

Electrophysiological Evidence for Different Colour Receptors in One Ommatidium of the Bee Eye

R. Menzel

Zoologisches Institut TH Darmstadt

(Z. Naturforsch. 30 c, 692–694 [1975]; received May, 23, 1975)

Colour Receptors, Fused Rhabdom, Electrophysiology

Spectral and spatial sensitivity were determined in several retinula cells of the worker bee eye during one penetration with a microelectrode. Pairs of retinula cells were found, which differed in their spectral sensitivity, but had nearly identical fields of view. From this result it is concluded that ommatidia in the worker bee eye are not colour specific, but consist of different colour receptor types. The consequences for the functional organisation of the fused rhabdom are shortly discussed.

The ability of the honey bee to discriminate between colours of wavelengths between 360 and 540 nm^{1–3} is best described by a colour vision system consisting of UV, blue and green receptors. Autrum and v. Zwehl⁴ demonstrated these colour receptor types by intracellular recordings from retinula cells, which then prompted the question of whether the ommatidia are colour specific or whether each ommatidium contains differing colour receptors. Selective adaptation experiments together with fine structural analysis^{5,6} indicated that each ommatidium consists of 4 green receptors, 2 UV, 2 blue and 1 proximal, short UV-receptor. This finding, however, could not be confirmed and several aspects (e.g. differentiation between blue and green receptors, no appearance of blue receptors in the ventral eyepart) were not convincing and in disagreement with behavioural colour discrimination experiments⁸. Selective radial pigment movement in retinula cells in response to chromatic illumination gave evidence for UV and green receptors in one ommatidium⁹, but the results are not as clear cut as in other hymenopteran eyes^{10,11} and did not demonstrate blue receptors.

The knowledge of the composition of the ommatidium is of importance for any functional analysis because the rhabdomeres of each retinula cell in one ommatidium join together to form a fused rhabdom which acts as an uniform light guide¹². We therefore searched for distinctive evidence of different colour receptors in one ommatidium by using electrophysiological techniques.

Requests for reprints should be sent to Prof. Dr. R. Menzel, Fachbereich Biologie (10), Zoologisches Institut der Technischen Hochschule, D-6100 Darmstadt, Schnittspahnstr. 3.

Honey bee "workers" were collected at the hive entrance, mounted on an adjustable balljoint and positioned in the centre of a perimeter device. The dark adapted left eye was illuminated with a light guide (visual angle 45'). Monochromatic light was produced by a 900 W Xenon arc and a high intensity grating monochromator (Schoeffel, GM 250) together with broadband cut-off filters. Conventional electrophysiological recording techniques were used. The KCl-filled glass microelectrodes had a resistance of 100–250 M¹¹.

The retinula cells with their rhabdomeres are fused together and share the same field of view. In the bee eye the acceptance angle is narrow (2.5° at the 50% sensitivity level¹⁴) and the inter-ommatidial angle in the median frontal part of the eye, where the recordings were made, is in the same range¹⁵.

If, as the microelectrode is advanced, cells are encountered whose optical axes lie less than 0.5° apart they can be presumed to lie in the same ommatidium. During experiments the microelectrode was advanced slowly and the tip jumped from one retinula cell to the next. The optical axis for each cell was determined and the *x* and *y* coordinates of the perimeter were noted.

The spectral sensitivity was determined for each cell from one intensity function at, or close to, the most effective wavelength and a spectral scan, with 21 different wavelengths between 300 and 650 nm, at intensities which gave about 50% of the maximal response. In four animals more than 10 retinula cells in one eye were held long enough to allow careful centering of the light source and determination of their spectral sensitivity functions. The example in Fig. 1 comes from one experiment where 31 retinula cells were recorded during 1 penetration. Only those spectral sensitivity functions are shown which come from retinula cells with very close or overlapping fields of view.

Most of the retinula cells are green receptors ($\lambda_{\max} \approx 520$ nm); only a few UV receptors ($\lambda_{\max} \approx 340$ nm) were recorded. Blue receptors ($\lambda_{\max} \approx 420$ nm) were very rarely found. In Fig. 1 eight retinula cells have overlapping fields of view, two pairs of green receptors (Nos. 10 and 11, 16 and 17) one pair of a blue and a green cell (Nos. 6 and 7) and one pair of a UV and a green cell. (Nos. 13 and 14). In the 3 other eyes I found 4 pairs of green cells and 2 pairs of UV and green cells.

This result proves that ommatidia in the worker bee eye are not colour specific but consist of different colour receptor types. The accumulation of recordings from green receptors and from pairs of green photoreceptors with overlapping fields of view



Dieses Werk wurde im Jahr 2013 vom Verlag Zeitschrift für Naturforschung in Zusammenarbeit mit der Max-Planck-Gesellschaft zur Förderung der Wissenschaften e.V. digitalisiert und unter folgender Lizenz veröffentlicht: Creative Commons Namensnennung-Keine Bearbeitung 3.0 Deutschland Lizenz.

Zum 01.01.2015 ist eine Anpassung der Lizenzbedingungen (Entfall der Creative Commons Lizenzbedingung „Keine Bearbeitung“) beabsichtigt, um eine Nachnutzung auch im Rahmen zukünftiger wissenschaftlicher Nutzungsformen zu ermöglichen.

This work has been digitalized and published in 2013 by Verlag Zeitschrift für Naturforschung in cooperation with the Max Planck Society for the Advancement of Science under a Creative Commons Attribution-NoDerivs 3.0 Germany License.

On 01.01.2015 it is planned to change the License Conditions (the removal of the Creative Commons License condition "no derivative works"). This is to allow reuse in the area of future scientific usage.

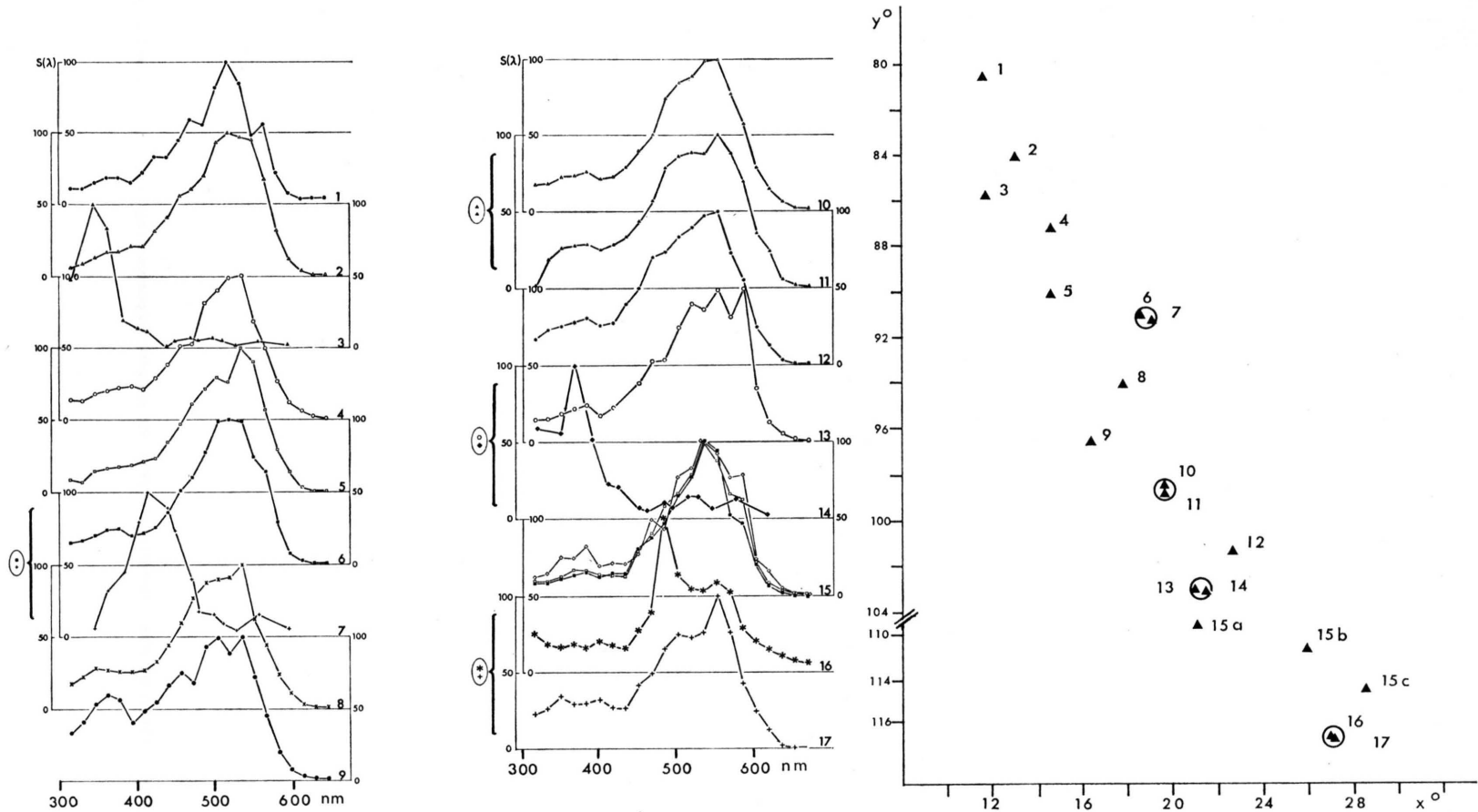


Fig. 1. Spectral sensitivity function of 19 different retinula cells in one eye of the worker bee. All retinula cells had close or overlapping fields of view and were located in the median frontal part of the eye. The retinula cell No. is given in the right corner of each diagram and marks also the abscissa for the retinula cell in question. No. 15 gives three different retinula cells with different fields of view. The retinula cell numbers describe the succession of the recordings. The pair Nos. 6 and 7, 10 and 11, 13 and 14, 16 and 17 (marked with a bracket) have overlapping fields of view. The centers of their acceptance angles were less than $\pm 0.5^\circ$ apart. All other neighbouring retinula cells had their centres of view between 1.5 and 4° apart (these values refer to the vertical large circle of the perimeter, the change in the horizontal circle of the perimeter was small, because the microelectrode was advanced vertically). The differences between the spectral sensitivity functions of the green receptors are not discussed here. Menzel, in preparation).

makes it very likely that green receptors have the highest frequency. In general this is in agreement with the fine structural analysis^{5,6}. The ratio of green: UV: blue receptors, however, differs markedly between the electrophysiological recordings and the fine structural determinations (*e.g.* in Fig. 1 this ratio is 17:2:1 in Gribakin's^{5,6} and Kolb's⁹ experiments: 4:2:2 and 6:2:0, respectively). The reasons for these differences are not yet known. One possibility is that the smaller diameter of UV and blue receptors compared with green receptors reduce the chance of stable, long lasting intracellular recordings.

The consequences of combining different colour receptors into one light guiding structure have been discussed in detail elsewhere^{10,11}. Briefly, the rhabdomers of different colour receptors act as lateral spectral absorption filters to each other. This results in spectral sensitivity functions which are close to the spectral extinction of their photopigment even in long rhabdoms with high total absorption. The ommatidium in the worker bee compound eye is thus capable of supplying "fine grain" colour information.

¹ K. Daumer, *Z. vergl. Physiol.* **38**, 413–478 [1956].

² R. Menzel, *Z. vergl. Physiol.* **56**, 22–62 [1967].

³ O. v. Helversen, *J. Comp. Physiol.* **80**, 439–472 [1972].

⁴ H. Autrum and V. von Zwehl, *Z. vergl. Physiol.* **48**, 357–384 [1964].

⁵ F. G. Gribakin, *Nature* **223**, 639–641 [1968].

⁶ F. G. Gribakin, *Vision Res.* **12**, 1225–1230 [1972].

⁷ O. J. Grundler, *Cytobiol.* **9**, 203–220 [1974].

⁸ R. Menzel, *The Compound Eye and Vision in Insects*, G. A. Horridge, ed., Oxford University Press 1975.

⁹ G. Kolb and H. Autrum, *J. Comp. Physiol.* **94**, 1–6 [1974].

¹⁰ F. Menzel and R. Knauth, *J. Comp. Physiol.* **86**, 125–138 [1973].

¹¹ R. Menzel and M. Blakers, *Cytobiol.*, in press.

¹² A. W. Snyder, R. Menzel, and S. B. Laughlin, *J. Comp. Physiol.* **87**, 99–135 [1973].

¹³ R. Menzel and A. W. Snyder, *J. Comp. Physiol.* **88**, 247–270 [1974].

¹⁴ S. B. Laughlin and G. A. Horridge, *Z. vergl. Physiol.* **24**, 329–339 [1971].

¹⁵ J. del Portillo, *Z. vergl. Physiol.* **23**, 100–145 [1936].