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Visual lateral fixation and tracking in the haematophagous bug *Triatoma infestans*

C. Lazzari* and D. Varjú

Lehrstuhl für Biokybernetik, Universität Tübingen, Auf der Morgenstelle 28, D-7400 Tübingen, Federal Republic of Germany

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Summary. *Triatoma* bugs turn away from a vertical black stripe on the inner surface of a rotating or oscillating drum by keeping it in the lateral visual field at an angle α relative to the long axis of the body. The value of α depends on the angular velocity w of the drum. Below $w = 5° \text{ s}^{-1}$, α increases with increasing w, and the stripe can lie to either side of the animal. Occasionally, the bugs switch between these two tracking modes. Above $w = 5° \text{ s}^{-1}$, α remains nearly constant at about 120° and the stripe lags behind the animal. We call this *lateral tracking*. At velocities over $5° \text{s}^{-1}$ the animals track the leading edge of a wide black stripe in the same manner as they track a narrow stripe. Below $5° \text{ s}^{-1}$ they walk towards the centre of the stripe (skototaxis). Objects moving towards the insect above the horizon are also fixated at an angle of about 120°. Lateral tracking is mediated mainly by the dorsal part of the visual field, as can be shown by occluding either the dorsal or ventral halves of the eyes. The walking speed of the bugs increases significantly during lateral tracking of an oscillating stripe compared with that during frontal fixation of a stationary one. We therefore interpret lateral tracking as an escape response.

Key words: Bug – Object fixation – Lateral tracking – Escape response – Regional eye specialization

Introduction

Visual stimulation causes several types of behaviour in animals. In insects, the fixation and tracking of objects are elementary functions of the visual system, although stimulation may also cause escape reactions or freezing. The physiological mechanisms underlying the visual behaviour of flying and walking insects have been extensively analysed. Several models have been proposed to account for movement perception, object fixation or course stabilization (see review by Buchner 1983).

In experiments with the haematophageous bug, *Triatoma infestans*, we observed a hitherto undescribed fixation response to moving objects. These animals turn away from an approaching object, but keep it in their lateral visual field. We report here on a detailed analysis of these responses, which we refer to as *lateral fixation*, and *lateral tracking*, respectively, and on the involvement of the dorsal and ventral part of the compound eyes in this behaviour. Some of the results have been presented earlier in a preliminary form (Lazzari and Varjú 1989).

Material and methods

The experimental animals were males of *T. infestans* reared in the laboratory at 30 °C and 50–70% relative humidity, and fed on citrated sheep blood. The experiments were performed 20–30 days after the imaginal moult. For 1 week prior to the experiments the animals received no food.

In the experiments the animals were placed on a locomotion compensator in the centre of a drum, the height and diameter of which were both 16.5 cm. The tethered bug walked on a lightweight hollow styrofoam ball (diameter: 10 cm) supported by air current. The walking animal turned the ball. The position of the panorama, the orientation of the longitudinal axis of the body, and its direction of locomotion and speed could all be recorded simultaneously with a sampling rate of 10 Hz. For further details see Dahmen (1980). The drum had a panorama on its surface and could either be rotated with a uniform angular velocity or oscillated around the animal, the head of which was fixed with wax to the thorax. The bugs could rotate freely. The panorama consisted of a black stripe on a white background, either 9.8° or 113° wide, subtending 58° above and 22° below the insect's horizon. The drum was homogeneously illuminated from the outside by means of regularly spaced incandescent light bulbs. The luminosity at the position of the animal amounted to 60 lux.

In one experiment a motor-driven black disc 2 cm in diameter was moved along a straight path towards and away from the animal just above its horizon with a speed of 1.5 cm s^{-1}.

To elucidate the contributions of different regions of the eye to the response, the visual fields of the animals were partially occluded. Either the ventral or the dorsal halves of both eyes were covered with black acrylic paint.

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* *Present address:* Departamento de Biologia, Facultad de Cs. Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, (1428) Buenos Aires, Argentina

Results

Lateral tracking

When a drum with a 9.8°-wide black stripe was rotated around the bugs, they also rotated, keeping the centre of the stripe at an angle α relative to the longitudinal axis of the body (Fig. 1a). The value of α varied with the angular velocity w of the drum (Fig. 1b).

Above $w = 5^\circ\,\mathrm{s}^{-1}$, α remained nearly constant at an average value of 123° as the insects turned away from the stripe approaching from behind (Fig. 1b; for the geometry of the situations, see insets).

Within the range of $w = 0^\circ\,\mathrm{s}^{-1}$ to $w = 5^\circ\,\mathrm{s}^{-1}$ the value of α increased with w from 0° (stationary drum, frontal fixation) to its final value (lateral fixation). Here, however, the stripe could lie to either side of the animal, which switched between these two tracking modes, with the same value of α in each direction (Fig. 2c).

The response to a wide black stripe

In these experiments the black stripe was 113° wide. When the drum was stationary or its angular velocity remained below $5^\circ\,\mathrm{s}^{-1}$, the insects walked towards the centre of the stripe, a response termed skototaxis. Above $w = 5^\circ\,\mathrm{s}^{-1}$ the leading edge was kept at the same angular position as the narrow stripe in the previous experiments (Fig. 3).

The response to approaching objects

The above experiments indicate that *Triatoma* avoids rotating objects by keeping them fixated in the lateral

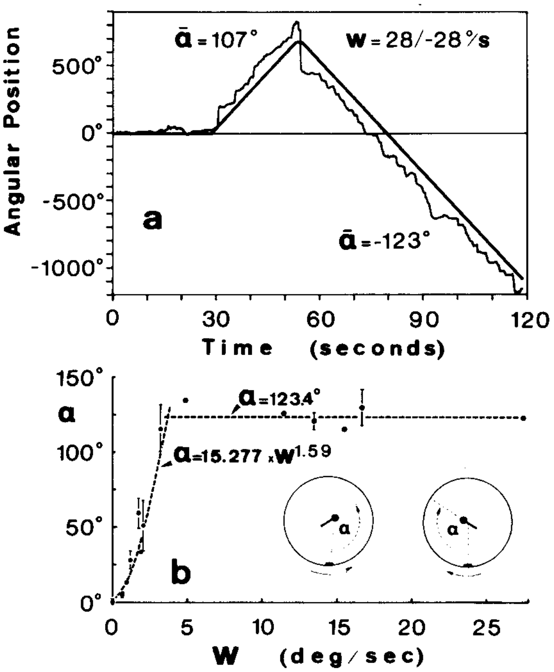

Fig. 1a, b. The sample record shows the angular position of the centre of a black stripe (*smooth line*) on the inner surface of a white drum rotating with angular velocity w, and that of the longitudinal axis of the animal's body (*jerky line*). Here and in all subsequent similar records a positive slope indicates counterclockwise rotation. α Average angular position of the stripe relative to the longitudinal axis of the body (tracking angle). **b** Tracking angle α versus angular velocity w of the drum. Average values with standard error obtained using 33 animals. Dashed lines: Power function fitted to the data within $0 \leq w \leq 5^\circ\,\mathrm{s}^{-1}$, average value above $w = 5^\circ\,\mathrm{s}^{-1}$. *Inset*: Geometrical situation during counterclockwise (*left*) and clockwise rotation of the drum

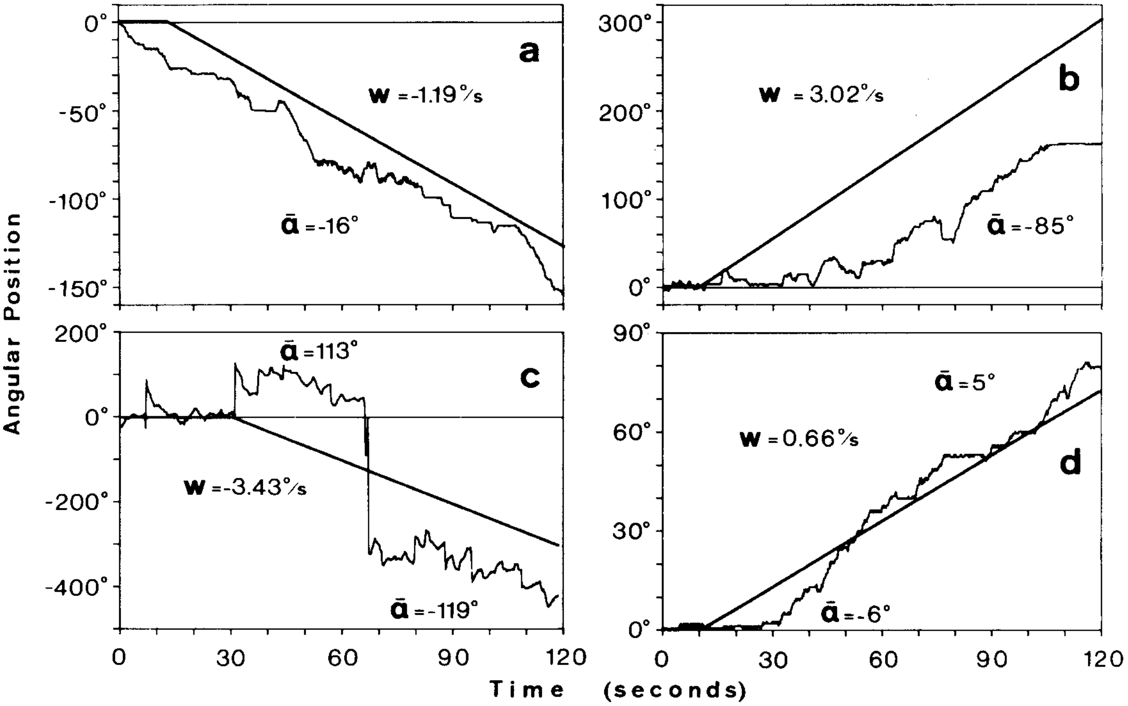

Fig. 2a–d. Sample records of tracking under the same condition as in Fig. 1a, but with angular velocities w below $5^\circ\,\mathrm{s}^{-1}$. Same conventions as in Fig. 1. The tracking angle α shows considerable scatter and the stripe can switch from one side of the animal to the other while the direction of drum rotation remains the same

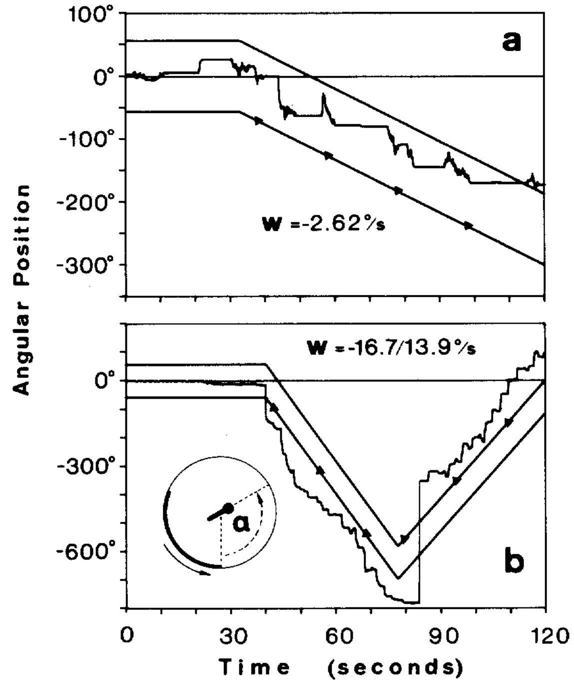

Fig. 3a, b. Sample records of tracking a 113°-wide black stripe at different angular velocities *w* of the drum. Same conventions as in Fig. 1. *Triangles* mark the leading edge of the stripe. At low velocities the bug walks towards the centre of the stripe. Above $w = 5° \text{ s}^{-1}$ the leading edge is kept in the lateral part of the visual field

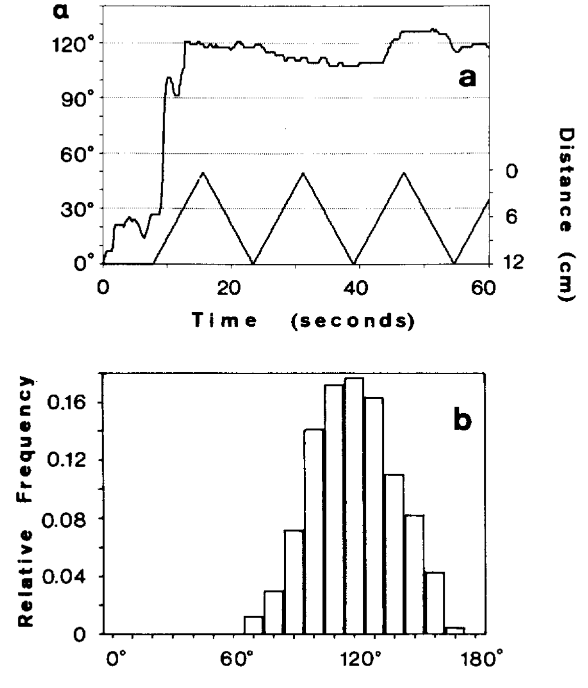

Fig. 4a, b. Response of the bugs to an approaching target. A black disk, diameter 2 cm, was moved towards and away from the insect above its horizon with a speed of 1.5 cm s^{-1}. **a** Sample records of the angular position between the longitudinal axis of the body of an animal and the path of the approaching object (*jerky* lines, left ordinate), and the distance of the object to the centre of the drum (*smooth line*, right ordinate). **b** Frequency of the α values obtained in 10 experiments with 5 bugs. Mean value: 119.8° ± 22.6°

part of the visual field. Under natural conditions objects do not rotate around the bugs, but approach along straight or curved paths. We therefore asked whether or not such objects also elicit lateral fixation.

A black disk 2 cm in diameter was moved straight towards and away from the animal above its horizon, with a uniform velocity of 1.5 cm s^{-1}. In Fig. 4a we show a sample record of the angular deviation α between the path of the object and the longitudinal axis of the body. Note that both the approaching and retreating object elicit lateral fixation, while a stationary object can be anywhere within the visual field. In Fig. 4b the distribution of α is plotted. The data were obtained in ten experiments with five animals, and with a total of 6000 samples. The response resembled that for rotating stripes. The animals tried to run away from the object, keeping it at an average angle of 119.8° ± 22.6° (SD) relative to the longitudinal axis of the body.

Oscillating drum

Other insect species investigated so far fixate and track narrow black stripes or the edges of wide stripes with the frontal part of the eyes. Object fixation in flies (Reichardt 1973) and edge fixation in the mealworm beetle (Varjú 1976, 1987) require relative motion between the animal and black stripe.

However, the panorama does not have to be rotated around the animal; oscillation with a suitable frequency and amplitude is sufficient. Now *Triatoma* avoids approaching or rotating objects, but keeps them within

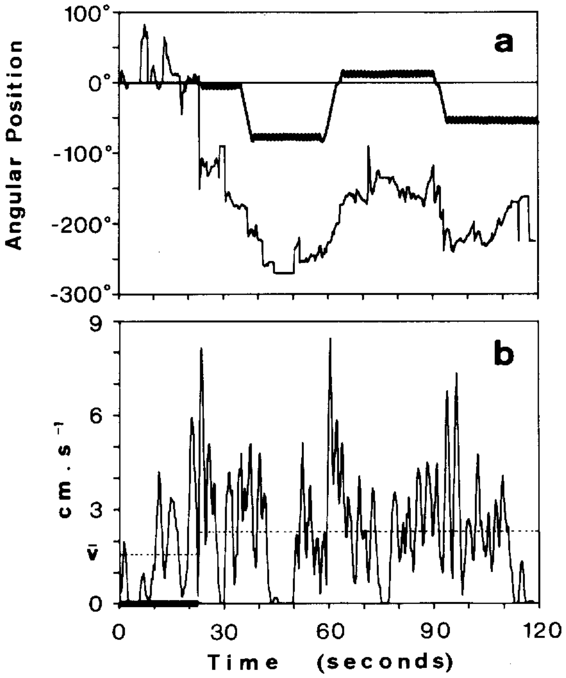

Fig. 5a, b. Lateral fixation of a 9.8°-wide black stripe that oscillates sinusoidally with 1 Hz frequency and 9° amplitude at different angular positions in the absolute coordinate system. Sample records of the angular positions **a** and the translational velocity *v* of the bug **b**. *Dashed lines* in **b**: Average values before and after the onset of oscillation

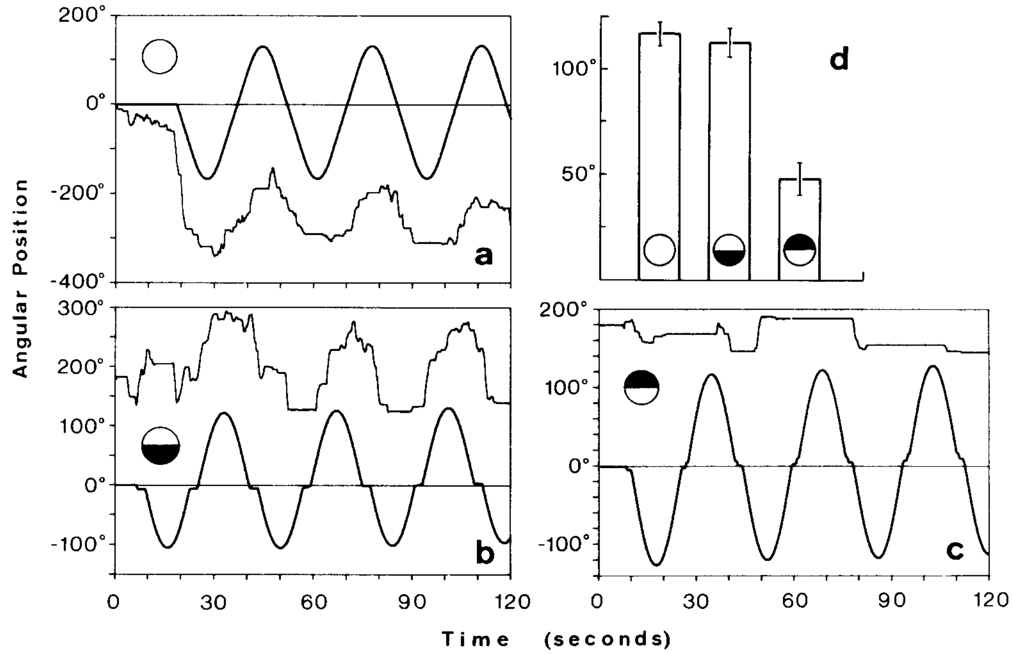

Fig. 6a–d. Tracking of a 9.8°-wide black stripe subtending 26° above and below the horizon oscillating sinusoidally with a frequency of 0.04 Hz and amplitude of 120°. **a** Unimpaired animal. **b** ventral, **c** dorsal half of the eyes occluded. Conventions as before. **d** The average amplitude of the body oscillation under the above conditions (cf. pictograms). The response of the ventrally blinded animals does not differ from that of the unimpaired ones. That of the dorsally blinded ones is significantly reduced (*t*-test, $P<0.0001$). Ten experiments with five animals under each experimental condition

the lateral part of the visual field. It was therefore of particular interest to see whether a small amplitude oscillation of the drum also elicits lateral fixation.

A sample record of the angular position of a 9.8°-wide black stripe and that of the walking direction of the animal versus time is shown in Fig. 5a. In this experiment the drum oscillated at 1 Hz with an amplitude of 9°. The centre position of the stripe was shifted three times in a steplike manner. The bug kept the oscillating stripe at the same position in the visual field as a rotating stripe.

The animals vigorously increased their walking speed v when the rotating stripe entered their visual field. This was also the case when the oscillating and laterally fixated stripe changed position, as shown by the sample record in Fig. 5b. Walking speed could increase fivefold compared to the average value during frontal fixation, after which the initial peak v declined and the animal seems to become habituated. However, even the average value during lateral fixation of a repeatedly displaced oscillating stripe was significantly higher than that during frontal fixation, the values being 1.71 ± 0.04 (SD) and 2.10 ± 0.03 (SD) cm s^{-1}, respectively ($P<0.001$, 6000 samples). We therefore interpret lateral fixation as an escape response.

The regional specialization of the compound eye

Regional specializations of the eyes have been described in several arthropods. Structural (Zeil 1983; Dahmen and Junger 1988) and functional (Reichardt 1973; Wehrhahn 1984; Varjú 1987) specializations are considered to be adaptations to the environment and habits of the animals (see review by Land 1989).

The compound eyes of *T. infestans* have a rather small number of facets, about 300 in adults (Settembrini 1984). They are spherical with a cuticular ridge at the posterior zone and extend far ventrally. Although no exact data are available on the visual field of the bugs, our anatomical measurements indicate that the antero-posterior extent of the visual field in the horizontal plane is somewhat more than 140°.

In order to investigate the involvement of the different regions of the eyes in lateral tracking we covered either the ventral or the dorsal halves of both eyes with black paint. In these experiments a 9.8° wide black stripe oscillated at 0.04 Hz with an amplitude of 120°. The amplitude of the oscillation of the long axis of the body was measured in both experimental groups and in a control group of unimpaired animals.

Sample records of the angular position versus time for all three groups are shown in Fig. 6a–c. The bars in Fig. 6d represent the average values with twofold standard error obtained in ten experiments with five animals in each group. The number of samples amounted to 6000 in each case. The response of the bugs with their eyes occluded ventrally did not differ from that of the controls. However, covering the dorsal half of the eyes drastically reduced the response of the bugs ($P<0.0001$).

Discussion

To our knowledge this kind of lateral tracking has not been described before in insects. A different kind of lateral tracking has been observed by Collett and Land (1975) in the hoverfly *Syritta pipiens*. In rare instances male hoverflies attempt to keep a target in a lateral position at about 30° and not straight ahead.

The biological function of the response described here seems to be related to defensive behaviour. The regional specialization of the compound eyes, the increase of the walking speed and the response to an approaching disk all support this interpretation. Approaching predators appear, as a rule, in the dorsal visual field of the insects. Antiparasitic actions of the hosts are also perceived within this region. In contrast, the visual field below the horizon might serve to perceive conspecifics.

It is worth noting that an object does not have to increase in apparent size in order to elicit the response. A retreating object is as effective. If the response is an escape, as we believe, then the underlying mechanism is quite different, for example, from that in crabs. There, looming detectors have been postulated to be crucial for eliciting escape (Nalbach 1990). The bug apparently perceives any fast-moving object as potential enemy.

The defensive value of keeping a potential enemy at a particular angle relative to the longitudinal axis of the body is obvious. The ideal value of the escape angle α might be 180°, but in this case the insects could not see the predator since the anteroposterior extent of the visual field is only about 140°. Keeping the enemy at an angle of about 120° rather than further behind can thus be understood. An object tracked at the limit of the visual field could easily come into the posterior blind area if it moved backwards or the insect forwards. Not to see the predator would be more dangerous than the adoption of a suboptimal escape direction.

It would be interesting to know whether the escape angle is changed when a potential shelter is seen nearby, as observed in crabs (Nalbach 1990). In these arthropods the escape direction can be predicted by calculating the sum of two vectors, one of which points directly away from the predator, and the other towards a possible shelter, such as a hole, the coastline or a shadow.

We are also puzzled by the way fixation changes at low angular velocities (Fig. 1b). We thought that two stable fixation angles might exist, 0° for stationary and slowly moving objects, and about 120° for objects with angular velocities higher than $5° \mathrm{s}^{-1}$. If this were the case, one would expect a bimodal distribution of the angle α around these two values. With increasing angular velocity w, the animal would fixate the stripe more and more frequently at 120° than at 0°, and the average value of α would smoothly shift from 0° to 120°. Such a process could easily be modeled on the basis of our knowledge of fixation mechanisms in other insect species. Nevertheless, we needed additional information to explain why the stripe can lie to either side of the animal at low angular velocities. However, our data did not reveal a bimodal distribution; the transition was smooth and not the consequence of averaging. We suggest, therefore, that at low angular velocities the animal simply tries to keep to a straight course by fixating the stripe frontally. Since the target rotates, the animal must turn, and leg proprioceptors might signal deviations from the intended straight course. The concurring visual and proprioceptive input would lead to a stable angle α off midline, the value of which would increase with increasing angular velocity. To find out what mechanism underlies this transition, the characteristic function of the feedback loop, that is the amplification as a function of the angular deviation between objects and longitudinal axis of the body, should be determined in open-loop experiments, as has already been done in the case of the fly (Reichardt 1973) and the mealworm beetle (Varjú 1976).

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