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Honey Bees: Photoreceptors Participating in Orientation Behaviour to Light and Gravity*

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Summary. The ability of honey bees to dance compromise directions when confronted with conflicting light and gravity references was used to determine their spectral sensitivity. The action spectrum has peaks at 450 nm and 550 nm and thus indicates the contributions of the blue and green receptors of the bees' compound eyes. There is no obvious contribution from the UV receptors. The dance directions indicate that blue and yellow-green light is regarded as sunlight. UV light seems not to be so interpreted, though it clearly influences the bees' orientation to gravity, if it is polarized. This result is consistent with our earlier findings which demonstrated that the bees' 350 nm receptors are used as detectors of blue skylight rather than sunlight. Because the receptor contributions differ, there is a clear distinction between the sun compass behaviour apparent in the dances and the phototaxis responses observed in other contexts.

Introduction

Light and gravity serve as two interchangeable reference stimuli in the orientation of the honey bee waggle dance (see von Frisch, 1967, for summary). Inside the dark hive a bee uses gravity for orientation, translating the food-to-sun angle into a waggle angle with respect to the upward direction on an inclined comb surface. On the other hand, bees also dance in the sun on the horizontal alighting board. Here the food-to-sun angle is transformed directly into a waggle angle with respect to the sun: the bee waggles in the direction of the food source. For experimental purposes the latter situation can be simulated by using an artificial light source in place of the sun and setting the combs on which the dances occur horizontally. If the light source emits light of wavelengths longer than 410 nm (i.e. blue, yellow) the bee dances as if the direction of the light source were the direction of the sun. However, if the light source emits only ultraviolet light (between 300 and 400 nm) then the animal dances in the opposite direction – indicating that it interprets a spot of UV light as an area of the sky in the opposite direction of the sun – "anti-sun orientation" (Edrich, 1977b, Edrich et al., 1979).

On an inclined surface, the honey bee selects a compromise direction if it can see a light source to the side of the vertical. The selected direction depends on the component of gravity in the dance plane (which varies with its angle of inclination), on the brightness of the light source and on the angle between the directions of light and gravity (von Frisch, 1967; Edrich, 1972, 1977a). The bee's compromise dance behaviour under such competing light and gravity references provides an experimental means of evaluating the animal's spectral sensitivity to light within this behavioural task.

We have used this method to determine whether all three colour receptor systems of the honey bee contribute positional information for the interaction with gravity. In particular we have examined the role of the UV receptors in this interaction, both as colour and as polarization detectors.

Materials and Methods

The experiments were conducted near Freiburg using a colony of locally-bred honey bees (predominantly from the subspecies *Apis mellifera carnica*) housed in a two-framed observation hive that was kept in a wooden experimental hut. The bees could leave the hive for free flight by passing through a flexible tube 200 mm

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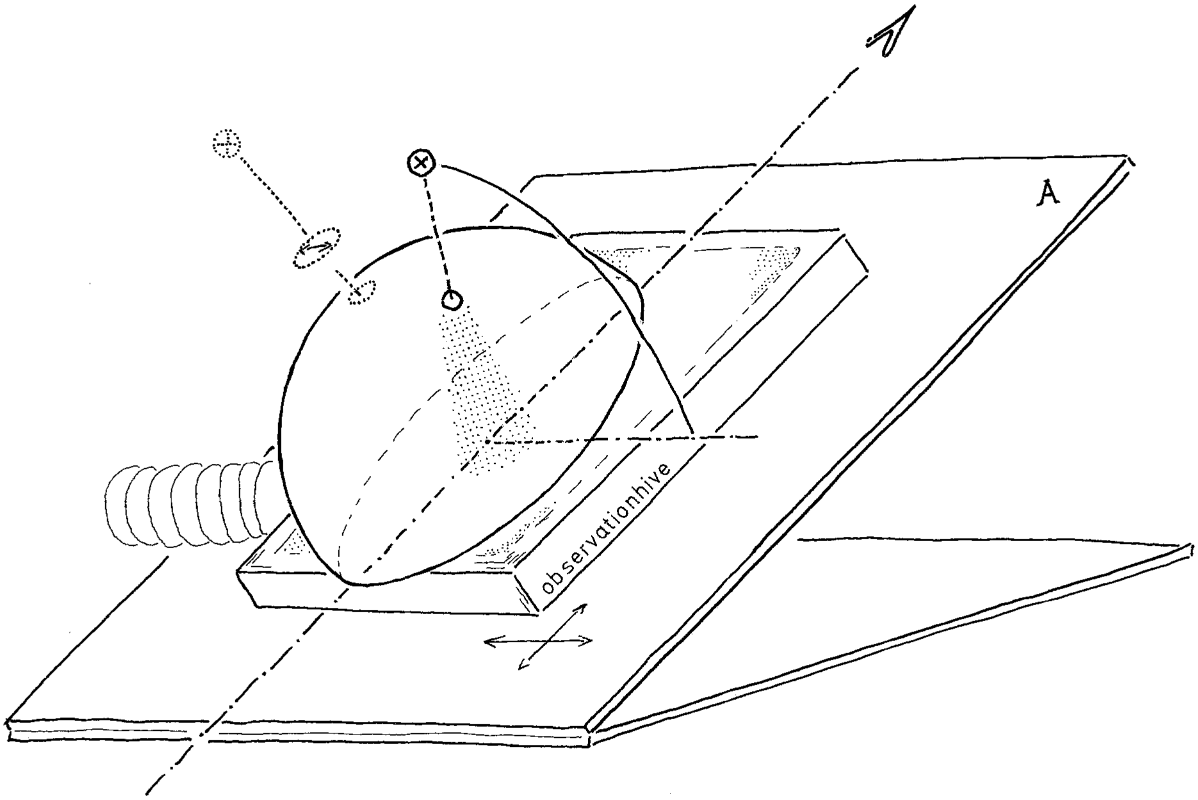

Fig. 1. Schematic plan of the experimental set-up. An observation hive covered with netting could be moved freely in the (inclined) plane "A". The dance plane inside the hive was at the same angle of inclination. The vertical in this plane is indicated by an arrow, which was directed towards north. In the main experiment individual bees were centered in the set up by translational movement of the whole hive. In this position they were exposed to a field of unpolarized light of variable wavelength and intensity in a direction 90° with respect to the vertical. In an additional experiment the bees were exposed to a field of polarized UV light directly above their backs in the apex of the dome (UV filter: UG1 Schott & Gen.; polarizing foil: KS-W68 Käsemann)

wide. Approximately 6 individually tagged forager bees were permitted to collect concentrated sugar syrup from an artificial feeder 300 m away from the hive. Their waggle dances with which they advertised the food source were performed on a flat area inside the hive. A piece of corduroy was glued to this platform to ensure a good grip for the bees. The dancing bees were centered underneath a diffusely lit dome. In this position they could see a disk of light in the dome which subtended an angle of 2.3° at the bee's eye and appeared 45° above the dance plane (Fig. 1). This disk of light was produced by a diffusing foil mounted in the wall of the dome which was illuminated from outside by a 250 W slide projector with objective removed. Grey and interference filters were used to alter the intensity and colour of the light.

During the experiments the dance plane was set at an inclination of $27 \pm 2°$ with respect to the horizontal, with the upper end of the dance platform directed towards magnetic north, while the light fell into the center of the dome from the east of the vertical. For the dancing bee this arrangement produced a 90° deviation between the light and gravity references. The dancing bee was observed through an oval opening in the dome close to its apex. A dim indirect red illumination inside the dome (yielding 60 lux on the dance area) provided enough light to observe the bee, particularly when the experimental light source emitted little visible light. The indirect red illumination was obtained by covering tungsten light bulbs inside the dome with red plastic film which represented an edge filter ($\lambda = 590$ nm) for the spectral range of the bulbs' emission. A bee centered under the dome was seen through a measuring wheel and individual waggle runs were read off to the nearest 30° and dictated to a coworker who recorded the results. The applied reference grid for reading off the angles proved sufficiently accurate for reliably recording every single waggle direction in the dances of the bees under observation. For each selected light stimulus provided for orientation in addition to gravity about 100 individual dance angles were recorded. These data were normally obtained within half an hour for 4–6 experimental bees each dancing between 10 and 20 waggle angles in one dance. Then an average dance direction was calculated applying methods described by Batschelet (1965). The drift in the angles which arises from the gradual change of the food-to-sun angle during the day was eliminated from the data by comparing all mean dance directions during a particular interval only with the dance directions expected with respect to gravity for the middle of that interval, with constant stimulus conditions. This procedure is justified by results obtained from similar investigations made earlier. These showed that the actual food-to-sun angle does not influence the characteristic interactions of light and gravity orientations (Edrich, 1972, 1977a).

Our choice of the angle of inclination and the alignment of the dance plane was such that it was oriented perpendicularly to the field vector of the natural magnetic field at the experimental site. Dance angles performed on this plane can theoretically not be influenced by the earth's magnetic field (c.f. Martin and Lindauer, 1977). Only one part of our apparatus, the projector, contained ferromagnetic material. It was firmly fixed at a distance of 400 mm from the dance plane.

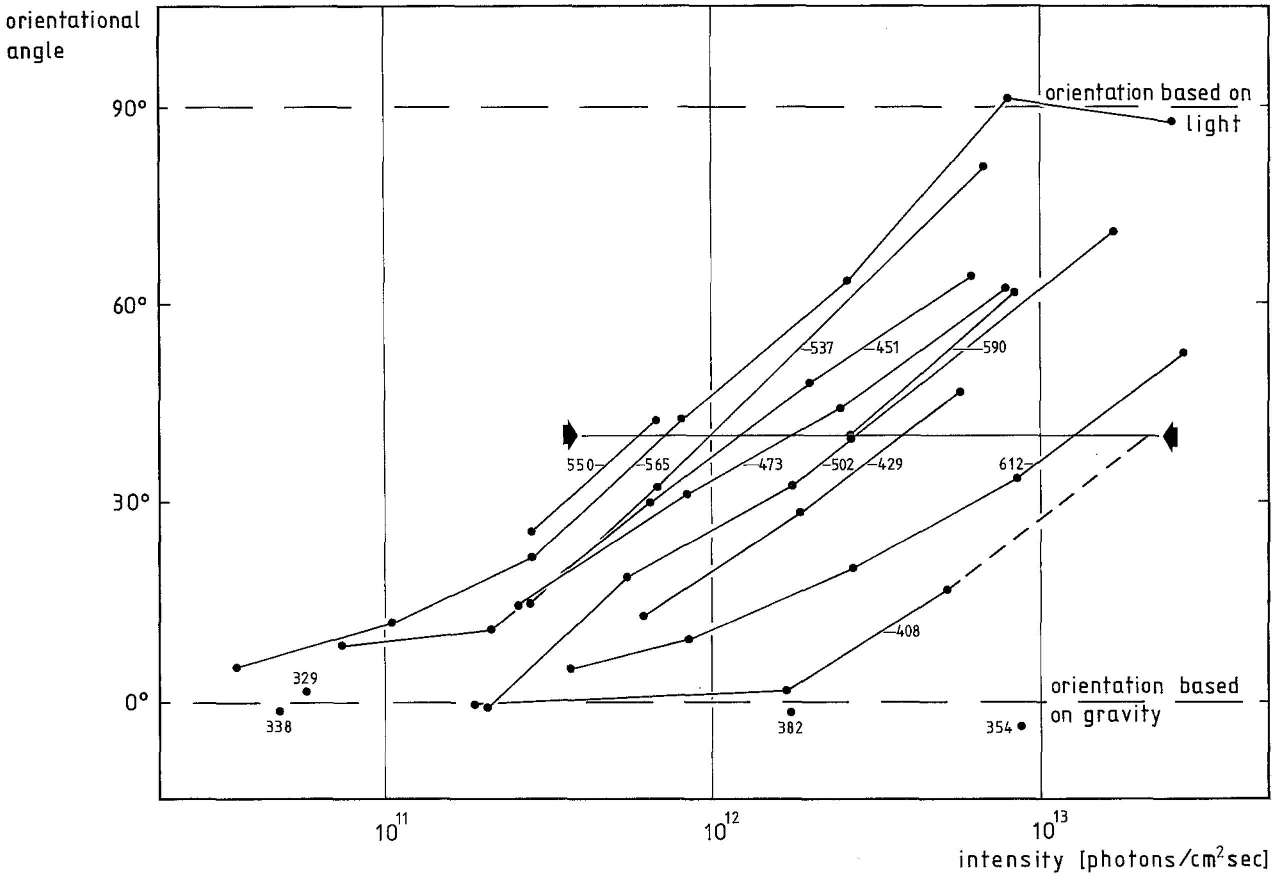

Fig. 2. Angular shift of dance directions from a gravity to a light-determined course, induced by light of various intensity and wavelength. The comb surface was inclined at 27° with respect to the horizontal and the bees could see the light source to the right of the vertical, yielding them a reference differing from gravity by 90°. The intensity-response curves are obtained from mean compromise dance directions. They are shifted along the intensity scale depending on the sensitivity which the bee shows for a specific wavelength of light in this particular situation

Results

When the honey bee responded to the experimental light it deviated from the gravity dance course. Orientation to the light source alone was indicated by a 90° deviation of the dance angles from the expected gravity dance direction because with the bee centered in our set-up the angle between the light source and the upward direction on the comb is 90°. Whenever a wavelength tested at the maximum intensity obtainable with our light source caused the dance angles to depart from the gravity course, the test was repeated at lower intensities by inserting neutral grey filters. An intensity-response curve could then be constructed for this particular wavelength. Intensity-response curves were obtained for ten different wavelengths of the light source (Fig. 2). The ordinate in the graph represents the angular deflection from the gravity dance course induced by light. The abscissa gives the light intensities presented in the experiments, in photons/cm · s. These curves show a smooth transition from orientation based exclusively on gravity (dashed line at the bottom of Fig. 2) at low intensities to an orientation based more on light than on gravity at higher intensities. The bees were quite sensitive to 550 nm and 451 nm light; the curves for these wavelengths are shifted towards lower intensities, as compared with those for other wavelengths. No response could be recorded in the UV range below 410 nm. (In an additional experiment a broad band UV light was presented to the dancing bees by inserting a UG1 filter (Schott & Gen.) into the light beam. Not even under this condition could a deflection be registered from gravity orientation: 132.6° ± 17.3° was registered as dance direction with respect to gravity when 132.5 was the food-to-sun angle. Basically the curves in Fig. 2 are log-linear where the biggest changes in the angle of orientation occur and have the same slope, when plotted on a logarithmic intensity scale. A regression analysis of data belonging to the 451 and 502 nm I-R curves revealed no significant difference in the slope of the two curves. How-

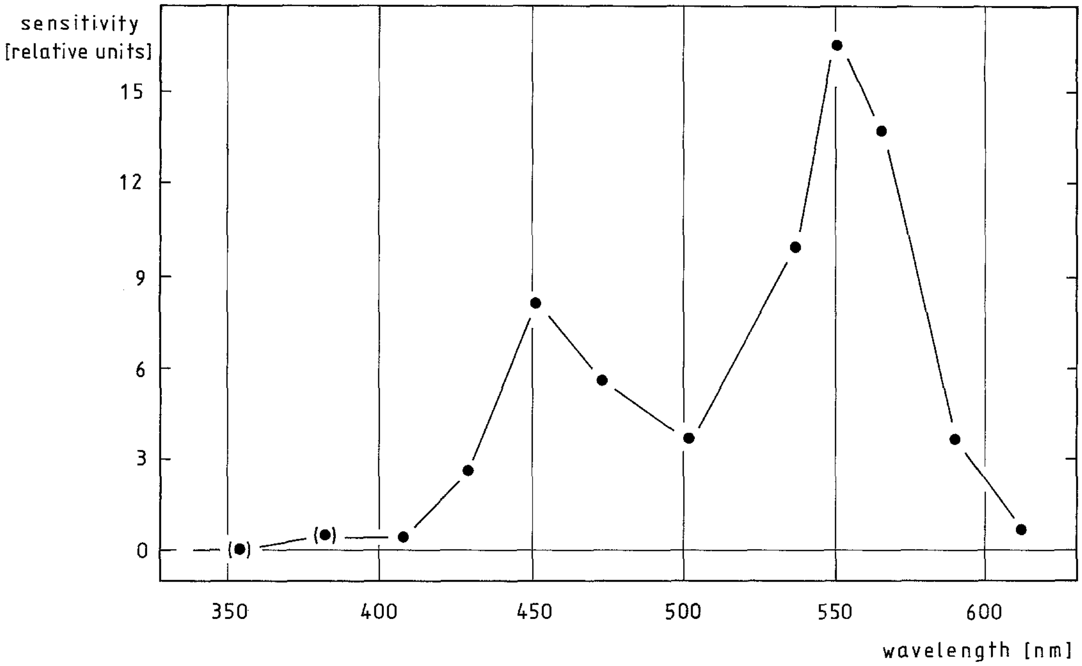

Fig. 3. Action spectrum of the orientational effect of a light source on waggle dances of honey bees orienting simultaneously with respect to gravity. The action spectrum is derived from data presented in Fig. 2, by plotting the reciprocal of he light intensity required to obtain a particular compromise angle (40° "sun reaction") for each wavelength tested with a constant gravitational cue. While the peaks reflect the contributions of the 450 nm and 550 nm receptors a contribution from the 350 nm receptor is not apparent. The sensitivity values for 382 and 354 nm lights (points in brackets) indicate the highest possible sensitivities which may be obtained by linear extrapolation from the corresponding single data points in Fig. 2

ever the shift obtained along the intensity scale between these two curves is significant; it exceeds threefold the error band of each curve derived from the standard deviation of the mean data points (±2.7° for the 451 nm and ±2.5° for the 502 nm light).

It is now feasible to construct an action spectrum, by extra- and interpolating those intensities of the differently coloured lights which caused the same deflection (40° was arbitrarily chosen) from the orientation with respect to gravity. The reciprocal values of these intensity readings reflect the spectral sensitivity of the bee in relative units.

The action spectrum obtained is given in Fig. 3. We find two peaks, one at about 450 nm and the other at about 550 nm. The lack of reaction in the UV range does not imply that the light source emitted insufficient light intensity in this part of the spectrum. The following results clearly refute this interpretation:

(1) The very same bees which did not respond to UV light in their dances hurried along the sloping comb towards the UV emitting light source when they had finished dancing and searched there – apparently in a positive phototactic state – for the exit of the hive. Since the hive exit was in the opposite direction we had to switch off the light source several times in the course of the experiment to let bees that had accumulated at the side find the exit.

(2) From investigations made by von Frisch and ourselves one can expect bees dancing on the inclined comb to respond to UV light if it is polarized (von Frisch, 1967; von Helversen and Edrich, 1974; Edrich, 1977a). We designed a test of this response which should give particularly clear results. A field of polarized UV light, 2.3° in diameter, was presented in the apex of the dome, above the back of the bee. Two directions of the plane of polarization were tested: parallel (P //) and perpendicular (P⊥) to the plane through the bee, the zenith and the apex of the dome. Finally, as a control, the projector light was switched off (P X) and the bees oriented with respect to gravity only. The circular distributions of raw data in Fig. 4 represent the waggle directions under the three conditions; in each case data were collected over 10 min.

With polarized light as the only stimulus honey bees have two reference directions for orientation, which lie perpendicular to the plane of oscillation. Consequently, the dance directions are divided into two groups, differing by 180° (cf. von Helversen and Edrich, 1974). If gravity provides an additional reference direction and this coincides, as in Fig. 4b, P⊥, with one of those from polarized light then the ambiguity in the resulting distribution disappears. If, as in Fig. 4c, P //, the reference directions from

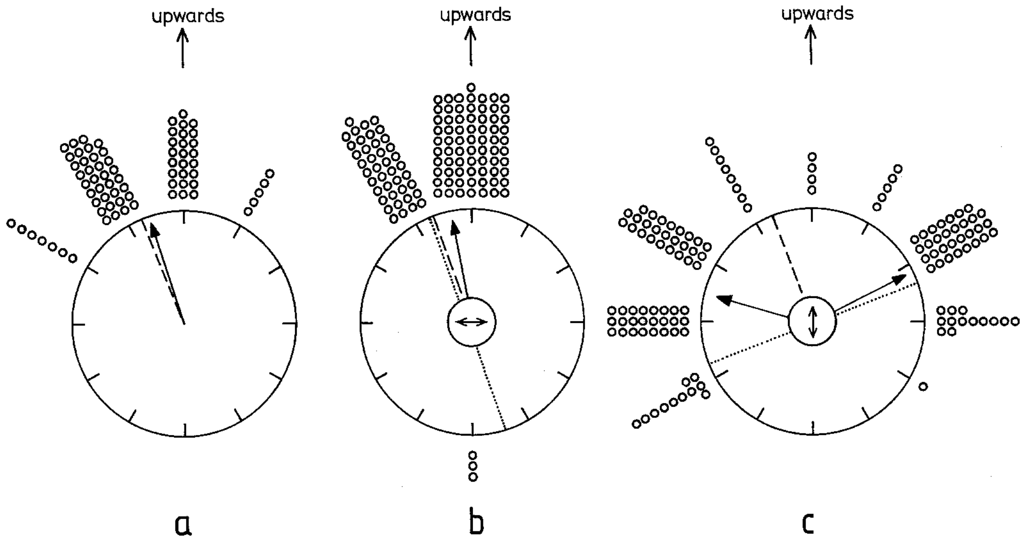

Fig. 4a–c. Dance directions related to gravity (**a**), and related to both gravity and polarized light (**b**), (**c**). The dance surface of the comb was inclined 20° with respect to the horizontal. Polarized UV light (Leitz Prado, UG1 filter, visual angle 2.3°, polarizer KS-W68) was presented at the apex of the dome directly above the back of the bee under observation. The experimental conditions were otherwise the same as in the main experiments. The polarizer was set in two planes indicated in the center of the distributions. Each small circle represents an individual waggle angle. A dashed line indicates the gravity dance direction calculated from the food-to-sun angle, dotted lines indicate the dance directions expected on the basis of polarized light orientation only. The mean dance direction is shown as an arrow, the length of which is proportional to the tightness of clumping of the data about the mean direction

polarized light lie orthogonal to the reference direction from gravity, then the dance angles are distributed between two directions. They do not lie exactly opposite each other because of the gravitational influence. The data for P X, no polarized light, do not differ significantly from those for P ⊥ whilst both differ from P //.

Thus the results clearly demonstrate that the animals responded to the change of the plane of polarization.

Discussion

From our experiments we obtained an action spectrum for the effect on the orientation of bees of a light source interacting with gravity. There are peaks in the action spectrum at approximately 450 nm and 550 nm which correspond to the combination of the spectral sensitivities of the bee's 450 nm and 550 nm receptor systems (Autrum and von Zwehl, 1964, von Helversen, 1972). We see no peak reflecting the animal's 350 nm receptors. (Nevertheless, the UV system could have an inhibitory effect on one or both of the other receptor systems. This possibility provides scope for further inquiry.)

The kind of compromise dance angles selected by the bees demonstrates that we are dealing with an interaction between sun and gravity compass behaviour. These results are consistent with the behaviour of bees on a *horizontal* plane where the direction of the sun is inferred from light perceived by the 450 nm and 550 nm receptors and not by the 350 nm system. The other type of orientation observed on the horizontal comb is the "anti-sun reaction" in response to stimulation of the 350 nm receptors (Edrich et al., 1979). This latter reaction can apparently not overcome a significantly orienting influence of gravity which already prevails at inclinations of the comb of 8° with respect to the horizontal.

Short-wavelength light is but one characteristic of the blue sky that could be used for orientation. It is generally assumed that the specific polarization of the sky light plays a predominant role in identification of specific patches of the sky by bees (von Frisch, 1967, for review; Rossel et al., 1978). However, it is difficult to assess the role of the skylight polarization for honey bee navigation independent of the effect due to the wavelength of the light. Polarized light is perceived only in the UV range (von Frisch, 1967; von Helversen and Edrich, 1974). In the above experiments with polarized UV light visible to bees dancing on an inclined surface, the observed response was due to the orientation of the plane of polarization (Fig. 4).

Taken together our results demonstrate quite clearly that UV orientation is qualitatively distinct from sun orientation. In view of the striking phototactic response to unpolarized UV light observed on the inclined surface, which contrasts with the behaviour during the dance, another distinction seems compelling: sun-gravity interaction within the dance is qualitatively distinct from phototaxis-geotaxis interaction; the light is perceived differently in the two behavioural contexts. Of course another distinction is that the responses to light and gravity in the dance allow for variable pre-set orientations, whereas the phototaxis and geotaxis responses do not.

A behavioural(neuro)geneticist working with *Drosophila* uses different photoreceptor mutants to elucidate the receptor functions and the associated nervous network. With bees we are in a position to tackle the same problems with normal (wild type) animals, because bees have assigned different light input channels to different orientation conditions. For these conditions quite a few action spectra are available now that document this specialisation within the visual system of the bee. Kaiser and Liske (1972) were the first to demonstrate that movements within the visual field of the bee are detected by its 550 nm (yellow-green) receptors. Polarized light is perceived exclusively with the 350 nm (UV) receptors (von Helversen and Edrich, 1974). The role of the 450 nm and 550 nm receptors as detectors of sunlight and the role of the 350 nm receptors as mediators for orientation with respect to scattered skylight have been discussed elsewhere (Edrich, 1977b; Edrich et al., 1979). Furthermore, the present study of the two types of interactions between visual and postural information from the gravity receptors has disclosed that different sets of photoreceptors are involved in the two cases and indicates two distinct central nervous levels of integration which in principle should also be detectable anatomically.

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