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On the response linearity of neurones in cat visual cortex

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Hubel & Wiesel's (1962) description of the receptive fields of cat visual cortical neurones suggests that simple cells may behave linearly, whereas complex cells are clearly non-linear. But Maffei & Fiorentini (1973) have reported that the modulation depth of the response of simple cells to drifting gratings is proportional to the *logarithm* of the grating's contrast. If simple cells were linear, the response would be directly proportional to the contrast.

We recorded extracellularly from neurones in the striate cortex of adult cats, using conventional techniques (see Movshon, 1975). Receptive fields were classified as simple or complex by the criteria of Hubel & Wiesel (1962). Drifting gratings of sinusoidal luminance profile, optimized for orientation and direction of movement, were generated by a PDP 11/20 computer and displayed on the face of an oscilloscope of mean luminance 150 cd m^{-2}, subtending 12·5° by 10° at a distance of 114 cm from the cat's eyes. Artificial pupils (3 mm diam.) were used, and stimuli presented monocularly. The computer also compiled histograms of the responses to successive cycles of the grating. Stimuli of nine different contrasts and a blank were presented for 10 sec each in random order to form one block of trials; the response to five blocks was accumulated for each cell, representing at each contrast the response to 100–200 cycles of the grating.

The responses of simple cells to drifting gratings were modulated in synchrony with the stimulus. The response wave form was not sinusoidal but appeared to be half-wave rectified since the resting discharge in these cells was low or absent. The responses of complex cells were usually unmodulated, but some cells gave a modulated discharge to gratings, superimposed on an unmodulated elevation of firing rate; the modulation, when observed, was most prominent at low spatial frequencies. In this respect, the behaviour of simple cells is reminiscent of that of the cat's X-type retinal ganglion cells; complex cells resemble Y-cells (Enroth-Cugell & Robson, 1966).

Eleven cells (eight simple and three complex) gave modulated responses at some spatial frequency; in each case, the modulation depth was linearly related to contrast but saturated at Michelson contrasts above about 0·3. Six complex cells gave unmodulated responses. In five cases the increase

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in discharge was approximately proportional to the square or cube of contrast and saturated at relatively low contrasts. In one case, the response seemed linearly related to contrast.

The amplitudes of the *modulated* responses of both cell types appear to be linearly related to contrast. Complex cells also show an *unmodulated* elevation of discharge (a non-linearity in itself), whose amplitude is usually not linearly related to contrast. Simple cells appear to be linear, apart from a half-wave rectification.

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REFERENCES

ENROTH-CUGELL, C. & ROBSON, J. G. (1966). *J. Physiol.* **187**, 517–552.
HUBEL, D. H. & WIESEL, T. N. (1962). *J. Physiol.* **160**, 106–154.
MAFFEI, L. & FIORENTINI, A. (1973). *Vision Res.* **13**, 1255–1267.
MOVSHON, J. A. (1975). *J. Physiol.* **249** (3) (in the Press).