

## INTERACTION BETWEEN COLOUR AND SPATIAL CODED PROCESSES CONVERGING TO RETINAL GANGLION CELLS IN GOLDFISH

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### SUMMARY

1. Extracellular recordings were made from ganglion cell units in the isolated goldfish retina. The discharge patterns of these units are spatial and colour coded.

2. Even for weak stimuli these ganglion cell responses are highly distorted. To a first approximation a rectifying element can account for the observed distortion.

3. A method is introduced to determine whether the interaction between the spatial and colour-coded processes occurs preceding or after the rectifying stage.

4. With various stimulus patterns such as checkerboards, bars, annuli, etc., not only the location of the interaction point but also the mode of operation underlying the colour and spatial interactions has been studied.

5. The presented data indicate that for the common phasic ganglion cells in the goldfish retina spatial and colour interaction occurs preceding the rectifying stage. Moreover an algebraic mode of operation governs this interaction.

6. The charm of the presented method lies in the fact that no assumptions need to be made about the dynamics of the various retinal transformations converging to the ganglion cells. Neither is a description required for the non-linear (rectifying) element in order to answer the question of the location and the mode of operation of the colour and spatial interaction mechanism.

### INTRODUCTION

The discharge pattern of the ganglion cell responses to illumination of the goldfish retina is a function both of the colour and of the spatial configuration of the stimulus. The ganglion cell response which is most frequently found in this retina consists of a short burst of spikes to the onset

or the cessation of the stimulus light. The most common type of these so-called 'phasic' units gives an 'off' response to stimuli whose wave-lengths are at one end of the spectrum and an 'on' response to stimuli in the other end of the spectrum (Wagner, MacNichol & Wolbarsht, 1960). Red 'on'-green 'off' and red 'off'-green 'on' processes can be distinguished in the centre of the receptive field. Surrounding processes can be revealed by stimulating such a ganglion cell with an annulus concentric to the electrode (Daw, 1967). The colour codings of centre and surrounding processes have been reported to be identical but the 'signs' of the surrounding processes are opposite to the 'signs' of the centre processes. If, for example, an 'on' response is obtained by stimulation with a red spot, an 'off' response will be found when a red annulus is used.

Many articles have been published in recent years about the interaction between the two mutually antagonistic, concentrically organized centre and surround regions. Most of these experiments have been performed on the retinal ganglion cells in the cat. It has been shown that the ganglion cell responses in this retina reflect a linear operation in the integration of the signals coming from antagonistic regions (Enroth-Cugell & Pinto, 1970). However, to a first approximation, the ganglion cells in the cat retina behave linearly when centre and surround processes are either simultaneously or separately stimulated (Maffei & Cervetto, 1968). They produce sinusoidal outputs when sinusoidally driven (Hughes & Maffei, 1966).

This is not the case for phasic retinal ganglion cells in the goldfish. Here, a strongly distorted response is evoked by stimulation with sinusoidally modulated light. The non-linear behaviour of these ganglion cells, even when weak stimuli are used, furnishes direct evidence for the existence of an essential non-linear element in the chain of retinal transformations in goldfish. Therefore the spike responses of the goldfish retina cannot be usefully described by the methods of linear system analysis.

In this paper a method will be presented to answer the question whether the spatial integration in the goldfish retina occurs before or after the essential non-linearity. In addition an account is presented of an investigation of the operation of the mechanisms that underlie both the spatial *and* colour interaction of the retinal processes converging to the goldfish ganglion cells.

#### METHODS

Common goldfish (*Carassius auratus*) measuring between 15 to 20 cm long were used in all experiments. The animals were kept in a dark room for at least several hours before the experiment. The eye was quickly removed from the head, opened, and the dark-adapted retina was lifted out after separation from the optic disk. Almost certainly some loss of rod outer segments occurred. The receptor side was usually fairly free of melanin pigment.

The retina was spread, receptor side up, upon a piece of glass in a moist chamber. The chamber was kept at 15° C and moist gas (95 % oxygen, 5 % carbon dioxide) passed over the preparation. Light for stimulation came from below, passing through the layers of the retina in normal direction. The micro-electrode entered from above.

The retina was stimulated by patterns of illumination generated by an optical stimulator which provides control of spatial configuration, wave-length and intensity. The light sources were two electronically controlled television projection tubes; Philips, MW 6/2 (Denier van der Gon, Strackee & van der Tweel, 1958). The phosphors had broad emission spectra and gave a colour temperature of approximately 6500° K. The intensities of the two light sources could be modulated; photocells monitored and controlled the outputs of the projection tubes. The peak-to-peak value of the spontaneous intensity fluctuations was smaller than 1 % of the mean intensity level. The stimulus intensity was limited to a maximum of about 2.5 log units above threshold for units in the goldfish retina.

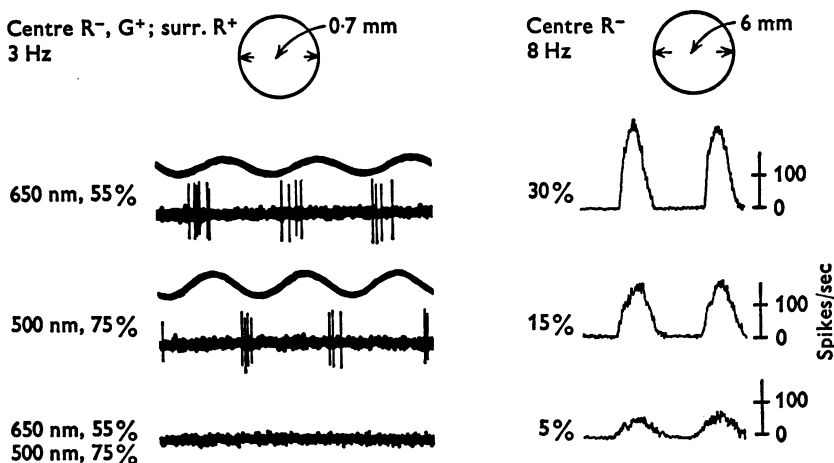
The optical system contained two independent but essentially identical pathways. Each pathway had a collimated region for placement of interference filters which determined the stimulus wave-length; the intensity was set by neutral-density filters. Two aperture stops which could be varied in size and position were focused upon the retina. In this way an image of spots, annuli and slits could be formed at the plane of the receptor layer. The two pathways were combined by a 50 % reflecting mirror. In the stimulus situations where more complicated patterns were used this half reflecting mirror was replaced by bar-, checkerboard-, etc., patterned mirrors. In the case of the checkerboard pattern, the mirror was patterned with alternate transparent rectangles and rectangles of reflecting material. The ratio of the lengths of the rectangle sides were  $1:\sqrt{2}$  so that when focused at an angle of 45° upon the retina, the mirror appeared to be patterned with squares. With the two light sources modulated in counterphase at equal intensities an alternating checkerboard was generated. In all situations the patterns were focused on the retina by viewing through a dissecting microscope; they were not noticeably distorted by passing through the retinal tissue, as can be seen in Pl. 1.

Recordings of the ganglion cell spike potentials were made with platinum-iridium micro-electrodes (Wolbarsht & Wagner, 1963). The indifferent electrode was a platinum wire placed in contact with the retina at some convenient point. The signals from the micro-electrode, which was centred under direct microscopic observation with respect to the stimulus field, were detected through conventional electronic amplification. The output of the amplifier was displayed, together with the signals of the photocells, on an oscilloscope. In order to improve the signal-to-noise ratio the responses, fed through a pulse shaper, were analysed by a computer of average transients (CAT). The number of summations was generally 50–600, depending upon the ganglion cell discharge rate. A final record was obtained by plotting the analogue output of the computer with an  $x$ - $y$  recorder.

## RESULTS

Initially, square-wave stimulation with a frequency of 0.5 Hz and 100 % modulation was used in order to isolate and classify a unit according to its colour and spatial coding. Next, other wave forms and stimulus configurations were applied in order to investigate the mechanism underlying the colour and spatial interaction. Sinusoidally modulated light was employed as a tool to detect the non-linear behaviour of the phasic ganglion cells in the goldfish retina.

The left column of Text-fig. 1 gives an example of such a response. This Figure shows that sine-wave stimulation produces a burst of action potentials only once during each stimulus cycle. For the red-off, green-on unit shown, stimulation with a sinusoid of 3 Hz resulted in discharges that were roughly in counterphase for the two colour-coded responses. The right



Text-fig. 1. Ganglion cell responses to sine-wave-modulated light. The degree of modulation is expressed as a dimensionless parameter,  $m = A/L_0$ , in which  $A$  is the amplitude of the sine wave and  $L_0$  is the mean intensity of the stimulus signal. The parameter  $m$  varies between 0 (0%) for unmodulated and 1 (100%) for fully modulated light.

*Left column* gives an example of the spike responses to sinusoidally modulated light of 3 Hz. The centre response of this particular cell (red-off, green-on centre) to a red sine-wave stimulus is roughly in counterphase with the response to an identical green coloured light. The bottom row shows that simultaneous stimulation with both coloured light does not result in any spike discharge at all. The mean intensity of the stimulus passed through Ealing-TFP interference filters is approximately  $6 \mu\text{W}/\text{cm}^2$  for the red and  $20 \mu\text{W}/\text{cm}^2$  for the green stimulus.

*Right column* gives the average spike response of a red-off centre process as a function of the modulation depth. It should be noted that even at 5% modulation the response is still highly distorted (half-wave rectified). The mean intensity of the stimulus passed through a Wratten 29 filter is approximately  $1 \mu\text{W}/\text{cm}^2$ . The number of summations with the CAT computer amounts to 300.

column of Text-fig. 1 gives the average response of a red-off unit. For half the stimulus period the density distribution of the nerve impulses had roughly the same shape as the sinusoidal stimulus, but during the other half of the stimulus cycle no spike discharge could be observed at all. The amplitude of the average response is approximately proportional to the strength (modulation depth) of the sine-wave stimulus. These data suggest that a

half-wave linear rectifier can model the distortions observed in the discharge pattern of the phasic ganglion cells to 'small' signal stimulation (see also Spekreijse, 1969).

*Spatial interaction for a centre colour-coded process*

In order to study the spatial interaction within the centre of the receptive field the retina was stimulated with a checkerboard pattern. Sine-wave modulation of exclusively one set of squares gives a response that, according to the data in Text-fig. 1, may be compared to a first approximation with a half-wave rectified sinusoid. Counterphase modulation of the other set of stimulus squares with the same mean intensity and modulation depth as the first set results, of course, in the same half-wave rectified sinusoid response shifted  $180^\circ$  in phase. Simultaneous counterphase stimulation of both sets of checkerboard squares could give one of the following two responses (Text-fig. 2): either a full-wave rectified sinusoid or no spike discharge at all. This can be understood as follows: if the spatial summation for a centre process takes place *after* the essential non-linear element, such as a half-wave rectifier, then the response would consist of a full-wave rectified sinusoid with the same amplitude as the original half-wave rectified response (Text-fig. 2*a*). On the other hand, if spatial summation occurs at a site *preceding* the non-linear element, then the two sets of input sinusoids counterbalance each other completely; and no response results (Text-fig. 2*b*). Text-fig. 2(*c*) gives the actual data for a green 'off' centre process. As is evident from this Figure, no spike discharge is observed when the two sets of squares are modulated simultaneously in counterphase. This holds, of course, only if the strengths of the responses to each set of squares are identical.

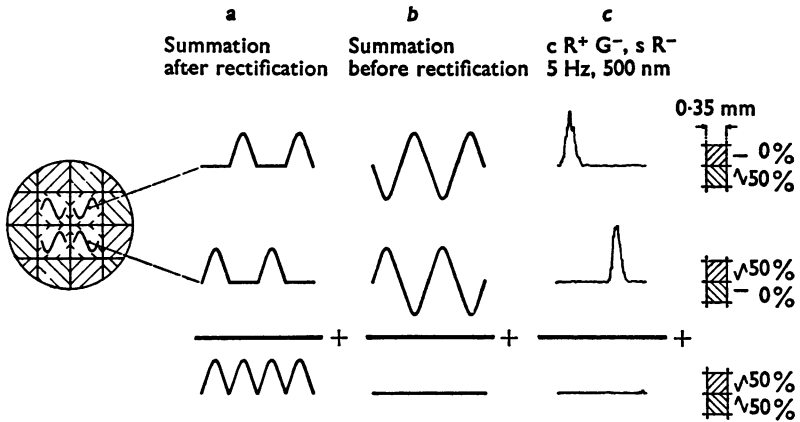
Neither the type of pattern nor the sizes of the pattern elements proved to be of importance in these experiments. Repeating the above experiments with bar as well as checkerboard patterns with various widths and square sizes, gave always similar results, as the ones depicted in Text-fig. 2*c*. Therefore the data demonstrate directly that in the goldfish retina the spatial interaction for a colour-coded centre process takes place preceding the essential non-linear element.

*Interaction between colour-coded centre processes*

As pointed out in the introduction, the type of ganglion cells most frequently found in the goldfish retina exhibits two antagonistic colour-coded centre processes: red and green. The spectral characteristics of each of these processes closely resemble the absorption spectra of the cones (Witkovsky, 1965). This indicates that cone outputs are grouped according to their

colour coding, and that the output signals of the two sets of cones travel separately through the retinal layers, or at least are only partly fused.

In order to investigate the functional location of the summing point between the red and green centre processes, we stimulated the retina with a red modulated light superimposed on a constant green background or vice versa. For each modulating signal, red respectively green, a modulation depth was chosen so that the responses were identical in size independently of the stimulus colour. An additional phase shift was necessary to have the



Text-fig. 2. Schematic representation (columns *a* and *b*) of retinal modes of summation between counterphase signals generated by the two sets of counterphase modulated squares of a checkerboard pattern.

Column (*a*) demonstrates that the summed response consists of a full-wave rectified sinusoid in the case that the retinal interaction takes place after the rectifying element.

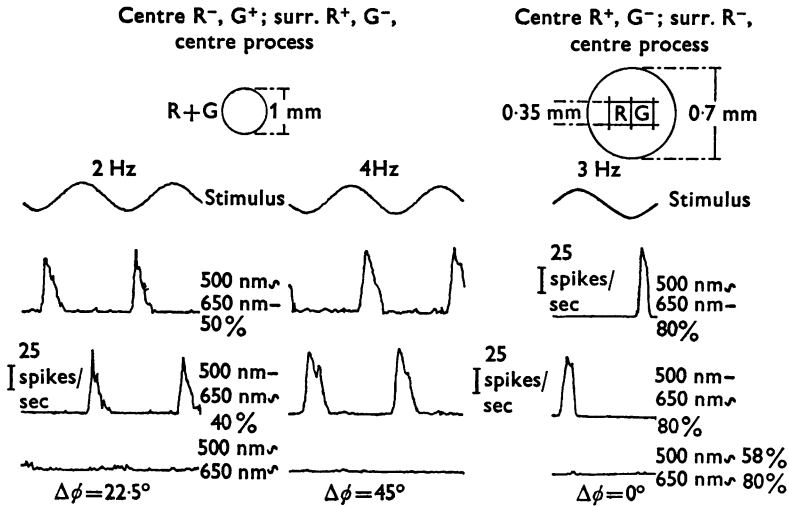
Column (*b*) shows that no response will be obtained in the case that the spatial summation of the two counterphase signals occurs preceding the rectifying element. This holds of course only if the strengths of the responses to each set of squares are identical.

Column (*c*) gives the actual data for a green-off centre process. The top figure is the average spike response to modulation (50%) of one set of squares (0.35 mm width). The other set of squares is not modulated at all but has a steady intensity identical to the mean intensity of the modulated set. Reversing the condition and modulating the other set of squares with the same depth, but in counterphase, results, of course, in the same rectified sinusoid but shifted 180° in-phase (mid figure). Simultaneous counterphase modulation of both sets of squares does not result in a spike discharge at all (bottom figure); an observation which suggests a location of the summing point at a stage preceding the rectifier.

The mean intensity of the stimulus light passing through an Ealing FTP interference filter is approximately  $4 \mu\text{W}/\text{cm}^2$ . The number of summations is 100; the modulation frequency is 5 Hz. The patterned spot focused on the retina has a diameter of 2 mm. For this particular unit a spot of even larger diameter could have been used, since no green colour-coded surrounding process could be detected.

individual responses to each stimulus colour exactly in counterphase. As can be seen in Text-fig. 3 (first column) under such condition simultaneous modulation of both coloured stimulus lights did not give a spike discharge (see also Text-fig. 3, left column).

Since twice this phase shift was required to cancel the two colour-coded responses when the stimulus frequency is doubled (Text-fig. 3, second column), this could suggest a latency difference between the red and green



Text-fig. 3. The Figure demonstrates the interaction between two different colour-coded centre processes. The left half Figure gives the average responses to two superimposed coloured spots. The first column gives the responses for a modulation frequency of 2 Hz and the second column for a frequency of 4 Hz. The right-hand column gives the responses to adjacent instead of superimposed coloured fields. In this case a modulation frequency of 3 Hz has been chosen. In all three columns the top row gives the stimulus. The second row gives the average responses to the modulated green fields (red fields steady) and the third row presents the average responses to the modulated red fields (green fields steady). In each column, except the third, the modulation depths of the red respectively green stimuli are chosen so that the average responses are identical in size, irrespective of the colour used. Under such a condition simultaneous in-phase modulation of both coloured stimulus fields does not result in a spike response (bottom row). To obtain this result, generally an additional phaseshift ( $\Delta\phi$ ) is required so as to have the responses to each of the coloured lights exactly in counterphase. For the superimposed condition the mean intensity of the 500 nm stimulus is approximately  $2 \mu\text{W}/\text{cm}^2$  and the intensity of the 650 nm stimulus is  $0.6 \mu\text{W}/\text{cm}^2$ . For the adjacent field condition these values are respectively 9 and  $1.2 \mu\text{W}/\text{cm}^2$ . The number of summations is 50 for the 2 Hz stimulus and 100 for the 4 Hz and 3 Hz stimuli. Calibration bars give the number of spikes/sec; the zero spike level is given by the lowest address points.

colour-coded centre process.\* However, for high stimulus frequencies ( $> 8$  c/s) the required phase shift difference between the red and green colour-coded processes was no longer proportional to the stimulus frequency. The origin of the phase difference remains therefore a point of further investigation.

It is well known that a large percentage of the cones in the goldfish retina are so-called double cones (Marks, 1965). It could be possible that only these cones contribute to the red-green centre processes. If so, the outputs of these cones would cancel each other already immediately after the absorption of the light quanta. To exclude such a point-to-point interaction mechanism, we studied also the interaction between the colour-coded centre processes with adjacent instead of superimposed coloured stimuli. The results obtained with a red-green in-phase modulated checkerboard are also presented in Text-fig. 3 (third column). These data indicate that the structure of the stimulus field does not affect the interaction between the red and green centre processes. Therefore it may be concluded that also the colour-coded components of the receptive field centre always interact, preceding the essential non-linear stage.

*Interaction between colour-coded components of centre and periphery*

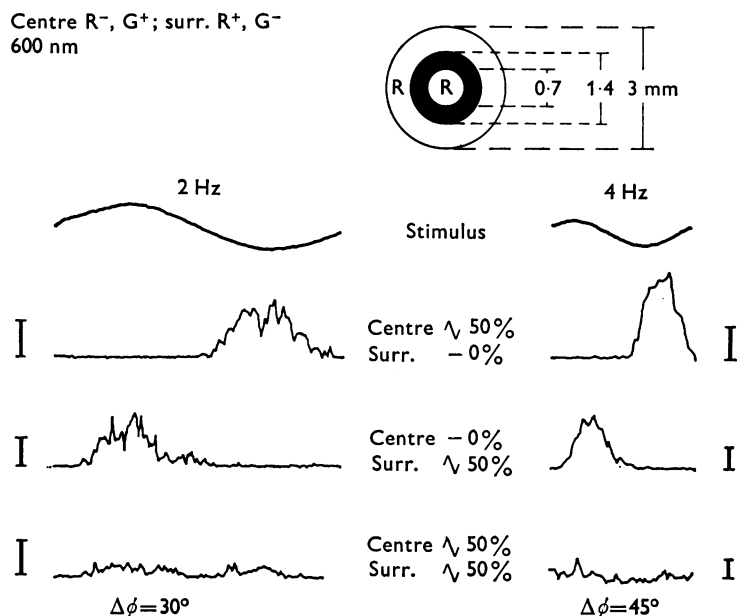
Having studied the interaction between the colour-coded central receptive field components, the next step was to investigate the interaction for a given colour between the two mutually antagonistic regions: centre and periphery. With *one* colour e.g., red, we stimulated centre and periphery simultaneously. The stimulus configuration consists of a central disk surrounded by an annulus. The two stimulus fields are not adjacent to reduce possible effects of scattered light. With steady illumination of one of the two stimulus fields we determined for centre and periphery separately the modulation depth required to obtain equally sized responses. Next we chose a phase shift between the central and peripheral stimulating signals such that the two responses themselves were in counterphase. Simultaneous stimulation under such a condition of the central and peripheral processes gives very weak spike discharges. This is illustrated in Text-fig. 4 for a red 'off' centre, red 'on' surrounding type unit. It follows that for central and peripheral processes also summation occurs, preceding the essential non-linear stage. Our experimental finding is that this holds not only for identical colour-coded components, but also for interactions between, for example, green-centre, red-surrounding processes.

\* Phase shift and latency are related to each other with the frequency as the proportionally factor ( $\phi = -\omega\tau$ ).



*Dynamics of the interactions mechanism*

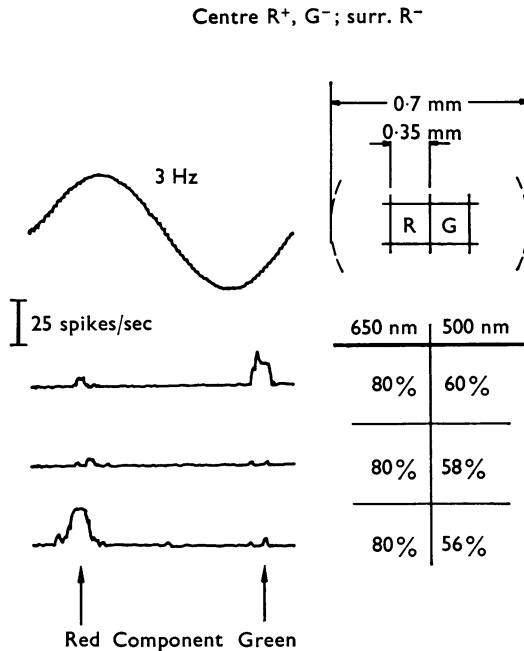
Up till now we have paid attention mostly to the location of the spatial interaction point in the chain of retinal transformations. However, the data presented here indicate not only that the spatial *and* colour interaction occurs preceding the essential non-linear stage, but also suggest an



Text-fig. 4. Interaction between the two mutually antagonistic regions: centre and periphery. The responses are from a red-off centre, red-on surrounding unit. Modulation of either the centre spot (annulus steady) or of the concentric annulus (spot steady) results in a highly distorted (rectified) response. Simultaneous in-phase modulation of both the centre spot as well as the annulus gives a very weak spike discharge (bottom row). An additional phase-shift ( $\Delta\phi$ ) is needed to have the individual responses exactly in counterphase. Generally it is more difficult to obtain a zero spike response for this condition than for any of the previous situations. The smaller strength of the 2 Hz response in comparison to the size of the response to the 4 Hz stimulus suggests a low-frequency attenuating process. Such a differentiating process is characteristic for phasic units. The mean intensity of the centre spot amounts to  $15 \mu\text{W}/\text{cm}^2$ ; the intensity of the annulus is  $30 \mu\text{W}/\text{cm}^2$ . The number of summations is 25; the calibration bars are 100 spikes/sec. The zero spike level is given by the lowest address points.

algebraic mode of interaction. This follows directly from the observation (Text-fig. 5) that only subtractive interaction of *equally sized* responses results in a zero response. The slightest difference in the sizes of the subtracting signals results in a spike discharge. The data of Text-fig. 5

illustrate the sensitivity of this zero-setting for the red-green interaction mechanism. A modulation depth increase or decrease of no more than 2% for the green stimulus resulted in a clear dominance of the green or the red component in the spike response. Such a sharp minimum means that the positive and negative halves of the stimulating sinusoid are treated



Text-fig. 5. The slightest difference in the strengths of the responses to the green, respectively red modulated set of checkerboard squares results in a disturbance of the zero-spike-response setting. The Figure shows that, keeping the modulation depth of the red stimulus constant, a 2% increase of the modulation depth of the green stimulus light results in a dominance of the green component in the final response. Similarly, a 2% decrease of the modulation depth of the green stimulus light results in the dominance of the red component of the final response. The unit from which these data are taken is the same as the one depicted in the right-hand column of Text-fig. 3. For the stimulus settings see the legend of that Figure.

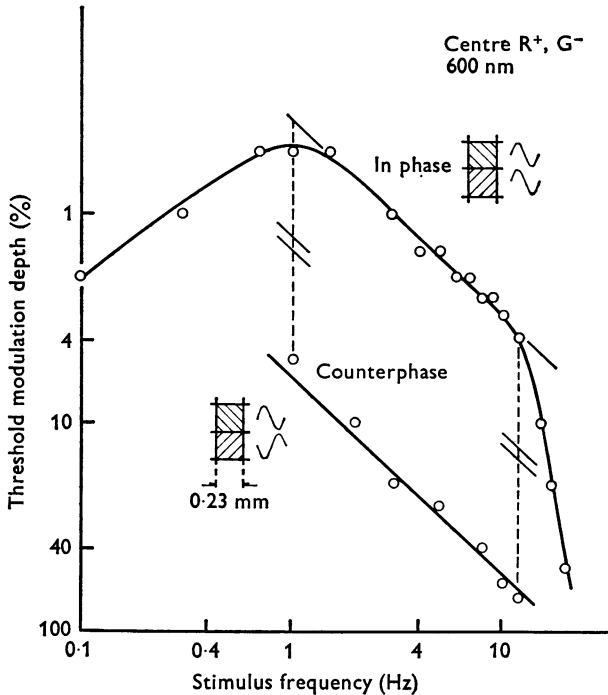
identically by the retinal processes preceding the interaction point. Therefore for weak stimuli an approximately linear input-output relationship holds for the primary processes; suggesting an algebraic mode of operation for the spatial and colour interaction.

#### *Saturation*

In applying the checkerboard method we assumed that only *one* non-linearity accounts for the distortion in the ganglion cell responses. As the

observations in, for example, Text-fig. 2(c) indicate, this is practically true; but only to a first approximation! In reality none of the elements in the chain of retinal transformations behaves linearly. Any element has a restricted dynamic range and, when driven sufficiently strongly, each of them will exhibit non-linear behaviour such as saturation.

In terms of Fourier analysis this means that early elements may generate



Text-fig. 6. The so-called de Lange curves for a red-on centre process. The modulation depth required to reach a constant threshold criterion is plotted as a function of the frequency of the sine-wave modulated checker-squares. The upper curve gives the threshold modulations for in-phase modulation of the two sets of squares. The bottom curve represents the data points for counterphase modulation of these two sets. The mean intensity of the 600 nm stimulus is approximately  $0.4 \mu\text{W}/\text{cm}^2$ . The diameter of the circular patterned spot focused on the retina is 1.5 mm; the width of the checker squares amounts to 0.23 mm.

harmonics. If such harmonics (in particular even harmonics) are formed at a stage preceding the summing point of the receptive field centre, then they can never be cancelled by counterphase stimulation of the two sets of checkerboard squares. This offers the possibility of determining at which modulation depth distortion occurs early in the system, i.e. before the 'rectifying' stage. The results of this experiment are presented in Text-fig. 6.

The upper curve in this Figure is the so-called de Lange curve. This curve is determined for a red 'on' centre ganglion cell by in-phase stimulation with identical settings of the two sets of checkerboard squares; thus no structure is present in the stimulus plane. For a constant mean intensity the de Lange curve represents the modulation depths requested as a function of the sine-wave frequency to reach an arbitrarily chosen, constant-response criterion. As is evident from the curve, for higher stimulus frequencies, larger modulation depths are necessary to reach the criterion. Also, at lower stimulus frequencies some elevation of modulation depth is required in order to reach the chosen threshold.

Next the same unit was stimulated with the two sets of checkerboard squares modulated in counterphase, and the modulation depth was determined to reach the threshold using the same constant intensity as for the in-phase measurements. The results are very clear. As can be seen in Text-fig. 6, lower curve, counterphase stimulation of the two sets of squares needs at least a ten times as high modulation depth to reach the in-phase threshold condition. The surprising finding in this Figure is that the increase in threshold is independent of the modulation frequency of the checkerboard pattern. This means that in the frequency range measured the first effective non-essential distortion (for example, saturation) manifests itself *after* the high-frequency attenuation, but *preceding* the essential non-linear stage (i.e. the rectifier). Otherwise the threshold criterion would never have been reached (see also Text-fig. 3).

#### DISCUSSION

In all the experiments to study the spatial and colour interaction reported in this paper, sine-wave modulated light was used. The advantage of this stimulation above any other type of stimulating signal lies in the fact that application of this stimulus does not require any knowledge about the dynamic characteristics of the interacting processes. For example, if these characteristics differ, the responses of the interaction processes can never be equalized for any other type of stimulus without changing the modulating wave forms. In contrast, equal responses can always be obtained with sinusoidal stimulation merely by choosing the correct amplitudes and phases of the input sinusoids.

In addition, the zero-response method described in this paper has an advantage over the commonly used phasor representation to study the interaction mechanism (Maffei & Cervetto, 1968). As discussed already by Enroth-Cugell & Pinto (1970), the phasor technique can be successfully applied only if precise assumptions are made about the characteristics of the non-linear process involved. This is not so for the zero response method.

As is illustrated in this paper, this method can answer the question of the mechanism underlying the spatial *and* colour interaction without the necessity of a description of the characteristics of the (essential) non-linearities involved.

Not all ganglion cells in the goldfish retina are silent when no stimulus is applied. When such units are sinusoidally modulated, their dynamic behaviour is similar to that of the ganglion cells in the cat retina. The observations presented here hold also for these ganglion cells, but for moderate modulation depths the essential non-linearity is masked by the spontaneous activity (Spekreijse, 1969). Therefore for these units the location of the interacting point cannot be determined by the methods described in this paper; only the mode of operation can be investigated. Our observations indicate that for the spontaneous units also an algebraic operation underlies the colour *and* spatial interaction.

The results described here do not give any specific answers to how the coding of the sensory information is at the stage where the colour and spatial interaction occurs. However, taking into account the present concepts about spike-generating mechanisms, it seems unrealistic to suppose that at the interaction point the nerve impulses are already generated. Only direct investigation from the nuclear layer between photoreceptors and ganglion cells can give an answer to this question. Such a further investigation is also needed to determine at which pre-ganglion level the interaction occurs.

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#### REFERENCES

- DAW, N. W. (1967). Goldfish retina: organization for simultaneous color contrast. *Science, N.Y.* **158**, 942-944.
- DENIER VAN DER GON, J. J., STRACKEE, J. & TWEEL, L. H. VAN DER (1958). A source for modulated light. *Physics Med. Biol.* **3**, 164-173.
- ENROTH-CUGELL, C. & PINTO, L. (1970). Algebraic summation of centre and surround inputs in retinal ganglion cells of the cat. *Nature, Lond.* **226**, 458-459.
- HUGHES, G. W. & MAFFEI, L. (1966). Retinal ganglion cell response to sinusoidal light stimulation. *J. Neurophysiol.* **29**, 333-352.
- MAFFEI, L. & CERVETTO, L. (1968). Dynamic interactions in retinal receptive fields. *Vision Res.* **8**, 1300-1304.
- MARKS, W. B. (1965). Visual pigments of single goldfish cones. *J. Physiol.* **178**, 14-32.
- SPEKREIJSE, H. (1969). Rectification in the goldfish retina: analysis by sinusoidal and auxiliary stimulation. *Vision Res.* **9**, 1461-1472.

- WAGNER, H. G., MACNICHOL, E. F. & WOLBARSH, M. L. (1960). The response properties of single ganglion cells in the goldfish retina. *J. gen. Physiol.* **43**, suppl. 2), 45-62.
- WITKOVSKY, P. (1965). The spectral sensitivity of retinal ganglion cells in the carp. *Vision Res.* **5**, 603-614.
- WOLBARSH, M. L. & WAGNER, H. G. (1963). Glass-insulated platinum micro-electrodes: design and fabrication. *Medical Electronics*, Proc. 5th Int. Conf. on Med. Electr., ed. BOSTEM, H., pp. 510-515. Liège: University of Liège Press.

#### EXPLANATION OF PLATE

Fig. 1. The left-hand photograph shows an isolated retina in the moist chamber. A circular light spot is projected from below on to the retina (*a*); the micro-electrode (*b*) enters from above; the retina is placed in contact with the indifferent electrode (*c*). The circular spot has a diameter of 5 mm. The right-hand photograph illustrates that a checkerboard pattern focused on the retina is not much distorted by passing through the retinal tissue. The circular patterned spot has a diameter of 2 mm; the width of the checker-squares amounts to 0.35 mm.

