Set point of retinal velocity of ground images in the control of swarming flight of desert locusts

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Summary. 1. The visual control of ground speed in the flight of gregarious desert locusts, *Schistocerca gregaria*, was investigated under open- and closed-loop conditions. Locusts were flown tethered in a wind tunnel, and ground pattern motion in line with their longitudinal body axes was used to simulate the visual effects of headwind and tailwind while the locusts' flight thrust and yaw-torque were monitored.

2. In open-loop experiments, a correlation between thrust and pattern speed modulation was observed only when pattern speed modulation crossed $0°/s$, (i.e. when the pattern direction of movement reversed). Otherwise thrust was kept constant at one of two extreme levels, depending on whether patterns moved progressively or regressively. When pattern motion was stopped intermittently, thrust production approached a mean level between the two extremes, which was assumed to be a "preferred" value.

3. In closed-loop experiments, a regressive bias of pattern motion used was counteracted by a compensatory modulation of thrust. Pattern speed was in this way minimized. Quality of bias compensation differed both between experiments and during an experiment. In some of the experiments, the residual mean slip speed, though variable, was proportional to the strength of the bias. In other experiments the pattern was stopped, except for a small amount of positional jitter, over a wide range of bias modulation.

4. Compensation for the pattern motion bias was restricted to a limited range of bias modulation. Beyond this range, thrust was always strongly increased, independent of whether the biased motion was too slow or too fast for compensation by thrust modulation.

5. The thrust response was often combined with a modulation of yaw-torque, especially when the biased pattern speed was beyond the range of compensation by thrust.

6. The results from both open- and closed-loop experiments indicate that in visual control of ground speed locusts tend to minimize the retinal velocity of ground images. It is suggested that this may be a general charac-teristic of the visual flight control system in swarming desert locusts.

Key words: Locust – *Schistocerca* – Optomotor flight control – Visual orientation – Swarming flight

Introduction

Numerous observations on the behaviour of day-flying locusts in the field have led to the generally accepted hypothesis that wind plays an important role in determining the orientation of desert locusts in flight. As first pointed out by Kennedy (1951), this wind-related orientation seems to be mediated by optomotor responses to the apparent movement of ground images over the ventral ommatidia ("optomotor anemotaxis"; Kennedy 1939). This movement results from the vectorial addition of the locust's own flight manoeuvres and motion induced by wind.

It was originally thought that the direction of orientation depended rather simply on wind speed, with locusts tending to fly into the wind while their flying speed exceeded that of the wind, but otherwise turning out of the wind or downwind, in order to avoid drifting backwards over the ground (Kennedy 1951). At high wind speeds, downwind orientation is indeed observed to dominate, but at wind velocities up to about 5 m/s (as most frequently measured during swarming flight in the field), close observation has shown that swarms consist of large numbers of groups of flying locusts with a wide diversity of mean orientations; in addition, at both the leading and trailing edges of the swarms, locusts actively head into the swarm and so contribute to its cohesion (Waloff 1972). The cumulative effect of the varied and changing orientations of individuals is that swarms as a whole tend to simply drift downwind (Rainey 1963; Waloff 1972), although evidence for off-wind bias has been reported by Casimir (1987). Typically the speed of swarm displacement observed is only a fraction of the

wind speed (Rainey 1963); an effect which would be produced if individual locusts settle periodically (behaviour which has been observed in low flying swarms; Kennedy 1951; Waloff and Rainey 1951), or, if in high flying swarms, upwind orientation predominates.

The observed variability of locusts' wind-related orientation behaviour in the field was confirmed by laboratory experiments in which locusts were flown tethered in a wind tunnel, and ground pattern motion was used to simulate the visual effects of wind drift (Preiss and Gewecke 1991). Three of the locust flight parameters (yaw-torque, thrust and lift) were seen to be modulated, correlated with direction-reversing cycles of pattern motion. Thereby, two opposing types of response were observed for each flight parameter and they occurred with equal frequency. The polarity of responses was maintained throughout an experiment or reversed repeatedly. The yaw response thus revealed a tendency for locusts to orient either upwind or downwind; in addition, indications of a menotactic orientation to wind were obtained. The thrust and lift responses confirmed that locusts attempt to compensate for deviations from a preferred retinal image flow rate, as has been postulated from field observations, by adjusting both air speed and altitude (Kennedy 1951; Waloff 1972). Neither field nor laboratory studies, however, have to date revealed the value of this preferred rate (the set point of the underlying control circuit); the present paper deals with its determination by means of open- and closed-loop experiments.

Materials and methods

Desert locusts, *Schistocerca gregaria* Forsk., of both sexes from a crowded laboratory culture were used. The test animals were at least 10 days past their imaginal moult, and their body-colour was no longer pink. For the experiments, a small metal pin was waxed to the locust's dorsal pronotum. The pin was subsequently used to attach the locust to a friction-free force transducer which prevented both rotatory and translatory movements of the animal, but allowed simultaneous measurement of the instantaneous yaw-torque and thrust generated by the locust. Details of the measuring device have been decribed elsewhere (Preiss and Gewecke 1991).

The locusts were flown in a continuous air current within the perspex flight chamber ($36 \times 25 \times 25$ cm) of a horizontal wind tunnel. Onto the floor of the flight chamber a movable ground pattern could be projected. Air current within the tunnel simulated the locust's air speed, and was adjusted for each locust to produce optimum flight action: In most cases this occurred at an air speed of 2.5 m/s. The ceiling and sides of the flight chamber were lined with opaque white paper. The floor was covered with translucent plastic, acting as a projection screen for visual stimuli subtending an angle of 69° from side-to-side and 98° fore-and-aft. A black/white periodic grating with a spatial wavelength of 53° (defined as the angular width of a stripe-pair, as seen looking downwards from the locust position) and a contrast $(I_{max} - I_{min})/(I_{max} + I_{min})$ of 0.7, was projected onto this screen (average pattern luminance 400 cd/m²). In some experiments, a pattern with a spatial wavelength of 22° was used instead, and this gave essentially the same results. The experiments, therefore, will be discussed together. The patterns were produced by moving a 35 mm film-loop with black and clear stripes of equal width through the focal plane of a slide projector. The film-loop was driven by a 548:1 reduction gear linked to a DC motor equipped with a tachometer. In closed-loop experiments, the movement of the pattern was, in addition, measured directly by a

ring-potentiometer coupled to the film-loop. Pattern motion, simulating ground speed of the locust, was in line with the animal's longitudinal axis. In open-loop experiments, pattern speed was controlled by a function generator, and followed a trapezoidal pattern with time. In closed-loop experiments, pattern speed was controlled by the thrust component of response, which was amplified and, with negative sign, fed back to the motor. The coupling between thrust and the resulting angular velocity of the pattern was 6×10^{4}°/Ns, calculated for directly underneath the locust. Zero adjustment of the feedback loop was done before the locust was attached to the measuring device; any inaccuracy would only be equivalent to an error in simulated wind speed and thus of minor importance. The signal of a function generator was subtracted from the thrust-related signal, thus reducing pattern speed and visually simulating the effect of a headwind. The biased pattern speed thereby followed a triangular pattern with time. Thrust, yaw-torque, and visual stimuli were registered on a chart recorder and, in addition, digitized and stored in a computer for off-line averaging (Commodore PC 40/20, combined with a CED 1401 signal averaging programme, Cambridge Electronic Design, U.K.). The locust's behaviour was observed from behind using a mirror, and was noted.

Results

Open-loop experiments

It was shown in earlier experiments (Preiss and Gewecke 1991) that pattern speed changes in the ventral visual field in line with the locust's long body axis, effectively simulate passive changes in displacement. When the direction of movement was periodically reversed from progressive (anterior to posterior) to regressive (posterior to anterior), a correlated modulation of yaw-torque and thrust either in combination or independently was induced. In half of the experiments, the thrust was low when the pattern moved progressively and high when it moved regressively. In the other half, the opposite occurred. The amplitude of thrust either decreased when pattern speed was reduced, or it showed a step-like character, remaining at the maximum value, independent of pattern speed down to 0.15°/s, the lowest speed tested. The latter kind of response was formerly attributed to an extreme gain in the stimulus-response conversion (Preiss and Gewecke 1991).

In order to determine the locusts' preferred retinal velocity, we selected test animals which showed step-like changes in thrust of this type (Preiss and Gewecke 1991). The rationale for this choice was that a well defined step change in thrust could be expected to occur whenever the preferred pattern speed was crossed by the speed modulation. This would not occur if thrust production was a function of pattern speed. In this case, any speed modulation would induce a modulation of thrust, independent of whether it crossed the set point or not.

As seen in Fig. 1B, the amplitude of thrust response was constant, independent of whether pattern speed was modulated between ± 1.2°/s or ± 0.27°/s. The latter speed modulation was used throughout for determination of the set point of retinal image velocity. This was done by offering the locust the pattern speed modulation either about 0°/s or shifted into either the progressive or regressive range. In the latter case, of course, movement direction was no longer periodically reversed, and it was
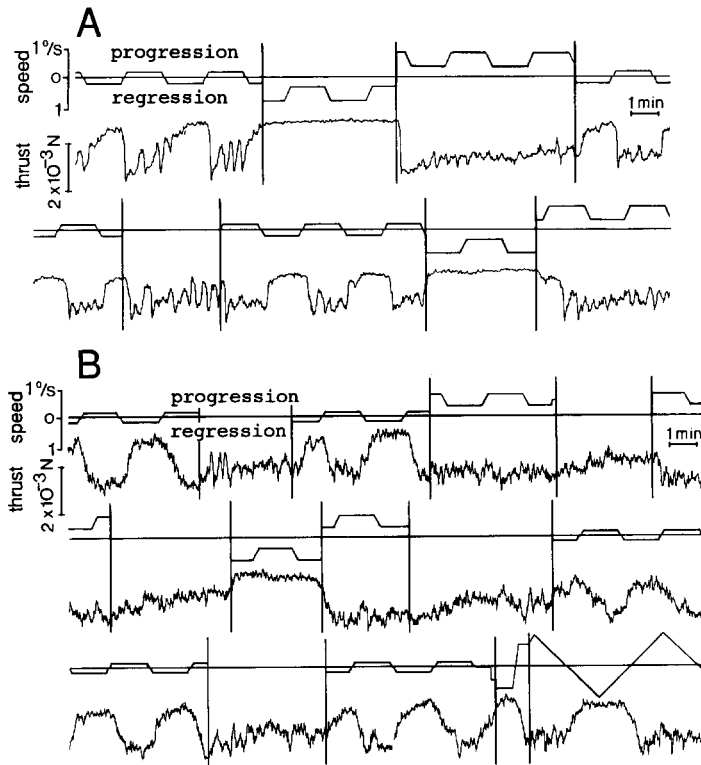
Fig. 1. Modulations of thrust of two individual locusts (**A** and **B**) in response to motion of a ground pattern in line with their long body axis (open-loop experiments). Modulation of pattern speed was either around zero and the direction of motion periodically inverted from progression to regression, or it was shifted into either the progressive or regressive range. Intermittently, the pattern was kept stationary. A correlated modulation of thrust was only induced when speed modulation was around zero. Otherwise thrust was kept constant at one of the extreme levels. During periods of stationary pattern, thrust approached a mean level. Pattern speed is calculated for directly underneath the locust

Fig. 2A, B. Closed-loop experiments on the compensation of a biased regressive ground pattern motion (R) in line with the locusts' long body axis. Speed of the biased motion was reduced by the locusts' compensatory modulation of thrust. (**A**) The remaining difference between the biased motion and the locust's adjustments *(slip speed)* was proportional to the strength of the injected bias. (**B**) Within a wide range of bias modulation the mean slip speed was zero, as also indicated by the signal of a ring-potentiometer sensing the actual displacement of the pattern (quantified by the number of displaced pattern periods). $n =$ number of averaged stimulus periods. Speed values [°/s] are calculated for the position at right angle to the locust

then found that no modulation of thrust occurred as it did when speed was modulated around zero (Fig. 1). Instead, thrust was kept constant at one of the two extreme levels depending on whether the pattern moved progressively or regressively. In the example depicted in Fig. 1, thrust was maximal at regression and minimal at progression, but was reversed in half of the experiments as expected when thrust was negatively correlated with the direction of pattern motion (Preiss and Gewecke 1991). This lack of a correlated thrust modulation indicates that a 0.27°/s modulation of speed around zero crossed the locust's set point of retinal image velocity. When pattern motion was intermittently stopped during an experiment, thrust approached a mean level (Fig. 1B); in such cases, the amplitude of thrust fluctuations was often increased as well (Fig. 1A).

Closed-loop experiments

When, under closed-loop conditions, the locust's thrust production was negatively fed back to pattern speed, and a triangular modulation of regressive bias additively
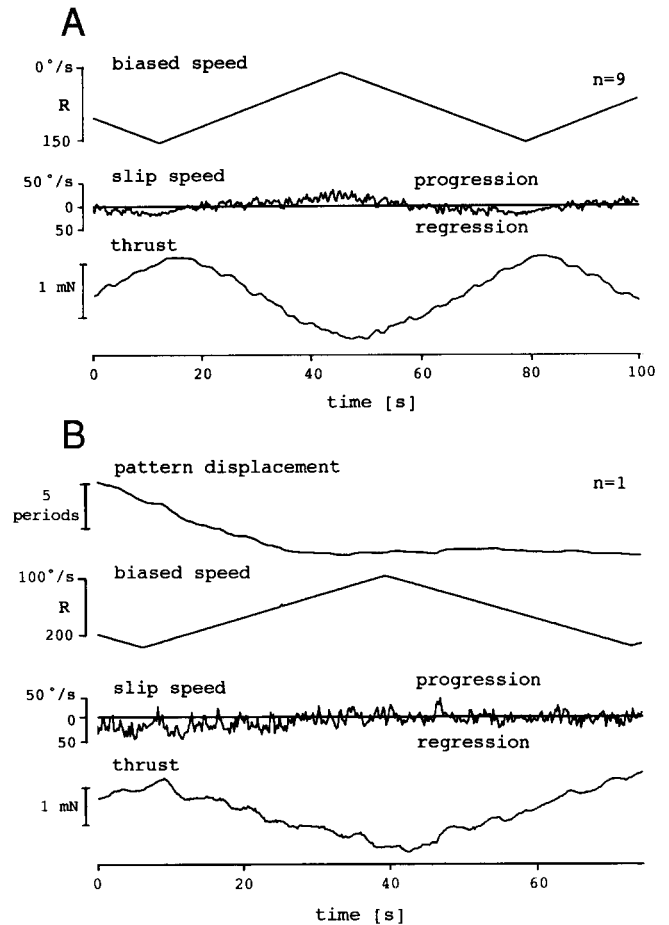
superimposed, a correlated modulation of thrust was observed (Fig. 2). The polarity of response was always such as to counteract the bias motion indicating a reduced variability of response under closed-loop conditions. Therefore, test animals had not to be selected for experiments. Ground speed was reduced by the thrust response and maintained at about 0°/s, with a residual modulation (slip speed) proportional to the bias used. In the example depicted in Fig. 2A, a 160°/s bias modulation of ground speed has been reduced to about ±20°/s, as indicated by the averaged response curves. This result, however, does not entirely describe the peculiarities which were observed in many cases. In many experiments, the pattern was instead kept stationary, except for a small amount of positional jitter, over a wide range of bias modulation. Pattern displacement was then often below the resolution of the potentiometer; the mean slip speed was then actually zero (Fig. 2B).

It is important to note that in all of these cases (as also in case of the open-loop experiments) the locusts had adopted the typical long-term flight posture with the hindleg tibiae pressed against the femora, midlegs pointed backwards, and forelegs drawn up within the groove between head and pronotum; the abdomen was extended horizontally. This posture differed from the landing posture, observed after a long duration (up to 5 h) of uninterrupted flight. The hindlegs were then stretched out and, in most cases bent downwards together with the midlegs and the abdomen. The locusts then usually struggled with their legs and sustained wing beating no longer occurred. The smooth modulation of the flight parameters, observed when the locust had adopted the long-term flight posture, then changed into an erratic modulation with high amplitude, not correlated with the visual stimulus, and flight stopped intermittently.

Stabilization of the ground pattern could occur either over the whole range of bias modulation (Fig. 2), or it could be restricted to a more or less narrow range (Fig. 3). Beyond this range, when thrust had reached its minimal value and progressive pattern speed increased, thrust (in most cases) strongly increased, whereupon slip speed grew even further. With regressive pattern motion, thrust was usually kept at high level. In many experiments, this was accompanied by an increase of yaw-torque, indicating the locust's tendency to turn out of the wind to compensate for the retinal image velocity. Within the range of bias compensation, modulation of thrust was often also combined with a turning response, when incomplete compensation caused regressive or progressive motion of the pattern.

Compensation of the pattern motion bias used by means of thrust modulation was thus critically dependent on the relation between self- and bias-generated motion.
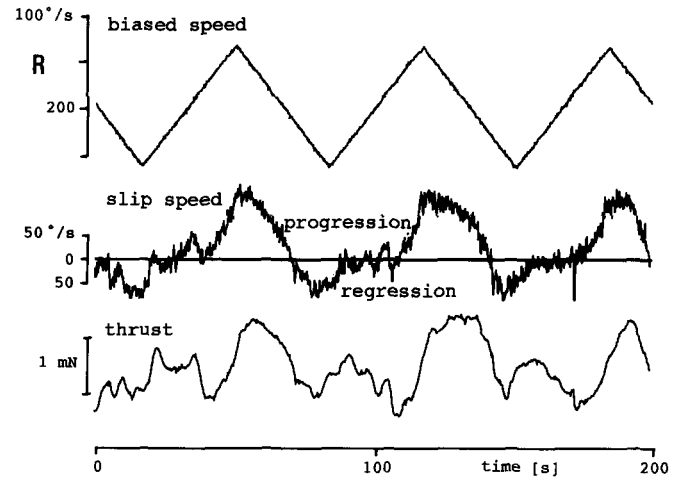

Fig. 3. Closed-loop experiment as in Fig. 2, but with an increased strength of the regressive biased pattern motion (*R*). Only within a limited range of speed modulation the locust succeeded in compensation of the biased motion by modulations of thrust. Beside this range thrust and concomitantly slip speed were strongly increased

This relation had to be individually adjusted, since thrust can only be modulated by an animal within a certain range. This adjustment was done by changing the mean level of the bias, whereas the coupling between thrust and angular velocity of the pattern was kept constant at $6 \times 10^{4\circ}/Ns$, throughout the experiments. Figure 4 shows the whole set of a locust's response capabilities to changes of the mean value of the bias modulation. At the beginning of this experiment (0–310 s), the biased motion was compensated by thrust modulation, though the amplitude of slip speed modulation slightly increased over time. Upon reduction of the mean level of the biased
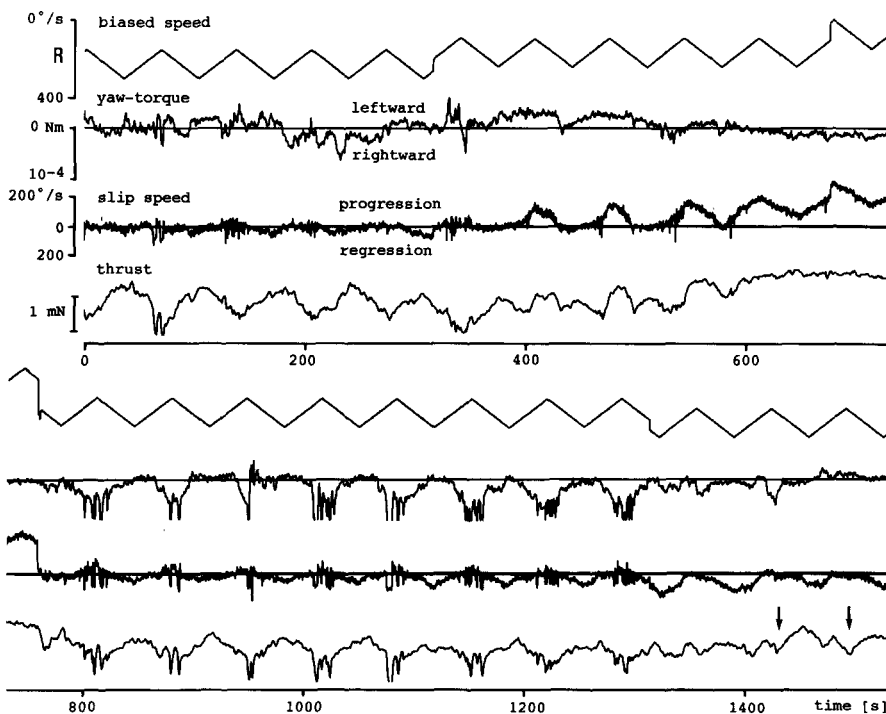

Fig. 4. Closed-loop experiment as in Fig. 2. The mean value of the biased regressive pattern motion (*R*) was stepwise altered after a variable number of stimulus periods. While thrust production was negatively fed back to pattern speed, the locust's yaw-torque modulation, measured simultaneously, had no effect on pattern speed. For further explanation see text

motion (310–640 s), pattern speed was kept minimized for one stimulus period even during the phase of low biased speed made possible by an extreme reduction of thrust. Thereafter, during the phases of low biased motion, thrust and concomitantly, slip speed was instead strongly increased. The time interval during which slip speed was kept minimized was continuously shortened. During the last stimulus period, as well as upon further reduction of the mean level of biased motion (660–750 s), thrust production was kept at a high level throughout, as described before. Readjustment of the biased motion to the same mean level as at the beginning of the experiment, was now answered by the locust's combined modulation of thrust and yaw-torque (750–1300 s). Slip speed again was minimized, though during the phases of high biased motion, thrust was not sufficient for compensation and pattern motion became regressive. This became dominant when the mean level of biased motion was further increased (1300–1500 s) though short periods with thrust modulated in a compensatory manner remained (arrows).

If, however, the mean level of bias modulation was adjusted correctly, the compensatory thrust modulation could persist over hours. It was only the quality of bias compensation, i.e., the amplitude of slip speed modulation, that could vary during the experiment.

Discussion

Our experiments to investigate the visual control of ground speed in the flight of gregarious locusts produced a very surprising result: the locusts modulated their thrust to minimize their movement relative to the ground. This sort of response seems analogous to that of waterstriders (Gerridae) on the surface of a flowing stream, where it serves to keep the animal from being swept downstream (Junger and Varjú 1990), but it is not the kind of behaviour that has been seen in flying insects, where "preferred" (although sometimes context-related, Preiss and Kramer 1983; Willis and Baker 1988) positive values of retinal image velocity have always been found (Heran and Lindauer 1963; Marsh et al. 1978; David 1982; Preiss and Kramer 1986). It is especially not the kind of behaviour to be expected in highly migrant insects like locusts. Our results thus need an explanation.

It seems *possible* that our locusts attributed the biased pattern motion to disturbances in their pitch angle, and that the measured alterations in thrust were simply a by-product of their attempts at pitch correction. Certainly, in flight at high altitude, pattern motion caused by pitch changes would greatly exceed any caused by changes in translation speed. We think, however, that this is unlikely to be the explanation of our results, because it has been found in similar experiments with gypsy moths *(Lymantria dispar)*, that there is functional specialization of the eye which causes pattern motion in the ventral visual field to be interpreted as translation rather than pitch change (Preiss 1991). Hints of a similar specialization are also found in the flight behaviour of *Drosophila* (Blondeau and Heisenberg 1982), and we

believe that the same is likely in locusts. Furthermore, the occurrence of two opposing types of thrust responses in open-loop experiments contradicts the assumption that the observed behaviour serves flight stabilization instead of the control of ground speed. Stabilization of flight requires only one type of response for compensation of rotatory disturbances.

It is also unlikely that minimization of ground speed was associated with an intention to land. Both the full flight posture maintained by the locusts and the duration of uninterrupted flight typical in our experiments might have been characteristics of long-range flight (Kennedy 1951; Rainey 1963; Casimir 1987). This indicates that the observed behaviour is related to migration or swarming, but not to the normal behaviour of solitary grasshoppers. A preferred zero ground speed could, however, be of advantage to the solitary grasshoppers where it would ensure that they dont fly out of their habitat. The rearing conditions (crowded laboratory culture), however, ensured that the experimental locusts were in the gregarious phase. Mature animals of this phase are characterized by their tendency to migrate except when engaged in mating or egg-laying (Kennedy 1951).

If we assume that the locusts' preference for minimized retinal image velocity is a real phenomenon, some evidence for this preference ought to be available from field observations. Swarming locusts are seen to maintain, at least to some extent, their positions relative to their immediate neighbours (Kennedy 1951; Waloff, 1972). They presumably do this by stabilization of their visual surroundings, but the stabilization responses are believed to be primarily activated by stimuli in their lateral visual fields (Kennedy 1951). It thus seems improbable that this kind of behaviour would be triggered in the present experiments, where ventral stimuli are presented, appropriate to flight over the ground. It is, however, difficult to refute entirely the possibility that the behaviour observed in our experiments might reflect a tendency for swarming locusts to maintain station relative to others flying below them.

To understand the biological significance of the observed flight behaviour, it is of primary importance to consider whether minimization of the retinal image velocity really could prevent locusts from migrating.

Unfortunately, due to technical reasons (slackness between motor and film loop), our experiments did not allow us to finally decide whether locusts prefer a stationary surrounding over very low retinal image velocities, i.e. close to threshold level (the threshold of optomotor responses in the visual control of translation is below $0.15°/s$; Preiss and Gewecke 1991; optomotor steering responses are induced down to $4 \times 10^{-3}°/s$; Thorson 1966). However, two pieces of evidence indicate that locusts prefer the stationary ground pattern. In many closed-loop experiments, the pattern was stabilized over a wide range of bias modulation without any mean displacement. When, in open-loop experiments, the pattern was kept stationary, locusts adopted a medium thrust production. This might indicate a preferred flight speed as postulated by Kennedy (1951) though the frequently observed concomitant increase in the amplitude of thrust

fluctuations might indicate the locust's intention of gaining visual feed back in response to changes in thrust, as found in *Drosophila* during steering (Heisenberg and Wolf 1988).

Secondly, retinal image velocity depends not only on ground speed but also on flight altitude and is inversely proportional to the latter. Long-range flight in the field in fact often takes place at high altitudes (up to about 1.5 km), during which the angular speed of ground features would be expected to be close to threshold level. For example, during downwind flight the retinal velocity would be less than 0.3°/s if the locusts' air speed amounts to 3 m/s and wind speed does not exceed 5 m/s, most frequently measured during swarming flight in the field. It has also to be taken into account that the quality of bias compensation could vary during the experiments, most probably due to spontaneous gain modulations in the stimulus-response conversion as formerly described by Eggers et al. (1991) and Preiss and Gewecke (1991). Slip speed was then proportional to the strength of the bias used. This uncomplete compensation, in addition, would enable migration though the set point of the underlying control circuit remains at zero.

It thus seems conceivable that the animals in our closed-loop experiments were trying to adjust image speed to a value appropriate from their (assumed) high altitude perspective. Low-flying locusts in the field do not try systematically to minimize retinal image velocity but zoom around all over the area (Riley, pers. comm.). In accordance, migratory locusts, *Locusta migratoria*, within low-flying swarms (average flight altitude: 6.2 m) adjust the retinal image velocity to a variable but positive preferred value (Baker et al. 1984). It is, therefore, tempting to infer that ground speed is set to different values according to their flight altitude, i.e. during long-distance and short-distance flight.

However, a preference for minimized retinal image velocity might also indicate a preference for upwind flight (in wind speeds comparable to flying speed). It is in fact tempting to infer that winds which are so weak that a locust can make headway against them are not useful for transport to wind convergence zones, such as the Inter-Tropical Convergence Zone, where rainfall is most probable (Rainey, 1963, 1978). Such weak winds ought, therefore, be largely counteracted by minimizing ground speed in order to stay in the same place. However, it is known from field observations particularly on high-flying swarms (above 900 m altitude) that the speed of displacement is in most cases only a fraction (less than 40%) of the wind speed in which the locusts fly (Rainey 1963, 1978). A predominance of upwind flight may thus be an important factor in reducing the rate of swarm movement to less than the wind speed. This might be important to ensure that the direction of swarm displacement is not dominated by the daily weather but is primarily guided by the mean wind direction towards the Inter-Tropical Convergence Zone, according to a "low-pass filtering" of wind directions. Minimization of the retinal velocity of ground images is, therefore, believed to be a basic requirement for long-distance, wind-related orientation of swarming locusts in the field.

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