

# Motion-induced blindness is not tuned to retinal speed

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Motion-induced blindness is a visual phenomenon in which a moving pattern can cause superimposed static targets that remain physically present to intermittently disappear from awareness. To date, there has been little systematic investigation of the type of motion that induces the most robust perceptual disappearances. To address this issue, we investigated the temporal frequency and stimulus speed sensitivity of this phenomenon in two experiments. In the first, we used radial gratings and waveform modulation to decouple spatiotemporal frequency and retinal speed characteristics. The results suggested that motion-induced disappearances are tuned to temporal frequency, but not to stimulus speed. In the second, we showed that luminance flicker-induced disappearances were tuned to the same temporal frequency as motion-induced disappearances. In combination, these data suggest that motion-induced blindness does not depend on retinal stimulus speed. Rather, it seems to be broadly tuned for moderate rates of temporal modulation. This observation is reminiscent of other instances where motion and spatial coding interact to modulate visibility.

Keywords: motion-induced blindness, perceptual switching, motion, temporal frequency, speed

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## Introduction

Situations in which conscious visual perception can change despite consistent retinal input provide fascinating opportunities to explore the nature of visual awareness (Alais & Blake, 2005; Arnold, Grove, & Wallis, 2007; Blake & Logothetis, 2002; Crick, 1994; Kim & Blake, 2005; Leopold & Logothetis, 1996, 1999; Logothetis & Schall, 1989). One example of such a situation is motion-induced blindness (MIB; Bonne, Cooperman, & Sagi, 2001). This remarkable phenomenon is characterized by intermittent perceptual disappearances of usually salient visual targets in the presence of a superimposed moving dot display. In this situation, when the targets disappear, they can remain suppressed for several seconds.

Several explanations for MIB have been proposed. Bonne et al. (2001) have suggested that MIB disappearances are caused by attentional competition between different display elements. Graf, Adams, and Lages (2002) have shown that disappearances are strongly modulated by occlusion cues. A perceptual filling-in mechanism (Hsu, Yeh, & Kramer, 2004, 2006), adaptation of target borders (Hsu et al., 2006; Kawabe & Miura, 2007), interhemispheric switching (Carter & Pettigrew, 2003; Funk & Pettigrew, 2003), and more recently gain control reduction accompanied by a response bias shift (Caetta, Gorea, & Bonne, 2007) have also been implicated. However, the role of motion itself has not been addressed in detail by any of these accounts.

In their original paper, Bonne et al. (2001) manipulated the speed of different types of dot masks (a kinetic depth sphere, a 2D rotating surface of crosses, and a 1D translating cross surface). They found that disappearance proportions increased with increasing mask speeds. However, these stimuli all contained broadband spatial and temporal information that makes Bonne et al.'s findings regarding speed impossible to disentangle from the plausible influence of temporal frequency.

Kawabe and Miura (2007) have recently shown that temporal luminance modulations (flicker) are sufficient to induce subjective MIB-like disappearances. Specifically, they showed that a ring surrounding the MIB target produced significantly more disappearances when it was flickered (at 9.38 Hz) compared to when it was static. These disappearances were greatest when the ring was near, but not overlapping, the target (Kawabe & Miura, 2007). Kawabe and Miura's findings suggest that the critical determinant of MIB might be temporal modulation rather than retinal motion per se.

However, at present the link between flicker-induced blindness (FIB; Kawabe & Miura, 2007) and MIB (Bonne et al., 2001) is unclear, and it is at least possible that the two are unrelated. For instance, flicker-induced disappearances could be a consequence of some form of temporal masking (Anderson & Burr, 1985; Cass & Alais, 2006; Hess & Snowden, 1992; Snowden & Hess, 1992), whereas MIB might be a consequence of some combination of the aforementioned MIB explanations. The suggestion that a common mechanism underlies both phenomena

(Kawabe & Miura, 2007) would be strengthened if their temporal tuning characteristics were found to be similar.

To assess this possibility, the present study will disambiguate the roles of temporal luminance modulation and retinal stimulus speed. Speed is a product of both the temporal frequency (TF) and the spatial frequency (SF) of a stimulus. If disappearances are sensitive to retinal speed, the TF at which disappearances are greatest will vary as SF changes. Alternatively, if disappearances are insensitive to retinal stimulus speed, the temporal frequency at which disappearances are greatest will not vary even if SF is changed.

## General methods

### Observers

The two authors participated in both of the experiments reported, in addition to two different naive observers in each experiment. All observers had normal or corrected-to-normal visual acuity.

### Procedure

Observers tracked subjective disappearances of two targets over 45-s trials by holding down one of two buttons whenever the target seemed to disappear (left button for the left target, right for right target). Observers were first shown an example animation of MIB and were instructed to use complete disappearance of the target as a criterion (not just fading). The inter-trial interval was  $\sim 4$  s (slight variations may have occurred due to drawing operations between trials). The number of trials in each experiment varied (see the methods section in each experiment). Each observer repeated the run of trials four times.

### Stimuli

Visual stimuli were generated using Matlab software to drive a VSG 2/3F stimulus generator (Cambridge Research Systems) and were displayed on a gamma corrected 21-in. Samsung SyncMaster 1100 p+ monitor ( $1024 \times 768$  resolution; 120 Hz refresh rate). All stimuli were viewed from 57 cm, with the observer's head restrained by a chinrest. A white cross ( $0.54^\circ$  by  $0.54^\circ$ ) was presented at the centre of the display to aid fixation. Details of the stimuli used in each experiment are given in the methods of the relevant section.

### Data analysis

We measured the proportion of each trial in which at least one of the targets disappeared. Observers also

reported disappearances during static trials, in which the displays were not modulated.

Individual proportions of disappearances during static trials were subtracted from individual proportions of disappearances during other trials to control for any influence of Troxler (1804) fading and spatial crowding (Bex & Dakin, 2005; Bouma, 1970; He, Cavanagh, & Intriligator, 1996). This also isolated the influences of temporal modulation. All analyses were conducted on these corrected proportion disappearances.

Repeated measures ANOVAs were then performed to assess whether disappearance proportions varied across different conditions. When main effects of TF were detected, tuning functions were determined by fitting gamma functions to the grouped corrected disappearance data from each condition. We then compared estimates of the fitted peaks to speed tuning predictions using 95% confidence intervals associated with the peak estimates.

## Experiment 1

### Method

To determine if MIB is tuned to TF or to retinal stimulus speed, we used radial grating (or “windmill”) stimuli (see Figure 1). In these stimuli, speed increases with eccentricity, but the rate of temporal modulation is constant. The average speed in these stimuli will therefore double and halve respectively if the radial frequency (RF) is halved or doubled. Thus, if disappearances are tuned to a particular stimulus speed, we would expect the TF at which disappearances are maximal to double if we double the RF, and to halve if we halve the RF.

We used stimuli with different RFs (3, 6, and 12 c/360°) and cycled the waveforms of the stimuli at a range of different TFs (1.33, 1.6, 2, 2.67, 4, 6, 8, 10, and 12 Hz) to create different rotation speeds.

The display background was green (CIE 1931  $x = 0.28$ ,  $y = 0.61$ ,  $Y = 6.2$ ). The radial gratings were sinusoidally luminance modulated from dark (CIE 1931  $x = 0.28$ ,  $y = 0.61$ ,  $Y = 0.3$ ) to bright ( $Y = 12.4$ ) green. The windmill had a radius subtending  $6.84^\circ$ . An overlay the same coordinates as the background was superimposed over the radial grating to isolate the targets. The eccentricity of the inner and outer borders of this ring was  $3.06^\circ$  and  $5.00^\circ$ , respectively. A circular overlay, also of the same coordinates as the background ( $0.8^\circ$  diameter), was presented at the centre of the display surrounding the fixation cross.

Two targets were presented  $4.03^\circ$  to the left and right of fixation. The target stimuli were Gaussians subtending  $1.8^\circ$  with a space constant (s.d.) of  $0.30^\circ$ . They ranged along an image vector from central red (CIE 1931  $x = 0.62$ ,  $y = 0.33$ ,  $Y = 24.8$ ) to the background green (CIE 1931  $x = 0.28$ ,  $y = 0.61$ ,  $Y = 6.2$ ).

Trials with static waveforms were completed for each RF at the start of each run of trials. These were displayed

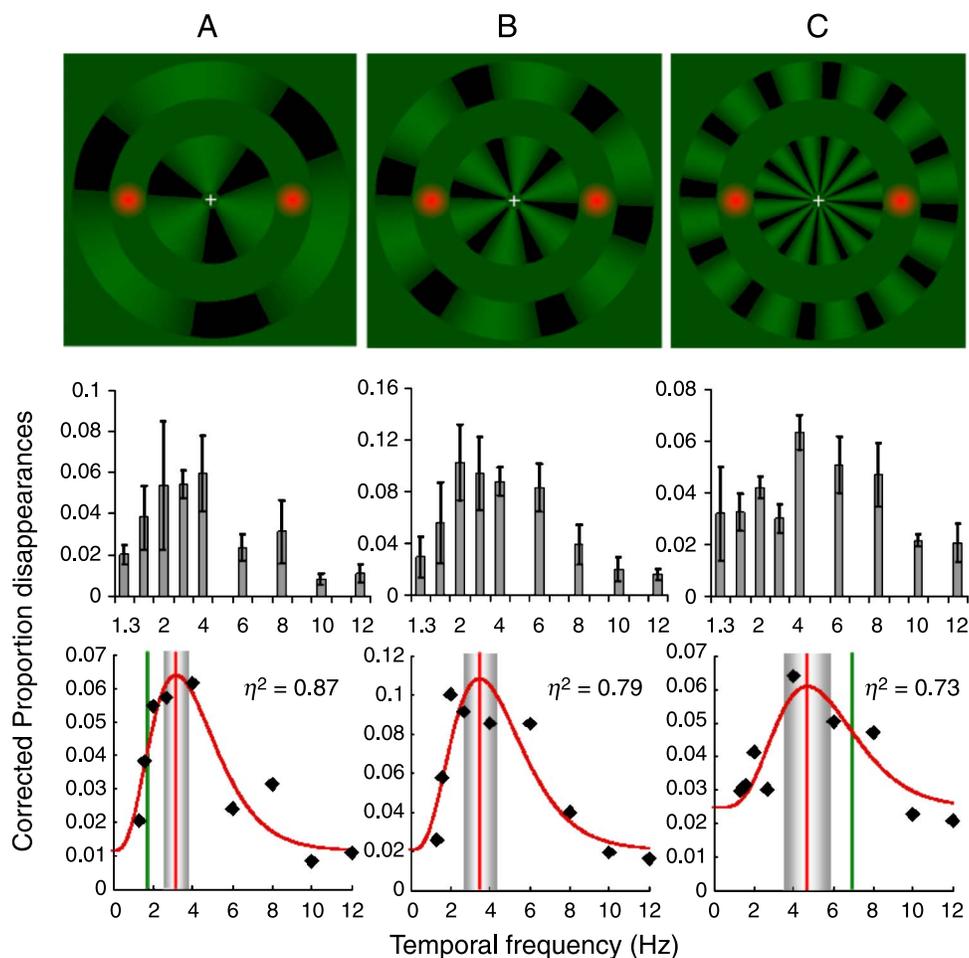


Figure 1. Depictions of stimuli and results for Experiment 1. Stimulus depictions and associated data are shown for (A) 3 c/360°, (B) 6 c/360°, and (C) 12 c/360° (click here to play animations). All linked stimulus animations contain ~4 Hz TF modulations of the waveforms. In all charts the ordinate depicts corrected proportion disappearances (see text) and the abscissa temporal frequency (Hz). Bar plots of corrected disappearances averaged across 4 observers (error bars denote *SEM*) are shown below the relevant stimulus depiction. Scatter plots are shown below the bar charts and depict the averaged data from the bar chart above fit with a gamma function (red curve,  $\eta^2$  estimates goodness-of-fit). Red vertical lines show the position of fitted peaks, and the shaded grey bars depict the extents of the 95% confidence intervals associated with the fitted peaks. Green vertical lines (in A and C) show speed tuning predictions (based on tuning in B). Note that the limits of the confidence intervals never overlap the speed tuning predictions.

prior to presentations containing movement in order to avoid the possible influence of illusory motion produced by motion aftereffects. During a run of trials, these three initial baseline trials were followed by test trials during which each RF was paired with each TF in a random order. The direction of drift was reversed on each trial to minimize the build up of motion aftereffects. There were therefore 30 trials per run. Each observer completed four runs of trials, providing 120 individual trials per observer.

## Results

A 3 (RF)  $\times$  9 (TF) repeated measures ANOVA revealed a significant main effect of RF [ $F(2,6) = 5.16, p = 0.049$ ]

and a significant main effect of TF [ $F(8,24) = 9.05, p < 0.01$ ] (see bar plots in Figure 1). However, there was no significant interaction between RF and TF [ $F(16,48) = 1.49, p = 0.14$ ]. Follow up pairwise *t*-tests with a Bonferroni correction demonstrated that the stimulus with an RF of 6 c/360° produced more disappearances than did 3 c/360° [ $t(3) = 4.89, p = 0.049$ ] but not more than did 12 c/360° [ $t(3) = 1.81, p = 0.51$ ]. There were no differences between the proportions of disappearance induced by stimuli with an RF of 3 c/360° and 12 c/360° [ $t(3) = 0.61, p = 0.99$ ]. These data show that the spatial scale of the waveform within the inducing stimulus influences the proportion of disappearances. However, our primary interest here is the possibility that disappearances might be maximal at specific rates of luminance modulation or of retinal stimulus speed.

As the repeated measures ANOVA had indicated that disappearances varied with TF, we fitted gamma functions to estimate the temporal frequencies that coincided with maximum disappearances. We found that the gamma functions peaked at 3.21 Hz (95% CI+ = 3.83, CI- = 2.63) for data collected using a grating with an RF of 3 c/360°, at 3.49 Hz (95% CI+ = 4.38, CI- = 2.69) for a grating with an RF of 6 c/360°, and at 4.72 Hz (95% CI+ = 5.93, CI- = 3.61) for a grating with an RF of 12 c/360° (see scatter plots in Figure 1).

We made speed tuning predictions by halving (1.75 Hz) and doubling (6.98 Hz) the TF associated with the fitted peak to the 6 c/360° condition (see green lines Figure 1). In both cases, these speed tuning predictions lie outside the confidence intervals associated with the peaks of the fitted gamma functions. We can therefore conclude that these motion-induced disappearances are not tuned to retinal stimulus speed. Additionally, since the confidence intervals between the three levels of RF overlap, we can conclude that maximal disappearances are well predicted by TF, with an average estimate of this tuning across the three conditions being ~3.81 Hz.

## Experiment 2

### Method

It has been shown previously that luminance flicker can be used to induce MIB-like disappearances (Kawabe & Miura, 2007). In Experiment 2, we assessed whether the temporal tuning of MIB from our previous experiment could predict the temporal tuning of FIB (Kawabe & Miura, 2007). We used 32 green (CIE 1931  $x = 0.28$ ,  $y = 0.61$ ) inducing Gaussians arranged in concentric circles centered at eccentricities of 2.52° and 5.94°, respectively (see Figure 2A). These were shown against a green background (CIE 1931  $x = 0.28$ ,  $y = 0.61$ ,  $Y = 12.4$ ). The inner inducing Gaussians subtended 0.9° (with space constants of 0.15°), and the outer inducing Gaussians subtended 1.8° (with space constants of 0.30°).

Two target Gaussians were presented 4.03° to the left and right of fixation. They subtended 1.98° with a space constant (s.d.) subtending 0.33° and ranged along an image vector from central red (CIE 1931  $x = 0.62$ ,  $y = 0.33$ ,  $Y = 24.8$ ) to the background green (CIE 1931  $x = 0.28$ ,  $y = 0.61$ ,  $Y = 12.4$ ).

The peak luminance of the inducing Gaussians was sinusoidally modulated ( $12.4 \pm 9.94$  cd/m<sup>2</sup>) to create luminance flicker. The TF of the flicker was manipulated across trials in 1 Hz steps (1 to 15 Hz). Presentation order was randomized. A static trial was also included in the random sequence, in which the green inducing Gaussians were not flickered but were presented at the peak or trough luminances (randomly determined), to control for

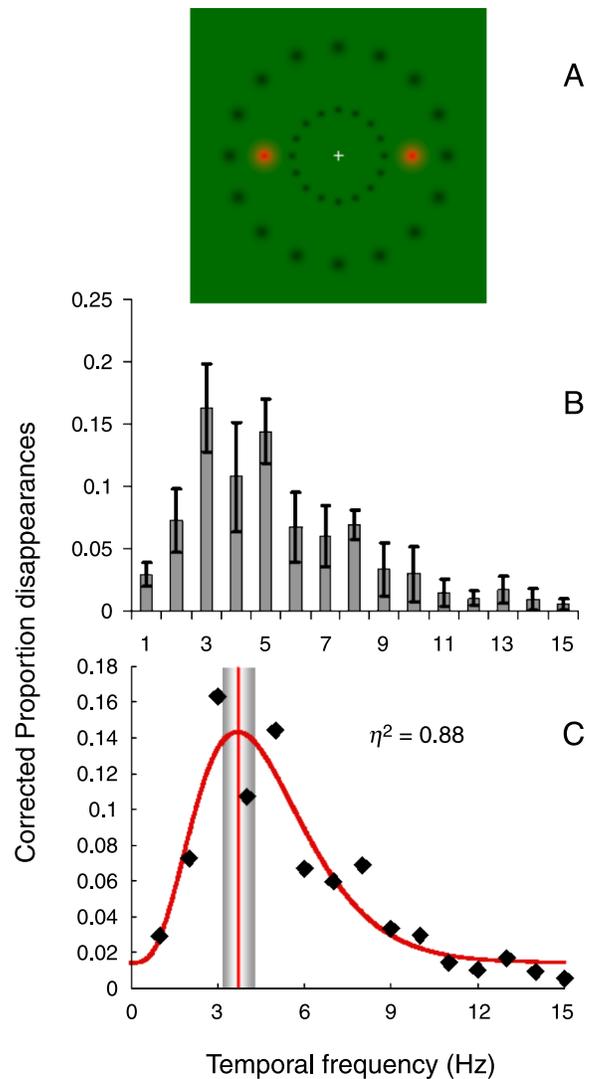


Figure 2. Stimulus depiction and data from Experiment 2. (A) A graphic depiction of the stimulus configuration used in Experiment 2. The linked stimulus animation contains ~4 Hz luminance flicker ([click here to play animation](#)). (B) Bar plot depicting corrected proportion disappearances across four observers. (C) Scatter plot of the data depicted above fitted with a gamma function ( $\eta^2$  estimates goodness-of-fit). The red vertical bar depicts the peak of the fitted function, and the shaded grey bar depicts the extents of the confidence intervals associated with the fitted peak.

Troxler fading and spatial crowding as per the static trials in Experiment 1.

### Results

TF had a significant effect on disappearances, as revealed by a one-way repeated measures ANOVA [ $F(14,42) = 10.15$ ,  $p < 0.01$ ] (see Figure 2B). Since the ANOVA revealed a main effect of TF, we fitted a gamma function to determine the TF at which most disappearances

were induced. The fitted gamma function peaked at 3.69 Hz (95% CI<sup>+</sup> = 4.25, CI<sup>-</sup> = 3.16, see [Figure 2C](#)). The average peak TF from [Experiment 1](#) (3.81 Hz) falls well within the confidence limits associated with the peak of the gamma function fitted to these data. Note that this is true even though two of the observers who participated in the two experiments differed. These data therefore suggest that subjective disappearances induced by luminance flicker and by displays containing smooth motion have similar TF tuning characteristics, supporting the possibility of a common causal mechanism.

## General discussion

Our first experiment demonstrated that disappearances in displays containing directional motion do not vary with retinal speed. Instead they reflect temporal frequency sensitivity, with maximal disappearances occurring at ~4 Hz. The results of [Experiment 2](#) showed that quantitatively similar rates of luminance modulation were also optimal for flicker-induced disappearances.

In combination, the two experiments show that MIB is not tuned to stimulus speed. The mechanism(s) underlying MIB are therefore likely to depend on local luminance modulations at moderate temporal frequencies. This primarily implicates neurons sensitive to separable spatial and temporal information (Foster, Gaska, Nagler, & Pollen, 1985; Priebe, Lisberger, & Movshon, 2006; Tolhurst & Movshon, 1975; for a review, see Lennie & Movshon, 2005). However, the present data do not speak to the possible influence of other aspects of motion, such as direction.

We have shown that flicker-induced disappearances are tuned to the same rates of temporal modulation as motion-induced disappearances. Our data therefore corroborate Kawabe and Miura's (2007) finding that disappearances produced by luminance flicker are likely to be caused by the same mechanism as traditional MIB displays.

These data may seem to be inconsistent with Bonneh et al.'s (2001) finding that faster stimulus speeds induce more disappearances. However, in Bonneh et al.'s study, TF modulation was confounded with stimulus speed. It is therefore likely that their findings primarily reflect changes in the average TF content of the display.

We should also note that, while our data show that MIB-like disappearances are not tuned to stimulus speed, [Experiment 1](#) did show a slight non-significant trend in the direction of speed tuning. Of course this could be coincidental. However, it is also possible that speed tuned neurons exert a weak influence upon a phenomenon that is primarily driven by mechanisms tuned to specific rates of TF.

The ~4 Hz temporal tuning found in the present study is similar to rates found for motion-induced position shifts

(De Valois & De Valois, 1991; Whitney & Cavanagh, 2000). Interestingly motion-induced position shifts seem to be driven by the effective disappearance of specific stimulus regions due to apparent contrast modulations (Arnold, Thompson, & Johnston, 2007; Chung, Patel, Bedell, & Yilmaz, 2007; Liu, Ashida, Smith, & Wandell, 2006; Tsui, Khoo, & Hayes, 2007; Whitney et al., 2003). Functionally, these effects might be related to a motion deblurring mechanism (Arnold, Thompson, et al., 2007; Burr, 1980; Burr & Morgan, 1997; Whitney et al., 2003).

Given the similar TF tunings, and the fact that both motion-induced positions shifts (Arnold, Thompson, et al., 2007; Chung et al., 2007; Whitney et al., 2003) and motion-induced disappearances (Caetta et al., 2007) have been tied to reductions in contrast sensitivity, it is at least possible that these two phenomena are related. We shall explore this possibility in future experiments.

## Conclusions

The present study demonstrates that subjective disappearances of static targets during MIB are tuned to TF, but not to retinal stimulus speed. Flicker-induced disappearances have similar temporal tunings to those induced by motion, suggesting that a common mechanism may underlie both phenomena.

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