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Enroth-Cugell C & Robson J G. The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiology* 187:517-52, 1966.
[Biomedical Engineering Center, Technological Inst., Northwestern Univ., Evanston, and Dept. Physiology, Northwestern Univ. Med. Sch., Chicago, IL]

This paper introduces the use of sinusoidal grating patterns as stimuli for studying the functional characteristics of visual neurones. The utility of spatial-frequency response measurements is demonstrated, and a new classification of retinal ganglion cells based on the linearity or nonlinearity of spatial summation is adopted. [The SCI® indicates that this paper has been cited in over 865 publications since 1966.]

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The experimental work reported in this paper was undertaken during a four-month period spent with Christina Enroth-Cugell in the Biomedical Engineering Center at Northwestern University in 1964 while I was on leave from my home university. Our collaboration was prompted by Fergus Campbell, who had, while notionally supervising my PhD research on muscle control systems, involved me in his work on vision. This work (finally published in 1968)¹ showed that spatial vision could usefully be studied using a small-signal linear systems approach and suggested that this should be extended to visual neurophysiology. Fortunately, Campbell had recently met Enroth-Cugell, who had just started to make recordings from single fibers of cat optic tract. Seizing this opportunity for scientific matchmaking, Campbell hustled me off to take advantage of Enroth-Cugell's equipment as well as her considerable experience of retinal neurophysiology gained as a student of Granit in Stockholm.

Arriving in Evanston with the bits and pieces necessary to convert an eviscerated oscilloscope

into a stimulus pattern generator, we were soon listening to the beguiling crackle of action potentials generated by ganglion cells so sensitive that they responded to low-contrast gratings that we could not always see ourselves. Though understandably gratified by our initial success, we were disappointed that the D(ull)-cells whose spikes we recorded so readily behaved much more nonlinearly than we had hoped. Particularly frustrating was our conviction that there were other more linear I(Interesting)-cells, whose small spikes we thought we could hear through the background noise of our amplifier. Fortunately, we were able to devise a simple electronic circuit to improve the audibility of these smaller spikes, so that at last we could study the cells I had come to find.

Although our experiments were quite soon completed, gestation of a publishable manuscript was laborious and, despite all the heroic efforts and the imprecations of my coauthor, prolonged. However, it was finally accomplished and with little enough trauma that within 10 years we were sufficiently recovered to take up where we had left off, first looking at image quality in the cat eye and later at temporal aspects of ganglion-cell behaviour,² a program that could occupy us until we retire.

This paper seems to have been so often cited partly because it has appealed to several different groups. Visual neurophysiologists have been interested not only in the spatial-frequency response method of studying the spatial characteristics of visual neurones³ but also in the linear/nonlinear classification of retinal ganglion cells (by the time of publication, "I" and "D" had become less emotive "X" and "Y"), which has been extended to other cells in the visual pathway. Visual psychophysicists, particularly those attracted by the spatial-frequency approach to vision, have recognised the advantages of describing the behaviour of retinal ganglion cells in a way that is easily related to psychophysical observations. For the same reason, the paper has interested engineers and applied scientists who have preferred its approach to that of more traditional neurophysiology.

The work described in this paper has been recognised by the 1983 Friedenwald Award of the Association for Research in Vision and Ophthalmology.⁴

1. Campbell F W & Robson J G. Application of Fourier analysis to the visibility of gratings. *J. Physiology* 197:551-66, 1968. (Cited 565 times.)
2. Enroth-Cugell C, Robson J G, Schweltzer-Tong D E & Watson A B. Spatio-temporal interactions in cat retinal ganglion cells showing linear spatial summation. *J. Physiology* 341:279-307, 1983.
3. Robson J G. Frequency domain visual processing. (Braddick O J & Sleigh A C, eds.) *Physical and biological processing of images*. Berlin: Springer-Verlag, 1983. p. 73-87.
4. Enroth-Cugell C & Robson J G. Functional characteristics and diversity of cat retinal ganglion cells. *Invest. Ophthalmol. Visual Sci.* 25:250-67, 1984.