## This Week's Citation Classic <sup>®</sup>\_

Campbell F W & Green D G. Optical and retinal factors affecting visual resolution. J. Physiol.—London 181:576-93, 1965; and Campbell F W & Robson J G. Application of Fourier analysis to the visibility of gratings. J. Physiol.—London 197:551-66, 1968.

[Physiological Laboratory, University of Cambridge, England]

These papers measure the optical transfer function of the optics of the eye and the contrast sensitivity function of the retina-brain. The second one gave rise to the concept that the visual cortex of man had neurones tuned to spatial frequency (size). [The *SCI*<sup>®</sup> indicates that these papers have been cited in more than 705 and 600 publications, respectively.]

## Probing the Human Visual System

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When I joined, in 1952, the Physiological Laboratory in Cambridge, Edgar Adrian, Alan Hodgkin, and Andrew Huxley were the dominant scientists and all had Nobel Prizes by 1963. The research tradition was a "string and sealing wax" affair and most of the apparatus was handmade by each research worker. I once asked Adrian how he dealt with the exponentially increasing research literature and he replied, "It is only necessary to read the first paper which proposes the problem and the last paper that solves it. The ones in-between do not matter."

Among my childhood hobbies were microscopy, photography, and radio electronics; by 1955 the Fourier approach was becoming popular for the study of optical, television, and photographic systems, and I began to wonder whether this new approach might help us to understand how the human visual system operated. In 1957 John G. Robson took over my tiny laboratory to undertake his PhD research on "muscle tremor." After several years of acrimonious argument, we ultimately published the above paper, which neither of us had set out to produce. By 1962 David Hubel and Torsten Nils Wiesel had established the startling discovery that neurones in the cat's visual cortex were tuned

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to orientation.<sup>1</sup> The idea that these same neurones might be also selectively sensitive to spatial frequency provided a mathematical tool to replace a verbal vacuum about how we see objects. Perception psychologists quickly adopted this quantitative approach and abandoned their verbal approach.

Christina Enroth-Cugell and Robson, working at Northwestern University, found that cat ganglion cells could be divided into two types.<sup>2</sup> The X neurone behaved linearly and the Y very nonlinearly. At that time everyone assumed that the visual system was very nonlinear, and they had great difficulty with the referees!

Dan Green, from the University of Michigan, visited me in 1963 when I had become intrigued with the potential use of the laser in vision research. We used it to bypass the optics of the eye and were able to establish the transmission properties of the human retina when it was operating well at high luminance levels. It turned out that the optics of the eye were well matched to the transmission properties of the retina. At that time most textbooks maintained that the resolving power of the eye was solely due to the optics. This paper is also often quoted for the methodology of using a laser in visual research. At that time lasers were thought to be very dangerous to look at; 25 years later I still have not developed cataract!

Colin Blakemore returned from the University of California, Berkeley, to join the staff in 1967. We accidentally discovered a way of proving that the human visual cortex had neurones that were tuned not only to orientation, but also to spatial frequency.<sup>3</sup> Although this was known to be occurring in the cat cortex, there was no positive evidence that the human cortex was similarly organised. This led to a detailed examination of the cortical neurones in the mokey (see the review by R. De Valois and K. De Valois<sup>4</sup> for subsequent developments, including their own very substantial contributions).

This is still a very active field of research, and it is with regret that I cannot find Lord Adrian's "last paper."

4. De Valois R L & De Valois K K. Spatial vision. Oxford, England: Oxford University Press, 1988. (Cited 5 times.)

Hubel D H & Wiesel T N. Receptive fields. binocular interaction and functional architecture in the cat's visual cortex. J. Physiol.—London 160:106-54, 1962. (Cited 2,590 times.) [See also: Hubel D H. Citation Classic. Current ContentsLife Sciences 28(19):23, 13 May 1985.]

Enroth-Cugell C & Robson J G. The contrast sensitivity of retinal ganglion cells of the cat. J. Physiol.-London 187:517-52, 1966. (Cited 1,065 times.) [See also: Robson J G. Citation Classic. Current Contents/Life Sciences 29(8):18, 24 February 1986.]

Blakemore C & Campbell F W. On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. J. Physiol.—London 203:237-60, 1969. (Cited 660 times.) [See also: Campbell F W. Citation Classic. Current Contents/Life Sciences 28(45):24, 11 November 1985.]