

The ocelli control the flight course in honeybees

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Abstract. Fully-sighted honeybees and bees with all ocelli occluded were trained to fly through an arena to arrive at a feeding place. After training, the bees were exposed to side-light flashes during their feeding flights. The flight paths were recorded on video and analysed frame by frame at 40 ms intervals with reference to the main parameters, the coordinates of the thorax and the yaw angle of the bee. Course angles, translational course velocities and accelerations were calculated, and the responses to side light flashes evaluated with respect to 'on' and 'off'.

Immediately after light on, fully-sighted bees respond slightly positively by yawing and flying toward the side light. Bees in which all ocelli are occluded are greatly disturbed and respond with negative yawing and flight path directions.

The ocelli apparently help to control phototactic alertness in the bee. They determine whether phototactic orienting or pattern-induced orienting behaviour is more important in a particular state of motivation. They help to minimize the level of disturbance in flight course control, obviously by activating a neuronal circuit with comparator attributes. It is assumed that this kind of compensation or suppression of phototactically guided reflexes occurs only for a few 100 ms. Consequently, the biological significance of light flashes shorter than 400 ms is very slight.

Fully-sighted bees decelerate strongly when a side light is switched on. Bees in which the ocelli are occluded behave less cautiously: they generally fly faster and need more reaction time. Thus, the ocelli help the bee to react photokinetically to photic stimuli in a much shorter time than do the compound eyes alone.

Key words. Honeybee, flight control, compound eyes, ocelli, phototaxis, flight course, yawing.

Introduction

The function of the ocelli in orientation is still

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very unclear (for summary, see Milde, 1987). Many authors have shown that they play a role in flight stabilization (dragonflies: Stange & Howard, 1979; Stange, 1981; locusts: Taylor, 1981; flies: Wehrhahn, 1984) or phototactic behaviour (locusts and crickets: Jander, 1963; Jander & Barry, 1968; bees; Schrickler, 1965;

Kral & Heran, 1983; Frisch, 1986; flies: Hu & Stark, 1980; moths: Eaton *et al.*, 1983). Ocellar participation in turning behaviour during phototactic runs and flight has also been reported (Kral & Heran, 1983; Frisch, 1986; Kastberger & Kral, 1985; Kastberger, 1987, 1988a, b).

Phototaxis is often taken as a convenient measure of an animal's visual capacity because this stereotyped behaviour is easily elicited and relatively stable (Menzel & Greggers, 1985). Yet there is the danger of reducing natural behaviour to stereotyped and simple responses while motivational dynamics, complex sensory input relations or complex processing of signals are ignored. The sensory and motivational state of the test animals may influence the phototactic response (Menzel & Greggers, 1985). Moreover, in many behavioural conditions phototaxis may be less important than other orientational factors.

These basic problems explain why so little information about the role of the ocelli has been obtained up to now. There is strong evidence now that the ocelli are more than a simple phototactic control device. This led us to choose an approach similar to that of Menzel & Greggers (1985). Honeybees were tested during their natural foraging cycle and experimentally induced orientational behaviours were compared with naturally occurring behaviours. The bees under test conditions were in a similar

motivational state as on natural feeding tours: they were trained to cross an arena in free flight. Temporal and spatial parameters of responses to light stimuli were measured using an inertialess method. The bee was stimulated artificially and observed to see how it compensated for flight course errors. Fully sighted bees and bees with all ocelli occluded were compared in this respect. To this end, the main parameters for phototactic and photokinetic course control in free flight were measured, that is course direction, yawing behaviour and ground velocity.

Materials and Methods

Experimental setup. Honeybees (*Apis mellifera carnica* Pollm.) were trained to collect sucrose solution at a feeding place inside the laboratory. To arrive at the feeding place the bee had to pass through a flight arena which was a glass box measuring $70 \times 50 \times 40$ cm (Fig. 1). On a feeding tour, the bee flew from the hive to the window of the laboratory (100 m) to land in front of the entrance hole of the flight arena. Then it had to walk up the vertical front of the arena from the landing site to the entrance hole, fly through the arena (50 cm) and finally land in front of the feeding place. It had to walk the last 10 cm to the feeding place outside the

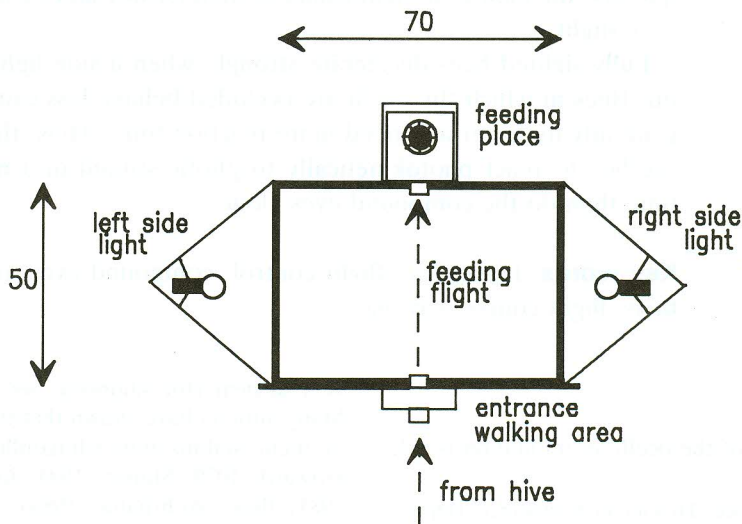


Fig. 1. Floor plan of flight arena. The numbers give the dimensions in cm.

arena. The way back to the hive (homing tour) was simply the reverse route.

During its feeding flight a bee was stimulated by wide-field light flashes. For that reason, at the sides and top of the arena, outside the frosted-glass plates, 100 W lamps were installed in aluminium reflectors to produce diffuse bright areas inside. One of the side lights (right or left) was switched on or off by hand after a bee had started to fly across the arena from the entrance hole to the feeding hole. The light was switched on at different times and positions after the start from the entrance hole. Usually it was switched off 1 s later. The side with the stimulation light on defined the sign (+/-) of responses with respect to the arena: positive coordinates are defined on the side with light on. Positive angles resulted if the bee faced the on side. The intensity of the light on the top of the arena was *c.* 1 kLux, and of the side light 1.5 kLux if measured in the main and direct path of trained bees. The difference in illumination between the side with light on and the other side with light off was at least 1 kLux. If the side light was switched off, the side areas were also illuminated indirectly by the diffuse top light.

The bee was tracked by a video camera in the arena to measure the positional coordinates and

the angle of the body's long axis (Fig. 2) during feeding flights. This was achieved by providing the arena with a transparent floor. The whole arena was mounted on a bracket 1.5 m high to permit video recording from the bottom. A curtain kept light out of the space below the arena where the video camera was located (Camcorder SONY).

Occlusion of the ocelli and marking with colour codes. Well-trained bees which have visited the feeding place over a period of days pass through the arena on straight flights within 1 s. Such bees were taken from the feeding place for marking and occlusion of the ocelli. Experiments were done during 3 weeks in August 1988. Each day, two groups with five to ten bees were tested; the first group consisted of fully-sighted bees and the other group consisted of bees with all ocelli occluded. Fifty fully-sighted bees and twenty-five occluded bees were evaluated here. The colour codes were chosen so that the individual bee could be recognized quickly and easily during its walk from the landing site to the entrance hole and during its flight course through the arena. Each group was marked with a special colour combination. An individual code was obtained by varying the marking site on the thorax or abdomen. The

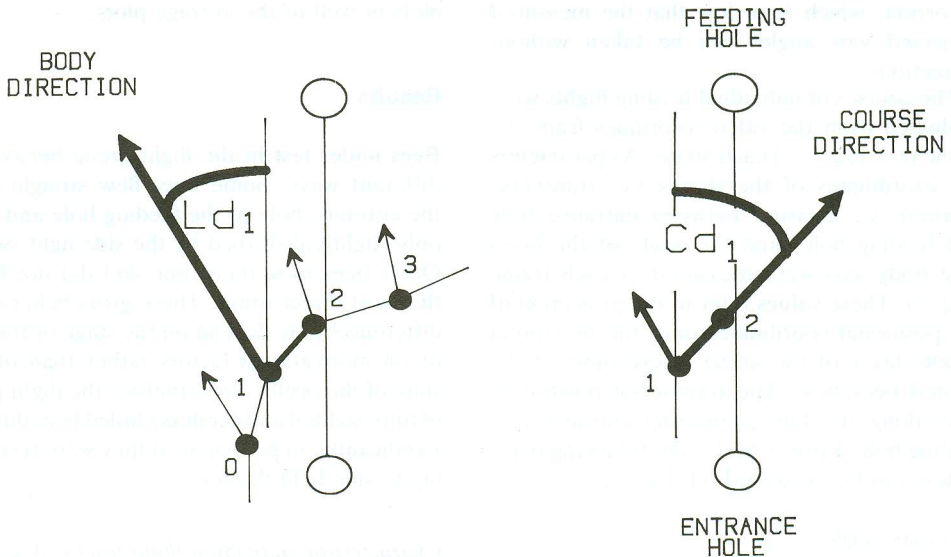


Fig. 2. Definition of flight angles. 0, 1, 2, 3 are four successive positions of a bee during free flight. The line between entrance and feeding holes gives the shortest flight path. The arrows at each position give the angles of the bee's long body axis. Definition of the body angle Ld_1 (left graph), the course angle Cd_1 (right graph), and the body and course directions at position 1.

ocelli were occluded with black water-soluble paint which dries within 1 min. The occluded ocelli were additionally coloured with the group code to enable the check of the status of occlusion during test. Bees recently colour-coded and occluded were either released at the feeding place, or they were set in the sun at the window from where they soon homed. Marking and occlusion of the ocelli were performed within 3 h before testing. The occlusion remained effective in *c.* 50% of the individuals 1 day after the experiment.

Evaluation of the data. The video camera was placed at a distance of 100 cm from the horizontal midsection of the arena. As only one video camera was used, it was not possible to calculate the true three-dimensional trajectories of the flight tracks. The experiment was designed to detect and quantify only gross effects in the flight course with and without sighted ocelli. The video images of the flight courses were evaluated as if they were projections onto the horizontal midsection of the arena. This simplification brings about two main error potentials when the bee flies to peripheral zones: first, the parallax error, which can be neglected here because the individual bias in flight course would be much higher than the maximal parallax error of projection; second, the perspective distortion, which is so low that the measured projected yaw angles can be taken without corrections.

The courses of individual feeding flights were evaluated from the video recordings frame by frame ($i = 1, 2, \dots$) each 40 ms. As parameters the coordinates of the thorax (x_i , transverse position; y_i , measure between entrance hole and feeding hole) and the angle of the bee's long body axis were measured in each frame (Fig. 2). These values refer to the projection of the positional coordinates onto the horizontal middle layer of the arena where most of the trained bees flew. The transversal position is zero along the line connecting entrance and feeding hole. From x_i and y_i the following parameters can be calculated (cf. Fig. 2):

- (1) Course angle:

$$Cd_i = \text{ARCTAN}((x_{i+1}-x_i)/(y_{i+1}-y_i)) \text{ [degrees]}$$

- (2) Ground velocity:

$$Vg_i = \text{SQRT}((y_{i+1}-y_i)^2 + (x_{i+1}-x_i)^2) * 25 \text{ [cm/s]}$$

- (3) Ground acceleration:

$$Ag_i = (Vg_{i+1}-Vg_i) * 25 \text{ [cm/s}^2\text{]}$$

The data were evaluated in relation to the transition to light-on or light-off. Generally, the responses to right side light on or off were evaluated in detail. The experiments where the left side light was used were evaluated only for a gross check of the symmetry of effects. Five frames were observed before the light on or off stimulus, and twenty frames thereafter. The data were related to light-on or light-off, adequately pooled and the basic statistics (mean, standard error) calculated. The Chi-square test (Sachs, 1978) was used to see whether the rates of positive and negative responses referring to a certain time interval are equally distributed. If the Chi-square values were higher than 2.77, the positive rate differed significantly ($P < 0.05$) from the negative rate. This way of proving the significance of response levels was chosen because of its simplicity and its nonparametric nature. The relative difference between positive and negative rates is given by

$$(4) \text{relDIFFrate} = R_{\text{pos}} - R_{\text{neg}} * 100 / (R_{\text{pos}} + R_{\text{neg}})$$

where R_{pos} (R_{neg}) is the rate of positive (negative) cases. The proper rates of the given time intervals were calculated as the sums of the neighbouring rates in four individual 40 ms intervals (running average). The rate difference plots fit well to the average plots.

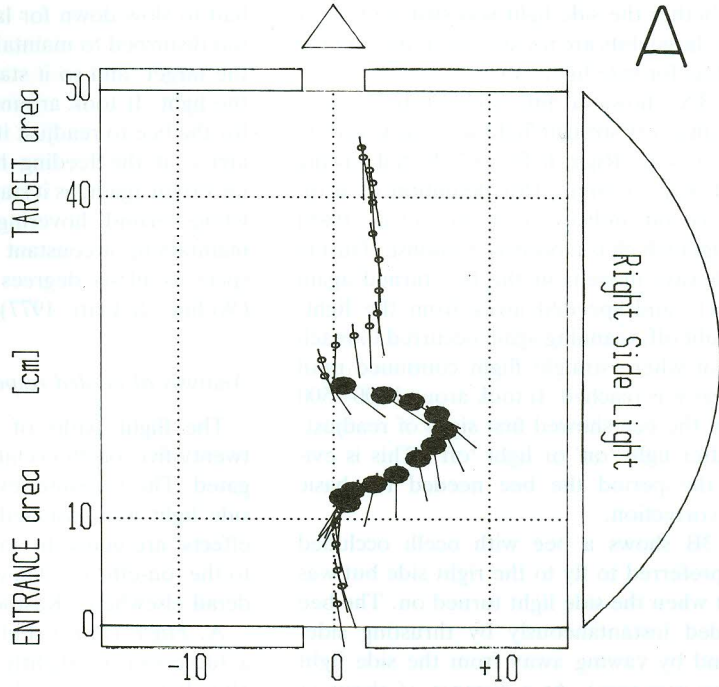
Results

Bees under test in the flight arena behaved in different ways. Some bees flew straight from the entrance hole to the feeding hole and were only slightly disturbed by the side light switch. Other bees took their time and did not fly by the most direct route. These gross behavioural differences may depend on the stage of training or on motivational factors rather than on the state of the ocelli. Nevertheless, the flight paths of fully-sighted and ocelli-occluded bees differed significantly, in particular, if they were responding to side light flashes.

Characteristic individual flight tracks of fully sighted and bees with their ocelli occluded

The flight behaviours of two individuals are shown in Fig. 3 by the flight path coordinates, by the yawing of the bee and by the information

FULLY SIGHTED



ALL OCELLI OCCLUDED

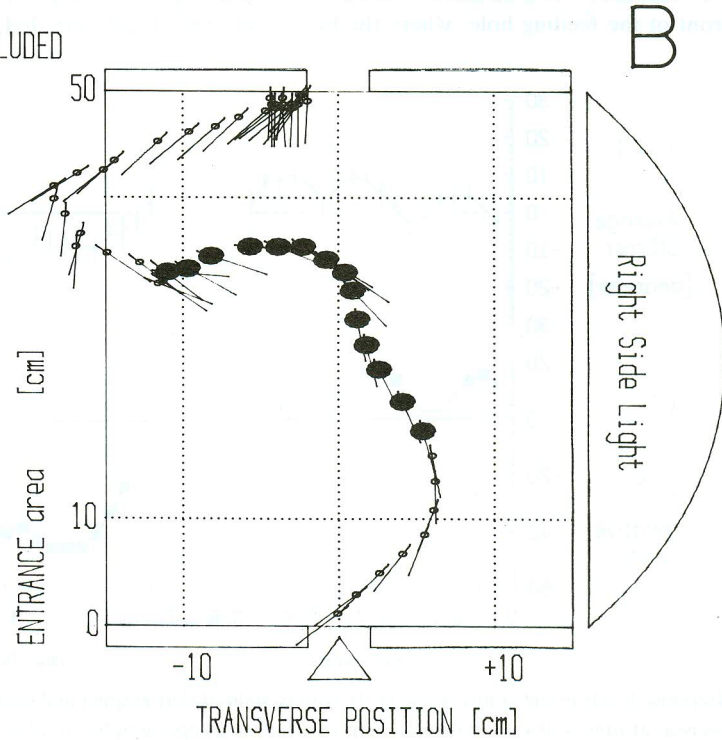


Fig. 3. Flight paths of a free-flying, fully-sighted bee (A) and a bee with its ocelli occluded (B) on feeding flight in the arena. The entrance hole was at the lower side of the graph (entrance area), the feeding hole at the upper side (target area). The right side light was briefly flashed on and off; small dots refer to light 'off', large solid dots to light 'on' periods: the tails on the dots give the direction of the abdomen of the bee at the respective position. For further details see text.

as to whether the side light was switched on or off. The large dots are for side light 'on' and the small dots for side light 'off'.

Fig. 3A shows a fully-sighted bee which started on a very straight flight with slight yawing to the left side. Right light 'on' elicited yawing and sideways scanning (for definition of scanning behaviour in bees, see Lehrer *et al.*, 1985) to the light which is a positive response. During this sideways movement the bee turned again negatively and speeded away from the light. After light off, scanning again occurred to reach the point where straight flight continued until the target was reached. It took around 300–500 ms until the bee showed first signs of readjustment after light 'on' or light 'off'. This is evidently the period the bee needed for basic course correction.

Fig. 3B shows a bee with ocelli occluded which preferred to fly to the right side but was straight when the side light turned on. The bee responded instantaneously by thrusting sideways and by yawing away from the side light (negative response). At a distance of about 15 cm in front of the feeding hole, where the bee

had to slow down for landing, it was evidently too disturbed to maintain the straight course to the target, and so it started to scan away from the light. It took around 400 ms after light off for the bee to readjust its flight direction and to arrive at the feeding hole. Here it was very uncertain again, as it stayed there scanning for a whole second, hovering in front of the target, maintaining a constant flight position with respect to all six degrees of locomotor freedom (Wehner & Flatt, 1977).

Analysis of pooled responses to side light

The flight paths of fifty fully sighted and twenty-five ocelli-occluded bees were investigated. The response levels are calculated after side light was switched on and off. The 'off-effects' are generally in the opposite direction to the 'on-effects'. They will be documented in detail elsewhere (Kastberger, in preparation).

A. *Flight course.* Fully-sighted bees showed a succession of slightly positive course angles after light 'on' (Fig. 4), reaching mean angles of $+8^\circ$. Light 'off' led to a negative course.

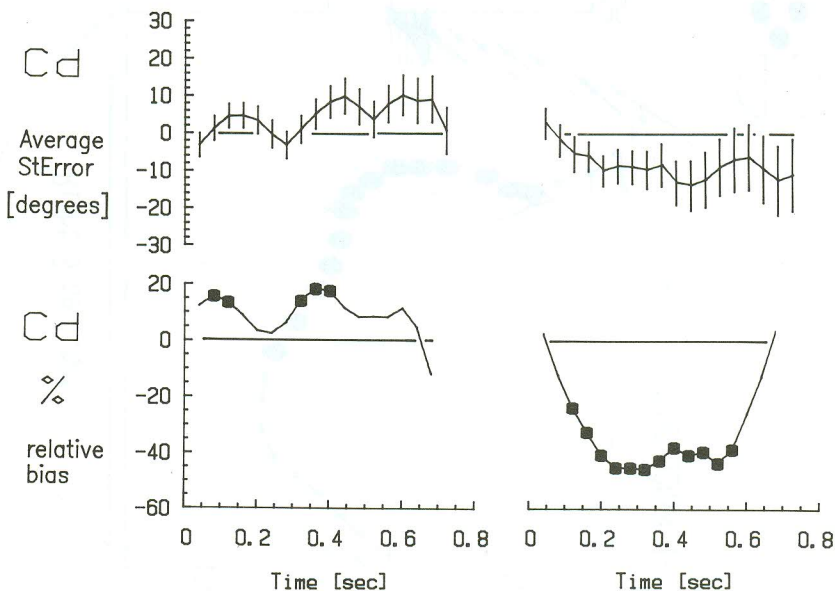


Fig. 4. Response levels in the course angle (Cd) of fully-sighted (left graphs) and ocelli-occluded (right graphs) bees. Abscissa: at time = 0 s the right side light switched on; upper graphs are plots of averages and standard errors (vertical bars); lower graphs are plots of the relative difference between the rates of positive and negative cases (see Methods); the rate 100 (%) corresponds to the sum of positive and negative cases at a certain time. The dots refer to significant bias ($P < 0.05$) between positive and negative cases. The curves refer to fifty fully-sighted and twenty-five ocelli-occluded bees.

Ocelli-occluded bees showed an opposite and stronger response (mean course angles up to -12°) to that of fully-sighted bees. In particular, this contrast is very clear in the rate plots (Fig. 4).

B. Yawing. After light 'on' fully-sighted bees yawed positively and instantaneously within 100 ms. This is seen in the pooled data (Fig. 5) and also in the individual flight in Fig. 3. Yawing was the first response observed after light 'on'; even earlier than changes in course angle, in transversal position or in ground velocity. The mean body angles are $+5^\circ$, the response is very low, but significant ($P < 0.001$). Ocelli-occluded bees yawed massively away from the side light after light 'on', reaching mean angles of 20° within 300 ms. After 300 ms this negative body angle was reduced. Average and rate plots are here very similar (Fig. 5).

C. Ground velocity and acceleration. Fully-sighted bees flew in the arena with mean ground velocities up to 60 cm/s. Ocelli-occluded bees usually flew significantly ($P < 0.001$) faster at more than 70 cm/s. After light 'on' fully sighted bees were more 'cautious' than occluded bees, they decelerated instantaneously (Fig. 6). Ocelli-occluded bees started to decelerate with

a delay of at least 100 ms, but then decelerate more rapidly (Fig. 6, Ag). Light 'off', led to instantaneous and negative responses in both categories of bees. The negative course acceleration response is interrupted by characteristic positive effects, which are much stronger in occluded bees than in fully sighted bees.

Discussion

Our way to determine the role of the ocelli in the control of free flight was to subject the bees to light flashes with moderate light intensity changes and to compare the instantaneous responses of fully-sighted bees with those of bees in which the ocelli were occluded. Fully-sighted bees respond slightly positively; occluded bees react strongly to light flashes and respond predominantly negatively. At first sight it might be postulated that the ocelli influence only the sign of the response and that occlusion of the ocelli will not lead to further consequences. But there are some indications that the ocelli are essentially more than just a simple phototactic control device for switching the phototactic mode from negative to positive when on feeding tours.

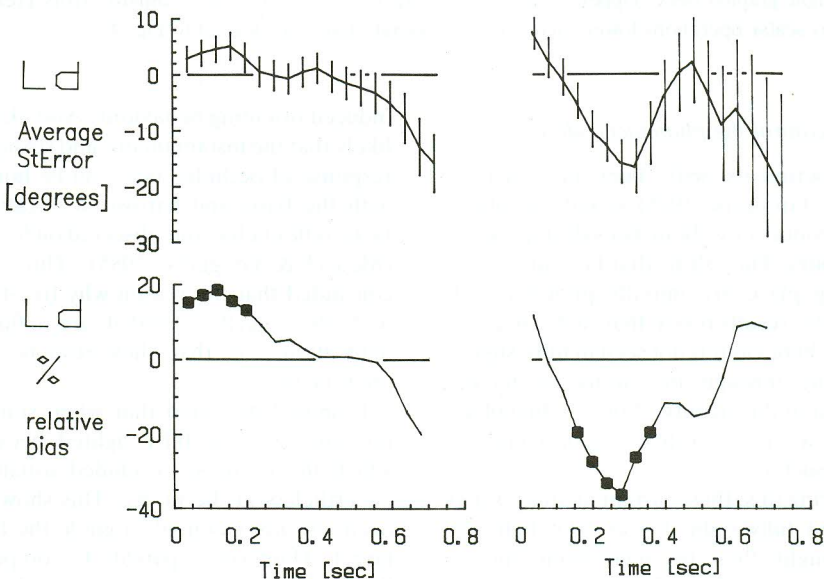


Fig. 5. Response levels in the body angle (L_d) of fully-sighted (left graphs) and ocelli-occluded (right graphs) bees. For more detail see legend to Fig. 4.

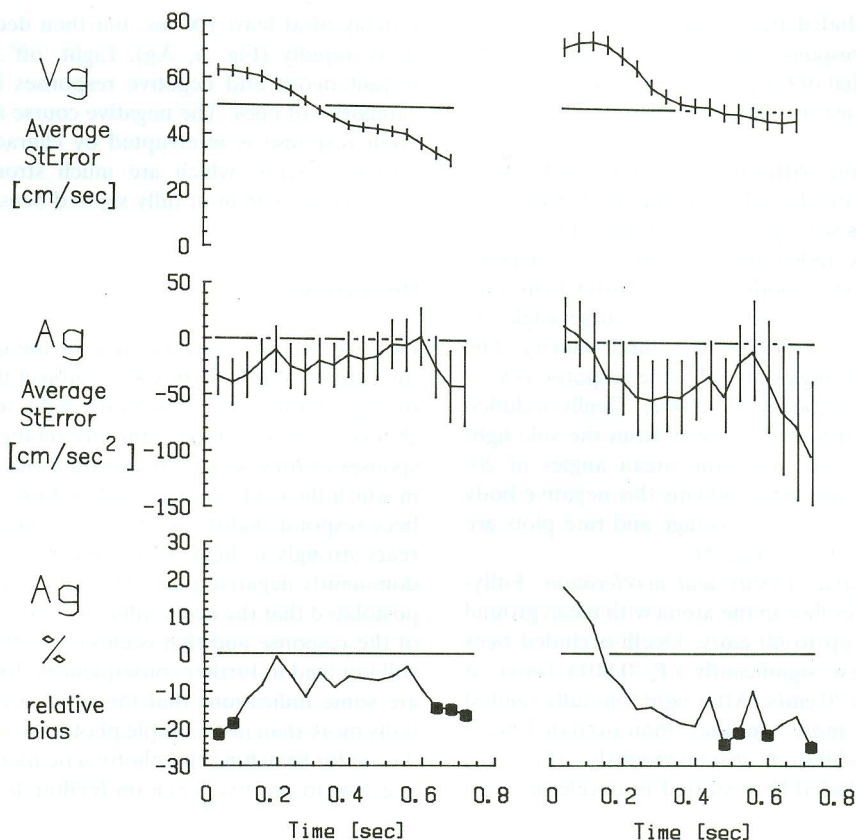


Fig. 6. The response levels in ground velocity (V_g) and acceleration (A_g) of fully-sighted (left graphs) and ocelli-occluded (right graphs) bees. Upper curves V_g and A_g refer to means and standard errors (vertical bars), calculated by scalar operations lower curves refer to A_g rate plots (see legend to Fig. 4).

The ocelli control the phototactic alertness

The experiments with bees in a y-maze (Menzel & Greggers, 1985) tested the phototactic behaviours of walking bees during natural foraging tours. They show that bees arriving at the feeding place are initially phototactically negative. Our results reveal that such a negative phototactic behaviour is not seen in fully-sighted bees passing through the arena on feeding flights, even in the vicinity of the feeding place. Moreover, a slight positive responsiveness is evident in such bees.

Considering this, these instantaneous positive responses of fully sighted bees after light-'on' switches might then be seen from another aspect: during feeding flights in the arena phototactic orienting might be less important for finding the feeding place than pattern-

induced orienting behaviour. And likewise, it is likely that the instantaneous and strong negative response of occluded bees can be homologized with the basic and hardwired negative phototactic reflex behaviour observed on feeding tours (Menzel & Greggers, 1985). Thus, it can be concluded that the reason why free-flying bees with their ocelli occluded are influenced by light flashes is that they respond primarily phototactically.

It should be noted that when stimulated in the same way as fully sighted bees, bees in which the ocelli are occluded usually arrived nevertheless at the target. This shows that the ocelli are not essential to guide the bee to the target. Thus, this capability to compensate for flight course errors must be based mainly on fixation (Wehner & Flatt, 1977) or on related strategies of pattern-induced orientation like

smooth fixation, quantum search (Reichardt & Poggio, 1981; Bülthoff *et al.*, 1982) or even scanning (Lehrer *et al.*, 1985).

The ocelli control the biological significance of light flashes

Our results let suppose that the ocelli help the bee to minimize errors in tracking during feeding flights, that they help to compensate for extremely phasic photic events by suppressing hardwired phototactical responses. This will result in helping to prevent negative course errors due to very short light-'on' signals. In other words, the bee on feeding flights is not orienting primarily phototactically, and therefore the biological significance of light flashes shorter than 400 ms is much diminished. This confers an important advantage to the bee: while tracking under shady trees on sunny days it is not severely disturbed by the light and shadow sequences along its flight path. The results of this paper produce a new view of the role of the ocelli in flight stabilization, supporting the postulation of Taylor (1981) that the ocelli are especially important for stabilization of the retinal image of the compound eyes during flight, when disturbances are frequent and sudden.

The ocelli are part of a comparator system

Fully-sighted bees can compensate for phasic photic events, probably by suppressing the hardwired phototactic reaction. On the other hand, free-flying ocelli-occluded bees show a marked negative response to such stimuli. Thus, the disruption of the flight course through short photic disturbances can be kept low only if both compound eyes and ocelli receive the same photic event. As it has often been discussed for the ocelli (for summary of this aspect, see Schricker, 1965), the simplest way of gating this kind of compensation is to activate a neuronal circuit with comparator attributes. A comparator is a very fast tool which can compare two inputs in order to calculate differences between two signals, or which can eliminate artefacts that form equal parts of both signals. Comparators as neuronal circuits are known in processes that have to work in the time domain of action potentials or even faster. Here, feedback circuits including successive sensory input cannot be

involved, because this kind of control would need too much time to elicit a reaction.

This hypothesis leads to the interesting conclusion that the classical postulate whereby the ocelli may act to adjust compound eye sensitivity (Kerfoot, 1967; Hu & Stark, 1980; Kral & Heran, 1983; Milde, 1987) can be considered to be updated by the observations presented here: the obvious comparator function of the visual system, with the ocelli playing a major role, prevents the bee from being guided primarily by phototactic principles when other modes of orientation are more appropriate. As a consequence, the hardwired reflexes eliciting negative phototactic responses are suppressed or even replaced by counter-directed ones. In other words, this fast ocellar mechanism helps to minimize course errors and makes up for the slower processing through fixation.

The ocelli control the photokinetic behaviour

When flying through the arena, a fully-sighted bee trained for a straight flight adjusts its speed depending on the distance to the feeding hole. It decelerates strongly when a side light is switched on and speeds up slightly if the side light is switched off. Bees with their ocelli occluded generally fly faster under normal arena conditions, need more reaction time to start to decelerate and then have to decelerate more strongly to arrive at the target without damaging themselves. Thus, the ocelli enable the bee to react photokinetically to photic stimuli in a much shorter time than the compound eyes alone, thus helping to compensate for flight course errors with higher precision.

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