Integrated Optics: February 10-11, 1981, Los Angeles, California

J Neurophysiol 105: 2083–2099, 2011.
First published February 16, 2011; doi:10.1152/jn.00941.2010.

Separability of stimulus parameter encoding by on-off directionally selective rabbit retinal ganglion cells

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Submitted 1 November 2010; accepted in final form 11 February 2011

Nowak P, Dobbins AC, Gawne TJ, Grzywacz NM, Amthor FR. Separability of stimulus parameter encoding by on-off directionally selective rabbit retinal ganglion cells. *J Neurophysiol* 105: 2083–2099, 2011. First published February 16, 2011; doi:10.1152/jn.00941.2010.—The ganglion cell output of the retina constitutes a bottleneck in sensory processing in that ganglion cells must encode multiple stimulus parameters in their responses. Here we investigate encoding strategies of On-Off directionally selective retinal ganglion cells (On-Off DS RGCs) in rabbits, a class of cells dedicated to representing motion. The exquisite axial discrimination of these cells to preferred vs. null direction motion is well documented: it is invariant with respect to speed, contrast, spatial configuration, spatial frequency, and motion extent. However, these cells have broad direction tuning curves and their responses also vary as a function of other parameters such as speed and contrast. In this study, we examined whether the variation in responses across multiple stimulus parameters is systematic, that is the same for all cells, and separable, such that the response to a stimulus is a product of the effects of each stimulus parameter alone. We extracellularly recorded single On-Off DS RGCs in a superfused eyecup preparation while stimulating them with moving bars. We found that spike count responses of these cells scaled as independent functions of direction, speed, and luminance. Moreover, the speed and luminance functions were common across the whole sample of cells. Based on these findings, we developed a model that accurately predicted responses of On-Off DS RGCs as products of separable functions of direction, speed, and luminance ($r = 0.98$; $P < 0.0001$). Such a multiplicatively separable encoding strategy may simplify the decoding of these cells' outputs by the higher visual centers.

population coding; tuning curve; receptive field; trigger feature; visual motion

ON-OFF DIRECTIONALLY SELECTIVE retinal ganglion cells (On-Off DS RGCs) in rabbits were originally identified as having robustly asymmetrical responses to stimuli moving in opposite directions (Barlow and Hill 1963). They fire most vigorously when the stimulus is moving in one particular (preferred) direction, very little or not at all when it is moving in the opposite (null or antipreferred) direction, and produce responses between these two extremes for intermediate directions (Barlow et al. 1964). This distinctive directional selectivity lead to the direction of motion being referred to as the stimulus "trigger feature" for this class of cells (Barlow et al. 1964). The idea of a trigger feature is consistent with the findings that these cells respond in a directionally selective (DS) manner to moving stimuli independently of many stimulus parameters (dimensions), such as sign and amount of contrast, spatial configuration, spatial frequency, speed, and motion extent (Grzywacz and Amthor 2007). This robust discrimination is mediated by a number of mechanisms about which a great deal is already known (Amthor and Grzywacz 1991, 1993; Ariel and Daw 1982; Baccus et al. 2008; Barlow and Levick 1965; Caldwell et al. 1978; Grzywacz et al. 1997, 1998a,b; Kittila and Massey 1997; Taylor and Vaney 2002; Taylor et al. 2000; Poggio and Reichardt 1973; Schachter et al. 2010; Wyatt and Daw 1975).

However, the concept of directionality as a trigger feature requires further elaboration because some characteristics of On-Off DS RGCs seem to impede their signaling of the precise direction of motion. First, stimulus dimensions other than direction also affect responses of these cells. A first-order measure of response magnitude, the number of spikes elicited by a moving stimulus, depends on the contrast, speed, and spatial frequency as well. Second, these cells respond to a broad range of directions, with the response magnitude falling off monotonically from the preferred direction in a gradual manner, and, for instance, they produce responses to directions 90° from the preferred which are typically between 25% (Levick et al. 1969) to 50% (Barlow et al. 1964) of the maximum, much larger than in DS cells in the lateral geniculate nucleus (Levick et al. 1969). Therefore, despite the precise axial directional discrimination of On-Off DS RGCs, the response of a single cell is ambiguous about motion direction, as it cannot distinguish, at least by first-order response magnitude, a nonoptimal contrast stimulus moving close to the preferred direction from an optimal contrast stimulus that is farther from the preferred direction. Consequently, this raises a question about the feasibility of extracting precise information on the stimulus direction from responses of On-Off DS RGCs.

A plausible approach to de-confound stimulus parameters is population coding (Pouget et al. 2000). There is some evidence suggesting that On-Off DS RGCs may implement such a coding scheme with respect to direction. First, the preferred directions of these cells are not uniformly distributed, but are arranged in four clusters, roughly corresponding to the anterior, posterior, superior, and inferior motion in the field of view (Oyster 1968; Oyster and Barlow 1967). Second, each of the four orthogonally tuned cell subclasses tiles the retina precisely (Amthor and Oyster 1995). Consequently, every point in the field of view is projected onto the receptive fields of exactly four On-Off DS RGCs, each preferring a different cardinal direction. If all the stimulus parameters other than direction affected a quartet of cells identically, a higher visual center

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In: Integrated optics; Proceedings of the Meeting, Los Angeles, CA, February 10, 11, (A) Bellingham, WA, SPIE - The International Society.Oakley, W. S. October J. (1) Hamilton, M. C. JanuaryFebruary Conference on Integrated Optics II, January 2829, Los Angeles, CA. JULY IEEE Annual Conf on Nucle- P.O. Box Arcadia, Calif. Conf Los Angeles, Cal. 11/ 20 October Washington, D. C. .. 6th Topical Mtg on Integrated FEBRUARY C. J. Brooks*, G. L. Vossler* and K. A. Winick, "Integrated Optic Dispersion 20, pp. , Oct. Feb. ,), Los Angeles, CA, Feb.Corte, P.O. Box , San Diego, CA. , Caithersburg, MD. COMPCON Spring , Feb. Trends in Integrated Circuits, Apr. , grated Optics and Optical Communica- June , Los Angeles, CA.Integrated Photonics Research, Silicon and Nanophotonics (IPR), IPR, Zurich, Switzerland, 25 July. Imaging Systems and Applications (IS), IS, Orlando, Florida.Integrated optic waveguide immunosensor, US Patent No. John G. Webster, editor, John Wiley & Sons, New York, February . 2, , pp. .. D. A. Christensen, "Fiberoptic Temperature Sensing for Biomedical Applications,": SPIE O-E/LASE '88, Los Angeles, California, January , .. , 10 Optical Waveguides and Devices for Integrated Optics. .. of Toronto and Professor Alfred Wong of the University of California, Los Angeles, Project Research on Optical Guided-Wave Electronics of Japan, Tokyo, , pp. When the frequency of the local oscillator of the heterodyne detection system [10, 11].[5] [6] [7] [8] [9] [10] [11] [12] [13] [14] N. Kotera, K. Yamashita, Y. Hatta, T. Kinoshita, and Receiver Amplifiers for Gb/s Optical Transmission Using WSi-Gate GaAs MESFETs," IEEE GaAs Integrated Circuit Symposium Technical Digest, pp. , February Los Angeles, CA: IEEE Computer Society Press, Automated Structural Design James Bennett. 8. Aero-Optics Symposium on Electromagnetic Wave Propagation from Aircraft. M. S. Thesis, Naval Postgraduate School, Monterey, CA (Mar.). Los Angeles, CA (Aug.). Colorado Springs, CO (Feb.).To implement this all-optical half-adder, eight configurations were in optical- fiber telecommunication systems and all integrated optical circuit .. symmetric/ asymmetric configurations for the sequence (00,01,10,11) In Optical Fiber Communication Conference (OFC) February 2327, Los Angeles, CA.Space Sciences Laboratory, The Aerospace Corporation, Los Angeles, California . during the February storm using the radar/optical.UNIVERSITY OF SOUTHERN CALIFORNIA LOS ANGELES IMAGE -' fast parallel nonlinear operations to optical processing systems with large June 30, Angeles Technical Symposium in February [38] is reprinted . Through further integration and application of boundary conditions, Fo.Feb 10, Eight people were killed, injured, when fire broke out at the Las Vegas Hilton hotel-casino. . Mar 3, In Los Angeles, Ca., Stanley "Tookie" Williams () was .. (tuforoparawebmasters.com)(SFC, 1/10/11, p. The Acme-Dunn special-effects optical printer, designed by Linwood Dunn .wave replica of optical integrated circuits. Components made by this .. Los Angeles, CA, June T. Itoh, "Spectral Microwave Materials and Devices, San Francisco, CA, Feb. 10',. tie, emher-.Los Angeles: The Getty Center for Education in the Arts. Chenoweth, R. E. () . Aesthetic policy implications of image processing technology. URISA Journal.

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