

# The vergence eye movements induced by radial optic flow: Some fundamental properties of the underlying local-motion detectors

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## Abstract

Radial optic flow applied to large random dot patterns is known to elicit horizontal vergence eye movements at short latency, expansion causing convergence and contraction causing divergence: the Radial Flow Vergence Response (RFVR). We elicited RFVRs in human subjects by applying radial motion to concentric circular patterns whose radial luminance modulation was that of a square wave lacking the fundamental: the missing fundamental (*mf*) stimulus. The radial motion consisted of successive  $\frac{1}{4}$ -wavelength steps, so that the overall pattern and the  $4n+1$  harmonics (where  $n = \text{integer}$ ) underwent radial expansion (or contraction), whereas the  $4n-1$  harmonics—including the strongest Fourier component (the 3rd harmonic)—underwent the opposite radial motion. Radial motion commenced only after the subject had fixated the center of the pattern. The initial RFVRs were always in the direction of the 3rd harmonic, e.g., expansion of the *mf* pattern causing divergence. Thus, the earliest RFVRs were strongly dependent on the motion of the major Fourier component, consistent with early spatio-temporal filtering prior to motion detection, as in the well-known energy model of motion analysis. If the radial *mf* stimulus was reduced to just two competing harmonics—the 3rd and 5th—the initial RFVRs showed a nonlinear dependence on their relative contrasts: when the two harmonics differed in contrast by more than about an octave then the one with the higher contrast completely dominated the RFVRs and the one with lower contrast lost its influence: winner-take-all. We suggest that these nonlinear interactions result from mutual inhibition between the mechanisms sensing the motion of the different competing harmonics. If single radial-flow steps were used, a brief inter-stimulus interval resulted in reversed RFVRs, consistent with the idea that the motion detectors mediating these responses receive a visual input whose temporal impulse response function is strongly biphasic. Lastly, all of these characteristics of the RFVR, which we attribute to the early cortical processing of visual motion, are known to be shared by the Ocular Following Response (OFR)—a conjugate tracking (version) response elicited at short-latency by linear motion—and even the quantitative details are generally very similar. Thus, although the RFVR and OFR respond to very different patterns of global motion—radial vs. linear—they have very similar local spatiotemporal properties as though mediated by the same low-level, local-motion detectors, which we suggest are in the striate cortex.

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## 1. Introduction

A moving observer who looks in the direction of heading experiences a radial pattern of optic flow, and such visual stimuli have been shown to elicit horizontal vergence

eye movements at very short latencies,  $\sim 85$  ms in humans (Busettini, Masson, & Miles, 1997; Yang, FitzGibbon, & Miles, 1999) and  $\sim 60$  ms in monkeys (Inoue, Takemura, Suehiro, Kodaka, & Kawano, 1998). Centrifugal (expanding) flow, which signals forward motion of the observer, results in convergence of the two eyes and centripetal (contracting) flow, which signals backward motion, has the opposite effect. These Radial-Flow Vergence Responses (RFVRs), as they are termed, would be useful to the

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moving observer insofar as they help to keep both eyes aligned on the object of regard in the scene ahead and hence can be thought of as “compensatory”. The gain of the initial RFVRs was shown to be a linear function of the preexisting vergence angle and hence would be inversely proportional to viewing distance under normal viewing conditions (Yang et al., 1999). Given that the vergence eye movements required to compensate for a given forward motion of the observer are inversely proportional to the square of the viewing distance, it was suggested that this dependence on the preexisting vergence angle would help the observer who wants to fixate far ahead to avoid making vergence eye movements in response to the optic flow created by nearby objects. In monkeys, bilateral lesions of the Medial Superior Temporal (MST) region of the cerebral cortex, which is an area known to contain many neurons sensitive to radial optic flow (Duffy, 2000; Duffy & Wurtz, 1991a, 1991b, 1995, 1997a, 1997b, 1997c; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Saito et al., 1986; Tanaka & Saito, 1989; Tanaka et al., 1986), result in major impairments of these eye movements (Takemura, Inoue, & Kawano, 2002; Takemura, Murata, Kawano, & Miles, 2007).

The RFVR is one of three ocular tracking mechanisms that are activated at ultra-short latencies by large-field visual stimuli: for review, see Miles (1998) and Miles, Busetini, Masson, and Yang (2004). One of these other mechanisms, referred to as the Disparity Vergence Response (DVR), is thought to work in parallel with the RFVR, generating vergence eye movements to help maintain binocular alignment on objects that lie ahead by utilizing the binocular parallax (Busettini, Miles, & Krauzlis, 1996; Masson, Busetini, & Miles, 1997; Masson, Yang, & Miles, 2002b). The third mechanism, the Ocular Following Response (OFR), generates conjugate (version) eye movements in response to motion perpendicular to the line of sight and is thought to help stabilize gaze on objects that move within the plane of fixation (Barthelemy, Vanzetta, & Masson, 2006; Busettini, Miles, & Schwarz, 1991; Masson, Busetini, Yang, & Miles, 2001; Masson & Castet, 2002; Masson, Rybarczyk, Castet, & Mestre, 2000; Masson, Yang, & Miles, 2002a; Masson et al., 2002b; Miles & Kawano, 1986; Miles, Kawano, & Optican, 1986). These three mechanisms have previously been shown to have a number of features in common—including mediation by the MT/MST region of cortex, at least in monkeys (Takemura et al., 2007)—and have been suggested to work in harmony to help stabilize gaze in 3-D: for review, see Miles (1998) and Miles et al. (2004). The present experiments were undertaken to determine if the RFVR also shares with the OFR and DVR several additional features that we have uncovered only recently. Experiments 1 and 2 in the present study used broadband radial-motion stimuli and indicate that the RFVR depends critically on the Fourier composition of the stimulus, consistent with mediation by local spatio-temporal filters; this is in line with recent findings on the OFR (Chen, Sheliga, FitzGibbon, & Miles, 2005; Sheliga, Chen, FitzGibbon, & Miles, 2005a) and

the DVR (Sheliga, Chen, FitzGibbon, & Miles, 2005b; Sheliga, FitzGibbon, & Miles, 2006b) using broadband stimuli. Experiment 3 in the present study used two competing radial-motion stimuli and indicates that the RFVR displays a highly nonlinear dependence on the relative contrast of the two stimuli, whereby the one with the higher contrast can totally dominate RFVRs; a similar winner-take-all (WTA) outcome has also been reported for the OFR (Sheliga, Kodaka, FitzGibbon, & Miles, 2006c) and the DVR (Sheliga, FitzGibbon, & Miles, 2007) when competing stimuli are used. Lastly, Experiment 4 in the present study used apparent radial-motion stimuli consisting of single steps (“two-frame movies”) and indicates that the RFVR can be reversed by a brief inter-stimulus interval (ISI), consistent with the idea that the visual input to the underlying motion detectors has a biphasic temporal impulse response; this is in line with recent findings on the OFR using an ISI with single-step motion stimuli (Sheliga, Chen, FitzGibbon, & Miles, 2006a). A quantitative comparison of these new RFVR data with the previously reported OFR data leads to the hypothesis that these two reflexes rely upon the same low-level, local-motion detectors.

## 2. Experiment 1: Dependence of the RFVR on the harmonic content and the contrast of the stimulus

Recent studies manipulated the Fourier composition of the visual stimuli used to elicit the OFR and the DVR (Sheliga et al., 2005a, 2005b, 2006b), employing a variety of 1-dimensional spatial patterns including a square wave lacking the fundamental, which is the so-called missing fundamental (*mf*) stimulus. As first pointed out by Adelson (1982), the *mf* stimulus has the special property that, when advanced in  $\frac{1}{4}$ -wavelength steps its harmonics all shift  $\frac{1}{4}$  of their respective wavelengths, the  $4n+1$  harmonics (like the 5th, 9th etc) in the forward direction and the  $4n-1$  harmonics (like the 3rd, 7th etc) in the backward direction. Importantly, the amplitude of the *i*th harmonic of the *mf* stimulus is proportional to  $1/i$ , so that the major Fourier component is the 3rd harmonic. It has been known for some time that when *mf* stimuli are moved in successive  $\frac{1}{4}$ -wavelength steps, the direction of perceived motion is often opposite to the actual motion (Adelson, 1982; Adelson & Bergen, 1985; Baro & Levinson, 1988; Brown & He, 2000; Georgeson & Harris, 1990; Georgeson & Shackleton, 1989). It was generally argued that 1st-order-motion detectors were responsible for the perception here and that these detectors were not sensing the motion of the raw images (or their features) but rather the motion energy in a spatially filtered version of the images, so that the perceived motion depended critically on the harmonic composition of the spatial stimulus and especially the principal Fourier component, the 3rd harmonic. On the other hand, subjects sometimes perceived motion in the correct direction and this was generally attributed to higher-order detectors sensitive to the motion of specific features in

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