Vision Res. Vol. 9, pp. 577–590. Pergamon Press 1969. Printed in Great Britain.

THE RESPONSE OF THE HUMAN VISUAL SYSTEM TO MOVING SPATIALLY-PERIODIC PATTERNS

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(*Received* 31 *October* 1968; *in revised form* 29 *November* 1968)

INTRODUCTION

IF A ROTATING radial grating of low spatial frequency is viewed monocularly, the observer fixating the centre of the disc, it is found that as the speed of rotation is varied, two frequencies are critical (FOSTER, 1968). These two critical frequencies divide the visual sensation into three distinct ranges: an upper range where conventional fusion takes place (analogous to the fusion of spatially uniform flashing sources), a middle range where a sensation of motion is present, but the directional information is ambiguous, or non-existent, and finally, a lower range where both the sensation of motion and the sensation of direction are well defined. Under some circumstances, a stationary stroboscopic effect is also observed (FOSTER, 1968).

In the present work, the variation of these two critical frequencies with both stimulus area and grating period are examined, and a model developed which describes the behaviour of that portion of the visual system defined by the range of inputs tested.

There are several mathematical techniques available for the analysis and synthesis of systems. The one adopted here is the classical transform approach, where if a system is linear and time-invariant, it can be characterised by its transfer function. More complex systems can be described by linking together individual units, each with its associated transfer function, and the behaviour of the entire system analysed in the complex frequency domain. However, as PORTER (1966) points out, other, more powerful techniques are available; in particular, the state variable approach, where the behaviour of the system is described in the time domain and the restriction of linearity and time-invariance no longer apply, and secondly, the considerably more sophisticated function theoretic approach, where the input-output relationships are investigated using set theory (see WYMORE, 1967). Thus the model derived in the work reported here is only one of a number of possible, equally valid representations of the logic of the system. Furthermore, it must be emphasized that although units representing various functions such as addition and multiplication will be introduced, they do not necessarily near any relation to the morphology of the system (see CHERRY, 1961).

It will be shown that two of the major elements of this model of the human visual system (defined by the inputs tested) are the de Lange filter (DZN, DE LANGE, 1952, 1954 and 1958), and the Hassenstein and Reichardt model (discussed in detail by REICHARDT and VARJÚ, 1959). Both use the transform approach. The de Lange filter is a low pass filter which describes the frequency response of the human visual system at fusion (obtained by measuring the modulation depth of a sinusoidal stimulus as a function of f.f.f.). The

Hassenstein and Reichardt multiplicative interaction model was developed in the analysis of the optomotor response of the beetle, Chlorophanus, to a rotating striped drum, and formed the basis of the analysis of similar, subsequent studies by, among others, THORSON (1964) and McCANN and MACGINITIE (1965). Two of the main features that emerged from these studies of the insect optomotor response were the phenomenon of phase insensitivity to the drum pattern, and the existence of a range of spatial periods of the pattern for which it was possible to evoke a negative response. On the basis of the latter an estimation of the ommatidial separation was made.

A possible objection to the use of the Hassenstein and Reichardt model in the analysis of the human visual system is that it was designed originally to describe the insect optomotor response. However, as long as the inputs of the model can be meaningfully related to a pair of receptors, or group of receptors, in the human retina (which is possible since the image is fixated), and that the response of the system can in some way be measured, or at least fixed (achieved by working at motion threshold), then the relevance of the model in the present experiments depends purely on its description of the observed phenomena.

Since frequent reference has been made and will continue to be made to the Hassenstein and Reichardt model, its 'construction' and major properties will now be discussed.

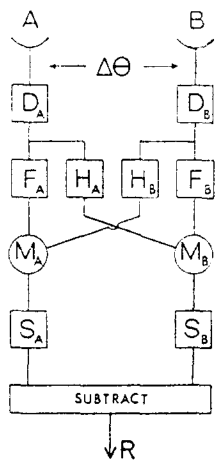

FIG. 1. The Hassenstein and Reichardt multiplicative interaction scheme. D, F, H and S are linear filters and the M units, multipliers. The system gives a net response R to a moving pattern passing in front of the input receptors A and B.

The units D, H, F and S (see Fig. 1) are all linear filters (i.e. if the input of such a filter is multiplied by some constant k, then the output is also multiplied by the same constant k) and except for the D filters, each are basically integrators with different time constants. The D-filters are 'fractional-order' differentiators (see CHAPMAN, 1963) and have transfer functions of the form $s^{\frac{1}{2}}$, where s is the complex frequency (i.e. the Laplace variable). The M-units are multipliers in the time domain, their action therefore being equivalent to convolution in the complex frequency domain. All these units are linked together by lines which lead the 'signal' from one process to the next. Where a line splits into two, say, the same quantity is considered to be present in each of the two new paths as in the original path.

Thus, when a pattern consisting of sinusoidal variations in intensity is moved across the pair of receptors A and B (representing two ommatidia in Chlorophanus) the signals, after various modifications in the two channels, are multiplied together and after further filtering are compared by subtraction.

In general, the response, R, of the model has the form:

$$R = G\,(f).\ \sin\,(2\pi\,\Delta\theta/\lambda) \tag{1}$$

where $\Delta\theta$ is the separation of the 'receptor' input pair,
λ, the spatial period of the rotating pattern,
f, the temporal input frequency at a fixed point (McCann and MacGinitie's 'contrast' frequency),
and $G\,(f)$, a function of the input signal and model structure.

It can be seen that when $\Delta\theta = n\lambda/2$, $R = 0$, and when $n\lambda/2 < \Delta\theta < n\lambda$, R is negative, the latter indicating that the response is in the opposite direction to the stimulus (the 'pattern-reversal' phenomenon). The form of the function, $G\,(f)$, is such that the phase information in the stimulus pattern is lost (the transform of the input function appears in $G\,(f)$ as the square of the modulus, thus predicting 'phase insensitivity').

To summarize, it will be shown that in the human visual system, if we associate the lower critical frequency, f_l, with a fixed output, R, of the Hassenstein and Reichardt model, then it is possible to predict qualitatively, the observed variation of f_l with both grating period and aperture. Furthermore, by incorporating this model within a larger scheme, including de Lange filters, the characteristics of the upper critical frequency f_u, may also be described.

APPARATUS AND METHODS

The apparatus was set up as in Fig. 2.

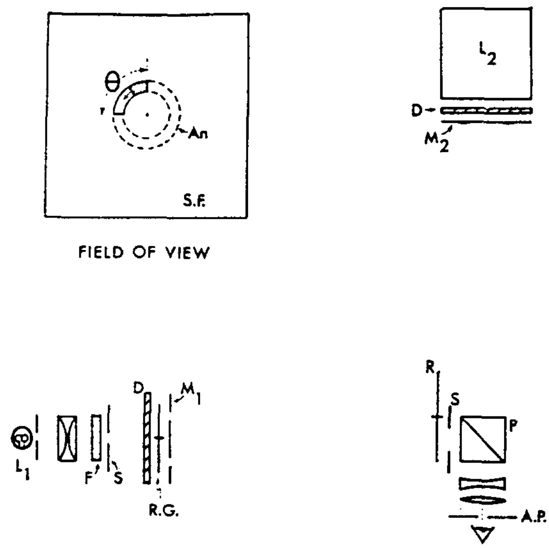

FIG. 2. The apparatus: L_1 and L_2 are incandescent light sources; F, liquid filter for colour correction; S, stop; D, diffusing screen; R.G., radial grating; M_1 and M_2, positive and negative masks; R, slow rotating sector; P, split prism; A.P., artificial pupil.
In the inset: An, annular aperture; S.F., surround field.

The rotating radial grating, R.G., was illuminated from behind by the incandescent lamp, L_1, via the filter, F, stop, S, and diffusing screen, D. A rectangular, rather than sinusoidal waveform was chosen for the radial grating since in this form, the grating could be prepared with considerably more accuracy, and thus the subharmonic content was minimised. No diffusing screen was introduced in front of the grating to reduce the higher harmonic content (cf. McCANN and MACGINITIE, 1965); the contribution of these higher harmonics to the response is discussed later.

The view of the pattern was restricted with the annular mask, M_1, portions of which could be sectioned off. The remaining section of the annulus was specified by the coordinate θ. (See insert of Fig. 2.)

An annular field was chosen so that the density of receptors constituting the input of the system remained fairly uniform, and the angular subtense of the entire annulus at the eye (1·5°) sufficiently large so that the consequent coarsening (reduction of visual acuity) of the system enabled a simpler functional representation. (For a discussion of acuity, see JONES and HIGGINS, 1947.) The angular subtense of the width of the annulus was 0·21°.

A uniform background field was provided with the light box, L_2 and diffusing screen, D, in front of which was the mask, M_2, the negative of M_1. The two fields were combined using the beam splitter, P, and the whole viewed via the 2 mm artificial pupil, A.P. The retinal illumination was 390 trolands, and colour temperature of the source approximately 2,500°K. A slow rotating sector, R, was included to cycle the viewing period.

The observer fixated, monocularly, the centre of the annulus, and was able to control the speed of rotation of the radial grating, the angular velocity of which was read from an electronic tachometer. In order to ensure that the stimulus remained at a constant retinal location, it was necessary to maintain 'good' fixation. 'Good' fixation in the present context was judged to have ceased when the eye movements involved were great enough to stop the otherwise gradual 'washing-out' of the field. (See RIGGS *et al.*, 1953.) Sharp eye movements, or flicks (DITCHBURN and GINSBORG, 1953) could be identified by the sudden brightening of some dark contours which were part of stimulus surround (LORD and WRIGHT, 1950). A further consideration, in defining the stimulus was that each period of observation had to be sufficiently long for the transients to vanish, and steady state conditions to be established (HOUSEHOLDER and LANDAHL, 1945). The 5 sec on, 5 sec off cycling of viewing period was a compromise between achieving this latter condition, and still maintaining 'good' fixation. At low contrast frequencies, five seconds is not sufficient for steady state conditions to be reached, and so the slow-rotating sector was removed, and steady state judged to have been reached when the stimulus appearance remained constant at the end of the period of observation.

Before commencing measurements, it was necessary to standardise the stimulus intensity against the background field intensity. The stimulus pattern (fused by the observer) was superimposed on the negative mask, M_2, and the two fields matched for colour and brightness. M_2 was then removed, leaving a uniform background field, and a ten per cent neutral density filter introduced between the grating and the beam splitter. Thus the stimulus intensity variation was within ten per cent of the surround intensity, and superimposed upon it. The principal observer (the author) was marginally protanomalous, judged by colour matching data (although making no mistakes on the Ishihara test), was aged twenty-three, and wore contact lenses.

RESULTS

In order to determine the general characteristics of the system, the following three preliminary experiments were performed.

Experiment 1. *The uniformity of the field*

All but a 20° sector of the annulus was masked off and the lower critical frequency, f_l, measured for sector orientations of 0° to the vertical, 45°, 90°, 135°, and so on around the annulus. There was no significant variation in f_l, and thus the field was concluded to be uniform.

Experiment 2. The symmetry of the system with respect to reversal of stimulus direction

The variation of the lower critical frequency with the field size, θ for a spatial period of grating equal to 60°, was determined for both directions of grating rotation. Again no significant variation was found between the two curves, and the system was concluded to be symmetric with respect to reversal of stimulus direction.

Experiment 3. Phase insensitivity to the pattern structure

To investigate whether the system was sensitive to the phase relationships of the Fourier components making up the stimulus pattern, a radial grating with the waveform shown in Fig. 3 was substituted for the conventional square wave type.

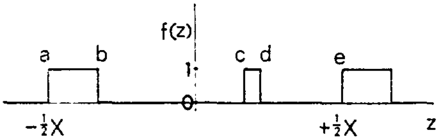

FIG. 3. The waveform of the radial grating used in the phase sensitivity experiment. The angular distance z around the grating is measured from the arbitrary origin indicated; $f(z)$ is the normalised intensity transmitted by the grating as a function of z. $f(z)$ is periodic in z, with period X.

This radial grating was modified in the following way.

By keeping the angular distance '*bc*' and '*de*' constant (at 180 and 100° respectively), and by varying the position of '*bc*' from the extreme left, *a*, to the extreme right, *d*, it was possible to change the magnitude and phase of the Fourier components making up the stimulus pattern. It can be shown that if the system is insensitive to phase content of the stimulus, then the curve obtained by plotting f_l as a function of the angular distance '*ab*' (for a given aperture, θ) would be a symmetric about the point ('*ad*' – '*bc*')/2 = 40°. (See Appendix A.)

With $\theta = 360°$, f_l was measured as a function of angular distance '*ab*' on the grating, and the results are shown in Fig. 4.

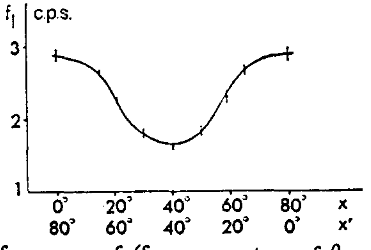

FIG. 4. The lower critical frequency, f_l (for an aperture of $\theta = 360°$) as a function of the grating waveform, defined by the 'shift' variables, x and its complement, x' (see text).

As can be seen f_l is indeed a symmetric function of x (='*ab*') and x' (='*cd*') about $x = x' = 40°$.

The system defined by the range of inputs tested, was concluded to be insensitive to the phase structure of the stimulus.

The principal experiment

The upper and lower critical frequencies, f_u and f_l, were determined as functions of the area of stimulus, θ, exposed, for a range of grating periods. The curves were taken in both directions to reveal the presence, if any, of drifting. The results are shown in Figs. 5a, 5b and 6.

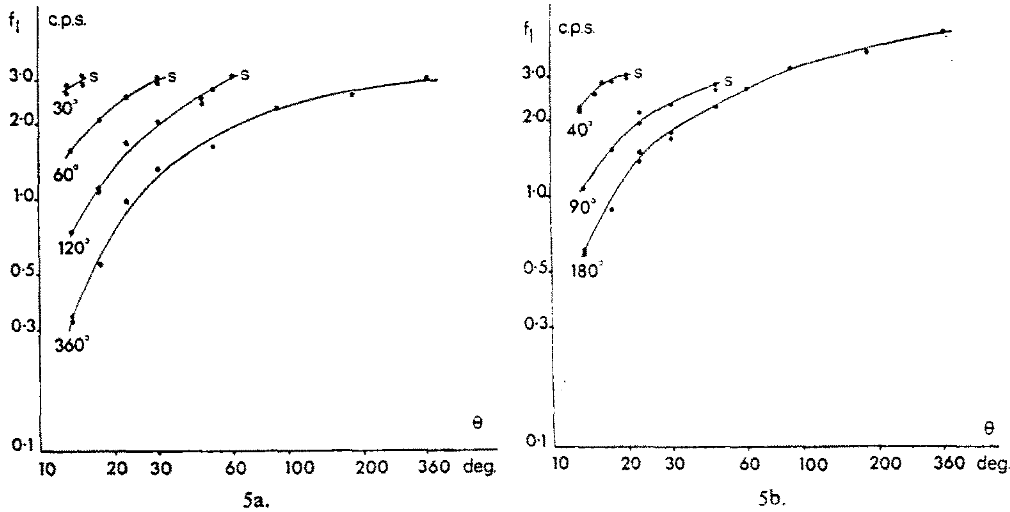

FIG. 5a and 5b. The variation of the lower critical frequency, f_l with annular area, θ. The grating period, λ, in degrees, is shown at the left of each curve. The onset of the stationary stroboscopic effect is indicated at the points marked *S*. The mean deviation associated with each point is less than ten per cent.

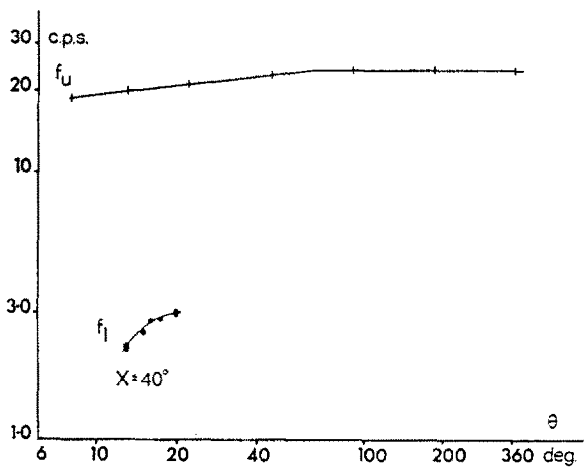

FIG. 6. The variation of the upper critical frequency, f_u, with annular area, θ. The spread of the curve for values of the grating period, λ, equal to 30, 40, 60, 90, 120, 180 and 360°, is indicated by the short vertical lines. Also included in the set (within the spread shown) is the special case of f_u equal to c.f.f. A 40°, f_l curve is shown for comparison.

In Figs. 5a and 5b is shown the general upward trend of f_l with both θ and λ; the onset of the stroboscopic effect (verified by K.H.R.) is indicated at the points marked '*s*' and occurs for all values of grating period λ, except $\lambda = 180°$ and $\lambda = 360°$. For $\lambda = 20°$, the stroboscopic effect was observed for all values of aperture tested. Two other features of the f_l curves are the smooth transition of f_l from the full ($\theta = 360°$) annulus, to the semi-annular case of $\theta = 180°$, with the two terminating edges perpendicular to the pattern direction, and secondly, the very strong relationship between the onset of the stroboscopic effect, s, and the corresponding value of $\lambda/2$.

The upper critical frequency, f_u, as a function of θ, for a range of spatial periods, λ (Fig. 6), proved to be independent of λ (within experimental error). Included in this set of curves is the special case where the stimulus is that of a spatially uniform flashing source, and f_u is conventional c.f.f. with ten per cent modulation depth. An f_l curve is included in the figure for comparison.

DISCUSSION

In order that the transform approach can be employed in the analysis of the system, certain characteristics must first be specified or determined. The non-linearity of the eye with respect to intensity variation is well established (DZN, DE LANGE, 1954 and 1958). It may be shown however, that using a Taylor expansion (see appendix B) that an input modulation depth of ten per cent enables the system to be adequately represented by a linear approximation, within the experimental accuracy of the present work (see SCHWARZ and FRIEDLAND, 1965). Hence the introduction of the ten per cent neutral density filter in the apparatus. Two other factors, the spatial uniformity of the system and its symmetry with respect to reversal of stimulus direction were established by Experiments 1 and 2. Having defined the input characteristics of the system, we can now deduce some of the more general functions that take place within it from the form of the f_u and f_l curves.

The upper critical frequency

The observed non-dependence of the f_u v. θ curves on λ (Fig. 6) implies that the processes responsible are insensitive to spatial variations in phase across the input (receptor) mosaic. Also included within this set of curves is the limiting case of f_u equal to the critical fusion frequency.[1] Because the variation of c.f.f. with θ is the same as that of f_u with θ, the simplest inference is that each of the processes determining the upper critical frequency, f_u, is identical with the low pass filter mechanism defined by de Lange (DZN, DE LANGE, 1952), and to which the same comments on spatial phase insensitivity apply. [The spatial phase insensitivity described here should not be confused with the phase insensitivity of the motion perception investigated in Experiment 3, nor with the single channel temporal phase insensitivity found by FORSYTH (1960). All three are distinct phenomena.] Since f_u increases with area, some form of functional summation takes place, but whether the actual mechanism responsible is input facilitation, or simple output summation, it must be spatially phase blind.

The lower critical frequency

Because the f_l vs-. θ curves, for λ equal to 180° and 360°, were monotonic (Figs. 5a and 5b), and in particular there was no sharp change in f_l going from $\theta = 360°$ to 180°, it

[1] As λ increases, the phase lag, Δt say, between one receptor and the next decreases, for a given contrast frequency f_u (i.e. $\Delta t \propto \frac{1}{\lambda}$). The limiting case is where there is no phase lag between receptors (i.e. $\Delta t=0$), and the temporally varying stimulus is spatially uniform across the receptor mosaic. Here f_u has become c.f.f. and λ infinite.

was concluded that contributions from the edges of the semi-annulus (perpendicular to the motion direction) were not significant. A more obvious feature of the curves is the strong functional relationship between the onset of the stroboscopic effect (s), and the spatial period of the grating (i.e. 's' occurs when $\theta > \lambda/2$). If the higher harmonics present in the stimulus were of proportional significance, then one might expect a similar 'secondary' stroboscopic sensation at values of θ around $1/3$ $(\lambda/2)$ for the second harmonic, around $1/5$ $(\lambda/2)$ for the fourth harmonic, and so on. (Even multiples of the fundamental spatial frequency in a square wave are absent.) No such secondary strobing was observed.

Since the system seems to be dominated by its response to the fundamental, the contribution of the higher harmonics will be neglected in the following brief analysis.

We consider now the stationary stroboscopic phenomenon in more detail. Since the Hassenstein and Reichardt model gives negative response values for $\Delta\theta/\lambda > \frac{1}{2}$, and in the present experiments, the visual system was found to give rise to the stroboscopic effect when $\theta > \lambda/2$, i.e. $\theta/\lambda > \frac{1}{2}$, a possible description of the processes present in the system is the following. When the aperture, θ, is sufficiently large to introduce motion perception units with input pair separations of greater than $\lambda/2$, the resulting negative (by analogy with the Hassenstein and Reichardt model) output of these units remains distinct from the positive response contributions of perception units with input pair separations of less than $\lambda/2$. The total response then consists of contradictory elements. Thus, it is necessary to postulate that the outputs of these individual motion perception processes do not undergo 'algebraic' summation. (If such summation did occur, then the resulting net output would give rise to a net sensation of motion with a well defined lower critical frequency, f_l.)

VALIDITY OF THE HASSENSTEIN AND REICHARDT MODEL

The property of the Hassenstein and Reichardt model of giving negative response values for a certain range of pattern periods was invoked to describe the stationary stroboscopic effect. The other necessary condition that the system (defined by the inputs discussed) should satisfy is that it should show insensitivity to the phase structure of the stimulus pattern. This was established by Experiment 3.

To show that the Hassenstein and Reichardt model is also capable of indicating the general trend of the observed f_l curves, the following skeletal analysis is put forward.

The response, R, of each motion perception process in order to give rise to the sensation of motion, must exceed some minimum value, say threshold, T.

Thus: $R = G(f).\sin(2\pi\Delta\theta/\lambda) = T =$ constant, at threshold. (From equation 1).

Thorson has shown (THORSON, 1966) that the Hassenstein and Reichardt model can be simplified and yet still retain its essential characteristics (in particular, by removing the D, F and S filters). In this case we may write for $G(f)$ in the above:

$$G(f) = \frac{kf}{a^2+4\pi^2 f^2}$$ where k is some constant, and a is the rate constant for the cross filter, H.

We now choose a small and obtain the following, remembering that f_l is defined for threshold.

$$f_l \simeq k.\sin(2\pi\Delta\theta/\lambda), \text{ where } 4\pi^2\, T \text{ has been incorporated in the constant } k. \tag{2}$$

In Fig. 7 the results of Figs. 5a and 5b are replotted with f_l as a function of λ for constant θ

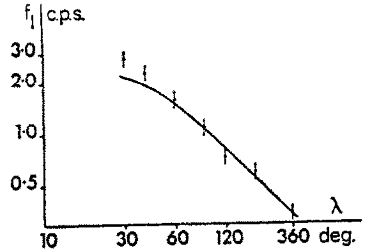

FIG. 7. The lower critical frequency, f_l, as a function of the spatial period of the grating, λ, for fixed aperture, θ, equal to 13°. The ten per cent error associated with each point is indicated. The continuous curve is the result calculated on the basis of the proposed model.

($\theta = 13°$). The theoretical curve from equation 2, with $\Delta\theta$ set arbitrarily equal to 7°, is also shown (the continuous curve). The fit can be further improved at the high frequency end by making $\Delta\theta$ smaller.[2] The foregoing is not intended to be a rigorous analysis, but merely an indication that the model is at least a possible description of part of the system's behaviour.

A model describing both f_u and f_l

We now review the major elements that must be part of the model of that portion of the visual system, defined by the present experiments.

(1) Two threshold mechanisms associated with the two transition frequencies, f_u and f_l; threshold mechanisms since the lower critical frequency, f_l, may be thought of as being that frequency at which the 'signal' carrying the directional information fails to reach some minimum value, and similarly the upper critical frequency, f_u, that frequency at which the 'signal' carrying the remaining non-directional motion information (see Introduction) also fails to reach some other minimum value.

(2) From the discussion of the upper critical frequency, the processes which describe the behaviour of f_u must include the de Lange low pass filters (and as the most economical assumption, be equal to the de Lange filters).

(3) The summation mechanism for these processes must be spatially phase blind (see discussion of f_u).

(4) The mechanisms which represent the behaviour of f_l must be capable of showing the stroboscopic effect, and if we base each of these mechanisms on the Hassenstein and Reichardt model, then the further properties of the system, implied by their model, must also be satisfied.

Finally, the model as a whole must be capable of representing in an integrated manner the range of phenomena described in these experiments.

Accordingly, the network shown in Fig. 8 is proposed.

The 'processing' part of the system model consists of inputs, R (each representing single, or possibly, groups of receptors), low pass de Lange filters, V, and horizontal units, H, which are some modification of the Hassenstein and Reichardt multiplicative interaction model.[3] These H-units are shown extending over more than adjacent channels.

[2] The value of f_l for $\lambda = 360°$ was included for completeness, but not too much weight should be attached to the point, in view of the pulse like nature of the stimulus at this frequency.

[3] These H units, each of which represents a complete Hassenstein and Reichardt multiplicative interaction model, should not be confused with the individual H filters within the Hassenstein and Reichardt model, discussed in the Introduction.

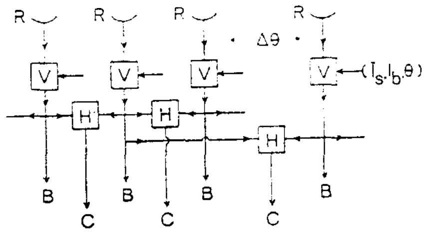

FIG. 8. A model of the processing part of the system. R are receptors (or groups of receptors); V, de Lange low pass filters; H, essentially Hassenstein and Reichardt multipliers. The sites at which the parameters, $\bar{I}_s$, the mean stimulus intensity, I_b, the background intensity, and θ, the stimulus area, can act, are indicated.

The sites at which parameters like the mean stimulus intensity, $\bar{I}_s$, the background intensity, I_b, and the area of stimulus, θ, can exert an influence are indicated.

From this network, two kinds of 'signal' are produced. Signals corresponding to local temporal fluctuations in stimulus intensity but carrying no information on the spatial phase distribution of the signal across the receptor mosaic are carried by the B channels.

Information on the phase relationship of the stimulus intensity at one part of the field compared with that at another (i.e. motion information) is carried by the B channels. In order that the information carried in each of the two types of channel can exhibit a cut-off frequency (i.e. f_u and f_l), the B and C channels are fed into two separate threshold mechanisms (Fig. 9).

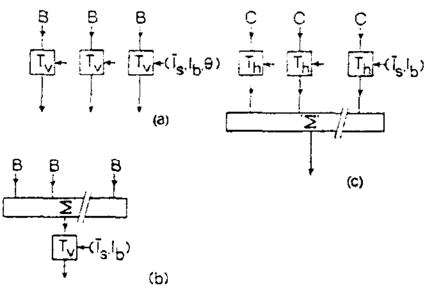

FIG. 9. The threshold/summation arrangements. T_v and T_h are the threshold mechanisms associated with the vertical (V) and horizontal (H) units respectively. The sites at which the parameters, $\bar{I}_s$, the mean stimulus intensity, I_b, the background intensity, and θ, the stimulus area, can act, are indicated. The units Σ and 'Σ' are defined in the text.

Because some form of functional areal summation of f_u occurs two possibilities exist for the threshold/summation mechanisms, viz. (a) and (b) in Fig. 9. In (a), the B channels retain their individuality, and the threshold units, T_v, are modified by the area, θ, and by the intensity parameters, $\bar{I}_s$ and I_b. An alternative representation is that of (b), where the B channels feed directly (via some weighting function, perhaps) into the summer, Σ, which by its nature, gives a larger output for a larger θ. In turn, the single output of Σ is fed into a single threshold mechanism, T_v, which no longer has θ as a parameter. (Such a scheme was proposed by LANDAHL, 1957.) Both types of summation/threshold arrangement (a) and (b), if defined to be spatially phase insensitive, are equally valid representations of the f_u behaviour.

For the lower critical frequency, f_l, it is necessary to postulate a more general kind of interaction of the C channels, bearing in mind the previously proposed origin of the stroboscopic phenomenon. Therefore, in Fig. 9 (c), the threshold mechanisms, T_h, are introduced separately into the channels, C, which in turn, feed into the unit, 'Σ', defined to give only non-zero outputs (i.e. unambiguous, directed motion information) for non-zero inputs of the same sign.

Thus to recapitulate, the information in the moving pattern is split into two portions by the model, consistent with the observed phenomena. One portion concerns local variations in stimulus intensity over the whole of the receptoral field, the information concerning the phase relationship of one locale with another being ignored. The other 'spatial' information relating one part of the field with another is channelled off and processed separately.

Because these two types of information are derived by units with different frequency characteristics (i.e. the H and V units), under some circumstances the information emerging from the system as a whole is incomplete. This is seen to happen for the range of contrast frequencies between the upper and lower limits, f_u and f_l.

Before going on to discuss the system model in operation and the subjective phenomena implied, some deductions are made concerning the 'receptor' separation.

Dimensions

The following refers to the separations of the input units of the model.

(1) *Minimum separation of motion perception inputs*, $\Delta\theta$ min. In the discussion of the validity of the Hassenstein and Reichardt model in the present work, it was shown that fair agreement could be achieved between the predicted curve of the model, and the recorded variation of f_l with λ, for fixed θ ($\theta = 13°$), if the assumption was made that the input pair separation was of the order of 7°. This would seem to imply that an aperture of $\theta = 13°$ behaves as if it consists of two receptors (or two groups of receptors) separated by approximately 7°. This, in conjunction with the observation that no value of f_l could be recorded with $\theta = 10°$, for any λ, in turn indicates that the 'width' of each receptor (or group of receptors) forming the input pair to the motion perception unit is of the order of (13–7°), i.e. 6°, so that an aperture of $\theta = 10°$ fails to reveal both 'receptors' completely, and consequently, also fails to give rise to a unidirectional sensation of motion.

(2) *Maximum separation of motion perception input units*, $\Delta\theta_{max}$. For sufficiently large values of the aperture. θ, $\lambda = 120°$ would give rise to the stroboscopic effect, but not $\lambda = 180°$, nor $\lambda = 360°$. (Because of the form of the stimulus, intermediate values of λ could not be obtained.) Remembering the previous discussion on the stroboscopic effect and the introduction of negative components into the final response for values of θ (in practice) and $\Delta\theta$ (in theory) greater than $\lambda/2$, it can be deduced that since for $\lambda = 180°$ there is no strobing, $\Delta\theta_{max}$ must be less than 180°/2, and by similar reasoning, must be greater than 120°/2. This assumes that the width of each 'receptor' in each input pair is of the same order as that obtained for the minimum input pair separation, $\Delta\theta_{min}$. Thus $\Delta\theta_{max}$ lies between 60 and 90°.

Hence it seems that in this model representing the response of the human visual system to this class of stimuli, interaction leading to motion perception can occur between units considerably more removed from one another than observed by Hassenstein and Reichardt in Chlorophanus.

We now finally examine qualitatively, the behaviour of the entire system model, and its relation to the observed phenomena, as the contrast frequency, f, of the rotating radial grating is steadily increased.

For near zero values of f, the input signals pass virtually unattenuated through the low pass filter V-units, and then undergo comparison (i.e. cross-correlation, see REICHARDT and VARJÚ (1959)) in the H-units. The two signals carried by their respective channels pass into and providing their magnitudes are sufficiently large, out of their respective threshold mechanisms. Thus both portions of the information contained in the original system remain intact at the output, and the sensation is that of unidirectional motion (providing there are no negative contributions). As f increases, a point will be reached where the V-unit attenuation of the input is sufficient for the V-unit output to surmount its associated threshold (T_v) but not sufficient for the eventual output of the H-units to surmount their threshold (T_h), and the resulting sensation is that of motion without a unique direction, since temporal changes in the stimulus are being observed over the receptoral field, but any sequential relation between one part of the field and another is absent. Here $f = f_l$. If f is made larger still, the input signal is further attenuated by the V-units (DZN, DE LANGE, 1952), until it is insufficient to surmount even the thresholds, T_v, and finally fusion occurs. Here f equals f_u.

In conclusion, it is emphasized once again that this functional model of that portion of the visual system defined by the inputs tested, does not necessarily bear any similarity to the morphology of the system; the model is certainly crude, and like most models, is a compromise between comprehensiveness and tractability (e.g. no attempt has been made to take into account other visual phenomena). Having in this paper established the functions of the various units comprising the model, it is hoped to present later a paper giving the detailed mathematical analysis and further predictions of the model.

Acknowledgements—I thank Professor W. D. WRIGHT and Dr. K. H. RUDDOCK who supervised this work.

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APPENDIX A

Phase insensitivity

Consider the function, $f(z)$, defined in Fig. 3.

i.e.
$$f(z) = 1, \text{ if } a<z<b$$
$$= 0, \text{ if } b<z<c$$
$$= 1, \text{ if } c<z<d$$
$$= 0, \text{ if } d<z<e$$

We can expand $f(z)$ in a complex Fourier series with spatial frequency ω, and period X, thus:

$$f(z) = \sum_{n=-\infty}^{n=+\infty} F_n e^{in\omega z} \quad \text{since } f(z) \text{ is well behaved,}$$

$$\text{where} \quad F_n = \frac{1}{X}\int_{-X/2}^{+X/2} f(z)e^{-in\omega z}dz \tag{1}$$

Substituting for $f(z)$ in (1), we obtain:

$$F_n = \frac{1}{X}\left[\frac{e^{-in\omega z}}{-in\omega}\right]_a^b + \frac{1}{X}\left[\frac{e^{-in\omega z}}{-in\omega}\right]_c^d \tag{2}$$

If we put $b\text{-}a = x$, $c\text{-}b = \Delta x$, $d\text{-}c = x'$, and $e\text{-}d = \Delta x'$, substitute in equation 2, and simplify, then:

$$F_n = \frac{i}{2\pi n}e^{+in\omega X/2}\left\{e^{-in\omega x} - 1 + e^{+in\omega\Delta x} - e^{-in\omega(x+\Delta x)}\right\}$$

To remove the phase content of F_n, we take the modulus squared. Noting that $(x+\Delta x+x'+\Delta x') = X$, we obtain:

$$|F_n|^2 = \frac{1}{4\pi^2 n^2}\Big[4 - 2\cos(n\omega x) - 2\cos(n\omega x') + 2\cos\left\{n\omega(x+\Delta x)\right\} + 2\cos\left\{n\omega(x'+\Delta x)\right\} - 2\cos(n\omega\,\Delta x) - 2\cos(n\omega\,\Delta x')\Big] \tag{3}$$

In equation 2, $|F_n|^2$ remains the same when x and x' are interchanged; i.e. if $x = p$, say, (and $x' = q$), then $|F_n|^2$ has the same value for $x = q$ (and $x' = p$). Thus $|F_n|^2$ is symmetric about the point $x = x' = \frac{1}{2}(X-\Delta x-\Delta x') = \frac{1}{2}(360\text{–}180\text{–}100) = 40°$.

Thus, if the system under investigation is insensitive to the phase content of the pattern $f(z)$, (i.e. it responds to $|F_n|$ rather than F_n, in the frequency domain), then the response of the system to variation of x in $f(z)$ should be symmetric about $x = 40°$.

APPENDIX B

Linearity of the system

Suppose the response of some non-linear system to an input, x say, is $f(x)$, then for a small change, Δx, in x, let the corresponding change in the output be Δf.

$$\text{So:} \quad f(x) + \Delta f = f(x+\Delta x) \tag{1}$$

If the right hand side of equation 1 can be expanded in a Taylor's series about x, we obtain:

$$f(x+\Delta x) = f(x) + \Delta x.f'(x) + \frac{(\Delta x)^2}{21}f''(x) + \text{higher terms} \tag{2}$$

If Δx is sufficiently small, the above reduces to:

$$\Delta f = \Delta x.f'(x) \tag{3}$$

Thus the system, described by equation 3, behaves linearly for small changes in the input (i.e. $k\,\Delta x \Rightarrow k\,\Delta f$).

To obtain some indication of how small 'sufficiently small' must be in the approximation of equation 3, we consider $f(x) = \log(x)$, the non linear function examined by both DE LANGE (1954) and VERINGA (1958) in a similar context.

Substituting for f in equation 2, we obtain:

$$\log\left[\frac{x+\Delta x}{x}\right] = \frac{\Delta x}{x} - \frac{(\Delta x)^2}{2x^2} + \frac{(\Delta x)^3}{3x^3} -$$

if $\Delta x = 0{\cdot}1x$, then the left hand side of the above becomes 0·092 and the first term of the right hand side, 0·100.

Therefore, in approximating $\Delta f = \Delta x . f'(x)$ in the above, an error of a little under 10 per cent is introduced in the predicted output for a modulation depth of 10 per cent in the input. This is within the tolerances of the experimental technique and this was the input modulation depth accordingly chosen.

Abstract—The work is concerned with the two critical frequencies that are associated with the visual observation of a moving, spatially periodic pattern. Data are given for the dependence of these frequencies upon the input parameters of the stimulus (e.g. spatial period, and area). On the basis of these data, it is concluded that the system has features in common with the known optomotor response of certain insects. In particular, the system demonstrates the property of phase blindness and also a phenomenon probably related to the 'pattern reversal' effect found in the case of the insect. It was further found that the de Lange c.f.f. filters are insensitive to spatial variations in the phases of the input stimuli. A network, capable of detailed analysis, is suggested that functionally describes the behaviour of the system.

Résumé—On étudie les deux fréquences critiques associées à l'observation visuelle d'un réseau périodique spatial en mouvement. On détermine ces fréquences en fonction des paramètres d'entrée du stimulus (période spatiale et aire). On en déduit que ce système a des traits en commun avec la réponse optomotrice connue chez certains insectes. En particulier, ce système possède la propriété de cécité à la phase et aussi un phénomène en relation probable avec le renversement du réseau trouvé chez l'insecte. On trouve en outre que les filtres de fréquence critique de de Lange sont insensibles aux variations spatiales dans les phases des stimuli d'entrée. On suggère un réseau de conducteurs capable d'une analyse détaillée et qui décrit fonctionnellement le comportement de ce système.

Zusammenfassung—In dieser Arbeit handelt es sich um die zwei kritischen Frequenzen, welche im Zusammenhang mit der Betrachtung eines sich bewegenden, raum-periodischen Musters stehen. Es werden Ergebnisse für die Abhängigkeit dieser Frequenzen von den Eingangsreizparametern (z.B. Raumperiode und Flächengrösse) geliefert. Auf Grund dieser Ergebnisse wird geschlossen, dass das System Kennzeichen hat, welche von den Optomotorreaktionen gewisser Insekte her bekannt sind. Das System veranschaulicht insbesondere die Eigenschaft der Phasenblindheit und auch ein anderes Phänomen, welches möglicherweise mit der Musterverkehrung, die bei Insekten beobachtet werden kann, verwandt ist. Es wurde auch gefunden, dass die de Langeschen Fusionsfrequenzen für räumliche Änderungen der Reizphasen unempfindlich sind. Ein Netzwerk, welches im Einzelnen untersucht werden kann, wird für die funktionelle Beschreibung des Betragens dieses Systems vorgeschlagen.

Резюме — В работе изучались две критические частоты, связанные со зрительным наблюдением движущегося периодического пространственного паттерна. Приведены данные о зависимости этих частот от параметров, поступающих на вход зрительной системы (периодичность и площадь раздражителя в пространстве). На основании этих данных заключается, что изучаемая схема сходна с известными оптомоторными реакциями некоторых насекомых. В особенности ясно, что система обнаруживает свойство фазовой слепоты, а также феномен, родственный, по-видимому, эффекту «обращения паттерна», встречаемому у насекомых. Было найдено так же, что фильтры Lange, для исследования критической частоты слияния мельканий, нечувствительны к пространственным изменениям фазы на входе. Предлагается сетевая схема для подробного функционального анализа поведения системы.