Evidence against the temporal subsampling account of illusory motion reversal

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An illusion of reversed motion may occur sporadically while viewing continuous smooth motion. This has been suggested as evidence of discrete temporal sampling by the visual system in analogy to the sampling that generates the wagon–wheel effect on film (D. Purves, J. A. Paydarfar, & T. J. Andrews, 1996; R. VanRullen, L. Reddy, & C. Koch, 2005). In an alternative theory, the illusion is not the result of discrete sampling but instead of perceptual rivalry between appropriately activated and spuriously activated motion detectors (K. A. Kline, A. O. Holcombe, & D. M. Eagleman, 2004, 2006). Results of the current study demonstrate that illusory reversals of two spatially overlapping and orthogonal motions often occur separately, providing evidence against the possibility that illusory motion reversal (IMR) is caused by temporal sampling within a visual region. Further, we find that IMR occurs with non-uniform and non-periodic stimuli—an observation that is not accounted for by the temporal sampling hypothesis. We propose, that a motion aftereffect is superimposed on the moving stimulus, sporadically allowing motion detectors for the reverse direction to dominate perception.

Keywords: visual perception, illusory motion, temporal sampling, motion aftereffect

Introduction

Illusory motion reversal (IMR) of periodic moving patterns—such as ceiling fans and hubcaps—can be sporadically observed under continuous light sources (Kline, Holcombe, & Eagleman, 2004; Purves, Paydarfar, & Andrews, 1996; Schouten, 1967; VanRullen, Reddy, & Koch, 2005). One explanation for this phenomenon, offered by Purves et al. (1996), was based on the hypothesis that the visual system takes snapshots of the scene—in other words, it processes discrete epochs of sensory input, and concatenates them to construct a continuous percept (Andrews, White, Binder, & Purves, 1996). In analogy to the wagon–wheel illusion seen on film, it was suggested that spatiotemporal information between perceptual frames is lost, causing the visual system to mismatch the periodic elements of the stimulus between frames. Thus, through a process of correspondence matching (Burt & Sperling, 1981; Caelli, Manning, & Finlay, 1993), a wheel spoke traveling more than one half of a period clockwise between snapshots will erroneously be matched with its predecessor, giving the impression that the preceding spoke traveled less than half of a period counterclockwise between frames.

To explain the sporadic and unpredictable nature of the reversals, it has been suggested that the "frame rate" of the sampling drifts randomly around a mean value (VanRullen et al., 2005), yielding flexible episodes which may be context dependent. In a refutation of the sampling hypothesis, Kline et al. (2004) demonstrated that two side by side identical moving patterns do not undergo illusory reversal simultaneously, as would be required by a discrete sampling of the visual scene. This observation of independent reversals holds whether the two stimuli are in the same or different hemifields, precluding the possibility of independent sampling of the two hemispheres (Kline et al., 2004). However, these findings did not rule out the possibility that regions of the visual field are sampled independently, perhaps in an object-based manner (VanRullen, 2006). Given this uncertainty, several authors remain advocates of the snapshot hypothesis (Andrews & Purves, 2005; Rojas, Carmona-Fontaine, Lopez-Calderón, & Aboitiz, 2006; Simpson, Shahani, & Manahilov, 2005; VanRullen, 2006, 2007; VanRullen et al., 2005).

In this paper, we put the snapshot hypothesis to the next level of testing. First, to address the possibility of localized snapshots, we designed a stimulus consisting of two spatially overlapping, orthogonal periodic motions. The experimental question was whether IMR of the two motions would occur separately or simultaneously. If illusory reversals of the two motions occur independently, that will rule against localized snapshots.

Second, both the cinematographic wagon–wheel effect and the temporal sampling mechanism proposed by others (Purves et al., 1996; Simpson et al., 2005; VanRullen et al., 2005) require periodicity. That is, the pattern must be composed of identical (or very similar) repeating

elements for incorrect token matching to occur. If the perceptual snapshot hypothesis is responsible for IMR, then the illusion should not occur with stimuli such as a random texture or a periodic pattern with distinct elements. In contrast, the rivalry hypothesis of IMR (Kline et al., 2004; Kline, Holcombe, & Eagleman, 2006) proposes that IMR is related to the motion aftereffect but is essentially a motion "during-effect." That is, the continuous stimulation of one direction of motion eventually causes rivalry with the opposite direction of motion, and the balance of the rivalry eventually tips, engendering the perception of reversed motion. Note that in this framework, non-periodic patterns and those containing non-repeating elements should also induce IMR, a prediction we will take advantage of below. To pit these two hypotheses against each other, we here present observers with two different stimuli that should not appear to reverse direction if temporally subsampled.

For clarity, in this paper we refer to the illusion of reversed motion under continuous input as illusory motion reversal (IMR), while reversed motion caused by sub-sampling is called the wagon–wheel effect (WWE). Note, however, that despite the phenomenological differences between the two, other authors have referred to IMR as a wagon–wheel illusion under continuous illumination (e.g., Purves et al., 1996).

Methods

All stimuli were viewed in the dark from 61 cm on a CRT monitor with a refresh rate of 100 Hz, which provided the appearance of smooth motion. Stimuli were generated using Matlab and the psychophysics toolbox. In the first experiment, participants observed a "windmill," turning clockwise at 1 revolution/s and consisting of 5 radial fan-blades (17° of visual angle in diameter; Figure 1a; demonstration at http://neuro.bcm.edu/eagleman/imr). Superimposed on the radial blades was a dynamic, periodic pattern of contracting concentric rings (0.35 cycles/degree). Temporal periods of the windmill and rings were matched at 5 Hz, thereby ensuring that temporal subsampling would lead to a WWE in both motions simultaneously. With the right hand, observers reported the perceived direction of rotation (clockwise or counterclockwise) by holding one of two keys. With the left hand, observers simultaneously reported their perception of concentric motion (inward or outward) by holding one of two keys, corresponding to veridical and illusory motion. Two subjects were excluded because they never perceived IMR in at least one of the motions. The remaining 4 observers perceived reversals in both motions at various points in the experiment.

In the second experiment, 10 observers watched six different moving stimuli for 4 minutes each (randomly ordered and each divided into two 2-minute blocks).

Observers fixated on a point centered 1° below the stimulus. The physical direction of stimulus motion was the same for all blocks for an observer; in half the subjects, this was to the left, in the other half, to the right. Stimuli subtended 23.4° of visual angle, traveling 18.7 cm/s. (corresponding to 8.4 Hz for the stimuli shown in Figures 2a, 2b, 2d, and 2e). Five of the stimuli were periodic, each on a white background with a sigmoid edge mask to prevent the distraction of sudden element
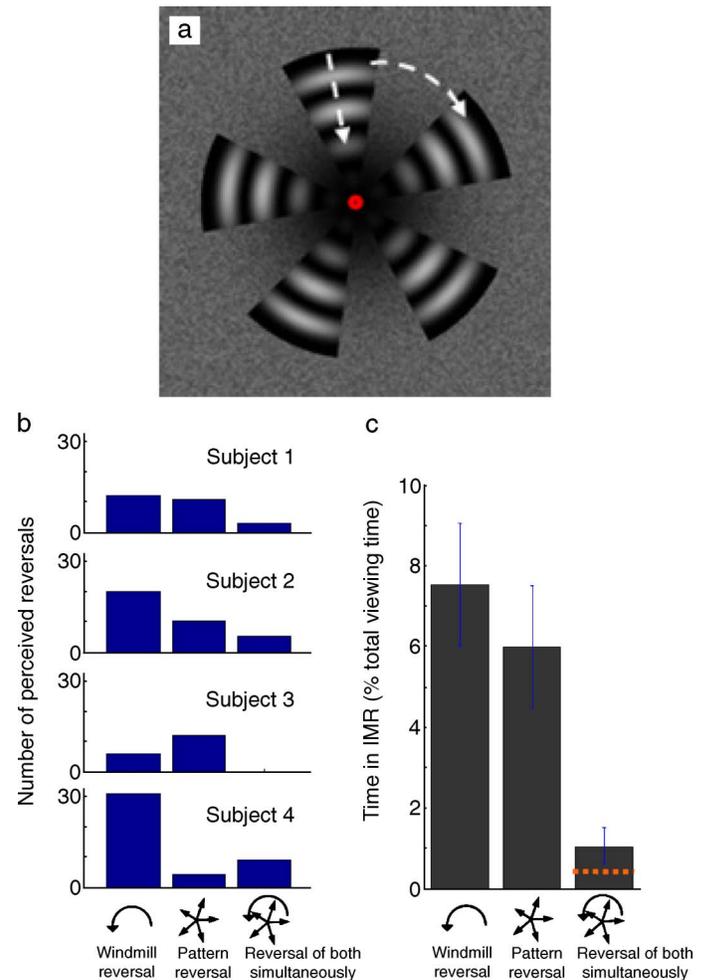

Figure 1. The dual motion windmill experiment tests discrete processing of a restricted region of visual space. (a) Observers fixated at the center of the rotating stimulus composed of five radial blades with a superimposed contracting pattern. The temporal frequencies of the rotating and contracting motions were matched at 5 Hz, such that temporal subsampling would be predicted to cause reversal in both motions simultaneously (see Methods). (b) Results do not support the temporal subsampling hypothesis. Instead, 4 observers saw simultaneous reversals of both motions only a small fraction of the time, if at all. (c) Results averaged over the 4 observers and plotted as the amount of time during which IMR was experienced, as a percentage of the total time of the experiment. Error bars represent the standard error of the mean. In the rightmost column, the dotted red line represents the amount of coincident IMR expected by chance.
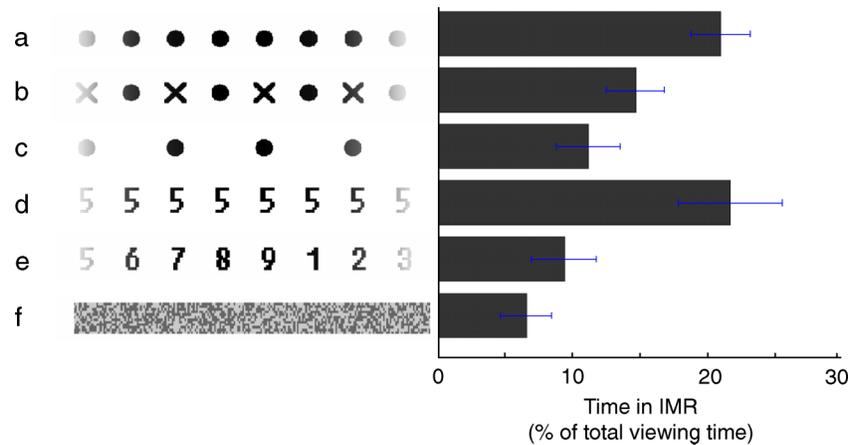
Figure 2. Repeating periodic patterns are not necessary to induce IMR. (a–f) Each of six moving patterns was presented in random order for 2 blocks of two minutes each. A fixation point was centered 1° below the stimulus. Nine of 10 participants perceived IMR in at least one of the non-uniform stimuli. Error bars represent standard error of the mean.

appearance and disappearance. These periodic stimuli consisted of solid black circles (3.1°/c; Figure 2a), alternating black dots and Xs (3.1°/c; Figure 2b), sparse solid black circles (6.2°/c; Figure 2c), a string of identical digits (3.1°/c; Figure 2d), and a series of unique digits (1–9, 3.1°/c; Figure 2e). Observers also watched a non-periodic random dot pattern (each check in the pattern subtended ~0.1° visual angle, speed of pattern = 18.7 cm/s or 17°/s; Figure 2f; demonstration at http://neuro.bcm.edu/eagleman/imr). Observers held down one of two keys to report veridical or illusory motion. Reports of IMR lasting less than 250 ms were rejected as false alarms, following subject self-report.

Results

Addressing snapshots restricted to a region of the visual field

In the dual motion windmill experiment (Figure 1), observers were asked to report IMR while viewing two overlapping, orthogonal motions. Because the temporal periods of both motions were matched, appropriately timed snapshots of the visual field encompassing the stimulus could cause reversal of both motions at once.

The results speak against the hypothesis of snapshots that are restricted to a region of the visual field. Instead, the rotating motion often appeared to reverse direction without simultaneous reversal of the inward motion or instead the inward motion reversed without reversal of the rotating motion (Figures 1b and 1c). The finding that the two motions can reverse separately rules out spatially localized discrete sampling.

We note that if reversals in the two motions are statistically independent, then coincident reversals should

occur 0.045% of the total viewing time (Figure 1c, dotted red line). The amount of coincident reversal appears to be slightly higher than the amount expected by chance. However, this difference is not statistically significant ($t(3) = 1.334$, $p = .274$, power = .09). Although it remains tenable that coincident illusions occur more frequently than expected by chance, the observed frequency falls far short of the predictions of discrete temporal sampling within a region of visual space, which would require that the two motions never reverse independently of each other.

Does the stimulus need to be periodic?

Although the cinematographic WWE requires a periodic stimulus (to allow for incorrect token matching), it is not known whether IMR requires the same. To date, all reports of IMR have used periodic stimuli, such as a moving strip of evenly spaced, identical dots. To address whether such stimuli are necessary for illusory reversals, we presented observers with six different stimuli (Figures 2a–2f), three of which contained non-uniform patterns (Figures 2b, 2e, and 2f).

In contrast to the results predicted by the snapshot hypothesis, 9 subjects perceived IMR while viewing all six of the stimuli (Figure 2). Note that temporal subsampling of stimulus 2b could cause the WWE if the stimulus traveled slightly less than two periods between frames, or if matching between non-identical tokens occurred between frames (Xs matched with Os). However, this cannot explain the reversal of the broadband stimulus (Figure 2f). Moreover, 5 observers subjectively reported that during IMR of the ordered strip of numbers, distinct numbers were perceived. The numbers did not appear to blur or morph as the illusion occurred, but instead, reversed motion seemed to be "painted onto" the stimulus (for a discussion of the idea that motion is painted onto

stimuli, see Crick & Koch, 2003). This volunteered verbal report seems to speak against token matching.

One might argue that a WWE reversal of the broadband stimulus (Figure 2f) only requires the stimulus to *contain* a periodic component at the correct temporal frequency (VanRullen, personal communication). However, this would not explain the *unified* perception of a single strip moving in the opposite direction. Instead, in a discrete sampling framework, only portions of the stimulus would appear to reverse direction while others continued veridically.

We have previously suggested that illusory reversals are caused by the spurious activation of motion detectors tuned for the reverse direction (Kline et al., 2004, 2006). Some spatial frequency tunings are presumably more common than others among the population of detectors (presumably matching the demands of the natural statistics of vision), and this may explain why the frequency of reversals is reduced for the non-periodic stimuli in Figure 2. In any case, the key finding is that all versions of the stimuli indeed give rise to illusory reversals.

Discussion

We have previously ruled out global or hemispheric visual snapshots as an explanation for illusory motion reversal by demonstrating that two identical rotating drums in the same or opposite hemifields do not appear to reverse simultaneously (Holcombe, Clifford, Eagleman, & Pakarian, 2005; Kline et al., 2004, 2006). We here extended that observation by designing two motions in a single object placed within a small portion of the visual field (Figure 1a). While a snapshot model would predict that both motions should reverse simultaneously, we found instead that illusory reversal of one motion most often occurred independently of reversal in the other (Figure 1b), demonstrating that snapshots spanning the entire stimulus cannot account for the illusion. We cannot at present rule out attentionally partitioned object-based snapshots (VanRullen, 2006) since at times the radial elements and the concentric rings could be perceived as separate objects.

In a second experiment, we addressed the fact that the cinematographic wagon–wheel effect requires a periodic moving pattern; the illusion should not occur with stimuli composed of distinct elements or a random textured pattern with no periodicity. In contrast, however, we found that IMR indeed occurs with such stimuli (Figure 2), although less frequently than when viewing periodic stimuli composed of identical elements. Note that discrete temporal sampling of the broadband noise stimulus used in Experiment 2 cannot account for a cohesive reversal of the entire stimulus. Instead, in a sampling framework, illusory reversals would occur independently for particular frequency bands in the stimulus, creating the perception that portions of the stimulus moved in reverse while other portions continued in the veridical direction. In contrast to this, subjects had a clear, strong sensation of the entire stimulus reversing as a unified whole. This can be verified by the reader with the online demonstrations. The snapshot hypothesis of vision does not seem to account for illusory reversal of this and other non-repeating periodic stimuli.

Given the current data, we suggest that adaptation of motion detectors signaling the veridical direction induces (Kline et al., 2004, 2006) or at least contributes to (VanRullen, 2007) the occurrence of IMR. The well-known motion aftereffect demonstrates that populations of opposing motion detectors compete to drive perception. We propose that the motion aftereffect (MAE) can be superimposed on a moving stimulus, creating a motion during-effect that can lead to illusory motion reversal. A potential problem with this "during-effect" framework may be the recent demonstration by VanRullen (2007) that certain manipulations that led to increased MAE concomitantly led to decreased IMR. However, if the veridically and spuriously activated motion detectors (which are proposed to be in competition, Kline et al., 2004, 2006) are differentially affected by manipulations of contrast and eccentricity, the during effect hypothesis may still apply. Future experiments will be required to clarify these possibilities.

Acknowledgments

Commercial relationships: none.
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