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More than colour attraction: behavioural functions of flower patterns

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Flower patterns are thought to influence foraging decisions of insect pollinators. However, the resolution of insect compound eyes is poor. Insects perceive flower patterns only from short distances when they initiate landings or search for reward on the flower. From further away flower displays jointly form larger-sized patterns within the visual scene that will guide the insect's flight. Chromatic and achromatic cues in such patterns may help insects to find, approach and learn rewarded locations in a flower patch, bringing them close enough to individual flowers. Flight trajectories and the spatial resolution of chromatic and achromatic vision in insects determine the effectiveness of floral displays, and both need to be considered in studies of plant–pollinator communication.

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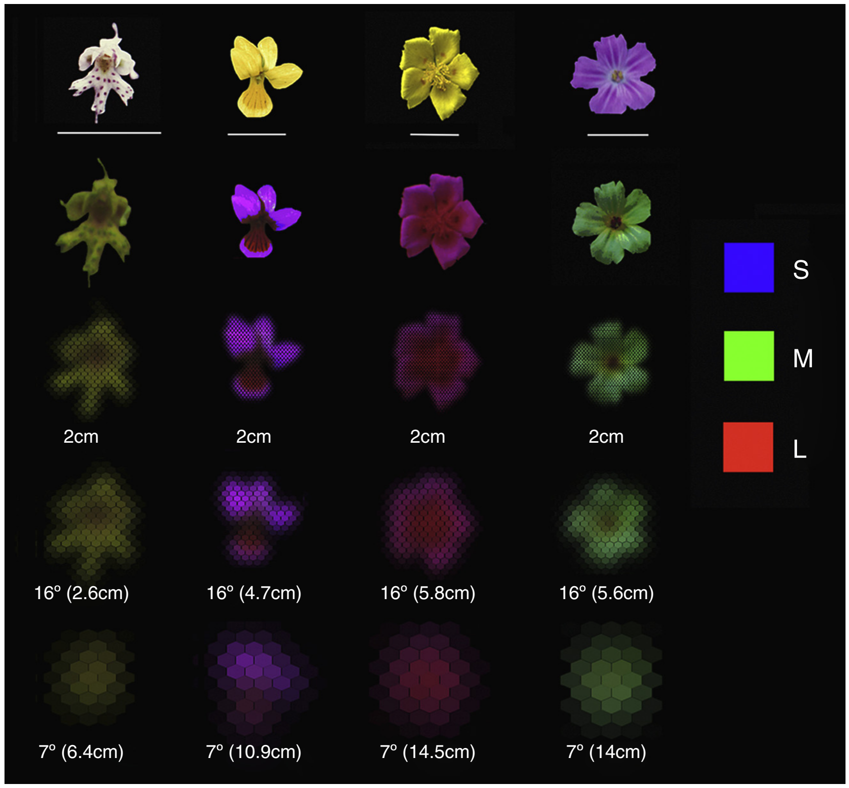
Introduction

Visual information is indispensable for insect pollinators to locate, choose and interact with flowers. However, insect vision is constrained by the poor optical resolution of their small compound eyes, which is about a hundred times lower than that of our single-lens eye [1]. Unlike single-lens eyes, which are able to focus on objects at different distances, insect eyes have the same angular resolution at far and close distances. Therefore, insects are unable to resolve spatial details of distant objects, though they can use vision at extremely close distances. Theoretical analysis of the optical resolution of insect eyes demonstrates that most flower patterns can be resolved only when the insect is millimetres away [2] (Figure 1). Hence small-sized flower patterns do not play a role when insects approach flowers from some distance, as spatial details simply cannot be optically resolved. Resolution of chromatic vision is predicted to be lower than the eye's optical resolution. Different spectral types of photoreceptors that contribute to colour coding are randomly located across the eye [3]. Hence, chromatic vision requires that signals from more than one ommatidium are integrated which reduces the resolution below the limit set by the optics of the eye [4].

Under dim light conditions the spatial and temporal resolution of insect vision decreases further in order to improve contrast sensitivity. Many nocturnal insects, such as moths and beetles, have compound eyes with superposition optics, which confer higher sensitivity but lower spatial resolution than the apposition eyes of most diurnal insects. Several species of night-active bees are special in possessing diurnal-type apposition eyes with sufficient sensitivity to allow visually-guided foraging in twilight, and even during the night [5••]. The contrast sensitivity of such eyes can be enhanced by neural mechanisms, and anatomical evidence suggests that nocturnal bees sum signals from many ommatidia, albeit with the necessary reduction in spatial resolution [6]. Vision becomes slower under low light levels, due to temporal summation of receptor and neural signals that can occur in both types of eyes, and affect the insect's flight speed and trajectories [7,8,9••]. Interestingly, some nocturnal insects have not sacrificed colour vision in order to increase their visual sensitivity and can identify flowers on the basis of their colours even during moonless nights [10,11].

Insect views of flowers differ fundamentally from ours, and human observers usually overestimate the signalling distance range and functions of floral displays [e.g. 12]. The low spatial resolution of insect eyes defines their perception of flower colours, shapes and patterns. Behavioural experiments confirm that insects cannot resolve small objects or small-scaled variations of shapes and patterns over long distances. For instance, the detection limit for single-coloured discs is 5° of angular size in honeybees, around 2° in large-sized bumblebees and 1° in swallowtail butterflies, which can be related to differences in eye size [13,14,15•]. For a 1 cm flower, this corresponds to a viewing distance of 11–57 cm, respectively. Dissectedness of the outline shape in flower-like targets impairs the detection range [16], as predicted by the optical model of the honeybee eye. The behavioural resolution of chromatic vision is even worse — honeybees

Figure 1



Flowers through bee eyes. Shown are pattern displays of small flowers (1 cm scale) in human colours (first row) and 'bee colours' (second row, high spatial resolution), for methods see [2,29]. From left to right: *Traunsteinera globosa, Viola biflora, Helianthemum nummularium, Geranium robertianum.* Spectral sensitivities of the S, M and L-receptors of honeybees (peak sensitivities 344 nm, 436 nm, 556 nm) were used to calculate quantum catches in each pixel of the multispectral images. To show 'bee colours' (second row) quantum catches were converted into RGB values for the three primary monitor colours (see legend). The third row shows the images of single flowers projected onto the ommatidial lattice of the honeybee eye at a close distance (2 cm). Images in the fourth and lowest row simulate views at distances where the flower subtends a visual angle of 16°, which is above the chromatic threshold, or 7°, which is below the chromatic threshold (and approximately at the detection limit, within the range of the achromatic (brightness) visual system). Note that above the chromatic threshold, at short distances, only larger-sized patterns are optically resolved. Visually contrasting small ornaments or flower parts are visible when the insect is already on the flower and invisible during its approach flight (shown here for a distance of 2 cm at which a bee prepares for landing).

cannot detect and discriminate targets on the basis of chromatic cues if they subtend a visual angle less than 13–15° [17,18]. As viewing distances vary with an insect's movements, the appearance of flowers will change considerably, and consequently the insect must be able to rely on different visual cues when foraging and navigating in flower patches. To evaluate the functions of floral displays it is therefore not only important to know how they are resolved and processed by the visual system of an insect pollinator but to also consider an insect's flight trajectory at different distances from flowers.

Why are flower patterns so widespread and diverse?

It is usually assumed that flower patterns increase the diversity of floral displays and help pollinators to discriminate between flowers and to identify the best-rewarding ones. However, when taking into account the poor resolution of compound eyes and typically small sizes of individual floral displays, it is evident that flower patterns can be seen by an insect and influence its behaviour only when it is already close to the flower, initiating a sequence of motor actions that lead up to landing and interactions with the flower. In that phase flowers can use patterns to exploit visuo-motor responses guiding an insect's movement [19,20] to optimise pollen transfer and reduce potential damage from handling of the flower by the insect.

To communicate with insect pollinators over a distance, flowers must increase individual display sizes considerably or contribute to shared displays in inflorescences, mass displays or multi-species patches (Figure 2). Shared displays in a scene can produce effective signals with