A SECOND ORDER FEEDBACK MODEL OF VISUAL TRANSDUCTION IN CONES OF THE MONKEY *MACACA FASCICULARIS*

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Abstract

A representative existing model of visual transduction in the retinal cones of the macaque monkey combines parametric curves and feedback models to give a detailed description of cone response dynamics. Here, we approximate this previous model with a second order feedback control system, capturing key dynamic characteristics of cone responses, namely, a system with a natural frequency of 5 Hz and peak response time of 50ms. Even if considerably simplified when compared to the original model, the second order feedback system is found useful as a computational tool to simulate blurring of moving visual cues. Comparison with a signal averaging model - an accepted approximation of motion blur - shows that second order feedback more closely follows visual perception of motion smear in various stimulus patterns. The finding that cone dynamics capture perceptual phenomena that has been hitherto associated with motion pathways raises questions about the neurological origins of motion blur effects.

Visual transduction in rods and cones of the retina constitutes the earliest step in neural representation of optical signals in the visual system. Understanding the nature of these early neural representations provides clues to the building blocks on which consecutive processing stages are based, and is hence fundamental to a truer understanding of not only feature representation, but also the perceptual and cognitive utility of different stages of visual processing.

For example, rods are sensitive to small perturbations in luminance intensities, respond fast to changes in luminance, but are distributed at relatively low spatial resolutions. Rods are considered a constituent of the *magno* cellular pathway, that culminates in representation of motion and spatial depth signals, and most of the visual regions connected with the *magno* cellular stream share the processing of depth and motion signals to some extent. Similarly, cones are slow receptors sensitive to high levels of luminance, wave length selective, and distributed at higher spatial resolutions, and constituent of the *parvo* cellular pathway, a visual stream mostly involved in colour and form representation (DeYoe & van Essen, 1988; Livingstone & Hubel, 1988).

The fact that photoreceptors are distributed at a finite spatial resolution and responds with a temporal delay implies that neural representations introduce distortions in visual information, even at the earliest levels of vision. Neural mechanisms in various stages of the visual system are thought to deal with such distortions to some degree, and the effect of their ability or failure to deal with spatio-temporal distortions should be evident at the perceptual level. The still radii illusion is an example of a motion blur distortion (Fig. 1a), believed to result from slow responsiveness of the visual system to fast changes in luminance when the stimulus is displaced relative to the viewer. Due to the dynamic nature of the perceptual effect, this type of illusion has been associated with the motion pathway, and debates about a retinal or cortical origin of the illusion are still ongoing (Gregory, 1980).

In this paper, we challenge the idea that motion blur originates in the motion pathway, by simulating the still radii illusion with an approximation of cone transduction dynamics. In what follows, we first present the computational model, and then compare its performance with an excepted model of motion blur, to distinguish key differences.The implications are discussed in the conclusion.

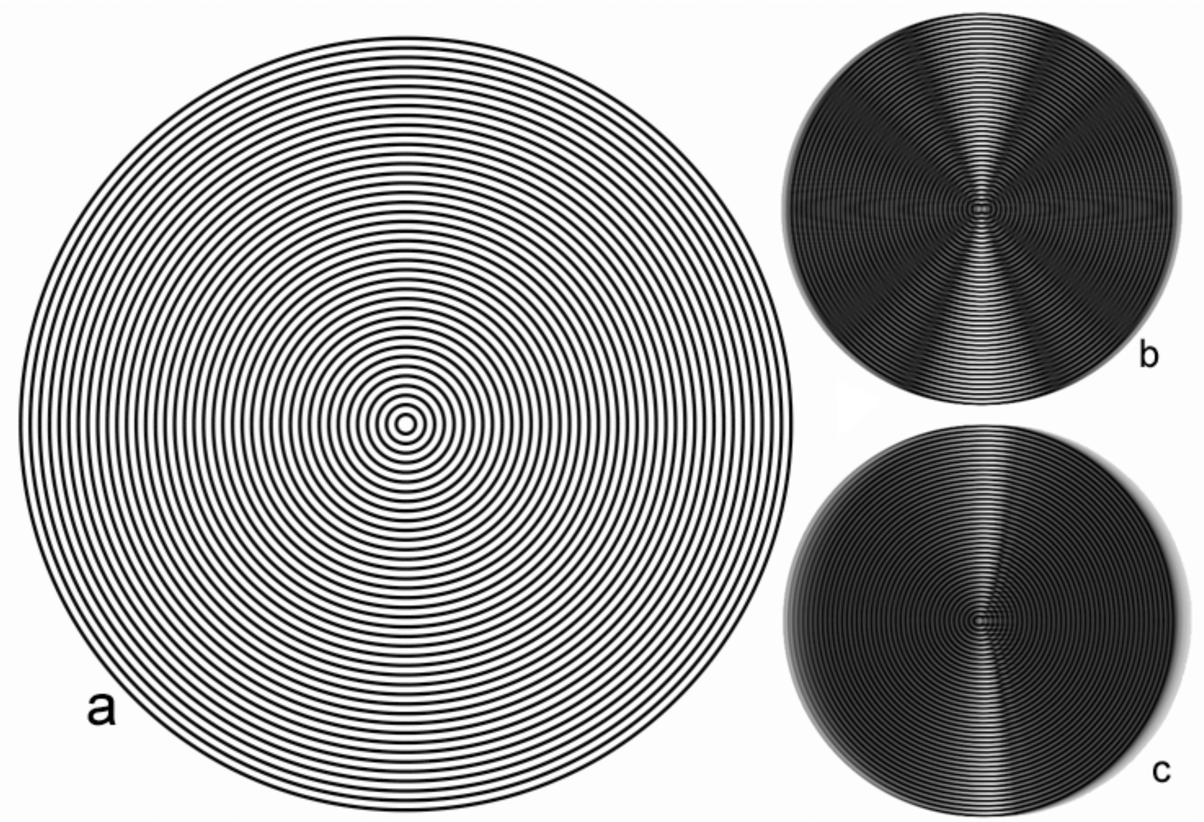

Fig. 1. Originally created by Purkinje in 1823 to investigate contrast illusions and later investigated by Helmholtz, this concentric line pattern (a) has lead Cobbold (1881) to propose the still radii illusion, seen as a vertical hour-glass figure when looking at the tip of your finger while moving it horizontally over the discs. Motion blur simulated with signal averaging (b) and second order feedback, as presented here (c), for leftward horizontal motion.

Method

Schnapf *et al* (1990) provides one of the most detailed accounts of visual transduction in cones of the Macaque monkey. Following the incidence of an impulse of light onto a given cone, there is a delay of about 50ms before the cone reaches a maximal activation potential, after which the output signal of the cone oscillates at 5Hz for about another half second, constituting a rather large distortion of what should be 'veridically' registered as an impulse. The response amplitude is non-trivially affected by the initial luminance of the incident light and other factors. However, here we will use an approximate model of visual transduction in retinal cones, sufficient to demonstrate blurring of texture and other visual cues for the purpose of this paper. Standardized second order feedback control system theory (Abramovici & Chapsky, 2005) offers a concise and reliable design methodology for constructing a stable transfer function that meets the dynamic requirements (Schnapf *et al*, 1990) of a system with rise time of 0.05 s, natural frequency of 5Hz, peak time of 50ms, settling time of 150ms (Fig. 2). The Laplace domain second order transfer function is:

$$F(s) / U(s) = 30(s + 117) / (s^2 + 50s + 3520) \quad (1)$$

U(s) is the system input, in the form of a movie sequence of image frames of the stimulus as it is displaced from one moment to the next, and F(s) is a movie sequence of image frames, showing the simulated cone response at each spatial location in the stimulus at each time step.

Following standard control system design methodology, with discrete simulation frame rate $\tau_{\mathbf{k}} = N_{\mathbf{k}}^{-1} = 240^{-1}$s = 0.0042s, conversion of the transfer function into discrete state space yields the following algorithmic formulae:

$$x_1(\mathbf{k}) = 0.894\, x_1(\mathbf{k-1}) - 6.936\, x_2(\mathbf{k-1}) + 0.002\, u(\mathbf{k}) \quad (2)$$

$$x_2(\mathbf{k}) = 0.002\, x_1(\mathbf{k-1}) - 0.9927\, x_2(\mathbf{k-1}) \quad (3)$$

$$y(\mathbf{k}) = 30\, x_1(\mathbf{k}) + 3500\, x_2(\mathbf{k}) \quad (4)$$

y(**k**) is the system output at time step **k**, and u(**k**) is the **k** th frame in an input animation sequence representing the input image at time step **k**.

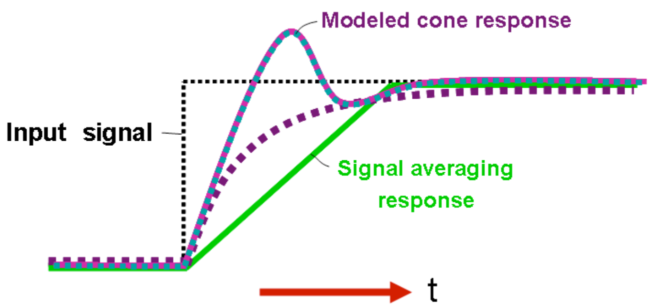

Fig. 2. Comparison of step responses of a signal averaging model and the second order feedback model. Overdamping the second order feedback model (dotted line), equivalent to low pass filtering, renders the model more resistant to discretization errors during simulation.

Simulation movie sequences were based on viewing conditions where two experienced participants in psychophysical experiments (GVT and AT) effortlessly perceived the still radii illusion, with both manually moved stimuli, printed on cardboard, and as Quicktime movie sequences, viewed at a distance of 40cm, subtending 20cm on a Dell E196FB series 19 inch TFT display monitor, at a resolution of 38 pixels per centimeter and frame rate of 60 Hz. Stimuli were displayed at average luminance of 80 cd/m^2, 98% peak-to-peak Michelson contrast. Salient illusions were reported for a translational constant of T^N =145 pixels (stimulus features moving at velocity of 3.8cm/s), with frame rate, N.

Algorithmic implementation and generation of input stimulus animations were implemented in MATLAB on a TOSHIBA Dynabook SS 1610 computer (1.1GHz, 752MB RAM). Input animations were created with parameters obtained in the above psychophysical setting. A higher frame rate, $N_{\mathbf{k}} = 4N$, was used to reduce discretization errors. Note that this model still generated sampling errors during discontinuous motion of the stimulus image, a problem that can be overcome by increased damping of the control system (Fig. 2). Here, we avoided this problem by choosing stimulus displacement paths without abrupt discontinuities.

Results and Discussion

The second order simulated response (Fig. 1c) of the still radii illusion during leftward horizontal movement of Fig. 1a reveals a distinctly bilaterally asymmetric hour glass shaped region of high contrast in the stimulus pattern. In a simple informal test, not described here, 12 out of 15 subjects reported an asymmetric illusion, confirming the qualitative structure of the simulated illusory figure.

Signal averaging (Gosselin & Lamontagne, 1997) – an accepted model of motion blur - averages different stimulus values over a specified time window, and thus does not distinguish between the temporal order in which luminance values change at each image location, resulting in a bilaterally symmetric simulated high contrast region for the still radii illusion (Fig. 1b). With a small increase of complexity, the second order feedback approach more closely follows perception of this well known illusion. Model results also suggest that other perceptual phenomena, such as scintillating phase contours (Fig. 3) may originate at the earliest levels of visual processing, and may be related to motion blur phenomena.

The results imply that transduction dynamics of cones account for the still radii illusion – a phenomenon usually associated with the failure of rods, and consequently motion detectors, to correctly register changes in image luminance. The findings presented here strongly suggest that this type of illusion relates to processes within the *parvo* cellular pathway, and concerns locally stationary regions within stimuli undergoing relative displacements.

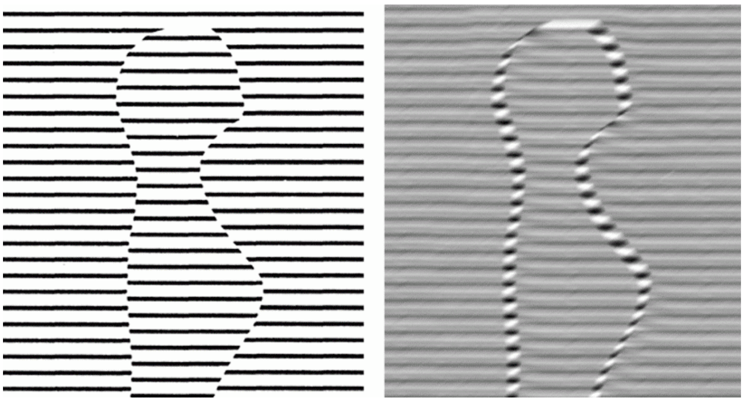

Fig. 2. A phase contour figure (left), after Ehrenstein, and simulated second order feedback transduction response (right).

Acknowledgements

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