, and consequently increase the likelihood of temporal reversals between the object and the other newly presented stimulus. However, our results demonstrated that this is not the case. We found that participants with longer MIB durations experienced less illusory temporal reversals than participants with shorter MIB durations, and vice versa. Additionally, after correcting for chance performance, a within-participant analysis confirmed the inverse relation between the temporal reversal illusion and the duration of MIB. Our results clearly show that the unconscious target representation “aged” over time to an equivalent state as if it were a new stimulus presentation, leading to a progressively smaller temporal advantage for its reloading to visual awareness as compared to a new visual event. This implies, in turn, that the observed temporal advantage (which decreases over time) is not a direct reflection of the strength of the unconscious MIB target representation (which presumably increases over time), and that multiple mechanisms might be at play in the generation of the observed temporal advantage.

One might argue that more direct evidence for the decay of the conscious perceptual reloading could be obtained from a correlation between MIB duration and temporal reversal occurrence across trials, rather than across observers. However, to obtain the temporal reversal illusion, a dot probe (or any external stimulus) has to be presented during MIB so as to trigger an early target reappearance. This experimental intervention makes it impossible to determine what the actual MIB duration for a given trial would have been without the probe interference. Therefore, it is not feasible to study the within-participant correlation across trials between the duration of MIB and the frequency of illusory temporal reversals. To overcome this limitation, we used different quartile values extracted from the individual MIB duration distributions of the pretest sessions as an estimate of the MIB duration, and then examined the temporal advantage for re-entering conscious access. Note that the baselines refer to the expected percentages of ring-first responses that would occur due to a natural termination of MIB.

Figure 3. Negative correlations across participants between the percentage of ring-first responses and the corresponding quartile value. In each of the probe onset delay condition, participants with longer quartile values show less illusory temporal reversals (as indicated by less ring-first responses), suggesting that the unconscious target representation decays over time in MIB and gradually loses its temporal advantage for conscious access. Note that the baselines refer to the expected percentages of ring-first responses that would occur due to a natural termination of MIB.

Acknowledgements

This study was supported by Ministry of Science and Technology in Taiwan (MOST-102-2923-H-002-002-MY3) to H.-M.S. and C.-T.W. as well as L’Agence Nationale de la Recherche in France (ANR-12-ISV4-0001-01) to M.I. and R.V. The authors thank the editor, Prof. Anil Seth, and the two anonymous reviewers for their constructive feedback. The authors declare no conflict of interest. Data are available on request.
References
Ansorge U, Kunde W, Kiefer M. Unconscious vision and executive control: how unconscious processing and conscious action control interact. Conscious Cogn 2014;27:268–87.
Blake R. What can be “perceived” in the absence of visual awareness?. Curr Dir Psychol Sci 1997;6:157–62.
Blake R, Brascamp J, Heeger DJ. Can binocular rivalry reveal neural correlates of consciousness?. Philos Trans R Soc B 2014;369:1471–2970.
Bachmann T, Poder E, Luiga I. Illusory reversal of temporal order: the bias to report a dimmer stimulus as the first. Vis Res 2004;44:241–6.
Bonneh YS, Cooperman A, Sagi D. Motion-induced blindness in normal observers. Nature 2001;411:798–801.
Brainard DH. The psychophysics toolbox. Spat Vis 1997;10:433–6.
Broggaard B. Are there unconscious perceptual processes?. Conscious Cogn 2011;20:449–63.
Donner TH, Sagi D, Bonneh YS et al. Opposite neural signatures of motion-induced blindness in human dorsal and ventral visual cortex. J Neurosci 2008;28:10298–310.
Donner TH, Sagi D, Bonneh YS et al. Retinotopic patterns of correlated fluctuations in visual cortex reflect the dynamics of spontaneous perceptual suppression. J Neurosci 2013;33:2188–98.
Faiivre N, Berthet V, Kouider S. Sustained invisibility through crowding and continuous flash suppression: a comparative review. Front Psychol 2014;5:475.
Graf EW, Adams WJ, Lages M. Modulating motion-induced blindness with depth ordering and surface completion. Vis Res 2002;42:2731–5.
Hofstoetter C, Koch C, Kiper DC. Motion-induced blindness does not affect the formation of negative afterimages. Conscious Cogn 2004;13:691–708.
Hsieh PJ, Colas JT, Kanwisher N. Pop-out without awareness: unseen feature singletons capture attention only when top-down attention is available. Psychol Sci 2011;22:1220–6.
Hsu LC, Yeh SL, Kramer P. A common mechanism for perceptual filling-in and motion-induced blindness. VisRes 2006;46:1973–81.
Kawabe T, Yamada Y, Miura K. How an abrupt onset cue can release motion-induced blindness. Conscious Cogn 2007;16:374–80.
Kiefer M, Ansorge U, Haynes JD et al. Neuro-cognitive mechanisms of conscious and unconscious visual perception: from a plethora of phenomena to general principles. Adv Cogn Psychol 2011;7:49–61.
Kim CY, Blake R. Psychophysical magic: rendering the visible “invisible”. Trends Cogn Sci 2005;9:381–8.
Kouider S, Dehaene S. Levels of processing during non-conscious perception: a critical review of visual masking. Philos Trans R Soc B 2007;362:857–75.
Mitroff SR, Scholl BJ. Forming and updating object representations without awareness: evidence from motion-induced blindness. Vis Res 2005;45:961–7.
Montaser-Kouhsari L, Moradi F, Zandvakili A et al. Orientation-selective adaptation during motion-induced blindness. Perception 2004;33:249–54.
New JJ, Scholl BJ. Perceptual scotomas: a functional account of motion-induced blindness. Psychol Sci 2008;19:653–9.
Pelli DG. The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 1997;10:437–42.
Sato W, Okada T, Toichi M. Attentional shift by gaze is triggered without awareness. Exp Brain Res 2007;183:87–94.
Schölvinck ML, Rees G. Neural correlates of motion-induced blindness in the human brain. J Cogn Neurosci 2010;22:1235–43.
Schwarz W, Eiselt AK. The perception of temporal order along the mental number line. J Exp Psychol Hum Percept Perform 2009;35:989–1004.
Tsuchiya N, Koch C. Continuous flash suppression reduces negative afterimages. Nat Neurosci 2005;8:1096–101.
Walsh V. Visual perception: an orderly cue for consciousness. Curr Biol 2009;19:R1073–4.
Wu CT, Busch NA, Fabre-Thorpe M et al. The temporal interplay between conscious and unconscious perceptual streams. Curr Biol 2009;19:2003–7.
Yamamoto S, Kitazawa S. Reversal of subjective temporal order due to arm crossing. Nat Neurosci 2001;4:759–65.