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Drift compensation and its sensory basis in waterstriders (*Gerris paludum* F.)

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Summary. Watestriders (*Gerris paludum* F.), displaced by flowing water or wind, compensate for this by periodic jumps against the direction of drift so that they keep their average position – relative to the river bank, for instance – constant over long periods of time. To identify the cues used by the animals to compensate for drift, they were kept on an artificial stream with visual patterns along one or both sides. The velocity of the water flow and the pattern motion were varied. It is not possible to induce compensatory jumps in darkness by water or air current alone. Visual cues are indispensable for the reaction. The product of jump amplitude and jump frequency equals the drift velocity on average. The jump amplitudes are more or less independent of the flow velocity while the jump frequency is adjusted to it.

Key words: Visual behaviour – Position control – Retinal image processing

Introduction

Flying insects need visual information to control their speed and flight direction over ground. Heran and Lindauer (1963) have demonstrated for bees, Collett (1980) for hoverflies, and Preiss and Kramer (1983) for moths that these animals are equipped with a visual feedback mechanism to control flight velocities over ground. Walking insects, on the other hand, can detect changes in speed and deviations from a straight course not only visually but also with various other senses. Proprioception plays an important role (cf. Jander et al. 1970; Görner 1973; Mittelstaedt and Mittelstaedt-Burger 1973; Zanker and Collett 1985). It provides reliable information of self-motion which is independent of other influences such as wind velocity.

Various species of waterstriders live on flowing water. Usually they prefer quiet or slowly moving water zones but often leave these areas to forage at sites with stronger currents. At a narrow passage, waterstriders will find a rich supply of prey (Wilson et al. 1978), provided they compensate for drift. They can indeed be observed in the field to keep their position in space stable for hours.

Moreover, investigations by Rubenstein (1984) revealed that the strongest females, i.e. those which are able to maintain their position in areas with strong current, have a mating advantage. Large males copulate preferably with such females.

Waterstriders are also displaced on still waters by wind. This kind of displacement is also compensated for, often over long periods of time.

The locomotor system of waterstriders, however, does not allow them to compensate for drift continuously. Instead, compensation is achieved by single powerful rudder strokes of the middle legs. Consequently, they must tolerate an increasing deviation from the set position for a certain time, that is until the next jump is performed. To be effective, such a rudderstroke has to be fast and carried out simultaneously on both sides. The rapid translocation of the body after a rudder stroke is referred to hereafter as a compensatory jump.

Animals which can maintain their position against water currents or wind must be able to sense the amount and direction of position changes and to control their own motor activity accordingly.

In the following, we describe the animals' behaviour on a flowing water surface and present experimental results to identify the senses which enable them to detect deviations from a chosen position.

Materials and methods

Animals. Waterstriders (*Gerris paludum* F.) were collected from ponds and quarry lakes around Tübingen. They were kept in a 50 × 90 cm aquarium and fed on wingless *Drosophila*. The behaviour of captive animals did not differ from that of free-living ones, as far as this can be concluded from observation. Hungry animals react better in experiments than satiated ones. Before an experiment, therefore, the animals received no food for 2 days.

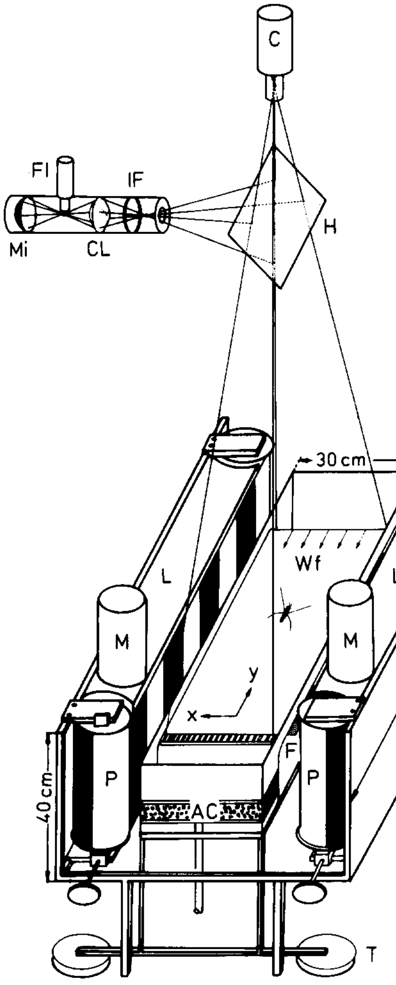

Fig. 1. Artificial canal with laminar water flow (*Wf*). *AC* active carbon; *M* step-motors; *L* light sources; *P* stripe pattern, *C* video camera; *H* half-silvered mirror; *F* reflection foil; *IF* infrared filter; *Fl* flash light; *Mi* mirror; *CL* condenserlense; *T* rubber tubes

Artificial canal. The experiments were carried out in a Perspex canal, 110 cm long and 30 cm wide (Fig. 1). It was levelled out exactly and placed on air-filled rubber tubes to prevent the transfer of vibrations from the building. A centrifugal pump raised water into a vessel that served as a buffer and opened into the canal. The overflowing water flooded the canal. The water level was controlled by a gate at its outlet. The outflowing water was collected in a second vessel and recycled by the pump. The water current was laminar; its velocity could be adjusted to values between 0.5 and 25 cm/s.

Black and white vertical stripe patterns (wavelength 10 cm, height 20 cm) were placed along one or both sides of the canal. They were homogeneously illuminated from behind with DC-operated light bulbs and could be moved horizontally by means of step motors. To prevent transfer of vibration from the pattern, the stimulation apparatus was mounted on a separate frame without mechanical connection to the canal.

Recording. The animals were filmed from above with a video camera (Ultricon) and a 3/4" U-matic video recorder. The scene was illuminated by an infrared flash; flash and camera were synchronized (frame interval 20 ms). The light was directed through a condenser and a half-silvered mirror tilted at 45° to the optical axis of the camera. A reflection foil (Scotch 3M) was placed underneath the transparent bottom of the canal, which reflected the light back to the lens of the camera through the half-silvered mirror. Through this arrangement the animals could be recorded without motion blur in spite of the fast rudder strokes which last less than 10 ms. The energy of the infrared flash could be kept very low because nearly the total amount of light reflected by the foil was captured by the aperture of the camera. Waterstriders are not sensitive to infrared light of wavelengths over 800 nm (Hamann and Langer 1980).

Data analysis. The video pictures were projected frame by frame onto a digitizing board, and the front and rear coordinates of the animal and also that of the pattern when it was moved were read into a computer with a sampling rate of 20 ms.

Results

Drift compensation on flowing water

Waterstriders placed on the water surface in the canal with laminar flow and patterned banks turn to face the current as soon as they drift. Thereafter, they periodically jump upstream (Fig. 2), keeping the distance from the banks relatively constant.

A compensatory jump can be divided into 2 phases:

1. Jumping phase T_j: The animal accelerates against the current and is then gradually stopped due to friction in air and on the water surface.

2. Drifting phase T_d: It begins when the velocity of the animal changes sign (relative to the canal coordinate system) and ends with the beginning of the next jump. The time interval between the initiation of two subse-

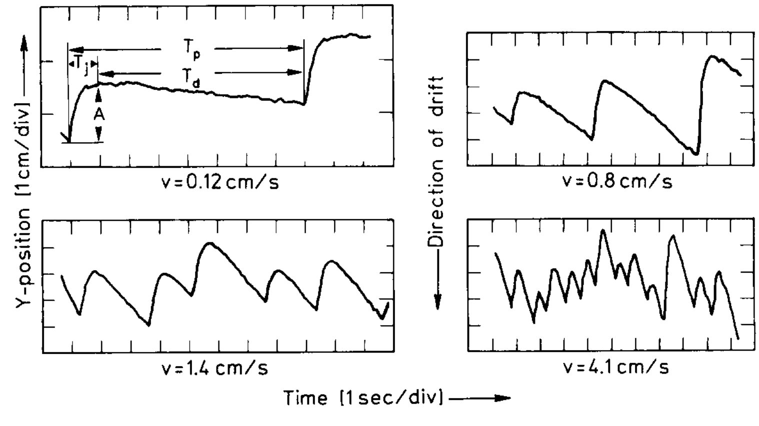

Fig. 2. The longitudinal coordinate Y of the animal's position (as defined in Fig. 1) plotted over time. Different flow velocities *v*. Stationary patterns (vertical black and white stripes, wavelength 10 cm, height 20 cm) are placed on both sides of the canal. T_d drifting phase; T_j jumping phase; T_p jump period; *A* jump amplitude

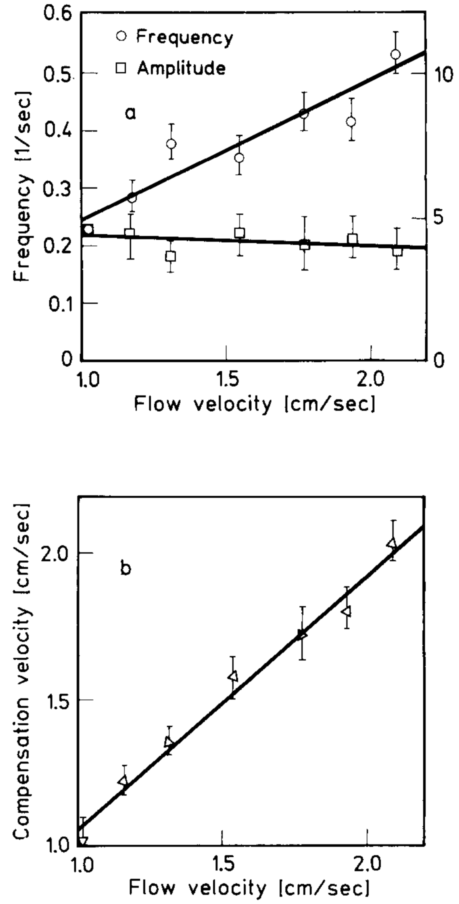

Fig. 3. **a** The amplitude of the compensatory jumps (□) is independent of the flow velocity to be compensated for (regression equation: $Y = a + mx$, slope $m = -0.036$; ANOVA test: not significant), whereas the jump frequency (○) is positively correlated with the flow velocity ($m = 0.237$; significance level $P < 0.002$). Lines are fitted by linear regression. The mean value of the jump amplitude is 4.18 cm. **b** The mean compensation velocity of the animal ($V = f \times A$) as a function of the drift velocity. A and f are the average jump amplitude and frequency as illustrated in **a**. The slope of the regression line is $m = 0.87$; significance level $P < 0.0001$. This means that the compensation velocity is always close to the flow velocity and hence that compensation is almost perfect

quent jumps is called the jump period, T_p, and its reciprocal value the jump frequency, f.

The compensatory jumps shown in Fig. 2 are typical. The longitudinal coordinate Y of the animal's position (relative to the external coordinate system) is plotted versus time.

The jump frequency and stream velocity are correlated when the pattern is motionless. The jump amplitude is by and large independent of the stream velocity (Fig. 3a). The product of the average jump frequency, f, and the average jump amplitude, A, is equal to the stream velocity (Fig. 3b).

This compensatory reaction is often interrupted by other types of behaviour. When a waterstrider catches prey dropped onto the water surface, it stops compensating drift for the time it needs to reach and seize the prey (Fig. 4a, arrow). The displacement during this period is compensated for afterwards by a series of jumps of increased frequency. The same can also be observed when the animals clean themselves. This happens usually when they are transferred from the aquarium to the canal, presumably as a reaction to differences in the water quality.

Frequently, waterstriders fixate one edge within the pattern and move with quick jumps towards and attack it (Fig. 4b). Excursion across the canal are even more frequent; the ends of the canal appear to be particularly attractive. This behaviour can be interpreted as searching.

The sensory basis of drift compensation

Waterstriders are thus able to sense and to compensate for passive displacement relative to their surroundings with a specific set of reactions. In general, they could perceive the amount and direction of the passive displacement relative to their environment by means of different sensory inputs.

1. Perception of air current: Waterstriders are provided with sensory hairs, which are very sensitive to air cur-

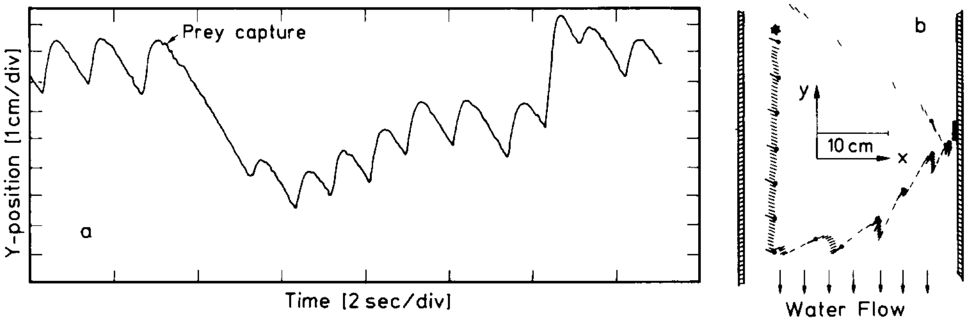

Fig. 4a, b. A waterstrider's behaviour in an optically structured environment. The longitudinal coordinate Y of the animal's position on flowing water in the artificial canal is plotted versus time. **a** In the left half of the picture it is shown how a waterstrider interrupts drift compensation and loses position when catching prey (arrow). Afterwards, by a series of jumps of increased frequency the former position is adopted again. **b** Successive positions of a waterstrider (top view), which passed a stationary black stripe and attacked it thereafter. The direction of water flow is indicated by arrows, the orientation of the animal by short lines. Head positions are indicated every second by black dots. The sequence starts at the asterisk. Flow velocity: 50 mm/s, stripe width: 2.5 cm

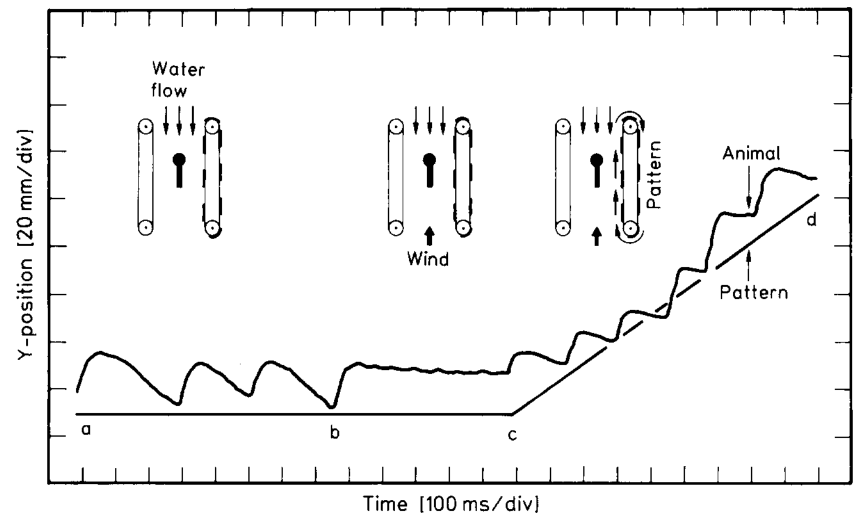

Fig. 5. Conventions as in Fig. 2. This experiment demonstrates that visual cues are essential for drift compensation. Section a–b: compensatory jumps, when the pattern is stationary and the water flows. If displacement is counterbalanced by an air current the animal stops drift compensation (section b–c). In this equilibrium state between water and air flow the animal follows a moving pattern (section c–d)

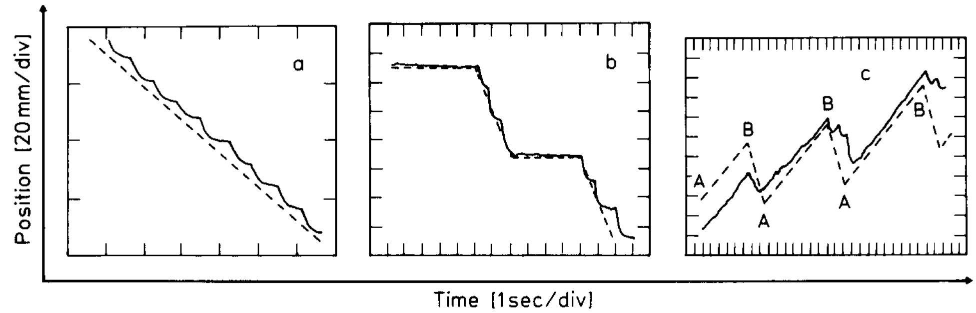

Fig. 6a–c. Conventions as in Fig. 2. Positional stability is guided by visually detected relative movements. **a** A waterstrider follows a stripe pattern which moves with uniform velocity at one side of the canal, while the water remains motionless. Pattern velocity: 1.1 cm/s. **b** The same experimental situation as in **a**, but the pattern motion is interrupted, and pattern velocity is incresased to 3.75 cm/s. **c** The pattern is moving either with (section A–B) or against (section B–A) the water current. Flow and pattern velocity are equal ($v = 1$ cm/s). The relative velocity between animal and pattern is zero, when the pattern is moving with the current. In this situation the animal does not compensate for drift (A–B)

rents (Rensing 1962). It is possible that a waterstrider uses air currents to perceive both drift direction and speed, at least when there is no competing wind.

2. Tactile perception of water current: When a waterstrider is displaced by wind on a motionless water surface, the tibial and tarsal mechanoreceptors are stimulated. This could provide a sensory input to perceive displacement relative to the water surface. Appropriate sense organs have been identified for the backswimmer *Notonecta glauca* (Wiese 1974), and it is probable that waterstriders have such sensors, too (Murphey 1971; Jamieson and Scudder 1979).

3. Analysis of retinal image motion: The structure and resolution of the waterstrider's compound eye are well-known (Bedau 1911; Rensing 1962; Schneider and Langer 1969; Hamann and Langer 1980; Junger and Dahmen 1986; Dahmen and Junger 1988). Presumably, waterstriders perceive and process optical stimuli in ways comparable with those identified in other insects such as optomotor response, fixation and landmark orientation.

The disadvantages of wind and/or water current perception are obvious. These receptors might mediate ambiguous – under unfavourable circumstances even contradictory – information regarding displacement, when water current and wind are present and perceived simultaneously.

The following experiments were performed to uncover the role of different senses in the compensatory behaviour. The animals were placed in the surface of flowing water in complete darkness. They were carried by the current downstream to the end of the canal; no compensatory strokes occurred. This proves that wind receptors are insufficient.

To corroborate this statement and to exclude tactile drift perception a striped pattern (wavelength 10 cm) was placed on only one side of the canal. The other side of the canal and the ground were homogeneous[1]. One consequence of this asymmetrical arrangement was that the experimental animals stayed – during compensation – more frequently close to the pattern rather than in the middle of the canal (cf. Kirchner and Srinivasan 1988). A bug was placed on the water surface that was flowing at a speed of 12.5 cm/s. The pattern was stationary. As soon as the animal had settled down and begun

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[1] We chose this optical environment in order to answer a number of different questions not dealt with in this paper

to compensate drift (section a–b in Fig. 5), a fan was switched on at the downstream end of the canal. Previously, the air current was set to a level at which the displacement of the waterstrider was exactly counterbalanced so that it came to a standstill relative to the banks (section b–c in Fig. 5). The bug immediately interrupted compensation. It behaved as if on a motionless water surface with no wind, although wind and leg receptors would have signalized displacement in the same direction. As soon as the pattern was set in motion, the animal began to compensate (section c–d in Fig. 5). Consequently in this experimental situation the animal reacted to an optical motion stimulus alone.

In another experiment the water and optical surround were motionless during the settling-in phase. Thereafter, the pattern had been moved with uniform velocity. The waterstrider adjusted the direction and frequency of its compensatory jumps to the velocity of the pattern, such that its mean velocity relative to the moving pattern became 0 (Fig. 6a, b). Finally, the water was set into motion as well, while the pattern was moving either with or against the current. The waterstrider responded to the relative movement of the pattern, i.e. to the difference between pattern and water velocity (Fig. 6c). This is an additional evidence that stabilization of position in waterstriders is guided by vision alone.

Discussion

Animals foraging in narrow passages with a strong current have a rich supply of prey, since many insects falling into the water further upstream will pass by. On the other hand, to compensate for their own drift costs energy. Whether such a trade-off is positive, and how much surplus energy is gained, could only be established in a detailed cost-benefit analysis which is rather difficult to carry out (cf. Hart 1987).

During drift compensation on the surface of flowing water, a waterstrider has to perform several tasks.

(a) It has to detect both longitudinal and transverse components of its passive translation velocity. This is required in order to face the water current. If the water current is inhomogeneous within the reach of the legs, the animal might be rotated around the yaw axis. In this case the rotation velocity has to be perceived, too.

(b) The displacement from the selected position has to be evaluated and compensated for.

(c) The animal has to be able to find its way back to a favoured site after extensive excursion.

According to the results presented here, waterstriders rely on vision during drift compensation. The question arises as to which one of the following types of optical information processing might underlie the animals' response.

1. Optomotor response

As demonstrated in numerous experiments in various species, animals perceive and compensate for the relative angular velocity between retina and their surroundings (e.g. Buchner 1976; Hausen and Egelhaaf 1989; Wehner 1981). When the animal or the panorama is rotated, the 'slip speed' is the same across the entire visual field, but during translation it varies for example with the distance between animal and objects. The optomotor response to rotating panoramas depends on pattern features such as luminosity, contrast and spatial frequency composition, and there is always a slip speed between the animal and its surroundings. To maintain a constant position by means of velocity-dependent sensory inputs a temporal integration of the signals is needed, as postulated also in connection with the vestibulo-ocular reflex in mammals (Precht 1978). While spatial integration of velocity signals seems to be an easy task and has been demonstrated, e.g. in flies (Hausen 1982), temporal integration on a neural level appears to pose high requirements to the nervous system (Shen 1989). Furthermore, mechanisms were needed to eliminate the dependence of the response on pattern properties, a problem extensively discussed in connection with the landing response of flies (Borst and Bahde 1986). Moreover, waterstriders are also able to compensate for drift when the only visible object is a faint pointlike light source, as will be described in detail in a forthcoming paper. It is therefore unlikely that the optomotor system might enable the animals to perform tasks (b) and (c).

2. Fixation

As demonstrated by ample research in several species (see references in Buchner 1976; Wehner 1981), insects are able to maintain their relative angular position to an object, a response referred to as fixation. Such a mechanism might enable waterstriders to maintain a desired position in space. The problem is, however, the selection of a distinct object in a richly structured environment, such as a stripe pattern among natural banks with abundant vegetation.

3. Landmark orientation

The use of the relative position of several landmarks in spatial orientation has also been demonstrated in different insect species (Wehner 1981; Collett and Land 1975; Cartwright and Collett 1982, 1983; Zeil and Wittmann 1989). This mechanism, in detail not fully understood, might participate in solving both tasks (a) and (b) in waterstriders. It cannot explain, however, the results of the above-mentioned experiment with a single pointlike light source. To perform task (c), landmark orientation is at present the only choice.

4. Analysis of the optical flow-field

Local analysis of the optical flow field would allow in principle for the exact assessment of self-motion with all possible degrees of freedom (Lounguet-Higgins and

Pradzny 1980; Koenderink 1986; Koenderink and van Dorn 1987). Such an mechanism requires, however, very sophisticated neural operations and a reliable perception of retinal position and velocity of contrast elements. It is questionable whether the central nervous system of waterstriders is capable of performing such pretentious tasks.

Our present results demonstrate that visual cues are essential for position stability of waterstriders, but they do not allow for secure conclusions as to what extent the various possible visual mechanisms contribute to the performance of this task. Current and future investigations centre on this question.

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