

## WING MOVEMENTS ASSOCIATED WITH COLLISION-AVOIDANCE MANOEUVRES DURING FLIGHT IN THE LOCUST *LOCUSTA MIGRATORIA*

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### Summary

1. Flying locusts will try to avoid colliding with objects directly in their flight path. This study investigated the wing movements and behaviour patterns associated with collision avoidance.

2. Tethered locusts were flown in a wind tunnel. Targets were transported at different speeds either directly towards the head of the animal or to one side of the midline but parallel to it. Changes in the form of the wingbeat for each of the wings were monitored using either a video camera or a high-speed ciné camera.

3. Animals attempted to avoid an impending collision by making movements interpreted here as (a) increasing lift to fly over the object, (b) gliding and extending the forelegs to land on the object, and (c) steering to one side of the object. Steering was monitored by observation of abdominal movements.

4. Steering to one side of an approaching target was reliably associated with an earlier and more pronounced pronation of the wings on the inside of the turn. Also, in the middle of the downstroke, the forewings were markedly asymmetrical. On the outside of the turn, the forewing was more elevated and separate from the hindwing. On the inside of the turn, the forewing was more depressed and often came down in conjunction with, or in advance of, the hindwing on that side.

5. The forewing asymmetry correlated with the position of the target such that most attempted turns were in the direction that would take the animal around the closest edge. High-speed cinematography showed that the asymmetry was caused both by changes in the timing of the two wings and by changes in the angular ranges of the wingbeats.

6. We propose that these changes in the form and timing of the wingbeats are likely to have swung the flight force vector around the long axis of the body to produce a banked turn around the closest edge of the object.

### Introduction

A casual observer of a dense swarm of migrating locusts might wonder how they manage to proceed without constantly colliding one with another, given that they

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are not all flying in the same direction or at the same speed (Waloff, 1972; Uvarov, 1977). Indeed, it has been stated that collisions between flying locusts have never been recorded (Uvarov, 1977). In the densest swarms the inter-individual spacing can be as low as 30 cm and could be even less at times of mass departure. At natural flight speeds of  $3\text{--}6\text{ m s}^{-1}$  (Baker *et al.* 1981) the ability to manoeuvre quickly and appropriately in such dense swarms is of considerable adaptive value and the motor control mechanisms of such directed behaviour are likely to be robust. Robust adaptive behaviours produced by experimentally accessible nervous systems provide the model systems of choice for those interested in understanding the cellular bases of motor control and behaviour. Visually guided collision avoidance during flight in the locust may be amenable to a detailed cellular analysis.

A wide variety of different aspects of the control of locust flight has been intensively studied for many years and the result of this scrutiny is that there is considerable information on locust flight control available in the literature (see Kammer, 1985; Gewecke and Wendler, 1985; Robertson, 1986; Reichert and Rowell, 1986; Rowell, 1988, 1989, for some recent reviews). It is significant that the knowledge extends from descending afferent influences (Reichert *et al.* 1985) through interneuronal circuitry (Robertson and Pearson, 1985), proprioceptive control (Möhl, 1985; Wolf and Pearson, 1988) and hormonal influences (Kutsch and Stevenson, 1984; Ramirez and Orchard, 1990) to motor patterns (Thüring, 1986), wing kinematics (Schwenne and Zarnack, 1987) and aerodynamics (Cloupeau *et al.* 1979). The processing of sensory information can be traced through interneuronal circuitry to adaptive behaviours. It is thus not surprising that the neuronal basis of visually induced steering movements is currently under investigation (see Rowell, 1989, for a review) and has already borne fruit (Reichert and Rowell, 1985, 1986; Reichert *et al.* 1985; Hensler and Rowell, 1990). In most of the previous studies, the manoeuvres under investigation are compensatory to maintain a particular course orientation (optomotor reflexes to correct roll and yaw deviations). Our intention has been to investigate the neuronal basis of collision avoidance in the hope that the more urgent nature of the behaviour would result in more obvious and invariant kinematics. It is already known that movement detector interneurons descending from the brain (e.g. Schlotterer, 1977; Rind, 1990) have synaptic connections with flight motoneurons in the thoracic ganglia (Simmons, 1980), although it is thought that these neurons may play no role in flight maintenance or steering (Rowell, 1989). However, it is important first to establish the repertoire of collision-avoidance behaviour patterns and, in particular, to describe the asymmetries in the wingbeat parameters associated with collision-avoidance steering.

The purpose of this investigation was to simulate the situation with which a locust is faced when it encounters an object directly in its flight path, and to observe the changes in wingbeat and posture elicited by the detection of the object. To do this, we presented stationary locusts, tethered in a wind tunnel, with targets approaching at closing speeds of  $0.4\text{--}2\text{ m s}^{-1}$ . We anticipated that the

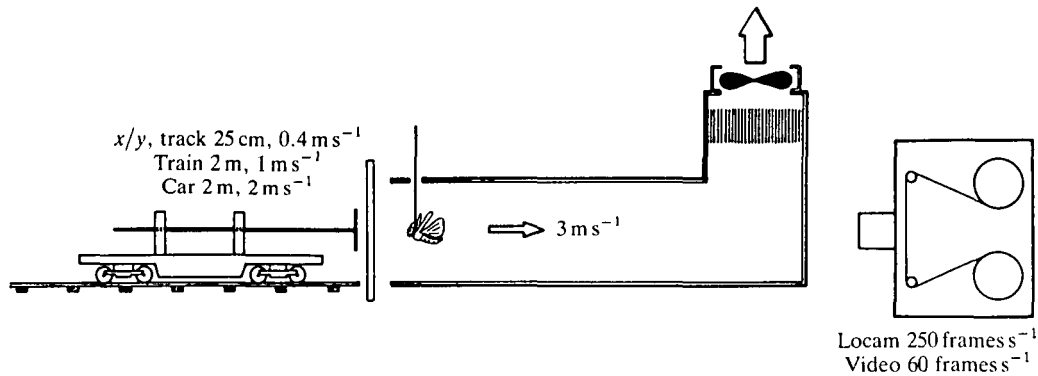


Fig. 1. Diagram of the apparatus used to monitor wing movements during collision-avoidance behaviour. The locust was suspended in the centre of the wind tunnel. Objects were presented to the head of the animal using three types of transport mechanisms with different characteristics. A wind shield was interposed between the approaching object and the head of the animal. The animal was filmed from behind using either a video camera or a high-speed ciné camera. Details in text.

locust would avoid collision by attempting to steer around the target and that the avoidance reflexes would be similar to, but more robust and consistent than, the compensatory steering reflexes described in the literature.

## Materials and methods

### *Tethered flight*

Adult male and female locusts, *Locusta migratoria* L., were obtained from a crowded colony in the Department of Biology at Queen's University. They were tethered to a rod either by attaching a spring-loaded clip to the anterior edge of the pronotum or by securing the rod to the pronotum using wax. Tethered animals were suspended in the centre of a square-section wind tunnel (14 cm × 14 cm) that had a wind speed of 3 m s<sup>-1</sup> (Fig. 1). Analysis of the wind flow using the fumes from dry ice and a hot-wire anemometer showed that the wind where the animal was to be suspended was laminar and at a constant speed. The wind tunnel was L-shaped to allow the animals to be observed from behind. The fan was oriented to draw air through the tunnel and the animal was suspended so that its head was 4 cm from, and facing out of, the square opening. In this way, different objects could be transported directly towards the head of the animal. The floor and lower halves of the sides of the tunnel were covered with black card, while the top halves of the sides were covered with white paper. This provided a lateral horizon to help maintain wing and postural movements appropriate for straight level flight in the absence of approaching targets. Three 150 W lamps were situated above the tunnel: one was used to illuminate and warm the animal while the other two were directed forward, primarily to illuminate the approaching targets. Animals were

flown for at least 15 min before starting experiments which could last for up to 3 h. Experiments were taken to conclusion or terminated whenever an animal started to show a reluctance to maintain steady flight in the characteristic tucked posture.

#### *Target transport*

The targets were squares (7 cm) of light cardboard. These were either black or covered with random dot patterns of uniform pixel sizes which gave the targets internal texture. Different pixel sizes were used on different targets. Three different methods of transporting the targets were used at different times. Initially, we used the locomotive of an electric model train set travelling at full speed along a 2 m length of straight track. The speed was about  $1 \text{ m s}^{-1}$  and constant over the last 1.5 m. The target and locomotive were brought to a halt over 1 cm when metal flanges projecting from both sides of the train were attracted to large magnets at the end of the track. The target remained in the mouth of the wind tunnel at the end of a trial. Using this mechanism the target initially subtended an angle of  $2^\circ$  at the animal and this expanded at an accelerating rate to  $82^\circ$  over 2 s.

To increase the speed of the target we next used a battery-operated radio-controlled model car. A 2 m track was constructed to guide the car in a straight line. The speed was about  $2 \text{ m s}^{-1}$  and constant over the last 1.5 m. The car was not a straightforward mechanism to operate and it was subject to considerable mechanical abuse. The most reliable transport mechanism was the last one that we used. The targets were attached to the moving pen-holder of a Hewlett Packard *x/y* plotter. Movement was initiated by applying a pre-determined voltage to the *x* input. The speed was  $0.4 \text{ m s}^{-1}$  and constant over most of the 25 cm of the bed of the plotter. The target remained in the mouth of the tunnel at the end of a trial. Using this mechanism the target initially subtended an angle of  $14^\circ$  at the head and this expanded at an accelerating rate to  $82^\circ$  over 625 ms.

Each of the tracks was shielded from the rest of the laboratory with sheets of cardboard covered with a random dot pattern to create a textured background for the target.

Each of the tracks created different sorts of noise interference – motors running as the target approached and various loud noises (for example, as the train came against the magnets). We controlled for the effects of these in two ways. First, we performed some trials with animals previously deafened by putting softened wax in their ears. Such animals made no obvious response to loud noises but showed the same asymmetrical wing movements in response to the approach of offset targets as did undeafened animals. Second, we performed some trials using the transporters without targets. The noises did cause startle responses, including upward flicks of the abdomen. However, these trials did not cause the consistent asymmetries in the wingbeat that are described here. Moreover, most of the startle responses were caused by the noises associated with the end of a trial, long after steering manoeuvres should have been complete.

Compensatory yaw manoeuvres can be caused by altering the characteristics of the wind flow over the head of the animal (Camhi, 1970; Zarnack and Möhl, 1977;

Schwenne and Zarnack, 1987). It could be argued that the moving target affected the flow of wind into the mouth of the wind tunnel as it approached and that this was the cause of the flight manoeuvres observed. To remove this possibility, in later trials we placed a 17 cm square acrylic wind shield 2 cm in front of the mouth of the wind tunnel. This had certain disadvantages in disrupting normal air flow into the tunnel but, provided the shield was placed symmetrically in front of the tunnel, apparently normal flight could be produced. The wind shield effectively isolated the animal from any possible directional information from the wake of the target. Figs 9–14 are taken from trials using the wind shield. Trials run with a wind shield showed no change in the form of the wing beat as the target stopped. However, trials run without a wind shield showed that the asymmetrical wind around an offset target markedly changed the character of the asymmetrical beat. They also showed that this happened only after the target had stopped (e.g. Fig. 15). Furthermore, the asymmetries in the wingbeat described here started before the target could have affected air flow into the tunnel. This is evident after considering the air flow rates that the target moved through as it approached the mouth of the wind tunnel and the points at which any turbulent wake could have affected the results (Fig. 2). Any wake would only have presented a problem when it travelled ahead of the target, i.e. when the target travelled in an air stream that was travelling faster than it and in the same direction. In our experimental situation, the air was accelerated over a relatively short distance near the mouth of the tunnel (Fig. 2). Air movement into the tunnel at  $1 \text{ m s}^{-1}$  first occurred 4 cm from the mouth of the tunnel. It was past this point on its approach that a target travelling at  $1 \text{ m s}^{-1}$  would have generated a wake travelling ahead of it. The video analyses (see below) (with  $1 \text{ m s}^{-1}$  target speeds) were started when the target was about 20 cm (about 5 wingbeats) from the mouth of the tunnel. When the target was at the critical distance of 4 cm from the tunnel there was time enough for only 1 wingbeat before the analysis stops and during at least half of this time the disturbed wake could not have reached the head of the animal. The asymmetry described here was observed long before the critical distance, and at least 90 % of the analyses were of wingbeats that could not have been affected by a disturbed wake. For targets travelling at  $0.4 \text{ m s}^{-1}$  on the  $x/y$  plotter, the critical distance when any wake travels ahead of the target was 9 cm. Targets were detected when they were about 10–12 cm away. Although these two figures are close, it is important to remember that the disturbed wake would take at least another 50 ms (2 cm of target travel) to reach the head of the animal. For the above reasons, the results described here could not have been caused by the detection of an asymmetrical turbulent wake.

#### *Video analysis*

Animals were filmed from behind using a Hitachi 5200A video camera with an effective shutter speed of  $1/1000 \text{ s}$ . Using a Panasonic videocassette recorder (model no. PV 4770 K), it was possible to freeze each of the two fields that make up a video frame. This allowed the wing and abdomen movements to be analysed with

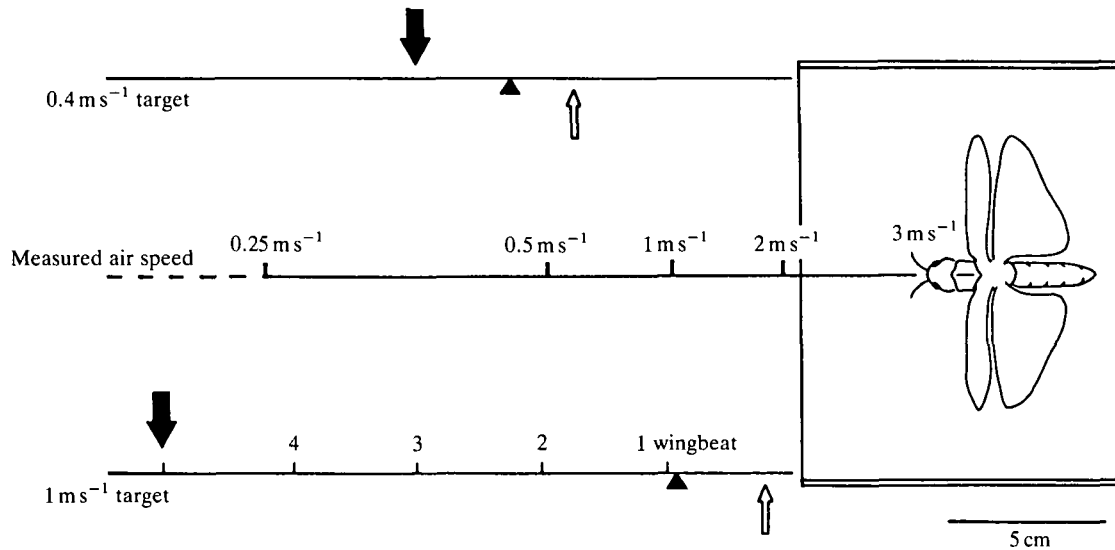


Fig. 2. Air flow measurements in the approach to the wind tunnel compared with critical distances of the target from the head of the locust. Measurements of wind speed at the height of the locust are shown along the central line. For a target travelling at  $0.4 \text{ m s}^{-1}$  (top line) or  $1 \text{ m s}^{-1}$  (bottom line) the black triangle indicates the position at which it entered an air stream travelling towards the animal faster than it was travelling; the open arrow indicates the maximum possible distance the target was from the animal when any disturbed wake reached the animal; the large black arrow indicates the position of the target when it was first detected ( $0.4 \text{ m s}^{-1}$ ) or when the analysis was started ( $1 \text{ m s}^{-1}$ , 5 wingbeats from the end of target travel). Note that detection or analysis was always before any disturbed wake could have reached the head of the animal. Further details in text.

a resolution of  $60 \text{ frames s}^{-1}$  (i.e. only 3 frames per wingbeat cycle). This resolution was insufficient to analyse the timing and amplitude of complete wingbeats. However, a consistent feature associated with the approach of a target was an asymmetry in the elevation angles of the two forewings that was most prominent during the downstroke. This asymmetry was quantified in the following way. For an image frozen during the downstroke, the angles of each of the forewings were measured to the nearest  $5^\circ$  from a zero position directed dorsally. The right forewing angle was given a positive value and the left forewing a negative value. The left (negative) value was added to the right (positive) value so that a positive difference would indicate a greater depression of the right forewing and a negative difference would indicate that the left forewing was more depressed. For each trial analysed, the asymmetry of the 5 downstrokes just prior to the target stopping was averaged to quantify the response to the target. This is presented as an absolute asymmetry in Fig. 4. Some of the animals showed steering biases as an artefact of tethering so the change in the asymmetry caused by the target was analysed by comparing the average asymmetry prior to stopping with the average

asymmetry of the 5 downstrokes just after the target had started. This is presented as a relative asymmetry in Fig. 5.

#### *High-speed cinematography*

Animals were filmed from behind using a Locam high-speed camera running at  $250 \text{ frames s}^{-1}$  with a shutter speed of  $1/2250 \text{ s}$ . This gave sufficient resolution (4 ms) to analyse the form of complete wingbeats (i.e. about 12 frames per wingbeat cycle). Selected trials were analysed in the following way. The image was projected *via* a mirror onto the underside of a sheet of glass covered with tracing paper. The orientation of the projection set-up was checked carefully to eliminate possible distortion. In each frame, the horizontal and vertical positions of the tip of the abdomen were measured relative to a fixed point (the end of the tether). Movements to the right and upwards were given positive values. The numerical values represent millimetres of movement of the projected image (enlarged two times). Also, in each frame the elevation angle of each of the four wings was measured relative to a zero position directly ventral with an accuracy of around  $2^\circ$ . For each beat of the forewings, the time of pronation was estimated as the time of the frame in which the wing profile changed from broad to narrow. It was unnecessary to analyse all the wingbeats during the complete approach of the target for the animal usually reacted only in the last 0.5 s. Consistently, the first indication that the animal was reacting to the approaching target was an elevation and lateral movement of the abdomen. We analysed 100 frames (400 ms) taken from two or three wingbeats before the first indication of abdominal movement and this usually passed the point at which the target stopped.

Owing to the relative difficulty of filming and the reliability of the  $x/y$  plotter as the transport mechanism, all trials analysed with high-speed cinematography were run with this mechanism.

#### *Database*

Thirty-eight animals of either sex were used. A trial refers to one approach of the target towards the head of the animal. The number of trials on each animal varied with the propensity of the animal to maintain flight. Some animals received 75 trials presented equally down the right, the left or down the centre line. Other animals received only 10 trials on each side. Ten animals were videotaped as the target was transported by the train. Seven animals were videotaped as the target was transported by the car. Twenty-one animals were presented with targets using the  $x/y$  plotter and, of these, 10 were videotaped and 11 were filmed using the Locam. Complete video analysis was performed for all the trials of the 10 animals using the train. Complete high-speed cinematographic analysis was performed for 23 separate trials of 7 animals all using the  $x/y$  plotter.

### **Results**

#### *General observations*

Within a few minutes of the wind stream being turned on, most tethered locusts

assumed the characteristic flight posture and flew continuously for up to 3 h. Some animals needed to be coaxed into flight with startling auditory stimuli (a hissing noise). However, animals that continually needed such coaxing were discarded and are not included in the database.

The stimuli presented to the locusts undoubtedly resulted in subtle alterations in posture and in the form of the wingbeat that were not detected in our analyses. The features that we describe below were relatively pronounced and consistent regardless of which transport system was used. There was some variability in the efficacy of each of the transport systems in eliciting a response. The slower speed of the target when carried with the  $x/y$  plotter was less effective in evoking steering manoeuvres. For example, of the 11 animals that we filmed using the Locam and the  $x/y$  plotter, 4 showed no response detectable with our methods. The remaining 7 gave expected manoeuvres and 5 of these responded particularly well. All the animals that we videotaped using the train responded sufficiently to indicate that they had detected the approach of the target.

*Forewing asymmetry associated with collision-avoidance steering*

Our study was restricted to analyses of movements viewed from directly behind the locust. During steady flight in the absence of stimuli that might induce steering manoeuvres, the wingbeats on the right and left sides were usually quite symmetrical with the hindwings leading the forewings by 10–30°. This is clearly evident during the downstroke (Fig. 3A). When presented with an approaching target offset to one side of the midline, the animal consistently assumed the posture characteristic of steering (Dugard, 1967; Camhi, 1970), with the abdomen and hindlegs transposed laterally and indicating the direction of the turn (Fig. 3B,C). In the majority of cases, the attempted steering manoeuvre was in the direction of the closest edge of the approaching target, which is likely to be the most rapid way to avoid the impending collision. The most obvious change in the form of the wingbeat associated with attempted steering was that during the downstroke the forewings became asymmetrical, with the forewing on the inside of the turn being markedly more depressed than the other forewing. The three video frames of Fig. 3 were taken at the same phase of the wingbeat (mid-downstroke), as indicated by the position of the hindwings, and they show clearly the forewing asymmetry produced by the targets. The increased depression of the inside forewing was often sufficient to bring it lower than the hindwing on that side (Fig. 3C, arrow).

The low temporal resolution of video analysis was insufficient to be able to determine what kinematic alterations led to these images. They could be produced either by altering the timing of the beat of the two forewings or by altering the range of elevation angles through which each forewing beats (or a combination of the two). However, the image was quite characteristic of attempted steering and could easily be detected in the videotapes. This enabled numerous trials to be analysed relatively simply in order to determine the consistency of such responses. As described in the Materials and methods, images of the forewings such as those



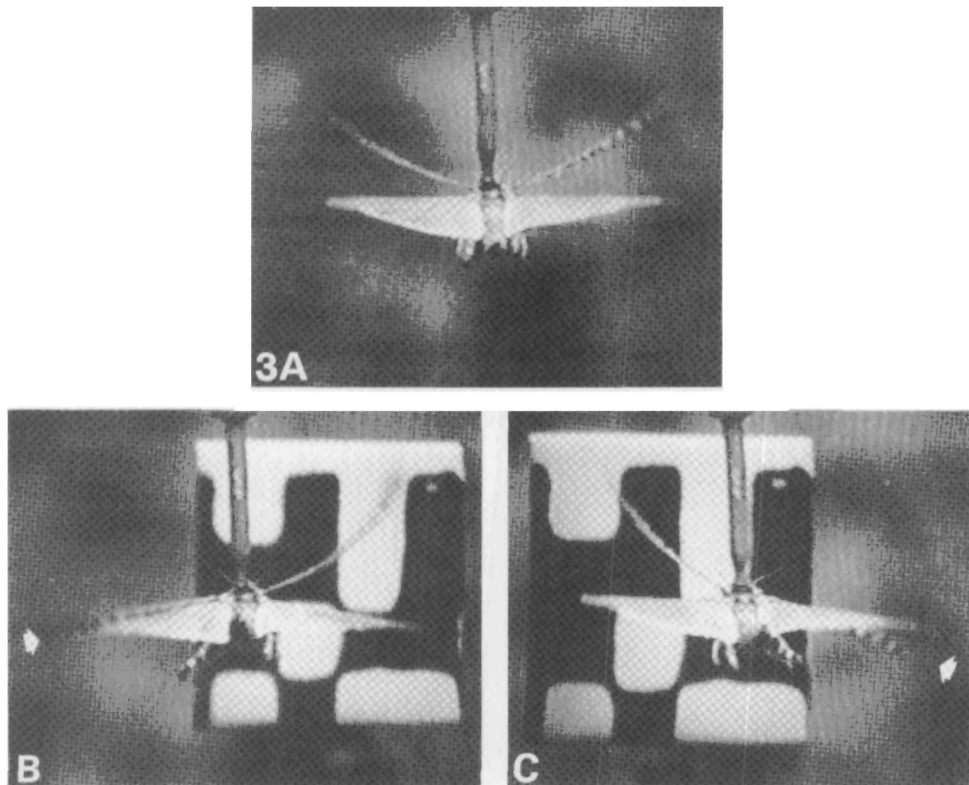


Fig. 3. Photographs of still images on the television monitor. The views are from the rear of a female locust during tethered flight in the wind tunnel. Each image is taken approximately at the middle of the downstroke. Hindwings (broad and white) lead the forewings (narrow and mottled). (A) Symmetrical wingbeat during straight flight. Note that the abdomen and hindlegs are pointing directly rearwards. (B) Changes in position initiated by the approach of an object offset from the direct midline by 2 cm to the right. Note that the abdomen and hindlegs have moved laterally and note the asymmetry in the position of the forewings. Position of left (lower) forewing is indicated with an arrow. (C) The mirror image of B as the object approaches on the opposite side. The lower forewing is arrowed.

shown in Fig. 3 could be quantified to give a value of angular asymmetry. If the angular asymmetry is negative, then the left forewing is more depressed than the right forewing by the value of that angle. An alternative way of thinking of this value is to consider that, if halved, it would indicate the direction of the line bisecting the angle between the two forewings, with zero being directly vertical and a negative value being rotated to the left. Analysis of the responses of 5 of the 10 animals videotaped and using the train to transport the target is shown in Fig. 4. Data from two animals were not included because these animals always responded by attempting to steer to the same edge of the target regardless of its line of approach, and three others were excluded because tethering had resulted in an

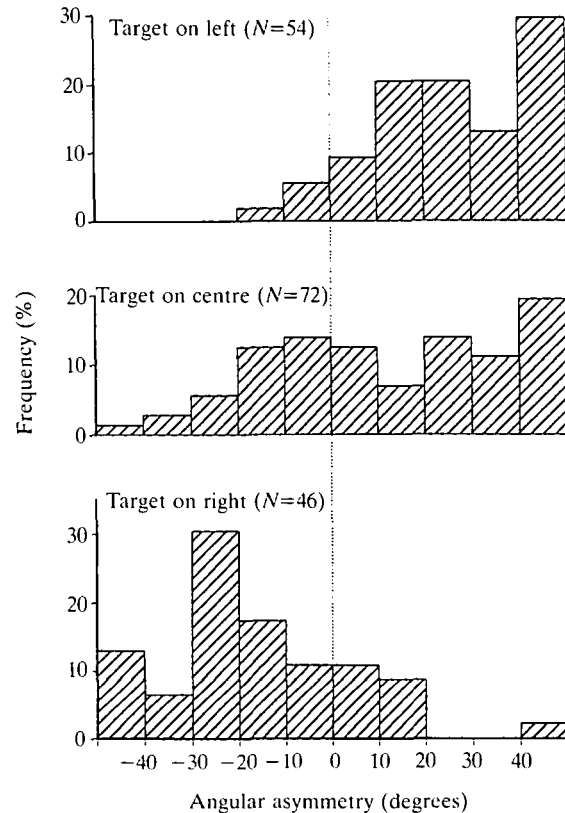


Fig. 4. Forewing asymmetry correlated with offset position of the target. The angular asymmetry of the forewings was calculated as outlined in the Materials and methods. A negative value indicates that the left forewing is more depressed. Data were taken from 172 separate trials on five animals. Upper graph, when the target was presented down the left side, the forewings were predominantly asymmetrical with the left forewing more elevated. Lower graph, when the target was presented down the right side, asymmetry was with the right forewing more elevated. Middle graph, when the target was presented down the centre line, the asymmetry could be to either side, although there was a slight bias to positive values of asymmetry.

unacceptable bias in the forewing asymmetry. The targets were presented either down the midline or 1, 2, 3 or 4 cm offset to either side. The data were pooled by including all trials within, and including, 1 cm either side of the midline as being on centre, and including all trials greater than and including 2 cm offset as being either to the left or to the right of the animal. When the target was on centre, the average angular asymmetry of the 5 forewing beats immediately prior to the target stopping was distributed between negative and positive values (Fig. 4). However, when the target was on the left, the average angular asymmetry of the forewing was predominantly positive, indicating that the right forewing was depressed (this corresponds to the image of Fig. 3C). When the target was on the right, the mirror image pertained, with the left forewing depressed (as in Fig. 3B).

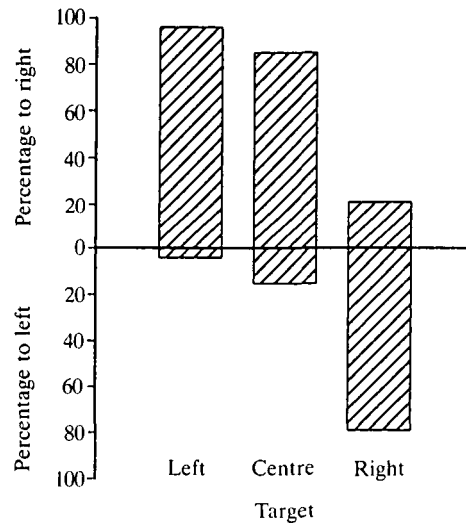


Fig. 5. Changes in the angle of asymmetry caused by the approach of targets. Each block shows the frequency of occurrence of changes in the asymmetry of the forewings relative to a starting bias (if present) and caused by the approach of a target on the left, on the right or down the centre line. Percentage to right, occurrences of trials when the angle of asymmetry becomes more positive, indicating a rightward rotation of the line bisecting the angle between the two forewings. Percentage to left, occurrences of trials when the angle of asymmetry becomes more negative, indicating a leftward rotation of the line bisecting the angle between the two forewings. Note that targets on the left predominantly caused a rightward rotation whereas targets on the right predominantly caused a leftward rotation. Targets down the centre line gave a biased response to a rightward rotation which may have been due to an inherent asymmetry in the apparatus. Data were taken from 181 separate trials on 10 animals.

The above analysis included only 5 of the 10 animals videotaped and using the train as the transporter. Although three animals were excluded because of a bias probably introduced as an artefact of tethering, these animals did respond to approaching targets in the appropriate way. To negate the effect of the bias, we compared the average asymmetry of the 5 forewing beats immediately prior to the end of the trial with the average of the 5 immediately after the target started to move. This gave a value for the change in asymmetry caused by the approach of the target. For all trials showing a shift greater than  $10^\circ$  ( $N=181$ ), in all 10 animals tested using the train, a positive shift in asymmetry (to the right) was associated with targets approaching on the left, whereas a negative shift was associated with targets on the right (Fig. 5). It is interesting that in Fig. 5, and less obviously in Fig. 4, there seemed to be a bias in the response such that targets on centre were more likely to cause positive forewing asymmetries (to the right) than negative ones. We did not investigate this further and attribute it to an unknown artefact caused by an unnoticed asymmetry in the set-up or procedure (e.g. between trials

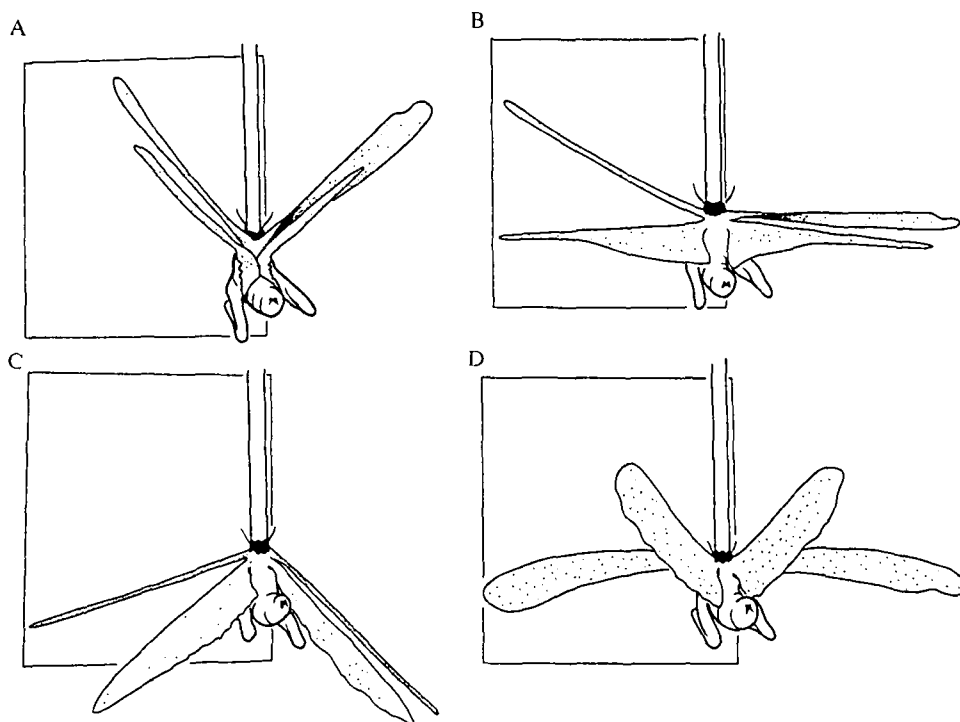


Fig. 6. Images of a wingbeat during attempted steering to the right (see abdomen) in response to the approach of a target (outlined) on the left. (A) Upstroke-to-downstroke transition. Note that the right forewing is considerably more pronated than the left forewing. (B) Mid-downstroke. Note the angular asymmetry of the forewings and the pronounced pronation of the right forewing. (C) Downstroke-to-upstroke transition. (D) Mid-upstroke. Note that both fore- and hindwings tend to be elevated symmetrically. The notch in the trailing edge of the right forewing is a convenient indicator of the quality of its angle of attack.

the experimenter consistently came into the animal's view on its right side in order to detach the train from the magnets).

#### *Angle of attack*

Videoanalysis enabled us to determine the frequency with which forewing asymmetry was caused by the approach of the target, and the extent to which the sign of forewing asymmetry correlated with the direction of attempted steering. However, to determine the details of the wingbeat, the higher temporal resolution of the Locam camera was necessary. Tracings from individual frames during particular trials show that both the angle of attack of the wings and the angular asymmetry of the forewings were asymmetric. At the top of the wingbeat, the wings on the inside of the attempted turn pronated in advance of the contralateral wings (Fig. 6A) and maintained a more pronounced pronation during the downstroke (Fig. 6B). At the bottom of the wingbeat, the right and left wings

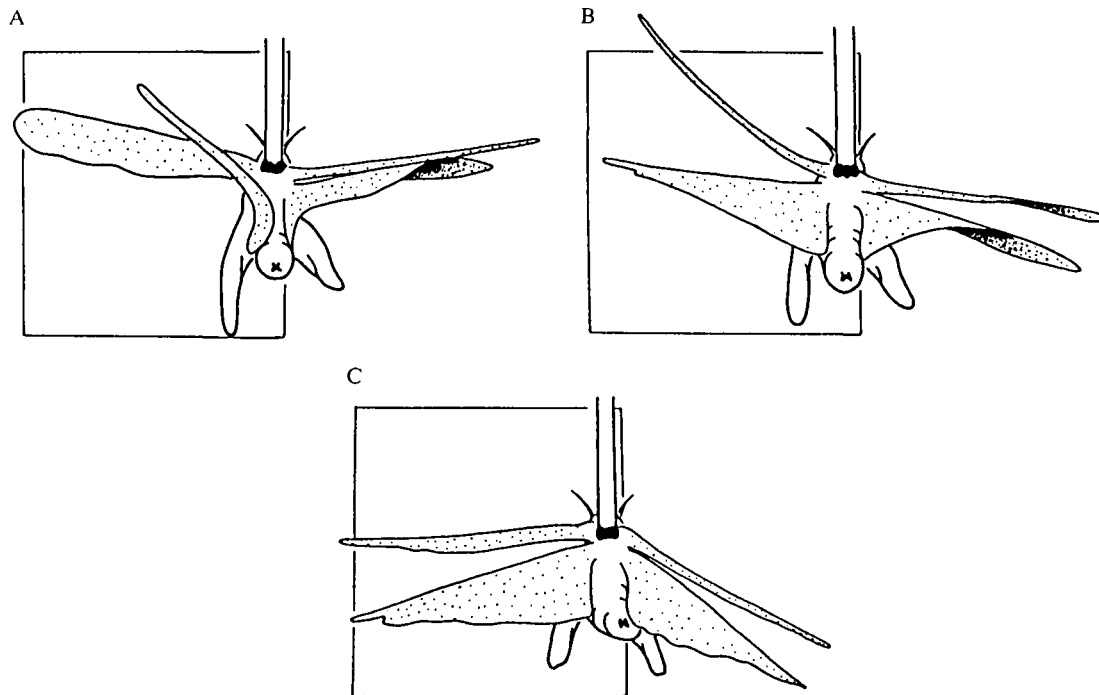


Fig. 7. Wing pronation on the inside of an attempted turn. (A–C) Tracings from frames during a single downstroke showing a pronounced pronation of the hind- and forewing on the right side. This occurred earlier than pronation of the left wings (compare profiles of forewings in A) and was of greater magnitude. Frames A and B are 8 ms apart and frames B and C are 12 ms apart.

supinated together (Fig. 6C) and they ascended during the upstroke relatively symmetrically (Fig. 6D). The asymmetry in the timing and extent of pronation (sooner and more pronounced on the inside of the turn) was evident for the hindwings as well as the forewings (Fig. 7).

#### *Clap-and-fling*

Another feature of the wingbeat that could be discerned in several trials only with high-resolution analysis was a clap-and-fling of the hindwings (Fig. 8). This wingbeat strategy to increase lift (Weis-Fogh, 1973; Ellington, 1984a) has been described in locusts in natural flight (Cooter and Baker, 1977). Further investigation of these unsteady mechanisms of generating increased lift was not undertaken.

#### *Kinematic analysis*

A full, high-resolution analysis of abdominal and wing elevation movements was undertaken for 23 trials using the  $x/y$  plotter as the transport mechanism. The

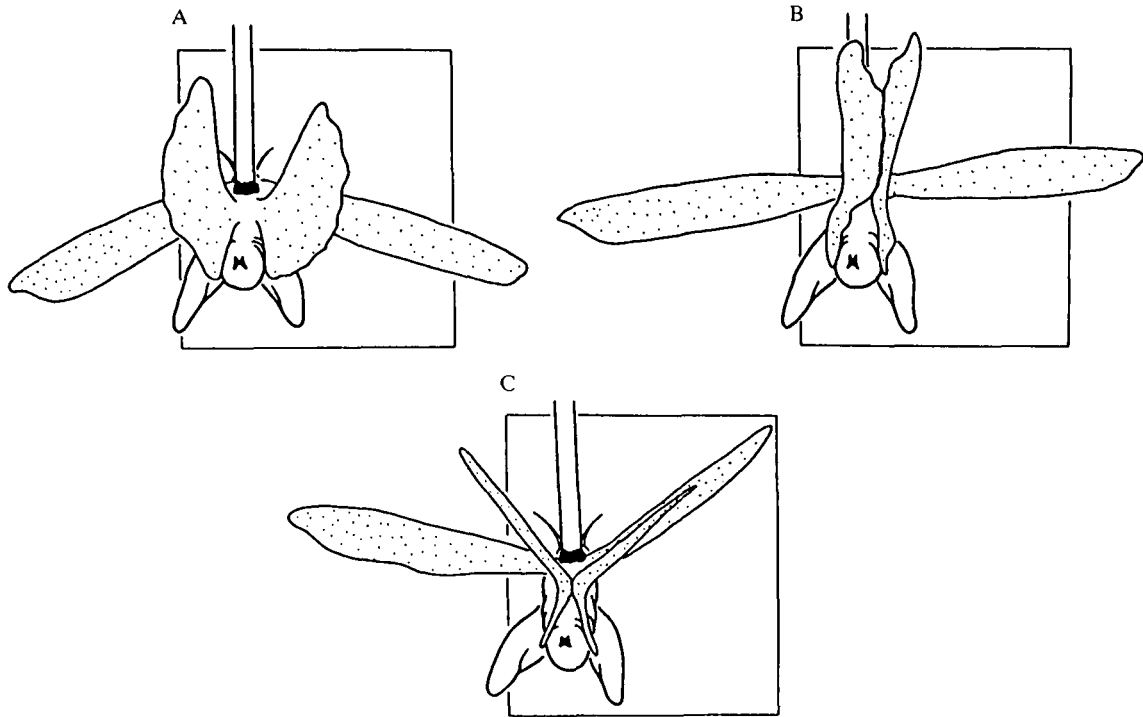


Fig. 8. 'Clap-and-fling' of the hindwings in response to the approach of a target on the right. A, B and C are 4 ms apart. Note that in B the hindwings come together at the top of the stroke and are then pulled rapidly apart. In C, the right forewing moves to a more elevated position than the left forewing in preparation for an attempted steering manoeuvre.

features consistently associated with attempted steering manoeuvres are described below using only a few selected trials to illustrate the points.

The first indication that the animal had detected and was responding to the approach of a target was an upward and lateral movement of the abdomen (Figs 9, 10). However, the abdominal movement preceded a change in the wingbeat usually by less than the duration of a single wingbeat. First detection of the target was 200–300 ms before the target stopped (12–16 cm from the head of the animal), which is equivalent to 300–400 ms before the projected collision. This time allowed only around 4 full wingbeats before the target stopped (around 7 full wingbeats before projected collision). At detection, the target subtended an angle of around  $30^\circ$  which was expanding at about  $85^\circ\text{s}^{-1}$  and about  $460^\circ\text{s}^{-2}$ .

The first change in the wingbeat after detection was often a shallow (low-amplitude) beat of all four wings created by eradicating most of the upstroke (Figs 9, 10). Thereafter, the forewings showed the most obvious changes. On the outside of an attempted turn the forewings moved into a more elevated range than the forewings on the inside. The rates of ascent and descent of the right and left forewings were similar and they were symmetrical in the middle of the upstroke.

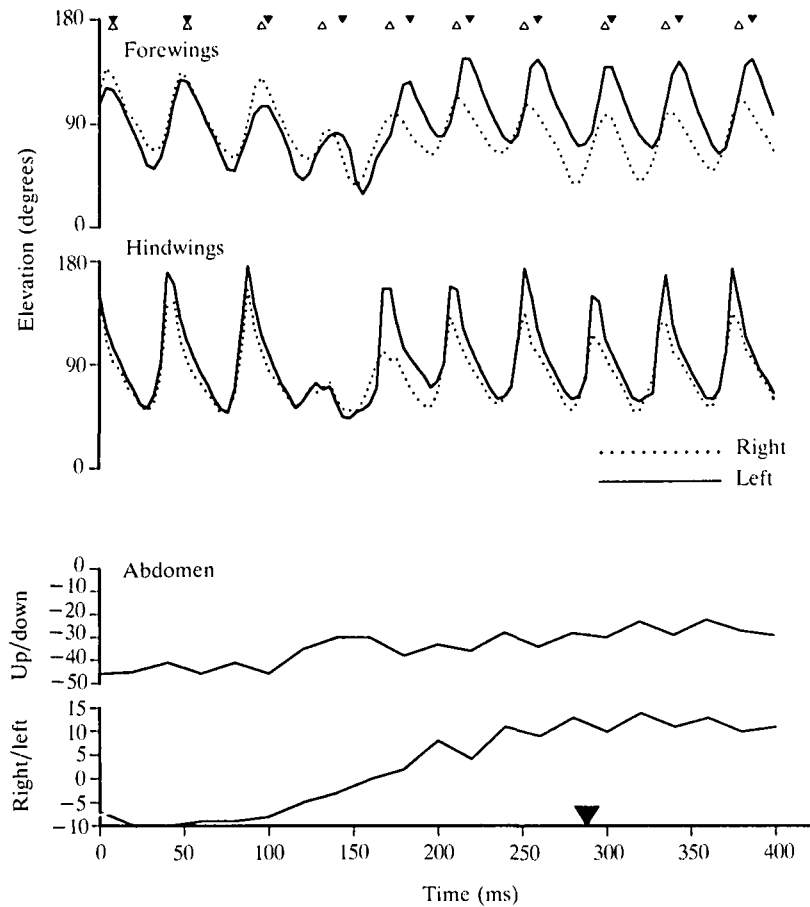


Fig. 9. Analysis of wing and abdomen movements in response to approach of an object offset to the left by 2 cm. Abdominal movement is indicated in millimetres of movement of the projected image (enlarged  $\times 2$ ): lateral movements were positive to the right; vertical movements were positive in the upward direction; the zero position was the bottom of the tether. Wing movements were plotted as angles of elevation, with  $0^\circ$  being directly beneath the animal. Triangles indicate the time of pronation for each of the forewings (open triangle, right; closed triangle, left). The object started to move at  $t = -350$  ms approximately. The large filled triangle on the time scale indicates the time at which the target stopped: collision would have occurred 100 ms after this time. The first reaction of the locust was at  $t = 100$  ms when the abdomen was raised and moved to the left. The first obvious change in wingbeat parameters was at  $t = 130$  ms with a shallow beat of all wings. This was followed by an extended elevation of the left forewing and slight phase shifting between the forewings, with the left forewing turning and pronating later than the right. Thereafter, the most pronounced change was an increased elevation of the right forewing relative to the left forewing. Hindwing asymmetry was present and of the same nature but mild in comparison with the forewing asymmetry.

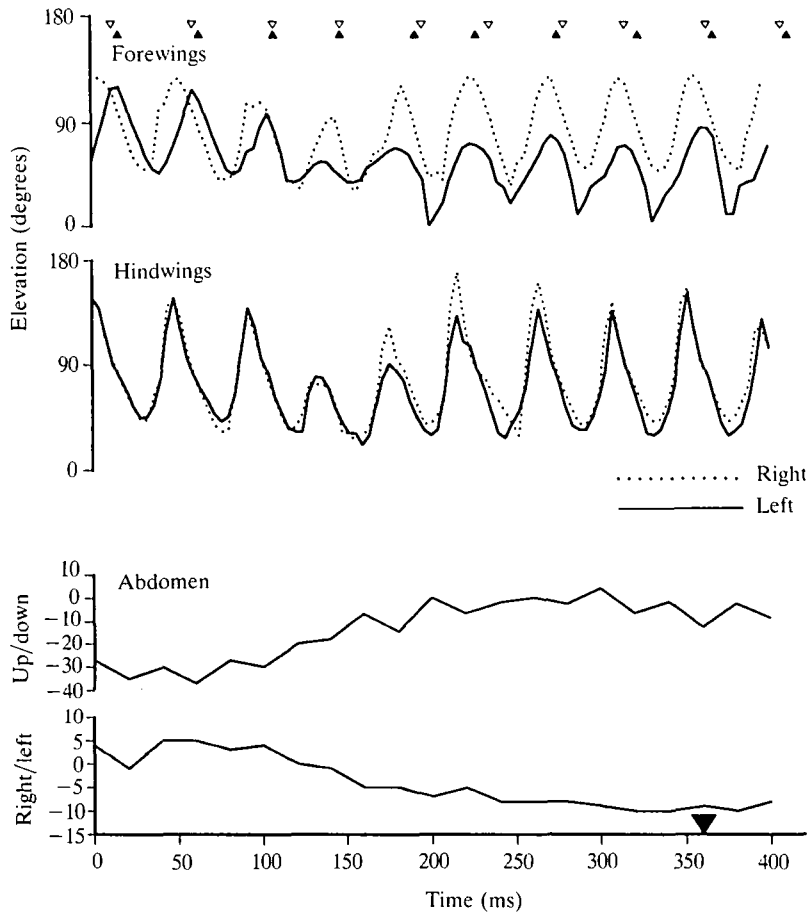


Fig. 10. Analysis of wing and abdomen movements in response to approach of an object offset to the right by 2 cm. Detailed description is similar to, but the mirror-image of, that for Fig. 9.

The asymmetry was caused by delaying the time of downstroke initiation of the forewing that became more elevated. Subsequent beats of the forewings remained out of phase by 4–8 ms (the temporal resolution of the analysis was 4 ms) with the inside wing leading. Amplitude asymmetries were often detected with the inside wing having a shallower beat. Pronation of the inside wing was earlier. The hindwings showed changes of a similar nature but to a lesser extent than the forewings. There was a slight increase in wingbeat frequency after target detection that was maintained for several cycles.

A shallow and early beat of the inside forewing brought it into line with the hindwing on the same side even though the upstroke/downstroke changes of the hindwing remained in advance of those of the forewing (Figs 11, 12).

The essential features of this movement pattern are summarised in Figs 13 and 14 from different trials. During an attempted left turn, the left forewing had a



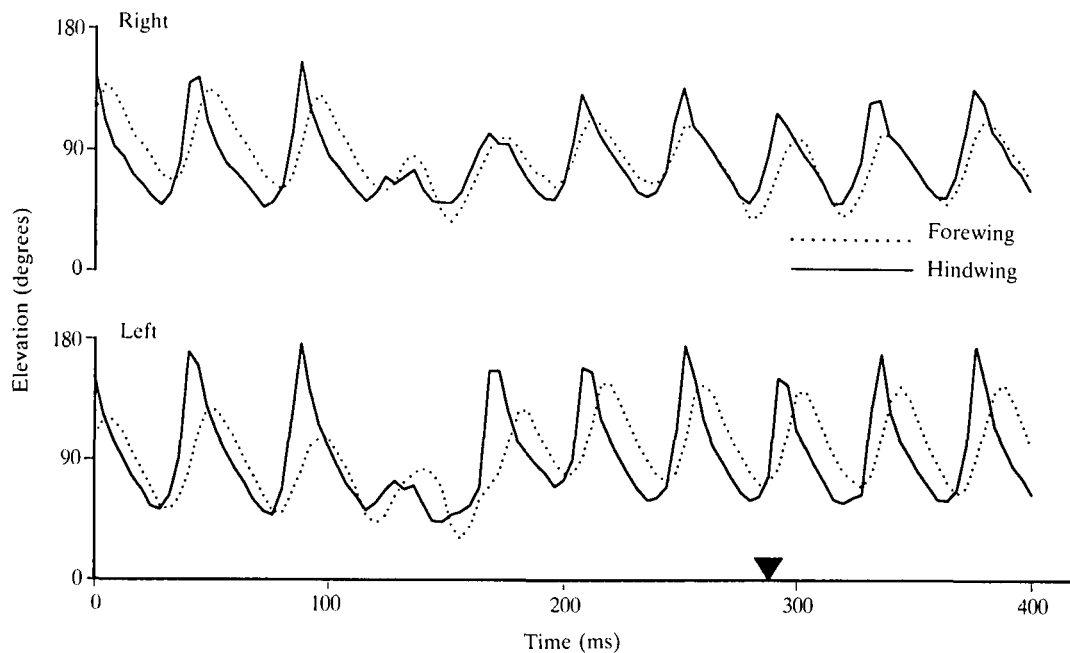


Fig. 11. Analysis of hindwing/forewing interaction in response to approach of an object offset to the left by 2 cm. This is the same trial as shown in Fig. 9 with the data presented differently. Note that after the target has been detected (shallow beat) the forewing and hindwing on the inside of the attempted turn (right side) had very similar elevation angles during each downstroke, whereas on the other side the forewing and hindwing are separated during each downstroke.

shallower, phase-advanced beat compared with the right forewing (Fig. 13). During an attempted right turn, the opposite was true. This had the effect of lining up the fore- and hindwings during the downstroke on the inside of an attempted turn while keeping them well separate on the outside (Fig. 14).

#### *Effect of target characteristics*

As well as black targets we also used targets covered with random dot patterns of different pixel sizes (see, for example, Fig. 3B,C). For the most part, such variations had no obvious effect on the movement patterns we observed and they are ignored in the following account. Nevertheless, for some trials we accidentally used a random dot pattern with a pixel size (3 mm square) that was not detected (as indicated by abdominal movement) by the animal until the target was close to collision (around 7 cm from the animals head; collision in about 175 ms). At detection, the target would be subtending an angle of  $53^\circ$  expanding at  $154^\circ \text{s}^{-1}$ , while each pixel would subtend  $2.5^\circ$  expanding at  $14^\circ \text{s}^{-1}$ . In these trials, at the top of the upstroke after target detection wingbeating stopped and the four wings assumed a gliding configuration (Fig. 15) that lasted until after the target had

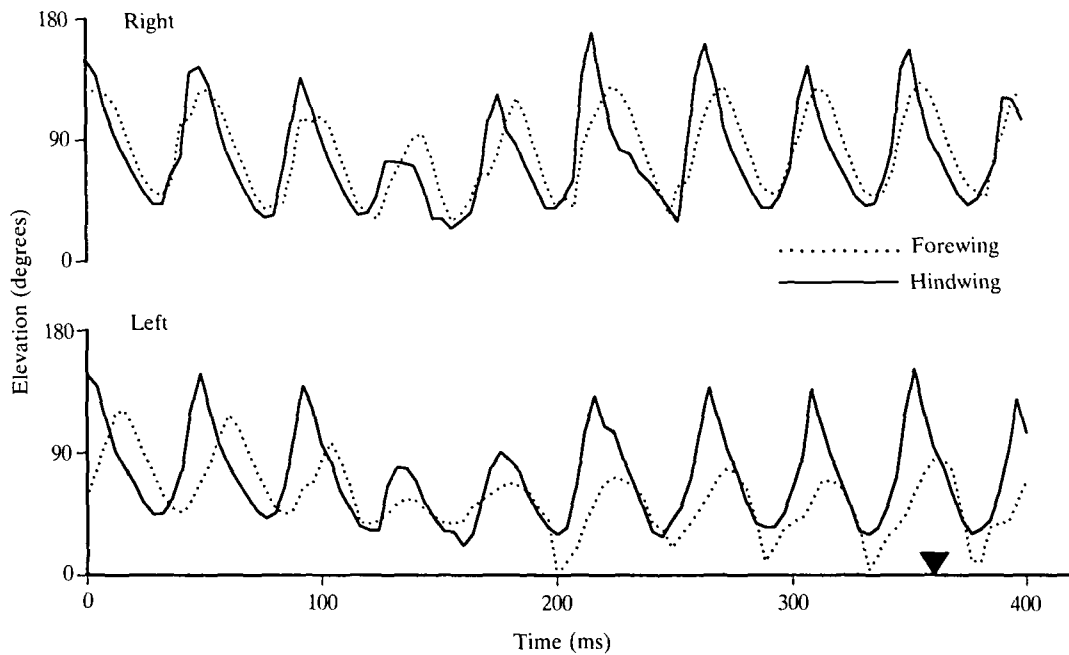


Fig. 12. Analysis of hindwing/forewing interaction in response to approach of an object offset to the right by 2 cm. This is the same trial as shown in Fig. 10 with the data presented differently. Detailed description is similar to, but the mirror image of, that for Fig. 11.

stopped moving. Before starting to glide, there was no detectable alteration in the form of the wingbeat. At the same time (not shown), the prothoracic legs rapidly extended forward in a landing-type reaction that would have prevented a head-on collision and absorbed some of the force of the impact, had the target continued to move.

### Discussion

The principal findings of this investigation are as follows: (1) presentation of a moving target towards the head of a tethered locust flying in a wind tunnel resulted in a marked asymmetry in the beat of the forewings; (2) the asymmetry involved the timing and extent of pronation at the top of the stroke and the angular position of the forewings at any point during the downstroke; (3) the side of the asymmetry (i.e. right or left wing more depressed) was predictable from the line of approach of the target; (4) the forewing on the same side as the target was more elevated than the forewing on the opposite side, which was depressed in conjunction with the hindwing on its side; (5) the asymmetry was brought about by relative shifts in the timing of stroke transitions (upstroke to downstroke and *vice versa*) and by a difference in the range of elevation angles through which each forewing beats. The possible interpretations of these findings depend on evaluating the limitations

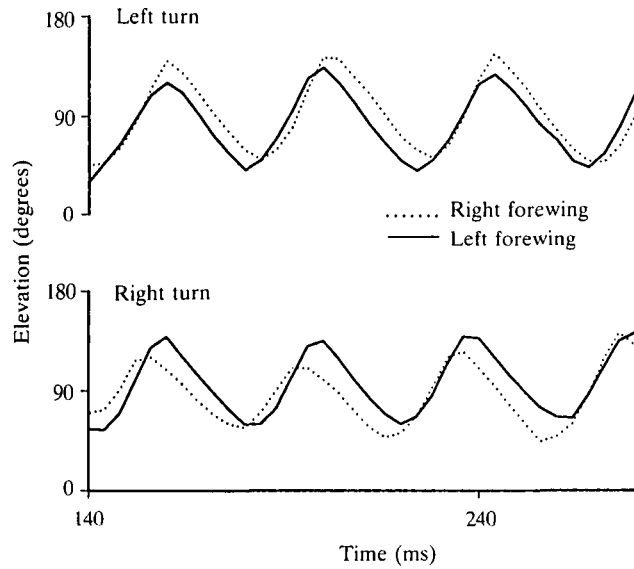


Fig. 13. Summary of forewing asymmetry during attempted turns to the left and to the right. Note the relative phase shift and the difference in the range of the beat between the left and right forewings. Also, the forewings are symmetrical for most of the upstroke and asymmetrical during the downstroke. These represent the three wingbeats just before the target stopped.

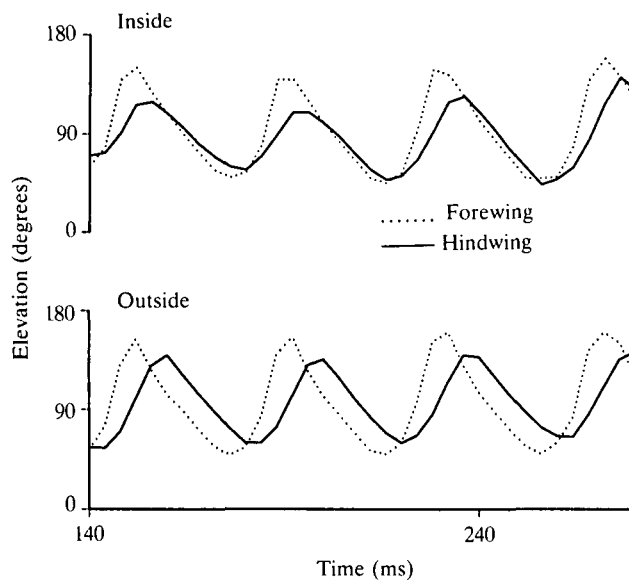


Fig. 14. Summary of hindwing/forewing interaction during attempted turns. On the inside of an attempted turn, the hindwing and forewing come down together whereas, on the outside, they are markedly separate. These represent the three wingbeats just before the target stopped.

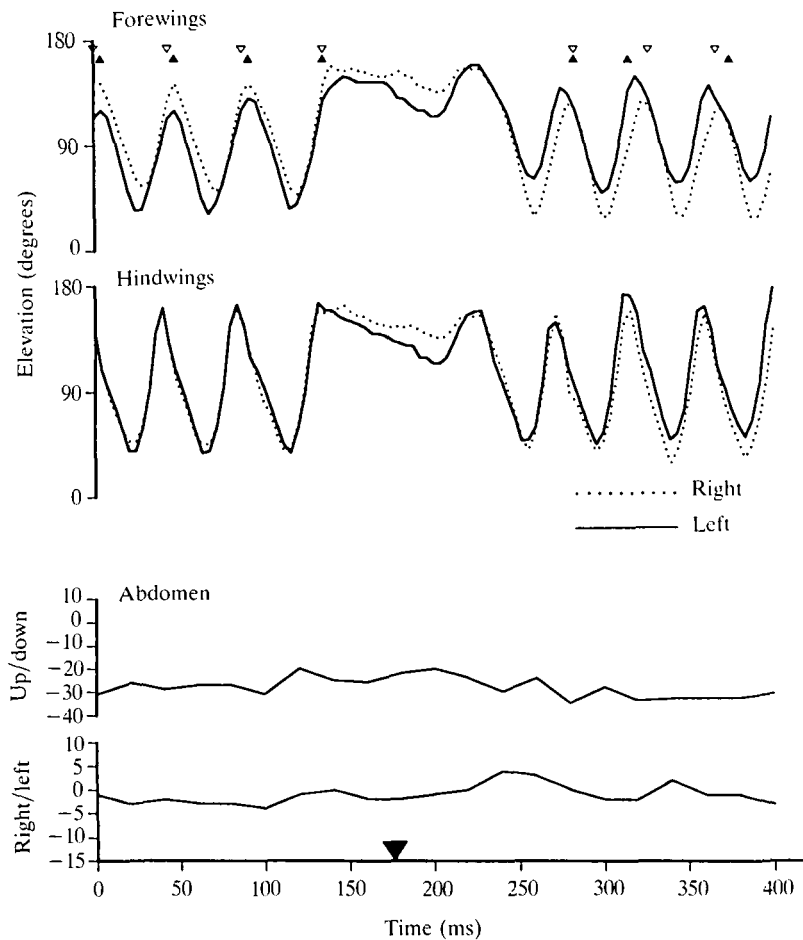


Fig. 15. Gliding and landing reaction. The target had a random dot pattern of small pixel size, preventing it from being detected against the background until late in the approach and it was offset 2 cm to the right. There was a slight bias, indicating attempted steering to the left. First reaction was at  $t=100$  ms, as indicated by the movement of the abdomen. Note that there were no additional asymmetrical forewing movements indicative of a steering manoeuvre but the animal glided and the wings started to fold. At the same time, the forelegs are extended towards the target (not shown). When the target stopped moving, wingbeating was resumed. The wind shield was not used for this trial and the forewing asymmetry on resumption of beating was due to an asymmetrical windflow around the target.

imposed by the experimental approach. It is thus important to consider the extent of these limitations, given that the intention was to mimic situations that would result in aerodynamic manoeuvres by a free-flying locust to avoid colliding with obstacles in its immediate flight path.

#### *Technical limitations*

The first question is whether our procedure adequately simulated normal flight.

Rigidly tethering the locust is arguably the most serious limitation. This is known to result in steering biases in recorded motor patterns (Möhl, 1985, 1988) and similar biases were clearly evident in the present investigation. Also, a preliminary analysis of the flight forces generated by tethered animals in our set-up has shown that they do not generate sufficient lift to counteract their body weight (R. M. Robertson and D. W. Lywood, unpublished results). Insufficient lift has been observed in numerous other studies using tethered animals (e.g. Kruppel and Gewecke, 1985) but is by no means a necessary consequence of tethering (Zarnack and Wortmann, 1989). Nevertheless, a rigid tether does avoid the problem that an animal free to move in the windstream may generate secondary compensatory reflexes for the altered wind flow over the head (e.g. Zarnack and Möhl, 1977), which could confuse the issue. This method of tethering also opens the reflex loop. Conceivably, the perception that a course of action is having no effect could induce other, more potent, or even spurious, reflexes. However, similar steering mechanisms to the ones described here have been described as underlying roll compensatory steering under closed-loop conditions (Waldmann and Zarnack, 1987). Accepting that most experimentation involves compromise, we believe that the rigid tether did not unduly influence our data and its interpretation for the following reasons. First, the movements generated by the approach of the target were sufficiently robust to be clearly evident in spite of the presence of pre-existing asymmetries, which are best interpreted as steering biases. Second, the movements described here had the characteristics of escape reflexes in that they were generated within a few wingbeats of the projected collision and they were thus less likely to be affected by opening the reflex loop. Third, the similarity of the wing movements described here with numerous descriptions in the literature of steering manoeuvres in other situations (see below) argues that the influence of the tether is minimal. A more serious problem with our method of tethering is that we have no measure of the effect of the wing asymmetries we have described on aerodynamic forces or on the direction of flight. Our behavioural interpretation is largely speculative but warranted, in our opinion, by the wealth of data on wing movements and aerodynamic manoeuvres in a variety of different insects, including a large body of data on locusts (see below).

The wind speed in the tunnel (laminar,  $3 \text{ m s}^{-1}$ ) and the variable speed of the target in different instances do not present problems. Indeed the consistency of our observations in the face of widely varying speeds and modes of target transport suggests that the phenomena we have described play an important part in a flying locust's aerodynamic repertoire.

The second question is whether these wing movements were induced by the visual properties of the approaching target. All the trials were contaminated with some form of auditory interference and the ends of some of the trials were contaminated with an asymmetrical wind flow. We believe that the controls we describe in the Materials and methods were adequate to discount the possibility that the forewing asymmetry was induced by anything other than the approach of the target. More compelling evidence, perhaps, is the observation that these

manoeuvres were initiated several wingbeats before the auditory and wind interferences could have had a confounding influence.

It could be argued that the fact that the reactions we describe were generated very late, within a few wingbeats of projected collision, betokens a problem with our set-up or procedure that prevented the locust from properly detecting the approach of the targets. We counter this with the argument that natural conditions in a swarm (Uvarov, 1977) are such that continual reaction to objects further away in the flight path would be maladaptive and that it seems sensible to manoeuvre only when absolutely necessary. Nevertheless, the visual environment of our tethered locusts was unnatural in that there was no optic flow field (Lee, 1980) before the target started to move. This may have prevented more gradual steering, which would be expected of animals not in a swarm, by preventing the perception of flight in a three-dimensional environment. Alternatively, the changes in wing kinematics and body posture that could cause slight variations in flight direction suitable for gradual collision avoidance may be so slight as to have escaped detection using our methods. It may be that we have monitored only the dramatic manoeuvres that come into play when all else has failed.

#### *Behavioural interpretation*

If confronted with an object directly in its flight path a locust could choose to fly around it, over it or under it, or it could land on it to prevent a head-on collision. The best strategy will depend on the position of the obstacle relative to the animal and the time to collision within which any manoeuvre has to be completed. Although we have concentrated primarily on steering movements around obstacles in this investigation, our results show, not surprisingly, that the locusts attempted each of the other behavioural strategies.

Clap-and-fling and clap-and-peel (Weis-Fogh, 1973; Cooter and Baker, 1977; Ellington, 1984*a,b*; Götz, 1987) of the hindwings were evident in numerous trials and this has been interpreted in other situations, and with other flying animals, as a means of generating extra lift. We also noticed for several trials in which the approach of the target was directly down the midline that all four wings increased the amplitude and rate of their beat without necessarily becoming asymmetrical, and the separation between the hindwing and forewing on each side became more prominent (data not shown). It has been demonstrated that lift is profoundly affected by the phase difference between the fore- and hindwings (Wortmann and Zarnack, 1987). The above tactics can be interpreted as an attempt to fly over the obstacle.

Short sequences (maximum 0.3 s) of gliding flight have been recorded for *Locusta migratoria* under natural conditions (Baker and Cooter, 1979). In these cases it was associated with a reduced forward speed, a sinking speed of around  $2 \text{ m s}^{-1}$  and a pitch forward of the animal, but the sensory conditions for initiation of gliding sequences were unknown. In our study, the occurrence of gliding was associated with a landing reaction and with the use of a random dot pattern of

small pixel size. It is likely that gliding in this situation would be useful in reducing forward speed in preparation for landing, or at least absorbing the impact of collision on the prothoracic legs. Cinematographic analysis of these manoeuvres showed that the locust made no reaction until late in the trial, indicating a late detection of the target. It may be that this was due to an inability of the locust to resolve the pattern and distinguish it from the background until it came close enough for the pixels to subtend a large enough arc at the compound eyes. Optomotor reflexes during flight generated by vertical gratings are elicited only if the gratings have spatial periods greater than  $5\text{--}10^\circ$  (Robert, 1988), indicating a limit to the resolving power of the visual system. An array of 3 mm pixels would have such spatial periods only when it was closer than 6.9 cm from the head. This corresponds approximately to the position of the target when it first generated a gliding response. Considering that response latencies for visually induced abdominal steering reactions are around 60 ms (Baader, 1990), this would put the target about 9.4 cm from the compound eyes at first detection. Whatever the reason for the late detection of this type of target, it is interesting that the wings went straight into a gliding configuration without any indication of an attempt to steer. One implication of this is that the time to collision had been computed and compared with the time to effect steering avoidance. It should be possible to determine which properties of the approaching target are detected and used to compute the time to collision.

In all of the trials analysed, the first indication that the animal had detected the target and was responding was a flick of the abdomen either directly upwards or upwards and to one side. Abdominal movement has been considered to be an effector of steering (Camhi, 1970; Arbas, 1986; Zanker, 1988) or at least an indicator of the direction of steering (Moiseff *et al.* 1978; Robert, 1989). The effect of moving the abdomen is twofold: first, it increases drag on the side to which it is moved, allowing it to act like a rudder (altering the yaw and/or pitch of the animal); second, it shifts the centre of mass around which the flight forces generated by the beating wings act (Zanker, 1988) and this renders the wings on one side of the animal more effective by increasing the steering moment of their forces at the expense of those on the other side. The role of abdominal bending in collision avoidance is debatable. Rudderlike movements of the abdomen are considered by some to have limited significance for steering (Thüring, 1986; Schmidt and Zarnack, 1987; May and Hoy, 1990), but this is by no means a universally held opinion (Gewecke and Philippen, 1978; Baader, 1990). Whether or not abdominal movements generate substantial steering torques, it is a testable proposition that they reduce the latency from detection of the obstacle to the first change in flight direction. The wing asymmetries involved in attempted steering are generated primarily during the downstroke, whereas any steering effected by the abdomen is independent of the phase of the wingbeat. If the thoracic response to first detection were to occur at the end of a downstroke, abdominal movement could theoretically provide an extra 25 ms in which to initiate a change in flight direction before the next downstroke (assuming the motor pathways to the

abdomen and to the forewings in the thoracic ganglia incurred similar response delays).

We interpret the changes in the form of the wingbeat in the following way. The changes in the angular ranges of the two forewings swing the direction of the flight force vector generated by them towards the side away from the line of approach of the target. Increased and early pronation of the wings on the side opposite to the line of approach of the target reduces their angle of attack and reduces the lift generated on that side. The separation of the forewing and hindwing on the same side as the approaching target promotes their action as independent flight force generators, whereas the interference between the fore- and hindwings on the opposite side compromises their efficiency as flight force generators. The increased beat amplitude of the wings on the same side as the target generates larger flight forces relative to those on the other side. All of these responses cooperate and would produce a banked turn around the closest edge of the target if the animal were not tethered. Based on what is known of the aerodynamics of flying insects (Cloupeau *et al.* 1979; Kammer, 1985; Wilkin, 1985; Nachtigall, 1985; Ellington, 1984*a,b*; Götz, 1987), these are reasonable statements. Clearly, in the context of the results presented here the statements are speculative but they can be considered as testable hypotheses generated by this investigation. In our opinion, it is almost indisputable that the movements we describe would result in steering around the closest edge of the target, however this may be achieved aerodynamically. This is supported by consideration of previous investigations into steering during insect flight.

#### *Comparison with previous work*

The kinematic mechanisms and motor patterns underlying steering during insect flight have been the subject of much investigation in the past (see Kammer, 1985; Rowell, 1988, for reviews). Although the steering of other insects has been investigated (Alexander, 1986; Blondeau, 1981; Wang and Robertson, 1988; May *et al.* 1988; Nachtigall, 1985), locusts have figured prominently and we consider only locust flight steering here. Much of the previous interest has been with steering manoeuvres to compensate for environmental perturbations and to maintain a constant flight direction (e.g. yaw of the windstream, Zarnack and Möhl, 1977; imposed roll of the horizon, Thüring, 1986; Schmidt and Zarnack, 1987; Waldmann and Zarnack, 1988). However, the control of manoeuvres, such as collision avoidance, that actively change the flight direction has also been studied (e.g. phonotaxis, Robert, 1989; phototaxis, Baker, 1979; steering towards a movement, Cooter, 1979). The type and level of investigation have varied considerably but a consensus is beginning to emerge (Kammer, 1985; Rowell, 1988). Pronation of the wing on the inside of the turn (Dugard, 1967; Baker, 1979; Waldmann and Zarnack, 1988), relative phase changes of the wings (Thüring, 1986; Schwenne and Zarnack, 1987; Waldmann and Zarnack, 1988) and aerodynamic coupling between the fore- and hindwings on one side (Schmidt and Zarnack, 1987; Schwenne and Zarnack, 1987) have all been implicated in steering.



Asymmetries in beat amplitude have been observed (Baker, 1979) but have been described as poorly correlated with steering torques (Thüring, 1986; Waldmann and Zarnack, 1988). The striking feature of the results presented here is the magnitude of the forewing beat asymmetry, which is mainly the result of the different ranges of angles through which each forewing beats rather than being due to simple phase changes. This changes the position of the forewings relative to the hindwings to such an extent that it is hard to escape the conclusion that aerodynamic coupling and/or interference between fore- and hindwings plays a prominent role in flight steering (see also Schmidt and Zarnack, 1987; Schwenne and Zarnack, 1987; Wortmann and Zarnack, 1987). Wing kinematics of a similar quality (asymmetry in the dorsal/ventral positions of the forewing beats), though not magnitude, as the ones described here have been described (Cooter, 1979), but these were associated with steering torques in the opposite direction and may have been incorrectly interpreted (Kammer, 1985). Based on our results, all the indications are consistent with the idea that the locusts in Cooter's investigation were attempting to steer away from a rapidly moving object in their field of view, in spite of the fact that the yaw-measuring device was indicating a yaw torque towards the object. Nevertheless, it is interesting that it is only in Cooter's study and the present one that asymmetries in the dorsal/ventral range of the forewing beat have been associated with presumptive steering. Other similarities, which may be related, are that in both studies the steering was directed, rather than compensatory, and the manoeuvres were in response to the detection of moving objects. These forewing angular asymmetries are large-scale and are likely to have profound effects on flight direction. It may be that they are more obvious in directed steering as a response to moving objects because collision avoidance is a matter of some urgency, whereas compensatory manoeuvring to control orientation is less important, especially when the resultant track of a locust in a swarm can be strikingly different from the orientation of its flight (Uvarov, 1977): the final destination may be less important than getting there safely.

In conclusion, the experimental paradigm described here has the advantage of being straightforward, yet eliciting wing movements and other behavioural strategies that are relatively consistent and robust. Determination of the motor patterns underlying these movements should be straightforward and, with the advanced knowledge of locust flight motor patterns during various flight manoeuvres (see e.g. references in Kammer, 1985), they should be readily interpretable. It may be possible to develop a preparation that would allow intracellular recordings to be made during the execution of collision-avoidance reflexes. The descending contralateral movement detector (DCMD) neurones (Rowell, 1971) descend from the brain, connect to flight motoneurones in the thoracic ganglia and have been implicated in collision avoidance (Simmons, 1980). There has been some debate about whether the DCMD neurones respond to looming stimuli (Schlotterer, 1977; Pinter *et al.* 1982). More recent work has confirmed that they respond to the acceleration of edges in the visual field and to looming stimuli (Rind and Simmons, 1990; Rind, 1990), and a recent re-evaluation of the physiology of

the DCMDs by one of us (D. N. Reye, unpublished results) has shown that they respond best to looming objects approaching the head at flight speed ( $3\text{--}5\text{ m s}^{-1}$ ). The combined activity of the right and left DCMDs contains sufficient information to identify the side of the closest edge of an approaching target whose edges overlap the visual fields of both eyes. This makes them prime candidates for mediating some of the behavioural patterns described here and future work will be directed towards understanding the cellular basis of collision avoidance during locust flight.

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