Motion-aftereffect-induced blindness

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Motion-induced blindness (MIB) describes the occasional disappearance of salient visual objects in the presence of moving features (Y. S. Bonneh, A. Cooperman, & D. Sagi, 2001). Here we test whether motion adaptation and the ensuing motion aftereffect (MAE) are sufficient to trigger disappearance of salient targets. In three experiments, observers adapted to either rotating or static stimuli. Immediately afterwards, a static test pattern was presented consisting of a mask with texture elements and three superimposed target dots in a triangular arrangement. Observers reported dot disappearance and reappearance. The results clearly show that illusory motion in a static test pattern, following motion adaptation, promotes the disappearance of target dots. Furthermore, disappearance is modulated by the depth relationship between test pattern and targets, increasing for targets placed stereoscopically behind the test pattern. We conclude that MIB is influenced by perceived relative motion between depth-segregated features.

Keywords: motion aftereffect, motion-induced blindness, surface completion, depth ordering, visual illusions

Introduction

Motion-induced blindness (MIB) is an arresting phenomenon in which salient visual stimuli disappear perceptually for up to several seconds at a time in the presence of a moving pattern (Bonneh, Cooperman, & Sagi, 2001). Explanations for MIB have included competition for attention (Bonneh et al., 2001), inter-hemispheric rivalry similar to binocular rivalry (Carter & Pettigrew, 2003; Funk & Pettigrew, 2003), perceptual filling-in (Hsu, Yeh, & Kramer, 2004, 2006), and motion-streak suppression (Wallis & Arnold, 2009). Previously, we demonstrated a role for surface competition, supported by the depth-contingent modulation of MIB disappearance (Graf, Adams, & Lages, 2002). In two experiments we found that disappearance was modulated by the depth relationship of the target and the moving pattern. In particular, when target dots were presented stereoscopically behind the moving pattern, disappearance increased relative to dots presented in front. In the present study, we revisit the surface interaction hypothesis and investigate the underlying mechanism of MIB, by asking whether illusory relative motion is sufficient to initiate target disappearances.

A motion aftereffect (MAE) occurs after prolonged viewing of coherent motion such as a waterfall. Subsequent fixation of a static pattern, such as rocks next to the waterfall, results in illusory perceived motion in the opposite direction (Addams, 1834; Purkinje, 1820; Wade & Verstraten, 1998; Wohlgemuth, 1911). The MAE cannot be completely accounted for by the fatigue of low-level pre-attentive motion detectors (Barlow & Hill, 1963) and is of at least cortical origin as demonstrated by substantial MAE transfer across the eyes (Steiner, Blake, & Rose, 1994; Wade, Swanston, & de Weert, 1993), even if the adapted eye is pressure-blinded to remove any retinal contribution (Barlow & Brindley, 1963). The precise stage or stages at which the motion aftereffect occurs, however, are difficult to determine, as the MAE depends critically on the characteristics of both adaptation and test pattern (Fang & He, 2004; Grunewald & Lankheet, 1996; Hiris & Blake, 1992; Nishida & Sato, 1995; Verstraten, Fredericksen, Grüsser, & van de Grind, 1994) and can be influenced by higher-level processes, such as attention (Chaudhuri, 1990; Culham, Verstraten, Ashida, & Cavanagh, 2000; Huk, Ress, & Heeger, 2001; Lankheet & Verstraten, 1995).

A binocular component of motion processing has been demonstrated by the existence of depth-contingent aftereffects between moving patterns and static test patterns (Anstis, 1974; Nawrot & Blake, 1989; Regan & Beverley, 1973; Sohn & Seiffert, 2006), with MAEs maximized when adaptor and test are presented at the same depth (Verstraten, Verlinde, Fredericksen, & van de Grind, 1994). We exploit this depth-contingent relationship to

explore the mechanisms of MIB. In the present study, we investigate target disappearance after prolonged adaptation to a moving pattern presented at the same or different depths. If a depth-contingent MAE systematically affects perception of salient target dots then this would indicate that not only stimulus motion but also illusory relative motion modulates visual awareness.

General methods

Apparatus

Computer-generated stimuli were presented stereoscopically in a split-screen Wheatstone configuration via haploscopic mirrors at a viewing distance of 114 cm and a frame-rate of 120 Hz. A chin and forehead rest stabilized observers' viewing position during stimulus display.

Observers

Six observers participated in the first experiment and eight observers in the second and third experiment. All observers had normal or corrected-to normal visual acuity, and none reported difficulties with binocular vision.

Observers were one of the authors (M.L.) and students of Glasgow University who received course credits for their participation. Students were naïve as to the aims of the experiments. The study was approved by the ethics committee at the University of Glasgow. All observers gave informed written consent.

Stimuli

Adaptation and test stimuli each subtended approximately 5.5 deg visual angle. Figure 1 depicts stimuli used in this study. Different adaptation stimuli were used in each experiment: In Experiment 1, it was a 7×7 matrix of blue crosses. In Experiment 2, the adaptation stimulus was a rotating sectored disc (Aitken, 1878) with 16 sectors alternating between black and white and in Experiment 3 we used a linear spiral with four alternating black and white segments (Thompson, 1880). The latter adaptation stimuli were presented at a mean luminance of 15 cd/m^2 whereas the blue crosses against the black background were shown at 1.8 cd/m^2 (adaptation and test). In randomly intermixed trials, the adaptation stimulus rotated clockwise (cw) or counter-clockwise (ccw) at 90°/s (0.75° per frame) or remained static.

The test stimulus included a mask surface, three target dots, and a white central fixation cross flanked by nonius lines. The mask consisted of a matrix of 48 blue crosses
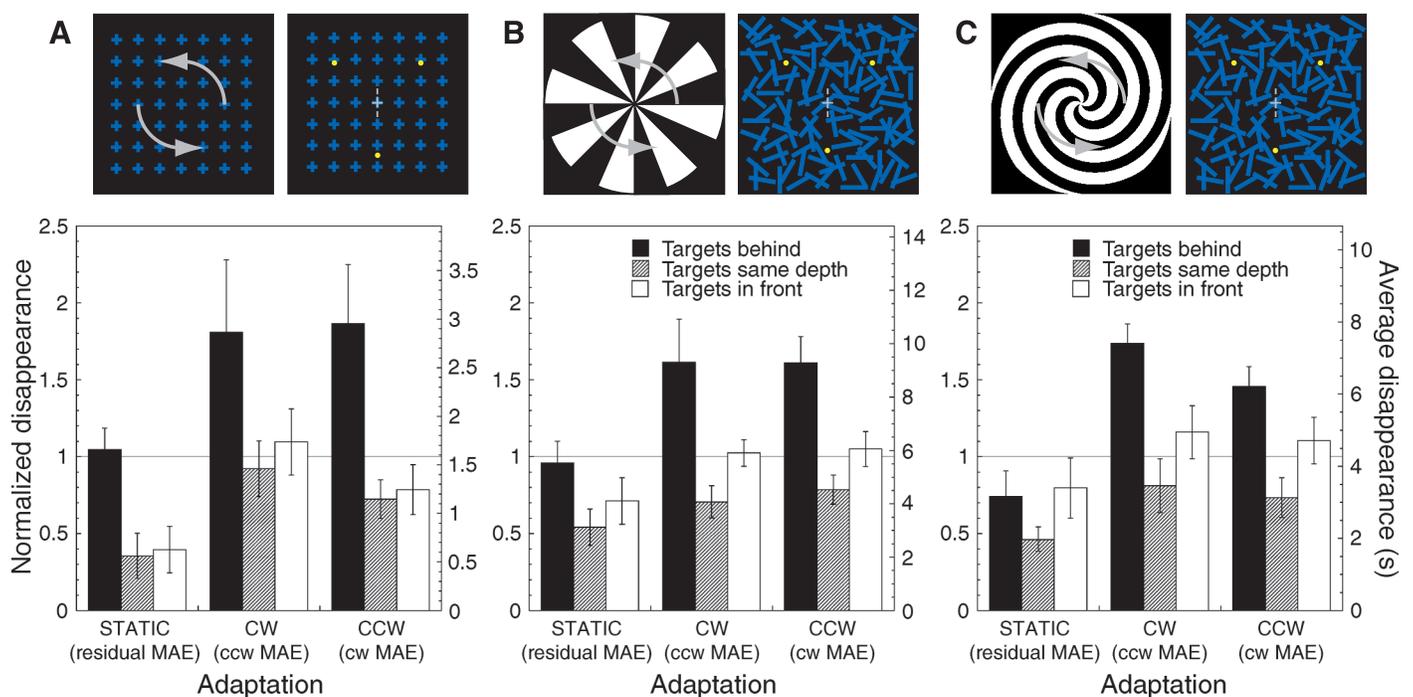

Figure 1. Adaptation and test stimuli are illustrated above the results for Experiments 1–3 in columns A, B, and C. Bar plots show normalized disappearance of target dots averaged across observers and trials for three adaptation conditions (static, clockwise, counter-clockwise) and three target depths (behind, same, in front). Error bars denote ±1 standard error. The horizontal line indicates average disappearance (in seconds) across conditions and observers.

(9 cd/m^2) in Experiment 1 and 110 randomly positioned and oriented blue bars (each 6 × 44 pixels) in Experiments 2 and 3, all on a black background. In all three experiments, the yellow target dots (22 cd/m^2) were placed in a triangular arrangement on an imaginary circle with radius 1.25 deg centered on the fixation cross. In three depth conditions, anti-aliased target dots were positioned behind, at the same depth as or in front of the mask and fixation cross but the mask never occluded the target dots.

Procedure

An experimental session consisted of three blocks of 18 trials each. There were three adaptation conditions and three depth conditions; all nine combinations were repeated twice per block with trials presented in randomized order.

During each trial, the observer fixated the center of a clockwise rotating, counter-clockwise rotating or static adaptation stimulus for 30 s. Immediately after this adaptation phase, the observer viewed the test pattern, also for 30 s. The observer indicated target disappearance by pressing and holding any combination of three keys (one per target dot) and releasing the key when the target dot reappeared.

Results

Experiment 1. Matrix of crosses

Total target disappearance (summed over the three targets) varied considerably across observers and experimental conditions. The smallest amount of disappearance, averaged across observers, was found in the static condition with targets at the same depth (0.8 s per trial with 30-s test phase). Disappearance increased to an average of 1.7 s per trial in MAE conditions where the targets were presented in front of fixation (−3 cm/ −5.3 arcmin) and 2.4 s per trial in MAE conditions with targets presented behind fixation (+3 cm/+5.0 arcmin). As a rough comparison with these data and for the following experiments, Graf et al. (2002) found an average target disappearance for continuous *apparent* motion of 4.8 s per 30 s trial for targets in front and 13 s per trial for targets presented behind. We note, however, that it is difficult to compare the MAE directly to an apparent motion stimulus (Castet, Keeble, & Verstraten, 2002; Hiris & Blake, 1992) due in part to a gradual decrease in the MAE strength over the 30-s testing phase. As such, it is the pattern of disappearance across the conditions that is most meaningful.

To enable meaningful comparisons across conditions and observers, target disappearance was analyzed in terms of normalized disappearance for each observer. The durations of all key presses for one observer were accumulated during the testing phase of each trial, averaged over the six repetitions of the same condition and then expressed as normalized disappearance across all conditions. These data are shown in Figure 1A together with average disappearance.

Normalized disappearance varied significantly across adaptation conditions (static, cw, and ccw) as confirmed by a two-factor ANOVA ($F(2,10) = 8.52$, $p = 0.007$, effect size expressed as partial $\eta^2 = 0.63$). Significantly more disappearance occurred in the two motion conditions than in the static condition (13.4% across cw and ccw vs. 6.7% for the static adaptor; $t(5) = 3.77$, $p < 0.05$, within-subjects contrast). Target depth influenced disappearance in the expected manner, with the largest amount of disappearance found when targets were stereoscopically presented behind the mask (17.5%) and less disappearance when targets were presented in front (8.4%) or at same depth as the mask (7.4%). This main effect of depth approached statistical significance after a conservative adjustment for heterogeneity ($F(2,10) = 3.55$, $p = 0.068$ Huynh–Feldt, partial $\eta^2 = 0.42$). No significant interaction between adaptation stimulus and target depth was observed ($F(4,20) < 1$).

Target disappearance was also analyzed in terms of two additional components (Graf et al., 2002): (a) the frequency of disappearances per trial and (b) the duration of each disappearance. Separate two-factor ANOVAs on normalized frequency of disappearances and normalized average duration of disappearance gave broadly the same results as our initial analysis: For average frequency, both main effects were significant (Adaptation: $F(2,10) = 7.56$, $p = 0.01$, partial $\eta^2 = 0.60$; Target Depth: $F(2,10) = 4.53$ $p = 0.04$, partial $\eta^2 = 0.48$). Average duration also showed a main effect of Adaptation ($F(2,10) = 5.51$ $p = 0.024$, partial $\eta^2 = 0.52$), whereas Target Depth approached significance ($F(2,10) = 3.55$, $p = 0.068$, partial $\eta^2 = 0.42$).

In summary, Experiment 1 suggests that illusory motion elicited by the motion aftereffect is sufficient to trigger disappearance in an MIB display. Informal reports from our naïve observers indicated that some experienced and interpreted the MAE as actual motion in the test pattern rather than illusory motion. Disappearance was also modulated by the relative disparity between target dots and test pattern according to the occlusion relation previously reported by Graf et al. (2002), with maximum disappearance when the target was presented stereoscopically behind the mask (although never physically occluded by it). Disappearance was minimized when the target dots were presented at the same depth as the adaptor and test patterns; depth-contingent MAEs affected the perceived motion of the targets and mask equally in this configuration, thus minimizing the perceived relative

motion between targets and mask. Disappearance is thus well predicted by perceived relative motion in combination with surface completion/occlusion mechanisms.

Experiment 2. Sectored disc

In the second experiment, we strengthened the MAE by using a disc with alternating black and white segments as a high contrast adaptation stimulus. In addition, the test pattern now consisted of blue bars with random orientations in order to create a more richly textured surface and thus a more robust MAE. Finally, we increased the displacement of targets in depth to ±4 cm from fixation (−7.1 and +6.6 arcmin) to facilitate segregation between surface and targets.

Stronger MAEs with the new stimuli, and the increased depth separation, resulted in increased target disappearance overall, relative to Experiment 1. In Experiment 2, the condition with least disappearance (static adaptor, same depth targets) produced an average of 3.6 s per trial. As before, disappearance was also maximized with moving adaptors and targets presented behind the mask; with the new stimuli, this disappearance was increased to 7.4 and 8.2 s per trial (for the cw and ccw motion, respectively).

As in Experiment 1, analyses were performed on accumulated disappearance, normalized for each observer (see Figure 1B). There was a significant main effect of Adaptation (static, cw, and ccw) on disappearance ($F(2,14) = 4.89$, $p = 0.025$, partial $\eta^2 = 0.41$; two-factor ANOVA). As before, moving adaptors (cw and ccw) produced significantly more disappearance than static adaptors (12.6% vs. 8.2%; $t(7) = 2.39$, $p < 0.05$, within-subject contrast). The main effect of Target Depth (−4, 0, and +4 cm) was also significant ($F(2,14) = 8.22$, $p = 0.018$ adjusted for heterogeneity, partial $\eta^2 = 0.54$). Presenting targets in the same depth plane as the mask produced significantly less disappearance (7.5%) than presenting targets either in front of or behind the mask (10.3% and 15.5%, respectively) as demonstrated by pairwise comparisons corrected for multiple testing. No significant interaction between Adaptation and Target Depth was observed ($F(4,28) = 1.67$, $p = 0.184$).

Interestingly, the difference in disappearance across adaptation conditions was driven mainly by changes in disappearance duration ($F(2,14) = 5.37$ $p = 0.038$ adjusted for heterogeneity, partial $\eta^2 = 0.43$). In contrast, the effect of target depth on disappearance was mainly due to changes in disappearance frequency ($F(2,14) = 6.66$, $p = 0.029$, adjusted for heterogeneity, partial $\eta^2 = 0.49$). No other significant effects were found in either analysis.

Experiment 3. Segmented spiral

Adaptation to a rotating black and white spiral at high contrast elicits a strong MAE with both rotational and

either expanding or contracting components (Wohlgemuth, 1911). The expanding MAE is known to be stronger than the contracting MAE (Scott, Lavender, McWhirt, & Powell, 1966). Accordingly, we might expect that in addition to the relative depth effects observed in Experiments 1 and 2, the expanding MAE resulting from clockwise motion adaptation will elicit more disappearances than the contracting MAE resulting from the counter-clockwise motion.

Averaging across observers (see Figure 1C), we found the lowest amount of total disappearance in the static condition with targets at the same depth (1.9/30 s) and the largest amount of total disappearance in the motion adaptation conditions with targets behind (cw 7.9 s and ccw 6.2/30 s).

As in Experiments 1 and 2, we analyzed normalized disappearance as a function of Adaptation condition and Target Depth in a two-factor ANOVA. We found a significant main effect of Adaptation ($F(2,14) = 7.38$, $p = 0.018$ adjusted for heterogeneity, partial $\eta^2 = 0.51$). This main effect was explored with pairwise comparisons (Sidak–Bonferroni). As predicted, adapting to clockwise motion (expanding MAE) produced more disappearance (13.7%) than adapting to counter-clockwise motion (contracting MAE, 12.2% disappearance), but this effect was not significant. Of the two motion conditions, only the cw motion condition produced significantly more disappearance than the static adaptation condition (7.4% disappearance). As in the previous experiment, there was a main effect of Target Depth ($F(2,14) = 8.11$, $p = 0.005$, partial $\eta^2 = 0.54$), with a significant difference between the "behind" and "same depth" conditions. There was no significant interaction between Adaptation and Target Depth ($F(4,28) = 2.36$, $p = 0.078$).

Separate analyses on the frequency and durations of disappearances as a function of Adaptation condition and Target Depth mirrored the pattern in Experiments 1 and 2: The effect of Adaptation on disappearance was driven more by changes in duration ($F(2,14) = 8.76$, $p = 0.003$, partial $\eta^2 = 0.56$) whereas the changes in disappearance across Target Depth were driven predominantly by frequency ($F(2,14) = 9.51$, $p = 0.002$, partial $\eta^2 = 0.58$). No other significant effects were found in either analysis.

Discussion

Using a range of stimuli, we have demonstrated that illusory motion, and in particular illusory *relative* motion, following motion adaptation, increases disappearance of salient targets. This is evidenced by greater disappearance after prolonged viewing of a moving rather than a static adaptor, particularly when the dot targets are displaced in depth from the mask. In this depth-segregated configuration, the MAE differentially affects the targets and mask,

creating perceived relative motion between the targets and a completed surface (although no motion, absolute or relative, is present in the test display). In contrast, when the target dots, adaptation, and mask are all placed in the same depth plane, the MAE affects both the dot targets and mask equally. In these instances, the targets and mask will be grouped into a single moving surface, thus substantially reducing disappearance.

In previous work, we have shown that motion-induced blindness is systematically modulated by the depth ordering of the target dots and rotating mask even when the mask consists of an illusory surface, implicating surface completion and occlusion mechanisms in MIB (Graf et al., 2002). In the present study, we have demonstrated a similar depth ordering effect with the *illusory motion* of a surface. With the illusory motion of the test surface, targets presented stereoscopically behind the mask disappear substantially more than targets in front (19% vs. 11% disappearance averaged across experiments). Together, these results support the notion that disappearance in MIB is, at least in part, mediated by principles of grouping and occlusion that dictate the interaction between depth-segregated features.

Surface completion mechanisms (Bakin, Nakayama, & Gilbert, 2000; Grossberg & Mignolla, 1985; Nakayama, 1996; Nakayama, He, & Shimojo, 1998; Nakayama & Shimojo, 1992) are critical for the successful interpretation of our three-dimensional environment. In the MIB display, motion stimuli typically involve feature arrays (e.g., crosses, lines, or dots) that move more or less coherently on a black background. Target suppression may help to resolve the spatial conflict between a perceptually completed surface and stationary targets so that the perceptual interpretation of the scene remains meaningful, particularly when the target is positioned in depth behind a moving surface. Such a description of MIB is consistent with recent evidence from fMRI. Using a very similar stimulus as in our Experiment 1, Schölvinck and Rees (2009) found that target disappearance was accompanied by *increases* in activation in retinotopic regions of V1 and V2 corresponding to target location. Such activity may reflect an active filling-in/surface completion process, similar to that suggested by single unit recordings during contour completion, also in V1 and V2 (Lee & Nguyen, 2001). In contrast, Donner, Sagi, Bonneh, and Heeger (2008) reported disappearance-related *decreases* in ventral visual areas V1 and V2 and an opposite response in dorsal visual areas V5/MT. They used masks comprised of a moving sphere of dots rather than a structured array of regular "surface texture." As indicated by Schölvinck and Rees (2009), such a stimulus may be less likely to create a stable surface representation, which might be more important for early areas. Interestingly, both studies report more general activation, correlated with disappearances, in V5/MT, which may feedback to earlier visual regions. Although depth relationships were not tested in either study, the activation in V5/MT complements our finding that depth-contingent motion aftereffects modulate target disappearance. It is known that V5/MT responds to the MAE (Tootell et al., 1995) and is sensitive to both motion and binocular depth (Bradley, Qian, & Andersen, 1995; DeAngelis & Newsome, 2004).

Conclusion

In summary, we have shown that adaptation to motion can disrupt subsequent perception of salient targets in a static test pattern, and this is modulated by the depth relationship between targets and mask. This MAE-induced blindness (MAE-IB) strengthens the case that motion processing (Wallis & Arnold, 2009) in combination with surface completion (Graf et al., 2002) must have a role in any comprehensive account of motion-induced blindness.

Acknowledgments

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