Simulated forward and backward self motion, based on realistic parameters, causes strong motion induced blindness

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Abstract

Motion Induced Blindness (MIB) is a well-established visual phenomenon whereby highly salient targets disappear when viewed against a moving background mask. No research has yet explored whether contracting and expanding optic flow can also trigger target disappearance. We explored MIB using mask speeds corresponding to driving at 35, 50, 65 and 80 km/h in simulated forward (expansion) and backward (contraction) motion as well as 2-D radial movement, random, and static mask motion types. Participants (n = 18) viewed MIB targets against masks with different movement types, speed, and target locations. To understand the relationship between saccades, pupil response and perceptual disappearance, we ran two additional eye-tracking experiments (n = 19). Target disappearance increased significantly with faster mask speeds and upper visual field target presentation. Simulated optic flow and 2-D radial movement caused comparable disappearance, and all moving masks caused significantly more disappearance than a static mask. Saccades could not entirely account for differences between conditions, suggesting that self-motion optic flow does cause MIB in an artificial setting. Pupil analyses implied that MIB disappearance induced by optic flow is not subjectively salient, potentially explaining why MIB is not noticed during driving. Potential implications of MIB for driving safety and Head-Up-Display (HUD) technologies are discussed.

INTRODUCTION

Motion Induced Blindness (MIB) is a visual phenomenon whereby highly salient visual targets become temporarily invisible despite their ongoing physical presence in one's visual field, when viewed against the background of a global moving mask (Bonneh, Cooperman & Sagi, 2001). MIB is one of many bistable perceptual phenomena (Kim & Blake, 2005) used with increasing popularity to investigate the mechanisms of perceptual organisation (Dieter, Tadin & Pearson, 2015; Kloosterman, Meindertsma, Hillebrand, van Dijk, Lamme & Donner, 2015; Libedinsky, Savage & Livingstone, 2009). These bistable phenomena allow subjects to experience varying phenomenology while receiving physically constant visual input, thus, they can help delineate the neural correlates of consciousness by dissociating physical stimuli from conscious perception (Bonneh, Donner, Cooperman, Heeger & Sagi, 2013; Dieter et al, 2015; Kim & Blake, 2005).

MIB has been extensively studied under stimulus parameters designed to optimise perceptual disappearances (Bonneh et al, 2013; Chang, Kanai & Seth, 2015; Wells & Leber, 2014). While it has been suggested that MIB may happen in the real world (e.g., Bonneh, et al, 2001), no research has yet explored MIB using parameters that approximate those experienced in real world movement. To date only two predominantly anecdotal studies have explored whether MIB may occur in the real world. Shimojo (2008) used a mirror ball to create a moving mask of bright spots across a room, and was able to cause the perceptual disappearance of a live person in their interactive museum display. Another demonstration of MIB in real life was reported by Inoue, Yagi and Kikuchi (2011), where they induced MIB by superimposing a target over the optic flow of a movie, filmed from the driver's point of view while travelling in a car. Perceptual disappearance was induced much more often while travelling in forward motion compared to viewing the target over a still frame. Our own pilot studies have also informally replicated this finding. This evidence suggests that the optical flow experienced in forward self motion can induce MIB in situations where a stable image is projected to the retina over a moving background. In the current study we aimed to lay the groundwork toward establishing the critical parameters of potential MIB phenomena in much more natural situations, focussing on variations of mask speed, trajectory of mask movement and target location.

The most frequently used display for demonstrating MIB consists of three yellow targets and a blue mask of rotating crosses, originally introduced by Bonneh and colleagues (2001). Using this display, various stimulus parameters have been studied (Bonneh et al, 2001; Hsu, Yeh and Kramer, 2004; Metzger, 2009; Mitroff & Scholl, 2005; Sakaguchi, 2006; Schölvinck & Rees, 2009; Shibata, Kawachi & Gyoba, 2010), among which are the effect of target location (Geng, Song, Li, Xu & Zhu, 2007; Nuruki, Oliver, Campana, Wash & Rothwell, 2013; Rosenthal, Davies, Aimola-Davies, & Humphreys; Schölvinck & Rees, 2009; Wells, Leber & Sparrow, 2011; Wallis & Arnold, 2009), mask speed (Bonneh et al, 2001; Grindley & Townsend, 1965; Libedinsky et al, 2009), and cues of mask depth (Graf, Adam & Lages, 2002; Rosenthal et al, 2013).

In terms of target location, a number of studies have reported greater disappearance when a target is located in the upper left quadrant of the visual display, compared to other tested locations (Bonneh et al, 2001; Bonneh & Donner, 2011; Nuruki et al, 2013; Rosenthal et al, 2013; Wells & Leber, 2014; Wells et al, 2011). A more frequent disappearance of upper left targets has been replicated several times (Bonneh et al, 2001; Bonneh & Donner, 2011; Geng et al, 2007; Grindley & Townsend, 1965; Rosenthal et al, 2013). However, research finding a significant upper left bias generally uses the original three target triangular display (Bonneh et al, 2001), and finds a significant bias only in relation to the lower central target (Bonneh et al, 2001; Bonneh & Donner, 2011; Nuruki et al, 2013). There has not yet been a controlled comparison of targets presented in all four quadrants of the screen to determine the effects of visual quadrant on disappearance, despite evidence suggesting that upper visual field may exhibit an effect over target disappearance. The trend regarding target location is important to consider when exploring MIB due to its potential relationship with the neural mechanisms of attention (Dieter et al., 2015; Geng et al., 2007). Indeed, Bonneh and colleagues (2001) interpreted the top-left bias as the result of processing the global mask at the expense of the local target, mediated by the right-hemisphere dominance of visuospatial attention.

It has previously been shown that mask speed influences MIB, with increased speeds leading to both an increased rate and duration of target disappearance (Bonneh et al., 2013; Libidensky et al., 2009). While it has been suggested that it is the temporal frequency rather than retinal speed of the mask underlying MIB (Wallis & Arnold, 2008), trajectory of motion has shown to be equally influential (Wallis & Arnold, 2009). As yet, no study has explored variations in the speed of masks that contract or expand in a way that occurs during self-motion.

Several studies have investigated the effects of other variations in mask composition and movement. In particular, Rosenthal and colleagues (2013) used a three dimensional (3-D) moving mask that mimicked the experience of real world movement and found that significantly more disappearances occurred when masks were perceived to be convex compared to concave, an effect restricted to targets presented in the left field of vision. This and related findings regarding depth ordered masks (Graf et al, 2002), suggests that the 3-D interpretation of the visual scene experienced during self-motion is likely to influence MIB, prompting a need for further research on how optic flow (with its implicit depth cues) may influence target disappearances.

We aim therefore to explore whether mask properties modelled on the real world are conducive to MIB, focussing on mask speeds that would typically occur in a driving situation, and the expanding and contracting optic flow experienced in (simulated) forward and backward self-motion. We also aim to explore the effect of target location on disappearance, to investigate the previously identified upper left bias for disappearance and to test the hypothesis that MIB is mediated by the right-hemisphere dominant attentional mechanism.

Finally, while it is possible that MIB might be occurring in real-life settings, it has not yet been reported. A reason for this may be that the saliency of MIB phenomenon is so low that we do not notice it in everyday life - and we cannot be aware of what is not consciously perceived. To estimate the saliency of MIB, phasic pupillary responses have recently been investigated during MIB events (Kloosterman, Meindertsma, van Loon, Lamme, Bonneh, & Donner, 2015). It was found that MIB produced larger pupillary responses than target re-appearance, suggesting disappearance is a more ‘subjectively salient’ and surprising event to the brain (Kloosterman, Meindertsma, van Loon et al, 2015; Naber, Frässle, Rutishauser & Einhäuser, 2013; Nassar, Rumsey, Wilson, Parikh, Heasly & Gold, 2012; Preuschoff, t'Hart & Einhäuser, 2011) . Previous research however, has not manipulated mask type to examine if such an interpretation of pupillary response as a proxy of subjective saliency holds across different stimulus conditions. Therefore we will also investigate the saliency of target disappearance and reappearance in our stimuli, measured by phasic pupil response, as well as the overall saliency of the different movement patterns by looking at 'tonic' (i.e., average) pupil dilation for each mask condition.

RESULTS

MIB can be induced by the optic flow of simulated forward and backward self-motion

We investigated the duration of MIB disappearance with optic flow patterns in two sets of non-overlapping subjects (Experiment 1: n = 18; Experiment 2: n = 19, see Method) comparing masks simulating forward (expansion) and backward (contraction) self motion with a static stimulus (see Figure 1 and Supplementary Video S1 for experimental display). The design of Experiments 1 and 2 were identical in all aspects, with the exception of the use of an eye-tracking device in Experiment 2 to monitor eye movements (as well as a small variation in viewing distance).

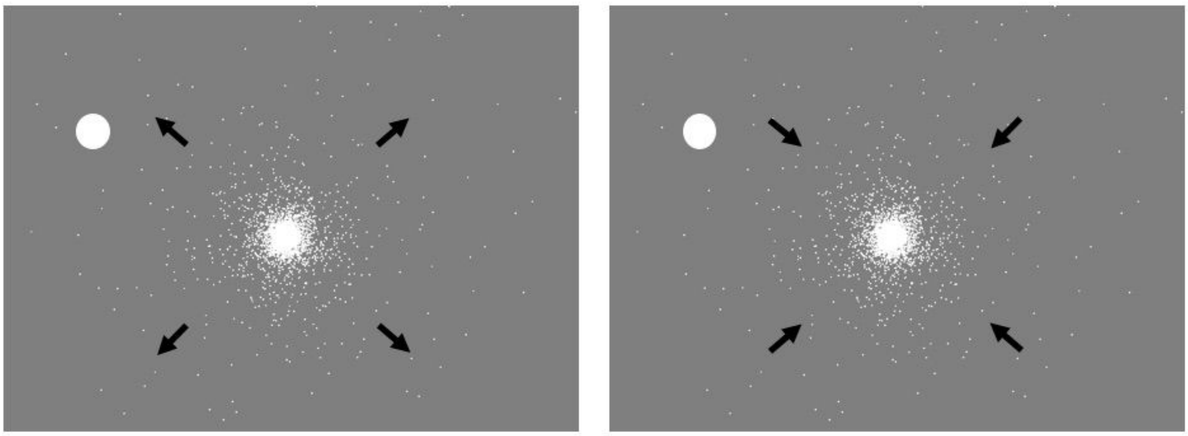

Figure 1. Experimental display for Experiments 1, 2 and 3. Black arrows depict expanding motion shown on the left, and contracting motion shown on the right.

In Experiment 1, repeated measures ANOVAs found a significant main effect of mask type on mean duration and mean rate of target disappearance (see Table 1). Experiment 2 replicated this finding for both mean duration and mean rate of target disappearance (Table 1). As the distribution of perceptual disappearances have been shown to follow a non-normal gamma distribution (e.g. Kloosterman, Miendertsma, van Loon et al., 2015), we also analysed the effect of mask type on the median duration and rate of target disappearance, for which similar results were obtained (see Table 1).

Table 1

Repeated Measures ANOVA Results for Experiments 1-4, Using Mean VS Median

Experiment & Analysis	Mean	Median
Exp 1: Duration	$F(2, 32) = 21.02, p < .001$	$F(2, 32) = 14.79, p < .001$
Exp 1: Rate	$F(2, 32) = 18.47, p < .001$	$F(2, 32) = 11.60, p < .001$
Exp 2: Duration	$F(2, 36) = 39.94, p < .001$	$F(2,36) = 30.78, p < .001$
Exp 2: Rate	$F(2, 36) = 54.04, p < .001$	$F(2,36) = 32.08, p < .001$
Exp 3: Duration	$F(3, 51) = 5.97, p = .001$	$F(3, 51) = 4.40, p = .008$
Exp 3: Rate	$F(3, 51) = 4.57, p = .007$	$F(3, 51) = 3.73, p = .017$
Exp 4: Duration	$F(3, 54) = 18.23, p < .001$	$F(2.0606, 37.0906) = 16.64, p < .001$ (GG)
Exp 4: Rate	$F(3, 54) = 15.51, p < .001$	$F(2.0319,36,574) = 11.60, p < .001$ (GG)

Note: GG indicates Greenhouse-Geisser correction of degrees of freedom due to violated Sphericity

Post-hoc paired-samples t-tests for Experiment 1 (Figure 2; using Bonferroni-corrected p-values) revealed that mean target disappearance in the static control condition was significantly shorter than during both expansion ($t(16) = 5.08$, $p < .001$, $r = .79$) and contraction ($t(16) = 5.40$, $p < .001$, $r = .80$). Mean rate of target disappearance was also significantly lower than during both expansion ($t(16) = 4.48$, $p = .001$, $r = .75$) and contraction ($t(16) = 5.36$, $p < .001$, $r = .80$). Post-hoc paired-samples t-tests for Experiment 2 (Figure 2; using Bonferroni-corrected p-values) also found mean target disappearance in static mask conditions to be significantly shorter than during both expansion ($t(18) = 6.60$, $p < .001$, $r = .84$), and contraction ($t(18) = 7.50$, $p < .001$, $r = .87$). Mean rate of target disappearance during a static condition was also significantly lower than during both expansion ($t(18) = 7.31$, $p < .001$, $r = .87$) and contraction ($t(18) = 9.60$, $p < .001$, $r = .91$). Mean duration of target disappearance for expansion and contraction were not significantly different from each other in Experiment 1 ($p = .95$) and Experiment 2 ($p = .41$). Likewise, mean rate of disappearance for expansion and contraction were not significantly different from each other in Experiment 1 and Experiment 2 ($p = 1.00$).

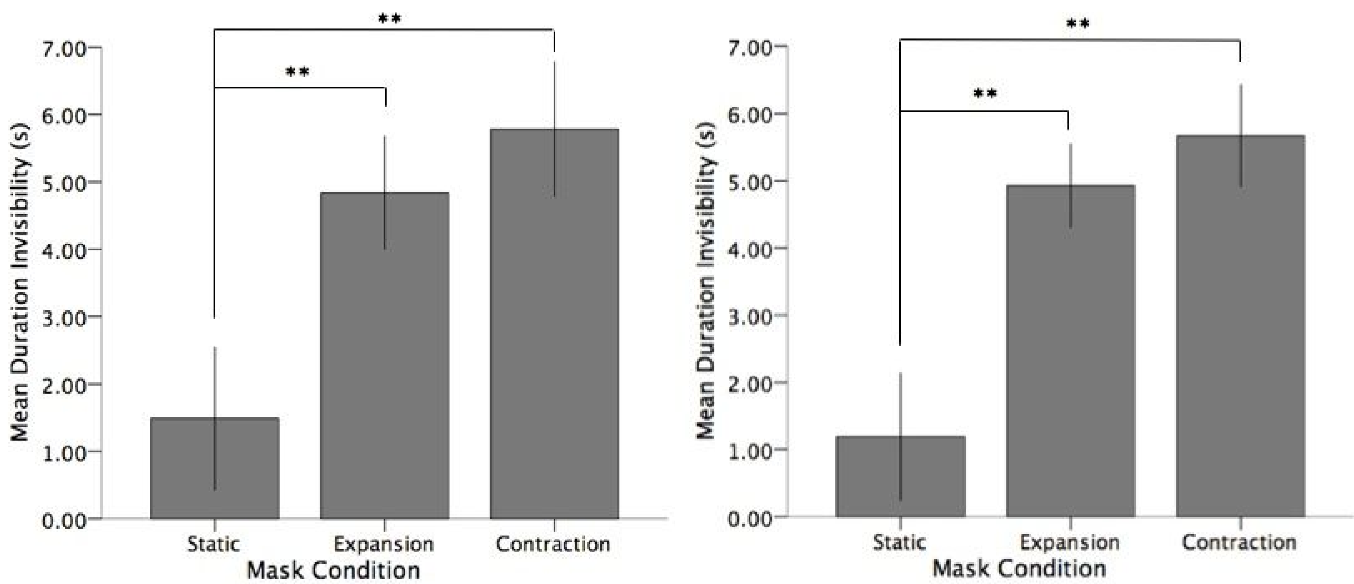

Figure 2. Mean duration of target disappearance dependent on movement type within Experiment 1 (left panel) and Experiment 2 (right panel)

The influence of saccades and target location

We recorded eye movements with an offline velocity-based saccade detection algorithm (Engbert & Kliegl, 2003) in Experiment 2 and 4, to ensure participants were fixating as instructed, as we expected that saccades towards the target would reduce MIB. The direct eye tracking also allowed us to quantify whether our results were attributable to eye movements. This is important because it is, for example, possible that the static condition induces more saccades, which then inhibit perceptual disappearances. Our analysis focussed on macro-saccades, because larger saccades have a stronger influence over the visual input, and may be most relevant in driving situations. However, we also confirmed that our results were not due to our imposed cut-off of 1° for macro-saccades, by also analysing all saccades (micro-saccades + macro-saccades). Using linear mixed effect (LME) modeling (Bates, Mächler, Bolker & Walker, 2014), we quantified how much of the total duration of target disappearance in each trial (MIBduration) can be accounted for by the number of saccades, alongside our main factors of interest of mask motion types and target position (see the details of LME in Methods). The significance of each factor was assessed with a likelihood ratio test (Bates et al, 2014).

LME and likelihood ratio tests confirmed the significant effects of mask type (Experiment 1: $X^2(1) = 40.53$, $p < .001$; Experiment 2: $X^2(1) = 95.16$, $p < .001$), even when taking account of the significant effects of saccades (Experiment 2: $X^2(1) = 12.68$, $p = .005$). Note the effect size of mask types, measured as X^2 value (Bates et al, 2014), is 2-4 times bigger than the effect of saccades. Thus we conclude that the effects of motion mask types on target disappearance cannot entirely be explained by the saccades in each condition. In addition, we found that the vertical position of the target also influenced the duration of MIB (Experiment 1: $X^2(1) = 3.45$, $p = 0.063$; Experiment 2: $X^2(1) = 27.64$, $p < .001$) while the horizontal position did not (Experiment 1: $X^2(1) = 2.42$, $p = 0.12$; Experiment 2: $X^2(1) = 0.074$, $p = 0.79$). Figure 3 shows the influence of these saccade effects. While the mean number of saccades negatively correlated with the mean MIB duration across subjects for expansion and contraction mask conditions, the differences between mask types cannot be explained by the number of saccades. This is further shown by a regression analysis with macro-saccades as the independent variable, which showed that 95% confidence intervals of the y-intercepts of both the contraction (*b*0 = 7.0, 95% CI [4.0, 10.0]) and expansion (*b*0 = 6.3, 95% CI [3.6, 8.9]) data did not overlap with the 95% confidence interval of the static (*b*0 = 1.6, 95% CI [0.6, 2.7]) data. The results of these regression analyses were not significantly changed when performed after combining both macro and micro saccades.

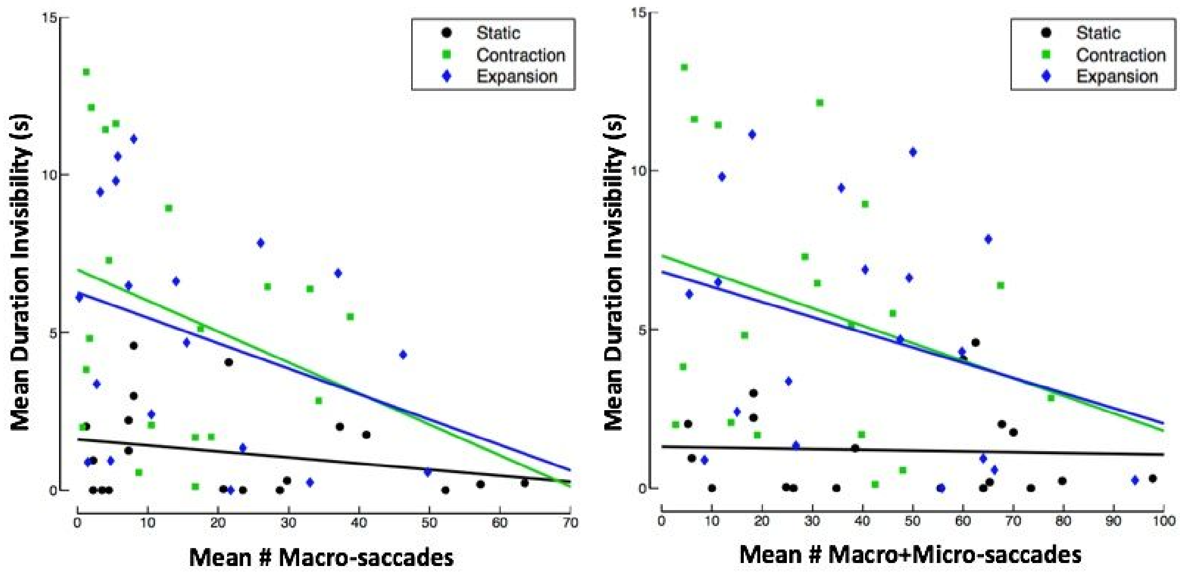

Figure 3. Relationship between mean number of macro and macro+micro saccades and target disappearance per minute within each mask condition of Experiment 2. A wide range of mean saccades, including a 0 intercept occur in all three conditions.

MIB is dependent on the speed of simulated forward self-motion

In Experiment 3, we examined the effects of the simulated speed of forward self-motion, comparing masks that simulated moving at 35 km/h, 50 km/h, 65 km/h and 80 km/h. There was a significant main effect of speed on mean MIB duration and mean MIB rate of target disappearance (Table 1, with similar results using median values), as seen in Figure 4. Regarding mean duration, post hoc paired-samples t-tests (using Bonferroni corrected p-values) revealed that disappearances for the lowest speed level of 35 km/h were significantly shorter than 65 km/h ($t(17) = 4.13$, $p = .004$, $r = .71$), and 80 km/h ($t(17) = 3.42$, $p = .02$, $r = .64$). Similar effects were found in post-hoc tests for mean rate, where number of target disappearances for the lowest speed level of 35 km/h were significantly less than 80 km/h ($t(17) = 3.53$, $p = .015$, $r = .65$) and also less than 65 km/h, although this difference fell short of significance ($t(17) = 2.93$, $p = .056$, $r = .58$). We also found that the mean duration of target disappearance showed linear dependency on the mask speed ($F(1, 17) = 14.09$, $p = .002$, $r = .67$) but neither quadratic ($p = .07$) nor cubic ($p = .87$) dependency was significant, although mean duration of invisibility appears to level off at higher speeds. The same effect was found for mean rate of target disappearance, with a significant linear dependency across conditions ($F(1, 17) = 11.50$, $p = .004$, $r = .64$), but neither quadratic ($p = .26$) nor cubic dependency ($p = .37$).

We again performed a linear-mixed effect analysis, investigating the influence of mask type and target location on mean target disappearance. The analysis showed that mask type had a significant influence ($X^2(1) = 13.20$, $p = .004$), vertical position had a near-significant influence ($X^2(1) = 3.50$, $p = .061$), while horizontal position had a significant influence ($X^2(1) = 3.99$, $p = .046$).

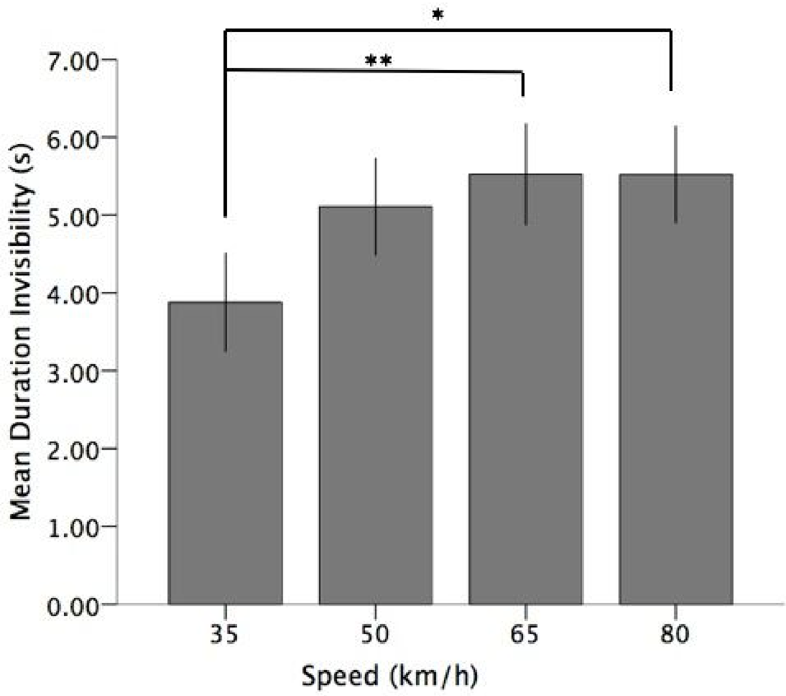

Figure 4. Mean duration of target disappearance for each mask speed condition within Experiment 3

MIB due to static, random and radial mask motion at a constant dot speed

Experiment 4 had two main purposes: 1) to compare our optic flow conditions to a condition with random motion that lacks any coherent 'motion structure', which has previously been shown to be important in MIB (Rosenthal et al, 2013; Graf et al, 2002) and 2) to investigate whether MIB still occurred as strongly when mask dots moved at a constant speed compared to an accelerating speed in our previous experiments.

Again, there was a significant main effect of the type of mask movement on mean duration (Figure 5) and mean rate of target disappearance (see Table 1, with similar results using median values). Post-hoc paired-samples t-tests (using Bonferroni corrected p-values) revealed that the static control condition had a significantly lower mean duration of disappearance than during 2-D random ($t(18) = 5.27$, $p < .001$, $r = .78$), 2-D radial expansion ($t(18) = 4.91$, $p = .001$, $r = .76$) and 2-D radial contraction conditions ($t(18) = 4.70$, $p = .001$, $r = .74$). Likewise, mean rate of target disappearance was significantly lower in the static condition compared to 2-D random ($t(18) = 4.96$, $p = .001$, $r = .76$), 2-D radial expansion ($t(18) = 4.77$, $p = .001$, $r = .75$) and 2-D radial contraction ($t(18) = 4.65$, $p = .001$, $r = .74$). However, in both rate and duration, 2-D random, 2-D radial expansion and 2-D radial contraction were not significantly different from each other (all $p = 1.00$).

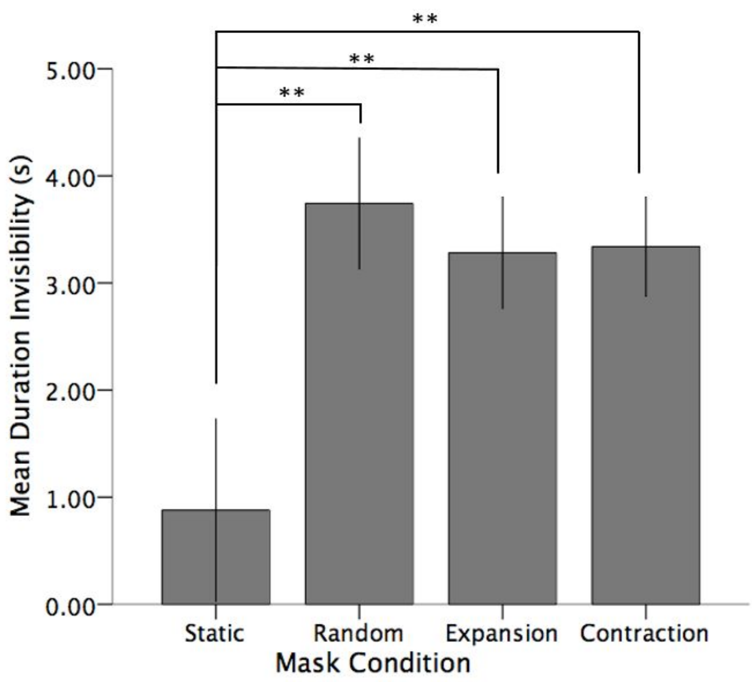

Figure 5. Mean duration of target invisibility dependent on motion type in Experiment 4

As the mean duration and rate of disappearance in Experiment 4 appeared to be lower than that of Experiments 1-3, we also compared the data of Experiment 4 to the 35 km/h condition of Experiment 3, which had a mask speed of 3.8°/sec around the target, which closely matched the 3.4°/sec in Experiment 4. This specific comparison between these mask types was necessary because the dot speeds *around the location of the target* were quite different (i.e., slower near fixation and faster towards periphery) in Experiment 1-3. In this comparison no difference in MIB between conditions was found for either mean duration (p = .81) or mean rate of disappearance (p = .50).

The linear-mixed effect analysis showed that saccades overall did influence MIB disappearance duration ($X^2(1) = 9.67$, $p = .046$). However the effect size was much smaller than the highly significant influence of mask type ($X^2(1) = 67.94$, $p < .001$). Vertical position of the target ($X^2(1) = 9.38$, $p = .002$), but not horizontal position ($X^2(1) = 0.010$, $p = .80$) accounted partly for the duration of MIB.

Phasic pupil responses as a proxy for subjective saliency during MIB disappearance and reappearance

Recent research (Kloosterman et al, 2015) has shown that phasic pupil responses are larger for target disappearances than reappearances. We sought to investigate whether this pattern of larger responses to disappearances would be replicated for our optic flow movement patterns, and whether there would be any difference in subjective salience (as measured by the pupil response) across mask motion types.

In terms of phasic pupil responses, target disappearances induced the largest pupil response in the static condition compared to the contraction and expansion conditions in Experiment 2 (FDR corrected comparisons are reported in Figure 6), while we found no differences in Experiment 4. The pupil size changes were smaller for target reappearances, consistent with Kloosterman et al (2015), and we did not find any significant differences between reappearance conditions in either Experiment 2 or 4. Our results suggest that perceptual disappearances were subjectively more salient events than reappearances, in support of Kloosterman et al (2015), regardless of mask types.

To further test if subjective saliency of the different motion types also modulated the overall tonic (i.e. baseline) pupil diameter, we also compared tonic pupil responses across Experiments 2 and 4, and across motion types (Figure 7). Interestingly, the average pupil diameter seems to correlate with the subjective saliency of the different motion types. Unnatural motion types that violate the optic flow of self-motion (e.g., the expansive 2-D motion in Experiment 4, which lacked an increase in dot speeds at greater eccentricities) showed the largest tonic pupil diameter, followed by 2-D contraction and random motion (Experiment 4). Natural motion stimuli (3-D expansion and contraction, Experiment 2), on the other hand, showed a smaller tonic pupil diameter. Quantitatively, average pupil diameter significantly differed across the conditions of the experiments, ($F(1, 132) = 6.04$, $p = .001$). More specifically, in Experiment 4, average pupil diameter remained comparable to the static condition for contraction (not significant; $t(18) = -0.18$, $p = .86$, $r = .04$), but increased significantly for the expansion condition ($t(18) = -2.44$, $p = .03$, $r = -.50$). In Experiment 2 tonic pupil diameter was greater in the static condition, compared to both contraction (not significant; $t(18) = 0.65$, $p = .52$, $r = .15$) and expansion conditions ($t(18) = 3.43$, $p = .003$, $r = .63$). Yet there were no significant differences in phasic or tonic responses dependent on target location, for both disappearance and reappearance. We present a potential interpretation of these pupil responses within a predictive coding framework below.

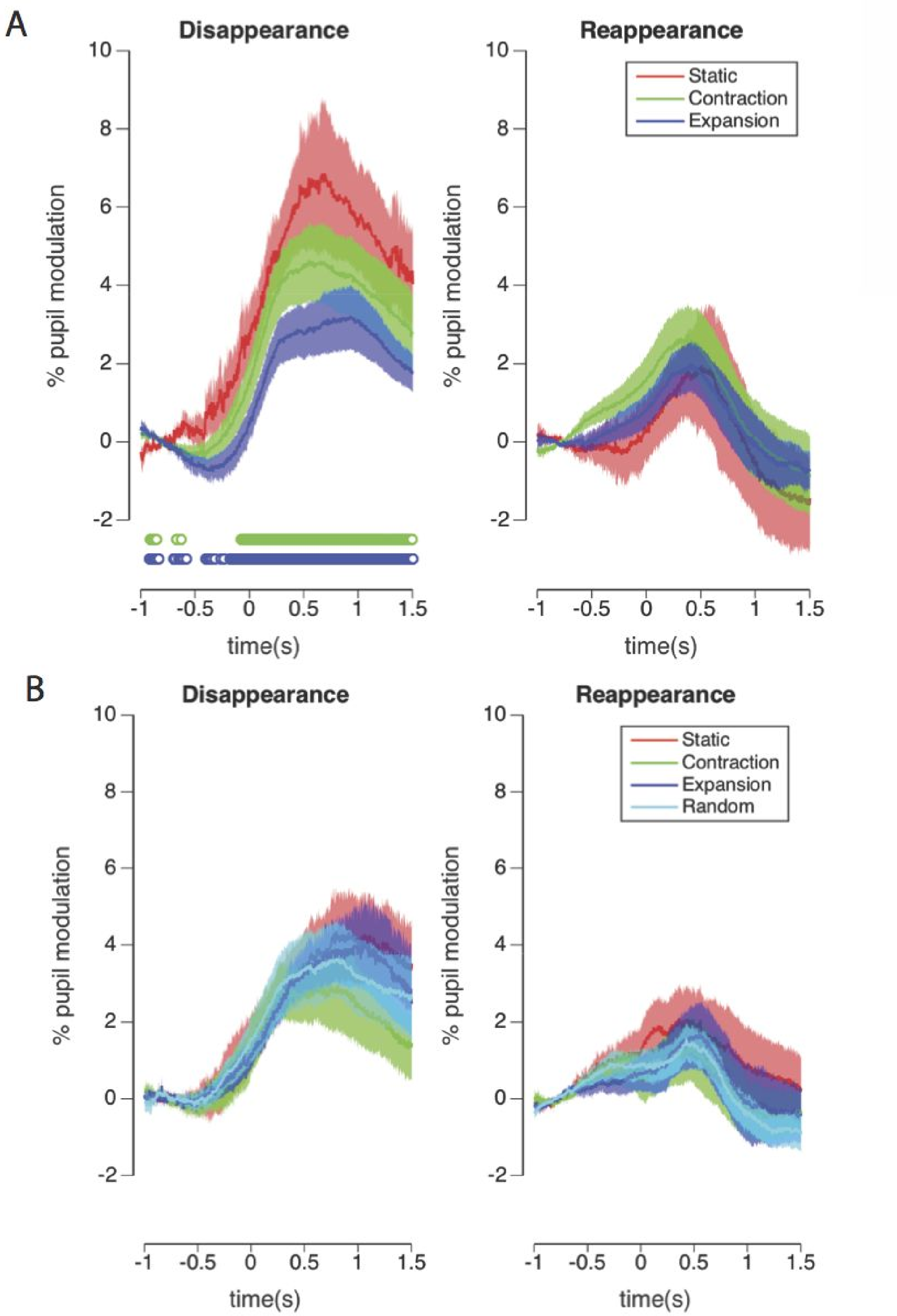

Figure 6: Phasic pupil diameter changes (in % modulation) in response to a reported

disappearance (left) and reappearance (right) for Experiment 2 (panel A) and Experiment 4 (panel B). Different conditions are displayed with different colors. Significance is indicated below the plot (green = contraction is significantly different from static, blue = expansion is significantly different from static at .05 level. There was no significant difference between contraction and expansion).

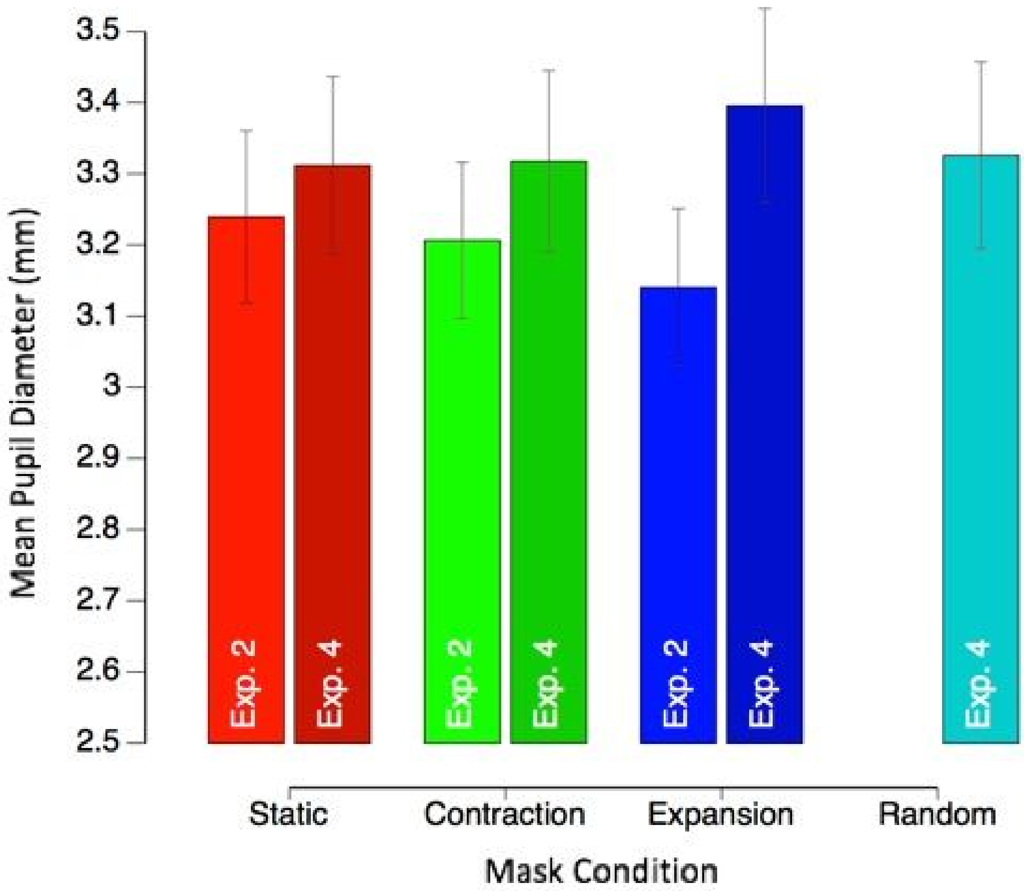

Figure 7: Mean pupil diameter per mask condition in Experiments 2 and 4.

DISCUSSION

In the current study we tested whether stimulus parameters modelled on optic flow simulating self-motion are able to induce MIB. Various other motion patterns have been used in the past (Bonneh et al, 2001; Rosenthal et al, 2013; Wallis & Arnold, 2009; Wells et al, 2011), but none have used a contracting or expanding optic flow analogous to when walking or driving, despite cues of self-motion being essential to safe navigation in altering environments (Britten, 2008). The present study showed that optic flow patterns similar to those experienced when driving a car in a realistic speed range, can reliably elicit MIB.

Mask movement

While mask movement was conducive to target disappearance, disappearance was not affected by variations in the direction of movement that we tested within each experiment, with optic flow expansion and contraction causing comparable target disappearance. While this effect may be expected based on the reliability of MIB occurring with a variety of mask parameters (Graf, Adam & Lages, 2002; Rosenthal et al, 2013; Wallis & Arnold, 2008; Wallis & Arnold, 2009; Wells et al, 2011; Wells et al, 2014), it is the first time that optic flow has been shown to elicit MIB. While claims regarding MIB in the real world cannot be made based on this finding alone, it nevertheless functions as a necessary first step in that direction. Expanding and contracting optic flow were shown to induce significantly more disappearance than radial expansion and contraction patterns with constant speed, but this difference disappeared once we controlled for mask speed differences between the experiments. However, the similar level of disappearance is still surprising, given that the dot density of the mask around the peripheral target within expanding and contracting optic flow was around 9-times lower, compared to 2-D radial expansion and contraction. Lower mask density necessarily results in less competition between the mask and target, causing less target disappearance (Wells et al, 2011; Bonneh et al 2001). Therefore, it is possible that a stronger disappearance effect within simulated forward and backward motion could have been observed if we were to equate dot density around the target in these conditions. Further research addressing inconsistencies between mask movement and dot density around the target will be needed to explore this possibility.

Mask speed

We found that target disappearance increased with mask speed, consistent with previous research (Bonneh et al, 2001; Libedinsky et al, 2009). Specifically, there was a significant positive linear dependency, with our two upper mask speeds of 65km/h and 80km/h eliciting significantly more disappearances than the lowest of 35km/h. While target disappearance did increase as a function of mask speed, the differences between the three upper speeds were not significant, suggesting that there may be a plateau effect of increased target disappearance that is reached at around 50 km/h. Further research is needed with a wider range of speeds to establish whether an optimal range of mask speed for inducing target disappearance exists, and where the upper threshold might be. Our current findings regarding mask speed may hold implications for driving safety, as it is known that driving speed is significantly related to accident rates (Centre for Road Safety, 2012; 2014), although further research in real world settings is needed before any claims can be made.

Target location

We found greater target disappearance for upper visual field presentation compared to the lower visual field across all four of our experiments. On the other hand, a bias for the left visual field was significant in only one experiment. To summarize the location biases in MIB,

Figure 8 shows the mean duration of disappearance for the different target locations across each experiment. Consistent with previous research (Bonneh et al, 2001; Rosenthal et al, 2013; Geng et al, 2007), there was a trend for target disappearance to be greatest for presentations in the upper left quadrant of the screen, and higher in the left visual field overall compared to the right, although these latter findings tended to fall short of significance. Past research has taken the increased disappearance of upper left targets to suggest a possible neural mechanism underlying MIB (Bonneh et al, 2001), such as spatial attention, which also shows strong visual field asymmetries (Mondor & Bryden, 1992; Rhodes & Robertson, 2002). However, most studies that report such a bias presented three targets in a triangular display with two targets in the upper field and one centred in the lower field, and found significant results only between the upper left and lower central target (Bonneh et al, 2001; Bonneh & Donner, 2011; Nuruki et al, 2013). If we interpret this in light of our current findings, in which the upper field bias was much stronger, it is possible that the upper left bias in MIB builds largely on a strong bias to the upper field overall.

Figure 8. Mean duration of invisibility according to target quadrant across all experiments

The upper field bias of perceptual disappearance is also compatible with previous research which suggests a greater visual acuity exists for the lower visual field (He, Cavanagh & Intriligator 1996), where object recognition in natural scenes is particularly important for our self-motion, hunting and general survival (He et al, 1996; He, Cavanagh & Intriligator, 1997). This lower visual field advantage has been reported in a range of visual tasks, including target detection and discrimination (Levine & McAnany, 2005), contrast sensitivity (Fuller, Rodriguez, & Carrasco, 2008; Skrandies, 1987), and the perception of illusory contours (Rubin, Nakayama, & Shapley, 1996). The present results extend this list to include MIB, as the trend for less target disappearance in the lower visual field may be explained as a consequence of greater visual acuity.

Saccades and the link to driving

We also considered the possibility that saccades may interfere with MIB. The results of our eye-tracking data showed that saccades influenced target disappearance, consistent with previous research (Bonneh et al, 2011; Hsieh & Tse, 2009). However, the magnitude of the effect was rather small compared to the influence of the mask, in both Experiment 2 and 4, and it did not explain our main findings, which is consistent with the observation that MIB occurs even with a moving target (Bonneh et al, 2001). This is also evident from our scatter plot analyses (Figure 3), which showed that, at the same level of saccades, MIB disappearances were larger in the motion mask types compared to the static masks. Thus, saccades did influence MIB, but cannot explain the difference in MIB between different mask types.

We recorded an average of 35 (macro+micro) saccades per minute in the optic flow mask conditions. Although around 80 saccades per minute typically occur while driving - a value considerably higher than found in our experiments - there is great variation in this according to the type of road and environment (Chapman & Underwood, 1998). While the frequency of saccades in our experiments were relatively low across subjects, there were some subjects who exhibited 30-40 macro-saccades or 50-70 (macro+micro) saccades per minute (Figure 3) and still reported substantial durations of target disappearance (~5 sec per minute). Assuming that 5 seconds of MIB can occur per minute for the saccade rates reported herein, then up to 10 minutes of MIB may occur during a two hour drive. Further, other known contributors to accidents such as fatigue and inattentional blindness, that are important factors in their own right (Centre for Road Safety, 2012; 2014), may interact with and increase any potential influence of MIB in traffic accidents. Further studies are needed to address such a possibility in settings which more closely approximate real-life.

Pupil size

While our study overall implies that MIB may occur during actual self-motion, such as when driving, spontaneous reports of MIB among the population are rare. Why is that so? One possibility is that MIB phenomena are so subtle that not many people notice them, regardless of the functional significance of object disappearance. As we did not ask participants how salient their MIB experiences were, we adopted phasic pupil responses as a proxy for subjective salience. Phasic pupil dilation is known to increase in response to surprising, novel or unexpected stimuli (Kloosterman et al, 2015; Naber et al, 2013; Nassar et al, 2012; Preuschoff et al, 2011), allowing us to investigate whether there were any differences in the saliency of MIB across mask conditions.

We found that phasic pupil responses were larger in response to target disappearances than reappearances, suggesting that disappearances were more salient, consistent with previous research (Kloosterman et al, 2015). We further found that in the optic flow conditions, target disappearances in the static mask condition induced larger pupil dilations than both the expansion and contraction conditions. This suggests that disappearances in the static condition were more salient, which might be explained by the fact that target disappearances were much less frequent in this condition. Conversely, and importantly, this means that target disappearances are less salient during optic flow stimulation. Reappearances did not show differences in terms of pupil size between mask conditions, probably because every disappearance is predictably followed by a reappearance after a relatively short period, making them less surprising. Interestingly, the differences in pupil responses between static and moving mask conditions were not significant in Experiment 4, perhaps because the target was embedded in a mask with higher dot densities, making the disappearance less salient. Overall, the pattern of pupillary responses we observed appears consistent with an interpretation that they signal the subjective saliency or surprise of events (Kloosterman et al, 2015; Naber et al, 2013; Nassar et al, 2012; Preuschoff et al, 2011). Importantly for our discussion here, disappearances are less salient in optic flow conditions than those in a static scene, which may explain why people seldom notice MIB during driving.

When analyzing the tonic pupil diameter (i.e. the average pupil diameter per mask condition), our results were again consistent with the phasic saliency account, though this time concerning a less-transient surprise measure that was dependent on motion mask type. Specifically, compared to the static mask condition, tonic pupil size was smaller during 3-D expanding optic flow, which is a condition that is frequently experienced during forward self-motion. Consistent with this idea, the opposite effect was found in Experiment 4, where average pupil size increased significantly for the 2-D radial expansion condition, where dots moved in an unnaturally constant speed across the screen - a situation we do not often encounter in our environment. Therefore, even though both conditions showed expanding patterns, the pupil size (and thus subjective saliency/surprise) results were in opposition. This can be explained by assuming that frequently experienced 3-D expansion (and contraction) caused by self-motion are well internalized in the visual system, producing small prediction errors, and thus little surprise (Rao & Ballard, 1999; Schindler & Bartels, 2016), while the visual system does not have good internal models for unnatural expansion patterns which therefore produce large prediction errors, and an increase in subjective saliency.

If realistic patterns of motion are indeed less salient, and thus attract less attention, it could mean that more attention is available to be directed toward other elements in the visual display, such as the targets. If there is indeed more attention paid to the targets embedded in realistic motion types, more target disappearance should result (Geng et al, 2007; Schölvinck & Rees, 2009). However, it is currently unknown how surprise-related pupillary responses are modulated by the allocation of top-down attention, requirement of reports, and subjective awareness of perceptual events, especially during MIB. Further research to dissociate these factors (van Boxtel & Tsuchiya, 2015; van Boxtel, Tsuchiya & Koch, 2010; Tsuchiya, Wilke, Frässle & Lamme, 2015) is necessary to properly understand how pupillary responses relate to these psychological constructs.

Limitations and implications

Collectively, our findings show that optic flow simulating self-motion successfully elicits MIB. While conclusions on the occurrence of MIB in the real world cannot be drawn from this finding alone, it provides support for further research into that possibility. If found to occur in the real world, MIB may hold implications for driving safety, where the most common point of gaze is at the centre of the expanding optic flow of the approaching road (Helander & Söderberg, 1972; Mourant & Rockwell, 1997; Shinar, McDowell & Rockwell, 1977). Additionally, items that need to be monitored, such as overtaking cars or GPS devices attached to the windscreen, reside mainly in (upper) peripheral quadrants, which we found prone to perceptual disappearance.

While drivers may often saccade to check mirrors, scan for other cars and so forth, there are also situations in which fixations lengthen and saccade frequency decreases. These include when driving on rural as opposed to urban roads (Chapman & Underwood, 1998; Underwood, Crundall & Chapman, 1997), during times of danger or hazard (Chapman & Underwood, 1998), when multi-tasking (May, Kennedy, Williams, Dunlap & Brannan, 1990; Reimer, 2009) and when experiencing fatigue (Di Stasi, McCamy, Catena, Macknik & Cañas, 2013). Given that fewer saccades and longer fixations result in greater target disappearance, MIB may be more likely to occur during hazardous situations or driver fatigue - two of the most influential factors relating to traffic accidents (Centre for Road Safety, 2015).

If confirmed to exist under more realistic visual settings, MIB may also hold implications for the development of Head-Up Display (HUD) technology. Using this technology crucial information is projected onto the windscreen or visor in the form of stable symbols and text, through which the moving background of road or land is viewed. Such technology can be found, for example, in the use of F-35 Fighter Jet helmets which have been developed to project flight information onto the visor viewed by the pilot over the moving background (The F-35 Helmet, 2015), or increasingly in commercially available cars with dashboard information projected onto the windscreen (Hyundai Future Transport Technology, 2015).

While providing support for future studies on the occurrence of MIB in the natural world, our research was still undertaken in an artificial setting. The experiment was conducted on a computer display, and while parameters were modelled on the real world, aspects of the display itself were also inconsistent with the type of motion perceived in daily life. Specifically, the mask dots did not increase in size as they approached the periphery, as would occur in normal optic flow movement (Wang et al, 2012). Additionally, the mask was based on a tunnel, yet driving through tunnels in reality is usually brief and infrequently experienced. Future research should attempt to measure the occurrence of MIB directly in conditions that approximate the statistics of the real world experience in a closer fashion, especially given its potential impact on driving safety. Such research could utilise a virtual reality environment to directly test the hypothesis of MIB occurring under driving circumstances, which would allow for stronger conclusions of the real-world implications than can be drawn from our stimuli.

METHOD

Participants

Ethics approval was obtained from the Monash University Human Research Ethics Committee, and informed consent was obtained from all participants in the form of written permission prior to participation. Methods were carried out in accordance with with the relevant guidelines and regulations. Thirty-seven participants were recruited at Monash University, all meeting the requirement of normal or corrected-to-normal vision. There was no overlap between the 18 participants for Experiments 1 and 3 (aged 18 – 59 years, $M = 24$, $SD = 9$; 15 females) and 19 participants for Experiments 2 and 4 (aged 18 – 34 years, $M = 23$, $SD = 4$; 13 females).

Apparatus

All experimental displays were created using Matlab (Mathworks, Natick, MA) and OpenGL, with the PsychToolbox extension (Brainard, 1997; Pelli, 1997). In Experiments 1 and 3, the experimental display was an IBM P275 CRT powered by a Dell Optiplex9010, and viewed from an approximate distance of 45 cm. In Experiments 2 and 4, the experimental display was a Tobii TX-300 powered by a MacBook Pro OS 10.9.5, viewed from an approximate distance of 60 cm. Experiments were run in an experimental room without natural light, with artificial lights dimmed in Experiments 1 and 3, and adjusted to a level enabling the proper performance of the Tobii TX-300 eye tracker in Experiments 2 and 4.

Hereafter, the stimulus specifications presented are for Experiments 1 and 3 with those for Experiments 2 and 4 in brackets. The stimulus consisted of a grey background at 31 Cd/m^2 (31 Cd/m^2), and white mask dots at 83 Cd/m^2 (169 Cd/m^2), each with a radius of .05° (.04°; Supplementary Movie S1). The mask was constructed as a 2-D rendering of a 3-D circular tunnel with randomly placed dots, through which the participant experienced simulated forward or backward motion. The tunnel was generated anew for each 1-minute trial, had a 5 meter radius, and was 3000 meters long. The mask consisted of 7500 white dots, placed randomly on the perimeter of the tunnel. Due to the trial length of 1 minute not all 7500 were seen by the participant. Dots moved progressively out of a central cluster (about .50° (.38°) radius), at which subjects were instructed to fixate during the experiment. During simulated forward self-motion the speed of dot movement gradually increased as each 'moved nearer' to the participant and approached the periphery of the screen, a pattern which was reversed for backward-motion conditions. Unlike real-life dot progression however, the dots did not change in size with expansion or contraction (Wang, Fukuchi, Koch & Tsuchiya, 2012), because we aimed to focus primarily on the influence of motion information.

The peripheral target for MIB was a white disc with a .84° (.63°) radius, surrounded by a thin exclusion boundary of .34° (.25°), through which no mask dots travelled. The disc was located 10.75° (9.32°) degrees diagonal distance from the central fixation cluster, 6.36° (4.61°) vertical and 8.70° (8.10°) horizontal, positioned in either the upper left, upper right, lower left or lower right quadrant of the screen in each trial.

Within each 60-second trial, one catch episode occurred in which the target physically disappeared from the display for a short period of time. The luminance of the target was linearly ramped off over 1.5 seconds, and stayed grey (i.e., the color of the background) for 1-4 seconds (randomly assigned in each trial), then linearly ramped up to white (i.e., the color of the original target) over another 1.5 seconds. The total duration of the catch episode therefore varied randomly from 4-7 seconds across trials. Each catch episode started randomly between 10 seconds and 50 seconds after the onset of each trial, to appear indistinguishable from perceptual disappearances. For the subsequent analyses, any reported perceptual disappearance of the target which overlapped with the catch was excluded from analysis. Participants were not told of the catch, but only encouraged to report all perceived disappearances. Accordingly, if the participants did not report physical disappearance of the catch appropriately, we regarded that they had not paid attention to the task in that trial. Debriefing with a number of participants revealed that they were surprised to hear of the catch disappearances, as they had not been able to tell the catch from the genuine perceptual disappearances. While three participants failed to record the catch on one or more trials, analyses with these participants excluded produced no significant difference to results. Their data was therefore included for analysis.

In Experiments 2 and 4, we also recorded participant fixation locations using an eye tracker. One purpose of eye tracking was to exclude participants who looked directly at the peripheral target, failing to fixate on the central point at any time. Fixations were defined as any duration between macro-saccades (>1 deg). If the fixation duration on the peripheral target per 60-second trial was longer than one second, the participant was considered for exclusion. Only three participants met this exclusion criterion on at least one trial. As including or excluding them did not significantly alter the results, we included their data for analysis. The other purpose of eye tracking was to quantify the influence of eye movements on MIB (Bonneh et al, 2011; Hsieh & Tse, 2009), which might to some degree explain the effects of our experimental manipulation of motion stimuli.

Experiments 1 & 2. In Experiments 1 and 2, three different types of mask were presented – expansion (simulated forward motion); contraction (simulated backwards motion), and a static still frame in which there was no dot movement. The simulated movement speed was 65 km/h for both expansion and contraction. The four different target locations were balanced and randomised over trials. Both Experiments 1 and 2 consisted of

12 1-minute trials, presenting each possible combination of mask (3 types) and target location (4 quadrants). Eye-movements were recorded during Experiment 2.

Experiment 3. In Experiment 3, only forward motion was simulated, resulting in an expanding motion pattern. Four different movement speeds were simulated: 35 km/h, 50 km/h, 65 km/h and 80 km/h. Experiment 3 consisted of a total of 16 1-minute trials, presenting each possible combination of speed and target location.

Experiment 4. Experiment 4 had two purposes: 1) to compare optic flow conditions to a condition with random motion and 2) to investigate whether MIB still occurred as strongly when the mask dots moved at a constant speed compared to an accelerating speed as in the optic flow conditions. In Experiment 4, instead of a central cluster, the fixation point was explicitly presented as a white cross with a size of 0.50° x 0.50° (Supplementary Video S2). The cross was surrounded by an exclusion radius of 2.35°, through which no mask dots travelled. In addition, only in Experiment 4, all dots (500 in total) moved at a constant speed of 3.4° per second. Four different types of mask were presented: 2-D radial expansion, 2-D radial contraction, 2-D static and 2-D random movement. With the random type of mask movement, the dots moved in a random direction and had a 1% chance of being removed on each frame. Removed dots, and dots which crossed the outer edge of the display were replaced at a random position on the screen. Experiment 4 consisted of 16 1-minute trials, presenting each possible combination of mask type and target location. Due to the stimulus layout, this experiment had a uniform density of mask dots on the screen, while the other experiments had a decreasing density with increasing eccentricity.

Procedure

Experiments 1 and 3. Participants sat comfortably in front of the computer, with their head stabilised by a chin rest. They were instructed to fixate on the central area of the screen and to indicate the perceptual invisibility of the target by holding down the spacebar for as long as the target remained invisible. Participants were instructed to pay attention to the peripheral target, without looking at it directly.

Experiments 2 and 4. Experiments 2 and 4 followed the same procedure as 1 and 3, however eye movements were also recorded. Participants underwent a standard 9-point eye-tracking calibration before the experiment started, and did not move their heads away from the chin rest for the duration of the experiment.

Analyses

We ran two one-way repeated measures ANOVAs with mask condition as the sole independent variable (IV) for each experiment. The mean duration of target disappearance per condition was the dependent variable (DV) in the first analysis; the mean rate of target disappearance per condition was the DV in the second. For comparison, all analyses were also run using the median instead of the mean. The results did not change in a significant way (see Table 1).

To examine how much of the observed MIB disappearance (in each trial) could be explained by the frequency of saccades, which are expected to reduce MIB, and the location of the target, we used the linear mixed effect model (LME) in Matlab (ver 2016a). Likelihood ratio tests were performed through a X^2 test comparing the full model and a reduced model without the factor or interaction in question (Bates, Mächler, Bolker & Walker, 2015). We modeled the total duration of target disappearance in each trial (MIBduration) with a fixed effect of MaskType (for the different types of motion mask), NumberOfSaccades (per trial), and the target location (LeftRight and UpDown) as MIBduration ~ MaskType + NumberOfSaccades + LeftRight + UpDown + (1|SubjectID).

Subject variability was taken into account as a random effect. NumberOfSaccades was only entered when available (Experiment 2 and 4), in which case we included it in the unrestricted model as an interaction with MaskType.

Assumptions for all tests were met, with the exception of violated normality in several conditions across experiments. Therefore, unless otherwise stated a square root data transformation was performed for all ANOVA analyses, as small sample size (< 30) meant the Central Limit Theorem was not applicable in correcting normality (Field, 2012; Tabachnick & Fidell, 2013; Hair, Black, Babin & Anderson, 2009). A constant of 1 was added to all data when performing the transformation, due to the dataset containing 0 values (Field, 2012).

Despite the transformation, normality was occasionally still violated in the static mask condition across Experiments 1, 2 and 4, with skewness Z-Scores exceeding the alpha =.05 cutoff of 1.96 (Field, 2012; Tabachnick & Fidell, 2013). Alternate transformations (Log10, Reciprocal) also failed to correct normality in this variable. The violation in the static mask control condition was due to the majority of participants recording disappearance scores of zero for this condition, as expected. Given that negative values were not possible in our study, this necessarily led to a skewed distribution in the static condition. As the violated static condition was serving as a control for comparison only within our ANOVA analyses, the square root transformation was retained and parametric tests run despite the violation. However, non-parametric Friedman's tests corroborated our findings in all cases. All graphical representations of data were created using within-subjects error bars displaying a 95% confidence interval, as recommended by Cousineau (2005). In all figures, double asterisks (**) indicate significance at a < .01 level, and a single asterisk (*) indicates significance at a < .05 level.

Eye-movement analyses

Saccades and fixations: Eye movements were recorded binocularly using a Tobii TX-300 Eyetracker (Tobii Technology, Danderyd, Sweden) at a sampling rate of 300Hz, controlled through the software package T2T (http://psy.cns.sissa.it/t2t/About_T2T.html). Saccades and fixations were detected offline using a velocity-based algorithm (Engbert & Kliegl, 2003). Saccades with an amplitude larger or less than 1 degree of visual angle were categorised as macro-saccades or micro-saccades, respectively.

Pupil size: Pupil diameter was also recorded by the Tobii TX-300 Eyetracker. We analysed the left eye and followed procedures by Kloosterman et al (2015). Briefly, to obtain phasic pupillary responses, we took excerpts from the pupil trace from -1 second to +1.5 seconds around the time of a reported disappearance or reappearance. The pupil diameter over the first 400 ms of each excerpt was subtracted from the signal, and the result was then divided by the mean pupil diameter over the entire experiment (dividing by the mean per condition yielded identical results in terms of passing statistical significance). This was done per participant separately. Results were then analysed over participants, with multiple comparisons corrected with a False Discovery Rate (FDR) 0.05. To estimate the sustained, baseline tonic level of pupillary diameter for each motion stimulus, we calculated the mean pupil diameter for each of the movement conditions separately, without normalisation.

STATEMENT OF CONTRIBUTION

VT and JVB conceptualised and designed the research reported in this article, with feedback from NT and MD. VT collected and analysed the behavioural data, with help from JVB. VT wrote the article, with feedback from JVB, MD and NT. MD programmed the experiments, with help from JVB. PZ analysed the saccade data, JVB analysed the pupil data.

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