Visual Fixation in Freely Flying Bees

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Compound Eye, Fixation, Fovea

A foraging bee approaching a food source visually fixates the food source before it lands on it. During this process of fixation the bee adjusts its rotatory and translatory flight components to fixed values with respect to all six degrees of freedom.

In human vision a moving object has first to be fixated visually before it can be analysed. During fixation the object is viewed by a specialized region of the retina, the fovea, that is characterized by increased acuity and associated with binocular vision. In insects which locomote by often rapid flight, images get blurred and distorted unless fixation movements adjust the target in the direction of flight.

In predatory insects such as dragonflies, mantids, some beetles, bugs and wasps as well as in male flies that pursue females during mating behavior, frontal or dorsal regions of the compound eyes have relatively small interommatidial angles (associated with large facets and a decreased radius of curvature) and hence exhibit increased visual acuity. Recently it has been shown by optical and behavioral analysis that large-facet parts of compound eyes are especially designed to fixate and track small objects (*e. g.* females) against a bright background [1, 2]. In worker bees, no part of the eye strikes by facets as conspicuously large as in the dorsal parts of the eyes of many flies.

However, do bees fixate? Although pattern recognition in bees has been studied for many years [3], the data available do not allow one to answer this question convincingly. In most experiments where bees have been trained to discriminate between visual patterns, these figures have been presented on a horizontal plane. There the flying bee has been allowed to adjust its longitudinal body axis in arbitrary directions relative to the figure and finally had to land on it. Neither position nor angular size of the figure as experienced by the receptor array could be controlled by the experimenter.

In order to avoid these uncertainties, in the experiments described here the pattern disks were presented in front of the approaching bee at a certain distance behind a translucent Plexiglass screen. The bee had to land on the opening of a small Plexiglass tube that penetrated the translucent screen as well as the center of the figure. Using this apparatus we were able to define a particular "fixation point", where the bee decides to land on the tube and where its body axis are adjusted such as to maintain space constancy.

A bee approaching the patterns in free flight has three degrees of freedom for both *rotatory* as well as *translatory* movements: it can perform translatory movements along and rotatory movements around the *longitudinal*, *transverse* and *dorsoventral* body axis (Fig. 1 a). Reichardt and his co-workers have used an ingenious experimental advice to study visual fixation in tethered flying insects [5–7]. In our experiments freely flying bees are used. As will be shown, however, during the process of fixation the

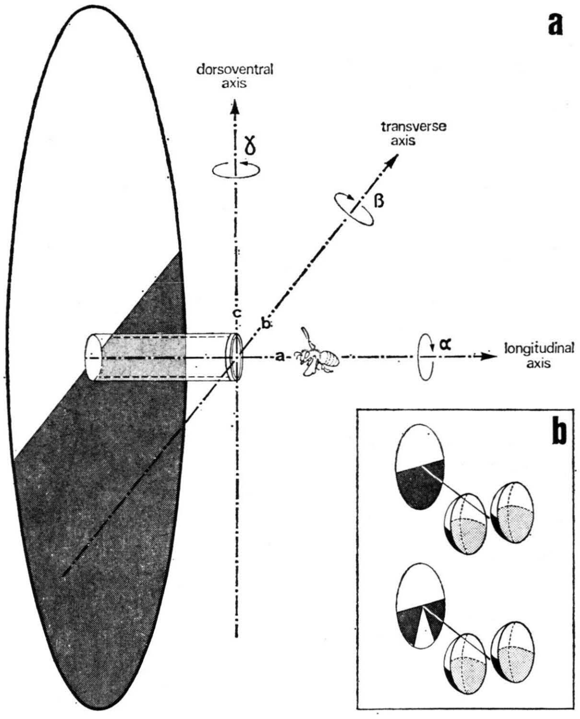

Fig. 1. a) A bee approaching a test pattern. The test pattern consists of a black-and-white disk with the contrast line adjusted horizontally. The bee has to crawl through a Plexiglass tube which penetrates the pattern disk and a translucent Plexiglass screen (*not shown*). The Plexiglass screen extends parallel to the pattern disk at the level of the entrance hole of the tube. The flying bee experiences 6 degrees of freedom: the rotatory components *roll* (α), *pitch* (β), *yaw* (γ) and the translatory components of *backward-forward* (a), *left-right* (b) and *upward-downward* movement (c). b) If the lower halves of both eyes of the bee are covered with light-tight paint, the two patterns shown *above* and *below* are no longer discriminated.

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bees behave like tethered flying bees in a fixed position in space.

There are three lines of direct evidence from which this conclusion can be drawn: *First,* high-speed cinematography, *second,* discriminatory capacities of bees that have parts of their visual fields excluded by light tight paint, and *third,* training bees to patterns that coincide in angular size, but differ in absolute size and in the distance from the opening of the Plexiglass tube. Frame by frame analysis of motion pictures reveals that roll and pitch are stabilized during visual fixation. In determining the possible amount of *roll*, the approaching bee was filmed from ahead through the opening of the Plexiglass tube. Irrespective of whether or not the patterns contained a horizontal line that could be used by the bee for visual course stabilization, the transverse axis of the head was always held in a horizontal position (Table I A). In lateral view the dorsoventral axis of the head is nearly constantly inclined by about 70° to the horizontal (constant *pitch*), irrespective of whether the ventral or dorsal halves of the eyes were occluded by paint (Table I B).

A more sophisticated strategy than just taking motion pictures has to be used if one wants to decide whether *yaw* is restricted to a certain angle during visual fixation. A bee can approach the Plexiglass tube from different directions, and it is only in the final phase of the approach flight that the longitudinal body axis is perpendicularly adjusted to the pattern screen. Only then fixation takes place. This result was obtained by occluding the bee's right or left visual field by means of light tight eye caps. When the right visual field was occluded, patterns that exclusively varied in their right halves could no longer be discriminated, but there was no significant reduction in discrimatory capacity for patterns varying in their left halves (and *vice versa*). If during fixation the bee did not adjust its longitudinal body axis to match that of the Plexiglass tube, it would be able to look at the left part of the pattern with its right visual field. According to the highly significant results in the

Table I. Position of the bee's body axes during visual fixation.

	Rotations around body axes	Translations along body axes
Longitudinal axis	A. *Roll*: $\alpha=0^\circ$ Standard error around 0°-position (horizontal) according to motion picture analysis: (1) S.E.$=0.33^\circ$, $n=69$	D. *Forward-backward movement*: $a=10$ mm Discrimination frequencies (D.F.) between circular black disks of different absolute sizes (training disk: r_1; reference disk: r_2), but equal angular size ($\varrho_1=\varrho_2=59^\circ$) as seen from the fixation point. (1) $r_1/r_2=0.25$, D.F.$=0.55\pm0.08$, $n=69$ (2) $r_1/r_2=0.50$, D.F.$=0.56\pm0.06$, $n=128$ (3) $r_1/r_2=0.75$, D.F.$=0.51\pm0.04$, $n=177$ (4) $r_1/r_2=2.00$, D.F.$=0.52\pm0.07$, $n=60$
Transverse axis	B. *Pitch*: $\beta=70^\circ$ Inclination of the dorsoventral head axis towards the horizontal (1) $\beta=71.7^\circ\pm1.0^\circ$ S.E., $n=625$ (both eyes uncovered) (2) $\beta=69.9^\circ\pm1.0^\circ$ S.E., $n=1293$ (eye caps excluding *upper* visual fields) (3) $\beta=73.2^\circ\pm0.8^\circ$ S.E., $n=1206$ (eye caps excluding *lower* visual fields)	E. *Sidewise movement*: $b=0$ mm see C.
Dorsoventral axis	C. *Yaw*: $\gamma=90^\circ$ Discrimination frequencies (D.F.) for pattern differences in the *right* visual field after excluding the right or left parts of the bee's eyes: (1) D.F.$=0.87\pm0.03$, $n=151$ (controls, both eyes uncovered) (2) D.F.$=0.57\pm0.03$, $n=265$ (eye caps excluding *right* visual field) (3) D.F.$=0.86\pm0.02$, n$=218$ (eye caps excluding *left* visual field)	F. *Upward-downward movement*: $c=0$ mm Discrimination frequencies (D.F.) for pattern differences in the *upper* visual field after excluding the upper or lower halves of the bee's eyes: (1) D.F.$=0.91\pm0.01$, $n=458$ (controls, both eyes uncovered) (2) D.F.$=0.58\pm0.02$, $n=1376$ (eye caps excluding *upper* visual field) (3) D.F.$=0.91\pm0.02$, $n=582$ (eye caps excluding *lower* visual field)

discrimination tests, this "oblique fixation" does not occur (Table I C). Concomitantly, it is proved by the same kind of experiment that the bees do not fixate when they perform translatory movements *to the right* or *to the left* from the axis of the tube (Table I E). The same rationale was applied in checking translational *upward-downward* movements during fixation. If *e. g.* the ventral halves of both eyes were covered, stimulus differences in the lower part of the figures could no longer be detected by the bees (Fig. 1 b, Table I F). Hence, during fixation translatory movements are also excluded along the dorsoventral body axis.

What remains to be tested is the *distance* of the fixation point *from the opening* of the Plexiglass tube, where the bee has to land. The fixation point can be determined by using two black disks of different absolute sizes presented at different distances behind the translucent Plexiglass screen. In this situation the fixation point is then defined as that distance in front of the Plexiglass screen, at which two disks which appear to have identical angular size are mixed up by trained bees. This distance was found to be about 10 mm (Table I D). Bees significantly discriminate between disks that coincide in angular size at distances of either 3 mm or 20 mm.

In conclusion, a freely flying bee fixates a visual pattern by adjusting its translatory and rotatory flight components to constant values relative to a fixation point. As a consequence of this fixation process, a bee ready to land on a food source always views the same parts of the figure with the same parts of the retina. It has been shown by previous experiments that a space-constant internal representation of the visual surround is built up in the visual system of a foraging bee. If subsequently the bee is confronted with a different visual surround, the behavior of the bee is determined by the goodness of fit between the memorized image and the actual retinal image[4] (see also hoverflies[8]). Fixation and cross-correlation of the actual distribution of landmarks with the memorized ones would provide an insect with a fairly simple strategy for re-orientation towards food sources and nest entrances.

Although the problem of visual fixation in insects has only recently come into vogue by the sophisticated and painstaking behavioral work performed in flies[1, 5], it already seems safe to conclude that fixation and foveal vision is in no way restricted to lens eye systems.

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