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COLOUR-CODED GANGLION CELLS IN THE GOLDFISH RETINA: EXTENSION OF THEIR RECEPTIVE FIELDS BY MEANS OF NEW STIMULI

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SUMMARY

1. Receptive fields of colour-coded ganglion cells of the goldfish retina were investigated.

2. Only a few cells (5%, Type P) were found to be as simple as those described by Wagner, MacNichol & Wolbarsht (1960, 1963), with an 'on' response to red light in the centre, and an 'off' response to green light over a rather wider area, or vice versa.

3. Most cells (49%, Type O) also gave a peripheral response with an 'on' response to green light, and an 'off' response to red light in the periphery, as well as an 'on' response to red light and an 'off' response to green light in the centre (or vice versa).

4. When a small spot of light was used to stimulate the periphery of a Type O cell, the peripheral response usually was not obtained. The organization of the periphery is such that a stimulus of large area and low intensity (annulus) is much more effective than a stimulus having equal energy with small area and high intensity (spot). If only small spots are used, the Type O cell is indistinguishable from the Type P cell.

5. Spectral sensitivity measurements show that one central and one peripheral process are fed primarily by red-absorbing cones, and the other central and the other peripheral process by green-absorbing cones or rods.

6. The diameter of the receptive field as a whole is very large, being 5 mm or more on the retina.

7. When red spots in green surrounds, or red/green boundaries are used as stimuli, the response can be predicted by summing the responses to the components of the stimulus.

8. This type of receptive field organization is appropriate to mediate

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simultaneous colour contrast. The 'opponent colour' organization previously reported is appropriate for successive colour contrast, but not for simultaneous colour contrast.

9. The component of the response coming from the green-absorbing cones was masked or hidden by the component of the response coming from the red-absorbing cones in 14% of the units (Type Q units). The component from the green-absorbing cones was revealed by using a high intensity of stimulation, or by observing the response after bleaching pigment with an intense red light.

INTRODUCTION

Opponent colour units are found in several vertebrate species. The criterion for such a unit is that its response to light of one colour should be opposite to its response to light of some other colour. Usually one can discover this by illuminating the retina with diffuse light, as was done in the original work on the monkey lateral geniculate cells (De Valois, Smith, Kitai & Karoly, 1958) and fish S-potentials (Svaetichin, 1956). More detailed stimuli reveal the nature of the receptive fields of the units. Work on the receptive fields of such units has been done in fish (Wolbarsht, Wagner & MacNichol, 1961; Motokawa, Yamashita & Ogawa, 1961), monkey (Hubel & Wiesel, 1960; Wiesel & Hubel, 1966) and ground squirrel (Michael, 1966).

Wagner *et al.* (1960, 1963) showed that the majority of recordable ganglion cells in the goldfish retina give opponent colour responses. They found wave-lengths that isolated the two opposing responses, and mapped the receptive fields with small spots of light. Typically, the cell fired several spikes when a red light was turned on ('on' response), and was silent when a green light was turned on, but fired when the latter was turned off ('off' response). The receptive field mapped with a red spot was found to be concentric with the receptive field mapped with a green spot, and nearly always smaller. Thus there were two basic types of unit—'on' to red in the centre and 'off' to green over a wider area, or 'off' to red in the centre and 'on' to green over a wider area. Wagner *et al.* (1963) noticed some exceptions, but believed that the fundamental organization was similar in all cases to the two basic types.

Motokawa, Yamashita & Ogawa (1960, 1961) performed parallel experiments on the carp. Their studies suggested some differences from the results of Wagner *et al.*, but the differences were not clear and they state that the organization they found was basically the same as the organization found by Wagner *et al.* (1960, 1963).

The present paper describes experiments in which annuli and other

stimuli were used, and shows that the results cannot be predicted from the experiments done with small spots of light. The basic organization of the receptive field is, in fact, rather more complex than that described by Wagner *et al.*

METHODS

Goldfish retinae (*Carassius auratus*) were isolated and maintained according to the method described by MacNichol & Svaetichin (1958). The neural retina was removed from the eye and placed receptor side up in a cool chamber (retinal temperature approx. 11·5 °C). The fish were well dark-adapted before removal of the retina, to make use of the photomechanical response and ensure that as few receptors as possible were torn off, in separating the retina from the pigment epithelium. Moist gas (95% oxygen, 5% carbon dioxide) flowed over the retina. Most fish had eyeballs of diameter 7–10 mm, so that 1 mm on the retina corresponded to 6–9° visual angle.

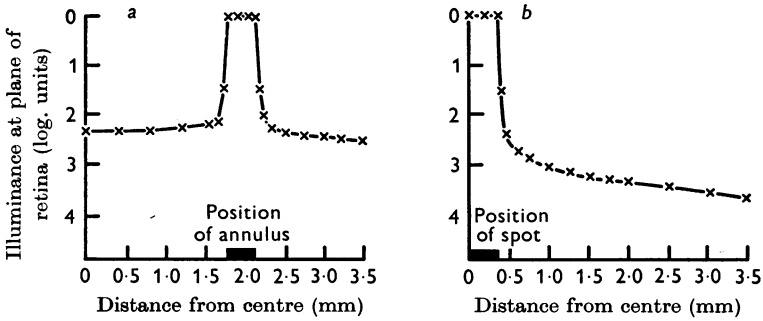

Fig. 1. Scatter by an annulus (*a*) and a spot (*b*). Without scatter, the annulus would have an inside radius of 1·8 mm, outside radius of 2·16 mm, and the spot would have a radius of 0·36 mm at the plane of the retina. Both graphs represent the illuminance of this plane, taken across a diameter through the centre.

The stimulating and recording system was designed and built by Dr Edward F. MacNichol, Jr., with minor modifications by the author. Light was focused on the retina from below, through the glass on which the retina lay. Two monochromators of modified Czerny–Turner design were used. Each illuminated a stimulus plane in focus with the retina. Various spots and annuli could be placed and moved around in the stimulus planes. They were either cut from metal, or made on high-contrast photographic material with a density of 0·15 log units in the clear areas, and more than 5 log. units in the dense areas. Over-all intensity was controlled by Kodak Type M carbon neutral-density wedges. After each beam passed through its stimulus plane and neutral wedges, the two beams were combined.

Some light was scattered by the lenses and prisms between the stimulus planes and the retina: this was measured in order to interpret the results. A small aperture was placed in the plane of the retina, the retina being absent, with a photomultiplier behind it. Measurements were made at various distances from the centre of various spots and annuli, and curves were drawn for the intensity of stimulation across the diameter of all the spots and annuli used (Daw, 1967*a*). The results for one spot and one annulus are given in Fig. 1.

Figure 2 outlines the recording and timing system. Platinum–iridium micro-electrodes were made according to the method of Wolbarsht, MacNichol & Wagner (1960) and inserted into the retina from the receptor side. Signals from the micro-electrode passed through a cathode follower and a low-level differential amplifier (MacNichol & Bickart, 1958) to a

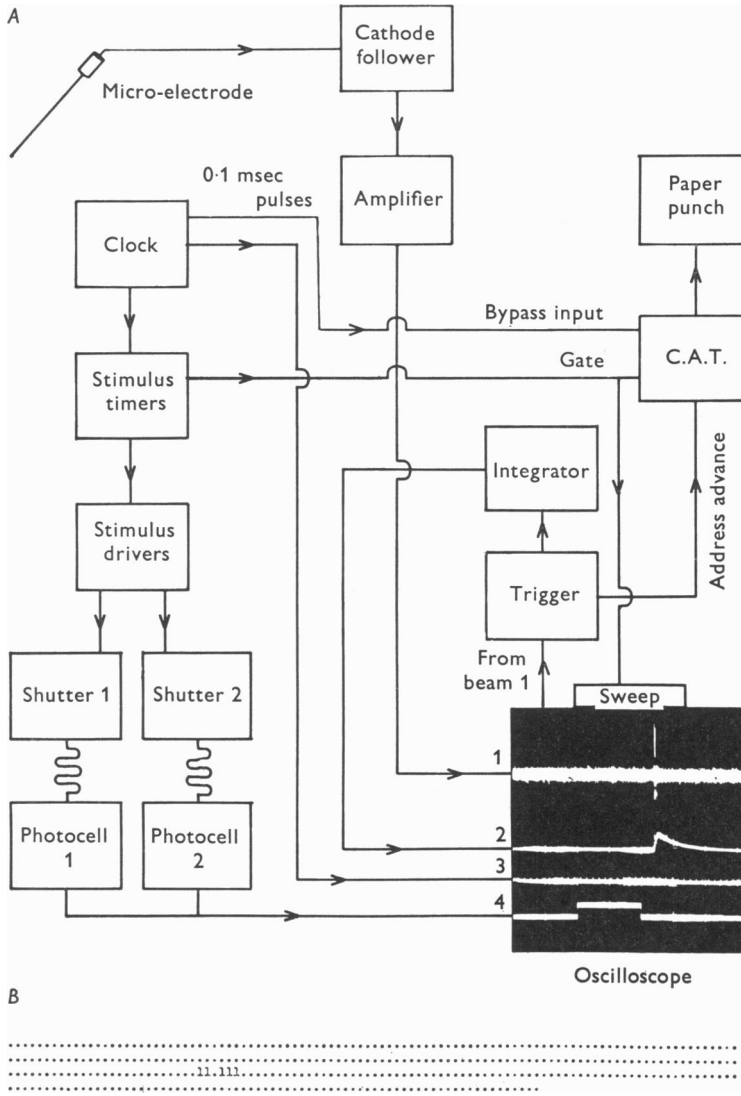

Fig. 2. (*A*). Diagram of the recording system and the timing system for the stimuli. The four beams on the face of the oscilloscope screen show: beam 1, output of the amplifier giving the spike train; beam 2, output of the trigger, after passing through a network which turns each pulse from the trigger into a step with an exponential decay; beam 3, pulses at 100 msec and 500 msec intervals from the clock; beam 4, output of the photocells, showing when the stimulus was turned on and off. It was clear in the original photograph that there were five spikes and five pulses from the trigger. (*B*) Output from subsequent computer processing of the data, giving 3·7 sec of the spike train seen on beam 1, in the form of a single stimulus histogram with time bins of 10 msec.

trigger. This fed into a computer of average transients (Mnemotron CAT 400 A), which stored the interspike intervals as multiples of 0·1 msec, and fed out this information on paper tape at the end of each stimulus. The tape was subsequently processed on an LGP-30 computer, which printed out the spike train for each stimulus (Fig. 2*B*). The performance of the whole system was continually observed on a Tektronix Type RM 561 four-beam oscilloscope, which showed the original recording, the output of the trigger, pulses from a Tektronix Type 180 A Time Mark Generator, and signals from two photo-cells monitoring the two light beams (Fig. 2*A*).

Spectral sensitivity curves were plotted as the logarithm of the inverse of the quantum flux required to reach some criterion; usually one spike fired on two occasions out of three. For cells with spontaneous activity, a higher criterion was chosen.

RESULTS

After a number of preliminary experiments were performed, quantitative results were obtained on 136 cells. The majority of these gave opposite responses to diffuse red light and green light—either 'on' to red light and 'off' to green light or vice versa—and were consequently called colour-coded. Only a few of these colour-coded cells were found to have receptive fields as simple as the basic type described by Wagner *et al.* (1960, 1963). This type is called Type P in the present work. Over half the colour coded cells had a more extended receptive field, and these were called Type O.

Type O cells

Typically, when the whole receptive field of a Type O cell was illuminated with red light of wave-length 650 nm, the cell gave an 'off' response while, if light of complementary colour (500 nm) was used, the cell gave an 'on' response. With a small spot of light placed in various positions in the receptive field of the cell, the cell responded as it did to diffuse illumination, no matter what the position of the spot. In the middle of the receptive field, the cell responded more sensitively, and the centre of the most sensitive region was called the mid-point. Units giving an 'on' response to red light and an 'off' response to green light were found almost as frequently, but the diameter of the sensitive region found with green light was always as large or larger than the diameter found with red light.

These properties do not distinguish the Type O cells from those described by Wagner *et al.* (1960, 1963). However, when annuli centred on the mid-point of the receptive field were used, some new properties emerged (Fig. 3). The cell gave an 'off' response to spots and small annuli of red light (650 nm) and an 'on' response to spots and small annuli of green light (500 nm), but an 'off' response to large annuli of green light and an 'on' response to large annuli of red light. (Strictly speaking light of 500 nm is not a pure green, but slightly longer wave-lengths gave similar results, so the word 'green' will be used to describe experiments done with 500 nm,

for the sake of clarity and brevity.) Thus the large annuli reveal peripheral responses which are opponent to the central responses for the same wave-lengths.

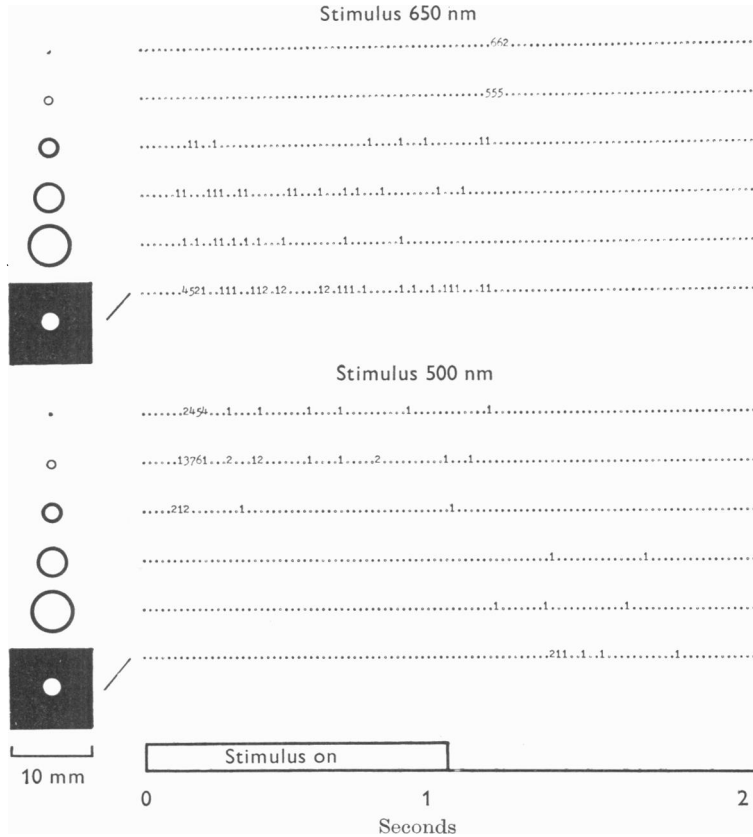

Fig. 3. Response of a Type O unit to various spots and annuli. Red light (above) was 650 nm of irradiance $1{\cdot}3 \times 10^{10}$ quanta.mm^{-2}.sec^{-1} and green light (lower series) was 500 nm of irradiance $6{\cdot}5 \times 10^{9}$ quanta.mm^{-2}.sec^{-1}. Illuminated areas are shown black and non-illuminated areas white. Dimensions at the plane of the retina were: diameter of spot 0·36 mm; diameters of annuli 0·72–1·08 mm, 1·44–2·16 mm, 2·88–3·60 mm, 4·32–5·04 mm and 2·16–10 mm square. The stimuli are drawn approximately to scale opposite the responses which they elicited. Each line of response represents two seconds of data, divided into 100 time bins of 20 msec each.

Other Type O cells with reverse properties were found. They gave an 'on' response to red light in the centre, an 'off' response to green light in the centre, an 'off' response to red light in the periphery, and an 'on' response to green light in the periphery. In general, the results with annuli suggested that the centre for red was smaller than the centre for green,

agreeing in this respect with the results from small spots of coloured light placed in various positions in the receptive field. This can be seen in Fig. 3, where the third annulus gave an 'on' response to both wave-lengths. Thus the receptive field consisted of three areas, the centre, the periphery, and an intermediate area which was in the centre for green and in the periphery for red. This intermediate area corresponds to the periphery described by Wagner *et al.* (1960, 1963). It was always quite narrow in relation to the rest of the receptive field, and sometimes did not exist at all.

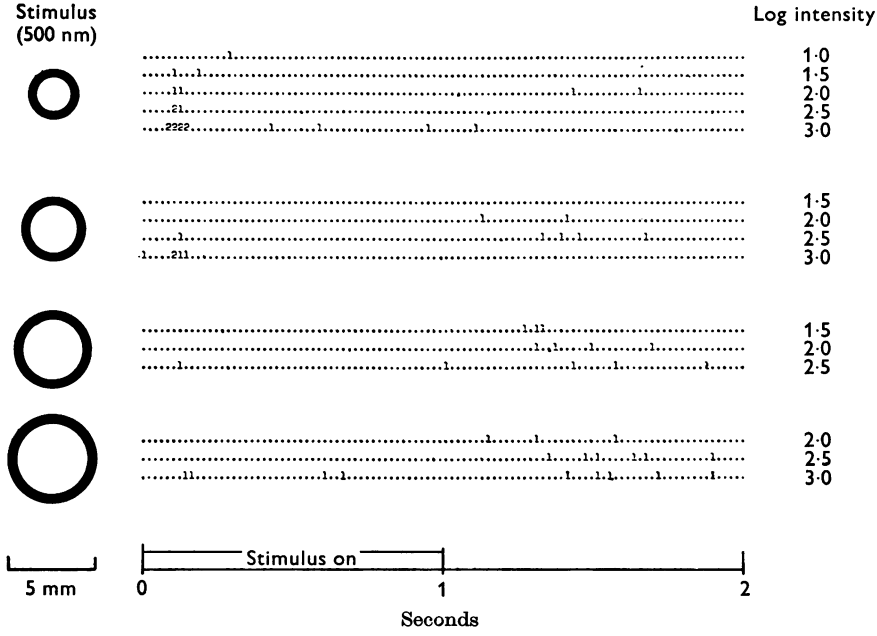

Fig. 4. Response of a Type O unit to various annuli of 500 nm at various intensities. Zero log intensity was $6{\cdot}5 \times 10^7$ quanta.mm^{-2}.sec^{-1}. Diameters of the annuli were 2·16–2·88 mm, 2·88–3·60 mm, 3·60–4·32 mm and 4·32–5·04 mm.

The response to diffuse light was always the same as the response to the same wave-length in the centre of the receptive field of the cell, for both red light and green light, and for both subtypes of Type O cell, with the exception of one red–on green–off centre cell. The responses to all annuli were stable for a log unit or so above threshold, even annuli which straddled the boundary between the centre and the periphery of the receptive field (Fig. 4). However, at high intensities of 1 log. unit or more above threshold, large annuli elicited the central response as well as the peripheral response appropriate for the wave-length concerned, and at very high intensities, only the central response was seen.

Size of receptive field. Obviously the larger annuli were very big in

relation to the retina, extending over a substantial fraction of it, but the cell gave a response to them, and this response was the peripheral response at threshold. Was this response due to scattered light, or was the receptive field enormous?

One can show that the receptive field was indeed enormous, and obtain an indication of its size. The argument follows from the nature of the scattered light, and the fact that diffuse illumination gave the central response. As already mentioned, the scatter in the optics was equivalent to a uniform veil. There is also scatter within the retina. However, one would expect the curve for retinal scatter to fall off with distance, rather than flatten out like the curve for optical scatter, because each element of

TABLE 1. Average size of receptive field for Type O units

Wave-length	Outer bound for size of centre of receptive field (mm)	Inner bound for size of whole of receptive field (mm)
650 nm	$1{\cdot}35 \pm 0{\cdot}36$	$5{\cdot}4\text{–}D \pm 1{\cdot}55$
500 nm	$1{\cdot}6 \pm 0{\cdot}84$	$5{\cdot}8\text{–}D \pm 1{\cdot}45$

retina through which the light passes absorbs and scatters the light further. Consequently one would expect retinal scatter to be unimportant compared to stimulator scatter beyond some distance D mm, which is small compared to the size of the larger annuli, and one can say that the scatter is equivalent to diffuse illumination beyond this distance.

Annuli, even larger than those shown in Fig. 3, gave the central response at threshold. The threshold intensity agreed well with the threshold for uniform stimulation of the whole field by direct light, and the measurements of stimulator scatter alone, without considering scatter within the retina. The diameter at which the threshold response changed from peripheral to central must be related in some way to the size of the periphery of the receptive field. Optical scatter will tend to bring out the peripheral response for annuli up to D mm larger than the periphery of the receptive field. Thus D mm less than the value obtained is an inner bound for the diameter of the periphery of the receptive field.

The same method can be used to measure the diameter of the centre of the receptive field, by noting the size of annulus at which the response changes from central to peripheral. In this case the value obtained is simply an outer bound because both stimulator and retinal scatter tend to bring out the central response.

Measurements were made on 22 units, with the results given in Table 1. In six cases, the measurements were checked by drawing area–threshold curves (Barlow, 1953) for both red and green light, which minimized the scatter problem, and gave values in agreement with the annulus measure-

ments for the size of the centre of the receptive field. The size of the centre for both red and green compared well with the size of the receptive fields found by Wagner *et al.* (1960, 1963). The size of the field as a whole, however, was much larger than this, being at least $5{\cdot}5 - D$ mm in diameter for both red and green. This is approximately half-way across the retina of the average fish, which has an eyeball of diameter 7–10 mm.

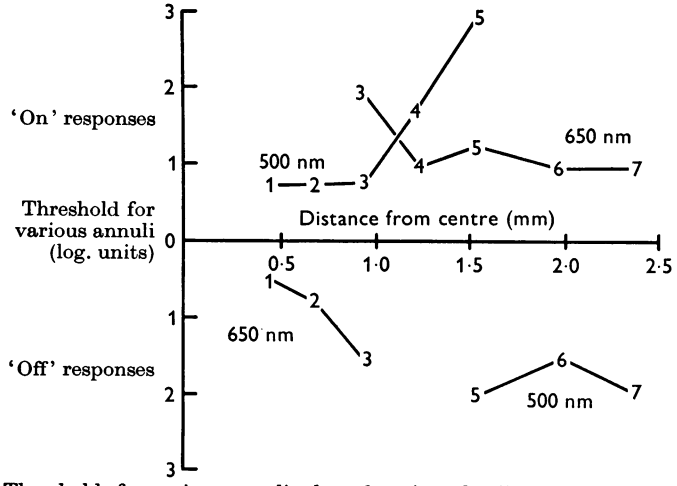

Fig. 5. Thresholds for various annuli, plotted against the distance between a point half-way across the illuminated portion of the annulus and the centre of the annulus. The results were taken from the same unit as that described in Fig. 3, where the responses to annuli, 1, 3, 5 and 7 are shown. Responses to annuli 4–7 were not due to scatter, for the reason that scatter would have brought out the central response, rather than the peripheral response.

Threshold in various parts of the receptive field. Threshold was measured for various annuli centred on the receptive field. The results for one unit are given in Fig. 5. If the system were such that the response depended on the product of area and intensity alone, each threshold given in Fig. 5 could be divided by the area of the relevant annulus, to give the threshold per unit area for various parts of the receptive field. There were indications that the system does not behave like this.

Figure 6 illustrates an experiment demonstrating this point, performed on a red–on green–off centre Type O unit. The first three lines show the 'on' responses obtained from three narrow annuli, all falling on the periphery of the receptive field, the 'on' response being due to light scattered into the centre of the receptive field. Measurements showed that each of these annuli scattered the same uniform veil of light over the field (Daw, 1967*a*). Thus the wide annulus of one-third the intensity shown on the fourth line must have also scattered the same uniform veil. Yet the wide

annulus gave an 'off' response. The difference in response can only be accounted for by the difference in stimulation of the periphery, since the stimulation of the centre was identical in all four cases. This was a difference of area and intensity—the wide annulus has 3 times the area and one-third the intensity. Since the wide annulus was the sum of the three narrow ones, the results of the experiment cannot be explained by the hypothesis

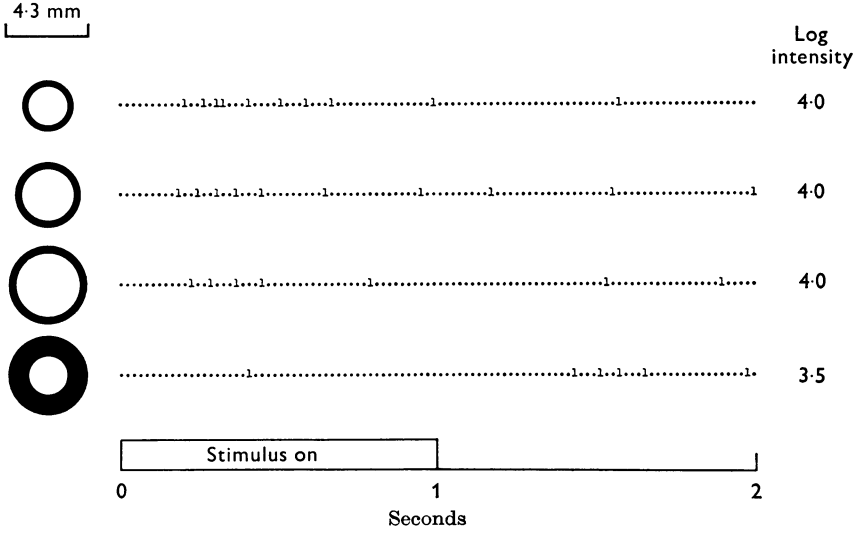

Fig. 6. Response of a Type O unit to three annuli which lie inside each other, and to a fourth, which is the combination of the first three at a lower intensity. All annuli were illuminated by 650 nm; the first three all had irradiance 3×10^{10} quanta.mm^{-2}.sec^{-1}, and the fourth had irradiance one-third of this. The diameters were 2·16–2·88 mm, 2·88–3·60 mm, 3·60–4·32 mm, and 2·16–4·32 mm.

that the wide annulus included some highly sensitive part of the periphery, which the three narrow annuli did not. The results were not critically dependent on the intensities used: the intensities could be varied by 0·2 log. units without changing the results. The experiment was repeated on four other units with similar results.

In several experiments, the periphery was searched with a small spot, to obtain the peripheral response, but the central response was always seen. Larger spots gave the peripheral response, and when this was so the same response was seen north, south, east and west of the mid-point of the receptive field, with threshold the same within 0·3 log. units. Figure 6 suggests an explanation for this: a small spot of intensity 1000 covering an area $\frac{1}{1000}$ of the periphery will scatter the same amount of light into the centre as a large annulus of intensity 1, covering the whole of the periphery, but if area and intensity are not reciprocal in stimulating the periphery the small spot will be much less effective.

Spectral sensitivity. Spectral sensitivity measurements were made on 14 units. Figure 7 shows the results from one unit which gave an 'off' response to red in the centre or to green in the periphery and an 'on' response to green in the centre or to red in the periphery. The spectral sensitivity of the centre was measured with a spot of diameter 0·72 mm, and that of the periphery with an annulus of inside diameter 2·88 mm, outside diameter 4·32 mm. The spot was chosen to be fairly small, so that

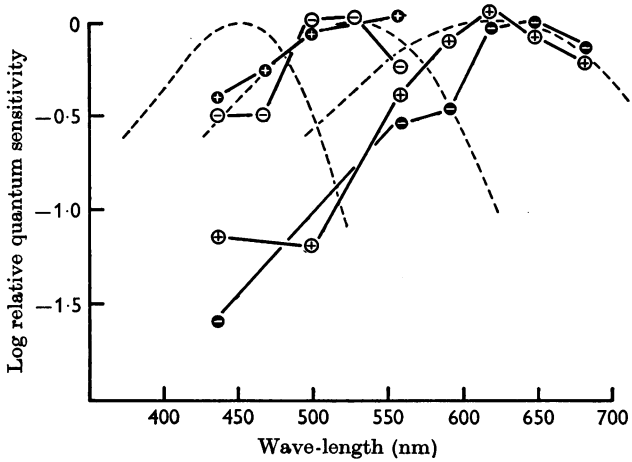

Fig. 7. Spectral sensitivities for the centre and the periphery of a Type O unit. Pluses refer to 'on' responses, minuses to 'off' responses, white symbols on a black ground to central responses, and black symbols on a white ground to peripheral responses. The dashed lines give the difference spectra for the goldfish cone pigments (Marks, 1965). The curves have been displaced upwards relative to the central 'off' response curve, to fall close to the difference spectra, by the following amounts: central 'on' response 0·3 log. units, peripheral 'on' response 2·2 log. units, peripheral 'off' response 1·7 log. units.

it fell within the centre for both red and green. The annulus was chosen to have a sufficiently large inside diameter, and a sufficiently small outside diameter, that it fell entirely within the periphery for both red and green. (Spectral sensitivity measurements were not attempted on any units until the measurements of field size had been completed.) Some scatter was unfortunately inevitable in the apparatus used, and the width of the annulus was chosen in an attempt to minimize this problem.

The spectral sensitivities for the central 'off' response and the peripheral 'on' response were nearly identical; so were the spectral sensitivities for the central 'on' response and the peripheral 'off' response.

Figure 7 also shows the difference spectra of pigments in the goldfish cones measured by Marks (1963, 1965). Two of the ganglion cell spectral sensitivity curves follow the difference spectrum for the red-absorbing

pigment, and two follow the difference spectrum for the green-absorbing pigment with some deviation where the pigment curves overlap. This was true for all the spectral sensitivity curves measured, except for one rather unstable unit, whose curve peaked at about 475 nm. The discrepancy between spectral sensitivity and difference spectrum was reduced when measurements were made against a coloured background.

Latency. Measurements of latency were made on 16 units. Eleven of these were units which gave an 'off' response to red and an 'on' response to green in the centre, and five were the reverse. All the latencies were long, ranging from about 100 msec for central red responses to 400 msec or more for peripheral green responses. In general, it was true that the latency for a peripheral response tended to be longer than the latency for a central response. It was also true, however, that the latency for a 500 nm response tended to be longer than the latency for a 650 nm response. The combination of these two effects meant that the latency for a 500 nm central response was about the same as, sometimes even shorter than, the latency for a 650 nm peripheral response, whereas the latency for a 500 nm peripheral response was much longer than the latency for a 650 nm central response. The 500 nm peripheral response always had a particularly long latency when it was an 'off' response. Raising the temperature shortened the latencies a little, but did not alter these qualitative generalizations.

The latency for the 500 nm peripheral 'off' response was so much longer than the latency for the 650 nm central 'off' response that it was possible to obtain a double latency by stimulating with a 650 nm spot in a 500 nm surround. Figure 8 illustrates this. The first line shows the 'off' response to a 650 nm spot—a burst with a latency of about 140 msec. The second line shows the 'off' response to a 500 nm surround—a burst with a latency of about 380 msec. The third line shows the response to the 650 nm spot plus the 500 nm surround—two bursts, one with a latency of about 135 msec, the other with a latency of about 380 msec.

Combination of responses. There is no reason to assume that the results presented so far can be used to predict the response in more complicated situations where different areas are illuminated by different wave-lengths. In other words, the units might be complex in the sense defined by Hubel & Wiesel (1962).

Some experiments were performed with spots of one wave-length in surrounds of another. When a red 'off' green 'on' centre unit was being recorded, a red spot in a green surround gave a strong 'off' response, and a green spot in a red surround gave a strong 'on' response, while uniform illumination of the whole field with either red or green gave a fairly weak 'on–off' response (Daw, 1967*b*). The fact that the centre for green was larger than the centre for red meant that the diameter of the spot could

not fit the demarcation line between centre and periphery for both red and green at the same time. Taking this into account, the responses for spots in surrounds were predictable from the responses to spots and surrounds seen separately, and from the responses to narrow annuli such as those given in Fig. 3.

Other experiments were performed with red/green two-part fields (Daw, 1967*b*). A square area of 10×10 mm was illuminated and the boundary between the two colours was kept parallel to one edge of the

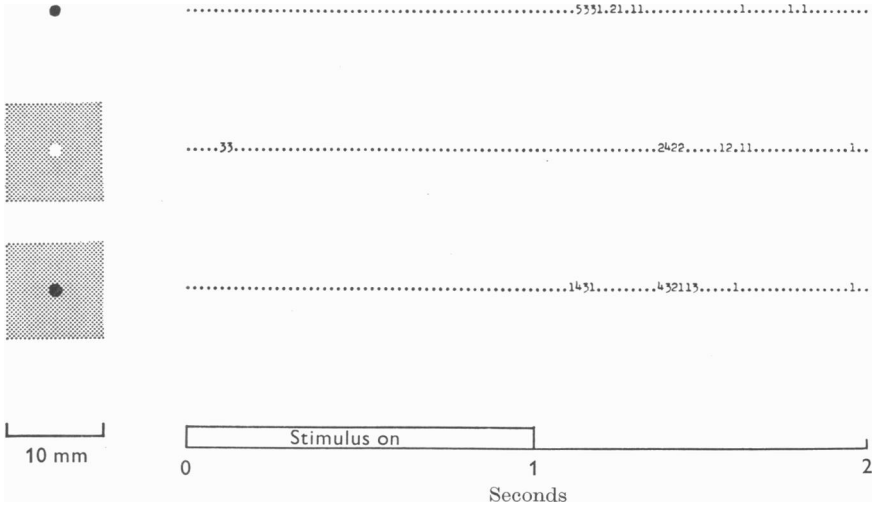

Fig. 8. An example of 'double latency'. The spot had a diameter of 1·08 mm, and the surround the same inside diameter. Solid areas were illuminated by light of 650 nm, dotted areas were illuminated by light of 500 nm, white areas were not illuminated. Stimuli are drawn approximately to scale. The latency for red in the centre was short, and for green in the periphery was long. The 'double latency' appears when the two stimuli occur together.

square. The slide was behind the 10 mm square mask, so that the whole area was illuminated in all positions of the boundary. The response was measured for various distances of the boundary on each side of the midpoint of the receptive field of the cell.

Figure 9 gives results for red/green, red/black, black/green and yellow/black fields, the yellow being the superimposition of the red (650 nm at $3{\cdot}8 \times 10^8$ quanta $.\mathrm{mm}^{-2}.\mathrm{sec}^{-1}$) and green (500 nm at $1{\cdot}9 \times 10^9$ quanta $.\mathrm{mm}^{-2}.\mathrm{sec}^{-1}$). Two curves are plotted for each boundary. The upper one shows the number of spikes occurring between 0·1 sec after the light was turned on and 0·1 sec after it was turned off, plotted upwards from the base line for the 'on' response. The lower one shows the number of spikes occurring between 0·1 sec after the light was turned off, and 1·1 sec after the light

was turned off, plotted downward from the base line for the 'off' response. The response was observed for eight boundaries with fourteen positions for each, ranging from 3·15 mm on one side of the mid-point of the receptive field of the unit to 3·85 mm on the other side.

The green/black and black/red boundaries gave curves which were qualitatively similar ('on' response to the right, 'off' response to the left) and so did the green/red boundary which was the combination of them. The red/black and black/green boundaries both gave curves of opposite

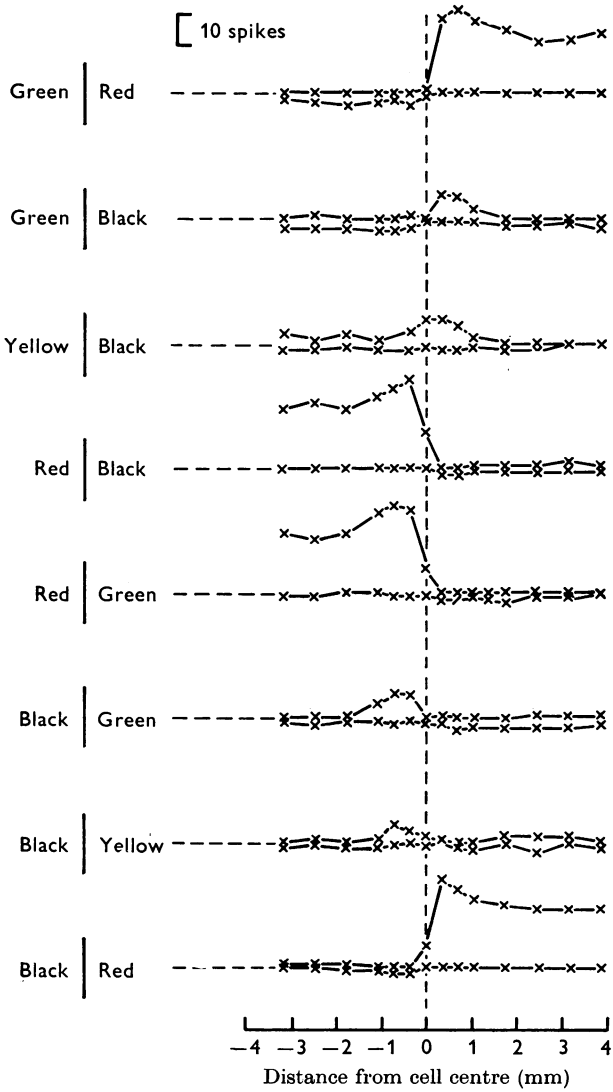

Fig. 9. For legend see opposite page.

shape ('on' response to the left, 'off' response to the right) and so did the red/green boundary which was the combination of them. On the other hand, both the yellow/black and the black/yellow boundaries showed responses which were qualitatively rather different, being 'on–off' and small for most positions of the boundary. The 'off' responses were always small compared to the 'on' responses, but were associated with a significant inhibitory effect: for example, the 20–30 'on' spikes seen with the red/black boundary to the left, combined with the 2–3 'off' spikes seen with the green/black boundary to the left, yielded the 2–3 'on–off' spikes seen with the yellow/black boundary to the left. This point may be appreciated more if the figure is viewed sideways. The responses seen with both yellow/black and black/yellow boundaries in certain positions may have been due partly to the fact that the centre of the receptive field for red was not the same size as the centre of the receptive field for green, and partly to the possibility that the relative intensity of 650 nm and 500 nm was not quite correct for cancellation.

The peaks of the 'on' response curves for green/red and red/green occur further from the receptive field mid-point than the peak of the curves for black/red and red/black. This is doubtless related to the fact that the centre of the receptive field for green was larger than the centre of the receptive field for red. One can also see from Fig. 9 that reversing a boundary gives a mirror image response curve. In other experiments response curves were plotted for boundaries orientated in orthogonal directions: for example, a red/green boundary, with the boundary going from left to right in the first

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Legend to Fig. 9.

Fig. 9. Response of a Type O unit to various boundaries placed in various positions on the receptive field. The type of boundary is shown on the left. The red areas had irradiance $3{\cdot}8 \times 10^8$ quanta.mm^{-2}.sec^{-1}. The green areas had irradiance of $1{\cdot}9 \times 10^9$ quanta.mm^{-2}.sec^{-1}. Yellow areas were made by superimposing red on green without changing the intensity of either. Two curves are plotted for each boundary. The upper curve in each case is the number of spikes occurring while the light was on, adjusted by 100 msec for latency (i.e. the number of spikes occurring between 100 msec after the light was turned on, and 100 msec after the light was turned off). The lower curve is the number of spikes occurring during the second after the light was turned off, also adjusted by 100 msec for latency. Each of the upper curves for the 'on' responses is plotted upwards from the base line, and each of the lower curves for the 'off' responses is plotted downwards from the base line. The base lines are given by dashed lines between the descriptions of the boundary and the curves. Each boundary was placed in fourteen positions, ranging from 3·15 mm on one side of the mid-point of the receptive field to 3·85 mm on the other side. Each cross represents the response at one of these positions, given by the scale at the bottom of the figure.

series and top to bottom in the second series. Again, the response curve did not depend on the orientation of the boundary. This reinforces the conclusion above that the sensitivity did not vary greatly from one part of the periphery of the receptive field to another.

Nine units were investigated for combination of responses. In all units, with all stimuli, the responses to the more complex stimuli were in accordance with what one would predict from a summation of the responses to the component parts of the stimulus. Sometimes the antagonistic influence of the periphery was strong, so that stimulation of the whole field uniformly gave little response for 500 nm, 650 nm, or other wave-lengths (Daw, 1967*b*). Sometimes the periphery was not as effective as this (Fig. 9). The summation did not always hold quantitatively, taking a linear addition of the number of spikes, but the qualitative generalization was always true.

Type Q units

Nineteen units were classified as Type Q—another type of colour-coded unit with a rather involved organization. Illumination with diffuse light clearly showed that the units were colour-coded. In the case of the unit illustrated by Fig. 10, the response was 'off' for long wave-lengths, and 'on', or 'on–off' for short wave-lengths. A spot in the centre, irrespective of its wave-length, gave an 'off' response, similar to the discharge to long wave-length diffuse light. An annulus in the periphery gave the short wave-length diffuse light response ('on') irrespective of wave-length. The reverse kind of cell was also found, the central response always being the same as long wave-length diffuse illumination, and the peripheral response the same as short wave-length diffuse illumination.

At first glance, these units would appear to be like the Type I units described by Wiesel & Hubel (1966) in the lateral geniculate of the monkey—either red 'off' centre green 'on' periphery or red 'on' centre green 'off' periphery. Further experiments showed that this was not true. First, the spectral sensitivity for a spot in the centre was the same as the spectral sensitivity for an annulus in the periphery (Fig. 11). Both central and peripheral spectral sensitivities tended to follow the difference spectrum for the red-absorbing pigment of the goldfish cones. Secondly, the details of the response (Fig. 12) and bleaches with long wave-lengths (Fig. 13) revealed an opposing short wave-length component, always present in the centre, and often present in the periphery.

Figure 12 shows the response of a Type Q unit to spots of light centred in its receptive field. The response is 'on' for both red and green light for several intensities up to 1·5 log. units above threshold. However, the response to red light is sustained, while the response to green light is transient. This proves that more than one receptor type is involved, and

suggests that there is an inhibitory short wave-length process which cuts short the response to green light.

Figure 13 shows the response of a Type Q unit to spots of light centred in the receptive field, before and after a bleach with a strong red light (3·5 mm circle of 650 nm, at maximum intensity of stimulator for 30 sec—this should bleach up to 50% of the pigment; see Daw, 1967*a*). Before

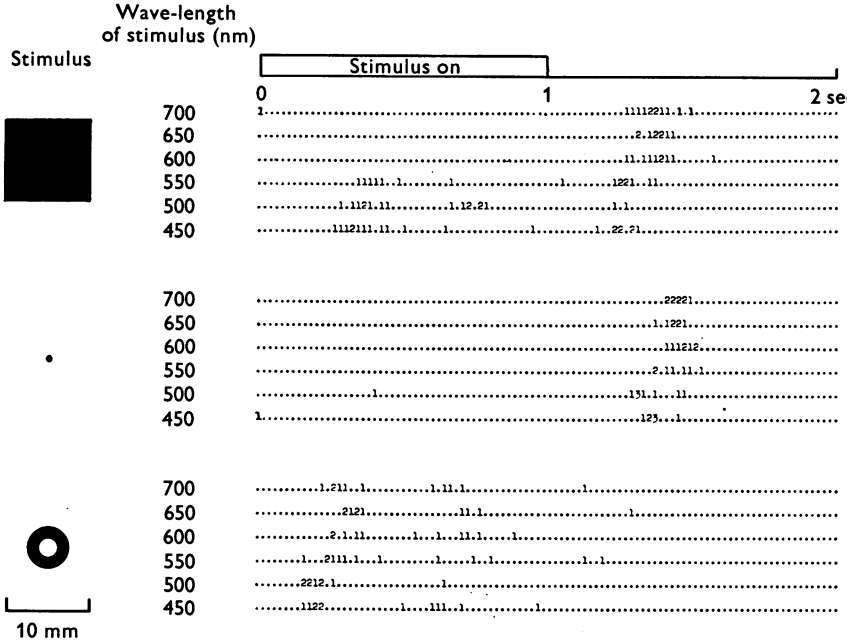

Fig. 10. Response of a Type O unit to stimulation of the whole field, the centre, and the periphery, with light of various wave-lengths. The spot for the centre was 0·72 mm in diameter. The annulus for the periphery was 2·16 mm inside diameter, 4·32 mm outside diameter. Each response given is for an intensity between 0·5 and 1·0 log units above the threshold for the stimulus concerned: in general, the type of response did not vary between threshold and 1·0 log units or more above threshold. Stimulation of the centre gave an 'off' response for all wave-lengths; stimulation of the periphery gave an 'on' response for all wave-lengths; stimulation of the whole field gave an 'off' response for long wave-lengths and an 'on' response for short wave-lengths.

bleaching, both red and green light gave 'on' responses. After bleaching red light still gave an 'on' response, but green light gave an 'off' response. Thus the bleach with long wave-length light alters the response to green light, but not the response to red light. There was some recovery from the bleach, but its time course was slow, and it was not investigated in detail.

Both Figs. 12 and 13 show that there is an underlying opponent mechanism in the centre of the receptive field, which must be fed by short

wave-length receptors. Was there also an underlying short wave-length opponent mechanism in the periphery of the receptive field? In three cases such a process was directly apparent. For the on-centre subtype, this meant that both red and green light gave 'off' responses at threshold in the periphery, but that the response to green light changed to 'on–off' or

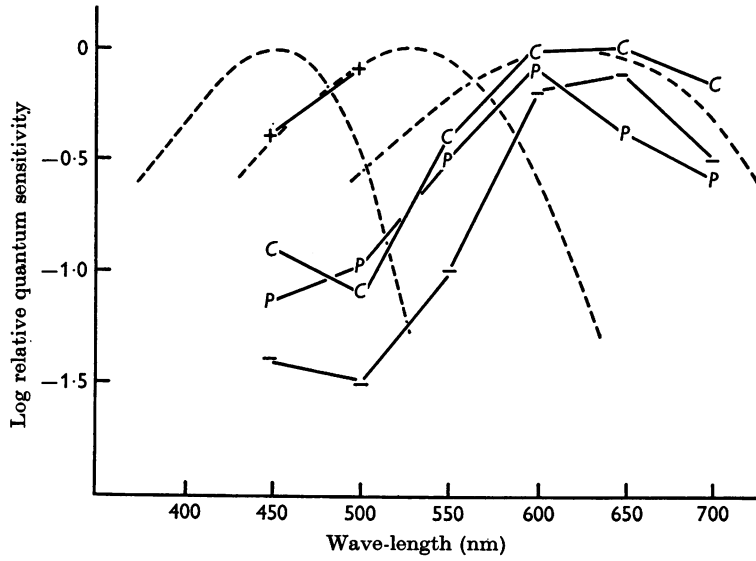

Fig. 11. Spectral sensitivities for a Type Q unit. The curve marked by *C* shows the spectral sensitivity for a 0·72 mm spot in the centre of the field, which gave an 'off' response for all wave-lengths. The curve marked by *P* shows the spectral sensitivity for an annulus of inside diameter 2·16 mm, outside diameter 4·32 mm, centred on the receptive field, which gave an 'on' response for all wave-lengths. The curve marked with + shows the spectral sensitivity for illumination of the whole receptive field, for those wave-lengths which gave an 'on' response. The curve marked with − shows the spectral sensitivity for illumination of the whole receptive field, for those wave-lengths which gave an 'off' response. The dashed lines give the difference spectra for goldfish cones (Marks, 1965). The curves are displaced upwards relative to the 'off' response curve for the whole field, to fall close to the difference spectra, by the following amounts: centre 0·8 log units, periphery 0·75 log units, and whole field 'on' response 0·5 log units.

'on' closely above threshold. For the off-centre subtype the reverse was true. In six other cases the spectral sensitivity measurements showed a curve which was pushed down from the difference spectrum of the red-absorbing pigment on the short wave-length side, suggesting an antagonistic process operating at these wave-lengths. In the remaining ten cases there was no evidence either for or against an antagonistic short wave-length process in the periphery.

All this suggests that the Type Q units are basically organized like the

Type O units, with excitatory red and inhibitory green processes in the centre, and inhibitory red and excitatory green processes in the periphery, or vice versa. With Type O the green processes are readily apparent, but with Type Q, the red processes overwhelm the green processes in both centre and periphery.

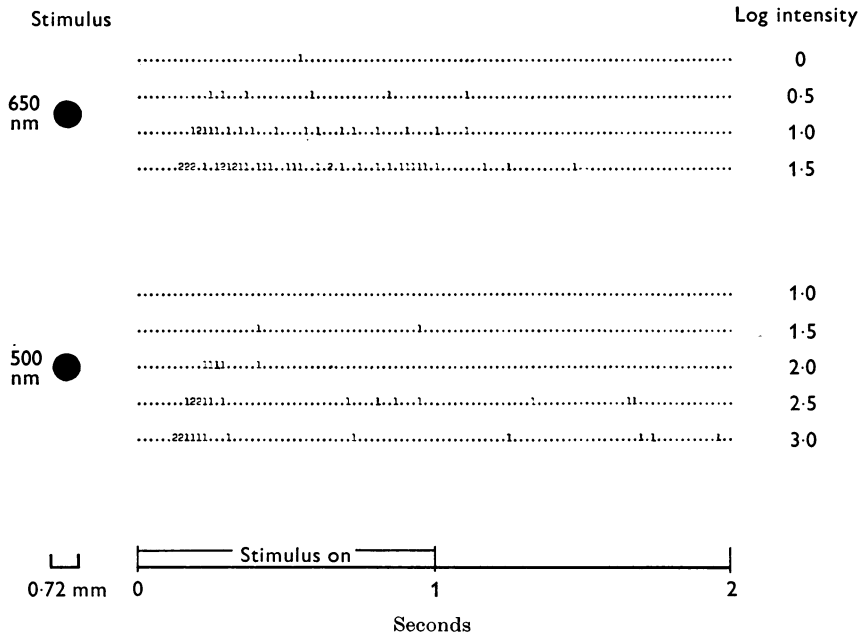

Fig. 12. Response of a Type Q unit to a spot of light centred on its receptive field. The spot had diameter 0·72 mm. The top four lines show an intensity series for a spot of 650 nm; the bottom five lines show an intensity series for a spot of 500 nm. In both series the responses are 'on'; in the series for 650 nm, however, the 'on' responses are sustained, and in the series for 500 nm transient. Zero log intensity is $3{\cdot}8 \times 10^6$ quanta.mm^{-2}.sec^{-1} for 650 nm, and $1{\cdot}9 \times 10^6$ quanta.mm^{-2}.sec^{-1} for 500 nm.

Numbers of various types of units

Table 2 gives the statistics for the 136 units on which quantitative measurements were made. It is noticeable that nearly all of them were colour-coded, and the majority of these were Type O. The Type P units, which were like Type O with the periphery missing, were comparatively rare. The Type Q units, which were like Type O with green components depressed were a little more common. There was no tendency for red to be associated with 'on' rather than 'off', in any of the types.

A fairly large number of units were unclassified. None of these was Type P, because some characteristic was found in each case to exclude this possibility. Many appeared to be a hybrid of Types O and Q, with both red

and green processes directly apparent in the centre, but only the red process apparent in the periphery. It may well be that Types O and Q just represent the ends of a spectrum of cells, in which the green processes are more or less overpowered by the red.

The non-colour-coded units were quite rare. Most of them were red 'on' centre, red 'off' periphery, or vice versa, like the units described by Kuffler (1953) in the cat retina, but with spectral sensitivity peaking in the red. Two were sensitive to orientation, responding to a bar pointing in one

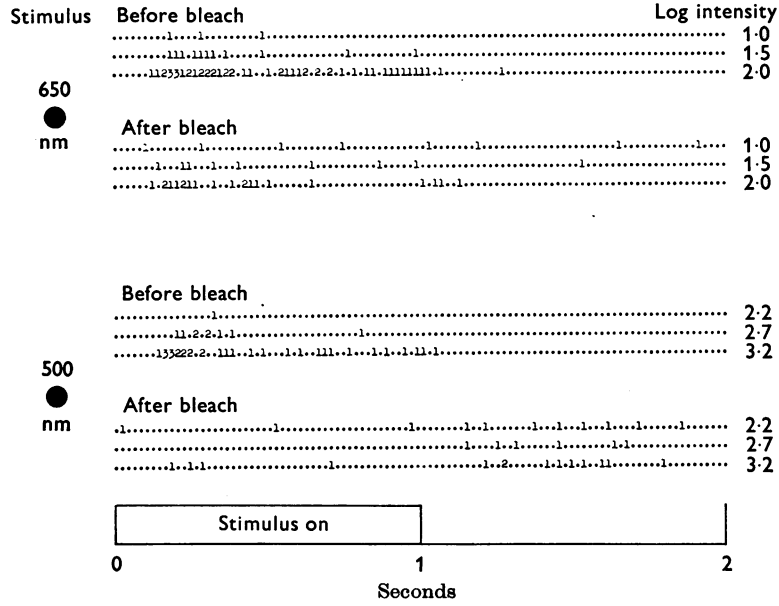

Fig. 13. Example of the response of a Type Q unit before and after a bleach with an intense 650 nm light. The stimulus was a spot of 0·72 mm diameter. Before the bleach it gave 'on' responses for both 500 nm and 650 nm. The area bleached had a diameter of 3·5 mm centred on the mid-point of the receptive field of the unit. After the bleach the 650 nm spot gave an 'on' response as before, but the 500 nm spot gave an 'off' response.

TABLE 2. Classification of units

		No.	Percentage
Type O units	'On' to red, 'off' to green in the centre, reverse in the periphery	30	22%
	'On' to green 'off' to red in the centre, reverse in the periphery	37	27%
Type P units	'On' to red 'off' to green	5	3%
	'On' to green 'off' to red	2	2%
Type Q units	'On' in centre 'off' in periphery	12	9%
	'Off' in centre 'on' in periphery	7	5%
Not colour-coded		8	6%
Unclassified		35	26%
		136	100%

direction but not to a bar pointing in the perpendicular direction, and giving 'on–off' responses to a small spot of light in all parts of the receptive field, without regard to wave-length.

DISCUSSION

It would appear from this work that the retinal organization of receptor classes in the goldfish is elegantly complete. The centre-surround organization exists for red receptors, an identical organization exists for green receptors, and the two systems impinge on one ganglion cell. The boundary between centre and surround is usually not the same for the red and green systems, but the difference in size is always minor compared to the diameter of the receptive field as a whole.

If the surrounds are absent (Type P), or not noticed in the O type, because small spot stimulation is used in the periphery, then the results of Wagner *et al.* (1960, 1963) are obtained. It is not surprising that area and intensity are not reciprocal in stimulating the periphery of the receptive field. At all stages of the visual system after the initial ones, the response is related to a compressive function of intensity (Davson, 1962; Graham, Bartlett, Brown, Hsia, Mueller & Riggs, 1965). Furthermore, at the ganglion cell level, the responses can be predicted by a linear summation of a compressive function of the intensity (Barlow, 1953; Easter, 1967). The mechanism for these results is not known, but they all point to the same conclusion, that a stimulus of large area and low intensity is likely to be more effective than a stimulus of small area and high intensity.

Function of Type O units. The Type O units would appear to be organized appropriately to respond to simultaneous contrasts of colour. Their maximal 'on' response comes from a red spot in a green surround, and their maximal 'off' response from a green spot in a red surround, or vice versa, depending on which subtype is involved.

As pointed out by Wiesel & Hubel (1966), this is not true of the 'opponent colour cells' found in the lateral geniculate and optic nerve of the monkey (Wiesel & Hubel, 1966; Hubel & Wiesel, 1960) and the optic nerve of the ground squirrel (Michael, 1966) or of the original description given by Wagner *et al.* (1960, 1963) for the colour-coded goldfish ganglion cells. The essential feature of such cells is that they give one response for one wave-length and an opposing response for another, often with spatial separation of the two stimuli. Thus the responses tend to oppose each other, not reinforce each other, when contrasting colours are presented to the two areas. The opponent colour cells are appropriate for successive colour contrast (De Valois, 1960*b*, 1965; De Valois, Jacobs & Abramov, 1964) but not for simultaneous colour contrast, although there may be some exceptions (De Valois, 1960*a*).

Size of the receptive field. One can describe the size of a receptive field in two ways. When the diameter of the field is given in terms of degrees, it tends to emphasize the functional significance of the field for the animal as a whole, and helps to relate the size to psychophysical measures of acuity. When the diameter is given in terms of microns or millimetres, it tends to emphasize the anatomical aspects. Correlations can then be attempted with the dendritic spread of the ganglion cells in the retina. The relationship between the size in degrees and the size in microns depends of course, on the focal length of the eye.

In terms of degrees, the Type O units had a red centre of 10–15°, a green centre of 15–20° and an overall receptive field of 40–60°. This has to be related to the colour acuity of the goldfish, rather than the brightness acuity, since several types of non-colour-coded units are found (Cronly-Dillon, 1964; Jacobson & Gaze, 1964). We know that some mammals have acuity which is finer than the diameter of the centre of the smallest receptive field found in their optic nerve by a factor of 5 or more (Brown & Rojas, 1965). Even so, the results suggest that the colour acuity of the goldfish is not good. Unfortunately colour acuity has not been measured behaviourally for the goldfish, or for any other fish.

In terms of millimetres, the size of the receptive field as a whole for the Type O units is extremely large, being 5·5 mm or more. McIlwain (1964) has reported that effects can be obtained over even greater distances than this in the cat retina. It may be that McIlwain's periphery effect is related to the present results on the goldfish, but two differences should be pointed out. First, the McIlwain results suggest a three part receptive field, consisting of centre, periphery, and far periphery, whereas the goldfish results so far do not suggest any far periphery, only a centre and periphery for red, superimposed on a centre and periphery for green. Secondly, the responses from the periphery of the goldfish receptive fields are direct, like the responses from the periphery of the cat receptive fields; that is, the responses show up directly upon stimulation of the periphery without a long time lag or prior stimulation of the centre. The responses from the far periphery in the cat would appear to be primarily indirect, seen through the effect on some stimulation of the centre of the receptive field, or as a change in the rate of firing, measured over a period of seconds.

Several authors have suggested that signals from the centre of the receptive field reach the ganglion cell via bipolar cells, while signals from the periphery pass through an interneurone, which may be a horizontal cell or an amacrine cell (Brown & Major, 1966; Dowling & Boycott, 1966; Gallego, 1965). The only direct evidence is that in the cat, the spread of the dendritic arborization of the ganglion cell corresponds to the centre of the receptive field, and is rather smaller than the size of the whole recep-

tive field. The ganglion cells in the fish do not appear to be much larger than those in the cat (Cajal, 1955), so that the same argument applies for the fish. The anatomical arrangement would have to be more complicated for the Type O cells in the fish, of course, requiring perhaps two kinds of bipolar cell in the centre, and two types of amacrine or horizontal cell in the periphery. It is interesting in this connexion that the internal horizontal cells (Cajal, 1892) and some amacrine cells (Cajal, 1892; Selvin de Testa, 1966) both extend laterally for a long way, which may be 0·7 mm or even more in the fish retina.

Spectral sensitivity. The question of concern in measuring the spectral sensitivity of various parts of the receptive field is this: which types of receptor feed into which parts of the receptive field? In most parts of the receptive field of colour-coded units there are two antagonistic processes. One may make the simplifying assumption that one type of receptor feeds each process, and try to identify the pigment involved. In trying to make this identification it is the shape of the spectral sensitivity of the long wave-length process on the long wave-length side of the peak, and of the short wave-length process on the short wave-length side of the peak which matter. These are both regions where the interaction between the two processes is minimal. It is not important to measure the wave-length of peak sensitivity for each process. The peak wave-length will depend on the strength of interaction between the two processes, which in turn will depend on several parameters, some of them changing during the course of an experiment.

The comparison between the spectral sensitivity of the Type O units and the difference spectra of the goldfish cones (Fig. 7) as measured by Marks (1965) suggests that the red and green pigments are the principal ones involved, in both centre and periphery. There is some discrepancy between the two measurements mainly on the short wave-length side of the long wave-length curves, and the long wave-lengths side of the short wave-length curves, in the sense that no short wave-length responses were obtainable for 590 nm. The discrepancy could be due to contributions from the blue pigment, or the very long wave-length red pigment postulated by Naka & Rushton (1966*a*, *b*). The most likely explanation on the basis of present evidence, however, is that the discrepancy is due to the interaction between the red and green processes. Experiments on spectral sensitivity against coloured backgrounds supported this explanation. The discrepancy may, in fact, be worse than indicated, since Marks's curves are difference spectra, rather than action spectra.

From previous work, one would expect to find some cells fed by blue cones. The reason that none were found may be statistical. Marks (1965) showed that the ratio of red:green:blue cones is approximately 11:15:2.

Bicking (1965) measured the sensitivity of ganglion cells at 480 nm, 540 nm and 660 nm for stimulation of the whole field and suggested from this that he had 46 red/green units, 5 green/blue units and 4 red/blue units. Given three classes of ganglion cell, with frequencies 10:1:1, the chance of taking a sample of 14 (the number of Type O units on which spectral sensitivity measurements were made) and finding all to be members of the first class is $(5/6)^{14} = 0{\cdot}08$. This is small, but not ridiculously so. It is possible that the initial test for identification for colour-coded units (stimulation of the whole field with 500 nm and 650 nm) selected red/green units. However, the units which were not colour-coded by this test were investigated further, and no red/blue or green/blue units were found among them.

The discussion so far has ignored the possibility of yellow/blue, red/cyan, or green/magenta units, or even more exotic combinations, the colours being taken to refer to the pigments involved rather than the peak wave-length of the action or difference spectra. Jacobson (1964), recording from the tectum of the goldfish, describes some yellow/blue units. Witkovsky (1965), recording from ganglion cells of the carp, which is closely related to the goldfish, states that all his 'on–off' units had one peak in the orange and another in the blue. In both these studies other properties of the units beside spectral sensitivity are not fully described, and the spectral sensitivity was only measured for one point in the receptive field of the unit. Consequently it is difficult to relate either Jacobson's or Witkovsky's work to the present study.

Type Q units. As mentioned in the results, the Type Q units behaved like the Type O unit, with the green process masked by the red in the centre, and either masked by the red or missing altogether in the periphery. This raises two interesting possibilities: (1) that a quantitative change in the anatomical connexions, without any change in the type of connexion involved, can lead to a response which is qualitatively quite different; or (2) that the Type Q units result from an abnormal condition of the preparation. (The latter would not be surprising since a retina is subjected to severe mechanical distortion during isolation.)

Type Q cells did not appear to result from a progressive degeneration of the preparation since a Type O cell was isolated on several occasions, followed by a Type P or Q, followed by another Type O. Temperature did not appear to affect the results. Witkovsky (1965) also found some units which were probably Type Q. They gave the same response to all wave-lengths, with peak sensitivity in the orange, from a 30–50 μ spot centred over the electrode. After bleaching with a red light, the response to long wave-lengths was the same, while the response to short wave-lengths was reversed. This result is similar to that shown in Fig. 13. Wagner *et al.*

(1963) also reported some cells in which one component was masked by another. One can only suggest that, if Type Q units are artifacts of the preparation, they are artifacts common to all these investigators There is no doubt that the Type O units were found more frequently than either of the other types,

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