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Motion Detection in Goldfish Investigated With the Optomotor Response is "Color Blind"

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The action spectrum of the optomotor response in goldfish was measured to investigate which of the four cone types involved in color vision contributes to motion detection. In the dark-adapted state, the action spectrum showed a single maximum in the range of 500–520 nm, and resembled the rod spectral sensitivity function. Surprisingly, the action spectrum measured in the light-adapted state also revealed a single maximum only, located in the long wavelength range between 620 and 660 nm. A comparison with spectral sensitivity functions of the four cone types suggests that motion detection is dominated by the L-cone type. Using a two colored, "red–green" cylinder illuminated with two monochromatic lights separately adjustable in intensity, it could be shown that motion vision is "color-blind": the optomotor response disappeared whenever "isoluminant" red and green stripes were offered. Under this condition, calculations revealed that the L-cones were only slightly modulated by the "red–green" stimulus. Copyright © 1996 Elsevier Science Ltd.

Motion Color vision Goldfish (*Carassius auratus*) Optomotor response

INTRODUCTION

The perception of motion is one of the major abilities of animal visual systems. Additionally, most animals are capable of color discrimination. Are the same photoreceptor types used for both visual tasks? In early studies, the optomotor response elicited by a rotating drum with alternating grey and colored stripes was used as a convenient test for color vision mainly in insects but also in vertebrates. Most animals behaved as if they were "color blind" in this context. This was interpreted as an absence of color vision until Schlieper (1927) detected that honeybees also behaved in that way although known to possess an excellent color vision from training experiments by Karl von Frisch (1914) and Alfred Kühn (1927). Much later, when it was clear that color vision in honeybees is trichromatic (Daumer, 1956) and based on three different types of retinula cells (Autrum & von Zwehl, 1964), the optomotor response was investigated by Kaiser and Liske (1974) using a two colored striped drum illuminated by monochromatic light of different wavelengths. They found that bees did not show any response when the stripes were adjusted to a certain intensity ratio. The action spectrum of the optomotor response indicated that bees use the "green" retinula cell type for detection of motion exclusively. The fact that one photoreceptor type only is involved explains why motion detection in bees was found to be "color blind".

In humans, separate pathways for color and motion are being discussed (Ramachandran & Gregory, 1978; Cavanagh *et al.*, 1984; Livingstone & Hubel, 1987; Logothetis, 1991; Merigan & Maunsell, 1993). One of the main arguments in this discussion is the disappearence of motion perception at isoluminance, when the stimulus only contains contrast in color, but not in luminance.

If two visual systems as different as that of the honeybee and that of some primates, both developed independently of each other during evolution, have similar properties, this indicates that there must be a general underlying principle. Therefore, we investigated the relationship between color vision and motion detection in a third system, in lower vertebrates, in goldfish (*Carassius auratus*) and turtles (*Pseudemys scripta elegans*) (in preparation).

Goldfish not only respond readily to moving stimuli, but also have a very well developed color vision (Neumeyer, 1986, 1992). Unlike in primates and honeybees, color vision in goldfish is based on four photoreceptor types which are maximally sensitive to wavelengths of 360, 450, 540, and 625 nm (Hárosi, 1976; Bowmaker *et al.*, 1991). All of them contribute to color vision. To find out which photoreceptor types contribute to motion vision in goldfish, we measured the action spectrum of the optomotor response in the dark- and in the light-adapted state in steps of 15–20 nm between 400 and 720 nm. The action spectra were then compared with the spectral sensitivity functions of rods or cones, respectively. In the light-adapted state, the function indicates a dominant influence of the long wavelength sensitive cone type. If motion detection is mediated by one cone type only, it should be "color blind". This was tested using a rotating drum with red and green stripes

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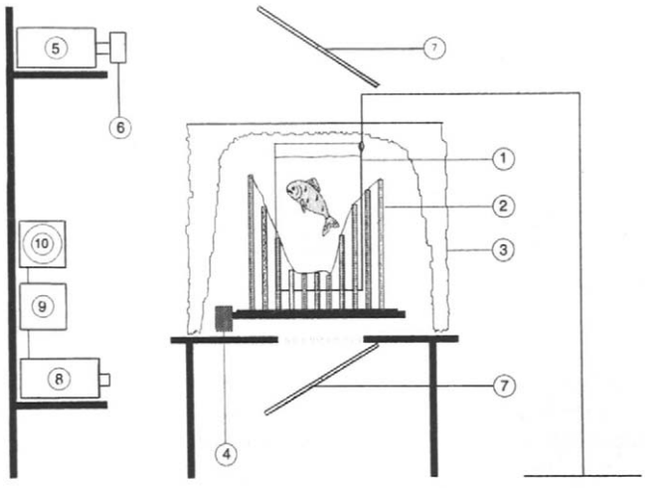

FIGURE 1. Setup to measure the action spectrum of optomotor response in goldfish. 1, Circular Plexiglas tank; 2, striped cylinder (equally wide white cardboard stripes and slits, or red and green cardboard stripes); 3, black velvet; 4, Plexiglas disk rotated by motor; 5, slide projector; 6, filter chamber for interference and neutral density filters; 7, mirrors; 8, video camera; 9, video recorder; 10, monitor.

illuminated by monochromatic green and red light providing an "isoluminant" stimulus at a certain intensity ratio.

METHODS

Animals

Eighteen goldfish of normal shape, 6–9 cm in length, were obtained from local suppliers. They were kept in a home tank at an average water temperature of 20°C, under an artificial light/dark regimen of 12/12 hr. They were transferred to the circular test tank only during measurements.

Setup

The setup used to measure the optomotor response is shown in Fig. 1. During the experiments, one goldfish was transferred into the circular tank, 11 cm in diameter. Water depth was about 7 cm so the fish could swim around freely in about the same plane. The tank was concentrically surrounded by a striped cylinder, 20 cm in dia, consisting of white cardboard stripes and equally broad slits. The drum was positioned on a rotatable Plexiglas disk which was driven by a motor (Fa. Faulhaber) adjustable to either direction and various speeds. At a distance of 25 cm, the striped cylinder was surrounded by black velvet to provide a high contrast between stripes and slits, and to screen stray light. The white cardboard stripes of the cylinder were illuminated from above by a slide projector (Leitz Prado Universal, 250 W) via a mirror. By using interference filters (type DIL, Schott and Gen, half-band width 8–14 nm) quasi monochromatic light was obtained. Neutral grey filters (Schott and Gen, type NG) attenuated the intensity of light in steps of half log units. The filters were inserted in a special filter chamber of the slide projector, and made it possible to test the spectral range between 400 and 720 nm in steps of 15–20 nm. The ultraviolet range was not investigated.

For experiments with the red–green cylinder, a second projector was positioned beneath the first, equipped with a different interference filter. In this way an additive mixture of colored light was obtained, in which the intensity of each spectral component could be varied separately (see below).

The swimming behavior of the goldfish was monitored from below by a video camera (Panasonic WV-F15E) and recorded on a VCR (Panasonic TL, AG 6720). Simultaneously, the fish could be observed on a monitor (Panasonic BT D-2020 PY). The monitor was also used to measure the strength of the optomotor response by using a mask corresponding in size and shape to the image of the circular tank. The mask was divided into sectors of 5 deg, so that the position of the fish's snout could be measured during stimulation.

The moving stimulus

Cylinders made of white cardboard stripes and equally broad slits were used for most of the measurements. In the first preliminary experiments, the width of the stripes was varied between 0.5, 1, 2, and 4 cm, corresponding to 2.86, 5.73, 11.46, and 22.9 deg per stripe, or 5.73, 11.46, 22.9, and 45.8 deg per cycle of stripe and slit. The cylinder used for the measurement of the action spectra was 22.9 deg per cycle, the velocity was 60 deg/sec. Experiments to test isoluminant colored stimuli employed a drum with alternating red and green stripes (without slits). Red and green colored cardboards were selected after measuring spectral reflectance: the green cardboard had a high reflectance (>60%) between 500 and 590 nm, and a low reflectance (30%) in the long wavelength range; the red cardboard reflected mainly above 600 nm (>80%) and not very much (<20%) at shorter wavelengths.

Light measurement

Light intensity was measured radiometrically by directing the detector head of the radiometer/photometer (EG and G, 550-1) perpendicular to the cardboard stripes from the outside of the cylinder. At the swimming height of the fish, it was positioned exactly in between two stripes, "viewing" horizontally through a slit. The tank was removed during the light measurements. The radiometric data obtained (in μW) were converted by calculation into the amount of quanta per square centimeter and second for each wavelength. As the spectral transmission of the neutral filters was known, only maximal light intensities (100% projector light) were measured, and the reduction by the neutral filters was calculated.

Procedure

Measurement of the action spectrum of the optomotor response in the dark-adapted state. A fish was transferred from the well lit laboratory to the circular tank, and the black velvet was draped evenly around the stationary

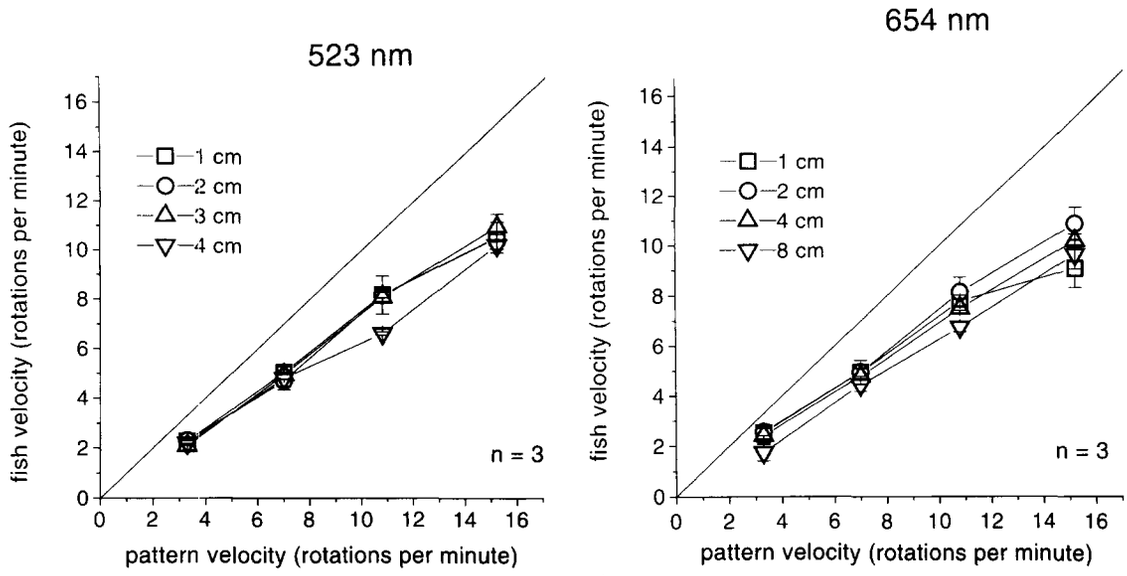

FIGURE 2. Optomotor response tested with two different wavelengths (523 and 654 nm) as a function of pattern velocity, using four different spatial frequencies (widths of stripes plus slits: parameter of the curves). The diagonal line represents a gain of one. Mean values for three fish (A, E, N).

cylinder. After a dark-adaptation period of 20 min, the monochromatic light was switched on and the stripes were set into motion. The optomotor response was recorded for 1 min. Then the cylinder stopped, and the light was switched off. The fish remained in the dark for 3 min before the test period started again, now with the monochromatic light of the same wavelength given in an amount of quanta reduced by half a log unit, and the cylinder rotating in the opposite direction. The measurements continued in this way till an intensity range was reached in which no optomotor response could be observed. Then, a second wavelength was tested. In succession, up to 30 measurements (1 min each) could be performed lasting for about 2 hr.

Measurements of the action spectrum of the optomotor response in the light-adapted state. The procedure was the same as for the dark-adapted state except that the white tungsten light of the slide projector was given in full intensity (126 lx) between two stimulus presentations. At the beginning of an experimental session the fish were brought into the circular tank, and adapted to the white light for 3 min. Then, within 5 sec, interference and neutral density filters were arranged in the projector chamber, and the motor was started to move the stripes. The recording started immediately, and the swimming behavior of the fish was measured for 1 min. Then, the rotation of the cylinder stopped, and white adaptation light was given for another 3 min, before the next test period of 1 min duration started. Direction of pattern movement was alternated after each measurement. Light intensities were reduced in half log unit steps until the fish showed no reliable optomotor response any more.

Measurements of the optomotor response with the red–green cylinder. In this experiment the red–green striped cylinder was illuminated by two slide projectors and interference filters providing quasi monochromatic light. Two pairs of filters were used: 532 and 685 nm, and 555 and 641 nm. The intensity of one monochromatic light was kept constant, while the intensity of the second increased in steps of 0.5 log units, starting about 1 log unit below threshold up to about 1 log unit above threshold (see Results section for more details).

Data acquisition

The optomotor response of a goldfish consists of following the rotating striped cylinder by swimming along the tank wall. As a measure for the optomotor response we used the "optomotor gain", which is defined as the number of rotations of the fish per minute divided by the number of rotations of the pattern per minute. Thus, the maximal response would be a "gain" of one. For the "standard" stimulus parameters of 60 deg/sec this would correspond to ten rotations of fish and pattern per minute. Therefore, we counted the rotations of the fish during 1 min of pattern motion, and related this value to the rotations of the pattern. A gain of 0.15 was found to differ highly significantly [ANOVA $F(5,4) = 0.264$; $P < 0.01$] from spontaneous swimming behavior. For more security, a swimming rate of two rounds per minute (gain = 0.2) was set as a threshold criterion for the optomotor response. To measure the scotopic action spectrum a threshold of four rotations per minute was chosen.

RESULTS

Search for the optimal stimulus parameters

When the cylinder rotated, the fish followed the stripes by swimming along the tank wall in the direction of the cylinder movement. Sometimes the animal stopped swimming and touched the wall of the tank with its mouth, but a few seconds later it started the optomotor response again. In order to define the optimal stimulus parameters for the optomotor response, pattern velocities

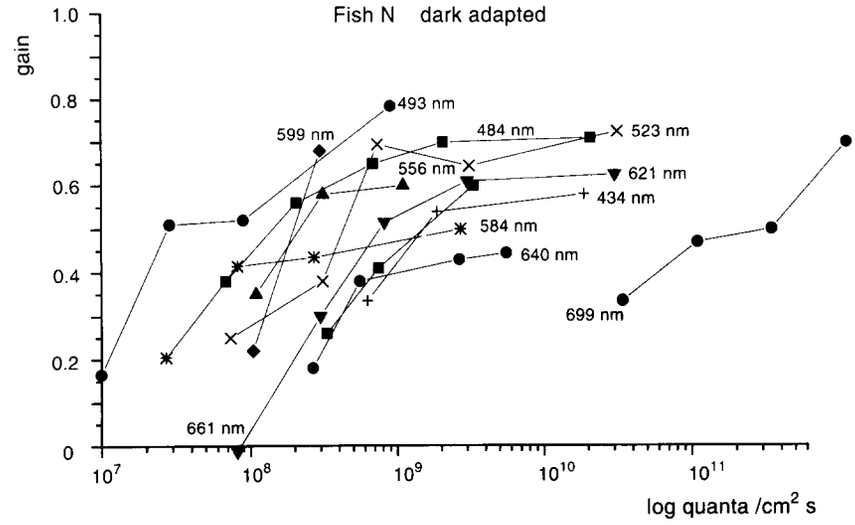

FIGURE 3. Optomotor response (dark adapted state) as a function of amount of quanta/cm^2 sec reflected by the white stripes. Parameter of the curves: wavelength (nm) of the monochromatic light illuminating the cylinder. The threshold criterion was a gain of 0.4. Results for one fish (fish N).

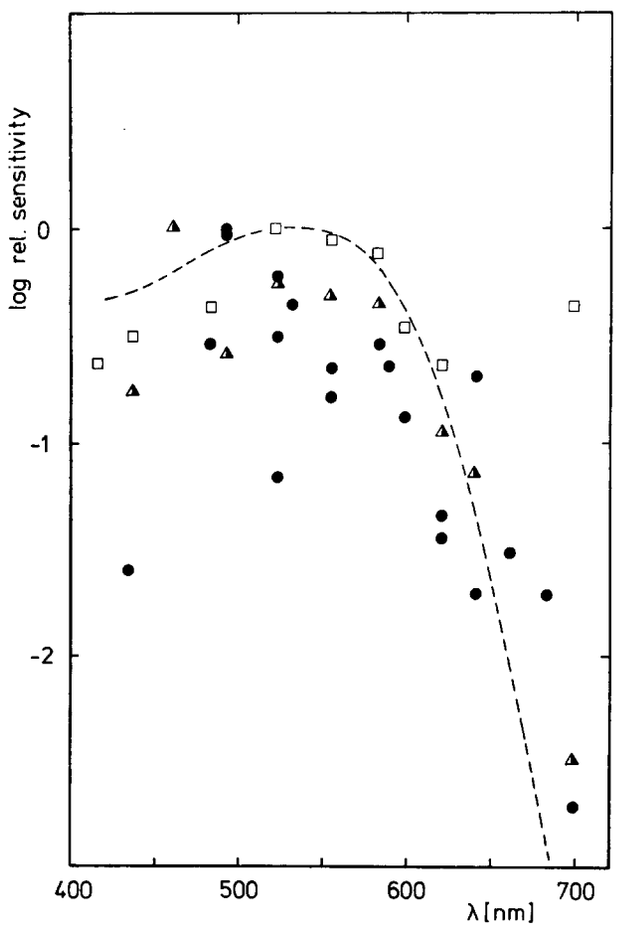

FIGURE 4. Action spectrum of the optomotor response in the dark adapted state. Data for three fish (□G, ●N, ▲M) normalized to the maximal value of each fish equal to one. Abscissa, wavelength; ordinate, log relative sensitivity. Broken line, rod spectral sensitivity (after van Dijk and Spekreijse, personal communication).

between 3.3 rounds/min (19.8 deg/sec) and 15.2 rounds/min (91.2 deg/sec), and widths of stripes between 1 and 8 cm/cycle were tested. For these measurements the fish were in the light-adapted state. In Fig. 2 the averaged data for three fish (A, E, N) are shown for monochromatic light of two different wavelengths given in a relatively high intensity (523 nm at 8×10^{11} Q/cm^2 sec, and 645 nm at 1.7×10^{11} Q/cm^2 sec). The fish's velocity increased with increasing velocity of the bars. The values are below the line for a gain of one, and correspond to an optomotor gain of 0.7 between 3.3 and 11 rounds/min. The values for 15.2 rounds/min were slightly lower. The results were about the same for stripe widths between 1 and 4 cm/cycle for both wavelengths. On the basis of these data a standard stimulus was selected which was used in further experiments. Its velocity was chosen as 10 rounds/min to obtain a response that differs highly significantly from spontaneous swimming behavior. Four centimeters per cycle was chosen as the spatial frequency of the standard stimulus.

The action spectrum of the optomotor response (dark-adapted state)

The goldfish were dark-adapted for 20 min before the first measurement. This adaptation time was found to be sufficient in preliminary experiments, in which the sensitivity for movement detection was measured at various periods (1, 2, 5, 10, 20, 30 min) after turnoff of the white adaptation light. A relatively steep increase in sensitivity was found within the first 5 min, and a smaller increase up to 30 min. (Two fish were tested with four wavelengths: 450, 483, 523, and 699 nm).

In Fig. 3 the strength of the optomotor response is shown as a function of the intensity of the monochromatic light for fish N as an example. The sensitivity of the fish's response to the moving bars varied with wavelength, which is indicated by the shift of the curves along the x-axis. At 699 nm, for example, the amount of quanta needed for a suprathreshold response was higher than that for all other wavelengths. About 2 log units less quanta were required at 523 nm indicating highest sensitivity of the optomotor response. The intersection of each

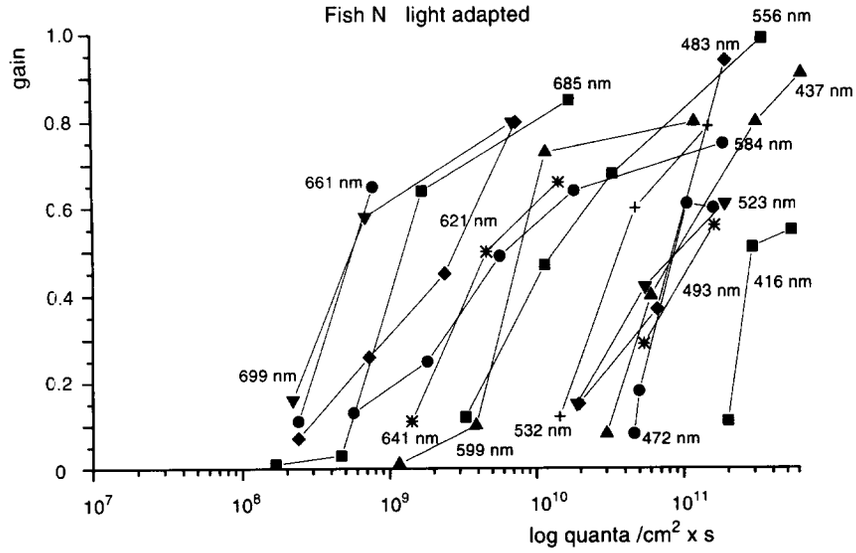

FIGURE 5. Optomotor response (light adapted state) as a function of amount of quanta/cm^2 sec reflected by the white stripes. Parameter of the curves: wavelength (nm) of the monochromatic light. Threshold criterion: gain 0.2. Results for one fish (fish N).

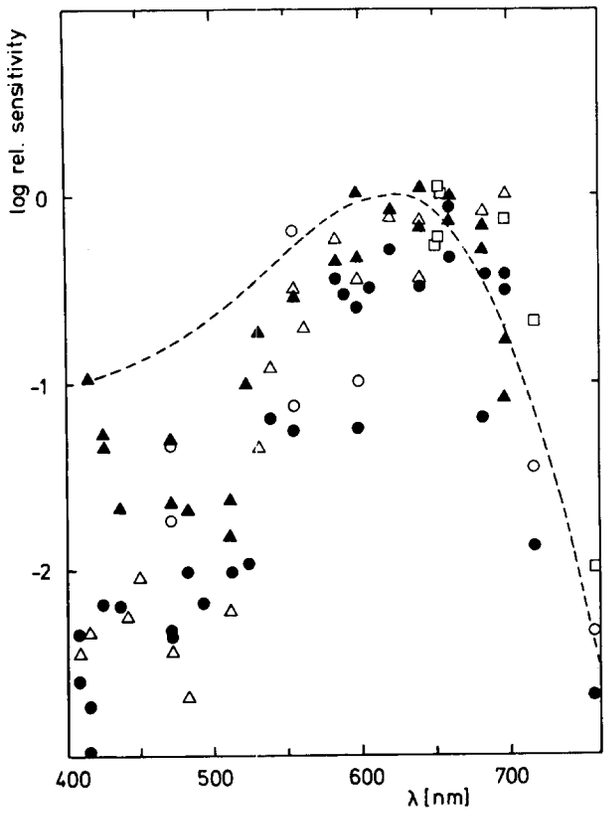

FIGURE 6. Action spectrum of the optomotor response in the light adapted state. Data for five fish (●N, △R, ▲M, ○B, □E), normalized to the maximal value of each fish. Broken line: spectral sensitivity of the L-cone type [from van Dijk & Spekreijse (1984)].

response curve with the threshold criterion at a gain of 0.4 was taken, and the amount of quanta required to reach threshold was interpolated. These values were plotted as a function of wavelength into a new graph to obtain the data points for the action spectrum. The action spectra for five goldfish are shown in Fig. 4. The maximal value of sensitivity of each fish was normalized to the value of one. Maximal sensitivity was located in the middle to short wavelength range, at 523 nm (fish G), 492 nm (fish N), and 461 nm (fish M) and reached absolute values of 2.3×10^7 (N), 4×10^7 (M) and 6.9×10^8 Q/cm^2 sec (G). The dashed line represents the spectral sensitivity function of the rods (van Dijk and Spekreijse, personal communication).

The action spectrum of the optomotor response (light-adapted state)

At each of 19 wavelengths, the optomotor reaction was determined as a function of stimulus intensity in light-adapted goldfish. Figure 5 shows the result for fish N as an example. Some wavelengths were measured twice (409, 416, 584, 599, 621, 699 nm) or three times (661 nm) to ascertain the values. As shown in the figure, the optomotor response increased with light intensity. Usually, a saturation of the response was reached, sometimes with a small decline of the reaction. The amount of quanta/cm^2 sec was interpolated for each wavelength at the threshold criterion of gain 0.2, and these values were plotted in the action spectrum shown in Fig. 6. The value of maximal sensitivity of each fish was normalized to the value of one. For all fish tested, there was only one maximum of sensitivity located in the long wavelength range, at about 640 nm. A comparison with the spectral sensitivity function of the long wavelength cone type [dashed line, after van Dijk & Spekreijse (1984)] indicates a close resemblance to the maximum and the long wavelength flank. The slope towards the middle and short wavelength range, however, declines very sharply. Only one fish (M) showed an increase of sensitivity in the short wavelength range. Measurements below 400 nm could not be carried out because the glass optics limited the amount of quanta in the ultraviolet range of the spectrum.

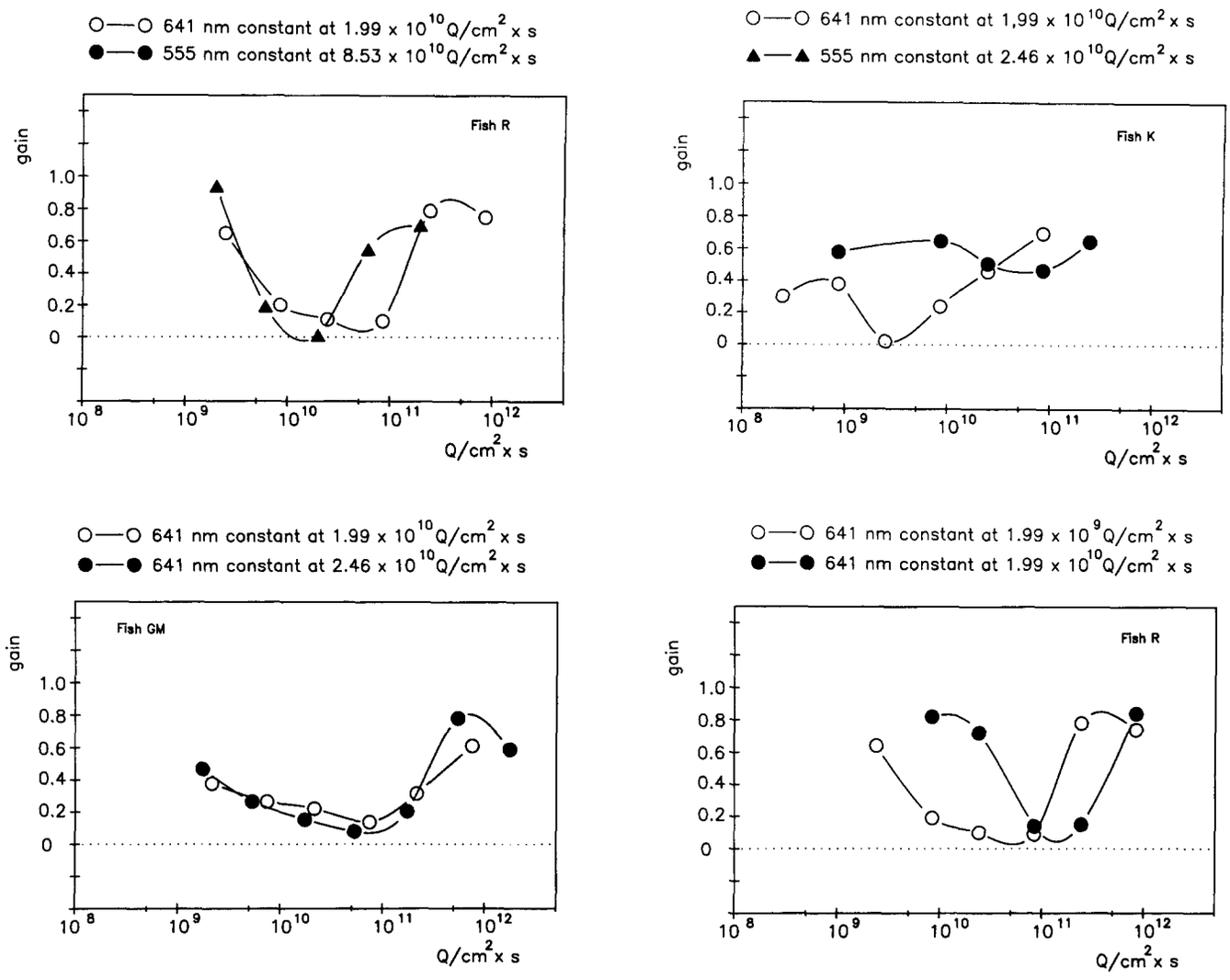

FIGURE 7. Optomotor response in the red–green cylinder illuminated simultaneously with two monochromatic lights (555 and 641 nm). The intensity of one monochromatic light was kept constant (as indicated on top of each diagram) while that of the second one was varied (abscissa). The results of three fish are shown as examples. The amount of quanta necessary to obtain zero optomotor response was read out of the figures and is given in Table 1. The values represent the amount of quanta reflected by the white cardboard for technical reasons.

The absolute values of maximal sensitivity found at 661 were in the range of 2.9×10^8 or 2.4×10^8 (fish N and R, respectively), and 1.3×10^{10} (fish M). Comparing the absolute sensitivity values of the photopic action spectrum (Fig. 6) with the values of the scotopic action spectrum (Fig. 4) for the same threshold criterion (gain 0.4), the sensitivity for the optomotor response in the dark-adapted state was >3 log units higher in the short wavelength range (430–523 nm), 2–3 log units higher in the middle wavelength range (532–584 nm) and 0.5–2 log units higher in the long wavelength range (590–683 nm). Only in the far red (699 nm) was a higher absolute sensitivity found in the light-adapted state.

Experiments with a red–green ("isoluminant") cylinder

A cylinder with red–green stripes was used to verify whether motion detection measured with the optomotor response is "color blind". As motion detection under these conditions is dominated by the long wavelength (L-)cone type, it seemed highly probable that the goldfish cannot see "motion" if the excitation of this cone type is not temporally modulated by "isoluminant" red and green moving stripes. To test this prediction we applied the method of "silent substitution" (Estévez & Spekreijse, 1982). The red–green cardboard cylinder was illuminated simultaneously with two monochromatic lights adjustable independently of each other in intensity. Two pairs of wavelengths were used: 532 and 685 nm, and 555 and 641 nm.

First, the threshold intensities for an optomotor response were determined when the cylinder was illuminated with each of the two wavelengths separately. Then, the amount of quanta of one of the two monochromatic lights was fixed at a value 1 log unit above threshold, and the second monochromatic light was added in steps of 0.5 log units starting about 1 log unit below threshold. The results for four fish are shown as examples for the wavelength pair 641 and

TABLE 1. Amount of quanta/cm^2 sec of 641 and 555 nm (measured at the white cylinder) at which the optomotor response was at zero or at minimum (a.o., from Fig. 7)

Fish	641 nm (quanta/cm^2 sec)	555 nm (quanta/cm^2 sec)	Modulation L-cone red:green	Modulation M-cone red:green
R	1.99×10^{10}	3.20×10^{10}	1:1.1	1:4.4
R	2.05×10^{10}	2.46×10^{10}	1:1.46	1:4.7
Ge	1.99×10^{10}	2.20×10^{10}	1:0.9	1:3.9
R	2.46×10^{10}	1.05×10^{10}	1:2	1:5.2
GM	1.99×10^{10}	2.90×10^{10}	1:1	1:4.3
GM	6.10×10^{10}	8.30×10^{10}	1:1	1:4.2
GM	2.90×10^{10}	8.53×10^{10}	1:1.6	1:5
K	1.99×10^{9}	2.00×10^{9}	1:3	1:5.6

The modulation of the L- and M-cone types was calculated (see text). For the L-cone type a mean value for the modulation: red : green stripes of 1:1.5 (SD = 0.7) was found, for the M-cone type a mean value of 1:4.7 (SD = 0.6).

TABLE 2. Amount of quanta/cm^2 sec of 685 and 532 nm at zero or minimal optomotor response. The mean modulation of the L-cone type was 1:1.4 (s = 0.6), that of the M-cone type 1:8.3.

Fish	685 nm (quanta/cm^2 sec)	532 nm (quanta/cm^2 sec)	Modulation L-cone red:green	Modulation M-cone red:green
K	1.00×10^{10}	2.30×10^{10}	1:1.7	1:8.3
K	1.36×10^{10}	5.00×10^{10}	1:2.4	1:8.3
M	1.36×10^{10}	2.50×10^{10}	1:1.5	1:8.3
Gr	1.28×10^{10}	2.30×10^{10}	1:1.5	1:8.3
R	1.28×10^{10}	1.70×10^{10}	1:1.2	1:8.3
R	3.40×10^{10}	6.80×10^{10}	1:1.6	1:8.3
R	3.00×10^{10}	2.04×10^{10}	1:0.5	1:8.3
Ge	1.28×10^{9}	8.30×10^{9}	1:0.34	1:8.3
Ge	1.00×10^{10}	2.30×10^{10}	1:1.8	1:8.3
Ge	4.70×10^{10}	7.50×10^{10}	1:1.4	1:8.3

555 nm in Fig. 7. When 641 nm was kept constant (open symbols), and 555 nm was added with increasing intensities, fish R showed a decline of the optomotor gain from about 0.7 to zero within about 1 log unit (between about 2×10^9 and 10^{10} quanta/cm^2 sec). A further increase of intensity brought the response back to high values (gain 0.8). A corresponding result was obtained when 555 nm was kept constant (filled symbols), and 641 nm was added in increasing intensities. Similar results are shown for fish GM and K in Fig. 7. In total, seven goldfish took part in this experiment keeping the intensity of 641 nm constant and increasing the intensity of 555 nm in small steps. All of them reduced or zeroed their optomotor response at a certain intensity of the added wavelength. In some measurements (4 out of 22) no pronounced dip was found, similar to the result of fish K (filled symbols). When the constant intensity of one monochromatic light was set at higher values (fish R and K in Fig. 7), the range of the minimal reaction was shifted accordingly to higher intensity values. The effects described were found also for the wavelength pair 532 and 685 nm (not shown). The results indicate that optomotor response is reduced or lost at a certain intensity ratio of red and green light, which means that motion perception in goldfish is "color blind".

Calculation of M- and L-cone modulation at "isoluminance"

How are the L- and M-cone types modulated by the red and green stripes at illuminations causing minimal or zero optomotor response? To answer this question, we obtained the amount of quanta of both monochromatic lights at which the optomotor response was zero or minimal from Fig. 7 and the other diagrams. For that purpose a second order function was fitted to the curves showing the most pronounced minimum of the optomotor response. The amount of quanta/cm^2 sec at the minimum of the regression function was read out of the figures for both wavelengths (e.g. in Fig. 7, fish R: 2.05×10^{10} Q/cm^2 sec at 641 nm, and 2.46×10^{10} at 555 nm). These values (listed in the Tables) give the amount of quanta reflected by the white cardboard which showed a constant reflectance of 0.95 between 500 and 700 nm. To obtain the relative amount of quanta of the monochromatic light reflected by the red and green stripes, the values were multiplied by the relative reflectance of the red and the green cardboard, respectively, at the corresponding wavelengths (for the red cardboard: 0.44 at 641 nm, and 0.09 at 555 nm; for the green cardboard: 0.27 at 641 nm, and 0.55 at 555 nm). Finally, to calculate the amount of quanta absorbed by the L- and M-cone type, respectively, these values were weighted by the absorption coefficients of the cone photopigments. Assuming

that maximal absorption is equal to one for both cone types, we used an absorption coefficient of 0.07 at 641 nm, and 0.89 at 555 nm for the M-cone type, and the coefficients 0.93 for 641 nm, and 0.7 for 555 nm for the L-cone type [from Bowmaker *et al.* (1991)].

In Table 1, the modulations of the M- and L-cone types are shown for all fish when the red and green stripes were illuminated by 555 and 641 nm. The mean value of modulation of the L-cone type at the minimum of the optomotor response for all fish tested was 1:1.5 (standard deviation: SD = ± 0.7), whereas the mean modulation of the M-cone type, 1: 4.66 (SD = ± 0.6), was much higher.

For 532 and 685 nm a similar result was obtained (Table 2): here we found a mean modulation of the L-cone type of 1:1.4 (SD = ± 0.6), and a mean modulation of the M-cone type of 1:8.3 (red:green stripe). (To calculate the modulation of the M- and L-cone types at the minimal optomotor response when illuminated by 532 and 685 nm monochromatic light, the relative reflectance of the green cardboard was 0.6 at 532 nm, and 0.22 at 685 nm, and for the red cardboard 0.07 at 532 nm, and 0.82 at 685 nm. The absorption coefficients of the M-cone type were 1.0 for 532 nm, and 0.001 for 685 nm, and of the L-cone type 0.48 for 532 nm, and 0.42 for 685 nm.)

The data suggest for both cases (Tables 1 and 2) that at the minimum of the optomotor response the L-cone type was hardly modulated at all, while the M-cone type was strongly modulated by the moving red/green cylinder.

DISCUSSION

The action spectra of the optomotor response

The optomotor response was easily elicited in all fish tested. In a wide range of stripe widths and pattern velocity the mean optomotor gain was 0.7 (Fig. 2). The same rate was found in goldfish by Easter (1972) while monitoring the eye movements in response to a moving background.

Under scotopic conditions maximal sensitivity was found in the mid wavelength range at about 530 nm with a high absolute sensitivity in the range of 10^7–10^8 Q/cm^2 sec. As shown in Fig. 4 the action spectrum resembles the rod spectral sensitivity function especially well at the long wavelength flank. This indicates that the scotopic action spectrum is most probably mediated exclusively by the rods.

The photopic action spectrum of optomotor response also showed very clearly a single maximum in the long wavelength range at about 640–660 nm with an absolute sensitivity in the range of 10^9–10^{10} Q/cm^2 sec (Fig. 6). This result strongly suggests a dominant role of the L-cone type in motion detection, as a comparison with the spectral sensitivity function of the L-cone type indicates a high similarity in the long wavelength range. Towards shorter wavelengths, however, the action spectrum declines much faster than L-cone sensitivity, reaching values more than one log unit lower at 500 nm. This steep flank of the action spectrum may be due to an inhibitory influence exerted by the M-cone type. A similar mechanism was also assumed to explain the pronounced and shifted maximum of the spectral sensitivity function at 660 nm obtained in training experiments (Neumeyer, 1984; Neumeyer & Arnold, 1989).

A single maximum in the long wavelength range was also obtained in an earlier measurement of the optomotor response by Cronly-Dillon and Muntz (1965) in goldfish. For a background illumination of 0.41 foot lambert they found that the sensitivity function increased from short towards longer wavelengths with a weak maximum at 635 nm. With a background adaptation light of 0.052 foot lambert they obtained a second maximum at 520–535 nm, which can perhaps be attributed to rod contribution due to the mesopic state of the retina. Grundfest (1932) investigated the perch *Lepomis* with similar methods and also found an action spectrum of optomotor response with a single maximum at 610 nm, resembling the shape of the goldfish curve. Northmore *et al.* (1978) suggested that the low sensitivity at short wavelengths could have its cause in a reduced spatial acuity. However, the action spectrum of visual acuity measured with a behavioral training technique showed an equally high spatial resolution of 1–2 c/deg between 450 and 700 nm with three pronounced maxima at 470, 540, and 660 nm (Neumeyer & Schaerer, 1992). Furthermore, in our experiment the optomotor response was measured with rather broad stripes covering a visual angle of 23 deg per cycle (seen from the center of the tank). Therefore, the possibility can be excluded that the steep decrease of the action spectrum towards shorter wavelengths has been influenced by visual acuity.

The photopic action spectrum of the optomotor response in goldfish has a similar shape to the action spectrum of temporal resolution obtained in a training experiment in which the fish had to discriminate between steady and flickering monochromatic light (Neumeyer & Schaerer, 1992; and in preparation). A similar result was also obtained in ERG-measurements (Burkhardt, 1966) using flicker stimuli at 20 Hz. It seems possible that flickering and moving stimuli are processed by the same mechanism, as is also suggested for humans (Anstis & Cavanagh, 1983; Kulikowski & Tolhurst, 1973).

The "color blindness" of goldfish motion detection

As the action spectrum of optomotor response in the light-adapted state indicated a dominant contribution of the L-cone type, it seemed likely that the goldfish would not show any optomotor response to a red–green cylinder providing color contrast but no luminance contrast. This was indeed the case in all goldfish tested. A calculation of the relative excitation values of the L- and M-cones revealed that the L-cones were only slightly, but the M-cones strongly modulated (Tables 1 and 2). Thus, motion detection was reduced or lost whenever the L-cones were "silenced" by the red and green stripes of the cylinder despite a high modulation of the M-cone type.

Taking into consideration that the action spectrum of the optomotor response showed a slope much steeper

than the L-cone sensitivity function in the short wavelength range, it is not easy to see why the calculation indicated only a slight or absent modulation of L-cones at the minimum of the optomotor response. If "isoluminance" is determined by a mechanism characterized by the action spectrum shown in Fig. 6, we would expect a modulation of about 1:3–4, as sensitivity of this mechanism is at least 0.5 log units lower at 550–530 nm than sensitivity of the L-cone type in this range. The modulation of only 1:1.4 of the L-cone type at zero optomotor response is difficult to explain. Perhaps it means that the modulation at the most peripheral level of the system is decisive: if L-cones are not modulated by the moving green and red stripes, the neural elements mediating motion detection are not activated. In this case we have to assume that the inhibitory action of the M-cone mechanism occurs more centrally.

It has to be emphasized that a "color blindness" cannot be assumed for motion perception in general, but only for large field stimuli which elicit an optomotor response and which are used in this study. It is possible that, for the detection of small moving stimuli, all cone types contribute, and that color contrast determines detection at isoluminance. Furthermore, even with large field stimulation a dominating role of the L-cone type could be restricted to the high velocities of 60 deg/sec used. A difference in the contribution of cone mechanisms with stimulus velocity was found in human motion detection by Gegenfurtner and Hawken (1995).

Comparison with electrophysiological findings

If we had to search for neurons most likely involved in motion detection using large field stimuli, we would look for "R+/G−" units. Such units are in general assumed to be "color-coding" because of their opponency and were described at the level of retinal ganglion cells a.o. by Daw (1968) and by Spekreijse *et al.* (1972). Whether these neurons play a role in color vision and, if so, which, are open questions. A first attempt to divide L-cone driven ganglion cells into cells involved in "color" vision and cells involved in "brightness" detection using the response behavior during light adaptation as an indicator showed that "color opponent" cells can be involved in both tasks (Neumeyer *et al.*, 1991). Despite the fact that the action spectrum of the light-adapted optomotor response resembles the action spectra of retinal ganglion cells which show maxima at 650 nm and rather steep decreasing short wavelength flanks (Spekreijse *et al.*, 1972) it is unlikely that they can be regarded as "motion detectors". Using conventional stimulation methods with moving bars, direction- or orientation-selectivity could not be shown in retinal ganglion cells of cyprinid fishes. Orientation and direction tuning have been found with black/white gratings of high spatial frequency in goldfish ganglion cells by Bilotta and Abramov (1989). Authors investigating the optic nerve termination area at the level of the tectum opticum report direction sensitive units (Jacobson & Gaze, 1964; Niida & Sato, 1972; Cronly-Dillon, 1964; Maksimova & Maksimov, 1981), however, without measuring action spectra. Daw and Beauchamp (1972) found three out of 113 cells in the optic nerve to be both color coded and direction selective. Schellart and Spekreijse (1972), who investigated the dynamic characteristics of goldfish ganglion cells, found the latency of the response to green light to be about 15–40 msec higher than to red light. The more rapid transmission characteristic could be an explanation for the long wavelength maximum of the action spectrum using high frequencies. Further levels of motion vision processing and the spectral properties of units in the accessory optic system still remain unclear.

Color blindness of motion vision as a general principle

Schlieper (1927) used the optomotor response for the investigation of spectral sensitivity in bees (*Apis mellifera*), dragonfly larvae (*Aeschna*), butterflies, mantids (*Mantis religiosa*), Crustaceans, beetles (*Coccinella septempunctata*), and lizards (*Lacerta viviparia*). He combined colored stripes with grey stripes of different degrees of light reflectance. In all cases he found a combination of color with grey which did not elucidate an optomotor response. In vertebrates he had to chose a very bright grey stripe for the combination with red, yellow and green stripes, suggesting that the tested animals were most sensitive in the long wavelength range. Birukow (1939) obtained the same conclusion with frogs. As mentioned in the Introduction, the most thorough investigation was conducted by Kaiser and Liske (1974) in the honeybee and came to the same results. The action spectrum corresponds to the spectral sensitivity function of the "green" retinula cell type which is the most sensitive to long wavelengths (maximal sensitivity at 540 nm). In the bee, other visual tasks seem to share with motion vision the fate of color blindness, as seen in the movement avoidance response (Srinivasan & Lehrer, 1984), scanning behavior (Lehrer *et al.*, 1985), and distance estimation (Lehrer *et al.*, 1988).

Srinivasan (1985) gives a theoretical explanation for the "color blindness" of movement detection. According to the model of Hassenstein and Reichardt (1956) a movement detector consists of two adjacent input channels responding with a certain time delay to the intensity variations of a complex visual stimulus moving in front of the eye. The excitation variations of the two input channels are interpreted as "movement" only if the two signals show a high correlation. In a complex "colorful" world optimal correlation is obtained only if the two input channels have the same spectral sensitivity. For the model it is not important whether the input channels are derived from a single class of receptors (as in the honeybee) or whether two or more receptor types are combined, additively (as in human visual system) or antagonistically (as in goldfish). According to Srinivasan the reason why the long wavelength receptors seem to dominate movement detection can be seen in the context of the spectral composition of the habitat (for example green leaves). It is also possible that the long wavelength

sensitive receptor is used because it is sensitive in the entire visible spectral range.

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