

In: Wiese K, Gribakin FG, Popov AV & Renninger G (eds)
Sensory Systems of Arthropods, pp 211-218
1993 Birkhäuser Verlag Basel/Switzerland

BEE COLOUR VISION - THE OPTIMAL SYSTEM FOR THE DISCRIMINATION OF FLOWER COLOURS WITH THREE SPECTRAL PHOTORECEPTOR TYPES ?

Lars Chittka, Michail Vorobyev*, Avi Shmida** and Randolf Menzel

Institut für Neurobiologie, Freie Universität Berlin,
Königin-Luise-Str.28-30, 1000 Berlin 33, Germany

* Sechenov Institute of Evolutionary Physiology & Biochemistry,
Thorez prospect 44, 194223 St. Petersburg, Russia

** Hebrew University, Department of Evolutionary Ecology,
Jerusalem 91904, Israel

SUMMARY

Two approaches are presented to measure the quality of trichromatic colour vision of Hymenoptera in terms of its suitability to discriminate between the colours of flowers. Templates of photoreceptor spectral sensitivity curves are shifted along the wavelength scale to search for the optimal set of three spectral receptor types. The criteria for optimality are: 1. maximal perceptual differences between all flower colours; and 2. a maximal number of distinguishable flower colours. We show that the set of three photoreceptor colour types as measured in a large number of Hymenoptera is optimally suited to the task of discriminating floral hues.

INTRODUCTION

Different animal species have different colour vision systems, and it is likely that the features of these systems reflect evolutionary adaptations to different classes of environmental colour signals. In this case, the quality of a particular colour vision system can be assessed in terms of its ability to discriminate between coloured objects of the respective class.

In flower-visiting Hymenoptera, the evolutionarily significant objects are comparatively easy to pin-point. Plants contain the major nutrition - pollen and nectar - for these insects, and they advertise these rewards by means of species-specific and conspicuous signals, the flowers (Feinsinger 1983, Kevan and Baker 1983). Bees have to make economic choices

within a multitude of different flower species with different colours and rewards. Generally speaking, selection will thus favour such flower-visitors that are able to learn the features of any plant species and distinguish it from all others in a community. Accumulating confusions of the labels of floral food sources may result in a decrease in foraging efficiency, and thus in a reduced fitness of the pollinator. Colour is a most important signal to guide the learning and choice behaviour of the insect (Kevan and Baker 1983). Consequently, the ability to discriminate colours is particularly important for Hymenoptera in the context of their food choices. Here, we present two approaches to investigate the question whether it might be possible to deduce the properties of bee colour vision from the characteristics of flower colour signals.

RESULTS

The spectral reflectance functions (300 to 700nm) of 180 flower colours in Israel were measured (methods and results in Menzel and Shmida, in press). We determined the set of photoreceptor colour types that yields an optimal distinction of these flower colours in a generalized colour opponent space, the colour hexagon (Chittka 1992). For this purpose, spectral sensitivity curves were modelled after Maximov (1988) and shifted systematically along the wavelength scale. The assumptions about the adaptation states of these photoreceptors are described by Chittka and Menzel (1992). If the wavelength position of a photoreceptor is altered, the two-dimensional spread of colour loci in the colour space changes (Fig.1). Correspondingly, the perceptual distances between colours change. The photoreceptor set is optimal for discrimination of objects if the perceived differences between all objects to be discriminated are maximal.

In each of three variations, one receptor was varied in 10nm steps, and the two others were held constant at the wavelength positions where they occur in Hymenoptera. For every such combination of photoreceptors all differences between flower colours in the hexagon are calculated and summed up (Fig.2). The resulting optima for these sums of perceptual differences at 330, 430 and 550nm agree well with the photoreceptor wavelength positions as found in the eyes of Hymenoptera (Fig.2, inset).

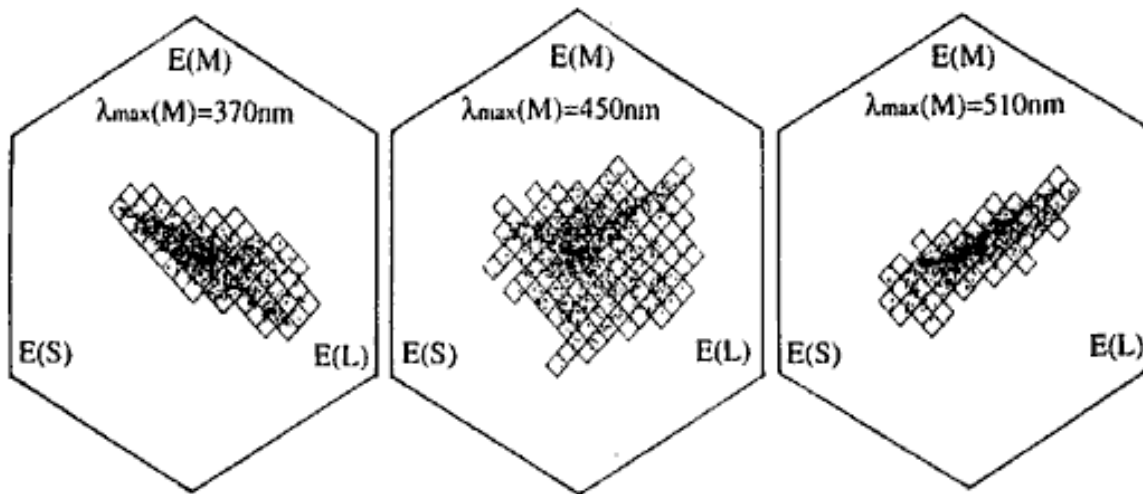


Fig. 1. The loci of 1144 flower and leaf colours in the colour hexagon, depending on which set of spectral photoreceptors is employed. Three examples are given; in all of them, the S (short wave)- and L (long wave)- receptors have λ_{max} values of 340 and 540nm. The position of the M (middle wave)- receptor is varied (values see figure). Each point marks the colour locus assigned to one spectral reflection function. Each square with a diagonal of 0.1 that is occupied by floral colour loci is marked. Colour loci on the outline of each given cell have equal distances from the center of this cell in a city-block metric (Backhaus 1991). The number of such squares is proportional to the number of colours that can be discriminated at a defined level of accuracy.

Similar results are obtained if two or three receptor template curves are varied (Chittka and Menzel 1992).

Govardovskij and Vorobyev (1989) introduced a somewhat handier measure of the quality of a colour vision system. Depending on the type of spectral photoreceptors, they calculated absolute numbers of distinguishable surface colours for birds and turtles. This concept can be readily applied to bees and flower colours. How many flower colours can a bee tell from each other? How does this number depend on the wavelength position of the photoreceptors? The following preliminary results are an excerpt from a current study by Vorobyev (in prep). They are based on the spectral reflectance curves of 1144 flowers and leaves from Israel, Norway, Brazil and the Austrian Alpine flora.

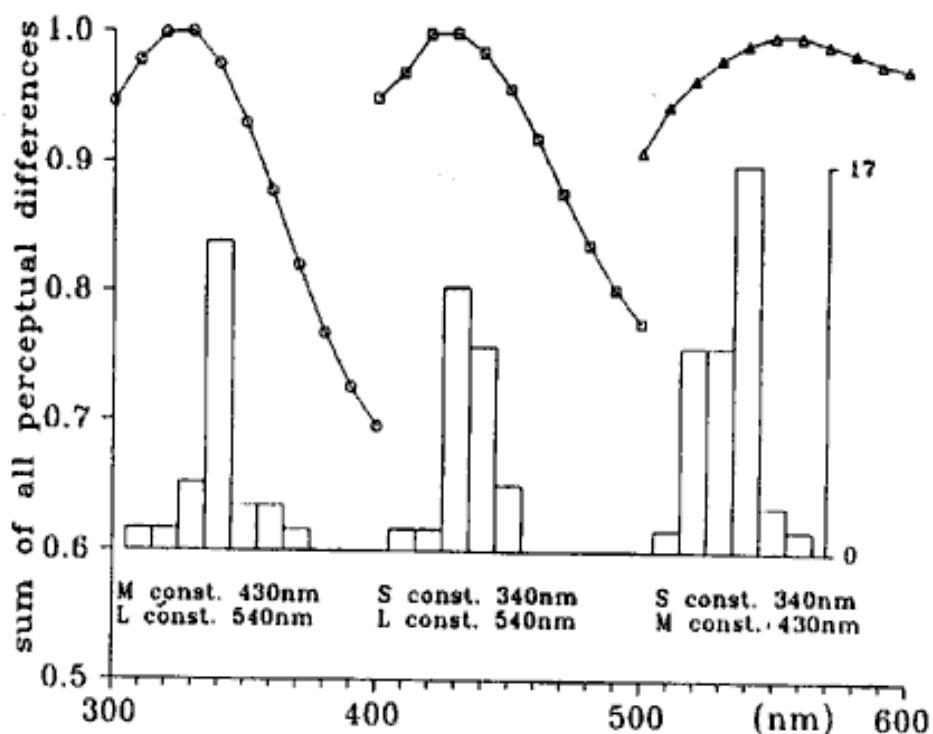


Fig. 2. The determination of an optimal photoreceptor set on the basis of maximal colour hexagon distances between colours of the Israeli flora. In each of three variations, two receptors were clamped at the wavelength positions where they most frequently occur in Hymenoptera (λ_{max} =340, 430, 540nm, see inset), and the third was shifted in 10nm steps from 300 to 400 nm, from 400 to 500 nm or from 500 to 600 nm. The spread of 180 flower colours was determined depending on which set of spectral photoreceptors was used. For every such set all the hexagon distances between every pair of colour signals were determined. All of these distances were summed up, and plotted in the diagram such that the maximum of each curve equals one. The inset shows the absolute number of photoreceptors recorded at every given λ_{max} for 40 different species of Hymenoptera (Peitsch et al. 1992). The calculated optimal photoreceptors thus deviate from the most frequent "real" receptors by maximally 10nm.

For a determination of the number of distinguishable colours, one needs a criterion of how well colours should be discriminated. Based on behavioural colour discrimination tests with several Hymenoptera (Chittka et al. 1992) it can be shown that a colour hexagon difference of 0.1 between two given colour stimuli will be discriminated with 70% accuracy

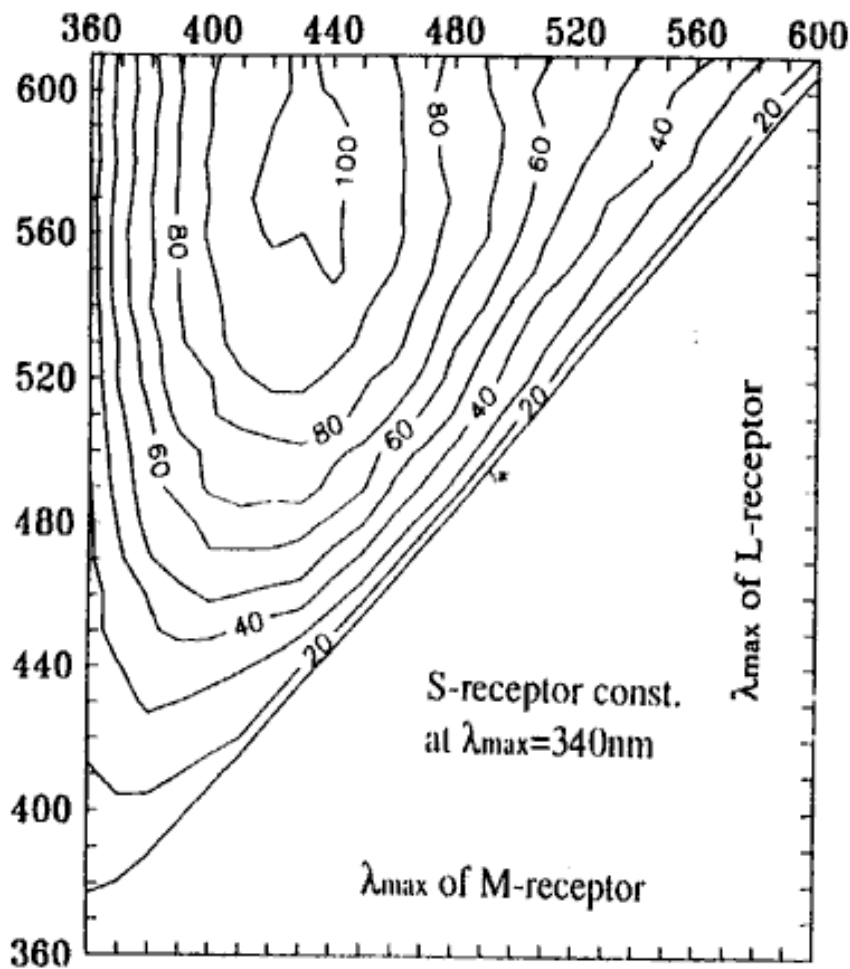


Fig. 3. The determination of an optimal photoreceptor set on the basis of the number of distinguishable colours. The S-receptor was set constant at $\lambda_{\max}=340\text{nm}$. The wavelength ranges over which the M- and L-receptors are varied in 10nm steps are given by the values next to the chart. For every combination of three photoreceptor colour types, the number of squares (diagonal of 0.1 in the colour hexagon, see Fig.1) covered by flower colour loci is counted. For the M-receptor an optimum is found at around 430nm. The L-receptor reaches a plateau at 550nm.

in a dual choice test that follows training to one of these two colours (Vorobyev and Chittka, in prep.). In terms of a city-block metric concept (Backhaus 1991), the number of distinguishable hues equals the number of squares occupied by flower colours (Fig.1). According to the criterion defined above, the diagonal of each square measures 0.1 in dimensionless

hexagon distance units. Consequently, the number of distinguishable flower colours can simply be determined by counting the number of squares that contain colour loci of flowers, depending on which photoreceptors are used. If an application of the colour hexagon to a large number of species is desired, the Euklidian metric might be more appropriate (Chittka 1992). The number of distinguishable hues in a Euklidian metric system is calculated by dividing the area covered with floral colour loci by the area of circular cells with a diameter of the defined threshold distance (0.1). Thus, the results differ simply by a linear factor, i.e. the number of distinguishable colours in a Euklidian space is 0.636 times the one in a city-block space.

The S-receptor was set to a constant value of $\lambda_{\max}=340\text{nm}$. Both the M- and L-receptors were shifted across the wavelength scale from 360 to 600nm, and for each combination the number of distinguishable hues is calculated (Fig.3). Variations including the position of the S-receptor have yet to be performed.

Thus, in the optimal case ($\lambda_{\max}(\text{M})=430$ and $\lambda_{\max}(\text{L})\geq 550\text{nm}$) a bee can discriminate approximately 100 different flower colours with an accuracy of 70% under the assumption of a city block metric (64 in a Euklidian space). Again, it appears that the most frequent hymenopteran M- and L-receptors ($\lambda_{\max}(\text{M})=430$ and $\lambda_{\max}(\text{L})=540\text{nm}$) are very close to optimal from this criterion. All other receptor combinations would reduce the number of distinguishable colours. Only the L-receptor may be shifted to longer wavelengths without a significant loss of information.

DISCUSSION

With the presented model calculations, we have shown that the bees set of spectral receptors is practically optimal for the discrimination of flower colours and that a better one can hardly be constructed. The approaches that yield this conclusion are based on precise measurements of the floral colour signals and take into account the detailed knowledge of the absorption properties of insect photoreceptors and their characteristics of light adaptation.

Did evolution, however, proceed along the same lines as our computer programs to optimize the bees colour vision? It is equally possible that our results simply reflect the selective pressure exerted by the bees on the

colours of flowers, and that, as a consequence, it is possible to derive the bees receiver features from the signals directed to this system. There are examples of insect trichromats which do not feed on flowers, but have similar sets of photoreceptor colour types as bees do (e.g. *Hemicordulia tau*, Odonata (Laughlin 1975): λ_{\max} =350, 440 and 510nm; *Gryllus bimaculatus*, Orthoptera (Zufall et al. 1989): λ_{\max} =332, 445 and 515nm). In these cases, only the L-receptor would have to be shifted to significantly longer wavelengths in order to generate an optimal flower coding system. Thus, the bees colour vision might have been evolutionarily "pre-tuned" according to criteria other than flower discrimination and flowers might then simply have occupied the ecological niches offered to them in the bees colour space.

So, we are left with the following questions: Can the bees (and other insects) colour vision be explained in terms of the discrimination of non-floral objects such as green leaves? Preliminary model calculations indicate that this is at least partially possible (Chittka, in prep.). Were the photoreceptors adjusted to tasks other than object discrimination (see Chittka and Menzel 1992 for some suggestions)? Or do the clusters of the wavelength positions of photoreceptors in insects reflect constraints of the molecular biology of the photopigments (Goldsmith 1991)? Why do most Hymenoptera not possess a red receptor, even though it exists in some species (Peitsch et al. 1992) and although there is information offered by floral signals in this spectral range (Chittka and Menzel 1992)?

An interesting, but entirely separate question is whether colours of sympatric flowers have reached an optimum in terms of being discriminated from each other by trichromatic bee colour vision, such as to favour pollinator constancy (Feinsinger 1983, Chittka and Menzel 1992). This would involve an investigation of distributions of flower colours in many different habitats and a proof that signals of different species influence each other to a degree that is significantly different from random.

REFERENCES

- Backhaus, W. (1991) Colour Opponent Coding in the Visual System of the Honeybee. *Vision Res.* 31: 1381-1397
- Chittka, L. (1992) The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J. Comp. Physiol. A* 170: 533-543

- Chittka, L., Beier, W., Hertel, H., Steinmann, E., Menzel, R. (1992) Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in hymenoptera. *J. Comp. Physiol. A* 170: 545-563
- Chittka, L. and Menzel, R. (1992) The evolutionary adaptation of flower colours and the insect pollinators colour vision. *J. Comp. Physiol.* 171: 171-181
- Feinsinger, P. (1983) Co-evolution and pollination. In Futuyma, D.J. and Slatkin, M. (eds.): *Co-evolution*. Sunderland, Mass.: Sinauer, 282-310
- Goldsmith, T.S. (1991) The evolution of visual pigments and colour vision, in Gouras, P. (ed.): *The perception of colour*. London: MacMillan Press. 62-89
- Govardovskij, V.I. and Vorobyev, M.V. (1989) The role of coloured oil droplets in colour vision. *Sensory systems (Sensornye systemy)* 3: 150-159
- Kevan, P.G. and Baker, H.G. (1983) Insects as flower visitors and pollinators. *Ann. Rev. Entomol.* 28: 407-453
- Laughlin, S.B. (1975) Receptor function in the apposition eye: An electrophysiological approach. In: *Photoreceptor optics*. Eds: Snyder, A.W. and Menzel R. pp479-498. Berlin-Heidelberg-New York: Springer Verlag
- Maximov, V.V. (1988) An approximation of visual absorption spectra. *Sensory systems (Sensornye systemy)* 2: 3-8
- Menzel, R. and Shmida, A. (in press). The ecology of flower colours and the natural colour vision of insect pollinators. *The Israeli flora as study case. Biological reviews*
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D.F. and Menzel, R. (1992). The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* 170: 23-40
- Zufall, F., Schmitt, M. and Menzel R. (1989) Spectral and polarized light sensitivity of photoreceptors in the compound eye of the cricket (*Gryllus bimaculatus*). *J. Comp. Physiol. A*: 164: 597-608