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DIRECTIONAL AND NONDIRECTIONAL CODING OF A SPATIO-TEMPORAL MODULATED STIMULUS

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Abstract—Contrast thresholds for *apparent flicker* and *direction of movement* were measured separately by using a subthreshold summation technique. The test stimulus consisted of a drifting grating superimposed on an identical grating moving in the opposite direction and set at different subthreshold contrasts. It was found that with increasing contrast of the subliminar grating that: (1) movement thresholds were increasing, (2) apparent flicker thresholds were slightly decreasing and (3) percentage of apparent flicker reports was increasing from 0 to 100. The distinction between flicker and movement thresholds was shown to be justified by two subsidiary experiments which showed that flicker is not to movement what movement is to flicker. A moving subliminar grating facilitates the detection of an objectively flickering grating whereas the reciprocal is not true. This might indicate separate detection of drifting and flickering gratings.

INTRODUCTION

The diochotomy between flicker and movement detectors may be analysed in terms of: (1) a phenomenal difference between two distinct sensations elicited at threshold by a drifting grating and (2) an objective difference between two kinds of stimulations, namely a grating flickering ON–OFF and a drifting grating.

Van Nes *et al.* (1967) mentioned that their subjects could sometimes experience phenomenal (or apparent) flicker at threshold although their stimuli were drifting gratings which were implicitly supposed to elicit some "direction" response. These two kinds of sensations at threshold lead to the idea of a possible distinction of thresholds and furthermore they raise the question as to what extent "apparent flicker" and "direction of movement" are the phenomenal correlates of the activation of one or two detecting mechanisms. Nevertheless, such a distinction of thresholds for a drifting grating is frequently overlooked in the literature although careful definition of threshold criteria seems quite important when one tries to get some information about distinct mechanisms in the visual system (Keesey, 1972; Kulikowski and Tolhurst, 1973; Kulikowski and Gorea, 1978). In the particular case of a drifting grating, the operational distinction between "apparent flicker" and "direction of movement" thresholds might shed some new light on the claim of independence of channels tuned to the detection of opposite directions of movement (Levinson and Sekuler, 1973, 1975a) as opposed to their strong interinhibition at suprathreshold levels (Levinson and Sekuler, 1976b). The first and second experiments reported here are intended to complement Levinson and Sekuler's observations when using some experimental conditions supposed to facilitate an operational distinction between "apparent flicker" and "direction of movement" thresholds and to provide some evidence on the possible existence of distinct mechanisms responsible for the two above-mentioned kinds of sensations.

The third and fourth experiments are more directly concerned with the distinction between mechanisms detecting objective (ON–OFF) flicker and movement and with their possible interactions at threshold. Such a dichotomy has already been mentioned by Tolhurst (1973) who showed that absolute thresholds for flickering and drifting gratings were quite different although such stimuli were generally supposed to be detected by some common transient mechanisms (Kulikowski and Tolhurst, 1973). Breitmeryer (1973) brought some experimental support to this distinction, whereas King-Smith and Kulikowski (1975) advanced the existence of "pure flicker" detectors having "no surround inhibition" as opposed to the "motion" detectors having surround inhibition. The third and fourth experiments reported here are intended to test more directly the independence at threshold of these two hypothetical mechanisms and to question the possibility of some common detection of "apparent" and objective flicker.

METHOD AND MATERIALS

Either vertical or horizontal sinusoidal gratings were generated on the faces of two CRT (P31 phosphor). The gratings were stationary or made to drift and/or to flicker at different temporal frequencies. The two oscilloscope faces were superimposed by optical means. The inspection field was circular and it subtended 3.2° of visual angle at a distance of 120 cm. It was surrounded by a large field of similar chromaticity and mean luminance and it was viewed monocularly with natural pupils. The mean luminance was 3.5 cd/m^2 in the first two and 4.5 cd/m^2 in the last two experiments. Diagonal fixation cross hairs aided optical alignment.

Gratings were made to drift by desynchronizing the signals of the ramp and function generators and their velocity was read as the ratio of their respective frequencies.

When moving gratings were simultaneously generated on both oscilloscope faces their drift rates were rigorously identical since the modulation and ramp signals which generated them were derived from one single modulation and ramp generator, respectively. The optical device enabled the production of gratings drifting in opposite directions.

Square wave, ON–OFF flicker was obtained by means of an electronic device operating as a shutter of the modulating signal at continuously adjustable frequencies which allowed a good match between drift and flicker temporal rates. Two linear, ten turns, potentiometers were used to adjust the test and background contrasts.

Subjects

Three subjects were used in the first experiment. The most extensive data were collected from subject AG, the author. Another subject OP was used in experiment 2. This latter one was also used in experiments 3 and 4 and most extensive data were collected from him. A second subject, already used in the first experiment, also participated in these last two experiments. Three out of the four subjects had already participated in many previous experiments. Except for experiment 2 where only one subject was used, the main trends to be reported below for subjects AG and OP are confirmed by the other subjects. All the subjects, except one who was a corrected myopic, had normal vision. Their ages ranged from 20 to 40 yr.

EXPERIMENT 1

Procedure and stimuli

Contrast thresholds for the detection of a drifting grating were measured as a function of the subliminar contrast of an identical grating moving in the opposite direction. The background contrast was set by the experimenter at 8 or 9 equally spaced levels, from zero up to just below the threshold which had been previously determined. The subject was instructed to increase the contrast of the test grating up to his *first* threshold. He was then asked to specify the direction of drift. In case of no available answer the threshold was referred to as an "apparent flicker" threshold as opposed to an "objective flicker" threshold, which will designate in experiments 3 and 4 the sensation of flicker when the stimulus is an objectively flickering grating. The subject was then instructed to begin once again his contrast adjustment up to the point where he could assert the direction of movement. This new threshold was referred to as a "movement threshold". No such supplementary instruction was necessary if at his first threshold setting the subject indicated the correct direction of movement. This procedure, which departs from a similar technique previously used by Levinson and Sekuler (1975a), enabled the experimenter to plot two distinct curves, namely for "apparent flicker" and for "movement" detection. It is obvious that the number of "apparent flicker" threshold trials strictly depended on the subject himself and hence it was not necessarily equal to that of "movement" threshold trials.

The gratings were vertical bars and their spatial frequency was always 0.63 c/deg. They were temporally modulated at either 3.4 Hz or 8.6 Hz.

Results

Figure 1 shows that the movement thresholds (solid circles) are systematically higher than the apparent flicker thresholds (triangles) and that they are increasing with increasing background contrast. On the contrary, apparent flicker thresholds slightly decrease with increasing background contrast,

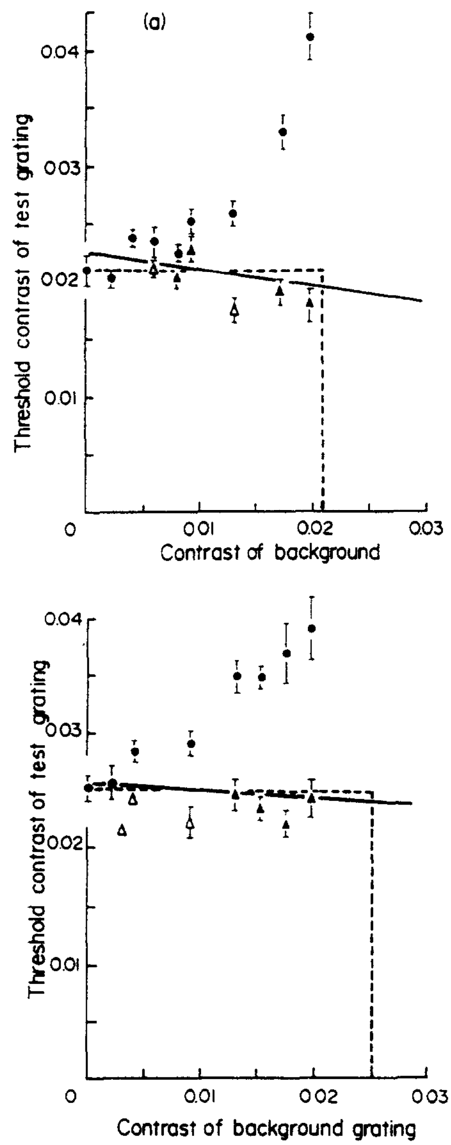

Fig. 1. Direction of movement (circles) and apparent flicker (triangles) thresholds for a drifting grating added to an identical grating moving in the opposite direction and set at different subthreshold contrasts. All solid symbols are averaged over five trials. Empty symbols are averages of less than five trials (see text). The horizontal and vertical dashed lines show movement thresholds without any background. The continuous lines are least square estimates for the movement and apparent flicker thresholds taken together (see text). The observer was A.G., the spatial frequency 0.63 c/deg. The temporal frequencies were 3.4 Hz (a) and 8.6 Hz (b).

although this trend is not statistically significant for the condition 0.63 c/deg, 8.6 Hz (Fig. 1a, slope −0.28, $p < 0.05$; Fig. 1b, slope −0.04, not significant).

The continuous lines in Fig. 1 show what would have been obtained by always recording the first threshold regardless of the phenomenal appearance of the stimulus. Mixing together direction of movement and apparent flicker thresholds would have led to taking into account for low subliminar contrasts either movement thresholds only (Fig. 1a) or some weighted average of movement and apparent flicker thresholds (Fig. 1b), and for high subliminar contrasts only apparent flicker thresholds. In this case and for both experimental conditions the slopes of the regression lines do not depart significantly from the horizontal although they have a negative sign, opposite to that reported by Levinson and Sekuler (1975a) (Fig. 1a, slope −0.14; Fig. 1b, slope −0.012).

EXPERIMENT 2

The observation that for low subliminar contrasts flicker sensation is either never experienced or only rarely reported raised the question as to what extent phenomenal flicker was related to the contrast of the subthreshold moving grating. This was the object of the second experiment.

Procedure and stimuli

The procedure was very similar to that already mentioned in the first experiment, excepting that only frequencies of apparent flicker reports at the first threshold were taken into account. Thus, once the subject had set the contrast at his first threshold, no further measurement was performed whatever the reported sensation. Ten trials were run for each level of subliminar contrast.

The gratings were vertical as previously. Two combinations of spatial and temporal frequencies were used, namely 0.63 c/deg, 3 Hz, and 1.5 c/deg, 7 Hz.

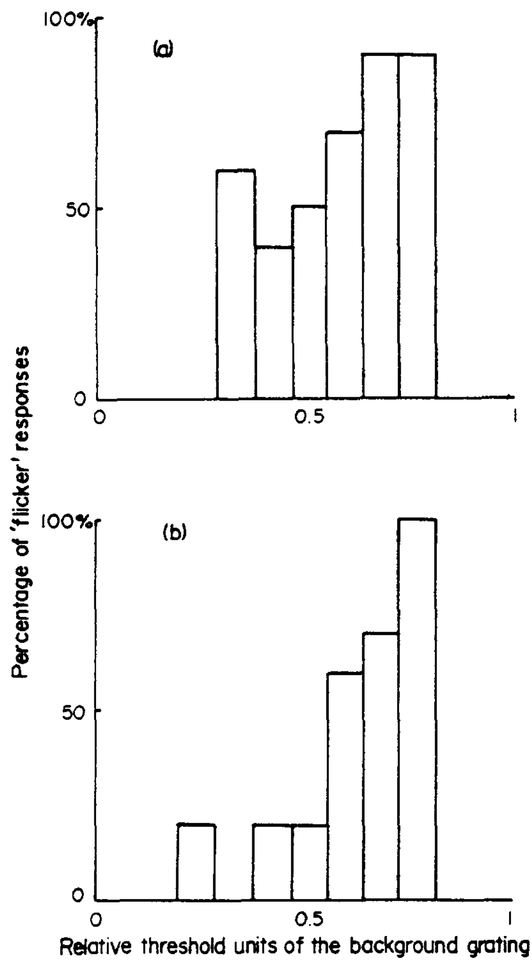

Fig. 2. Percentage of apparent flicker reports for a moving test grating within the same experimental conditions as in Fig. 1. The abscissa is given in relative threshold units of the backgroud grating, *1* representing a contrast equal to the threshold. The observer was O.P Each percentage is calculated over ten trials. The spatial and temporal frequencies were 0.63 c/deg and 3 Hz (a) and 1.5 c/deg and 7 Hz (b), respectively.

Results

Figure 2 shows that the number of apparent flicker responses increases significantly as a function of the contrast of the subthreshold drifting grating. Although probability of seeing curves have not been measured in this experiment, it can be advanced that the observed increase in percentage of apparent flicker sensation is not merely due to probability summation. Indeed, pure probability summation could not account in these experimental conditions for percentages of seeing as high as 90% (Fig. 2a) and 100% (Fig. 2b; see Discussion).

EXPERIMENTS 3 & 4

The flicker–movement dichotomy led to a more detailed investigation on the possible parallel between apparent and objective flicker (as previously distinguished) as well as on the possible interactions between objective flicker and movement.

Procedure and stimuli

The same subthreshold summation technique was used once again. A main modification was that the test and the background stimuli were no longer identical. They were a horizontal sinusoidal grating either stationary (in the control experiment) or drifting upwards or downwards in random order and a vertical sinusoidal grating turned on and off (objectively flickering grating). In experiment 3 the drifting or stationary stimulus was set at different subthreshold contrasts, whereas the subject was asked to adjust his contrast threshold for the flickering grating (objective-flicker threshold). The situation was reversed in experiment 4 where the drifting grating was the test stimulus and the flickering one the background. In this last experiment apparent flicker and movement thresholds were measured separately as before. The spatial and temporal frequencies of both test and background stimuli were always matched and they were 0.63 c/deg and 3.4 Hz respectively. The test and the background stimuli were orthogonally oriented in order to avoid any possible phase interference.

Results

Figure 3 shows nearly complete summation (solid squares, slope −0.87) for the detection of the objective flicker in presence of a drifting background. No such effect is obtained in the control experiment where the horizontal subthreshold grating is stationary (open squares, slope 0.03). This shows that the summation is purely temporal and not spatial.

Quite different results are obtained when the flickering grating is set at subliminar contrasts. No facilitation is noticed for movement detection (Fig. 4, solid circles, slope 0.05) and only slight facilitation is

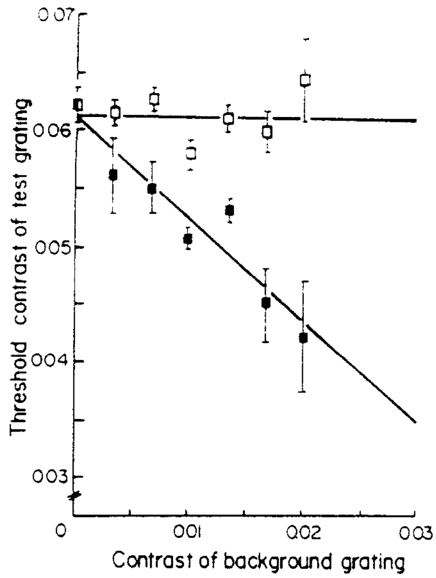

Fig. 3. Flicker thresholds for an objectively flickering grating as a function of the subthreshold contrast of an identical orthogonal grating which either moved (solid squares) or was stationary (open squares). The continuous lines are least square estimates. The observer was O.P. Each data point is an average of five trials. The spatial frequency was 0.63 c/deg the temporal frequency of the flickering and moving gratings was 3.4 Hz.

observed for apparent flicker detection (Fig. 4, open triangles, slope −0.13).

DISCUSSION

Experiments 1 and 2 point out that a distinction between apparent flicker and direction of movement thresholds might be useful when the test stimulus is a drifting grating. Within the subthreshold summation paradigm, apparent flicker and direction of movement thresholds (1) follow different curves as a function of the contrast of the background grating (experiment 1) and (2) are not randomly distributed over the same range of background contrasts (experiment 2). With respect to the first experiment it might be argued that the increase of movement thresholds as a function of the background contrast is due to mere probability summation. This necessarily implies that the increase in percentage of "apparent flicker" responses is also due to probability summation. Indeed, an increase in contrast of the subthreshold grating will enhance the probability of seeing both background and test grating at once. The detection of movement direction will thus be more difficult and consequently thresholds of movement direction will increase. Since the thresholds measured here cannot be directly matched to probability of seeing curves, such a claim cannot be completely dismissed. Nevertheless, it might be pointed out that probability summation should have induced, too, a pronounced decrease in "apparent flicker" thresholds which is evidently not the case in experiment 1. Whatever the role of probability summation, the second experiment seems to show that this latter could not entirely account for the increase in "apparent flicker" reports. Supposing complete independence between the detection of the test and the background grating, their probabilistic intersection would have never resulted in percentages of seeing "apparent flicker" as high as 90–100%. It might consequently be advanced that an explanation in terms of probability summation is not sufficient in order to account for these results. It can finally be argued that the decrease in movement sensitivity on one hand and the increase in "apparent flicker" reports on the other, are correlatives of a slight inhibition between channels of movement direction. Such an inhibition might be dependent on the experimental conditions used here, namely quite low spatial frequencies, small inspection field and reduced number of cycles on the screen.

Distinction between apparent flicker and direction of movement thresholds does not necessarily prove that an objectively moving grating stimulates two distinct mechanisms at once. Whereas experiments 3 and 4 definitely show that ON–OFF flickering gratings and drifting gratings are separately coded since their summation at threshold is not reciprocal, they also support the idea that apparent and objective flicker are not to be confounded. The entire picture of the results presented in this investigation may be understood in terms of directional and non-directional coding of a spatio–temporal modulated stimulus. Whereas direction of movement detecting mechanisms might be accounted for by some detectors presenting either some sort of asymmetric receptive fields (Hubel and Wiesel, 1962, 1968) or some unidirectional innervation of their inhibitory synapses (Barlow and Levick, 1965), flicker detectors might be free of such anatomo–physiological constraints, presenting receptive fields with insignificant surround inhibition. Conse-

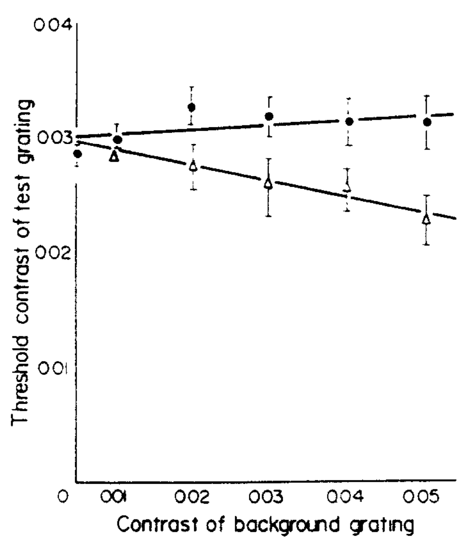

Fig. 4. Direction of movement (circles) and apparent flicker (triangles) thresholds for a drifting grating as a function of the subthreshold contrast of an identical orthogonal grating which was flickering at the same temporal rate. The continuous lines are least square estimates. The observer was O.P. Each filled symbol is an average of five trials. The open symbols are averaged over four trials or less (see text). The spatial and temporal frequencies were 0.63 c/deg and 3.4 Hz, respectively.

quently, it can be easily understood that an objectively drifting grating will stimulate, besides the movement detectors, the flicker detectors as well, since these latter will respond to any temporal modulation whatever. This would explain the strong summation between movement and flicker when the flickering grating is the test stimulus and the drifting one the background (Fig. 3, solid squares).[1] The reverse would not be true, since the background flickering stimulus will not elicit a directional response from the presumed movement mechanism and hence it will not facilitate the detection of the direction of movement (Fig. 4, circles).

Nevertheless some other explanation may partially account for this lack of reciprocity. It has already been suggested that orientational selectivity for drifting gratings is higher than for flickering ones (Sharpe and Tolhurst, 1973). Without directly testing it, Breitmeyer (1973) advances that flicker detecting mechanisms are not at all orientationally selective. It might thus be that in the particular experimental conditions of experiments 3 and 4 (where the test and the background gratings were orthogonal) lack of summation for movement detection was due to the large difference of orientation between test and background. At any rate, flicker and movement mechanisms should be distinguished since, within identical experimental conditions and for the detection of objective flicker, summation does take place.

The detection of apparent flicker seems much less, if at all, dependent upon the background flickering grating (Fig. 4, triangles) and it must be concluded that it is not monitored by the same mechanism as that responsible for the detection of objective flicker. It may be advanced on pure speculative grounds that, apparent flicker detection reflects the activity of movement detectors whose inhibitory responses are either too weak to convey directional information, or somehow disorganized by some interfering stimulation such as a pattern drifting in the opposite direction as in experiments 1 and 3. The growing percentage of apparent flicker responses illustrated in Fig. 2 might be a correlative of such an interference.

King-Smith and Kulikowski (1975) provide an extensive comparison between their results describing the psychophysical flicker detectors and the characteristics of the Y-cells, such as described by Enroth-Cugell and Robson (1966) and others, and conclude that the latter are the physiological basis of the former. Although distinguishing between flicker and movement, they assume that the Y-cells are equally responsive to these two types of stimulation. Whereas this might be the case, purely directional responses could be accounted for by W-cells which are known to be directionally selective (Stone and Hoffman, 1972; Stone and Fukuda, 1974; Fukuda and Stone, 1974). Although the physiological classification of X-, Y- and W-cells is still debated (see for a review Rowe and Stone, 1977) it may be advanced as a first approximation that whereas Y-cells are responsible for any temporal modulation whatever, W-cells specifically code the direction of movement. This classification would account quite well for the results of this investigation and would be consistent with the idea of two distinct mechanisms responding to flicker and movement.

[1] It is interesting to note at this point that the stated summation is linear whereas flicker detectors are known to be non-linear (King-Smith and Kulikowski, 1975). The significance of this discordance remains to be assessed.

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REFERENCES

Barlow H. B. and Levick W. R. (1965) The mechanism of directionally selective units in the rabbit's retina. *J. Physiol., Lond.* **178,** 477–504.

Breitmeyer B. G. (1973) A relationship between the detection of size, rate, orientation and direction in the human visual system. *Vision Res.* **13,** 41–58.

Enroth-Cugell C. and Robson J. G. (1966) The contrast sensitivity of retinal ganglion cells of the cat *J. Physiol., Lond.* **187,** 517–552.

Fukuda Y. and Stone J. (1974) Retinal distribution and central projections of Y-, X- and W-cells of the cat's retina. *J. Neurophysiol.* **37,** 749–772.

Hubel D. H. and Wiesel T. N. (1962) Receptive fields, binocular interaction and functional architecture in the cat visual cortex. *J. Physiol., Lond.* **160,** 106–154.

Hubel D. H. and Wiesel T. N. (1968) Receptive fields and functional architecture of monkey striate cortew. *J. Physiol., Lond.* **195,** 215–243.

Keesey U. T. (1972) Flicker and pattern detection: a comparison of thresholds. *J. opt. Soc. Am.* **62,** 466–448.

King-Smith P. E. and Kulikowski J. J. (1975) Pattern and flicker detection analysed by subthreshold summation. *J. Physiol., Lond.* **249,** 519–548.

Kulikowski J. J. and Gorea A. (1978) Complete adaptation to patterned stimuli: a necessary and sufficient condition for Weber's law for contrast. *Vision Res.* **18,** 1223–1227.

Kulikowski J. J. and Tolhurst D. J. (1973) Psychophysical evidence for sustained and transient mechanisms in human vision. *J. Physiol., Lond.* **232,** 149–162.

Levinson E. and Sekuler R. (1973) Spatio-temporal contrast sensitivities for moving and flickering stimuli. *J. opt. Soc. Am.* **63,** 12–96.

Levinson E. and Sekuler R. (1975a) The independence of channels in human vision selective for direction of movement. *J. Physiol., Lond.* **250,** 347–366.

Levinson E. and Sekuler R. (1975b) Inhibition and disinhibition of direction specific mechanisms in human vision. *Nature, Lond.* **254,** 692–693.

Rowe M. H. and Stone J. (1977) Naming of neurones. Classification and naming of cat retinal ganglion cells. *Brain Behav. Evol.* **14,** 185–216.

Sharpe C. R. and Tolhurst B. J. (1973) The effects of temporal modulation on the orientation channels of the human visual system. *Perception* **2,** 23–29.

Stone J. and Hoffman K. P. (1972) Very slow-conducting ganglion cells in the cat's retina. A major, new functional type? *Brain Res., Osaka* **43,** 610–616.

Stone J. and Fukuda Y. (1974) Properties of cat retinal ganglion cells. A comparison of W-cells with X- and Y-cells. *J. Neurophysiol.* **37,** 722–748.

Tolhurst D. J. (1973) Separate channels for the analysis of the shape and the movement of a moving visual stimulus. *J. Physiol., Lond.* **231,** 385–402.

Van Nes F. L., Koenderink J. J. and Bouman M. A. (1967) Spatio-temporal modulation transfer in the human eye. *J. opt. Soc. Am.* **57,** 1082–1088.