YAW-CORRECTING POSTURAL CHANGES IN LOCUSTS*

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INTRODUCTION

The mechanisms underlying locust flight include a central neuronal pattern generator determining the sequence of wing-muscle contractions, plus several systems for modulating flight and controlling its stability. One such control system stabilizes flight about the yaw axis. Weis-Fogh (1949) found that tethered locusts which were free to turn in the yawing plane re-oriented into an oncoming stream of wind whenever he rotated a wind jet about the head. He showed that the wind-direction receptors involved were the trichoid sensilla on the head. Camhi (1969a, b) showed that the sensory cell of each hair is tuned to read a specific wind direction, and that certain interneurons of the cervical connective further sharpen this directional response.

A second flight-control system consists of the optomotor response and dorsal light reaction which Goodman (1965) found to stabilize the locust in the rolling plane. Rotating an artificial horizon line or a dorsal light source results in a compensating tilt of the head. The locust detects the angle of head tilt through cervical proprioceptive hairs (Goodman, 1959) which signal the change in wing motion appropriate for re-orienting the thorax with the head, and thus with the visual input.

Direct observation of the specific manoeuvres used by locusts to correct yaws and rolls in flight have not been reported. It is generally assumed, however, as a result of electrophysiological studies (Wilson, 1962; Waldron, 1968) that locusts perform both these responses by changing differentially the amount of twisting of the two forewings on the downstroke. In tethered locusts showing a tendency to turn in one direction, however, Dugard (1967) and Gettrup & Wilson (1964) have also observed rudder-like movements of the abdomen, legs and wings, these members being held out on one side.

In this report I further describe and contrast some of the responses that tethered locusts use in correcting simulated yaws and rolls and in displaying a tendency to turn. I shall derive from these results implications concerning the neuronal integration underlying these flight mechanisms.

METHODS

Male *Schistocerca gregaria* ph. *gregaria* provided by the Anti-Locust Research Centre, London, were maintained as previously described (Camhi, 1969a). Locusts were tethered by waxing a glass rod, usually to the ventral pterothorax, at the animal's centre of gravity. I removed the antennae and in some cases the legs and/or wings,

plugging all wounds with wax. I mounted the insect with its head in front of a minia-
ture wind tunnel (14 mm inner diameter) capable of directing laminar flow over the head
at velocities of 0–4 m./sec. Yaw-correcting responses could be evoked by rotating the
wind tunnel about the head in the horizontal plane (aerodynamically simulating a yaw).
The motion of the wind tunnel was recorded on an oscilloscope (Tektronix RM 565)
through a potentiometer mechanically coupled to the tunnel's base. The room was
kept at 30° C., and totally dark to prevent visual detection of the tunnel's movement.

Alternatively, with the wind tunnel blowing air in the head-on direction, I could
evoke roll-correcting responses (i.e. the manoeuvres which would realign the body with
the rotated head). In a totally dark room I rotated the insect's head by a known angle
in the rolling plane (about the long axis of the body). The rotation was produced by
a sleeve fitted over the wind tunnel (but not projecting beyond the open end) such
that it could turn freely. Two pins waxed to the sleeve and to the sides of the locust's
head transmitted the rotation smoothly to the head. A needle on the sleeve marked off
on a graticle the amount of each rotation. (To assure that only the head rotated, it was
necessary to fix the pronotum in position by waxing it to a firm rod.)

Turn tendencies, the third type of response observed, could be induced by the
method of Dugard (1967)—shining a light on either side in front of the locust. (I shall
show later that the response thus evoked is in fact different from light-induced roll
correction.)

To measure delicate voluntary movements of the head or of individual abdominal
segments, it was helpful to wax very light-weight pins (size oo insect pins) to the
moving members. Movements of the pins could be read against a background graticle.
The length of the pins amplified all movements about 20-fold. The pins were in all
cases arranged symmetrically so as not to bias the movements. Since only comparative
readings were of interest, the inertia added to the system by the mass of the pins intro-
duced no error. Moreover, pins of three times the mass of the oo size produced the
same results as the lighter oo pins.

The necessity of keeping the room totally darkened during most measurements
made the following method of recording data very useful. For each yaw measurement
I opened the shutter of a 35 mm Nikon camera, previously focused on the locust, for
a 1-sec. interval. During that interval I triggered a strobe flash (General Radio
Strobotac) which recorded the initial posture of the insect. Immediately I rotated the
wind about the head and flashed the light again, creating a double exposure, from
which the change in position was easily measured. Included in the photograph was
the locust plus the oscilloscope screen, viewed through a mirror system which pre-
vented the light of the sweeping beam from reaching the insect. The oscilloscope trace
recorded the instantaneous position of the wind tunnel and, through an input from
the strobe light, the instant of each flash.

In this method the first flash of the light cannot provide any clue as to the direction
of the impending change of wind angle. The method allows observation of postures
over continuously variable intervals, by examination of different photographs. In some
experiments I changed the wind angle alternately from side to side, so it would have
been possible for the locust to predict through visual inputs during the flash the
direction of the next wind change. In all such cases, however, I very carefully painted
the compound eyes and ocelli with a mixture of wax and lampblack, probably abolish-

ing all visual inputs. Experiments on forced head rotation and turn tendency were recorded the same way, except that the input signals were not electronically monitored.

RESULTS

(1) *Responses evoked by changing wind angle*

Plate 1 A shows a typical double-exposure photograph of a locust responding to a 25 degree change of wind angle to its left. 300 msec. after the start of the change the abdomen is bent at an angle of 25 degrees to the left. Surprisingly, the head has also responded, rotating 15 degrees about the long axis of the body. Subsequent observations showed that the direction of head rotation was clockwise (as viewed from behind) for a right yaw, and counterclockwise for a left yaw, such as that in this photograph.
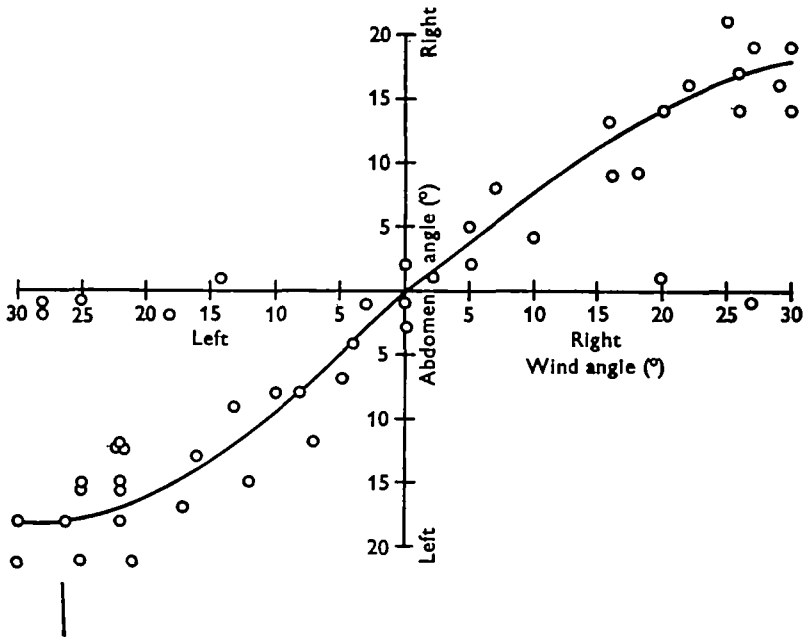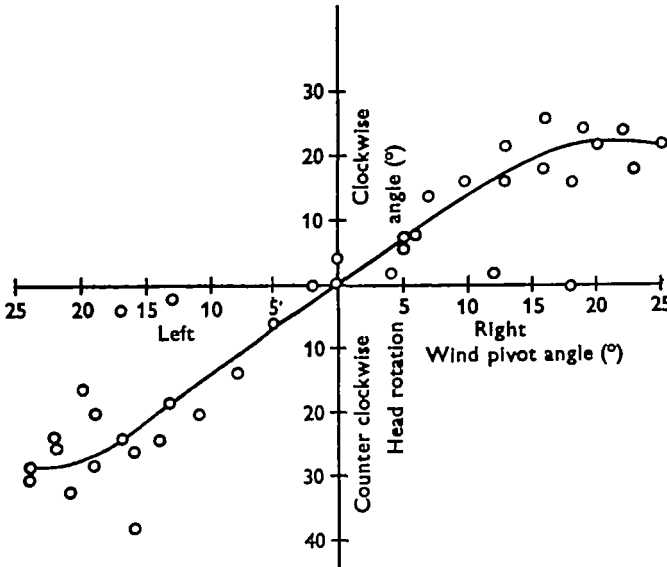

Text-fig. 1. Abdomen angle as a function of wind angle. Points indicating no response (those along abscissa) ignored in constructing curve. See text for further explanation.

Plate 1 B is a single-exposure photograph showing a locust with wings clipped and all legs intact in a right yaw-correcting posture. The metathoracic, and to a lesser extent the mesothoracic, legs move in the same direction as the abdomen in response to air flow from the side. A detailed view of the abdomen response, seen in Pl. 1 C, shows that virtually all the bending occurs at the joint between the first and second abdominal segments (segments A_1 and A_2). This is the closest movable joint to the inflexible thorax. Movements of the legs occur primarily at the coxa-trochanter joint.

For four locusts whose eyes and ocelli I had carefully blackened, and with the room lights very dim, I moved the wind jet from side to side at different frequencies to see how rapid a change of wind angle the insect could follow. In all cases the head, abdomen and legs were able to follow perfectly movements up to 3 per second (three

half periods per second). Thus a very rapid yaw should evoke a full response in about 300 msec. The presence of such rapid yaw-correcting movements contrasts with the view of Waldron (1968) that these responses require in general of the order of one to several seconds for completion.

I recorded the magnitudes of the movements of abdomen and head evoked in ten locusts by wind-angle changes of different magnitudes (same angular acceleration ± 10%). The sequence of these changes was randomized with respect to direction and angle. The graph of Text-fig. 1 plots abdomen movement, and that of Text-fig. 2 plots


Text-fig. 2. Head-rotation angle as a function of wind angle. Points indicating no response (those along abscissa) ignored in constructing curve. Clockwise designation, as viewed from behind. See text for further explanation.

head rotation, as functions of wind-angle change in a single, typical locust. Both responses are detectable for wind-angle changes of as little as about 5°. Both show a reasonably linear relationship for wind-angle changes of up to 20° (abdomen) and 15° (head). However, both curves show considerable scatter, and indeed neither response is evoked by every change of the wind angle.

The rudder-like movements of the legs appear generally much more sensitive to small wind-angle changes than movements of the abdomen. For large changes (over 10°) the leg excursion is far greater than that of the abdomen, occasionally resulting in leg postures at right angles to the thorax. However, it was very difficult to quantify leg movements because the legs vibrate considerably in synchrony with the wing beats.

Although I suspected that all these movements resulted from the sensing of wind direction by the cephalic hair receptors (Camhi, 1969a) several experiments were necessary to prove this point. First, by carefully cutting through the cuticle and muscles of the cervical region (taking care not to damage the gut or ventral nerve cord) the head could be rotated 180° about the long axis of the body and waxed firmly to the pronotum. One would expect any wind-angle detectors on the head now to respond

appropriately to the magnitude, but inappropriately to the direction, of a wind-angle change. A locust in this condition responds with movements of the abdomen and legs in the direction opposite to that of a normal locust. The response magnitude is about 20% less than that of the normal locust, a fact which may result from the slightly altered aerodynamic conditions produced by rotating the head. The experiment shows that receptors on the head provide at least 80% of the information useful in evoking the movements of abdomen and legs in yaw correction.
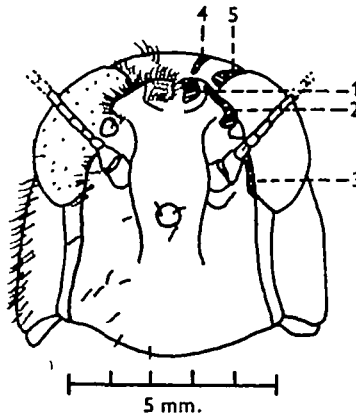
Text-fig. 3. Front view of locust showing locations of the five pairs of hair patches. After Weis-Fogh (1949).
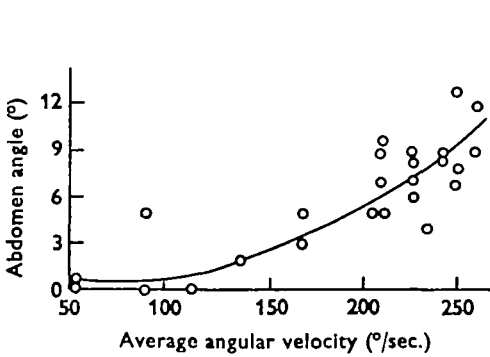

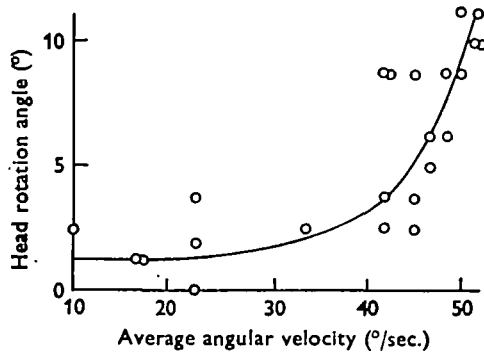Fig. 4   Fig. 5

Text-fig. 4. Abdomen angle as a function of average angular velocity of successive wind-angle changes from centre to 10° left. See text for further explanation.

Text-fig. 5. Head-rotation angle as a function of average angular velocity of successive wind-angle changes from centre to 10° left. See text for further explanation.

To locate the specific receptors on the head I waxed over increasingly extensive areas of cuticle. The head rotation and abdomen movements remained at full strength after waxing the compound eyes and the mouth parts. Both responses decreased to about two-thirds normal magnitude upon waxing bilaterally hair patches numbers 2 and 3 of Weis-Fogh (1949) (Text-fig. 3). Adding a small drop of wax to the top of the

head, thereby covering areas 1, 4 and 5 completely, abolished the response. Later peeling off this one drop of wax, thereby re-exposing hair patches 1, 4 and 5, re-instated the response to about two-thirds of its normal magnitude. In separate experiments, covering bilaterally patch 1 alone decreased the response to less than 50 % normal magnitude. These experiments suggest that the main system for recording wind direction consists of sensory hairs of area 1, which is situated on a horizontally oriented part of the cuticle. This contrasts with Weis-Fogh's view that the major yaw-correcting direction receptors are the hairs of area 3, on the lateral surfaces.

To determine whether the angular velocity of the wind-angle change affects yaw-correcting movements, I repeated, on four locusts, wind-angle changes of 10° to the left at different angular velocities which were determined later from the film records. Although the values of angular velocity were not strictly randomized, they were presented in a very varied sequence. Text-figs. 4 and 5 plot the positions of the abdomen and the head respectively 300–400 msec. after completion of wind-angle changes of 10° at different angular velocities. The graphs show that both responses are greatest for fast changes in wind angle, up to about 250°/sec., the most rapid turns possible with the device used.

(2) Co-ordination of movements of head, legs and abdomen

One question requiring attention was the way in which the movements of the head, legs and abdomen are co-ordinated. Does each move directly in response to the wind-direction information from the cephalic wind receptors, or does perhaps one of these movements induce, through proprioceptive feedback, the movements of the other members? The most likely proprioceptive source seemed the cervical hair plates which, as Goodman (1965) and Wilson (1968) showed, respond to rotation of the head and evoke rolling.

I investigated the question first using cine photography (24 frames/sec., Bolex 16 mm camera). Text-fig. 6 plots the sequence of changes of wind angle, head rotation and abdomen movement. As the curves show, the head usually begins its rotation one or two frames (about 40–80 msec.) later than the abdomen movement.

It was conceivable, nevertheless, that the detection of head rotation by the cervical sensory hairs might contribute to the magnitude of the abdomen movement. After cutting through all tissues in the neck (including all muscles) except the gut and the ventral nerve cord, and waxing the head firmly to the prothorax, double-exposure photographs of yaw-correcting responses revealed no detectable change in the magnitude of the abdomen response. (Of course, with the methods employed only change occurring within the first second after the wind-angle change would be noticed.)

In other experiments, cutting the nerves to the legs and those to the entire abdomen did not detectably diminish the head rotation. Clearly then, each of the three moving members—head, abdomen and legs—can give an apparently full response to changes of wind angle over the head without utilizing proprioceptive feedback from the other two members. Thus the neuronal control elements for the three movements probably proceed independently outward from some integrating circuit in the central nervous system.

One striking finding that corroborates the notion of central mediation is that if a tethered locust in a wind stream temporarily ceases to flap its wings, none of the

ʼmovements of head, legs or abdomen can be induced by even the most sweeping changes of wind angle. Even at heightened wind velocities all these output channels remain completely unresponsive to wind-angle changes. However, the instant flight is resumed, even at the same or at lower wind velocities, all three movements readily appear when one alters the wind angle. This inhibition does not result from proprioceptive stimulation by the closed wings, since the wings can be waxed in the open
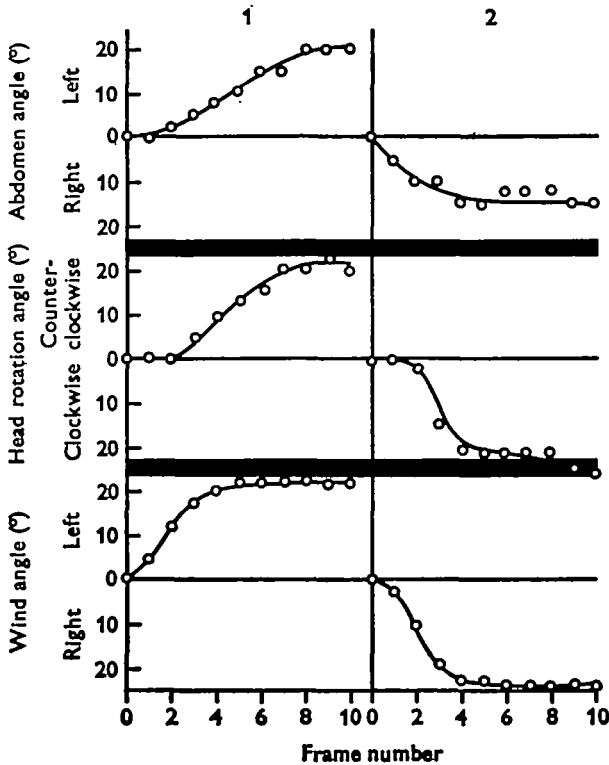

Text-fig. 6. Time courses of abdomen movement and head rotation following two changes of wind angle (1 and 2). Data plotted from cine film sequences. On both occasions the abdomen movement begins before the head rotation, by at least 1 frame. Filming rate, 24 frames/sec.

position or cut off at their bases without affecting the responses. Under these conditions, only when the remaining parts of the wings and the pterothorax vibrate from the action of the flight muscles do the legs, abdomen and head respond to wind-angle changes. These observations, which I have made countless times on numerous different locusts, suggest the presence of a central neuronal switch which is closed only when the flight system is in action, a condition which is apparently necessary to allow information to pass from the cephalic wind receptors to the motor-neurones of the neck, abdomen and legs.

The question now arises: once a wind-angle change evokes these responses of the head, abdomen and legs in a 'flying' tethered locust, how precisely are the magnitudes of each regulated, given the apparent absence of any proprioceptive 'crosstalk'? Text-fig. 7 plots the magnitudes of several abdomen movements against the magni-

tudes of the head rotations produced by the same changes of wind angle, the changes ranging from 5 to 20 degrees. On some occasions one of the two responses is almost totally lacking, while the other appears in full (points along the axes). The tremendous scatter indicates that the relative magnitudes of the movements are not very precisely controlled, again suggesting that feedback control between these two moving members is absent, the command system being essentially centrifugal.
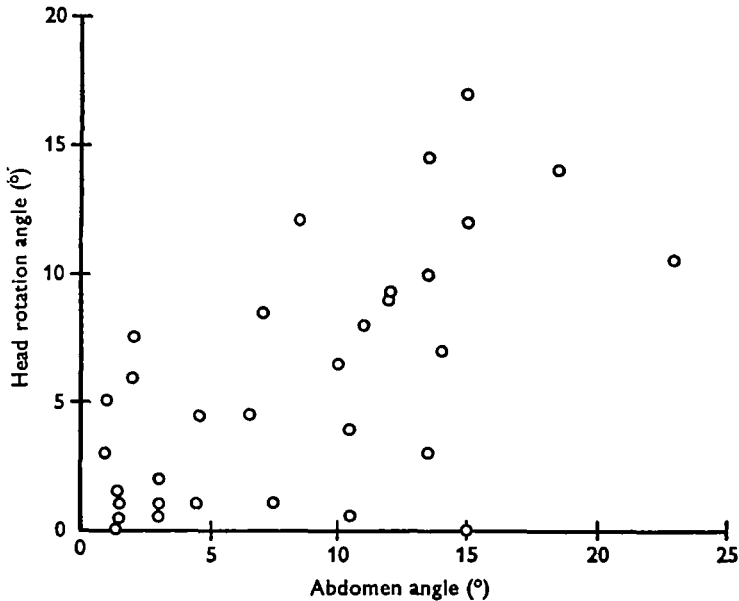
Text-fig. 7. Abdomen angle against head-rotation angle for the same wind-angle changes. Wind-angle changes ranged from 5° to 20°. See text for further explanation.

### (3) *Responses evoked by forced rotation of the head*

Of the postural changes induced by wind-angle changes, the movements of abdomen and legs are explicable as rudder-like yaw-correcting postures, while the head rotation is not. Goodman (1965) and Wilson (1968) have found that visually induced head rotations probably evoke, proprioceptively, differential changes in wing action which would stabilize the insect against rolls. It seemed important to see whether proprioceptive feedback from head rotations evokes any other aerodynamically meaningful responses.

Each of seven locusts was mounted in front of the wind jet and prepared for forced head rotation, as described in the Methods section. With the locust flapping its cut wing stumps, rotating the head clockwise (as viewed from behind) evoked a slight movement of the abdomen and legs to the right. These movements were much slower than those evoked by changing the wind angle, being unable to follow head rotations at frequencies above about one movement per second ($\frac{1}{2}$ cycle per second). If wing flapping stopped, no rotation-induced movements of abdomen or legs occurred, though these are re-instated the moment flight begins again.

In four of the seven locusts tested I carefully removed from both sides of the neck the cervical sclerites bearing the sensory hairs. In no case would forced head rotation

now evoke any movement of the abdomen, although I tested this for as long as 2 days postoperatively, and although all other aspects of flight appeared normal. These experiments suggest, then, that head rotation provides, through the mediation of the cervical sclerites, a command for slow rudder-like movements of legs and abdomen which is redundant to the more rapidly acting pathway coming directly from the cephalic wind receptors.

The finding that head rotation evokes specific, measurable responses predicts some correspondence between these responses and the known properties of the cervical hair receptors. It is known, for instance (Haskell, 1960), that the sensory cells of the cervical hairs adapt slowly, impulse frequency declining about 10 % in the first second, and then not at all for at least 5 sec. following. This suggests the possibility of a slowly
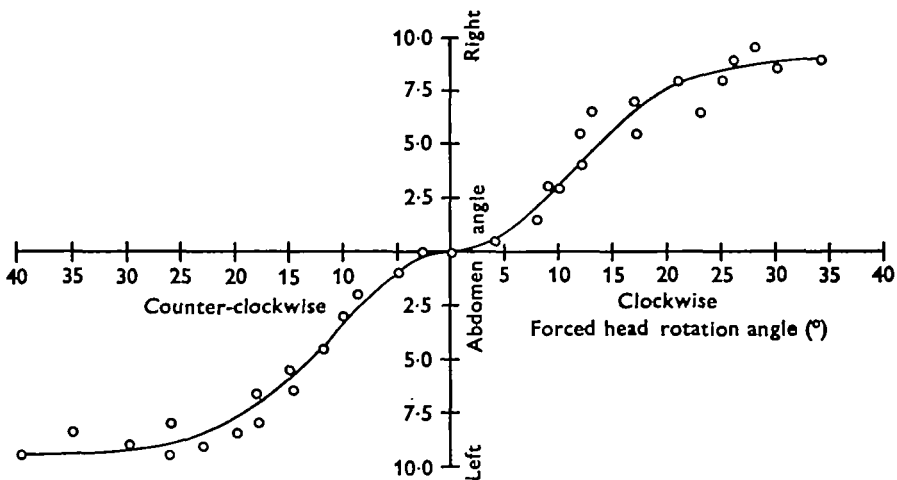
Text-fig. 8. Abdomen angle as a function of forced head angle. Final (sustained) abdomen positions plotted. See text for further explanation.

adapting response to head rotation. Four locusts held their abdomens sufficiently steadily in flight so that, in spite of spontaneous movements, it was possible to observe the duration over which the abdomen would retain its position following maintained forced head rotation. Each of these locusts held its abdomen at a constant angle (± 2°) for longer than a minute, thus adapting slowly as expected.

On four locusts I measured the abdomen position as a function of rotational head position. The graph of Text-fig. 8 plots the sustained (final) position of the abdomen of a typical locust following head rotations from the normal position toward either side. The relationship is roughly linear between 5° and 25° on either side. There was no detectable hysteresis, as tested by rotating the head from 30° on one side to some final position on that same side. Recalling that the largest head rotations evoked by a yaw (change of wind angle) were of the order of 25° (Text-fig. 2), this suggests that the output of the cervical receptor system is linear over practically its entire useful range.

(4) *Comparison of abdomen responses to wind-angle change,*
head rotation and turn tendency

As mentioned above, abdominal movements evoked directly by wind-angle in-formation from the cephalic wind receptors occur primarily through contraction of muscles in the A_{1-2} joint.

Careful photographic examination of movements of the abdominal segments (with pins attached) evoked by head rotation on eight locusts reveals that the contractions are distributed over the first three joints. This distribution, though irregular, has the following properties:

(1) Bending at joint A_{1-2} is always either greater than that at any other joint or is totally absent. That is, the controlling mechanism for this joint operates in an apparently all-or-none fashion. This probably does not result from the lack of fine muscular control, since wind-angle changes evoke finely graded contractions of muscles of this same joint (Text-fig. 1).

(2) Bending at joint A_{2-3} is graded with the magnitude of head rotation.

(3) Bending at joint A_{3-4} is also graded, and in 70% of the cases equals that of joint A_{2-3} ($\pm 5\%$).

(4) There is no apparent correlation between the occurrence of full or zero con-traction in A_{1-2} and any event in any other joint.

(5) Joints A_{1-2} and A_{2-3} return, upon re-centring the head, to within 10% of their original position on 90% of the trials. Joint A_{3-4} does so on only 50% of the trials.

Summarizing this information, joint A_{1-2} seems to bend in an all-or-none fashion and is independent of the other joints. Movements of joints A_{2-3} and A_{3-4} are graded with respect to the stimulus and are fairly well co-ordinated with one another. Posterior to segment A_4, no movements contribute to the response.

By contrast, the abdominal movements produced by light-evoked turn tendency, measured in the same way on six locusts, involves primarily the more posterior seg-ments. Another difference between abdomen posture induced by light and that induced by head rotation is that the former is often maintained for up to a minute after flight ceases, whereas a posture evoked by head rotation is abolished the moment flight ends. Finally, light-induced abdomen posture often occurs without any per-ceptible movement of the head.

These points suggest that while the fast yaw-correction, the slow yaw-correction and the turn-tendency responses of locusts are superficially similar, they actually involve different sensory inputs, differently distributed motor outputs, and some different central neuronal circuits.

DISCUSSION

(1) *Interaction of the abdominal command systems*

The results of the experiments presented here suggest that locusts possess two distinct mechanisms controlling the rudder-like movements of abdomen and legs in yaw correction. The first system is called into action by a change in the direction of the relative wind, monitored by the cephalic wind-receptor hairs. This evokes a rapid (300 msec.) contraction of the muscles of joint A_{1-2} and of the legs into the direction

of the required turn. The second, slower system is evoked by proprioceptive stimulation of the cervical hairs and results in bending at the first three abdominal joints. The locust completes this movement within approximately 1 sec. The slowness of this second response suggests that it serves as a 'failsafe backup' to the faster, more direct yaw-correcting mechanism. Whether the forewing-twist mechanism, which also operates in the time range of 1 sec. (Waldron, 1968), responds directly to information from the head hairs or to that from the cervical sclerites remains to be determined.

For the two yaw-correcting systems to operate in concert requires at least two conditions. First, the cephalic wind receptors must complete their measurement of an altered wind angle *before* the head rotates, as head rotation would decrease the apparent wind angle. Cine photography has shown that in fact the abdominal movement resulting directly from wind-angle measurements by the cephalic receptors usually begins before the head has started to rotate. This suggests that these hairs may actually complete the wind-angle measurement prior to this head movement.

The second requirement is that head rotation be accompanied by a command to ignore optomotor and dorsal light reactions (Goodman, 1965). Without this provision it would be theoretically impossible for the head to rotate in response to wind angle at all.

As already mentioned, Goodman (1965) and Wilson (1968) found that light-induced head rotations result in turns about the roll axis. This suggests that the head rotations evoked by a yaw (change of wind angle) might likewise evoke rolling through differential action of the wings on the two sides. This could produce a banked turn in the direction required to correct the yaw, and would supplement the aerodynamic effects of abdomen and leg posture.

(2) *Aerodynamic considerations*

The question of how the rudder-like movements of the abdomen and legs actually bring about a turn requires some comment. The most obvious mechanism is an increase in the aerodynamic drag on the side toward which these members are deflected. For small lateral movements such as those of the abdomen, the increase in drag, and therefore the torque produced, will be linearly related to the angle of the rudder. Clearly, the effectiveness of the abdomen as a rudder will increase, the greater the proportion of its length that moves. Thus bending at the A_{1-2} joint—the most anterior flexible joint—not only promotes speed of response, by limiting neuronal conduction time from the thoracic ganglia, but also increases the aerodynamic effectiveness of the rudder action. The slower movements of the proprioceptive neck reflex use joint A_{1-2} only on occasion, and more consistently employ joints A_{2-3} and A_{3-4}.

On lateral movements of more than a few degrees the abdomen and legs intercept the pathway of the beating metathoracic wing on that side. For large movements the interference with this wing is considerable, producing an audible click with each collision. Though seemingly an uneconomical way to make a turn, decrease in the lift and thrust of the powerful metathoracic wing on one side may well contribute to the yaw-correcting turn.

(3) *Motor pathways*

Three separate aspects of the organization of the motor output have emerged from this study. The first is the presence of a central switch which is thrown to the 'on' position by flight, allowing neuronal information originating at the head receptors and at the cervical hair receptors to be transmitted through and out of the central nervous system. Secondly, once the switch is 'on', non-interacting commands go out to the head, abdomen and legs. Thirdly, the three superficially similar movements of the abdomen (those induced by wind-angle changes, head rotations, and asymmetrical light sources) which function in identical ways (increasing drag and hindwing interference) appear on careful examination to result from three distinct command mechanisms in the central nervous system.

SUMMARY

1. Changes in the angle of the relative wind sensed by the facial wind receptors of a locust evoke fast rudder-like movements of the abdomen and legs whose magnitudes are proportional to the change of wind angle.

2. This system is sensitive to the angular velocity of the wind change.

3. Such wind changes also evoke rotations of the head about the long axis of the body.

4. The head rotation induces, through proprioception by the cervical hair receptors, slow, redundant rudder-like movements of abdomen and legs.

5. Control elements for the fast movements of abdomen and legs and for the head rotation appear not to be precisely co-ordinated and seem to include no proprioceptive 'crosstalk'.

6. All these responses are evoked by wind-angle changes only if the insect is flying at the moment, suggesting that flight closes a neuronal switch.

7. Separate motor pathways seem to be employed for the abdomen's rudder-like response to wind-angle change, head rotation and turn tendency.

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A

Strobe
flash

Wind
pivot

Head
rotation

Abdomen
movement

B

C

A₁
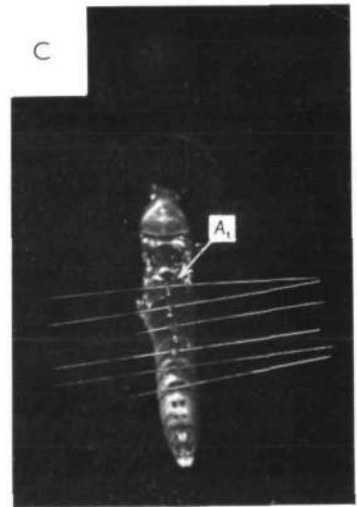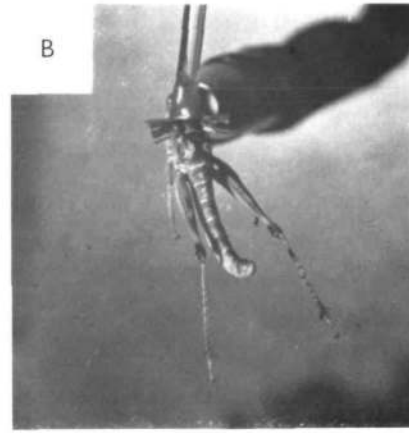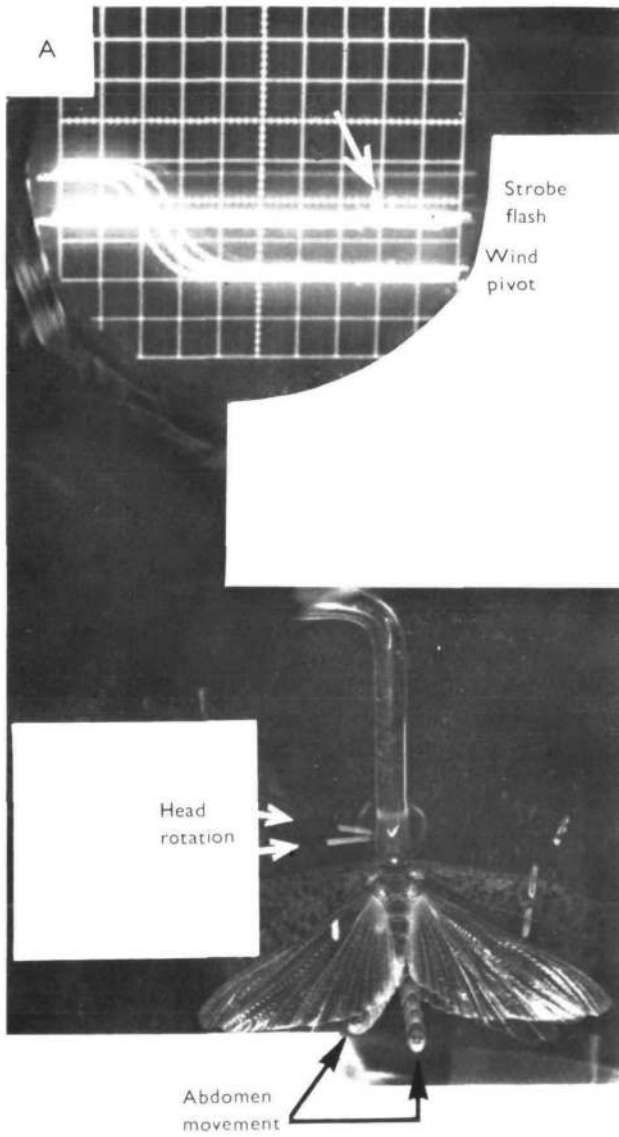
EXPLANATION OF PLATE

A. Double-exposure photograph of tethered flying locust subjected to change of wind angle. First strobe flash triggers oscilloscope sweep. Initially upper oscilloscope trace (wind-angle trace) calibration 9°/division. Sweep rate for both beams 50 msec./division. Arrow points to signal indicating instant of second strobe flash. Head rotated is 15° counterclockwise (viewed from behind). Abdomen is deflected 25° to left.

B. Single-exposure photograph of locust just after wind-angle change to the right. Abdomen, plus meta- and mesothoracic legs deflected to the right.

C. Single-exposure photograph of locust just after wind-angle change to the right. Pins on abdominal segments A_1 to A_6 show that virtually all bending occurs at the joint between segments A_1 and A_2. The joint between the metathorax and A_1 is inflexible.