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Vision Research xxx (2005) xxx–xxx
Vision Research
www.elsevier.com/locate/visres

Reply

Illusory motion reversal does not imply discrete processing: Reply to Rojas et al.

Under certain conditions a smoothly moving pattern viewed under continuous light is sporadically perceived to reverse direction (Purves, Paydarfar, & Andrews, 1996; Schouten, 1967). The existence of this surprising illusion has been taken as evidence that the visual system takes discrete snapshots of the visual scene (Andrews & Purves, 2005; Crick & Koch, 2003; Purves et al., 1996; Van Rullen, Reddy, & Koch, 2005). In our previous work we have provided evidence against this supposition (Kline, Holcombe, & Eagleman, 2004). Our key observation was that two identical rotating drums do not appear to reverse simultaneously, although simultaneous reversal is predicted by the hypothesis of discrete sampling of the scene. As a result, we proposed that illusory motion reversal results from rivalry between motion detectors tuned for the direction of the moving pattern in competition with spuriously activated detectors tuned for the opposite direction (Kline et al., 2004). In an effort to strike a middle ground between the snapshot theory of perception and our proposal of rivalry among Reichardt-like motion detectors (RLMDs), Rojas, Carmona-Fontaine, López-Calderón, and Aboitiz (2005) suggest that if RLMDs are *themselves* discrete samplers, then the snapshot hypothesis is still valid—but at the level of the individual motion detector rather than the whole visual field (Rojas et al., 2005). In other words, Rojas et al. attempt to salvage a theory of temporally quantized visual processing by suggesting it may happen at an extremely local level.

The main problem with Rojas' claim is that it is based on the idea that RLMDs are *temporally* discrete, and therefore subject to temporal aliasing. However, the motion detector model proposed by Reichardt (1961) is not temporally discrete and hence is not susceptible to *temporal* aliasing. A subunit of the RLMD receives asymmetrically delayed input from two visual receptive fields, such that sequential stimulation of the receptive fields (e.g., by a stimulus moving in the preferred direction) will result in the excitation of the motion detector. This produces a response that is continuous in time. RLMDs can be susceptible to *spatial* aliasing if they are not preceded by the appropriate pre-filters that Reichardt (1961) also proposed. That is, a periodic pattern moving in the anti-preferred direction may spuriously activate the detector (see Fig. 1 in Kline et al., 2004). This type of aliasing, which was proposed by Kline et al. (2004) to underlie illusory motion reversal, is very different from temporally-discrete processing, both at the level of the motion detector as described by Rojas et al. (2005), and at the full-field perceptual level.

We note, however, that we cannot currently rule out an intermediate level of temporally discrete processing. Our previous demonstration that two identical rotating drums do not appear to reverse simultaneously does not directly address the possibility of temporally discrete sampling restricted to limited portions of the visual field ('spatially-localized'), or to individual objects ('object-based') (Kline et al., 2004; van Rullen et al., 2005). In other words, discrete samples might be taken across the visual field, but at a limited scale, such that the samples of different parts of the field would be potentially out of synchrony, leading to independent illusory motion reversals. However, new observations in our laboratory speak against this possibility. Spatially overlapping motions, according to the localized snapshot theory, should appear to reverse simultaneously during illusory motion reversal. Yet we found that rotating fan blades may appear to reverse direction while moving patterns superimposed on the fan blades continue to appear to move in the veridical direction, and vice versa (Fig. 1). Although this experiment speaks against spatially localized sampling, it does not necessarily address object-based sampling, because of the difficulty in defining an 'object' (i.e., the fan blades and the concentric rings may be perceived as independent objects at times).

Unfortunately, a second misunderstanding of Reichardt motion detector function has led to a separate line of criticism against the rivalry hypothesis. It has been incorrectly supposed that RLMDs are tuned to velocity, not to temporal frequency (Andrews & Purves, 2005; van Rullen et al., 2005). As a result of this misconception, reports that illusory motion reversal occurs more often with stimuli presented at a temporal frequency around 10 Hz has been taken as evidence against our rivalry hypothesis (Andrews & Purves, 2005; Simpson, Shahani, & Manahilov, 2005; van Rullen et al., 2005). If RLMDs were truly tuned to velocity and not temporal frequency, then rivalry at the level of motion detectors could not account for the observed temporal

0042-6989/$ - see front matter
doi:10.1016/j.visres.2005.08.021

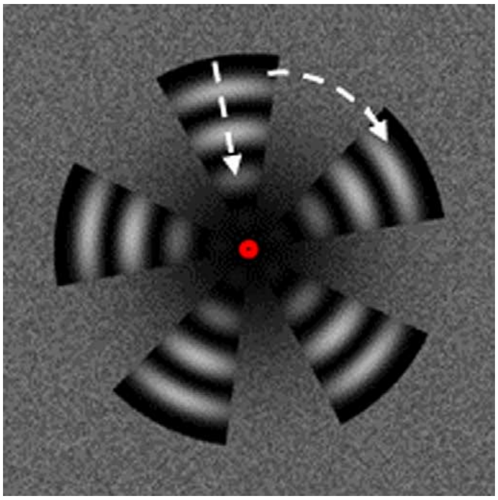

Fig. 1. Five fan blades rotate in the clockwise direction (temporal frequency of blades 3.3 Hz). Contracting concentric rings are superimposed on each blade (temporal frequency of rings 3.3 Hz). Since the temporal frequency of the two motions are matched, a temporal sub-sampling would have to reverse both motions at once. However, in contrast, observers often report that one motion appears to reverse while the other continues veridically. This result rules out a spatially-localized version of the snapshot theory. Fan stimulus subtended 17° of visual angle. The spatial frequency of the pattern on the fan blades was 0.44 cycles/degree. Demonstration available at nba.uth.tmc.edu/homepage/eagleman/imr.

frequency dependence. However, velocity tuning occurs only for the delay-and-compare subunit of the RLMD (Zanker, Srinivasan, & Egelhaaf, 1999). A full Reichardt detector, in which the activity of two delay-and-compare subunits tuned to opposite directions are subtracted from each other, is tuned to temporal frequency (Reichardt, 1961). If the illusion primarily results from extensive adaptation allowing detectors tuned to the anti-preferred direction to occasionally dominate the rivalry, this might be expected to occur most often with a stimulus that has the greatest potential to adapt the system—that which drives the system the most. In fact, the underlying mechanisms in the visual system are most sensitive to temporal frequencies around 10 Hz (Anderson & Burr, 1985; Snowden & Hess, 1992).

Purves et al. (1996) thought that discrete temporal sampling by our visual systems cause the motion reversal illusion, just as the discrete temporal frames presented in the cinema yield the wagon wheel illusion on screen. In the same spirit, Rojas et al. have argued that the illusion may arise from discrete processing in individual motion detectors. But our data, together with a better understanding of Reichardt motion detectors, undermine these arguments. Since the illusion does not provide good evidence for temporally discrete processing, it is misleading to refer to illusory motion reversal as a ''wagon-wheel illusion under continuous light'' (Andrews & Purves, 2005; van Rullen et al., 2005). With our current state of knowledge, it appears that illusory motion reversal does not provide support for temporally quantized processing either at the level of motion detectors, spatial regions, or the whole visual field.

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Received 9 August 2005