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Spatial and temporal contrast sensitivity of striate cortical neurones

THE human visual system detects discontinuities in the spatial or temporal pattern of light falling on the retina; it is relatively poor at detecting steady or slowly changing patterns in either domain. These insensitivities to low rates of change in space and time are not independent: a gentle gradient of illumination can be made more visible by moving it, or modulating its brightness in time. Patterns of alternating light and dark bars with a sinusoidal luminance profile across the bars—sinusoidal gratings—are commonly used to study spatial interactions in the visual system. Some of the earliest workers to use these stimuli noticed that human sensitivity to steady sinusoidal gratings of low spatial frequency is poor, but is markedly enhanced if the grating is moved or modulated in time[1,2].

It has often been proposed that the lateral inhibitory mechanisms responsible for the system's relative insensitivity to low spatial frequencies operate with a slower time course than excitory mechanisms, relatively reducing the effectiveness of lateral inhibition during the presentation of time-varying stimuli[2–6]. Adaptation studies, however, suggest that temporal modulation does not change the spatial frequency tuning of individual spatial filters ('channels') in the human visual system[7,8]; the increased detectability of temporally modulated low spatial frequency gratings could reflect the activity of a separate population of channels, sensitive to low spatial frequencies and relatively insensitive to steady stimuli[8,9].

The available neurophysiological evidence is equivocal. Lateral inhibition in the receptive fields of cat retinal ganglion cells is somewhat slower than excitation from their receptive field centres[10,11]. But at the next stage of visual processing, the lateral geniculate nucleus, there is no difference between the time courses of excitatory and inhibitory mechanisms[12]. We have examined the spatial frequency tuning of single neurones in cat striate cortex to establish whether their tuning is affected by the frequency of temporal modulation: does an increase in the temporal frequency of stimulation enhance a unit's sensitivity to low spatial frequencies?

Adult cats were prepared for electrophysiological recording using techniques described elsewhere[13]. Surgery was performed under short-acting barbiturate anaesthesia (Brietal); for recording, animals were artificially ventilated with a mixture of N_2O–O_2–CO_2 (78 : 20 : 2). The eyes were stabilised with an intravenous infusion of gallamine triethiodide (Flaxedil : 10–30 mg kg^{-1} h^{-1}), coupled with bilateral cervical sympathectomy. Pupils were dilated with homatropine, and the corneas were protected with clear contact lenses. Artificial pupils (3 mm diameter) were placed directly in front of the eyes, and supplementary lenses were chosen to focus them on a screen 114 cm distant. The activity of single neurones was recorded with tungsten-in-glass microelectrodes[14] hydraulically advanced into the cortex through a sealed chamber over a small craniotomy and durotomy. Amplification and display of action potentials were conventional; a standard pulse triggered by each spike was fed to an audiomonitor, from which the experimenter judged the activity of the cell.

Receptive fields were initially mapped on a tangent screen using flashed and moving stimuli, and classified according to the criteria of Hubel and Wiesel[15]. The dominant eye was chosen, and a cathode-ray oscilloscope, whose mean luminance was 150 cd m^{-2}, and which subtended $10° \times 12.5°$ was centred on its receptive field; the other eye was covered.

Drifting sinusoidal gratings of different spatial and temporal frequencies, optimised for orientation and direction of movement, were generated on the oscilloscope face by a PDP-11/20 digital computer. The temporal frequency of a drifting grating is the number of cycles of the grating which pass any point on the screen in 1 s; its contrast is the difference between the luminances of its brightest and dimmest points divided by their sum. For any one cell, as many as forty different gratings were used—eight spatial frequencies, each drifting at five different temporal frequencies. The computer presented the gratings once each in random order, and the experimenter adjusted the contrast of each and turned it on and off under computer control until he judged that its introduction and withdrawal caused a liminal change in the activity of the cell. When a threshold had been estimated for each of the stimuli, their order was re-randomised and they were presented again. Four estimates of each threshold were obtained in this way; the standard error of their mean was normally between 0.1 and 0.2 log units.

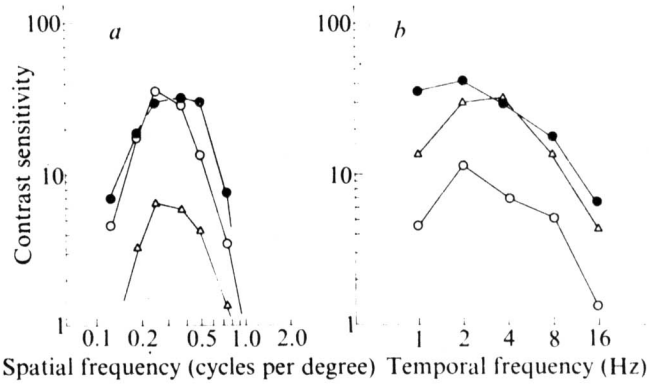

Fig. 1 Spatial and temporal contrast sensitivity functions of a simple cell. *a*, Spatial frequency tuning. The cell's contrast sensitivity as a functions of the spatial frequency is shown for gratings drifting at three temporal frequencies. ○, 1 Hz; ●, 4 Hz; △, 16 Hz. *b*, Temporal frequency tuning. The contrast sensitivity as a function of temporal frequency is shown for gratings of three spatial frequencies. Contrast sensitivity is the reciprocal of the contrast at threshold, $(L_{max} + L_{min})/(L_{max} - L_{min})$ ○, 0.13 cycles per degrees; ●, 0.25 cycles per degree; △, 0.5 cycles per degree.

We examined the spatial frequency tuning of 48 units from 10 cats. Of these, 27 were simple, 18 complex and two non-oriented. We examined spatial frequency tuning as a function of temporal frequency in the manner described above in 26 of these units, 15 simple and 11 complex.

Figures 1 and 2 illustrate the results of two such experiments, performed on a simple cell and a complex cell recorded within 70 μm of each other. Figures 1*a* and 2*a* show that both cells were well-tuned for spatial frequency, and that the general form of their tuning curves was little affected by a 16-fold increase in temporal frequency. Neither the optimum spatial frequencies nor the relative low-frequency sensitivity was systematically changed. Although their overall sensitivity varied considerably with temporal frequency (Figs 1*b* and 2*b*) it is clear that the shapes of their temporal frequency tuning curves at different spatial frequencies were rather similar, apart from a slight tendency

for the sensitivity to slow drift rates to be rather less at non-optimal spatial frequencies. This may reflect the fact that the responses of cortical cells to stimuli which are not optimal for the cell are more transient than those to optimal stimuli[16].

The cells illustrated are typical: in no case did we observe any tendency for cells to become less well-tuned for spatial frequency at high temporal frequencies.

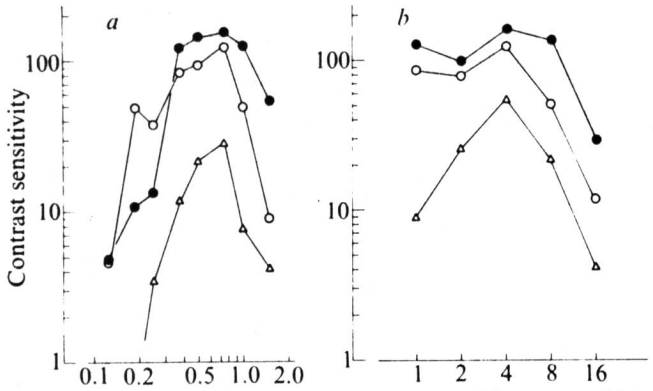

Fig. 2 Spatial and temporal contrast sensitivity functions of a complex cell. *a*, Spatial frequency tuning. ○, 1 Hz; ●, 4 Hz; △, 16 Hz. *b*, Temporal frequency tuning. Conventions as in Fig. 1. ○, 0.38 cycles per degree; ●, 0.75 cycles per degree; △, 1.5 cycles per degree.

The results shown in Figs 1*b* and 2*b* also show that the sensitivity of the units to the velocity of stimulus movement depends on its spatial frequency. Expressed in terms of velocity in degrees per second (temporal frequency divided by spatial frequency), the cells' optima vary by a factor of eight to twelve over the range of spatial frequencies used. This contrasts with the situation when single moving bars are used as stimuli: in that case, the preferred velocity is independent of bar width[13].

Our results may indicate that the effects of temporal modulation on human sensitivity to gratings of low spatial frequency cannot be explained by a change in the spatial frequency tuning characteristics of single neurones, unless neurones in the visual cortex of man are different from those in cat. Although we have not observed much variation among the temporal characteristics of striate neurones, it has been reported elsewhere[16] that visual cortical neurones can be subdivided into a sustained group sensitive to high spatial frequencies and a transient group more sensitive to lower frequencies, which may represent the two populations of neurones required to explain the increase in low-frequency sensitivity produced by temporal modulation seen psychophysically.

It is also interesting that, since the sensitivity of units to the temporal frequency of drift does not depend on the spatial frequency of the stimulus, their selectivity in the domain of stimulus movement seems not to be for velocity but for temporal frequency, or the local rate of change in luminance with time.

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