The role of mask coherence in motion-induced blindness

Erika T Wells, Andrew B Leber, John E Sparrow§

Department of Psychology, University of New Hampshire, Conant Hall, 10 Library Way, Durham, NH 03824, USA; e-mail: erika.wells@unh.edu, andrew.leber@unh.edu; § University of New Hampshire-Manchester, Manchester, NH Received 31 March 2011. in revised form 13 October 2011: published online 14 December 2011

Abstract. Motion-induced blindness (MIB) is the perceived disappearance of a salient target when surrounded by a moving mask. Much research has focused on the role of target characteristics on perceived disappearance by a coherently moving mask. However, we asked a different question: mainly, are there certain characteristics about the mask that can impact disappearance? To address this, we behaviorally tested whether MIB is enhanced or reduced by the property of common fate. In experiments 1, 2, and 3, we systematically manipulated the motion coherence of the mask and measured the amount of target disappearance. Results showed that, as mask coherence increased, perceived target disappearance decreased. This pattern was unaffected by the lifetime of the moving dots, the dot density of the motion stimulus, or the target eccentricity. In experiment 4, we investigated whether the number of motion directions contained in an incoherent mask could account for our findings. Using masks containing 1, 3, and 5 motion directions, we found that disappearance did not increase proportionally to the number of motion directions. We discuss our findings in line with current proposed mechanisms of MIB.

1 Introduction

Motion-induced blindness (MIB) is a psychophysical phenomenon whereby stationary peripheral targets are perceived to disappear when presented simultaneously with a moving mask pattern (Bonneh et al 2001). While this phenomenon has intrigued many researchers, the mechanism for the disappearance remains elusive. In an effort to solve the mystery of why disappearance of a salient target during MIB is so robust, many studies have focused on the interaction of different properties of the target with a mask possessing only one type of motion (ie 2-D or 3-D rotational). In this study, we took another approach, varying the motion properties of the mask as opposed to those of the target to reveal the effect on disappearance.

MIB is always the result of an interaction between the mask and target, and one characteristic common to disappearance phenomena in general and MIB in particular is the degree to which disappearance is affected by the shared featural organization between the mask and the targets. For instance, common Gestalt properties, such as continuity, proximity, and connectedness of the target in relation to the mask, can greatly impact perceived disappearance. In their seminal work on MIB, Bonneh et al (2001) reported an influence of continuity between the targets on their dominance in perception. When targets are two Gabor patches aligned in an orthogonal orientation within a moving mask, perception involves the alternation of an individual grating with both gratings rarely disappearing together. However, when the targets are arranged contiguously, both targets tend to appear and disappear more often as a group. The continuity of a border can also impact the perceived appearance and disappearance of a target. A circular target outlined with a dashed line will have a tendency to disappear as a complete object giving the illusion that the circular target alternates between present and absent. When the same dashed lines in the border of the target are rotated 90° , thereby disrupting the continuity, the individual components will more likely disappear independent of each other. Perception in this case tends to involve portions of the circular target disappearing compared to the entire object.

Perceived continuity between the mask and target can also have a profound effect on target disappearance (Hsu et al 2004). For instance, a target positioned in the center of a moving mask so that it is continuous with the array of moving mask elements produces far less disappearance than when the target is displaced from the center, eliminating the property of continuity.

Proximity cues can modulate the perception of completed objects, and thus the degree to which target components disappear separately (Shibata et al 2007). Targets separated by a smaller gap produced more instances of simultaneous and synchronous disappearance and reappearance of the individual targets as if they formed a completed object. As the gap between the individual elements increases, perceived grouping diminishes, and the individual target elements are more apt to disappear independently and asynchronously. A similar occurrence is observed with simple targets arranged linearly in the periphery. The smaller the spatial separation between the individual targets, the more often they disappeared together (Bonneh et al 2001). Distal targets, conversely, tended to disappear one at a time.

The Gestalt property of similarity, particularly between the target and mask, likewise affects the amount of MIB experienced. Hsu et al (2004) showed that contrasting features in the mask and target increased disappearance. When the mask contained rotating blue-cross elements, a yellow stationary target identical in shape experienced less disappearance compared to when the target was a completely different shape, such as a square.

While Gestalt properties of the targets can impact the degree of disappearance in MIB, we wondered whether a Gestalt property solely inherent to the mask could contribute to the perceptual disappearance in MIB. Specifically, we asked whether the property of common fate in the motion of the mask elements would impact perceived disappearance of peripheral targets in a manner similar to that observed with continuity, proximity, and similarity of the targets. While MIB has typically utilized coherently grouped mask elements moving with common fate, there are indications that a mask lacking the property of common fate may still produce incidents of MIB. Bonneh et al (2001) described evidence of disappearance with 'Brownian' or random-walk motion, although the amount of disappearance for this type of motion was not directly compared to more coherently structured motion. Leopold et al (2002) also found that randomly moving dots could induce disappearance, although they did not compare this stimulus to a coherent motion stimulus. Therefore, it is unclear to what degree motion coherence modulates MIB. The lack of systematic manipulation of Gestalt motion grouping in MIB makes it particularly ripe for further investigation.

In this study, we used random-dot stimuli to progressively increase the proportion of dots displaying coherent motion in order to evaluate behaviorally the effect of common fate on target disappearance.

2 Experiment 1

2.1 Method

2.1.1 *Subjects.* Fifteen and twenty-four participants with normal or corrected-to-normal visual acuity took part in experiments 1a and 1b, respectively. All were students from the University of New Hampshire, Durham, and received partial course credit. Informed consent was obtained from each participant.

2.1.2 *Stimuli*. Stimuli were generated with an Apple G4 desktop computer using Matlab (Mathworks, Natick, MA) with PsychToolbox extensions (Brainard 1997; Pelli 1997) and presented on a 19 inch CRT display (ViewSonic G90fb) at a viewing distance of 50 cm. Stimuli consisted of a mask containing 480 blue moving square dots, each subtending 0.20 deg² on a black background. A white fixation cross was located in the center



(a)

Figure 1. Representation of stimuli used for testing the effect of motion coherence on disappearance due to MIB. All square dots, comprising the mask, were blue and moved at the same speed (see text for details). Representative arrows indicate motion directions of individual dots and were not present in the actual stimulus. The stationary target (circle) was yellow.

of the screen and a yellow circular target (0.55 deg diameter) was displayed in the upper left quadrant at 3.36 deg to the left of fixation and 3.29 deg above it, yielding an eccentricity of 4.70 deg (see figure 1). Dot displays were confined within an area subtending 31.63 deg width \times 23.20 deg height, centered in the middle of the screen with a density of 0.65 dots deg^{-2} .

In experiment la, each dot's lifetime was 'eternal' (ie present for the duration of the trial). Specifically, each dot was drawn in a random location on the first frame of the mask presentation and then followed a predictable, linear direction path for each subsequent frame. In experiment 1b, each dot's lifetime was limited to 235 ms, at which point it was replaced by another dot in a new, randomly selected, location. Cycles of dot 'births' were distributed evenly at intervals of 47 ms. While 'alive', the dots traversed the screen until reaching the end of the aperture at which time they re-entered the display from the opposite side, maintaining the same trajectory as before (eg dots reaching the left border of the aperture re-entered at the same vertical position on the right side in the subsequent frame; dots reaching the top border re-entered at the same horizontal position on the bottom). Motion contrast in the mask was created by changing the proportion of dots moving in a coherent direction. Coherence was defined as the percentage of pattern elements moving in the same direction. Coherence varied between 0%, 33%, 66%, and 100% of the number of dots in the moving pattern. On a given trial, all coherent dots moved in one of four canonical global directions (up, down, left, right). Each incoherent dot was assigned a random number from 1 to 360 that determined the angle of trajectory. All dots moved at a fixed speed of 8.51 deg s^{-1} .

2.1.3 Design and procedure. Each participant completed a practice session of 6 trials, each lasting 30 s. Then, participants viewed a total of 96 trials, also lasting 30 s each, with coherence randomized across trials. A self-timed break after each set of 16 trials was provided. Participants were instructed to maintain gaze on the fixation cross and keep the peripheral target in their awareness. Participants were further instructed to press the right shift key when they saw the target disappear and release it upon target reappearance.

2.2 Results and discussion

2.2.1 Experiment la. Here, and in all subsequent analyses of variances, we used Mauchly's test of sphericity to assess whether our data violated this assumption. If significant, we used the Greenhouse-Geisser corrected degrees of freedom and the adjusted p-value in our

reported statistics. Holm-Bonferroni corrections were used to test the significance of all a posteriori pairwise comparisons.

An episode of target disappearance was defined as the time between the response button being depressed and then released. The total time of MIB episodes in a trial was used to determine the mean percentage of disappearance across all trials as a function of coherence (figure 2a).⁽¹⁾



Figure 2. Results for experiment 1a (eternal dot life). (a) Percent of target invisibility for the different coherence conditions for dots remaining on the screen for the duration of the trial. (b) Mean length of MIB episodes for the different coherence conditions for dots remaining on the screen for the duration of the trial. Error bars indicate within-subject ± 1 SEM.

The results were compared in a one-way repeated-measures ANOVA, which confirmed a statistically significant main effect of coherence ($F_{3,42} = 28.15$, p < 0.001, $\eta_p^2 = 0.67$). Specifically, the percent time of disappearance of the target increased as the motion coherence decreased. Pairwise comparisons revealed no difference in disappearance between 0% and 33% coherence. There was a significant difference in disappearance between the 0% and 66% coherence level (p = 0.005). However, the main effect seemed to be driven by a significant difference in disappearance at the 100% coherence compared to 0%, 33%, and 66% (all *p*-values < 0.001). Therefore, introducing a certain amount of random motion into the moving pattern significantly increased target disappearance.

We also investigated whether the increased percentage of time the target disappeared in the incoherent condition was due to an effect of longer episodes of disappearance compared to the coherent condition (figure 2b). The mean MIB episode across each trial was analyzed by a one-way repeated-measures ANOVA revealing that the episode duration was significantly longer in the incoherent condition ($F_{1.71,23.88} = 17.33$, p < 0.001, $\eta_p^2 = 0.55$). Again, the significant main effect seemed to be due to a difference between the incoherent masks (0%, 33%, and 66%) and the 100% coherent mask (all *p*-values < 0.001). There was no difference in disappearance between the masks containing intermediate degrees of incoherent motion.

Overall, we found that common fate had a detrimental effect on perceived disappearance in MIB. We will first describe additional results before discussing the implications of this finding.

2.2.2 *Experiment 1b.* We next tested the possibility that our pattern of results may have been impacted by temporal properties of the mask. In experiment 1a, the coherent dots remained on the screen for the entire trial duration. Here, we presented the same conditions as in experiment 1a, except now each dot remained on the screen for a limited lifetime before it was replaced by new dots (see section 2.1.2 above).

⁽¹⁾Some researchers have normalized individual subject data prior to statistical analysis to reduce intersubject variability in disappearance due to MIB (eg Libedinsky et al 2009; Wallis and Arnold 2009). To ensure that the specific analysis did not influence the pattern of results, we reanalyzed using normalized data from all of the experiments reported. Both the numerical patterns and statistical results were unchanged.

Results showed a similar pattern of percent disappearance to that of experiment 1a (figure 3a). That is, the percentage of time the target disappeared increased as the coherence level decreased. A one-way repeated-measures ANOVA found a significant main effect of coherence ($F_{1.55, 35.61} = 4.10$, p = 0.034, $\eta_p^2 = 0.15$). Pairwise comparisons revealed that the main effect was driven by a significant difference in disappearance at the 100% coherence compared to 0%, 33%, and 66% (all *p*-values ≤ 0.03). There was no difference in disappearance between the 0%, 33%, and 66% coherent condition. These results clearly show, once again, that the more coherence produced less disappearance in total.

Furthermore, similar to the results in experiment 1a, the mean length of an MIB episode was greater for incoherent motion than for coherent motion (see figure 3b). A one-way repeated-measures ANOVA showed that the difference was significant $(F_{3,69} = 18.17, p < 0.001, \eta_p^2 = 0.62)$. A significant difference in MIB duration was found for the 0% coherent mask compared to when the mask contained 33%, 66%, or 100% coherently moving dots (all *p*-values ≤ 0.001). Also, there was a significant difference in the mean length of an MIB episode when the mask contained incoherent motion compared to when it contained 100% coherent motion (all *p*-values < 0.001).

In summary, with both eternal and limited dot life (experiments 1a and 1b, respectively), a mask devoid of the property of common fate produced significantly more disappearance.



Figure 3. Results for experiment 1b (limited dot life). (a) Percent of target invisibility for the different coherence conditions for dots remaining on the screen for a limited time. (b) Mean length of MIB episodes for the different coherence conditions for dots remaining on the screen for a limited time. Error bars indicate within-subject ± 1 SEM.

3 Experiment 2

We also tested whether the target eccentricity affected the pattern of results. It has been shown previously that targets at greater eccentricities show greater initial time to fade (Hsu et al 2004). We questioned whether this phenomenon interacted with the present coherence manipulation. We varied the eccentricity of the target as well as the motion coherence of the MIB mask. If the relationship between mask coherence and MIB is specific to the eccentricity used in the previous experiment (4.70 deg), then we may fail to replicate this pattern at smaller or greater eccentricity values. Alternatively, the relationship between mask coherence and MIB may generalize across various eccentricities.

3.1 Method

The methods and procedure were the same as in experiment 1b. Here, we varied the target eccentricity, selecting randomly from one of three eccentricities $(2.00^{\circ}, 4.50^{\circ}, \text{ or } 6.00^{\circ})$ on each trial.

3.1.1 *Subjects*. Eighteen new participants with normal or corrected-to-normal visual acuity participated.

3.2 Results and discussion

The overall impact of coherence was not affected by eccentricity; the percentage of time a target disappeared as well as the mean length of an MIB episode was significantly greater when surrounded by an incoherent mask (figure 4). Using a 4 (coherence) by 3 (eccentricity) two-way repeated-measures ANOVA we first compared the percentage of time the target remained invisible (figure 4a). We found a significant main effect for coherence ($F_{3,51} = 4.73$, p < 0.01, $\eta_p^2 = 0.22$), replicating our results from experiment 1. Pairwise comparisons revealed that the disappearance of the target was significantly different between 0% and 100% (p = 0.005), as well as between 33% and 100% coherence (p = 0.008). A significant main effect was also found for eccentricity ($F_{2,34}$ = 51.68, p < 0.001, $\eta_p^2 = 0.75$). Pairwise comparisons revealed a significant difference in disappearance between all eccentricities (all *p*-values < 0.001). These eccentricity effects replicate previous findings showing enhanced MIB with increasing eccentricities (Hsu et al 2004). Importantly, a significant eccentricity by coherence interaction was not found ($F_{6,102} = 0.75$, p = 0.61, $\eta_p^2 = 0.04$).



Figure 4. Results for experiment 2 (eccentricity). Graphs show (a) percent of target invisibility for the different coherence conditions for three different eccentricities $(2^\circ, 4.5^\circ, and 6^\circ)$; (b) mean length of MIB episodes for the different coherence conditions for three different eccentricities $(2^\circ, 4.5^\circ, and 6^\circ)$. Error bars indicate within-subject ± 1 SEM.

We also tested the mean length of an MIB episode as a function of eccentricity and coherence using a 4 (coherence) by 3 (eccentricity) two-way repeated-measures ANOVA (figure 4b). Again, we found a significant main effect for coherence ($F_{1.97,33,42} = 9.67$, p < 0.002, $\eta_p^2 = 0.57$), replicating the results obtained for MIB duration in experiment 1. Pairwise comparisons revealed a significant difference for a mask containing 0% coherent motion versus masks containing 33%, 66%, and 100% coherently moving dots (all *p*-values < 0.02). A significant main effect of eccentricity ($F_{2,34} = 22.40$, p < 0.001, $\eta_p^2 = 0.57$) was also obtained, lending further support for an influence of target eccentricity on MIB (Hsu et al 2004). Pairwise comparisons showed a significant difference between all eccentricities (all *p*-values < 0.003). Finally, a significant eccentricity-by-coherence interaction was not obtained ($F_{6,102} = 0.85$, p = 0.53, $\eta_p^2 = 0.05$).

To summarize, the current findings show that the impact of mask coherence on MIB, described in experiment 1, is not specific to a particular range of eccentricities.

4 Experiment 3

We next found it necessary to investigate whether the effect of common fate on disappearance due to MIB would generalize across multiple dot densities. The role of dot density has previously been established to be central to both MIB and, more broadly, in the visual processing of moving stimuli. With respect to MIB, Bonneh and colleagues (2001) found that dot density had a pronounced effect on target disappearance, with greater disappearance at higher dot densities. For present purposes, it is prudent to understand whether the effect of motion coherence is influenced by dot density. Perhaps, more importantly, there is evidence beyond the MIB literature that the perception of coherent motion may be strongly influenced by dot density. On the one hand, studies using functional MRI (fMRI) and magnoencephelography (MEG) have shown that a high-density random-dot stimulus elicits greater activation in the motion-sensitive middle-temporal (MT/V5) area of the brain when the dots move with coherent motion, compared to when they move incoherently (Braddick et al 2001; Rees et al 2000). On the other hand, McKeefry et al (1997) obtained the reverse pattern with a much lower dot density; explicitly, fMRI revealed a greater activation for incoherent motion compared to coherent motion in MT. It has been argued that the lower density used by McKeefry et al explains the divergent results (Braddick et al 2001). Given that the neural processing—and perceptual consequences—of coherent motion may be influenced by dot density, it follows that the effect of coherence on MIB may be contingent upon dot density.

The dot density of experiment 1 may be judged to be somewhat sparse, at 0.65 dots deg⁻². Therefore, to test whether the overall pattern we obtained with incoherent motion in experiment 1 was specific to low dot density, we substantially increased the dot density, by a factor of 9.2, to 6.02 dots deg⁻². This exceeded the maximum dot density used by Bonneh et al (2001), which we calculated to be 5.3 dots deg⁻².

4.1 Methods

With the exception of the increased dot density (6.02 dots deg^{-2}), the methods and procedure were the same as in experiment 1b.

4.1.1 *Subjects*. Twenty-nine new participants with normal or corrected-to-normal visual acuity participated.

4.2 Results and discussion

Results were similar to those of experiments 1a and 1b, with respect to how MIB changed as a function of mask coherence (figure 5).

As in the previous experiments a one-way repeated-measures ANOVA on percent disappearance, across the four levels of coherence, produced a significant main effect $(F_{3,84} = 9.44, p < 0.001, \eta_p^2 = 0.25)$. Specifically, the target disappeared for a greater percentage of the time when the mask was incoherent compared to when it was comprised of coherent motion; pairwise comparisons revealed a significant difference in disappearance between 0%, 33%, and 66% compared to the 100% coherent condition (all *p*-values < 0.03). A significant difference in disappearance was also found between 0% and 33% as well as between 0% and 66% (p < 0.01). Similar to our findings in experiments 1a and 1b, incoherent motion still exhibited the greatest impact on disappearance.



Figure 5. Results for experiment 3 (higher dot density). Bar plots show (a) percent of target invisibility for the different coherence conditions for dots remaining on the screen for a limited time, (b) mean length of MIB episodes for the different coherence conditions for dots remaining on the screen for a limited time. Error bars indicate within-subject ± 1 SEM.

The main effect of the length of MIB episodes was also significant ($F_{3,84} = 9.26$, p < 0.001, $\eta_p^2 = 0.25$). Pairwise comparisons also found a significant difference between the masks comprised of incoherent motion and a mask containing coherently moving dots (all *p*-values < 0.02).

We also directly examined the effect of dot density by comparing the results from experiments 1b (low density) and 2 (high density). We tested whether the percentage of time a target disappeared was affected by a change in dot density using a 4 (coherence) by 2 (density) mixed-design ANOVA. We observed a significant main effect of coherence on the percentage of time the target remained invisible ($F_{2.13,108.86} = 12.35$, p < 0.001, $\eta_p^2 = 0.20$). A significant main effect was also found for dot density ($F_{1,51} = 5.44$, p = 0.02, $\eta_p^2 = 0.10$), replicating previous work showing increased MIB with increased density (Bonneh et al 2001). A significant dot density-by-coherence interaction for the percentage of time a target remained invisible was not found ($F_{2.13,108.86} = 0.23$, p = 0.81, $\eta_p^2 = 0.004$).

Similarly, we tested the average length of an MIB episode as a function of coherence and dot density using a 4 (coherence) by 2 (density) mixed-design ANOVA. Again, we found a significant main effect for coherence ($F_{3,153} = 23.16$, p < 0.001, $\eta_p^2 = 0.31$) and dot density ($F_{1,51} = 4.58$, p = 0.037, $\eta_p^2 = 0.08$) on the average length of an MIB episode. We did not observe a significant coherence-by-density interaction for the average length of an MIB episode ($F_{3,153} = 0.21$, p = 0.89, $\eta_p^2 = 0.004$), further confirming that the relationship between coherence and MIB was similar across the different dot densities.

In sum, the data from experiment 3 show that the results obtained in experiments 1a and 1b cannot be explained by the relatively low dot density used in the mask.

5 Experiment 4

In experiments 1, 2, and 3, we found that disappearance was reduced when the mask elements were grouped according to the Gestalt property of common fate. We manipulated common fate by physically changing the percentage of dots that moved in a coherent direction, and the trajectories of each of the non-coherent dots were determined randomly. Here, we questioned how the number of total motion trajectories influenced MIB.⁽²⁾ We constructed a stimulus for which the number of motion directions could move on 1, 3, or 5 motion trajectories, but separated these trajectories by diverse values of angular deviations. This type of stimulus was informed by the knowledge that the perceptual system averages across small divergences in motion direction to produce an overall percept of unidirectional motion indistinguishable from absolute coherent motion (Williams and Sekuler 1984). When the angle between different motion directions is very small, the visual system groups the different trajectories into a percept of coherent motion (or common fate), regardless of the number of directions contained in the stimulus (Watamaniuk et al 1989). However, if the motion diverges by more than $10^{\circ} - 20^{\circ}$, the visual system is unable to maintain the percept of coherent motion and will, instead, perceive dots moving in independent directions (Mather and Moulden 1980; Watamaniuk et al 1989). We thus set out to make two observations of this study. First, at what value of angular deviation does MIB begin to increase? Second, at the larger angular deviations, is MIB influenced by the total number of independent trajectories in the mask (ie 3 versus 5 directions)?

5.1 Method

The methods and procedure were similar to those in experiment 1b. However, in experiment 4 the moving stimulus could contain one, three, or five different motion directions. On 1-direction trials, dots traveled en masse in one of four cardinal directions

⁽²⁾We thank an anonymous reviewer for raising the possibility.

(left, right, up, or down-figure 6, left). On 3-direction trials, one third of the dots moved in the predetermined cardinal direction, one third of the dots maintained a fixed clockwise trajectory defined by an angular deviation (θ) from the cardinal direction, and the remaining one third of the dots maintained a fixed counterclockwise trajectory defined by the same angular deviation (θ -figure 6, middle). In the 5-direction trials, one fifth of the dots moved in the cardinal direction, another fifth of the dots moved at a fixed (θ) clockwise angular deviation from the cardinal direction, and another fifth moved at a fixed (θ) counterclockwise angular deviation, bearing similarity to the 3-direction condition. In addition, another fifth of the dots moved on a trajectory measuring $\theta/2$ in a clockwise angular deviation from the cardinal direction, while the final fifth moved with a counterclockwise angular deviation of $\theta/2$ (figure 6, right). The number of motions, the cardinal direction, and the angular deviation (θ) were randomly selected on each trial, and an equal number of all trial types were presented. To gain a robust sample of angular ranges, the values of θ were parametrically varied, using values of 10°, 20°, 40°, and 60°, and selected randomly on each trial.



Figure 6. Representation of stimuli used for testing motion directions on disappearance due to MIB. Motions in the mask were 1-direction (left), 3-direction (middle), and 5-direction (right). Trajectories for motion were separated by an angular deviation, θ or $\theta/2$ (see text for details). A white cross was located in the middle of the screen to aid in fixation (removed from depiction for clarity). The size, shape, and colors of dots and target were the same as in experiments 1 and 2.

5.1.1 *Subjects*. Eight new participants with normal or corrected-to-normal visual acuity each completed 288 trials over the course of two sessions.

5.2 Results and discussion

To examine the angular deviation at which MIB increases, we performed a series of planned comparisons for the percentage of time the target disappeared (figure 7a). Specifically, we averaged the 3-direction and 5-direction conditions at each angular deviation, comparing these means to the 1-direction baseline condition. Based on the visual system's ability to integrate multiple motion trajectories into a coherent percept at small angular deviations, we would predict that there would be no difference between a stimulus containing multiple trajectories separated by small angular deviations and 1-direction coherent motion (Watamaniuk et al 1989). In line with this prediction, we found that the multiple direction masks did not differ significantly from the 1-direction mask at 10° $(t_7 = -0.79, p = 0.45)$. However, as angular deviation increases to 60° , exceeding the limit of coherent motion integration (Mather and Moulden 1980), we should see more MIB for the multidirectional masks compared to a mask having only one coherent direction. In agreement with this line of reasoning, we found greater disappearance for the masks having more than one direction compared to the 1-direction mask $(t_7 = -3.11, p = 0.02)$. There was no significant difference between the 1-direction mask and the masks containing multiple directions with an angular deviation of 20° $(t_7 = -2.94, p = 0.05)$ and 40° $(t_7 = -1.93, p = 0.10)$.



Figure 7. Results for experiment 4 (angular deviation). (a) Percent of target invisibility for the varying number of directions in the moving mask for dots remaining on the screen for a limited time as a function of angular separation between the different motion directions. (b) Mean length of MIB episodes for the varying number of directions in the moving mask for dots remaining on the screen for a limited time as a function of angular separation between the different motion directions. Error bars indicate within-subject ± 1 SEM. The baseline 1-direction condition is represented as a dotted line with the height of the shaded area corresponding to ± 1 SEM.

We also tested the mean length of an MIB episode for the 1-direction mask compared to masks containing multiple motion directions using the same procedure described above (figure 7b). Planned comparisons revealed no significant difference between the 1-direction mask and the mask comprised of multiple directions when the angular deviation separating the motion trajectories was 10° ($t_7 = -0.20$, p = 0.85) as predicted by earlier work (Watamaniuk et al 1989). When the angular deviation increased to 60° , beyond the limits of motion integration (Mather and Moulden 1980), the mean length of an MIB episode was significantly greater for the multidirectional masks ($t_7 = -6.72$, p < 0.001). Again, no significant difference was seen for the intermediate angular deviations of 20° ($t_7 = -0.34$, p = 0.74) and 40° ($t_7 = -1.78$, p = 0.12).

Next, we specifically examined whether more motion directions in a mask would translate to increased MIB. Using a 2 (3-direction versus 5-direction) by 4 (θ), two-way repeated-measures ANOVA, we measured the percentage of time a target disappeared within a 30 s trial (figure 7a). The main effect of motion direction showed that more directions did not increase MIB; in fact, 3-directions produced significantly more disappearance than 5-directions (23.91% versus 22.55%, respectively, $F_{1,7} = 15.13$, p = 0.006, $\eta_p^2 = 0.68$). A significant main effect of θ was also found ($F_{1.39,9.72} = 8.03$, p = 0.01, $\eta_p^2 = 0.53$), reflecting the increased disappearance at increased angular deviation. Further, no significant interaction was found ($F_{3,21} = 0.90$, p = 0.46, $\eta_p^2 = 0.11$).

We also conducted a 2 (3-direction versus 5-direction) by 4 (θ) two-way ANOVA on the mean length of an MIB episode (figure 7b). No significant difference was observed between the 3-direction and 5-direction conditions ($F_{1,7} = 3.77$, p = 0.09, $\eta_p^2 = 0.35$). A significant main effect was observed for θ ($F_{3,21} = 11.68$, p < 0.001, $\eta_p^2 = 0.63$), with no interaction found between number of motion directions and θ ($F_{3,21} = 2.26$, p = 0.11, $\eta_p^2 = 0.24$).

To summarize this experiment, we found that at 10° there was no significant difference in MIB between a mask possessing 1-direction coherent motion and masks containing multiple motion directions. At 60° , when the process of coherent motion integration is exceeded (Mather and Moulden 1980; Watamaniuk et al 1989), we observed more MIB for masks with multiple motion directions. Furthermore, we found that, at the larger angular deviation of 60° , increasing the number of motion directions included in the mask—ie from 3 to 5—did not predict greater MIB.

6 General discussion

We found that perceptual organization of moving dots by common fate significantly influenced the perceived disappearance of a peripheral target in MIB. Specifically, the more the dots moved with coherent motion, the less often the target disappeared. This pattern was unaffected by the lifetime of the moving dots, the dot density of the motion stimulus, or the eccentricity of the target. Further, while greater angular deviation between dot trajectories gradually increased MIB, the total number of independent motion trajectories did not explain disappearance. Below, we discuss how the present results fit with other bistable phenomena, as well as several proposed mechanisms described in the MIB literature.

6.1 Filling-in and rivalry

How do our findings compare to other instances in which perceptual awareness fluctuates? One similar finding comes from studies of perceptual filling-in, in which episodes of such filling-in are also affected by common fate (Welchman and Harris 2000). Specifically, the initial time to fade for a target area comprised of incoherently moving dots surrounded by noise was significantly faster compared to when the target dots moved coherently. Another effect of coherence on filling-in was found when the coherence of the background was altered (Spillmann and Kurtenbach 1992). Here, a background of coherent motion significantly increased the time for a uniform peripheral target to initially fade. Perceptual filling-in may be analogous to processes of the visual system responsible for suppressing retinal anomalies (Ramachandran and Gregory 1991); a mechanism recently suggested to be a component of MIB (New and Scholl 2008). Binocular rivalry, characterized by the oscillating perceptions of different patterns when presented to different eyes, is similarly affected by coherence. In one study of this phenomenon that seems particularly analogous to the present MIB study, Silver and Logothetis (2004) found that an incoherent random-dot pattern presented to one eye produced greater periods of dominance of that eye (ie suppression of the stimulus in the other eye) compared to a coherent pattern. Comparable to the findings by Spillmann and Kurtenbach (1992) and Silver and Logothetis (2004), we found a significant impact of common fate, suggesting that these perceptual phenomena may share similar underlying mechanisms (Carter and Pettigrew 2003; Hsu et al 2004).

6.2 Suppression in early visual areas

Why might there be similar effects of coherence in the distinct perceptual illusions of MIB, perceptual filling-in, and binocular rivalry? The answer may lie in lower-level visual representations of the competing visual stimuli, particularly when motion is involved. Although Bonneh et al (2001) discounted the involvement of early visual areas in MIB, recent work by Donner and colleagues (2008), Libedinsky et al (2009), and Schölvinck and Rees (2010) points to a potentially important role for V1 in perceptual awareness of the target. Libedinsky et al (2009) reported that patterns of firing activity to target objects in monkey V1 cells were modulated in the presence of a moving mask, despite the use of a protection zone that ensured the mask elements would not appear within the classical V1 receptive fields of the recorded neurons. Donner et al (2008) observed a numerical, albeit non-significant, decrease in fMRI activation in human VI associated with the stationary target along with significant increases in activation in dorsal areas representing the moving mask (particularly V3A) during episodes of MIB. Similar modulation of neural activity in early visual areas has been found for other phenomena associated with periods of invisibility. For instance, during binocular rivalry, an object suppressed from visual awareness shows a significant reduction in V1 activity compared to when it is visible (Lee and Blake 2002). However, Schölvinck and Rees (2010) reported stronger fMRI activity in areas V1 and V2 compared to V5 with the perceptual disappearance of the target in MIB. The conflicting response of V1 activity related to the target during MIB may be a factor of the subtle differences in global motion between a random-dot 3-D structure from motion mask (Donner et al 2008) and a 2-D rotational mask (Schölvinck and Rees 2010). It is possible that any change in the global characteristics of the mask in MIB, including motion coherence, can impact the activity of V1, thereby affecting the amount of disappearance.

6.3 Suppression in higher visual areas

In contrast to invisibility that is precipitated by activity in V1, MIB could originate in higher visual-processing areas, such as the middle temporal area (MT) and V3A. According to one motion processing model, the perception of motion occurs when extrastriate areas such as MT and V3A combine the signals arising from many direction or orientation selective neurons located in V1 across space and time (Rust et al 2006). As alluded to above, Donner and colleagues (2008) observed a decrease in fMRI activation in human ventral visual areas associated with the stationary target along with an increase in activation in dorsal areas representing the moving mask (particularly V3A) during episodes of MIB. These results suggest that disappearance of a target during MIB may occur through suppression from higher motion-processing areas. Flickering and motion stimuli have been shown to produce similar activity in V3A (Liu et al 2004), and a suppressive mechanism may help to explain why flicker also induces MIB (Kawabe and Miura 2007; Wallis and Arnold 2008). Human brainimaging studies have shown that different types of global motion activate cortical area V3A differentially (Koyama et al 2005) raising the possibility that this area may also suppress activity in V1 preferentially. Extrastriate areas have also been implicated in the perceptual alternations with other bistable stimuli (Kleinschmidt et al 1998). Given the fact that MIB shares characteristics with other perceptual phenomena, such as binocular rivalry (Carter and Pettigrew 2003), it follows that an analogous mechanism of suppression by higher visual areas may also be involved in MIB. However, our results do not appear consistent with a high-level suppression account. That is, the high-level account would predict greater MIB with greater coherence, since areas such as MT and V3A favor coherent over incoherent stimuli (Braddick et al 2001; Rees et al 2000). Because we did not measure neural activity in this study, we cannot be sure how lower and higher visual areas would respond to the different levels of coherence during MIB. Thus, future work aimed at measuring neural activity during an MIB task with a coherence manipulation might help to reconcile the various findings supporting roles for early versus later visual areas in producing this disappearance phenomenon.

6.4 Motion streak suppression

We considered the possibility that processes fundamental to the integration of local motion signals were a factor in modulating disappearance with a coherent mask. As an object proceeds along a trajectory, each location in time is recorded by the activation of successive neurons in the visual system leaving a virtual trace of the spatial progression of motion (or a motion streak). These motion streaks are spatially integrated by the visual system to aid in our ability to determine the direction of global motion, but these residual clues are suppressed from awareness (Geisler 1999). Recent work by Wallis and Arnold (2009) presumes a mechanism of motion streak suppression in MIB, bolstered by their finding that MIB is greater at the trailing edge of motion as opposed to the leading edge. One might thus question how motion streak suppression influenced the present results. Specifically, it is possible that an incoherent mask creates greater motion streak suppression, producing the higher degrees of MIB we observed with this mask. It has been shown that a group of dots possessing incoherent local motion signals can produce motion streak suppression, provided the global motion signal is coherent— as is the case with Glass patterns (Ross et al 2000).

1515

However, little is known about the occurrence of motion streak suppression with a globally incoherent stimulus, which we used in this study. Therefore, further research is needed to expand our understanding of the relationship between motion coherence and motion streak suppression during MIB.

6.5 Surface completion

Surface completion in MIB has previously been discussed by others (Graf et al 2002; Lages et al 2009). For instance, grouping Kanizsa pacman elements to induce a completed surface produced greater disappearance than when the Kanizsa elements were rotated 180°, thereby eliminating the perception of a surface (Graf et al 2002). Gestalt processes are key to image segmentation, and common fate is advantageous for the determination of different depth surfaces—as evidenced by the pop out of a motion surface once a small percentage of static dots begin to move in a coherent direction (Ehrenstein et al 2003). Thus, with a mask grouped according to common fate, the visual system may easily process the elements into one good surface, while a mask with little common fate contains more complexity and may result in poorer surface segmentation. The ability of the visual system to more easily delineate a coherent motion surface, compared to an incoherent motion surface, may arise due to response differences in V1 (Lamme 1995) and/or V2 (Bakin et al 2000) receptive fields. In a V1 receptive field, motion in the preferred direction evokes an enhanced response when there are other similarly moving objects located in the surround (Lamme 1995). In comparison, a V1 cell's response to the preferred motion direction is inhibited when surrounding objects having a non-preferred motion direction (Lamme 1995). Likewise, V2 receptive fields show activation enhancement with complementary orientation in the surround as well as inhibition of activation when the surrounding area contains objects with a collinear orientation (Bakin et al 2000). Therefore, any decrease in disappearance when the mask elements are grouped according to common fate may merely reflect a decrease in surface processing load beginning in V1 and extending to V2.

6.6 Adaptation

It has also been suggested that adaptation contributes to target disappearance during MIB (Gorea and Caetta 2009). The mechanisms of target adaptation and/or prolonged inhibition by the moving mask may reduce the target's perceived brightness, such that it temporarily falls below its detection threshold, particularly in the presence of a mask that is moving (and thus not adapting to the same degree as the target). This adaptation/ inhibition process is thus hypothesized to produce transient perceptual disappearance (Caetta et al 2007; Gorea and Caetta 2009). Such an account is supported by the observation that MIB increases during the early stages of a trial, prior to reaching asymptote (Gorea and Caetta 2009). Our data may offer a novel contribution to this idea, as the time-course of MIB could vary as a function of coherence.

To this end, we combined the results from experiments 1a and 1b, dividing the data into bins as described in Gorea and Caetta (2009). Note that each bin in the present analysis encompassed 5 s epochs spanning the 30 s trial, as compared to 10 s epochs across a 60 s trial in Gorea and Caetta (2009).

Results are consistent with the interpretation that differential adaptation across coherence levels could underlie disappearance (figure 8). We performed a 4 (coherence) by 6 (bin) two-way repeated-measures ANOVA and found a significant main effect for coherence ($F_{2.33, 88.60} = 31.54$, p < 0.001, $\eta_p^2 = 0.45$), as our earlier analyses on these data revealed. More relevant to the current analysis, a significant main effect for bin was observed ($F_{3.24, 122.98} = 25.32$, p < 0.001, $\eta_p^2 = 0.40$). These findings are consistent with the basic adaptation effect of Gorea and Caetta (2009). Moreover, the interaction was also statistically significant ($F_{9.13, 346.92} = 3.77$, p < 0.001, $\eta_p^2 = 0.10$). Specifically, in the 0% coherence condition, the mean length of an MIB episode increased by

0% 33% 66% 1.2 **-**↓ 100% 0.8 0.4 1 2 3 5 4 6

Figure 8. Average length of an MIB episode in each 5 s bin within a 30 s trial. Data are averaged across experiments 1a and 1b. Error bars are ± 1 SEM.

35.75% between bins 1 and 4 and increased by only 4.20% between bins 5 and 6. The difference was less pronounced with the 100% coherent mask. Here, the initial increase for the beginning 20 s of the trial was 8.25% with a final increase of 4.04% between bins 5 and 6. Planned contrasts between the 0% and the 100% masks revealed a significant difference in the change in MIB for the initial 20 s of the trial ($t_{38} = 5.20$, p < 0.001). The change in mean duration of MIB episodes between bins 5 and 6 was not significantly different between the two types of masks ($t_{38} = 0.82$, p = 0.42).

The results described above reveal a novel pattern: adaptation effects increase dramatically as mask coherence is reduced. This pattern provides a plausible mechanism for why MIB varies with motion coherence. The explanation is two-fold, based on adaptation to the target coupled with inhibition by the mask, as put forth by Gorea and Caetta (2009). First, the adaptation to the stationary target could create a situation where the target dips temporarily below threshold reducing its visibility. Second, the simultaneous adaptation to a coherent mask reduces its inhibitory role on the target. However, an incoherent mask is subject to less adaptation, allowing it to continuously exert strong inhibition on the target throughout the duration of the trial. Future work will be able to more directly test this promising account of motion coherence and MIB.

7 Conclusion

In summary, we found that decreasing the motion coherence of the moving elements in the MIB mask significantly increased disappearance of the stationary target. We suggest that the result is consistent with a mechanism of adaptation of the target and differential inhibition by the coherence level of the mask. This result promises to inform mechanistic theories of MIB, and it also carries a practical recommendation: utilizing a mask composed of non-coherent moving dots enhances disappearance and will help reveal subtle effects of the local interactions of the mask on target disappearance that may not be discernible using a homogeneous mask.

References

- Bakin J S, Nakayama K, Gilbert C D, 2000 "Visual responses in monkey areas V1 and V2 to three-dimensional surface configurations" Journal of Neuroscience 20 8188-8198
- Bonneh Y S, Cooperman A, Sagi D, 2001 "Motion induced blindness in normal observers" Nature 411 798-801
- Braddick O J, O'Brien J M D, Wattam-Bell J, Atkinson J, Hartley T, Turner R, 2001 "Brain areas sensitive to coherent visual motion" Perception 30 61-72
- Brainard D H, 1997 "The Psychophysics Toolbox" Spatial Vision 10 433-436
- Caetta F, Gorea A, Bonneh Y, 2007 "Sensory and decisional factors in motion-induced blindness" Journal of Vision 7 1 - 12
- Carter O L, Pettigrew J D, 2003 "A common oscillator for perceptual rivalries?" Perception 32 295 - 305



- Ehrenstein W H, Spillmann L, Sarris V, 2003 "Gestalt issues in modern neuroscience" Axiomathes 13 433-458
- Donner T H, Sagi D, Bonneh Y S, Heeger D J, 2008 "Opposite neural signatures of motioninduced blindness in human dorsal and ventral visual cortex" *Journal of Neuroscience* 28 10298-10310
- Geisler W S, 1999 "Motion streaks provide a spatial code for motion direction" Nature 400 65-69
- Gorea A, Caetta F, 2009 "Adaptation and prolonged inhibition as a main cause of motioninduced blindness" *Journal of Vision* **9** 1–17
- Graf E W, Adams W J, Lages M, 2002 "Modulating motion-induced blindness with depth ordering and surface completion" Vision Research 42 2731-2735
- Hsu L C, Yeh S L, Kramer P, 2004 "Linking motion-induced blindness to perceptual filling-in" Vision Research 44 2857-2866
- Kawabe T, Miura K, 2007 "Subjective disappearance of a target by flickering flankers" Vision Research 47 913–918
- Kleinschmidt A, Büchel C, Zeki S, Frackowiak J, 1998 "Human brain activity during spontaneously reversing perception of ambiguous figures" *Proceedings of the Royal Society, Series B* 265 2427-2433
- Koyama S, Sasaki Y, Andersen G J, Tootell R B H, Matsuura M, Watanabe T, 2005 "Separate processing of different global-motion structures in visual cortex is revealed by fMRI" Current Biology 15 2027–2032
- Lages M, Adams W J, Graf E W, 2009 "Motion-aftereffect-induced blindness" *Journal of Vision* 9 1–7
- Lamme V F, 1995 "The neurophysiology of figure-ground segregation in primary visual cortex" Journal of Neuroscience 15 1605-1615
- Lee S H, Blake R, 2002 "V1 activity is reduced in binocular rivalry" Journal of Vision 2 618-626
- Leopold D A, Wilke M, Maier A, Logothetis N K, 2002 "Stable perception of visually ambiguous patterns" *Nature Neuroscience* 5 605-609
- Libedinsky C, Savage T, Livingstone M, 2009 "Perceptual and physiological evidence for a role for early visual areas in motion-induced blindness" *Journal of Vision* **9** 1-10
- Liu T, Slotnick S D, Yantis S, 2004 "Human MT+ mediates perceptual filling-in during apparent motion" *NeuroImage* **21** 1772-1780
- McKeefry D J, Watson J D G, Frackowiak R S J, Fong K, Zeki S, 1997 "The activity in human areas V1/V2, V3, and V5 during the perception of coherent and incoherent motion" *NeuroImage* **5** 1–12
- Mather G, Moulden B, 1980 "A simultaneous shift in apparent direction—further evidence for a distribution-shift model of direction coding" *Quarterly Journal of Experimental Psychology* 32 325-333
- New J J, Scholl B J, 2008 "Perceptual scotomas: A functional account of motion-induced blindness" *Psychological Science* **19** 653-659
- Pelli D G, 1997 "The VideoToolbox software for visual psychophysics: Transforming numbers into movies" *Spatial Vision* **10** 437–442
- Ramachandran V S, Gregory R L, 1991 "Perceptual filling in of artificially induced scotomas in human vision" *Nature* **350** 699–702
- Rees G, Friston K, Koch C, 2000 "A direct quantitative relationship between the functional properties of human and macaque V5" *Nature Neuroscience* **3** 716–723
- Ross J, Badcock D R, Hayes A, 2000 "Coherent global motion in the absence of coherent velocity signals" Current Biology 10 679-682
- Rust N C, Mante V, Simoncelli E P, Movshon J A, 2006 "How MT cells analyze the motion of visual patterns" *Nature Neuroscience* **9** 1421 1431
- Schölvinck M L, Rees G, 2010 "Neural correlates of motion-induced blindness in the human brain" Journal of Cognitive Neuroscience 10 1–9
- Shibata M, Kawachi Y, Gyoba J, 2007 "Combined effects of perceptual-grouping cues on object representations revealed by motion-induced blindness" *Perception* **36** Supplement, 103
- Silver M A, Logothetis N K, 2004 "Grouping and segmentation in binocular rivalry" Vision Research 44 1675-1692
- Spillmann L, Kurtenbach A, 1992 "Dynamic noise backgrounds facilitate target fading" Vision Research **32** 1941–1946
- Wallis T S A, Arnold D H, 2008 "Motion-induced blindness is not tuned to retinal speed" Journal of Vision 8 1-7
- Wallis T S Å, Arnold D H, 2009 "Motion-induced blindness and motion streak suppression" Current Biology 19 325-329

Watamaniuk S N J, Sekuler R, Williams D W, 1989 "Direction perception in complex dynamic displays—The integration of direction information" Vision Research 29 47-59

Welchman A E, Harris J M, 2000 "The effects of dot density and motion coherence on perceptual fading of a target in noise" *Spatial Vision* **14** 45-58

Williams D W, Sekuler R, 1984 "Coherent global motion percepts from stochastic local motions" Vision Research 24 55-62

1518

ISSN 1468-4233 (electronic)



www.perceptionweb.com

Conditions of use. This article may be downloaded from the Perception website for personal research by members of subscribing organisations. Authors are entitled to distribute their own article (in printed form or by e-mail) to up to 50 people. This PDF may not be placed on any website (or other online distribution system) without permission of the publisher.