Spectral Categories in the Learning Behaviour of Blowflies*

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Wavelength discrimination in the flower visiting blowfly *Lucilia* spec. was investigated in an attempt to elucidate the mechanisms underlying colour vision in this insect. The flies were subjected to a classical conditioning procedure in which they had to discriminate between a rewarded and an unrewarded monochromatic light stimulus. The results reveal large wavelength ranges within which no discrimination occurs, between which, however, a very distinct discrimination is found. The first range consists of the UV region up to 400 nm (UV). The second range comprises wavelengths between 400 nm and 515 nm (BLUE) and the third range all wavelengths longer than 515 nm (YELLOW). A simple model consisting of two colour opponent subsystems (R 7p/R 8p and R 7y/R 8y) can explain these results. Each of the two subsystems is assumed to evaluate only whether the sign of the difference between the excitations of R 7 and R 8 is positive or negative. For the whole system there are thus four possible conditions: p^+y^+, p^+y^-, p^-y^+, p^-y^-. Three of them correspond to the experimentally obtained wavelength ranges. The fourth condition (p^+y^-) might represent a still hypothetical PURPLE category in which the stimulus is made up of both short and long wavelengths.

Introduction

The functional organization of the dipteran compound eye is known in considerable detail [1]. Each ommatidium contains eight photoreceptors. Six of them (retinula cells R 1–6) are arranged in a trapezoidal pattern with separate rhabdomeres. The receptor axons project in the first optic neuropil, the lamina, where they are connected in an intricate order with axons of neighbouring ommatidia, forming the so-called neuroommatidia [2, 3]. These cells have broad, double-peaked spectral sensitivity functions (Fig. 1).

The axons of the central receptors R 7 and R 8 bypass the lamina and project directly into the medulla. The rhabdomeres of these cells are fused into a single light-guiding structure with the rhabdomere of R 7 located distally to that of R 8 [6].

Optical studies reveal two classes of R 7 cells. In transmitted light they appear pale and yellow and are respectively called R 7p and R 7y [7–9]. In accord, the underlying cells are termed R 8p and R 8y.

Electrophysiological recordings show that these classes correspond to different spectral classes [10–12]. Ommatidia containing pairs of either R 7p/R 8p or R 7y/R 8y are found over most of the retina, apparently randomly distributed, but with a preponderance (70%) of R 7y/R 8y [13, 14]. In total, the fly retina contains five spectral classes of photoreceptors: R 1–6, R 7p, R 8p, R 7y, R 8y (Fig. 1).

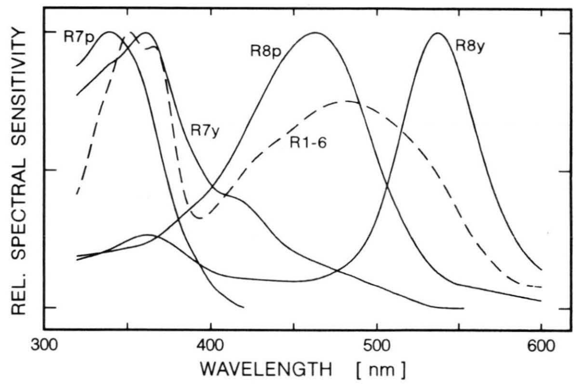

Fig. 1. Relative spectral sensitivity functions of the different fly photoreceptor classes. Sensitivity of R 1–6 after Kirschfeld *et al.* [4]. All other sensitivities after Hardie and Kirschfeld [5].

Although quite a lot is known about the physiology and the neuroanatomy of the blowfly retina and optic ganglia, comparatively little is known about the behavioural functions of the different receptor classes. In particular, the role of the

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photoreceptors R7 and R8 has not been fully appreciated.

The diversity in receptor spectral sensitivity is suggestive of colour vision and evidence for such comes from behavioural studies performed in different dipterans [15–19]. Of special interest are studies in the bigger nectar feeding species. These flies show a distinct "flower constancy" and it seems likely that this phenomenon is based on colour vision [16, 17]. This hypothesis is supported by training experiments, in which the colour could be identified as an important parameter for the fly's ability to recognize an artificial food source [20–22]. Furthermore, Fukushi [23] already found hints that the fly's colour vision is organized in a way that may be called "categorical".

The aim of this work is to investigate the wavelength discrimination properties of the flower visiting blowfly *Lucilia* spec. and to provide a model of the postreceptoral mechanisms underlying its colour vision.

For the investigations of wavelength discrimination, a classical conditioning procedure was used. The flies were subjected to a paradigm in which they had to discriminate between a rewarded and an unrewarded monochromatic light stimulus. A pair of light stimuli can differ in wavelength and in intensity. For colour training experiments it is important to exclude that learning is based on intensity differences. If intensity information can be stored by memory and used in learning, the relative efficacy of different wavelengths (action spectrum) has to be determined. Heterochromatic light stimuli could then be presented equally attractive with regard to the learning behaviour. It will be shown in this work that *Lucilia* is not able to learn on the basis of pure intensity differences. Thus it follows that learning success must be based on colour vision, regardless of how the intensities of the stimuli are adjusted.

Materials and Methods

Lucilia spec. larvae were reared on bovine liver until pupation. After emergence the imagos obtained water and sugar *ad libitum* for at least one day. Between the 2nd and the 6th day after emergence some 30 female flies were removed from the rearing cage and kept individually in small glass tubes. For the next 6 days the flies were allowed to take up water but otherwise no food was supplied. The tubes were placed in a chamber that provided a constant temperature of 15 °C and a daily illumination period of 13 h.

The experimental set-up is shown in Fig. 2. The flies could move freely in a small triangular arena (AR) with sides of 125 mm and a height of 15 mm. The walls and the floor of the arena were made of black anodized aluminium; the cover consisted of UV-transmitting perspex. Vertical screens (12 × 12 mm; SC) were placed in each of the corners of the arena. At any one time two of the screens could be illuminated from behind by means of two light guides (LG), which could be moved around the arena with a stepping motor (S1). With a second stepping motor (S2) the position of the two stimuli could be exchanged.

The screens subtended a visual angle of 5.7° when viewed by the fly from one of the other two corners. This means that the retinal image of the screen was sampled by about 17 ommatidia, provided that *Lucilia* has similar interommatidial angles as *Musca* (1.5°, [24]). Light was delivered by 100 W halogen lamps or a 75 W Xenon Arc lamp (LA), depending on the wavelength range under investigation. It passed through a narrow band interference filter (Schott IL; FI) and a motor driven intensity regulator (IR, S3) before being focussed onto the light guides. The light guides as well as all other optics consisted of UV-transmitting quartz glass. The halogen lamps were powered by 30 kHz AC current. At this frequency there is no flicker in the emitted light due to the inertia of the filaments of the lamps. The radiance of the light stimuli

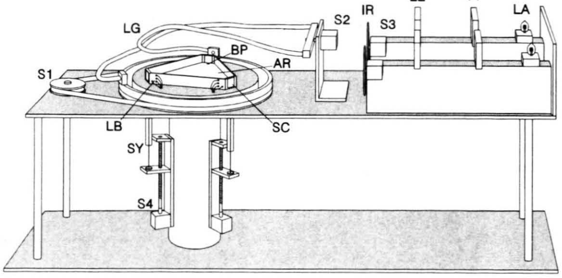

Fig. 2. Experimental set-up: AR, arena; BP, blotting paper; FI, holder for interference filter; IR, intensity regulator; LA, lamp; LB, light barrier; LE, lens holder; LG, light guide; SC, screen; SY, syringe; S1, S2, S3, S4, stepping motors. For further details, see text.

presented on the screens was measured with a calibrated PIN photodiode.

In front of each screen a small piece of blotting paper (2 × 2 mm; BP) was stuck onto the floor of the arena. Small amounts of sucrose solution could be diffused into the blotting paper from below. Every feeding dose consisted of 1 μl of 0.5 M sucrose solution, delivered from fine syringes (SY) which were driven by stepping motors (S 4).

The fly's approach toward one of the screens was registered by means of an IR light barrier (LB) when the fly passed within a distance of less than 10 mm from the screen. Extra light barriers were used to control whether the droplet was consumed by the fly. The whole apparatus was controlled by a PC (IBM 286).

The arena was uniformly illuminated from above by a 25 W tungsten lamp. Its spectral irradiance (Fig. 6a) was measured with a spectroradiometer (Spectra-Scan, Photo Research).

Upon entering the arena, the fly was confronted with two light stimuli, of which only one provided a reward (a droplet of sucrose solution as described above). Having consumed the droplet, the fly began to search for more food and eventually arrived at one of the other two corners. When this happened the first test run began: The two light stimuli were presented in the two opposite corners. Whenever the fly passed a light barrier in front of an illuminated screen, the pair of light stimuli were extinguished and appeared again in the two corners opposite to the new position of the fly. Repeating this procedure ten choices were demanded of the fly. When this was completed, the fly was fed a second time at the same spectral stimulus as before and subsequently again ten choices were registered (second test run). Altogether the procedure, consisting of feeding and test run, was repeated four times so that eventually the fly was required to perform 40 choices.

Data treatment

In every discrimination experiment between 10 and 20 flies were tested. Most experiments were repeated two or more times, so that for one pair of wavelengths up to 60 flies contributed to the results. As described above, each training and test experiment began with the presentation of two light stimuli, which may be called stimulus A and B. Which of the two stimuli was rewarded changed from one fly to another, so that half of the flies were trained to respond to stimulus A, the other half to stimulus B. Choice frequencies were determined as proportions of 1 and refer always to stimulus A, regardless of which of the two stimuli had been the training stimulus. Thus P = 0.3 means that the fly approached stimulus A in 30% of its choices and stimulus B in 70%. The mean choice frequencies over all four test runs of all flies trained and tested for stimuli A and B are denoted as P_A and P_B, respectively. The difference between the two mean choice frequencies is termed the conditioning index L (following [19]) and provides a measure of the fly's discrimination capability:

$$L = P_A - P_B.$$

A second important value relates to the spontaneous preference behaviour that might be confounding the learning behaviour (preference index M).

$$M = 0.5\,(P_A + P_B).$$

95% confidence intervals were calculated on the basis of the standard error. Over the whole range of possible values, choice frequencies are binomially rather than normally distributed. However, this is not of great importance except at the edges of the scale *i.e.* at extremely high or extremely low choice frequencies. As we are dealing only with values between *ca.* 0.25 and 0.75, we can assume normal distribution and homogeneity of variance and thus use the common methods for the calculation of the confidence interval of the difference between two means (*e.g.* [25]).

Results

The influence of intensity differences on spontaneous preference and on learning behaviour

The aim of these experiments was to determine whether flies can be trained to discriminate light stimuli purely on the base of intensity. Accordingly, the flies were presented with a pair of light stimuli, both of the same wavelength but with differing intensities. Six experiments were made at different wavelengths and intensity ratios (Table I). The results show that there is a strong correlation between the intensity ratio and the preference index M (Fig. 3a).

Table I. Six discrimination experiments, in which the two alternative light stimuli had been shown with equal wavelength but different intensity.

Wave-length [nm]	Intensity of stimulus A [W/str m²]	Intensity of stimulus B [W/str m²]	Total number of flies	Preference index M	Conditioning index L
438	0.640	0.200	10	0.640	0.093
501	1.680	0.168	16	0.783	0.092
540	0.640	0.200	14	0.627	0.018
540	1.820	0.560	14	0.618	0.105
580	2.000	0.640	16	0.633	−0.033
580	2.000	0.200	10	0.764	−0.028

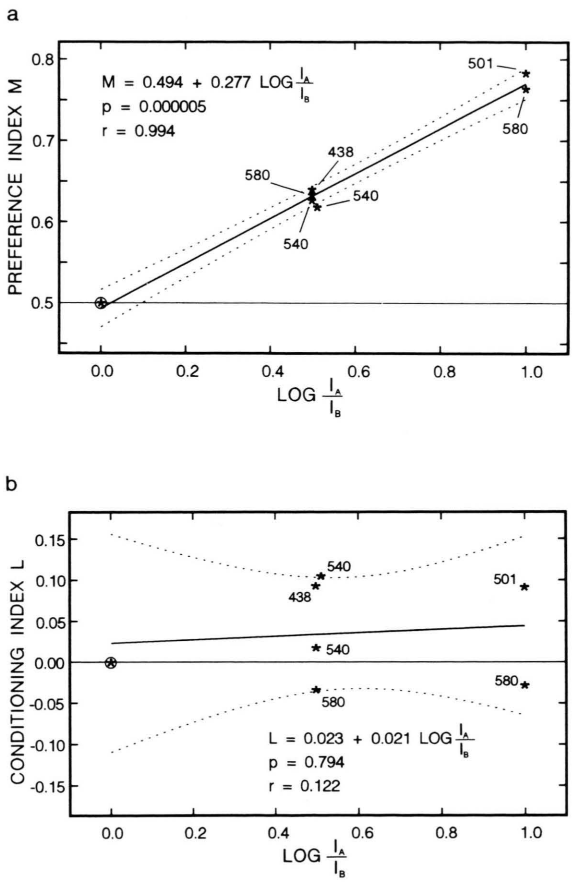

Fig. 3. Presentation of the experiments, listed in Table I. In each single experiment, two alternative stimuli were shown with equal wavelength but different intensity. Preference index (a) and conditioning index (b) were plotted against the intensity differences in log units. For the calculation of the regression line (solid line) the data point $I_A/I_B = 1$ ($L = 0$, $M = 0.5$) was added. The dashed curves show the 95% confidence interval for the regression line.

In contrast no correlation exists between the intensity difference and the conditioning index L (Fig. 3b). The discrimination performance expressed in the spontaneous preference behaviour is, therefore, not used for learning.

Since the flies are unable to learn different intensity levels of light sources, it is not necessary and actually not even possible to adjust the intensity of a heterochromatic pair of stimuli to equal "brightness" with regard to their learning behaviour. Nevertheless, the light stimuli were arranged so, that they were about equally attractive with respect to the spontaneous preference behaviour. Data were only used for further analysis when the preference index M had values between 0.4 and 0.6. These values correspond to the middle range of the scale of choice frequencies. This means that there is enough room in both directions to detect any learning effects clearly. In addition, the choice frequencies can be regarded as normally distributed in the range considered, and thus the statistical treatment of the data is simplified.

Colour discrimination

In a first series of experiments one of the light stimuli had a fixed wavelength of 438 nm, whereas the other was shorter or longer in wavelength. As can be seen from Fig. 4a, there is a broad wavelength range in which no discrimination occurs. At some distance from the reference wavelength, however, the conditioning index strongly increases. Beyond this wavelength the conditioning index remains constant and shows no further increase. The largest L-values are between 0.35 and 0.4. A L-value of 0.2 was defined as a criterion to account

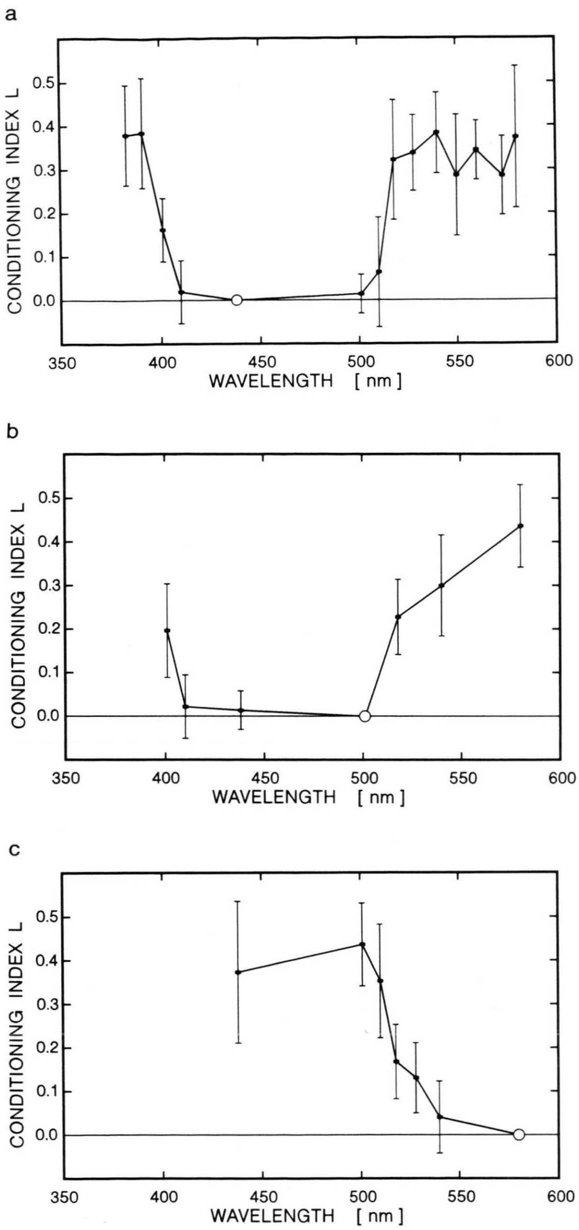

Fig. 4. Results of colour discrimination experiments. (a): Experiments in which one of the two alternative stimuli was of wavelength λ = 438 nm and radiance I = 0.2 W/str m^2. The radiance of the second stimulus had been adjusted such that the preference index M was between 0.4 and 0.6. The conditioning index L is plotted against the wavelength of the second stimulus. The vertical bars indicate the 95% confidence intervals of the L values. (b): Experiments in which the reference stimulus was of wavelength λ = 501 nm and radiance I = 0.64 W/str m^2. (c): Experiments in which the reference stimulus with wavelength λ = 580 nm and radiance I = 0.64 W/str m^2.

for successful discrimination. At this value the slope of the L-index/wavelength function (L/λ function) is steepest. With a 95% confidence interval of about $\pm$0.1 a discrimination effect of L = 0.2 is highly significant ($\alpha < 0.001$). The L = 0.2 criterion is reached at wavelengths of 399 nm and 515 nm. In the shorter and longer wavelength ranges the distance between the reference wavelength and the wavelength at which the criterion is reached are $\Delta\lambda^-$ = 39 nm and $\Delta\lambda^+$ = 76 nm, respectively.

In a second series of experiments the wavelength of the reference stimulus was 500 nm (Fig. 4b). Again it turns out that a wide wavelength range exists, in which the L-index is almost zero, but that on either end of this range (at 400 nm and at 516 nm), there is a sudden increase. Surprisingly, these values correspond to the ones observed in the previous experiment where the reference wavelength had a value of 438 nm. The L/λ function appears nearly unchanged and does not shift together with the reference wavelength along the wavelength axis as is the case in other colour discrimination experiments (*e.g.* [26]). Consequently a strong asymmetry between the two $\Delta\lambda$ values occurs ($\Delta\lambda^-$ = 100 nm, $\Delta\lambda^+$ = 16 nm).

In the third series of experiments the wavelength of the reference stimulus was 580 nm (Fig. 4c). Only the discrimination ability with respect to shorter wavelengths was investigated. Again the conditioning index reaches the criterion at 516 nm, though the slope is less steep than in the other two series of experiments.

Discussion

The results show that flies can learn to discriminate a set of stimuli on the basis of colour. Intensity is not involved in this ability, although it controls the fly's spontaneous preference behaviour.

In all three series of experiments concerned with colour discrimination, we find large wavelength ranges, in which no discrimination occurs. However, there are narrow ranges, in which the performance suddenly increases. For the two series of experiments, in which the reference wavelengths were 438 nm and 500 nm, respectively, the shape of the L/λ function is quite similar. The steplike increases are very pronounced and occur at *ca.* 400 nm and at *ca.* 515 nm, regardless of which wavelength was used as a reference. These results suggest the following interpretation: For flies the wavelength spectrum consists of three ranges or categories within which they are not able to discriminate. Between these regions, however, a precise discrimination is possible. The first range consists of the UV region up to 400 nm. The second range comprises the wavelengths between 400 nm and about 515 nm and a third range includes all wavelengths longer than 515 nm. The last series of experiments, in which the reference wavelength was 580 nm, confirms this interpretation, since there is almost no discrimination in the range of wavelength longer than 515 nm.

It cannot be excluded that there are additional, very narrow categories in the region of the slopes of the L/λ functions. The slopes are quite steep, but they are not completely vertical. This is probably due to variability among the flies, but it is also possible that there are wavelengths (*e.g.* 515 nm) which can be discriminated by each fly both from shorter and from longer wavelengths. However, this is very difficult to prove with our paradigm, because it is not possible to carry out all the necessary experiments with a single fly.

The colour vision in flies described here differs fundamentally from that found in all other known colour vision systems. Wavelength discrimination depends not primarily on the amount of the difference between two wavelengths, but rather on whether the wavelengths fall into two different categories or not. Thus, the colour vision found in the blowfly can be specified as categorical colour discrimination, in contrast to the continuous colour discrimination found in other species.

What kind of neural mechanisms could underly such a form of colour vision in *Lucilia?* Which photoreceptor classes are involved and how are they connected? Based on our findings, we will propose a simple model in which only the receptor classes R 7p, R 8p, R 7y and R 8y take part, without any involvement from the receptor class R 1−6.

We leave out R 1−6 because its spectral sensitivity is rather broad and therefore not very useful for colour discrimination. In fact, it is almost impossible to construct a pair of colour stimuli which is metameric for the tetrachromatic system, consisting of R 7p, R 8p, R 7y, and R 8y, but discriminable for the pentachromatic system, including R 1−6 [27]. Even if there were a neural participation of R 1−6 to a colour vision channel, discriminability would not be improved. It seems likely then, that the receptors R 1−6 do not participate at all to the fly's colour vision but are important in other visual tasks.

A plausible scheme in which only the central receptors are involved is the following (Fig. 5): There are two simple colour opponent mechanisms. One integrates signals antagonistically from the receptors R 7p and R 8p and the other from receptors R 7y and R 8y. Each opponent mechanism is equipped with a gain control which provides similar responses in R 7 and R 8 under adaptation conditions. In the presence of a transient, small field stimulus each of the two systems registers only whether the difference of the excitations of R 7 and R 8 is positive or negative. Boundaries be-

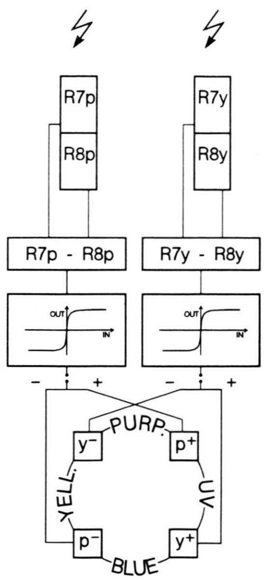

Fig. 5. This simple scheme can explain the experimental results. It consists of two subsystems, one containing the photoreceptors R 7p and R 8p, the other containing R 7y and R 8y. In each system, a gain control provides for equal responses of the two photoreceptors under adaptation conditions (not shown). R 7 and R 8 are antagonistically connected. The difference R 7−R 8 gives input to a threshold mechanism such that each subsystem can have only one of two values (+, −). For the whole system there are thus four possible conditions. Three of them correspond to the experimentally obtained wavelength ranges (y^+p^+ UV, y^+p^- BLUE, y^-p^- YELLOW). The fourth condition is the hypothetical PURPLE category (y^-p^+).

tween the distinct colour ranges would then result if the sign of the difference changes in one of the two opponent mechanisms.

This model thus makes predictions about the position of neutral points in the spectrum which can be compared with experimental data. One just has to calculate which wavelength λ_0 satisfies the equation:

$$G_7S_7(\lambda_0) = G_8S_8(\lambda_0).$$

The scaling factors (G_7, G_8) relate the relative spectral sensitivities ($S_7(\lambda)$, $S_8(\lambda)$) to the absolute sensitivities. Their ratio is fixed by the condition that the assumed gain control mechanism adjusts them so that the responses in R 7 and R 8 are the same under adaptation light I_{ad}.

$$\frac{G_7}{G_8} = \frac{\int I_{ad}(\lambda)S_8(\lambda)d\lambda}{\int I_{ad}(\lambda)S_7(\lambda)d\lambda}.$$

The equation for the wavelength λ_0 at the neutral point becomes then:

$$\frac{S_7(\lambda_0)}{\int I_{ad}(\lambda)\, S_7(\lambda)d\lambda} = \frac{S_8(\lambda_0)}{\int I_{ad}(\lambda)\, S_8(\lambda)d\lambda}.$$

For the calculations receptor sensitivities given by Hardie and Kirschfeld [5] were used. Most of their data come from *Musca* and *Calliphora*, but a few data are also available from *Lucilia,* suggesting that this closely related species has similar spectral sensitivities. For the adaptation stimulus I_{ad} the relative spectral power distribution of the illuminant was used.

The test arena was uniformly illuminated with a 25 W tungsten incandescent lamp, which has a rather reddish power spectrum (Fig. 6a). If the gain control factor is set in a way to give equal responses in R 7y and R 8y with respect to the tungsten light, the absolute sensitivity at the peak wavelength of R 7y is 10 times higher than for R 8y. Using the formula outlined above, we find that R 7y and R 8y produce equal responses when the wavelength of the light is 513 nm. This value agrees rather well with one of the experimentally obtained range boundaries.

Similar calculations for the pale system predict that R 7p will be about 60 times more sensitive than R 8p and that the corresponding neutral wavelength will be expected at 417 nm, as compared with 400 nm derived from the behavioural measurements.

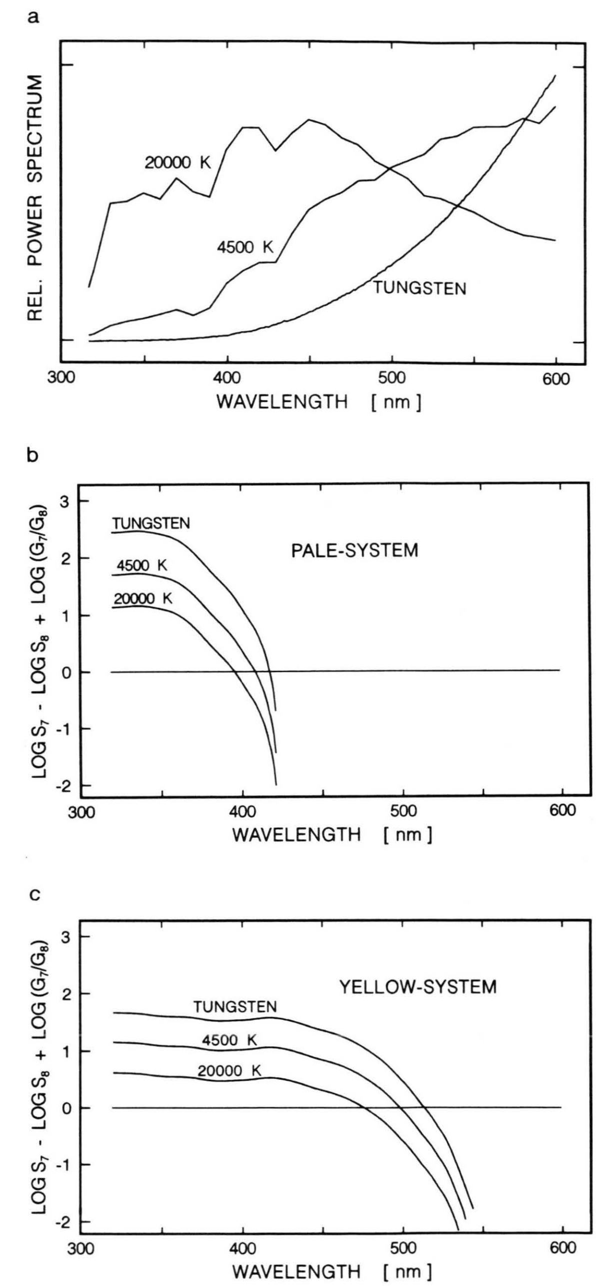

Fig. 6. The neutral points of the pale and yellow system were determined for different adaptation lights. (a): Relative power spectra (quanta per time) of the tungsten lamp used in the experiments and of two extreme natural daylights. (b): log (S_{7p}) − log (S_{8p}) + log (G_{7p}/G_{8p}) plotted against wavelength λ. S_{7p} and S_{8p} are the normalized spectral sensitivities of the pale system from Fig. 1. G_{7p}/G_{8p} is the ratio of the gain control factors, determined as described in the text. The neutral points are the points of intersection with the 0 line. (c): Same calculation for the yellow system.

The reason for the predicted very high absolute sensitivity of R7p compared with R8p is the artificial power spectrum of the tungsten lamp which has almost no overlap with the sensitivity spectrum of R7p. If the gain factors are set in such a way that R7p is only 10 times more sensitive than R8p, the neutral point becomes 407 nm, which is much closer to the experimental data. An extremely reddish natural daylight spectrum (4500 K, [28]) would produce such an adaptation state. It would be reasonable that the range of gain control does not much exceed the limits of natural light conditions. In Fig. 6b and c the output of hypothetical antagonistic interneurons, which are adapted to different lights, is plotted *versus* wavelength. A value of zero signifies the response to the adaptation light. Thus the intersections of the curves with the zero line mark the expected neutral points.

The model predicts at least three colour categories along the wavelength axis. A stimulus falls into the UV category, when R7p is more excited than R8p, and R7y is more excited than R8y. A stimulus belongs to the BLUE category when it excites R7p less than R8p, and R7y more than R8y. Finally, the YELLOW category is characterized by stronger excitation of R8 in both subsystems. These categories correspond to the three wavelength ranges determined in the discrimination experiments.

The model suggests a possible fourth colour category, manifested when R7p is more excited than R8p, and R7y less than R8y. None of the monochromatic stimuli, however, produces such an excitation pattern. Only a mixture of short and long wavelengths will belong to that category, thus it can tentatively be called the PURPLE category.

Neutral excitation of both subsystems might represent a further category that differs qualitatively from the others as it would correspond to an uncoloured condition such as the average background. None of the monochromatic lights would fall into this category. Fukushi [21] reports, that training to a green appearing paper was very difficult. The reflectance curve of the green paper had a broad maximum at 510 nm and a second one in the UV region. Such a reflectance spectrum could represent the expected "uncoloured" category.

It is interesting that the ranges of good discriminability in flies are about the same as in most other so far investigated colour vision systems [29]. This is especially true for flower visiting hymenoptera. The spectral discrimination function of honeybees shows optima at about 400 nm and 500 nm [26]. In other hymenoptera, where a spectral discrimination function has not been explicitly measured, the positions of the receptor sensitivity spectra on the wavelength scale suggest that there is also good discriminability in these regions [30].

Chittka and Menzel [31] measured a representative sample of spectral reflectance functions of angiosperm blossoms and pointed out that prominent slopes in these spectra accumulate in the regions of about 400 nm and about 500 nm. This means that the spectral reflectances of flowers produce large differences between the responses of the three different receptor classes, found in the eye of hymenopterans typically with sensitivity maxima at 340 nm, 430 nm and 540 nm [30].

Flies seem to take part in this consensus. The mutual adjustment of the location of slopes in blossom reflectance spectra and of the range boundaries in fly colour vision implies that the blossom colours fall very distinctly in one of the fly's categories. Thus they can be reliably distinguished – even under changing illumination conditions – not only from an uncoloured background, but also from each other.

The colour vision in the blowfly *Lucilia* spec. differs from the one in other investigated species as it is categorically rather than continuously organized. Our results suggest a simple model for colour vision in flies. This model, however, should now be verified by further experiments. It has to be shown how far the UV category projects into the short wave part of the spectrum. Moreover, it should be tested whether the colour categories can be shifted along the wavelength scale by varying the adaptation light. This would be a powerful prediction of the model. Another way of testing the model would be designing experiments to verify the existence of a fourth colour category (the PURPLE category).

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