

The evolutionary adaptation of flower colours and the insect pollinators' colour vision

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Summary. The evolutionary tuning between floral colouration and the colour vision of flower-visiting Hymenoptera is quantified by evaluating the informational transfer from the signalling flower to the perceiving pollinator. The analysis of 180 spectral reflection spectra of angiosperm blossoms reveals that sharp steps occur precisely at those wavelengths where the pollinators are most sensitive to spectral differences. Straight-forward model calculations determine the optimal set of 3 spectral photoreceptor types for discrimination of floral colour signals on the basis of perceptual difference values. The results show good agreement with the sets of photoreceptors characterized electrophysiologically in 40 species of Hymenoptera.

Key words: Colour vision – Flower colours – Evolution – Hymenoptera – Pollination ecology

Introduction

Many insects such as social and solitary bees are highly dependent on the pollen and nectar diet offered by flowers. Since flowers are unreliable and scattered food sources, the insects should be equipped with learning capacities and sensory systems that favour an efficient foraging strategy. All Hymenoptera so far tested have the ability to learn colours as a stimulus associated with a reward (von Frisch 1914, 1967; Mazokhin-Porshniakov 1962; Menzel 1979; Dukas and Real 1991; Menzel and Backhaus 1991; Chittka et al. 1992). This ability allows them to tell known from unknown flowers and, amongst the familiar ones, to discriminate profitable food sources and inefficient ones. An essential prerequisite for this capacity is a colour vision system that allows for optimal discrimination between flowers of different species.

Many angiosperm plant species compete with one another for animals as pollen vectors (Darwin 1876;

Kevan 1978; Feinsinger 1983; Rathke 1983; Waser 1983, 1986). For pollen to be effectively transferred, the plants generally "have an interest" that an individual pollinator visits con-specific flowers *exclusively*. The learning capacities of Hymenoptera offer a great opportunity in this regard. Making use of this, the plant does not have to restrict the pollinator type by means of morphological adaptations, which is may be an evolutionary deadlock and can also be rather insecure if it makes the plant exclusively dependent on one pollinator species. Instead, the flower has the possibility to "advertise" its reward by means of a species-specific label, which has two major consequences: 1. They potentially address a large spectrum of pollinator *species*. 2. *Individual* visitors that have experienced this particular flower as rewarding will have a high tendency to visit flowers of the same species more frequently, thus favouring an effective pollination. Hence, the flower signals must not only be well detectable, but also easy to distinguish from those of competing species (Daumer 1956; von Frisch 1914, 1967; Menzel 1967; Kevan 1978; Waser 1986).

The relationship between floral colours and the pollinators' colour vision may thus be regarded as a signal-receiver system whose components are likely to be evolutionarily adapted to each other (Menzel and Backhaus 1991) so as to allow optimal discrimination of flowers. Such processes of evolutionary tuning take place within the scope of certain physical and biological constraints (Lythgoe 1972, 1979; Lythgoe and Partridge 1989; Goldsmith 1991). On the signal side, the limits are set by the possibilities of obtaining flower colours through combinations of the available pigments and surface structures. With regard to the "receivers", the development is constrained by the optical design of compound eyes, the absorption properties of the photopigments, the mechanisms of signal transduction and light adaptation, and the neural processes evaluating the receptor of signals (Snyder et al. 1973; Menzel 1979; Laughlin 1981; Burkhardt 1983; Stavenga 1989).

The spectral reflection functions of angiosperm blossoms can be easily measured. The neural code underlying

colour discrimination has recently been identified for the honeybee (Backhaus 1991). The concept was successfully extended to several other Hymenoptera, these including social and solitary bees as well social and solitary wasps (Chittka et al. 1992; Chittka and Lunau, 1992). A standard measure of perceptual colour difference (colour hexagon distance) was developed (Chittka 1992) and found applicable to all the 10 species investigated.

This model of colour perception allows the assignment of numerical values to perceived colour differences between any two colour stimuli under a given spectral illumination. These values may be calculated for any trichromatic colour vision system with known receptor spectral sensitivities. We search for the set of spectral photoreceptor types which yields an optimum of discrimination between natural flower colours in an insect's system of colour perception.

Materials and methods

Spectral measurements of flowers. The spectral reflection functions of floral petals were measured from 300 to 700 nm by means of a flash photometer (resolution 1 nm). The white standard was a freshly pressed pellet of dry BaSO₄. The circular flash bulb illuminated the probe (\varnothing 10 mm) under an angle of 45°, and a light guide transmitting the light to the monochromator collected the reflected light under an angle of 0°. If the structures to be measured were smaller than \varnothing 10 mm, many petals were arranged like fish scales, such that only the identically coloured parts were exposed to the photometer (see Menzel and Shmida, in press, for details).

We selected the Israeli flora as a study case, because the interactions between angiosperm plants and their pollinators have been particularly well studied there (see Menzel and Shmida, in press, for review). As practically everywhere else, Hymenoptera have been found to be by far the most important flower visitors in Israel (Dukas and Shmida, in press).

It is important to note that only approximately 10 out of more than 1200 Israeli species of Hymenoptera are specialists (oligolectic) that appear to have an innately fixed preference to forage only on a restricted number of plant species (Shmida, personal communication). All others are generalists in the sense that individuals of the same species are found to visit several plant species. As mentioned above, in a flora dominated by generalists with learning capacities, there is a high selective pressure for plants to use their blossoms for species-specific labelling, i.e. to differ from each other with regard to the perception of the pollinators.

For all the following considerations, we evaluated a sample of 180 spectral measurements from plants that are known to be most predominantly visited by Hymenoptera.

Modelling of photoreceptor spectral sensitivity functions. We will proceed to extract an optimal photoreceptor set from the flower spectra by systematically shifting the spectral sensitivity curves along the wavelength scale. For this purpose, templates of photoreceptor spectral sensitivity curves are modelled according to Maximov (1988). This procedure is appropriate because of the structure of the fused rhabdom in Hymenoptera. The mutual filtering effects of the different visual pigments (rhodopsins) packed together in one light guiding structure results in spectral sensitivity functions of the single receptors which are very close to the spectral absorbance of a thin layer (Snyder et al. 1973). Consequently, the spectral sensitivity functions measured intracellularly with electrophysiological techniques correspond closely to the spectral absorbance of the respective photopigments (Menzel et al. 1986) although small deviations are found at scrutinized inspection (Gribakin 1988; Stavenga and Schwemer 1984). In this study, we do not

attempt to test whether and how strong these deviations affect the perceptual measures of colour vision. A discussion with regard to this point can be found in Menzel and Backhaus (1991), Peitsch et al. (1992). Since the spectral sensitivity functions follow a rhodopsin template function (Maximov 1988) closely, it is appropriate to characterize each function by its λ_{\max} value. The long wavelength photopigment templates ($\lambda_{\max} > 500$ nm) had to be corrected manually in the short wavelength part, because they deviate systematically from all measured spectral sensitivity functions in the uv ($\lambda < 400$ nm). The correction was performed such that it gave the best fit to a large number of spectral sensitivity measurements of photoreceptors in 40 species of Hymenoptera (Peitsch et al. 1992).

Calculation of photoreceptor excitations. The procedure for calculating the graduate potential in a photoreceptor with a known spectral sensitivity function $S(\lambda)$ stimulated by a given stimulus reflection curve $I(\lambda)$ which is illuminated by a light with the spectral composition $D(\lambda)$ is reviewed in detail by Backhaus and Menzel (1987), Chittka et al. (1992). The relative quantum flux P is defined by

$$P = R \int_{300}^{700} I(\lambda) S(\lambda) D(\lambda) d\lambda. \quad (1)$$

The coefficient R is adjusted such that it will yield a half maximal excitation (E in Eq. 2) in the photoreceptor when it is stimulated by the light reflected from the adaptation background (Laughlin 1981), following a von Kries (1905) type coefficient law.

We assume the receptors to be adapted to a background reflection function averaged from the reflections of various leaves and anorganic materials (sand and stones) found in close proximity of the plants of which the measurements were taken (Fig. 1, dashed line). The spectral illumination curve used in all the model calculations is the normfunction D65 (clear sky, Fig. 1, solid line).

The non-linear transfer function relating the receptor voltage signal (excitation E) with the quantum flux P follows Eq. 2 (Lipetz 1971; Backhaus and Menzel 1987, for reviews):

$$E = P^n / (P^n + 1). \quad (2)$$

The exponent n depends on the species in question and slightly on the adaptation state (see Backhaus and Menzel 1987; Chittka et al. 1992, for details).

As mentioned above, the adaptation process is assumed to adjust the sensitivity such that the excitation in each receptor will be half maximal for the light reflected from the background (Laughlin 1981). This regulation may not hold under the extreme low light

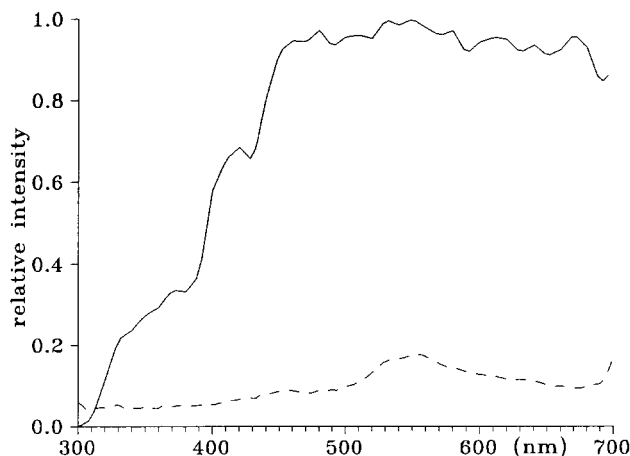


Fig. 1. The dashed line marks the spectral reflection of the background to which the photoreceptors are assumed to be adapted in the model calculations. This curve is averaged from the reflection functions of several leaves, sand and stones found in close vicinity of the flowers measured. The solid curve corresponds to the spectral composition of the daylight normfunction D65