J. comp. Physiol. 121, 241–252 (1977)

Journal of Comparative Physiology · A
© by Springer-Verlag 1977

# Specific Receptor Input into Spectral Preference in *Drosophila*

Karin G. Hu and William S. Stark

Department of Psychology, The Johns Hopkins University, Baltimore, Maryland 21218, USA

Received February 28, 1977

**Summary.** *Drosophila* have 3 types of retinal receptors, R1–6, R7 and R8. Using visual mutant strains lacking function in one or two receptor types, spectral preference in walking fast (30 s) phototaxis was measured. High correlations for intensity-response functions were obtained (Fig. 2 and 5).

With a 467 nm choice standard, which could saturate R1–6, white-eyed strains with only R8 or with R1–6 plus R8 functional exhibited similar spectral sensitivities with a broad peak at visible wavelengths (Fig. 3) not unlike the electrophysiological characterization of R8 (Fig. 1). Strains with R7 plus R8 or with all receptors intact exhibited similar functions with a high ultraviolet (UV) peak (Fig. 4), like the electrophysiological characterization of R7 plus R8. The presence of R1–6 did not alter the profiles mediated by R8 alone or by R7 plus R8.

With a 572 nm standard, which should maintain R1–6 function, white- and red-eyed wild-type strains with all receptors intact exhibited similar UV dominated spectral sensitivities, probably from R7 plus R8, with weak visible secondary peaks possibly from R1–6 or R8 (Fig. 6). However, even with a very dim 572 nm standard or with no standard at all, unequivocal evidence for R1–6 input was not found and intensity-response function correlations were low. This finding and other recent studies suggest that specific phototactic or optomotor tasks and conditions (e.g., adaptation level) determine the extent to which each receptor input is utilized.

Spectral preference with a bright 365 nm standard was difficult to measure because of the strong UV preference in phototaxis. In pilot studies, an ocelliless strain showed strong fast phototaxis.

## A. Introduction

*Drosophila* have three photoreceptor types in each ommatidium: R1–6 are six cells with peripheral rhabdomeres; R7 has a distal central rhabdomere; and R8 has a proximal central rhabdomere. Using chromatic adaptation to inactivate specific receptor types (Stark, 1975) and mutants lacking one or more receptor

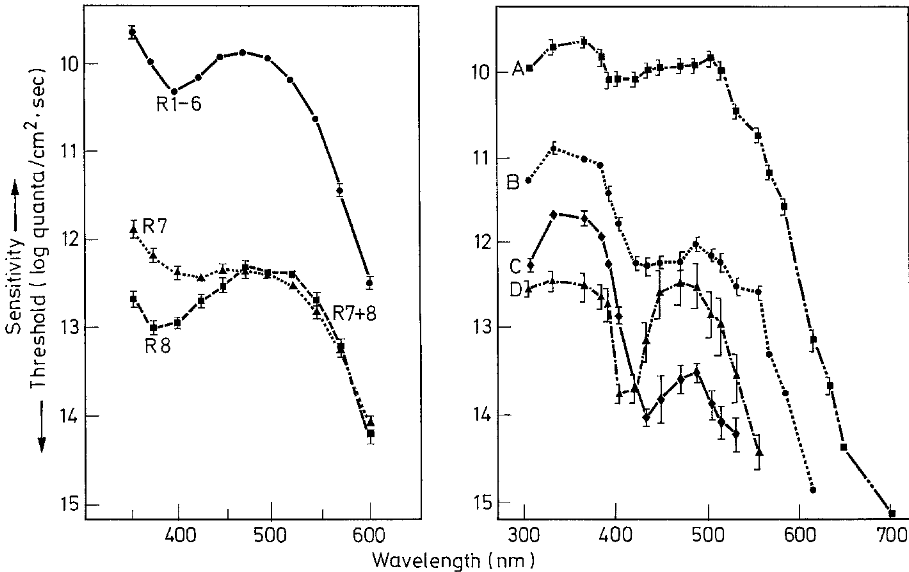


**Fig. 1.** ERG spectral sensitivity curves from white-eyed *Drosophila* with all receptors intact: dark-adapted (dots), 470 nm-adapted (triangles) and 370 nm-adapted (squares) (Harris et al., 1976). Standard errors of relative sensitivity are shown. The labels R1–6, R7+R8, R7 and R8 show which (portions of each) curve is generated by which receptor type (s) after Harris et al.'s analysis. Phototactic spectral sensitivity curves obtained by Schümperli (1973) (redrawn and transformed with permission of the author) from wild-type *Drosophila*. The intensity of the white light constant stimulus was varied: A: 0.05 erg/cm$^2$ s; B: 1 erg/cm$^2$ s; C: 10 erg/cm$^2$ s (all dark adapted) and D: 10 erg/cm$^2$ s after flies were given prior light adaptation

types (Harris et al., 1976), the different spectral sensitivities of each receptor type were characterized using electroretinographic (ERG) techniques. Such color receptor multiplicity could subserve Young-Hering trichromatic-opponent color vision as in the vertebrate eye (e.g., Svaetichin et al., 1965). On the other hand, the three types of receptors may mediate behavior at different adaptation levels as rods and cones mediate human scotopic and photopic vision respectively.

Color vision usually results from central integration of input from spectrally different receptors and is usually defined as the behavioral ability to discriminate between two wavelengths without using apparent intensity differences as a cue. The possibility of color vision or subtractive (opponent) receptor interactions in Diptera has been suggested in studies involving colored light stimuli in conditioned learning (Quinn et al., 1974), inhibitory interactions in optomotor responses (Kirschfeld and Lutz, 1974) and inhibitory interactions in higher order neurons (Mimura, 1976). Among invertebrates, insects like honeybees, which can be more easily taught conditioned responses, have provided the most unequivocal evidence for color vision (see von Frisch, 1971, for review) as well as early evidence for retinal multiplicity (Autrum and von Zwehl, 1964). Most investigations have used innate responses to study vision in flies. Evidence for color vision from such innate measures must, however, be interpreted with caution (Schümperli, 1973; Stark, 1970). Some literature addressed to the question of color vision in flies might be reinterpreted because it was obtained

before the present characterization of the retinal receptor types had emerged. For example, manipulating the adaptation level, Schümperli (1973, see Figure 1) obtained spectral sensitivities for walking phototactic preference in *Drosophila* which corresponded to the ERG characterization of each receptor type later presented by Harris et al. (1976, see Figure 1). With *Musca* the mean luminance and spatial frequency of the stimuli determine which of only two receptor systems input into optomotor behavior (Eckert, 1971). Since Schümperli obtained functions not expected from Eckert's earlier receptor spectral sensitivity data, he concluded that *Drosophila* have color vision.

The purpose of this study was to investigate spectral sensitivity and the question of color vision in walking phototactic preference in *Drosophila*. The present study was designed to determine each receptor system's input into innate spectral preference responses. Appropriate *Drosophila* strains with all receptor systems intact, lacking function in R1–6, R7 or R1–6 and R7 (see Methods) were compared to systematically deduce each receptor type's function and to disentangle the questions of receptor input from neural interactions. Light levels were controlled to produce functions which could appropriately be compared with Harris et al.'s (1976) electrophysiological and Schümperli's (1973) behavior data (see Fig. 1). Brief reports of some of these findings have been previously presented (Stark and Hu, 1976; Stark et al., 1976; Hu and Stark, 1977).

## B. Materials and Methods

*Animals. Drosophila melanogaster* were raised on a standard diet of yellow cornmeal, molasses, agar and brewers and live yeast under a 12:12 light:dark cycle at 23 °C. Receptor mutants used singly or in combination were $sev^{LY3}$, $rdgB^{KS222}$ and $ora^{JK84}$. The mutant strains had been characterized genetically, anatomically, electrophysiologically, photochemically and behaviorally by Harris et al. (1976). *Sev* eliminates R7 rhabdomeres. R8 should be indifferent to the absence of a distal R7 element in measures of whole eye response such as ERG or phototaxis. If reared in room light at 25 °C *rdgB* causes early light-induced R1–6 structural degeneration (Harris and Stark, 1977). More critically, light elicits an immediate and permanent R1–6 (but not R7 or R8) inactivation in white-eyed *rdgB*: R1–6 ERG activity is only observed in flies raised at 18 °C in the dark; R1–6 activity is completely absent after brief exposure to room or experimental lighting; only after careful preparation under dim, deep red (>650 nm) light can any R1–6 ERG activity be obtained (Harris and Stark, 1977). *Ora* reduces R1–6 rhabdomeres to about 4 μm by 0.5 μm diameter (i.e. to about 0.4% of the normal volume); it completely eliminates the R1–6 but not the R7 plus R8 ERG activity. Males or females usually within one week of pupal emergence of the following stocks were used: White-eyed flies lacking screening pigments were *rdgB sev*; *cn bw* having only R8, *w sev* having only R1–6 and R8, *w; ora* and *w rdgB* having only R7 and R8, and *cn bw* and *w* having all receptors intact. Red-eyed *rdgB* and Oregon-R wild-type (with all receptors intact) and white-eyed ocelliless *w oc ptg* flies were also studied. It is possible that phototactic spectral sensitivities do not show screening pigment leakage effects as do ERG data: Schümperli's (1973, Fig. 1, curve A) data from red-eyed flies looks more similar to an ERG spectral sensitivity from white- than red-eyed flies (Stark and Wasserman, 1972; Stark, 1973). However, white-eyed flies were used in most studies since they are readily phototactic and have been best characterized physiologically.

*Apparatus.* A straight choice arena or Y arena was used. Both arenas were painted flat black in the interior and had frosted glass endplates onto which the stimuli were projected. The straight arena measured 1.5 × 1.5 cm × 7.7 cm. Flies were randomly distributed throughout the arena by gentle shaking at the beginning of each trial. The Y arena arms were 1.9 cm by 1.5 cm, and the approximate distance from the midpoint to the endplate was 5.5 cm. Flies were shaken to

the bottom leg of the Y at the beginning of each trial. A central sliding guillotine door could be slid shut in each arena to finalize choices for counting.

*Optics.* A standard (constant) stimulus was from a GE ribbon filament T10/1P bulb approximately collimated with a glass achromat lens and filtered through a 365 nm, a 467 nm or a 572 nm Bausch and Lomb interference filter. These filters had been calibrated on a Carey recording spectrophotometer. The intensity was attenuated with Wratten neutral density filters. The 365 nm filter had a half-peak band width of 14 nm. Its long wavelength harmonic (inherent in Bausch and Lomb filters) was at 680 nm (to which the fly eye is slightly sensitive), while the glass optics blocked the short wavelength harmonic; thus a UV transmitting visible absorbing glass with a different long wavelength leakage was used to block the harmonic. The 467 nm interference filter had a half-peak bandwidth of 9 nm, and the short wavelength harmonic was blocked with a Wratten No. 2 UV blocking filter. The 572 nm interference filter had a half-peak bandwidth of 12 nm and the short wavelength harmonic was blocked with a Wratten Filter No. 8. The latter two interference filters had sufficiently long wavelength first order harmonics to not require blocking.

The variable stimulus was projected from a Bausch and Lomb UV-Visible 33–86–79 monochrometer with a regulated 150 W xenon arc adjusted for a 30 nm bandwidth. The beam was approximately collimated with a glass achromat lens and attenuated with a series of Bausch and Lomb 31–34–38 Inconnel-on-glass neutral density filters. These filters were calibrated for spectral absorption on a Carey recording spectrophotometer and had been found to be additive. Wavelengths used for testing ranged from 350 nm to 600 nm at about 25 nm intervals. At 600 nm an additional Wratten No. 12 filter was used to block the monochrometer's short wavelength harmonic.

*Calibrations.* The intensities of the full intensity variable stimulus were calibrated beyond the frosted glass end-plates with a calibrated (Stark, 1975) PIN-10 Schottky barrier photodiode (United Detector Technology). Intensity calibrations of the constant stimuli proved to be more of a problem because (1) Bausch and Lomb interference filters utilize the second harmonic, leaking an infrared harmonic to which the PIN-10 (but not the fly's eye) would be very sensitive; and (2) long wavelength blocking filters are difficult to use for calibration assistance because of poor wavelength specificity. The constant stimuli were thus estimated to be equal to the intensity of stimuli generated by monochrometer with neutral density filters to which flies (in all experiments conducted with that constant stimulus) responded in a 50:50 ratio. These intensity calibrations of the constant stimuli were validated by visual comparison with the monochrometer and neutral density generated stimuli.

*Procedure.* Constant stimulus wavelength and intensity were carefully chosen because of the influence on the level and shape of the resulting spectral sensitivity curve (e.g., see Schümperli, 1973). Constant stimulus wavelengths and intensities and variable stimulus intensity ranges at each wavelength were further selected to be within the dynamic range for R1–6, R7 and/or R8 as determined by Harris et al. (1976). These intensities, which produced criterion visual responses, were also close to those used by Schümperli.

Approximately 20 adult flies were lightly etherized and placed into the arena. The arena was sealed with a transparent top and testing began after flies had fully recovered from the ether. Room conditions were darkened. The straight arena was gently shaken or the Y arena flies were shaken to the bottom leg. The arena was then placed on a platform between the two stimuli, and covered with an opaque top. Flies were allowed 30 s to choose between stimuli, after which the central sliding door was shut. Flies on each side were counted under the white light of a standard flashlight. In some experiments, a dim red light was used for counting; this manipulation, chosen to maintain greater dark adaptation, did not alter the results. The next trial began after about 30 s dark adaptation with either a different intensity or different wavelength.

Each group of 20 flies was tested at each of 11 wavelengths at 5–11 different intensities flanking and ranging around the 50% (two stimuli equally attractive) response by about $\pm 1$–2 log units. This within subjects method of constant stimuli design usually used a total of 100 trials for each fly. Sequence of wavelength and intensity were varied between groups. After all of the flies had been tested, the cumulative proportion of flies counted in the variable stimulus arm to the total number of flies in the arena was tabulated for each intensity at each wavelength. The average correlation between intensity and proportion of flies attracted towards the variable stimulus was high, about $r = 0.9$ (Pearson's correlation coefficient), for experiments reported.

Linear regression by means of the least squares method was used to calculate which intensity

for each wavelength was required to elicit an equal number of flies to the left and right arms of the arena. The intensity which elicited the criterion response of 50:50 was a measure of the relative sensitivity of the eye to different wavelengths. Intensity, the reciprocal of sensitivity, was plotted (in log quanta/cm$^2$ s) against wavelength to produce a spectral sensitivity curve. For adaptation levels and fly strains reported below, the method produced stable results in that spectral sensitivities calculated from several 20 subject runs would be very similar. Thus, considerable pilot testing was used to determine appropriate intensity and experimental conditions.

## C. Results

Figure 2 shows the intensity-response data for straight-arena responses collected for males of the white-eyed strain *rdgB sev*; *cn bw* having only R8, *w sev* having only R1–6 and R8, *w rdgB* having only R7 plus R8, and *cn bw* with all receptor systems intact. All experiments were conducted with a 467 nm constant stimulus with an intensity of about 13.7 log quanta/cm$^2$ s. This intensity should give an estimated near-maximal R1–6 ERG of at least 15 mV. For this reason, we considered that the illumination level of the arena might prevent R1–6 of opposing eyes from providing behaviorally useful intensity difference information. Furthermore, although flies usually choose sides quickly, the 13.7 intensity would provide much of the approximate $10^{15}$–$10^{16}$ quanta/cm$^2$ required to inactivate R1–6 in 30 s if delivered without long wavelength stimuli (Stark and Zitzmann, 1976; Stark, 1977; Harris and Stark, 1977; Wright and Cosens, 1977). The high correlation coefficients (averaging across wavelengths $0.91 \pm 0.059$ (s.d.), $0.89 \pm 0.086$, $0.93 \pm 0.042$, and $0.94 \pm 0.032$ for each strain respectively) indicate that R8 alone or R7 plus R8 mediate phototaxis quite well (with or without a functional R1–6 system). The intensity-response function slopes averaged $0.18 \pm 0.055$, $0.13 \pm 0.039$, $0.13 \pm 0.042$, and $0.25 \pm 0.086$ (proportion vs. log intensity) respectively. It is important to point out that unresponsive flies, and reflection across the straight arena, would decrease intensity-response function slopes (without changing 50% point determination) which has been found to be higher and more experiment-specific by Schümperli (1973) whose methods (see Discussion) should count only responsive flies.

The experiments as in Figure 2 were performed on *w; ora*. The average intensity-response function correlation coefficient for 11 wavelengths was $r = 0.34$ with an average slope of 0.03. Although R7 and R8 function in the ERG the low correlations and slopes suggest a deficit or an absence of R7 or R8 behavioral input (confirming Harris et al.'s, 1976 behavioral report). Thus *ora* was not further used for eliminating R1–6.

Figure 3 shows the spectral sensitivities constructed from Figure 2 data for *rdgB sev; cn bw* and *w sev*. These functions have a broad visible wavelength peak and are similar to each other. Furthermore, they are not unlike the Figure 1 R8 ERG data and curve D behavior data in shape and are very similar in absolute level. Figure 4 gives the spectral sensitivities determined for *w rdgB* and *cn bw*. These functions are dominated by a high UV maximum just like the Figure 1 R7 plus R8 ERG data and curves B and C behavioral data; all are near the same absolute sensitivity level.

We attempted to more closely replicate Schümperli's experimental geometry, fly stocks, and illumination intensities to obtain an R1–6 dominated curve. Thus we used a Y arena and wild-type female white- and red-eyed flies to

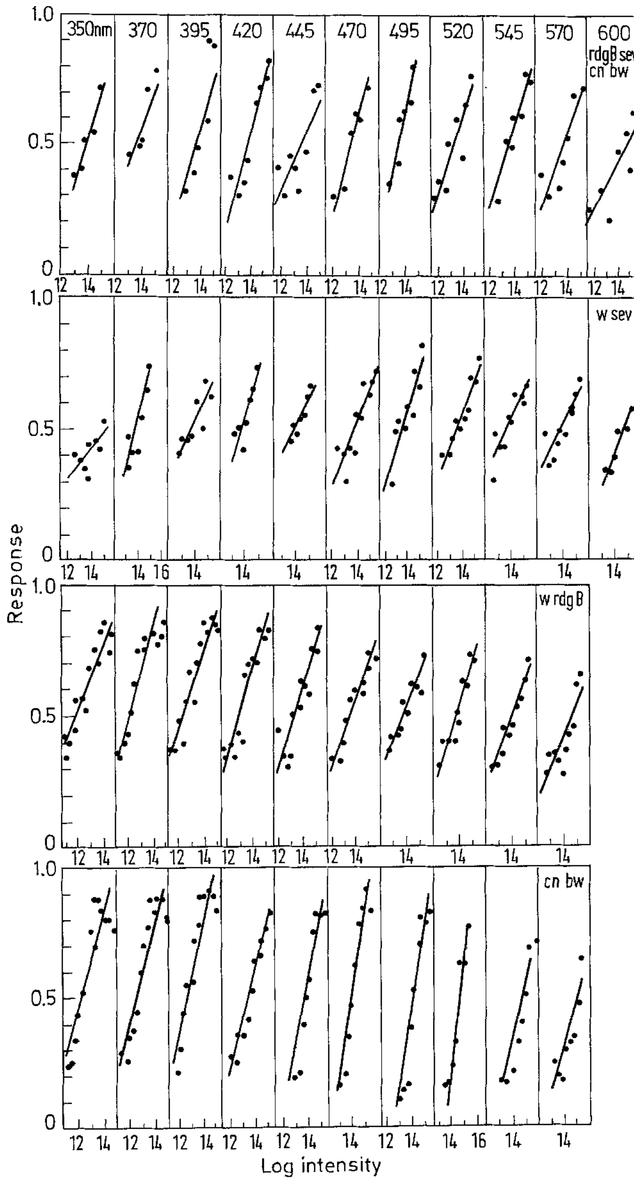


**Fig. 2.** Response (proportion of the number of flies choosing the variable stimulus/total number of flies) as a function of log intensity in quanta/cm$^2$ s (intensity-response functions). Each panel (and each point) represents approximately 100 flies tested with a 467 nm standard in a repeated measures (within subject) design. Four identical experiments using 10 or 11 wavelengths (on different strains) were performed (each row). See text for further details. Data at 600 nm was not included if a minimum of 50% of the flies were not attracted to the highest intensity of the variable stimulus

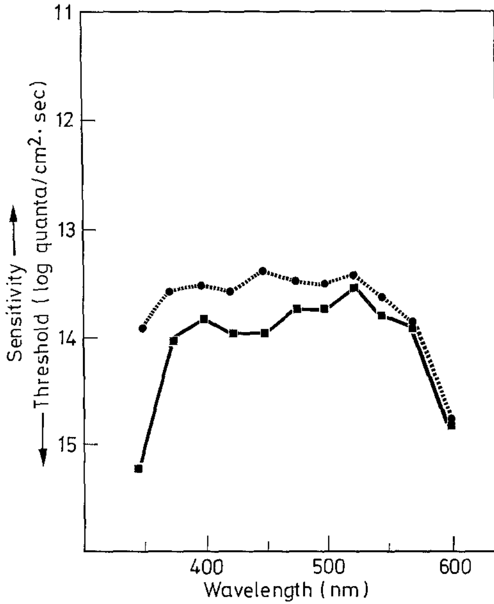


**Fig. 3.** Spectral sensitivities of *rdgB sev, cn bw* (dots; from Stark et al., 1976) having only R8, and *w sev* (squares) having R1–6 and R8. Each curve represents 100 subjects tested in an identical experiment, with a 467 nm standard

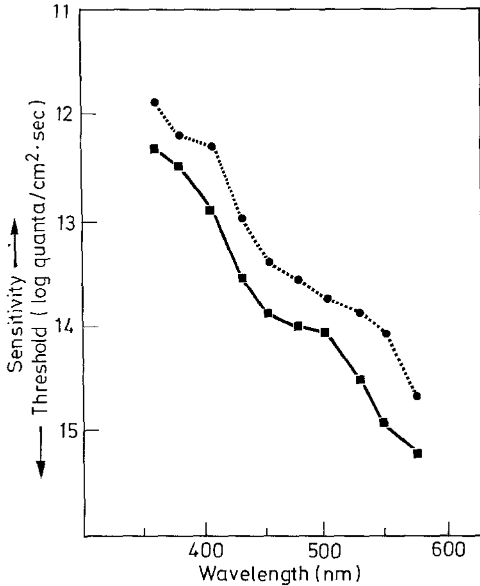


**Fig. 4.** Spectral sensitivities of *wrdgB* (dots; from Stark et al., 1976) having R7 and R8, and *cn bw* (squares) having all receptors intact. Each curve represents 100 subjects tested in the same identical experiment as in Figure 3 with a 467 standard

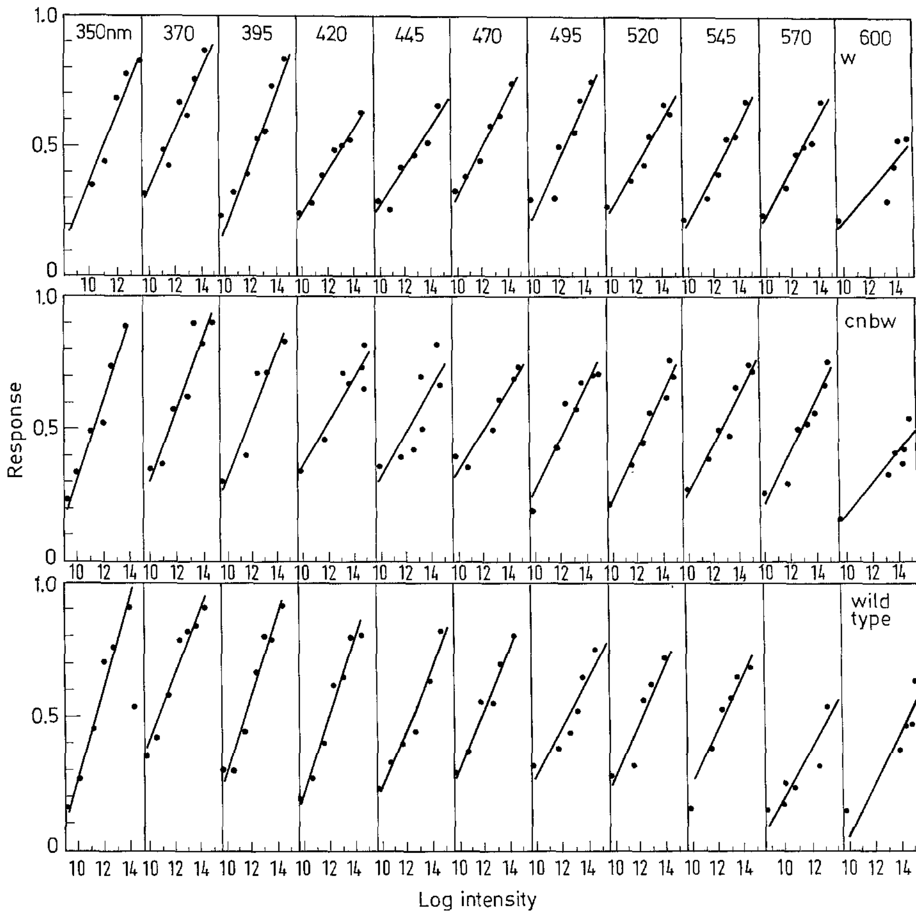


**Fig. 5.** Intensity-response functions as in Figure 2. For *w*: $n=100$; *cn bw*: $n=40$; red-eyed wild-type: $n=100$. All three were tested with a 572 nm standard at 11 wavelengths in an identical experiment. See text for further details

attempt to obtain the R1–6 behavioral profile obtained by Schümperli (curve A, Fig. 1). Schümperli's curve A has the same two-peaked shape as reported for R1–6 in numerous studies on flies using intracellular recording, ERG, microspectrophotometry and behavior (see Stark et al., 1976; Stark 1975, for reviews). Figure 5 gives the intensity-response function data for white-eyed (*w* and *cn bw*) and red-eyed wild-type strains (with all receptors intact) using a 572 nm stimulus of 13.2 log quanta/$cm^2$ s. This constant stimulus would be expected to give a substantially submaximal R1–6 ERG of about 5 mV and the wavelength should maintain R1–6 sensitivity. Intensity-response function correlations averaged $r=0.96\pm0.035$ for *w*, $0.95\pm0.047$ for *cn bw*, and $0.96\pm0.026$ for red-eyed wild-type with average slopes of $0.093\pm0.024$, $0.099\pm0.025$, and $0.119\pm0.03$ respectively. The spectral sensitivities constructed from this data (Fig. 6) are dominated by a UV peak more like the R7 plus R8 than the R1–6 ERG or behavioral data (Fig. 1) but have a secondary visible wavelength peak which

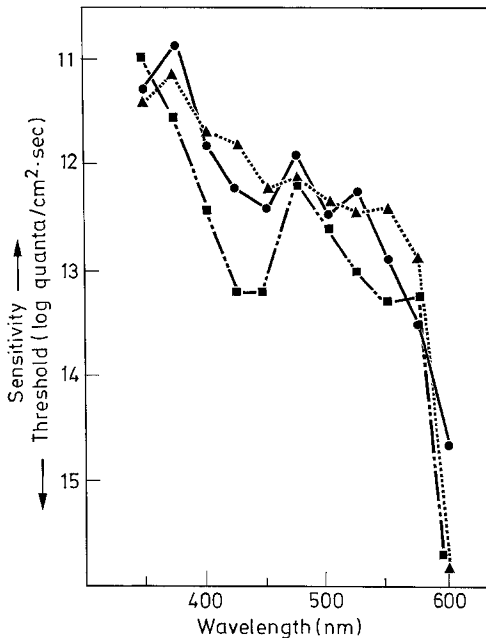


**Fig. 6.** Spectral sensitivities of *w* (squares), *cn bw* (triangles) and red-eyed wild-type *Drosophila* (dots), three strains with all receptors intact. For *w*, $n=100$; for *cn bw*, $n=40$; and for red-eyed wild-type, $n=100$. All three strains were tested with a 572 nm standard in an identical experiment with the Y-maze

could represent R1–6 or R8 activity. An experiment with *w sev* (lacking R7) using the same conditions ($n=100$, $r=0.89 \pm 0.047$, slope$=0.139 \pm 0.041$) resulted in about a 1 log unit reduction of the high UV peak, but no change in the secondary visible peak. Pilot studies done with *rdgB sev; cn bw* (with only R8 functional) and *rdgB* (lacking R1–6 function) tentatively indicate that R8 alone (or R8 plus R7) could mediate the visible wavelength sensitivity of Figure 6, i.e., that R1–6 still does not feed into behavior under this condition, which might be too bright for R1–6 input. Numerous pilot experiments using 1.0 log unit dimmer constant stimuli or no constant stimulus at all with extremely dim variable stimuli gave spectral sensitivities dominated by a UV peak, or, under very dim conditions, below estimated R7 or R8 threshold levels, gave poor intensity-response function correlations. It should be pointed out that the experimental tasks and adaptation conditions reported here and by Schümperli were different (see Discussion). Further pilot experiments showed no consistent differences between male and female flies or between straight and Y arenas.

Since Schümperli had obtained all of his Figure 1 functions from wild-type flies under different adaptation conditions, we attempted to reduce the UV peak in *w rdgB* and *cn bw* flies (which have R7) by studying phototaxis in the straight arena with a bright UV constant stimulus of 365 nm of intensity 13.26 log quanta/cm$^2$ s. Bright UV can selectively inactivate R7 (as well as R1–6 if present). While the derived spectral functions showed a slightly decreased

UV peak, the data were difficult to obtain due to the high UV preference; furthermore, subsequent ERG data (Stark, 1977) suggested that the time integrated intensity of our UV arena illumination was lower than the approximate $10^{17}$ quanta/cm$^2$ needed to inactivate R7.

Because the methods determined final choice placement of flies rather than directly observing phototaxis, we considered that the ocelli could contribute to such responsitivity. We thus replicated the experiments of Figure 2 on the strain *w oc ptg* which lack ocelli but have all three retinal receptor systems electrophysiologically functional and approximately normal (Stark, unpublished experiments). A pilot study ($n=44$) showed that any photokinetic influence from ocelli was not obvious in our task as the *w oc ptg* intensity-response correlation ($r=0.89\pm0.098$) was comparable to that of normal flies. Further studies of ocellar electrophysiological and behavioral function are in progress.

## D. Discussion

The results of this paper demonstrate that R7 and R8, as characterized by Harris et al. (1976), mediate fast positive (intensity-response function slope) phototaxis. When compared with the phototactic spectral sensitivities obtained by Schümperli (1973) they show: (1) that adaptation control and the methodology can determine which receptors dominate phototactic behavior; and (2) that all photoreceptor types, R1–6, R7 and R8, feed positively into phototaxis. That phototactic preference in wild-type *Drosophila* can have a predominant UV peak confirms a classic study by Bertholf (1932); Bertholf obtained spectral sensitivities with 365 nm primary maxima and much reduced 487 secondary maxima much like Schümperli's (1973, Fig. 1, curves B and C) data and the present (Fig. 6) data.

In our experiments, no unequivocal evidence of R1–6 behavioral input was found, while Schümperli (1973) presented convincing evidence of R1–6 input (Fig. 1) in his task which may not be fast phototaxis (see below). In a review of different techniques used to study *Drosophila* phototactic behavior, Rockwell and Seiger (1973) showed that phototaxis is operationally defined by the conditions and requirements of the task. Not only may task and arena design determine the response, but the internal state of the fly as well, such as receptor adaptation and state of agitation.

In the present study, through various pilot experiments, we eliminated several factors that might have contributed to the difference between Schümperli's and our findings, such as the use of red- vs. white-eyed flies, white vs. chromatic constant stimulus, females vs. males, straight vs. Y arenas, and being counted under red vs. white light. The remaining differences in design could be critical in explaining Schümperli's more unequivocal R1–6 data: (1) Our flies were gently agitated before each trial; (2) our flies were only dark-adapted for 30 s; (3) we scored position after a 30 s choice period which could include kinesis components while Schümperli scored initial turn; and (4) our task could be operationally considered to be fast phototaxis while Schümperli's could include fast and slow phototaxis and perhaps even optomotor turning. Heisenberg and Götz (1975) presented evidence suggesting physiological, in addition to behavioral, separation of fast and slow phototaxis. Using behavior techniques

to categorize visual mutants they were able to identify mutants which, under bright conditions, are able to mediate slow, but not fast phototaxis. In addition, these same mutants could not mediate slow phototaxis under dim conditions suggesting that not only are fast and slow tasks different, but also that dim or bright conditions use two different mechanisms as well. That adaptation level can determine which visual mechanisms dominate phototaxis is analogous to adaptation level determining whether rods vs. cones dominate scotopic and photopic vision in the human Purkinje shift. That R1–6 behavioral input in Schümperli's task is observed for extremely dim stimuli (Fig. 1) causes one to raise the question of under what naturalistic circumstances essentially diurnal flies would use such an extraordinarily sensitive behavioral mechanism.

Our results, as well as Schümperli's, must be considered not to provide critical evidence for (or against) color vision in *Drosophila* since the behavioral spectral sensitivities are like the corresponding receptor spectral sensitivities. The UV peak at low intensities suggests a high gain for the UV (R7) spectral input, consistent with Schümperli's conclusion. Harris et al. (1976) presented evidence of possible receptor interaction in studies of normal and mutant *Drosophila* phototaxis; yet their high levels of light adaptation and control stimulus intensities make their data less directly comparable to the present data (see Harris et al., 1976; Stark et al., 1976), than Schümperli's (1973, Fig. 1).

Optomotor behavior is another measure which has been shown to differentially use receptor input. Bees present an illustrative example of how task requirements can determine receptor input or whether color vision receptor interactions might be demonstrated. Although bees have color vision learning (von Frisch, 1971), they appear to be color blind in optomotor behavior (Kaiser and Liske, 1974). Studies of optomotor behavior in Diptera also suggest that not all receptors feed positively into this behavior. Eckert (1971), using *Musca,* obtained spectral sensitivity curves similar in shape and sensitivity level (personal communication) to the R1–6 and R8, but not the R7 ERG and behavioral spectral sensitivities (Fig. 1) in optomotor turning. Kirschfeld and Lutz (1974) used localized stimulation of retinal cells and found that receptors R1 and R6 from one ommatidium could mediate an optomotor turning response while R7 and/or R8 could inhibit it. Mimura (1976) has recorded inhibitory responses in the lamina which could mediate this or other receptor interactions. An R7–R8 interaction, rather than simple summation may be present, though not obvious, in our data. This, as well as Kirschfeld and Lutz's (1974) inhibitory interaction of R7 and/or R8 on R1–6 mediated optomotor turning, present the possibility of color vision in Diptera, a question which has been frequently raised in fly studies. By far the most strategic approach to studying color vision in flies is the recent learning study of Quinn et al. (1974). In this study, data for flies with eye color pigments were reported. Since wavelength-dependent leakage through these screening pigments (Stark and Wasserman, 1974) could influence spatial summation in the eye, these color vision studies do not necessitate the presence of subtractive opponent receptor color vision interactions.

Supported by NSF grants BMS-74-12817 and BNS-76-11921. We thank D. Lakin, A. Ivanyshyn, R. Greenberg, M. Chapin, D. Fritzberg, and W. Hamilton for technical assistance. We also thank R. Schümperli for suggestions, for his permission to redraw his data and for confirming the conversions we made.

## References


Autrum, H., von Zwehl, V.: Die spektrale Empfindlichkeit einzelner Sehzellen des Bienenauges. Z. vergl. Physiol. **48**, 357–384 (1964)

Bertholf, L.M.: The extent of the spectrum for *Drosophila* and the distribution of stimulative efficiency in it. Z. vergl. Physiol. **18**, 32–64 (1932)

Eckert, H.: Die spektrale Empfindlichkeit des Komplexauges von *Musca* (Bestimmung aus Messungen der optomotorischen Reaktion). Kybernetik **9**, 145–156 (1971)

Frisch, K. von: Bees: their vision, chemical senses and language. Ithaca (N.Y.) and London: Cornell University Press 1971

Harris, W.A., Stark, W.S.: Hereditary retinal degeneration in *Drosophila melanogaster*: a mutant defect associated with the phototransduction process. J. gen. Physiol. **69**, 261–292 (1977)

Harris, W.A., Stark, W.S., Walker, J.A.: Genetic dissection of the photoreceptor system in the compound eye of *Drosophila melanogaster*. J. Physiol. (Lond.) **256**, 415–439 (1976)

Heisenberg, M., Götz, K.G.: The use of mutations for the partial degradation of vision in *Drosophila melanogaster*. J. comp. Physiol. **98**, 217–241 (1975)

Hu, K.G., Stark, W.S.: Control of phototaxis by specific receptors in *Drosophila*. In: ARVO '77 Association for Research in Vision and Ophthalmology Meeting. (1977) (Abstract)

Kaiser, W., Liske, E.: Die optomotorischen Reaktionen von fixiert fliegenden Bienen bei Reizung mit Spektrallichtern. J. comp. Physiol. **89**, 391–408 (1974)

Kirschfeld, K., Lutz, B.: Lateral inhibition in the compound eye of the fly *Musca*. Z. Naturforsch., **29**, 95–97 (1974)

Mimura, K.: Some spatial properties in the first optic ganglion of the fly. J. comp. Physiol. **105**, 65–82 (1976)

Quinn, W.G., Harris, W.A., Benzer, S.: Conditioned behavior in *Drosophila melanogaster*. Proc. nat. Acad. Sci. (U.S.A.) **71**, 708–712 (1974)

Rockwell, R., Seiger, M.: Phototaxis in *Drosophila* : A critical evaluation. Am. Scientist **61**, 339–345 (1973)

Schümperli, R.: Evidence for colour vision in *Drosophila melanogaster* through spontaneous phototactic choice behavior. J. comp. Physiol. **86**, 77–94 (1973)

Stark, W.S.: Synaptic and receptor potentials as a function of wavelength in normal and mutant *Drosophila*. Masters Thesis, University of Wisconsin, Madison (1970)

Stark, W.S.: The effect of eye colour pigments on the action spectrum of *Drosophila*. J. Insect Physiol. **19**, 999–1006 (1973)

Stark, W.S.: Spectral selectivity of visual response alterations mediated by interconversions of native and intermediate photopigments in *Drosophila*. J. comp. Physiol. **96**, 343–356 (1975)

Stark, W.S.: Sensitivity and adaptation in R7, an ultraviolet photoreceptor in the *Drosophila* retina. J. comp. Physiol. **115**, 47–59 (1977)

Stark, W.S., Hu, K.G.: Sensitivity, adaptation and function of R7, an ultraviolet receptor, in *Drosophila*. In: Neuroscience Abstracts (Society for Neuroscience Sixth Annual Meeting), 1094 (1976) (Abstract)

Stark, W.S., Ivanyshyn, A., Hu, K.G.: Spectral sensitivities and photopigments in adaptation of fly visual receptors. Naturwissenschaften **63**, 513–518 (1976)

Stark, W.S., Wasserman, G.S.: Wavelength-specific ERG characteristics of pigmented- and white-eyed strains of *Drosophila*. J. comp. Physiol. **91**, 427–441 (1974)

Stark, W.S., Zitzmann, W.G.: Isolation of adaptation mechanisms and photopigment spectra by vitamin A deprivation in *Drosophila*. J. comp. Physiol. **105**, 15–27 (1976)

Svaetichin, G., Negishi, N., Fatehchand, R.: Cellular mechanism of a Young-Hering visual system. In: CIBA symposium on color vision (ed. A.V.S. de Reuck, J. Knight), pp. 178–205. Boston: Little, Brown and Co. 1965

Wright, R., Cosens, D.: Blue-adaptation and orange-adaptation in white-eyed *Drosophila*: Evidence that the prolonged afterpotential is correlated with the amount of M580 in R1–6. J. comp. Physiol. **113**, 105–128 (1977)