COLLISION AVOIDANCE OF FLYING LOCUSTS: STEERING TORQUES AND BEHAVIOUR

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Summary

1. Obstacles approaching in the flight path trigger postural and wing kinematic adjustments in tethered flying locusts. We sought to confirm that these behaviours were steering behaviours by measuring the changes in the flight forces associated with their execution. We also investigated the coordination of these behaviours in the execution of collision avoidance manoeuvres and the effect of speed or size of the obstacle on the timing and magnitude of the response.

2. Locusts were tethered and suspended in a wind tunnel from orthogonally arranged leaf springs mounted with strain gauges. Lift and yaw torque could be monitored unambiguously. We also monitored a forward translation force which combined pitch and thrust. During flight, the locusts were videotaped from behind while targets of different sizes ($5 cm \times 5 cm$, $7 cm \times 7 cm$, $9 cm \times 9 cm$, $11 cm \times 11 cm$) were transported towards the head at different speeds (1, 2, 3 or $4 m s^{-1}$).

3. Angular asymmetry of the forewings during the downstroke with the right forewing high, and abdomen and hindleg movement to the left, were temporally associated with an *increase* in yaw torque to the left. With the left forewing high, abdomen and hindleg movement to the right were temporally associated with a *decrease* in yaw torque to the left. Obstacle avoidance behaviours could be associated with either an increase or a decrease in the pitch/thrust component.

4. Leg, abdomen and wingbeat alterations in response to the approach of an obstacle were independent but tightly coordinated. Slower approaches increased the magnitude of the responses. However, the size of the obstacle had no effect on the magnitude of the response. Slower and larger targets generated earlier reactions (i.e. locusts reacted when the targets were further from the head).

5. We conclude that the behaviours we have described were steering behaviours which would have directed the animal around an obstacle in its flight path, and that there were at least two strategies for collision avoidance associated with slowing or speeding flight. Leg, abdomen and wingbeat alterations formed a coherent avoidance response, the magnitude of which was dependent upon the time available for it to develop. We further conclude that the manoeuvre was not initiated at a constant time to collision and we propose that the avoidance strategy was to initiate the manoeuvre when the targets subtended more than 10° in the insect's field of view.

Introduction

Rapid manoeuvrability is essential for individuals travelling at speed in a complex

environment. When the potential hazards in the environment are also travelling at speed and in different directions, then there is a clear need for effective and speedy motor control. Locusts flying in swarms are skilled exponents of such manoeuvres and the sensorimotor strategies, kinematics and neural mechanisms controlling this steering behaviour are of considerable interest.

There is a rich literature on mechanisms and control of steering in insects, particularly locusts (for reviews, see Kammer, 1985; Rowell, 1988). However, most of this concentrates on correctional manoeuvres to compensate for unintended course deviations (e.g. Thüring, 1986; Schmidt and Zarnack, 1987; Waldmann and Zarnack, 1988; Robert, 1988; Hensler, 1992; Robert and Rowell, 1992*a*) rather than intentional steering. Nevertheless, there has been some recent interest in active, intentional steering, such as phonotaxis in crickets (May *et al.* 1988; Wang and Robertson, 1988; May and Hoy, 1990*a*,*b*; Miles *et al.* 1992) and locusts (Robert, 1989; Robert and Rowell, 1992*b*) and collision avoidance in locusts (Robertson and Reye, 1992).

In locusts, a complete steering behaviour is likely to involve a coordinated response of the abdomen, hindlegs and wings (see Zanker *et al.* 1991, for flies). Lateral deflection of the abdomen (Camhi, 1970; Gewecke and Philippen, 1978; Baader, 1990; see also Zanker, 1988, for *Drosophila*) and the hindlegs (Arbas, 1986) can unilaterally increase drag and can shift the centre of action of the flight forces. The form and timing of the wingbeats have a major part to play. The changes in the wingbeat include pronation on the inside of the turn (Dugard, 1967; Baker, 1979; Zarnack, 1988), relative phase changes of the wings (Thüring, 1986; Waldmann and Zarnack, 1988) and aerodynamic coupling and interference between the forewings and hindwings on one side (Schmidt and Zarnack, 1987; Schwenne and Zarnack, 1987). Asymmetries in wing-stroke angle, particularly of the forewings, have been noted (Taylor, 1981) but are poorly correlated with turning (Baker, 1979; Zarnack, 1988).

One of the most dramatic kinematic adjustments to the wings described in tethered flying locusts is the response to the rapid approach of an obstacle in the immediate flight path. This is perhaps not surprising, given that the consequence of an inadequate response to the stimulus is likely to be collision. It has been demonstrated that, when locusts tethered in a wind tunnel are presented with rapidly approaching targets offset from the midline, the abdomen and hindlegs extend to the side away from the line of approach of the target. The forewings also become markedly asymmetrical during the downstroke, such that on the assumed inside of the turn the forewing depresses in conjunction with, or beneath, the hindwing, while on the opposite side the forewing remains more elevated and separate from the hindwing. The asymmetry is most pronounced at the middle of the downstroke and it has been proposed that it is likely to swing the flight force vector around the long axis of the body to produce a banked turn towards the most depressed forewing (Robertson and Reye, 1992). However, this proposal is speculative because the locusts were tethered and the consequences of the altered kinematics are unknown.

For many investigations of locust flight control (behaviour, kinematics, motor patterns), it has been necessary to tether the animals securely. There are obvious technical advantages resulting from this procedure, but there are also clear disadvantages (Zarnack and Wortmann, 1989). Rigid tethering prevents the response of the locust from having its

desired effect. This opens the reflex loop, rendering the stimulus unnatural, and also prevents the experimenter from determining what the effect would be. Other problems are that rigid tethering can cause steering biases in the motor patterns (Möhl, 1985, 1988) and in wing kinematics (Robertson and Reye, 1992) and can result in insufficient generation of lift (Krüppel and Gewecke, 1985). Some of these drawbacks can be alleviated by artificially closing the reflex loop (e.g. Robert, 1988; Möhl, 1988; Robert and Rowell, 1992*a,b*) but this uses a measure of the desired output either directly (Robert, 1988) or indirectly (Möhl, 1988) and assumes a knowledge of the gain of the reflex. For locust collision avoidance, it is necessary first to determine the output, which is the effect on flight orientation and direction of the observed kinematics. The constraints of the visual stimulation preclude free flight or the use of a long, loose tether such as has been used to determine motor patterns associated with zigzagging flight of moths in a pheromone plume (Willis and Arbas, 1991). The insect could be allowed some freedom of movement on a flexible tether or balance and be filmed during the execution of different manoeuvres (e.g. Baker, 1979; Alexander, 1986). Alternatively, a rigid tether could be used and the instantaneous forces generated during the manoeuvres in one or several of the axes of movement could be measured and correlated with the kinematics (e.g. Blondeau, 1981; Thüring, 1986; Robert and Rowell, 1992*a,b*). The first goal of the experiments described here was to test and confirm the hypothesis that the collision avoidance behaviours of tethered locusts (Robertson and Reye, 1992) are involved in steering by measuring the yaw torques generated during their execution.

An intriguing finding of the earlier study (Robertson and Reye, 1992) was that targets that generated late reactions, possibly because they were difficult to see, did not cause steering-like reactions but tended to generate landing reactions and gliding. This suggests that, in some way, the time to collision was being compared with the time to effect a steering manoeuvre, with the result determining subsequent behaviour. If information on time to collision is available to the locust, then it is possible that the steering-like reactions are initiated at a constant time to collision, thus perhaps avoiding unnecessary manoeuvring. Timing of behaviours according to specific times to collision has been demonstrated for other behaviours (Lee and Reddish, 1981; Wagner, 1982).

The second goal of the experiments described in this paper was to analyse collision avoidance behaviour in more detail, particularly with respect to the timing of, and the relationships between, the different components of the behaviour. We investigated the effects of differences in the size and speed of approach of the targets on the timing and magnitude of the avoidance response. Elsewhere we have briefly reported our conclusions on whether time to collision is involved in generating the avoidance reactions (Robertson and Johnson, 1993). In this paper, we describe the data set and the behaviour and its coordination in detail and consider its timing more fully.

Materials and methods

Animals

Adult female locusts, *Locusta migratoria*, approximately 3–4 weeks after the final moult were obtained from a colony maintained in the Department of Biology at Queen's

University. We used females because we surmised that their larger size would result in more obvious manoeuvres. Only large, apparently healthy animals with intact wings were selected (the wings tend to become tattered over time in the colony). Each animal was tested for its flight tendency by blowing on its head while holding its legs, and individuals that seemed reluctant to fly were returned to the colony. Many of the animals could not sustain flight for the required 2–4h of an experiment and these were discarded. Forty animals were used to obtain twenty complete experiments. The experiments described here were performed at all seasons of the year and the temperature in the laboratory ranged from around 19°C in the winter to around 25°C in the summer. There were seasonal and circadian variations in the willingness of the animals to fly for long periods. However, once an animal that would fly for the necessary length of time was found, there was no apparent difference in behaviour attributable to season or time of day.

The wind tunnel

Locusts were tethered by waxing a light aluminium tube to the pronotum and they were suspended in the centre of a 20cm×20cm wind tunnel (Fig. 1). Wind was drawn through the tunnel at $3 \, ms^{-1}$ and measured with a hot-wire anemometer. Wind flow was laminar and at a constant speed where the locust was tethered. Semicircular fairings around the entrance of the tunnel reduced eddy formation in the mouth of the tunnel. The L-shape of the tunnel allowed an unimpeded view from behind the animals for videography. The locusts were hung, facing outwards, 12cm in from the opening of the tunnel. This allowed the targets to be transported outside the tunnel, directly towards the head. The floor and bottom one-third of the sides of the tunnel were covered with black cardboard, while the top two-thirds of the sides were covered with white cardboard. This simulated a horizon to help the locust orient itself and maintain straight flight in the absence of an approaching target. Three 150W light bulbs were situated above the animal. Two of these illuminated the approaching target, while one illuminated the animal. Each animal was flown undisturbed in the tunnel for at least 15min before the start of an experiment.

Measurement of flight forces

The aluminium tether waxed to the locust's pronotum was suspended from a force transducer manufactured after an original design by Blondeau (1981; see also Thüring, 1986) (Fig. 2). The tether was connected to the centre of a light aluminium cross which was suspended at the end of its arms from four pairs of orthogonally oriented acrylic leaf springs using narrow silastic tubing which covered a rigid connecting rod (Fig. 2B). This allowed flexibility at the joints between the connecting rods and the cross and the leaf springs. Each leaf spring was mounted with a pair of semiconductor strain gauges (BLH Electronics, Canton, MA; SNB3-16-35-S13-211). Output from the strain gauges was amplified and combined in different ways in bridge circuits, as described by Blondeau (1981), to monitor translational and rotational forces exerted on the tether. The transducer was housed in an acrylic box mounted on top of the wind tunnel with only the tether protruding into the tunnel. The forces were recorded on a Vetter (model D) instrumentation tape recorder along with voltage transients from the three photosensors mounted on the track (see below).
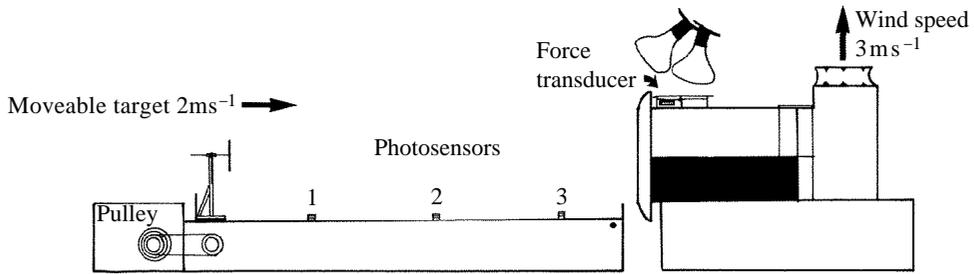
Fig. 1. The experimental set-up. Locusts were suspended from the force transducer. They faced out of the tunnel towards the target, which was propelled with a belt and pulley arrangement along the length of the track. Speed was altered by changing the diameter of the pulley and could be set at 1, 2 (shown), 3 or $4\,m\,s^{-1}$. The target's progress was monitored with three photosensors located 126, 76 and 26cm from the locust's head. Lamps above the transducer illuminated the locust for videotaping from behind through the L-shaped wind tunnel. The sides of the wind tunnel had an artificial horizon to help the locusts maintain proper flight orientation.
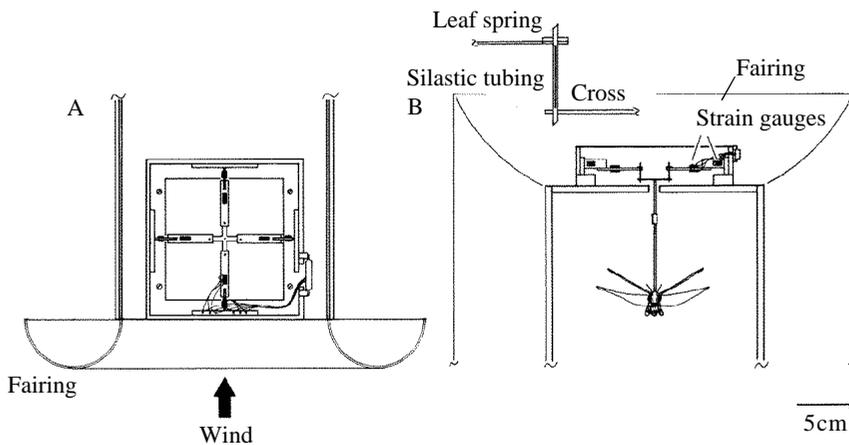

Fig. 2. (A) Top view and (B) front view of the wind tunnel showing the flight force transducer. The mouth of the wind tunnel was framed with a fairing that was semi-circular in cross section and made from half-cylinders of acrylic mitred around the opening (convexity out of page). Note that in B the frame around the tunnel opening represents this fairing, and that the force transducer is portrayed as visible through the clear acrylic of the fairing. The locust was waxed to an aluminium rod and suspended from the centre of an aluminium cross, which was in turn suspended from orthogonally arranged acrylic leaf springs. Each of the four arms had two leaf springs and each leaf spring was mounted with two strain gauges (16 strain gauges in total). The cross was connected to the leaf springs using connectors of silastic tubing stiffened along most of their lengths with rigid inserts (inset in B).

The reactions of a locust to presentation of a target were recorded by videotaping it from behind (60frames s^{-1}, i.e. with a resolution of 16.7ms; shutter speed 1/1000s). The photosensors activated light-emitting diodes (LEDs) visible in the field of view of the video camera. Thus, the timing of particular kinematics, of flight forces generated and of the progress of the target could all be related.

In Blondeau's design, the fly was tethered in the plane of the strain gauges and this avoids some ambiguity in the interpretation of translational and rotational forces. In our design, the locust was suspended some distance beneath this plane and translations in horizontal axes were constrained into arcs. Thus, an attempted translation of the animal could have been registered as an attempted rotation at the strain gauges. For example, a roll to the left measured by the transducer could have been produced by a sideslip of the animal to the right. There was a similar confusion between pitch and thrust. However, lift and yaw forces were unambiguous. Consequently, we used only yaw forces as a monitor of steering direction. The device was calibrated for torsion of the tether around a vertical axis (yaw), forces applied to the end of the tether in the vertical axis (lift or vertical) and horizontal forces along the sagittal midline of the locust (i.e. in and out of the tunnel) applied to the tether at the level of the locust, 11.5cm beneath the plane of the strain gauges (pitch/thrust). Most of the locusts showed less than 100% lift (i.e were not supporting their own body weight). This was probably an effect of tethering (Zarnack and Wortmann, 1989). Similarly, most locusts had biases in yaw torque probably resulting from tethering (motor patterns and wing kinematics are biased by tethering; see Introduction). In this study, we were concerned exclusively with changes in the forces generated by the approach of the target, rather than with absolute values.

Target transport

Targets were transported on a 2m straight track at nominal velocities of 1, 2, 3 or $4\,\mathrm{m\,s^{-1}}$. The targets were mounted on a car which travelled the length of the track at a height which resulted in the target being in the middle of the tunnel, and 5.5cm in from the opening, when it hit the end of the track. The track was either placed so that the target ran directly down the sagittal midline, or was offset parallel to this but 2cm to the right or left of the midline position. Three photosensors positioned along the length of the track (126 cm, 76cm and 26cm from the locust's head) monitored the progress of the target. Each photosensor turned on a small LED located in the wind tunnel behind the animal and in the field of view of the video camera. To prevent any possibility of the animal detecting the illumination of the LEDs and to improve their visibility in videotape playback, they were partially surrounded by a black cardboard shield which protruded about 2cm into the wind flow from the floor of the tunnel. This may have disrupted flow in the rear of the tunnel, but only after the wind had passed the animal. No difference in flow at the position of the animal could be detected with the LEDs and their shield in place.

The targets were squares of cardboard randomly patterned with uniformly sized black and white pixels (1cm×1 cm), and they varied in size depending on the experiment. The track and wind tunnel were isolated from movement in the room by a white-board barrier. The barrier behind, and on the back one-third of the sides of the track, was covered with the same spatially random pixel pattern as the target. Preliminary experiments showed that black targets on white backgrounds (and *vice versa*) were visible to the locust, and caused some steering behaviours, before the target started to move. Spatially random pixel patterns against similar backgrounds have been shown to be effective stimuli for initiating jump responses in peering locusts (Collett and Paterson, 1991), so we used a patterned background to camouflage the target before it started its approach.

Procedure

The first set of experiments was designed to examine the effects of target size on obstacle avoidance reactions. For ten animals, different target sizes (11cm×11cm, 9 cm×9 cm, 7cm×7 cm or 5 cm×5 cm) were transported towards the locust at a constant velocity of $2\,ms^{-1}$. During the period of analysis (first photosensor to target stop), the 11cm×11cm target initially subtended 5.0˚; this expanded at an accelerating rate over 0.85s to reach a final subtense of 63.4˚. The initial and final subtenses were 4.1–58.6˚ for the 9cm×9 cm target, 3.2–51.2˚ for the 7cm×7 cm target, and 2.3–42.3˚ for the 5 cm×5 cm target. Each size of target was presented to an animal three times to the left of the midline, three times down the midline and three times to the right of the midline. Each presentation was separated by 2min. The targets were presented in order of increasing size through the experiment. In a separate set of counterbalancing experiments, the target sizes were presented in order of decreasing size. The results from four animals in the counterbalancing experiments were compared with the results from four animals randomly chosen (using a random number table) from the set of animals to be described here. This comparison showed no significant difference and thus demonstrated that the effects described here were due neither to a habituation of the response over time nor to a result of presentation order.

The second set of experiments on a different set of ten animals used targets of a constant size (7cm×7 cm) but different approach speeds (1, 2, 3 and $4\,ms^{-1}$). Thus, the initial and final subtenses were the same as for the first set of experiments but the time over which they expanded was different (1.76s for $1\,ms^{-1}$; 0.85s for $2\,ms^{-1}$; 0.59s for $3\,ms^{-1}$; 0.44s for $4\,ms^{-1}$). The same format for target presentation was used (three left, three centre, three right) and the targets were presented in order of increasing speed. A similar comparison with results from counterbalancing trials in which target presentation was in order of decreasing speed showed no significant difference.

Video analysis

Animals were filmed from behind using a Hitachi 5200A video camera with an effective shutter speed of 1/1000s. The videotape of each trial was analysed frame-by-frame, with a resolution of $60\,frames\,s^{-1}$ (only about three frames in each wingbeat cycle), using a video and computer motion measurement system manufactured by PEAK Performance Technologies Inc. Analysis began at, or slightly before, the illumination of the LED triggered by the target passing the first photosensor (126cm from the head) and stopped when the target's car struck the buffer at the end of the track (5.5cm from the head). Nine positions were digitized on each video frame: (1) the point of connection between the tether and the pronotum; (2) the point directly vertical to this at the top of the video monitor; (3) the left forewing tip; (4) the right forewing tip; (5) the left hindwing tip; (6) the right hindwing tip; (7) the femoral-tibial joint of the left leg; (8) the tip of the abdomen; and (9) the femoral-tibial joint of the right leg. The PEAK system automatically calculated the elevation angles of each of the wings as the angles between the line created by joining points 1 and 2 (vertical zero position) and the lines created by joining point 1 to point 3, 4, 5 or 6, depending on the wing in question. The positions in
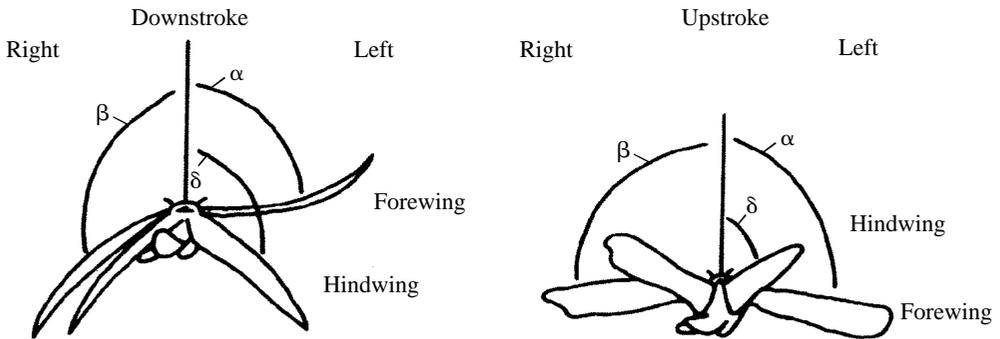
Fig. 3. Typical images of a locust attempting to steer to the left during the downstroke and the upstroke. Elevation angles of right forewing (α) and left forewing (β) and right hindwing (δ) are shown. Angular asymmetry of the forewing is given by ($\alpha-\beta$). Note that this is negative for attempted turns to the left (right forewing higher). Angular difference on the right side is given by ($\delta-\alpha$). Note that this is positive during the downstroke and negative during the upstroke.

the vertical and horizontal dimensions of the abdomen and hindlegs were measured relative to a zero position at the left-hand corner of the video monitor. These measurements were in real centimetres based upon a previous calibration of the video system.

The data from the PEAK system were further manipulated to yield the following variables in each frame (Fig. 3): (1) right minus left forewing elevation angle (resulting in a measure of angular asymmetry; $\alpha-\beta$); (2) right minus left hindwing elevation angle; (3) right hindwing elevation minus right forewing elevation (resulting in a measure of the angular difference between the wings on one side; $\delta-\alpha$); (4) left hindwing angle minus left forewing angle. Thus, a positive value for angular asymmetry indicates that the right wing is more depressed than the left, and a positive value for angular difference on a side indicates that the hindwing is more depressed than the forewing. Abdomen and leg movements were categorized as right (increase in value of position in the horizontal dimension), left, or no movement. For statistical comparisons, the magnitudes of these movements were grouped into large (>0.6cm), medium (0.4–0.6cm) and small (<0.4cm).

The forewing asymmetry associated with attempted steering reactions occurs primarily during the downstroke (Robertson and Reye, 1992). We extracted the data pertaining to the midportion of the downstroke in the following way. During straight flight the hindwings lead the forewings, which would give a positive value for the angular difference during the downstroke, whereas during the upstroke the angular difference would normally be negative (Fig. 3). Although this difference may be lost on the inside of a turn, on the outside it is accentuated. By selecting only those frames in which the value of the angular difference of the wings on the outside of the attempted turn was greater than +10°, we selected frames that occurred in the midportion of the downstroke.

The time of a locust's reaction to an oncoming obstacle was determined by the time at which the abdomen began to be elevated (increase in value of position in the vertical

dimension). All timing measurements are limited by the resolution of the videography and are ±17ms (the time between successive frames at $60\,s^{-1}$). The actual (not nominal) speed of the target was calculated from the time taken to pass between two photosensors. Speeds between the first and second photosensors did not differ from speeds between the second and third, indicating that the target was not accelerating during its approach. The position of the target on the track at the time of the reaction was determined using the actual speed and the time (number of frames) from the previous photosensor.

Statistics

The values for each variable measured were averaged for each animal such that there was one value for each variable per animal.

Paired *t*-tests were calculated for the results presented below. Since each level (e.g. 1, 2, 3 and $4\,ms^{-1}$) included data from the same animals, separate paired *t*-tests were performed on the differences between the levels tested against zero. Several of these paired *t*-tests were performed for each set of results being investigated and the *P* values were corrected for multiple comparisons using a sequential Bonferroni procedure (Rice, 1989). Differences were considered significant with *P* values less than 0.05.

Results

A total of 720 runs of a target towards a locust were videotaped (not including the counterbalancing experiments). Of the 720 runs, the locusts showed no reaction to the approaching obstacle in 144 runs. Most (85%) of these 144 runs used targets of $5\,cm\times5\,cm$ at $2\,ms^{-1}$ or targets of $7\,cm\times7\,cm$ at $4\,ms^{-1}$ and $3\,ms^{-1}$, indicating an increased difficulty of the task when the speed increased or the size decreased. In some of the trials, the locusts were biased (showing slight steering behaviours) in one direction or the other. However, this did not seem to affect the extent of the subsequent behavioural reaction to the oncoming obstacle.

One run (from one animal) has been chosen to exemplify the behaviour of a tethered flying locust to an oncoming obstacle (Figs 4, 5 and 6). In this run, a $7\,cm\times7\,cm$ target was transported towards the head of the locust at $1\,ms^{-1}$ and offset to right of the midline by 2cm. The angular asymmetry of the forewings varied considerably in sequential frames and showed a dislocation during the approach of the target (Fig. 4). This variability was a result of measuring at successively different positions in the wingbeat cycle (sampling rate $60\,s^{-1}$, wingbeat frequency around $20\,s^{-1}$). During the downstroke, the forewing angular asymmetry was initially around $+18°$ (right forewing lower), indicating a slight steering bias to the right. Around the point when the target passed the second photosensor (76cm from the head) the forewing angular asymmetry abruptly changed to values around $-35°$ (between $-20°$ and $-70°$), indicating that the animal had detected the approaching obstacle and was attempting to steer left around the closest edge. The remaining points (i.e. not mid-downstroke) in the plot of asymmetry in sequential frames show that during the upstroke the forewings remained symmetrical (Fig. 4). The hindwings showed no obvious change in asymmetry when the target was detected and remained with a bias of around $-10°$ (Fig. 5A). In this run, the angular
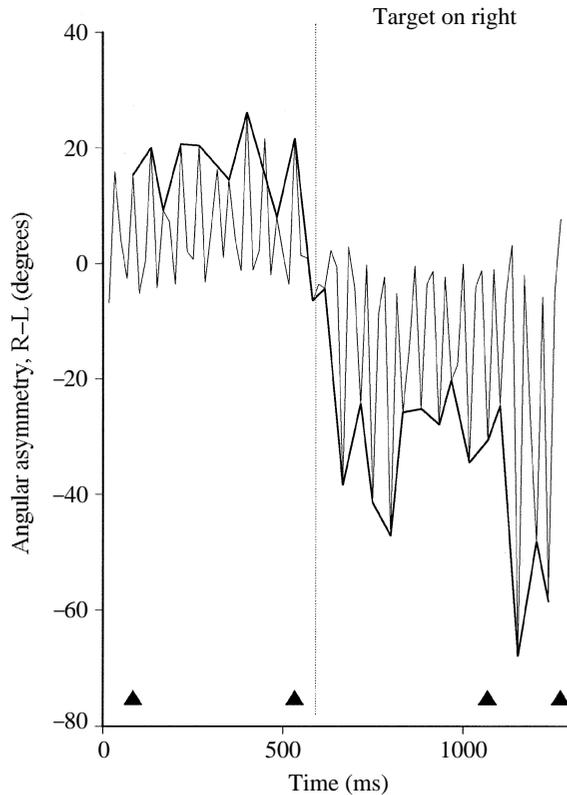
Fig. 4. Angular asymmetry of the forewings (i.e. $\alpha-\beta$ in Fig. 3) during the approach of a $7\,cm \times 7\,cm$ target travelling at $1\,m\,s^{-1}$ and offset from the midline by 2cm to the right. The light line indicates the asymmetry in every video frame ($60\,s^{-1}$). The heavy line indicates only those data points during the downstroke, selected as outlined in the Materials and methods. The first three black triangles indicate the times at which each of the three photosensors were activated (126, 76 and 26cm from the head) and the last indicates when the target reached the end of the track (5.5cm from the head). The dotted vertical line allows comparison between Figs 4, 5 and 6 and indicates the time of the reaction determined by the time of the first obvious change in forewing angular asymmetry. Note that angular asymmetry of the forewing during the downstroke was initially positive and that when the target was around the second photosensor (76cm distant) this asymmetry abruptly became negative. Also note that during the upstroke (data points not connected by the heavy line) the angular asymmetry of the forewings was, and remained, around zero.

difference (hind−fore) during the downstroke was initially slightly larger on the left than on the right (slight steering bias to the right) (Fig. 5B). The wings on the inside of a turn showed a decrease in angular difference from straight flight, while those on the outside of the turn exhibited an increase in angular difference (Fig. 5B). The abdomen (Fig. 6A) and the hindlegs (Fig. 6B) both moved towards the inside of the turn, with the inside (left) leg moving further than the outside (right) leg, presumably because its movement in that direction was not hindered by the abdomen. The abdomen also elevated. The three components of the behaviour (changes in wing asymmetry, in abdominal position and in
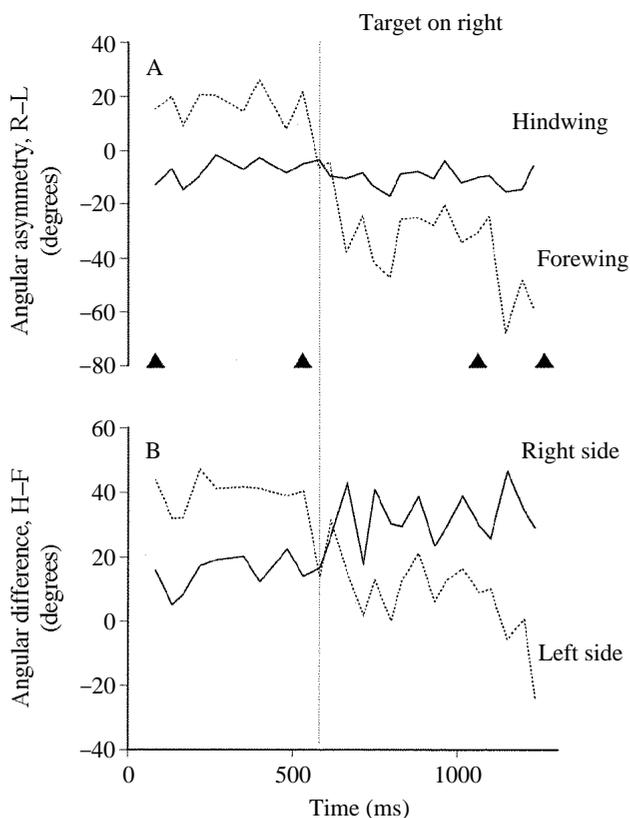
Fig. 5. (A) Angular asymmetry of the forewings and the hindwings and (B) angular differences between the right and left sides during the same trial as shown in Fig. 4. For reference, the dotted line in A is the same as the heavy line in Fig. 4. Note that the hindwing angular asymmetry did not obviously change at the time of reaction. Angular difference increased on the right and decreased on the left to negative values close to the end of the run.

leg positions) all occurred at approximately the same time with respect to the approach of the target. These results using a different wind tunnel, a different track and a low-resolution video analysis confirm the findings of Robertson and Reye (1992), which were obtained primarily using high-speed cinematography.

Steering torques

Of the twenty animals, eight animals exhibited discernible changes in force output during the approach of an obstacle. The output of the transducer was markedly oscillatory with considerable variation (Fig. 7). Variation at the wingbeat frequency (around 20Hz) was to be expected as instantaneous forces generated throughout the wingbeat vary, with a maximum during the downstroke (Cloupeau *et al.* 1979). Also, the forewing asymmetry associated with collision avoidance occurs during the downstroke (see above). However, there was also much that was spurious in the traces, particularly in the trace of yaw torque. The device with a locust attached had a resonant frequency of 3–5Hz. There was
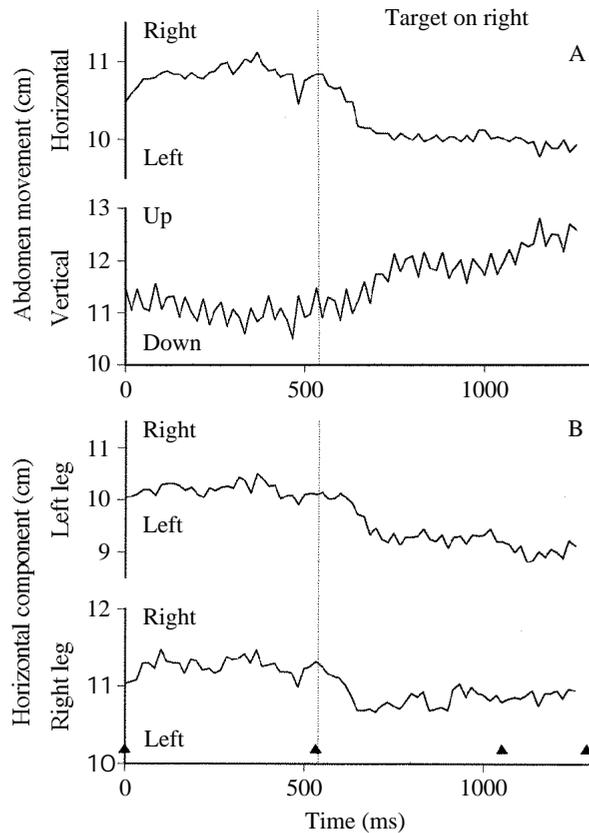
Fig. 6. (A) Movements of the tip of the abdomen in the horizontal and vertical dimensions, and (B) movements in the horizontal dimension of the femoral-tibial joints of left and right hindlegs during the same trial as shown in Figs 4 and 5. The dotted line indicates the time of reaction as determined by the first measurable change in forewing angular asymmetry (see Fig. 4). Note that for data collection the criterion for measuring the timing of an avoidance reaction was when the abdomen was first elevated which, in this case, is about 50ms later than the wing alteration. At this time, the abdomen and the right and left hindlegs also moved to the left. Note that the movement scales are different. The abdomen moved further in the vertical than in the horizontal dimension, and the left leg moved further horizontally than did the right leg. Oscillations in the vertical position of the abdomen are due to passive movements in time with the wingbeat.

also a problem with inadequate damping, so that a deflection generated by the locust in one direction would cause the tether to spring back and oscillate at the resonant frequency for several cycles. Beating at the different frequencies exacerbated the problem. Even the output produced by a dead locust suspended in the wind stream was not uniform because of turbulence generated by the locust. A compounding factor was that we were interested in forces produced by relatively few wingbeats during the last few hundred milliseconds before the target entered the mouth of the wind tunnel and disturbed the recording (Fig. 7). We filtered the traces using a wide variety of high and low cut-offs. However, this did not improve the appearance and interpretability of the traces. We chose instead to
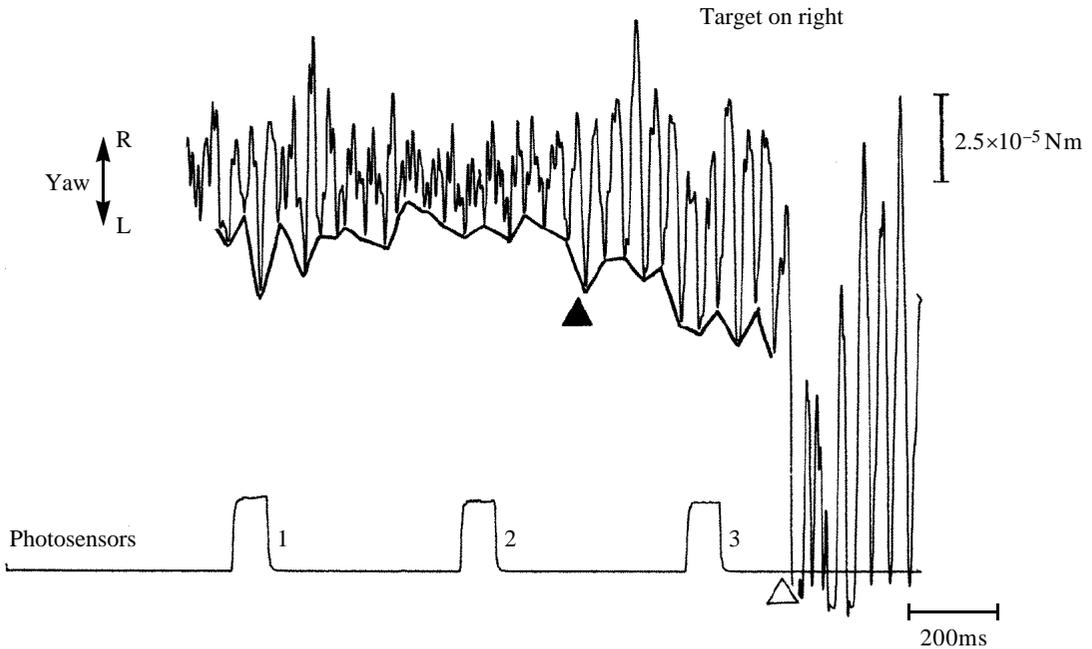
Fig. 7. Yaw torque measured during the approach of a 7cm×7cm obstacle at $1\,\mathrm{ms}^{-1}$ and shifted 2cm to the right of the sagittal midline. Yaw torque is contaminated with peaks at the wingbeat frequency and other spurious deflections. We have traced an envelope indicating maximum yaw torque to the left. The lower trace indicates progress of the target along the track (photosensors 126, 76 and 26cm from the locust's head). The open triangle indicates when the target entered the tunnel and disturbed the air flow. Force measurements after this point are artefactual. The filled triangle indicates the time of occurrence of the behavioural reaction monitored with the video camera and suggesting an attempted turn to the left (abdomen and hindlegs left, development of right-high angular asymmetry of the forewings in the downstroke). Note that the behavioural reaction is temporally associated with an increase in maximum yaw torque to the left.

trace an envelope around the trace of yaw torque indicating maximum yaw in one direction (usually to the left because of the steering bias of the animals in this set-up) (Fig. 7). This essentially connected the peaks of yaw torque generated by each wingbeat. Using this method, it was possible to distinguish changes in yaw torque associated with steering-like behaviours monitored videographically. Thus, an increase in the peak of yaw torque to the left was associated with hindleg and abdominal movement to the left and a change in angular asymmetry of the forewings during the downstroke (right higher than left) (Fig. 7). The timing of the increase was coincident with the occurrence of the behavioural reaction caused by an approaching target. Some, but not all, animals showed behavioural reactions to the right and left (depending on whether the target was on the left or right, respectively). For these animals, the maximum yaw torque to the left decreased when the target was on the left and increased when the target was on the right (Fig. 8). In all cases, this was coincident with the occurrence of the behavioural reaction. Note that in the trial depicted in Fig. 7 the target was travelling at $1\,\mathrm{ms}^{-1}$, whereas in the trials
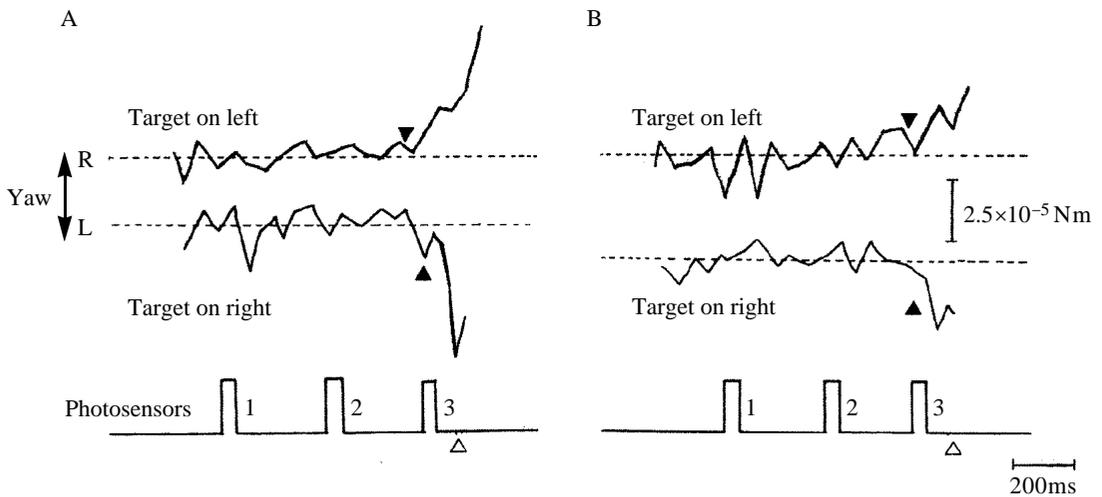
Fig. 8. Yaw torque changes associated with targets presented 2cm offset to the right or left sides. Conventions are as for Fig. 7. The raw trace of yaw torque is not shown; only the envelope of maximum yaw torque to the left. Targets (7cm×7cm) were presented at $2\,\mathrm{ms}^{-1}$. Dashed lines are horizontal and drawn by eye through the yaw torque at the beginning of the trial to accentuate the changes in yaw torque. A and B are from different animals. Each trace of torque in A or B is from a different trial aligned so that the photosensor trace beneath refers to both. Note that targets on the right were associated with an increase in maximum yaw torque to the left, which in turn was temporally associated with the time of occurrence of the behavioural reaction suggesting an attempted turn to the left (filled triangles). Note the similar, but opposite, effects when the target was on the left.

depicted in Fig. 8 the targets were travelling at $2\,\mathrm{ms}^{-1}$. The difference in the timing of yaw torque reactions associated with the change in target speed was the same as the difference in the timing of the behavioural reactions.

Some of the animals had a strong tendency to have the same behavioural reaction to the approach of the target regardless of whether it was on the right or the left (see below). It is an important observation that the direction of yaw torque reactions correlated with the direction of the behavioural reactions and not with the side of approach of the target (Fig. 9). Only for the third trace in Fig. 9B was there an indication on the videotape that the locust was attempting to steer to the right (judging by the behavioural reactions). It was for only this trial in the figure that maximum yaw torque to the left decreased.

Examples of the pitch/thrust and vertical forces produced during the approach of a target are shown in Fig. 10. Peaks of lift could be easily detected and each peak was probably generated by a downstroke (Jensen, 1956; Cloupeau *et al.* 1979). This made it possible to monitor the wingbeat frequency. In 80% of the trials where a change in vertical force was seen, the lift generated by each downstroke increased. Also, the wingbeat frequency increased during the reaction (from around 24Hz to around 29Hz in Fig. 10A,B). Three of the eight animals that showed changes in force production during the target's approach showed an increase in pitch/thrust towards the front of the tunnel. Five of the animals showed a decrease in forward pitch/thrust as the obstacle approached.

Behaviour

Behavioural components

Table 1 shows the types of reactions and the direction of the reactions seen in the 576 runs in which a reaction was observed. A change in wing asymmetry was chosen as the
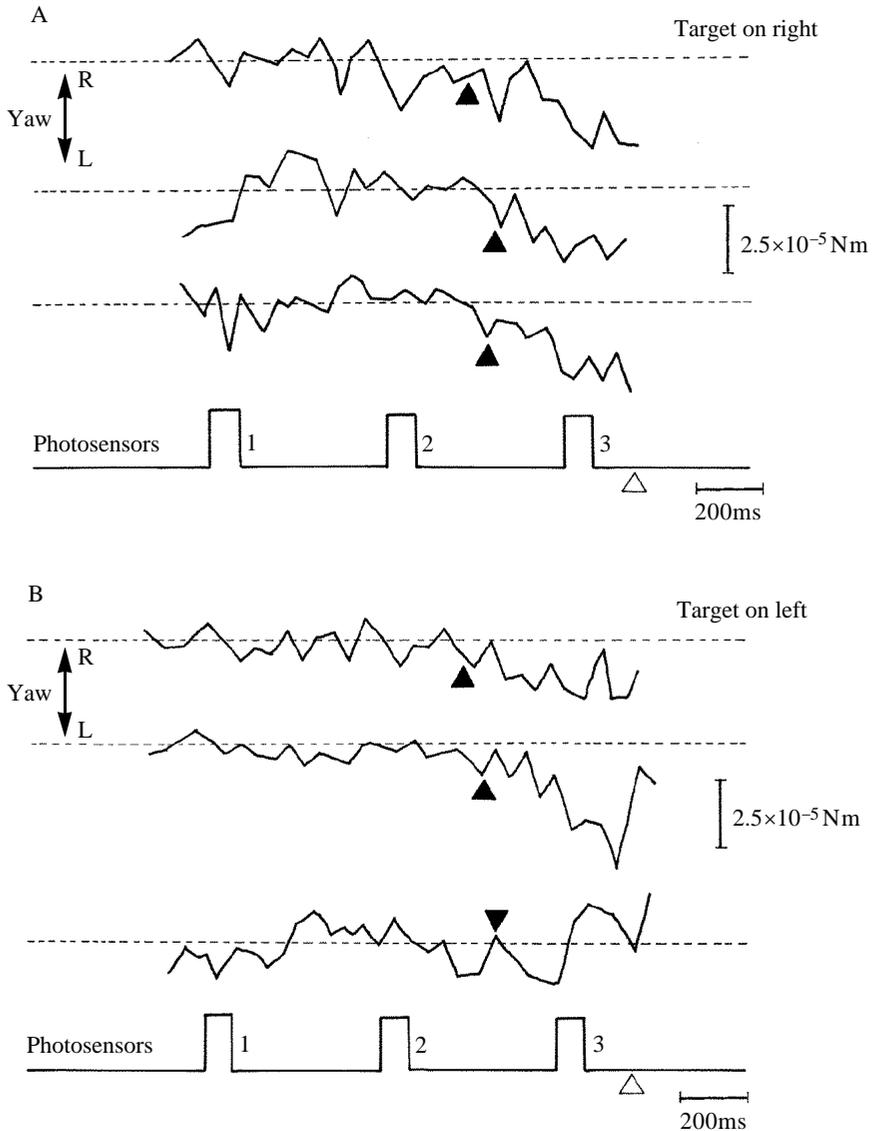

Fig. 9. Yaw torque changes associated with presentation of a $7 cm \times 7 cm$ target at $1 ms^{-1}$ offset by 2cm either to the right (A) or to the left (B) of the midline. Conventions as for Figs 7 and 8. A and B are from the same animal. For all trials except the third one in B the behavioural reaction suggested an attempted turn to the left in spite of the position of the target on the left for the first two trials in B. For the third trial in B, the behavioural reaction suggested an attempted turn to the right.
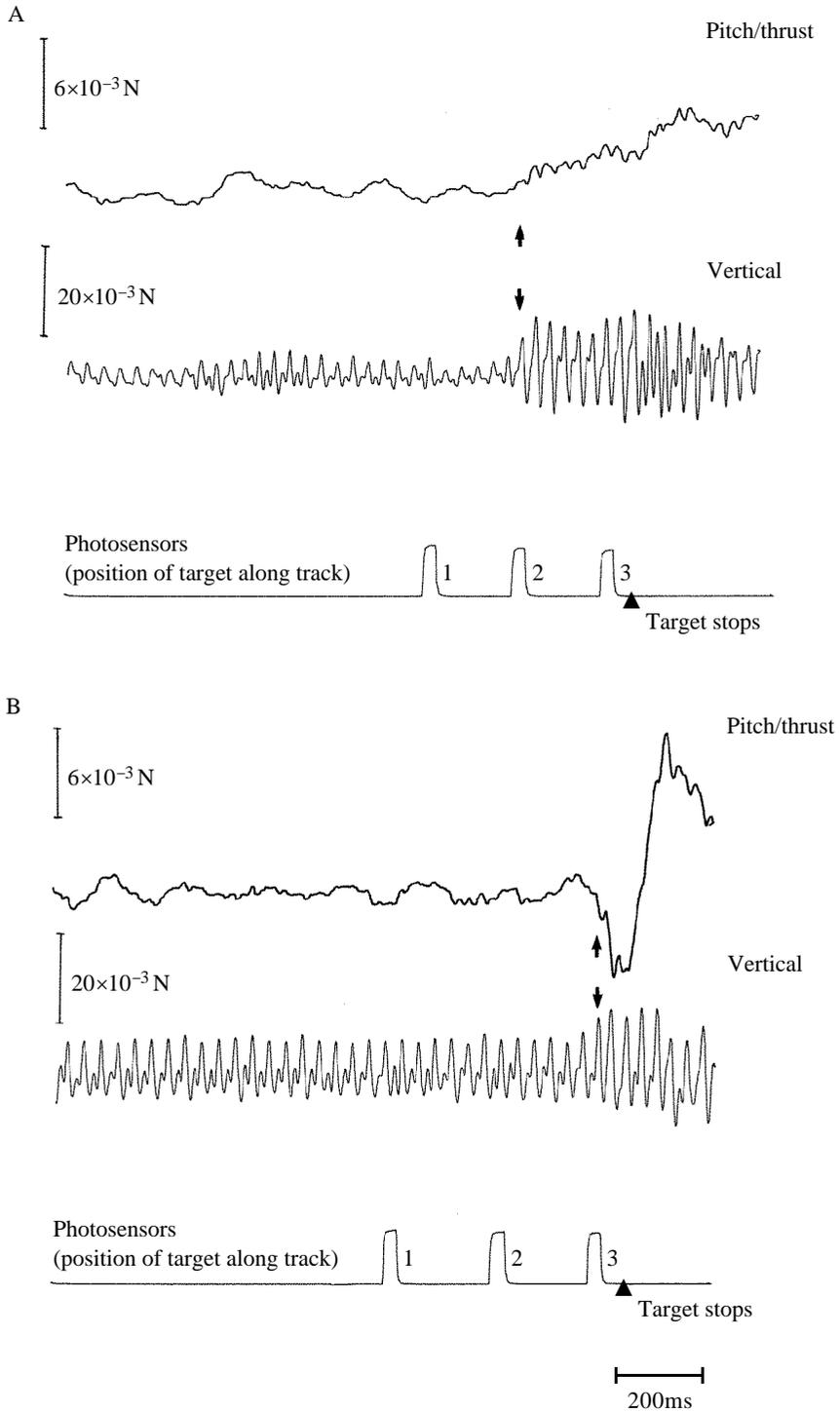
A

Pitch/thrust

6×10^{-3} N

Vertical

20×10^{-3} N

Photosensors
(position of target along track)   1   2   3

Target stops

B

Pitch/thrust

6×10^{-3} N

Vertical

20×10^{-3} N

Photosensors
(position of target along track)   1   2   3

Target stops

200ms

Fig. 10

Table 1. *Behavioural reactions of locusts to oncoming obstacles, showing the type of*
reactions seen in different trials as well as the direction of the steering movements

Number of runs	Type of reaction	Percentage of total	Left	Right	Neither
238	Wings, abdomen and legs	41	179 (75%)	15 (6%)	44 (19%)
338	Wings and/or abdomen and/or legs (not all three)	59	277 (82%)	27 (8%)	34 (10%)
Total					
576			456 (79%)	42 (7%)	78 (14%)

indicator of the presence of a steering reaction. When there was no wing asymmetry
change, the abdomen and the legs tended not to react either. The majority of the reactions
showed steering to the left. This strong bias in favour of attempted steering to the left was
an unexpected result. The side of approach of the target had a minimal effect on the
direction of the steering behaviours. All attempted turns to the right occurred when
targets approached on the left side. However, even when targets were on the left, the
reaction was most often an attempted turn to the left.

Although the locusts did not exhibit directional steering that was dependent upon the
side of the target approach, the abdomen movements, the leg movements and the wing
asymmetry changes that occurred tended to be in the same steering direction. For
example, the direction of the forewing asymmetry was related to the direction of
abdominal movement (Fig. 11). Similar histograms were obtained for forewing angular
asymmetry associated with movements of the right and left legs (not shown). The timing
of these reactions was also closely related. In approximately 85% of the trials, the wing,
abdomen and leg movements were initiated together. Leg movements occurred before the
other behaviours in only 1% of the trials. The magnitudes of the abdomen and leg
movements were also positively related to the magnitude of wing symmetry change (not
shown).

Effect of target characteristics

Calculation of actual target speeds showed that, when $4\,\mathrm{m\,s^{-1}}$ was intended, the speeds
were variable within a run and inconsistent between runs. Only 10 runs of 90 runs
intended actually proceeded at $4\,\mathrm{m\,s^{-1}}$. The data from these 90 runs were not

Fig. 10. Changes in lift and pitch/thrust associated with presentation of a 7cm×7cm target at
$2\,\mathrm{m\,s^{-1}}$ towards the head of the animal. A and B are from different animals. The traces
represent the raw output of the transducer. The filled triangle under the photosensor trace
indicates the time at which the target entered the tunnel and disrupted the recording. Arrows
indicate the time of occurrence of the behavioural reaction monitored videographically.
Primary oscillation in the vertical force represents the wingbeat frequency. Note that lift
normally increases (upward increase in vertical force) at reaction, but that the pitch/thrust
component can either increase or decrease. Wingbeat frequency increased from about 24Hz at
the beginning of each trial to about 29Hz during the reaction.
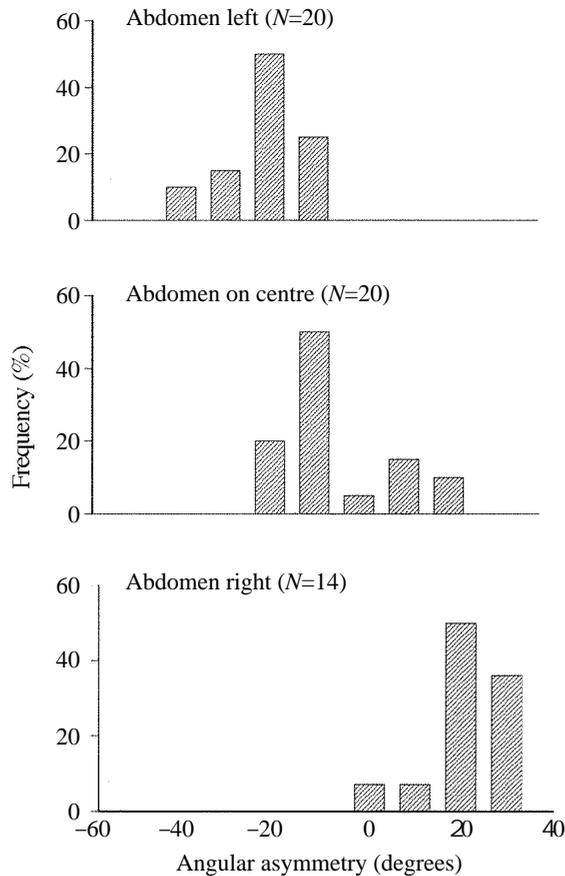
Fig. 11. Frequency distributions of forewing angular asymmetry (averaged for each animal to give one value) associated with the direction of abdominal movement. In the lowest histogram, $N=14$ because six of the locusts did not attempt to steer to the right. Positive asymmetry indicates an attempted turn to the right. Forewing angular asymmetries were significantly different when the abdomen moved left, remained on centre or moved right (t-tests, $P<0.001$), and positive forewing angular asymmetry occurred with rightward deviations of the abdomen.

incorporated into the following analysis (track speeds were grouped as $1\,ms^{-1}=1-1.5\,ms^{-1}$; $2\,ms^{-1}=1.5-2.5\,ms^{-1}$; $3\,ms^{-1}=2.5-3.5\,ms^{-1}$).

As the speed of the target increased, the magnitude of the change in forewing asymmetry decreased (Fig. 12). There was also a tendency for the magnitude of leg and abdomen movements to decrease as the speed of the target approach increased (not shown). However, the changes in target size did not significantly affect the degree of change in wing asymmetry or leg and abdomen movements (not shown).

More rapidly approaching targets caused later reactions, such that the target was closer to the head of the animal at the time of reaction (around 40cm at $1\,ms^{-1}$; around 25cm at $3\,ms^{-1}$; Fig. 13A). Smaller targets also caused later reactions (around 45cm for 11cm×11cm; around 20cm for 5cm×5 cm; Fig. 13B).
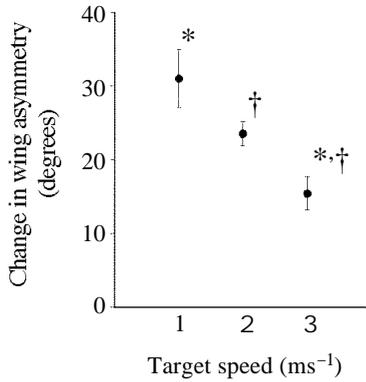
Fig. 12. Increases in target speed cause decreases in the magnitude of the change in angular asymmetry of the forewings. Each locust provided an average change in forewing asymmetry at each target speed. Values are given as mean ± standard error (*N*=10 animals). * and † indicate significant differences at the *P*<0.05 level after adjustment for multiple comparisons.
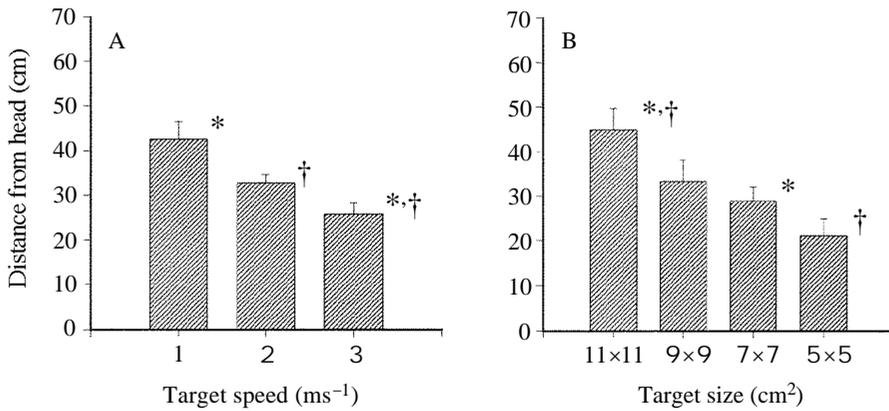

Fig. 13. (A) Increases in target speed and (B) decreases in target size result in reductions in the distance remaining to the head at the time of reaction. Each locust provided an average distance from the head for each target variable. Values are given as mean + standard error (*N*=10 animals). * and † indicate significant differences at the *P*<0.05 level after adjustment for multiple comparisons. Statistical comparisons are only within each target variable.

Discussion

The results we describe here confirm and extend the findings of Robertson and Reye (1992). Although there are likely to be subtle alterations in wingbeat and posture which contribute to collision avoidance manoeuvres (e.g. timing and extent of changes in angle of attack, Zarnack, 1988), the prominent reactions of tethered flying locusts to oncoming obstacles were changes in forewing asymmetry, abdomen position and metathoracic leg position. The following primary conclusions can be drawn from this study. (1) The behavioural reactions generate steering torques which would take the locust around one side of the obstacle. (2) Accompanying a yaw torque, the pitch/thrust forces either

Table 2. *Times to collision and angles subtended by the target at the time of reaction and at a time of detection assumed to be 65ms prior to reaction (see text)*

Target characteristics	Time to collision (s)[a]	Subtense at reaction (degrees)[b]	Subtense at detection (degrees)[c]
5 cm × 5 cm	0.12±0.02*	19.8±4.9	9.5±1.2
7 cm × 7 cm	0.15±0.02†	16.4±3.1	10.2±1.1
9 cm × 9 cm	0.18±0.03	20.0±5.0	12.5±1.8
11 cm × 11 cm	0.24±0.02*,†	15.2±1.8	11.4±1.0
1 m s^{-1}	0.44±0.05*	10.1±0.9*	8.6±0.7
2 m s^{-1}	0.17±0.01*	12.4±0.7†	8.8±0.3
3 m s^{-1}	0.09±0.01*	16.2±1.4*,†	9.0±0.4

Values are given as mean ± standard error, N=10.

Data previously published in Robertson and Johnson (1993).

[a]* and † indicate significant differences ($P<0.05$, adjusted for multiple comparisons as outlined in the Materials and methods) between the indicated values obtained when the target size and speed were varied. Statistical comparisons are only within either the speed group or the size group.

[b]There is no significant difference between values when size of the target was varied. Variation of target speed had significant effects.

[c]There is no significant difference between any of the values at the $P=0.05$ level when size or speed of the target was varied.

increased or decreased, suggesting at least two strategies for obstacle avoidance independent of the direction of the turn. (3) The three behavioural components of a steering reaction could occur independently. However, their timing, direction and magnitude were strongly related, suggesting that they jointly and coherently contribute to attempted avoidance manoeuvres. (4) The most consistently observed reaction was a change in forewing asymmetry, suggesting that collision avoidance manoeuvres most heavily depend on this aspect of the reaction. (5) The timing and extent of the reaction were strongly affected by the speed and size of the approaching target.

Before considering the significance of the results in more detail, it is necessary to consider their possible limitations. It could be argued that the locusts were responding to turbulence in the air flow as the targets approached. This possibility is refuted more completely elsewhere (Robertson and Reye, 1992), but it is worth noting here that the reactions described in this paper occurred on average between 20 and 50cm (some more than 70cm, see Fig. 4) outside the wind tunnel at positions where no air flow towards the mouth of the tunnel could be detected. These reactions were visually evoked.

A more serious problem is that changing the side of offset of the target had little effect on the side to which the locusts attempted to steer. Most of the reactions indicated an attempted turn to the left. We interpret this as being due to the experimental arrangement. The magnitudes of the offsets were chosen to be small (2cm), so that the small targets (5cm×5cm) would still overlap the centre of the head and thus stand more chance of being perceived as potential obstacles. Robertson and Reye (1992) found that offsets greater than 2cm would cause the strongest steering reactions. Indeed, in that study, offsets of 1cm and less were considered as being on centre. Thus, it appears likely that

most of the locusts were reacting to all of the presentations as being on centre. A few could apparently distinguish the disparity and these are responsible for the few instances when a target on the left induced an attempted turn to the right. The reason for most of the attempted turns being directed towards the left is probably an undetected asymmetry in the apparatus. In other arrangements of the set-up, a tendency to attempt to steer in the opposite direction (to the right) was noticed (Robertson and Reye, 1992; A. G. Johnson and R. M. Robertson, unpublished observations). Although the direction of the reactions seen in this study did not depend on the direction of offset of the target, the reactions are still steering reactions. They would be effective in avoiding collision, regardless of the fact that the choice of direction was based on factors other than object offset.

Steering torques

The force transducer that we used was a prototype and it had several limitations in the way it operated. The most serious of these was the confusion between roll torque and sideslip, especially as roll in one direction could be confused with sideslip in the opposite direction. Because of this ambiguity we did not monitor roll, although large roll/sideslip forces were generated by the behaviours. If the locusts were attempting to generate a banked turn around the target, a turn with a large roll component, then the yaw component of the manoeuvre may have been minimal. Small torques were more likely to be masked by the limitations of the transducer, for example, if they occurred during a period when the tether was exhibiting spurious oscillations resulting from the pendulum-like arrangement and the resonant frequency of the device. This could account for our difficulty in observing steering torques generated by animals, even though the videotapes showed that they were performing steering-like behaviours.

Yaw torque generated by locusts during correctional steering, in open- or closed-loop configurations, takes 2–5s to develop to a maximum which rarely exceeds 10^{-4}Nm (Robert and Rowell, 1992*a*; their Figs 2, 6, 11), using a different design of yaw torque meter (Robert, 1988). Roll torque takes a similar length of time to develop to around 10^{-5}N m in optomotor correctional steering reflexes (Thüring, 1986), using a device similar to ours. In our experiments, we had only 100–500ms (the period from the time of detection of the target to the time that the target entered the tunnel) within which to detect a development of steering torque. We observed changes in maximum yaw torque in one direction of around 2.5×10^{-5}N m after about 200ms. It is likely that this value would have increased with time and that we observed merely the initial yaw torque.

Thus, we suspect that the small and variable nature of the yaw torques we recorded was probably due, (1) to insufficient time for the torque to develop, (2) to the intended manoeuvre having a minimal yaw component, and (3) to the limitations of our torque meter. Nevertheless, when we could detect changes in yaw torque during the approach of the target there was a consistent pattern. An increase in maximum yaw torque to the left occurred at the same time as abdomen and hindleg movement to the left and development of a negative (i.e. right-high) angular asymmetry of the forewings during the downstroke. A decrease in maximum yaw torque to the left occurred at the same time as abdomen and hindleg movement to the right and development of a positive (i.e. left-high) angular asymmetry of the forewings during the downstroke. In these experiments, the particular

arrangement of the set-up resulted in a behavioural bias such that offsetting the target had only a small effect on the character of the response (see below). Importantly, the sign of the yaw torque changes was associated with the character of the behaviour and not with the offset of the target. This rules out any possibility that the change in yaw torque was an artefact resulting from target position and approach. We conclude that the behaviours caused by the looming approach of an obstacle in the flight path were steering behaviours (i.e. generate steering torques). The direction of the turn could be determined from the direction of abdominal movement, as has been well established in other studies (Camhi, 1970; Moiseff *et al.* 1978; Wang and Robertson, 1988; Zanker, 1988; Robert, 1989). These conclusions are not particularly surprising, but they did need to be confirmed for this behaviour.

We found that, when there was a detectable change in lift during the approach of the obstacle, it was usually an increase. This is probably a result of the increase in wingbeat frequency and consequently an increase in the speed of each downstroke. It is interesting that the animals showed both decreases and increases in pitch/thrust force production as the obstacle approached, regardless of the sign of lift change. Independent control of lift and thrust has been demonstrated in locusts (Zarnack and Wortmann, 1989; see also Nachtigall and Roth, 1983, for blowflies). It is possible that the locusts examined in our study were undertaking two separate strategies when presented with an oncoming obstacle. In some cases, the locusts may have been trying to execute sudden turns accompanied by braking in response to an object seen late in its approach. In other cases, the locusts may have been responding to an object seen early in the approach, allowing the animal to power through the turn and prevent a loss of height. It is important to remember that the forces we recorded from tethered animals could have different consequences in free flight. For example, an increase in forward flying speed generated by an increase in wingbeat frequency would be registered by our device as an increase in pitch/thurst. However, if such an increase in flight speed accompanied a roll, the result might be a more abrupt turn with a reduced loss of height, rather than pitching up or increasing forward translation. Similarly, what we registered as an increase in lift does not necessarily indicate that the intended manoeuvre was to fly over the obstacle. We constrained free movement of the locust and thus constrained any intention to fly dorsally into the vertical axis. Were the locust rolling, an intention to move dorsally would more rapidly remove the obstacle from the flight path (ventral to the locust, but to one side of the obstacle). Nevertheless, it seems clear that there were at least two strategies associated with obstacle avoidance in our experiments – one involved with speeding up and the other with slowing down. Roeder (1962) showed that moths have different responses to ultrasound depending on its intensity (simulating the distance of a potential bat predator) at the time of detection. Whether the two strategies described here can be related to characteristics of the target, its approach or the time of detection remains to be seen.

Behaviour

We found a high degree of coordination between the reactions of the wings, the abdomen and the hindlegs. A similar high degree of coordination has been described in the flight control system of houseflies (Zanker *et al.* 1991). However, in the case of

houseflies orienting in response to moving objects, the three motor output pathways are so tightly coupled that a failure in one pathway is always mirrored by simultaneous failures in the other two (Zanker *et al.* 1991). In the locust, the coupling was not as tight and, although the forewing asymmetry was the *sine qua non* of these collision avoidance manoeuvres, lateral abdominal deflections and movements of the hindleg were more variable in magnitude and occurrence. It is conceivable that, rather than indicating random fluctuations in the system, this variability was controlled and would have changed the character of an avoidance manoeuvre in ways appropriate for subtle changes in internal and external conditions.

Manipulation of the speed of approach or size of the target had effects on the magnitude of the avoidance responses. Yager and colleagues (Yager and May, 1990; Yager *et al.* 1990) have shown that the magnitude of the response of praying mantises to ultrasound increased with increases in stimulus intensity. In the study presented here, a slow speed elicited a larger response with respect to the magnitude of wing, abdomen and leg movements. It may be that slower targets provided a more intense stimulus. However, another consideration is that, at slow speeds, animals reacted sooner and therefore had longer to react before the target hit the end of the track. Time to collision, calculated from the distance remaining to the head (Fig. 13) and the actual speed of approach, was significantly increased with increases in target size and decreases in target speed (Table 2; Robertson and Johnson, 1993). The intensity of the reaction may have increased as the time to collision increased with decreases in target speed, allowing the steering reaction to develop fully. Increases in target size did not cause significant changes in the magnitude of the reactions. However, the effect of target size increase on time to collision (0.12–0.24 s) was not as large as the effect of target speed decrease (0.09–0.44s) (Table 2).

The significance of the effect of target characteristics on the timing of the reactions has been discussed elsewhere, using the same data set (Robertson and Johnson, 1993). For completeness, the values of variables presented in that paper are included here as Table 2. Briefly, the main point of that paper is that, unlike some other bird (Lee and Reddish, 1980) or insect (Wagner, 1982) behaviours, the timing of these obstacle avoidance reactions in locusts was not dependent on time to collision (obtainable from a parameter of optic flow; Lee, 1980). An attempt to find a target parameter (e.g. angle of subtense, angular velocity, angular acceleration, time to collision, relative retinal expansion velocity) that was constant at the time of reaction, and thus might have been acting as a trigger for the behaviour, was unsuccessful. However, using a latency of 65ms for the neural processing time from detection to reaction (e.g. Robert and Rowell, 1992*b*), we found that the angle of subtense at the assumed time of detection was not significantly different with changes in target size or speed. Our data suggest that the locusts initiated an avoidance reaction when the target subtended more than around 10˚. One point that we did not consider in our previous paper is how such a strategy could be effective. Assuming that avoidance could be effected in the duration of one wingbeat after the reaction had been initiated, the minimum time needed from detection of the obstacle would be around 115ms (65ms for neural processing and 50ms for the wingbeat). The natural flight speeds of locusts is 3–6 m s^{-1} (Baker *et al.* 1981). It is unlikely that, even in the confusion of a mass departure, two locusts will be flying directly towards each other.

Thus, the closing speeds of a locust and its potential obstacle will be less than $6\,\mathrm{m\,s}^{-1}$. From this, the minimum distance at which to detect the obstacle in order to manoeuvre safely would be 69cm (115ms at $6\,\mathrm{m\,s}^{-1}$). At this position, to subtend more than 10°, an obstacle would have to have one dimension of at least 12.2cm. At the more likely lower closing speeds, the minimum distance would be reduced. For example, at a closing speed of $3\,\mathrm{m\,s}^{-1}$ the obstacle would need to be detected about 35cm away and, for successful avoidance, would thus need to have a dimension greater than 6.2cm. It is interesting that the minimum spacing between individuals in dense swarms is around 30cm, with 1m being much more common (range 30cm to 9m; Waloff, 1972; Uvarov, 1977). Also, the wingspans of *Locusta migratoria* are around 11cm, which is close to the minimum size of objects that could be avoided safely with closing speeds of $6\,\mathrm{m\,s}^{-1}$ (12.2cm as calculated above). These rough calculations demonstrate that a simple strategy of initiating avoidance when looming obstacles subtend more than 10° of visual angle could be quite effective in preventing collisions with neighbours in a swarm.

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