INTRODUCTION

Imagine viewing the center of an imaginary square formed by four stationary dots while, in the background, an array of moving dots is drifting left to right. Surprisingly, after roughly five seconds of viewing the stimulus, one or more of the four stationary dots will appear to vanish (Grindley and Townsend, 1965). This phenomenon, which has been called Motion-Induced Blindness (MIB; Bonneh et al., 2001), would appear, at least in part, to involve relatively high-level processing of motion 'filling-in' the regions where there is no motion (Bonneh et al., 2014); perceptually, the regions occupied by the four stationary dots, or targets, appear to be filled in by the moving background, or mask. Color and form can fill in at different rates (Ramacandran and Gregory, 1991). Contrast adaptation contributes, but MIB clearly involves additional, high-level mechanisms (Gorea and Caetta, 2009; Bonneh et al., 2014). Depth ordering, with the mask behind the target, decreases MIB and the reverse increases MIB (Graf et al., 2002). Indeed, both perceptual filling in and MIB share depth-ordering effects and involve boundary adaptation (Hsu et al., 2006). Over and above the expected interactions between form and motion processing (see, Mather et al., 2013), MIB would seem to involve both sensory and decisional processes (Caetta et al., 2007). Eye movements will cancel the filling in (Grindley and Townsend, 1965) and modulate the probability of the disappearance or reappearance of the target (Martinez-Conde et al., 2006; Bonneh et al., 2010). Attending the target increases disappearance, and removing attention from the entire display decreases disappearance (Grindley and Townsend, 1965; Schöler and Rees, 2009).

Ventral V4 decreases responding with disappearance and dorsal visual areas around intraparietal sulcus increase responding (Donner et al., 2008). But, fluctuations in V1 are correlated with the duration of disappearance, suggesting that different areas of cortex, reflecting a processing hierarchy, are involved (Donner et al., 2013). For example, trans-
craniocerebral magnetic stimulation in posterior parietal influences the cycle of target disappearance with differential affects across hemispheres (Funk and Pettigrew, 2003).

One theory suggests that targets are treated like scotomas in the presence of a motion mask (New and Scholl, 2008; however, see Moors et al., 1974). Gorea and Caetta (2009) suggest that there are at least two processes associated with MIB. One is a reduction in response gain that gives a drop in brightness that has a time course similar to the case when either just a non-moving mask or no mask is presented (e.g., the Troxler effect (Troxler, 1804), which is due to retinal adaptation; Clarke and Belcher, 1962; Krauskopf, 1963). The second is a contrast gain reduction that results from transient, motion responses incrementally inhibiting sustained, form responses. Having demonstrated that increased coherence gave decreasing disappearance, though the result was not proportional to the number of motion directions, Wells et al. (2011) suggested that target adaptation drops the target below threshold, the putative drop in response gain, but that some adaptation to a coherent mask occurs that is, in turn, reduced when an incoherent mask is used. Of course, mask adaptation would decrease the contrast gain reduction due to the transient to sustained inhibition. Hence, incoherent motion should make a more effective mask than coherent motion.

The effects of the mask may be presumed to be relatively high-level effects, while those of response gain reduction described by Gorea and Caetta (2009) would seem to be low-level effects. While ganglion cells may be subdivided into roughly 17 categories based on anatomy, exhibiting a wide variety of behaviors (Dacey, 2004; Dacey et al., 2010), several of these categories of cells convey information about the presence of increments relative to the background, ON-cells, and others, decrements, or OFF-cells (e.g., Schiller et al., 1986; Schiller, 1992; Dolan and Schiller, 1994). There is strong physiological and behavioral evidence that ON- and OFF-processing channels flow through separate channels to cortex, and is maintained as a distinction to higher levels of cortex (Dacey, 2004; Yeh et al., 2009; Xing et al., 2010). Further, OFF-processing seems to have a stronger input, with lower contrast thresholds and faster response times, than ON-processing (e.g., DeMarco et al., 2000; Westheimer, 2007; Balasubramanian and Sterling, 2009; Jin et al., 2011; Komban et al., 2011).

Our aim was to measure both the effects of perceived mask coherence, while holding physical coherence roughly constant, and of increments and decrements in both the target and the mask on MIB in two experiments.

**EXPERIMENT 1**

**COHERENT MOTION, INCREMENTS, AND DECREMENTS**

In Experiment 1 we wished to explore the influence of coherent motion, both physical and perceived, and ON- and OFF-channels on motion-induced blindness. To that end, we measured the threshold duration for a mask to induce the disappearance of at least one of four targets using three mask types. The two-frame coherent motion mask was created by presenting a random array of dots during the odd frames of a movie sequence and then shifting those dots in one common direction to create the even frames. The odd to even frame transitions have non-zero coherent motion energy while the even to odd frame transitions have only incoherent motion energy. The appearance of such a mask is that of a twinkling array of random dots drifting in the direction of motion.

Our second mask type was the dynamic Glass pattern mask. A Glass pattern (Glass, 1969) may be formed by creating an array of random dots, then superimposing on that array an identical second array that is shifted in one direction by a given distance. The appearance is that of a random array of dot pairs where the distance between each member of a pair dots is constant and each pair is aligned along an axis that is parallel to that of the other dot pairs. Our dynamic Glass pattern mask was a sequence of independent Glass patterns that were aligned along a common axis. The dynamic Glass pattern has no coherent motion energy (Ross et al., 2000) although it appears to be a twinkling array of random dots drifting in one direction or the opposite along the common axis of the dot-pair orientations.

Comparing these two mask types, the two-frame motion mask appears coherent and has some measure of coherent and incoherent motion energy. The dynamic Glass pattern mask also appears coherent but with no coherent motion energy. Given recent evidence that incoherent motion masks are more effective than coherent motion masks, one might guess that the dynamic Glass pattern will be more effective than the two-frame motion mask. However, if the appearance of coherence, independent of motion energy, is the important variable, then one might expect essentially no difference in the effectiveness of the two masks.

With both of these mask types, we factorially varied whether the mask dots and the target dots were increments or decrements relative to the background. To the degree that the transient to sustained masking receives distinct input from the ON- and OFF-channels, one might expect increment masks to more effectively mask increment targets than decrement targets, and vice versa. As well, given the lower thresholds and greater representation of decrements than increments in the peripheral visual system, one might expect decrement masks to be more effective on increment targets than increment masks are for decrement targets.

Finally, our third mask type was a dynamic anti-Glass pattern mask. During the two-step process for creating a Glass pattern described previously, to create an anti-Glass pattern one might use increments for the first step and decrements for the second step, or vice versa (Glass and Switkes, 1976). A sequence of independent anti-Glass patterns forms a dynamic anti-Glass pattern mask. Viewing such a sequence gives the appearance of coherent motion in the direction of
the brighter dots, which may be due to the delayed processing of the OFF-channel relative to the ON-channel at the retinal level (Del Viva et al., 2006). The dynamic anti-Glass pattern will appear to have coherent motion energy in the decrement to increment direction with each frame, though only incoherent energy is nonzero between all frames. Further, the apparent coherent motion energy will be between ON-channels and OFF-channels, while the physical incoherent motion energy will be non-zero both within and between channels.

**METHODS**

**Participants.** Two female unpaid volunteers (AIL, who was naive with respect to our hypotheses, and MEL, a co-author of this paper), each in their early 20s, participated in Experiment 1. Both were undergraduates at the University of New Hampshire and had normal or corrected to normal visual acuity. Each subject signed informed consent and was debriefed consistent with University of New Hampshire Institutional Review Board policy.

**Apparatus and stimuli.** The experiment was conducted in a darkened room. Stimuli were rendered and the experiment controlled by a Mathematica program and presented on a 15 inch (381 mm) MacBook Pro running MacOSX. The fixation dot, four target dots, and 64 mask dots were presented on a 9.3 × 9.3 deg gray square of 107.5 cd/m². 200.0 cd/m² increment and 15.0 cd/m² decrement dots were used. The four target dots were plotted on the corners of an imaginary square with a side length of 3.1 deg centered over the fixation dot. The imaginary square was rotated from trial to trial in order to prevent target dot afterimages. The four target dots and the fixation dot were 16 min in diameter. Each mask frame contained 64 dots within a square region of side length 5.54 deg centered over the fixation dot. Each of the mask dots was 7.5 min in diameter, giving a density of 0.93 mask dots/deg². 0.018% of the stimulus was thus covered by masking dots. Three types of mask were created.

**Two-frame coherent motion mask.** The 64 dot mask moved linearly across the stimulus in a two-frame sequence. For the first frame the 64 mask dots were randomly placed in a square region of side length 6.2 deg centered over the fixation dot. For the second frame each dot was shifted in a common direction by 18.5 min, giving an overall velocity of 6.2 deg/s with a 20 Hz frame rate. If a dot’s shift left the 6.2 deg region, it reappeared at the opposite side. A set of two-frame sequences formed a stimulus trial. All two-frame sequences in a single trial shifted in a common direction, giving the appearance of coherent motion in that direction. The direction of mask movement varied from trial to trial randomly along the four cardinal directions.

**Dynamic Glass pattern mask.** For each frame the 32 pairs of mask dots (composing 64 mask dots) were randomly placed in a square region of side length 6.2 deg centered over the fixation dot. Each member of a pair of dots was separated in a common direction by 18.5 min, thereby forming a Glass pattern oriented along one axis. These Glass patterns were presented at a 20 Hz frame rate. A set of randomly-defined Glass patterns formed a stimulus trial. All Glass patterns in a single trial were oriented along a common axis, giving the appearance of coherent motion along that axis. The axis of the mask Glass patterns varied from trial to trial randomly along the four cardinal directions.

**Dynamic anti-Glass pattern mask.** For each frame the 32 pairs of mask dots (composing 64 mask dots) were randomly placed in a square region of side length 6.2 deg centered over the fixation dot. Each member of a pair of dots was separated in a common direction by 18.5 min, thereby forming a Glass pattern oriented along one axis. These Glass patterns were presented at a 20 Hz frame rate. A set of randomly-defined Glass patterns formed a stimulus trial. All Glass patterns in a single trial were oriented along a common axis, giving the appearance of coherent motion along that axis. The axis of the mask Glass patterns varied from trial to trial randomly along the four cardinal directions.

**Results.** The relative frequency for a target dot disappeared response was calculated as a function of log(t), trial duration, with 95% score confidence intervals based on n trials (Wilson, 1927; Agresti and Caffo, 1998; Agresti and Caffo, 2000). Equation (1), our Gaussian psychometric function, was fit
to these data for each of the four combinations of target/mask dot luminance and participant with lapse rate $\lambda$ (Klein, 2001).

$$F(\log(t)) = \frac{(1-\lambda)}{\sqrt{2\pi \log(\sigma)}} \int_{-\infty}^{\log(t)} e^{-\frac{(\log(1)-\log(t))^2}{2(\log(\sigma))^2}} \, d\log(t)$$ (1)

Note that we have a zero guess rate, reflecting the assumption that the target dots will be visible at the start of a trial. Threshold trial duration for a target dot disappeared response was estimated as $\mu$.

95% bootstrap confidence intervals (Efron, 1979; Efron and Tibshirani, 1993) were calculated for each threshold. For a given combination of target/mask dot luminance and subject, $n$ samples from a binomial pseudo-random number generator with the probability of success equal to the relative frequency for a target dot disappeared response at each trial duration were collected, and the relative frequency of successes calculated from the new, bootstrap, sample, where $n$ is the number of trials run by the particular subject. The psychometric function, Equation (1), was fit to these data and was estimated. This process was replicated 1000 times. The 2.5th and 97.5th percentile from the replications provided the lower and upper bounds for the 95% bootstrap confidence intervals.

Figure 1 shows example psychometric functions for MEL. As expected, the probability that at least one target dot vanishes increased with the duration of the trial. As well, Equation (1) captured the shape of the psychometric function well.

Figures 2 and 3 show the threshold trial durations for disappearance for AIL and MEL, respectively, with 95% bootstrap confidence intervals (Efron, 1979; Efron and Tibshirani, 1993).
rani, 1993). There was an interaction between increment versus decrement mask dots on the one hand and increment versus decrement target dots on the other. For decrement targets, both increment and decrement masks were equally ineffective, and mask type seemed to have no effect. Increment targets were more effectively masked by decrement masks with both two-frame motion and dynamic Glass patterns. The effectiveness of dynamic anti-Glass pattern masks matched that of decrement masks for AIL and fell between the former two types with increment targets for MEL. Decrement targets would appear to be more difficult to mask than increment targets, regardless of the luminance or contrast of the mask or the type of mask. Decrement masks were more effective than increment masks only for increment targets, and there seemed to be no overall effect of type of mask.

DISCUSSION

We essentially found no robust differences among the three mask types. Certainly, there is no evidence that a mask with coherent motion energy will be less effective than one with no coherent motion energy. Three rather different masks that all appear to move coherently are similarly effective. That decrement targets were more difficult to mask than increment targets is consistent with OFF-cells’ lower thresholds and stronger input. However, that decrement masks were more effective than increment masks only with increment targets complicates the interpretation.

EXPERIMENT 2

INCREMENTS AND DECREMENTS

Given the lack of effect for mask type, and the intriguing effects of decrements relative to increments, we decided to conduct a replication of Experiment 1 using just the two-frame coherent motion mask.

METHODS

Participants. Three female unpaid volunteers (AKS and HKH, who were naïve with respect to our hypotheses, and MEL, a co-author of this paper), each in their early 20s, participated in Experiment 2. All three were undergraduates at the University of New Hampshire and had normal or corrected to normal visual acuity. Each subject signed informed consent and was debriefed consistent with University of New Hampshire Institutional Review Board policy.

Apparatus and stimuli. The apparatus and stimuli were the same as those in Experiment 1 with the following exceptions. Only the two-frame coherent motion mask was used. We also added a control condition in which no mask was present.

Procedure. The procedure also matched that from Experiment 1. Target dot luminance (increment vs decrement),
mask dot luminance (increment vs decrement), and trial duration (3.1 s, 4.6 s, 7.0 s, 11 s, or 16 s) were factorially combined, and the no-mask control condition for increment and decrement targets was added (2 × 2 × 5 + 2 = 22), to create 22 trial types that were presented in random order. Nine trials per condition were presented during each session, for a total of 198 trials per session.

RESULTS
The data were analyzed using the same techniques outlined in Experiment 1. No subject exhibited a probability of disappearance greater than 0.2 in the control condition. The psychometric functions in the other conditions looked similar to that presented in Figure 1.

Figure 4 shows the threshold trial durations for disappearance for AKS, HKH, and MEL with 95% bootstrap confidence intervals (Efron, 1979; Efron and Tibshirani, 1993). Replicating Experiment 1, there was an interaction between increment versus decrement mask dots on the one hand and increment versus decrement target dots on the other. For decrement targets, both increment and decrement masks were equally ineffective for AKS and HKH. However, for MEL, the decrement target was more effectively masked by the increment mask than the decrement mask. Also, replicating Experiment 1, increment targets were uniformly more effectively masked by decrement masks than increment masks. Decrement targets would appear to be more difficult to mask than increment targets, regardless of the luminance or contrast of the mask. Decrement masks were more effective than increment masks only for increment targets for two participants.

DISCUSSION
Again, decrement targets were more difficult to mask than increment targets. Interestingly, decrement masks were more effective than increment masks only for increment targets. This pattern of results replicates that found in Experiment 1.

Asymmetries in the effects of various independent variables on targets and masks have been found before. For example, the ease with which a target can be masked increases with the contrast of the target; high contrast targets disappear more quickly than low contrast targets (Bonneh et al., 2001). However, high contrast masks are more effective than low contrast masks. The opposite effects of stimulus element contrast for target elements and mask elements suggest asymmetric mechanisms.

OVERALL DISCUSSION
Glass patterns seem to be processed in two stages, with structural aspects at higher levels in inferotemporal cortex (Tanaka, 1992). Dynamic Glass patterns stimulate motion areas of the superior temporal sulcus (Krekelberg et al., 2003). V1 and V2 cells in Macaca do not discriminate among the dot orientations in dynamic Glass patterns, though they do discriminate these patterns from dynamic anti-Glass patterns and drifting sine-wave gratings, as one would predict from their respective receptive field properties (Smith et al., 2002; Smith et al., 2007). That essentially no effect was observed among the mask types used in Experiment 1 would suggest that the appearance of coherent motion may be critical for the enhanced masking due to an incoherent mask reported by Wells et al. (2011). Since the dynamic Glass and anti-Glass patterns should have produced no oriented mask adaptation, they should have produced greater target contrast gain reduction from the tran-
sient to sustained inhibition; the dynamic Glass and anti-Glass patterns should have been more effective masks than coherent motion.

Interestingly, decrement targets were reliably more difficult to mask than increment targets, and decrement masks were more effective than increment masks when presented with just increment targets. Given the lack of mask type effects, the ON/OFF-dichotomy clearly carries its influence to the level of perceived motion coherence. Further, the asymmetry in the effects of increment and decrement masks on increment and decrement targets might lead one to speculate that they reflect the ‘importance’ of detecting decrements in the environment (see, for example, Ratliff et al., 2010).

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