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SENSORY CONTROL OF ABDOMEN POSTURE IN FLYING LOCUSTS*

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Flying locusts use their abdomens as rudders when executing a variety of flight manoeuvres. In the previous paper (Camhi, 1970) I described the lateral deflexions of the abdomen, which locusts presumably use in yaw correction. The sensory cue evoking this response is a change in the direction of the relative wind, monitored by the cephalic wind receptor hairs. The response appears in tethered locusts only while the wings are flapping in flight, suggesting that the activation of the flight mechanisms closes a neuronal switch, which permits wind-direction information from the cephalic hairs to be processed and translated into an abdominal movement.

In this report I discuss wind-stimulated deflexion of the abdomen in the *vertical* plane. I shall show that these movements, while of course serving a different function from the lateral postures, are evoked by stimulation of the same groups of hairs, and display similar switching properties.

METHODS

Male desert locusts (*Schistocerca gregaria* ph. *gregaria*) were provided by the Anti-locust Centre, London, and maintained as described earlier (Camhi, 1969*a*). I tethered individual locusts to a glass rod, usually ventrally on the pterothorax, and positioned them in front of a miniature wind tunnel, described earlier (Camhi, 1969*a*). A wind shield (Camhi, 1969*c*) restricted flow to the head surface. The active element of a hot-wire anemometer (Flow Corporation 55A1) was placed a few millimetres above the cephalic hairs. With a time constant of less than a millisecond, the output of this instrument displayed on an oscilloscope (Tektronix RM 565) could monitor instantaneous wind velocity and turbulence. The air flow was laminar for velocities up to about 4 m./sec.

I recorded the position of the whole abdomen by photographing, or simply viewing, the tip against a background graticle, placed just behind the abdomen. To measure contributions to the vertical movement by individual segments, I waxed an insect pin (size 00), vertically oriented, on to the side of each segment and recorded photographically any changes in the distance between their tips. Control experiments using pins three times their weight gave the same results, suggesting that loading by the pins did not appreciably affect the response.

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RESULTS

When wind flows faster than about 1·5 m./sec. over its head, a locust usually begins to fly. In a wind stream of normal flight speed* (3·5–4·2 m./sec., Weis-Fogh, 1956) the insect holds its abdomen approximately in line with the thorax, except for a slight upward curl at the tip. A sudden decrease of wind velocity to, say, 2 m./sec. evokes a rapid (less than 0·5 sec.) lowering of the abdomen to a new position which is specific to this velocity. A return to the original wind speed induces an equally rapid return to the original position. Though random movements of the abdomen sometimes occur within 15–30 sec. following a lowering of the abdomen evoked in this way, such random movements were often absent, and on these occasions postures were maintained for at least a minute. Slight abdomen elevations could be evoked by increasing the wind above flight velocity, though these elevations decreased by at least 20 % within the first minute.

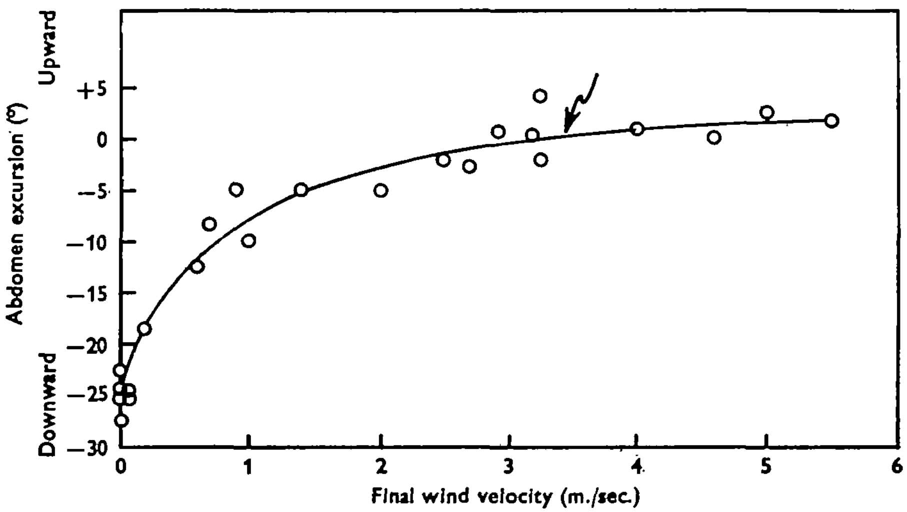

Fig. 1. Abdomen excursion during flight for wind-velocity changes from 3·5 m./sec. to final velocities shown. Arrow shows reference position for wind velocity at approximately normal flight speed. Increasing the wind evokes sligh televation, while decreasing it evokes marked depression of abdomen.

Many individuals would not continue strong flight when I decreased the wind velocity below about 2·0 m./sec. However, seven individuals flew sufficiently strongly at all air speeds from 0 to 8 m./sec. to allow repeated observation. The graph of Fig. 1 plots the initial peak excursion angle (maximal excursion) of the abdomen for changes of wind from a starting velocity of 3·5 m./sec. to various other speeds. Wind speed was re-set at 3·5 m./sec. and changed to a new value every 30 sec., in a highly varied sequence. The curve shows that abdomen angle changes only slightly at wind velocities above about 2·5 m./sec., but below this value the angle depends strongly on velocity. An almost identical curve results from measuring the bending of any of the first five abdominal joints as a function of wind speed.

* Wind blown over a stationary locust is fully analogous to the wind the insect creates when flying through air at the same speed.

Since normal flight speed is about 3·5–4·2 m./sec. (Weis-Fogh, 1956), the locust in free flight will presumably receive a cue to depress its abdomen only when its flight speed is drastically reduced. Such deceleration of any aircraft could result in a stall, and it seems reasonable to suggest that the abdomen depression may serve to avoid flight speeds dangerously close to stalling speed. Depressing the abdomen would result in increased lift along the posterior half of the body. Moreover, as I have previously shown (Camhi, 1969*c*), decreasing wind velocity also evokes a bilateral increase in pronation of the forewings on the downstroke. This would decrease the lift produced by the forewings, and thus by the front part of the insect's body. The net effect should be a dive, which would assist in restoring normal flight speed. Fig. 2 shows the graph of abdomen angle (from Fig. 1) together with a graph of forewing angle at mid-downstroke (from figure 4, Camhi, 1969*c*) against wind speed. The close similarity of two curves suggests again that these two responses comprise a concerted effort to avoid low flight speeds.

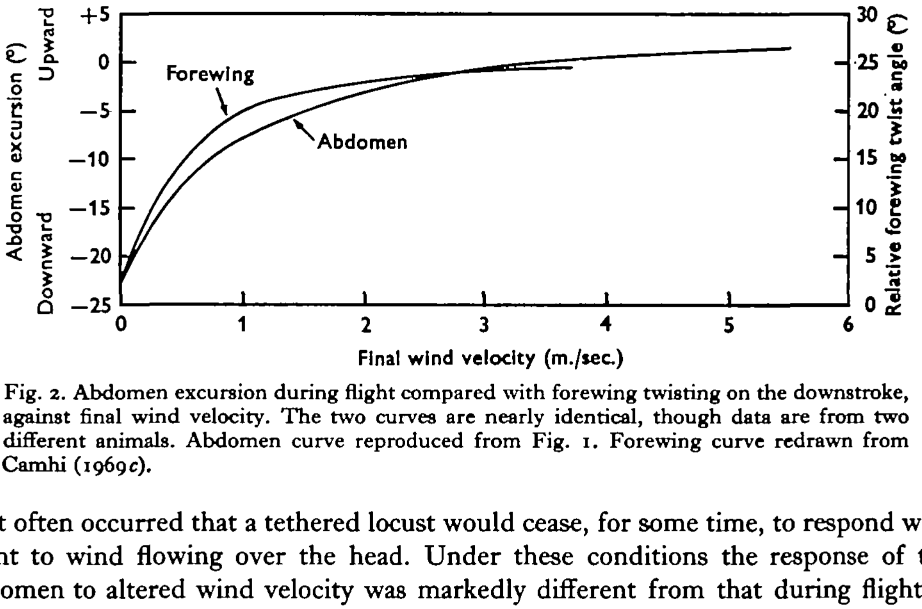

Fig. 2. Abdomen excursion during flight compared with forewing twisting on the downstroke, against final wind velocity. The two curves are nearly identical, though data are from two different animals. Abdomen curve reproduced from Fig. 1. Forewing curve redrawn from Camhi (1969*c*).

It often occurred that a tethered locust would cease, for some time, to respond with flight to wind flowing over the head. Under these conditions the response of the abdomen to altered wind velocity was markedly different from that during flight. I recorded the abdomen postures of eight locusts during such flightless intervals. (All of these individuals flew normally either just before or just following this flightless period, or both, and all appeared in good general condition.)

The graph of Fig. 3 plots abdomen angle as a function of wind speed for a typical, temporarily flightless locust—the same individual whose flight data are plotted in Fig. 1. (The data for this graph were taken just after the locust had ceased flying in wind, less than 40 min. after being tethered.) The response when not flying is very greatly diminished, compared to the response in flight, which is replotted from Fig. 1 for comparison. These results were strongly confirmed by one locust which, when exposed to wind, flew for several minutes in short bursts of about 15 sec. each, separated by flightless periods of about equal length. During flightless periods, the abdomen responded very little to wind-velocity changes, while during flight the response was dramatic.

This alteration of the response when the locust is not flying does not result from proprioceptive inhibition from the folded wings, for the wings can be waxed in the open position, or cut off at their hinges, without altering the response. The insect still shows a marked abdomen response only when the remaining parts of the wings and the thorax vibrate from the action of the flight muscles. There remains, of course, the possibility that the change in response derives from some muscle receptors in flight muscles, although no such receptors have ever been reported.

In order to locate on the head the receptors responsible for the wind-dependent abdomen movements, I waxed over increasing areas of the head. Covering the compound eyes and mouth parts had no effect on the response in flying locusts. Nor did covering hair patches 2 or 3 (Weis-Fogh, 1949; Camhi, 1969*d*) on the lateral surfaces of the head. Covering hair patch 1, at the front of the upper horizontal surface of the head, reduced greatly or abolished the response. (Presumably the remaining hairs, those of patches 4 and 5, provided the stimulus that evoked flight under these conditions.) Peeling off the wax covering hair patch 1 re-instated the response in full.

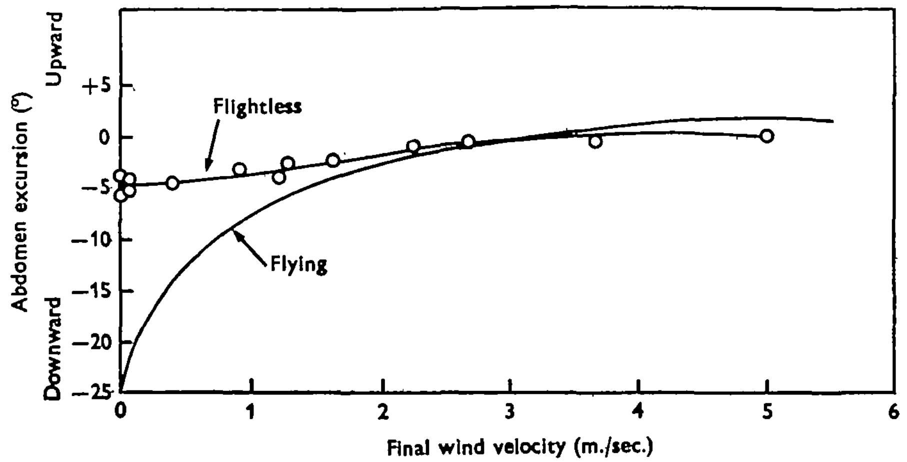

Fig. 3. Abdomen excursion against final wind velocity during flying and flightless intervals for the same locust. Points shown are for flightless condition. Curve labelled "flying" reproduced from Fig. 1. A marked response occurs only during flight.

DISCUSSION

The findings reported here suggest that tethered locusts exposed to deceleration of the relative wind make co-ordinated movements of the abdomen and the forewings which would increase lift posteriorly and decrease it anteriorly. Fig. 3 indicates that the wind dependence of both responses is very similar. Moreover, both occur within 0·5 sec., and both adapt slowly (Camhi, 1969*c*). It therefore seems reasonable to suggest that the two responses may result from separate readouts of the same central integrative process. Interestingly, the two differ in that the response of the abdomen is one continuous sweep, whereas that of the forewings is discontinuous, the twisting and its underlying muscle and motor neuron/activity appearing only at the beginning of each downstroke (Wilson & Weis-Fogh, 1962).

The results of this and the previous paper (Camhi, 1969*d*) suggest that wind-receptor hairs of patch 1 code essentially all the information used in the vertical responses of the abdomen to wind-velocity changes, and also provide sufficient information on wind direction to evoke lateral yaw-correcting postures of greater than half normal magnitude. To what extent individual sensory hairs participate in both responses cannot be determined from the data available. However, it is known (Camhi, 1969*b*) that sensory information from hairs of patch 1 flows to one group of interneurones which accurately monitor wind direction, and to another group which measure wind velocity.

As in the case of yaw-correcting abdomen postures, the locust must be engaged in flight while the change in wind is presented, if normal abdominal movements are to follow. Although no detectable yaw-correcting movement occurred without flight (Camhi, 1969*d*), the vertical movements persist, though very greatly diminished, in flightless intervals. Both responses suggest the presence of a switch (a 'leaky' switch in the case of vertical movements) which is closed by some central or peripheral part of the flight mechanism, permitting the passage and processing of wind information from the head hairs. Such switches are probably very common in nervous systems, though perhaps seldom appear so dramatically and quantifiably in the behaviour of animals.

SUMMARY

1. A flying tethered locust elevates its abdomen slightly in response to increased, and depresses it greatly in response to decreased, velocities of the relative wind over the head.

2. The wind-velocity dependence and time course of abdomen movement are very similar to those of forewing twist control on the downstroke. The two responses probably work in concert to rotate the animal into a dive when flying speed has fallen critically close to stalling speed.

3. The wind-velocity monitor is provided by a specific group of cephalic wind-receptor hairs.

4. The abdomen response is almost completely absent in tethered locusts which are temporarily flightless, suggesting the presence of a neuronal switch operated by the flight mechanism.

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