Locust flight steering

I. Head movements and the organization of correctional manoeuvres

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Summary. Locusts (Locusta migratoria) were flown in a flight simulator which converts yaw torque into angular motion of the visual environment (Fig. 1). The modalities and the time-course of steering behavior under these closed-loop conditions have been investigated.

1. Locusts flying under visual closed-loop conditions stabilize their visual environment by performing correctional steering manoeuvres. Besides torque production, due to differential wing movements and ruddering, correctional steering also involves head movements (Fig. 6).

2. During open-loop steering, ruddering and yaw torque begin some 60 ms after the onset of the visually simulated deviation from course. Head movements occur some 90 ms after stimulus onset, i.e. some 30 ms later than yaw torque (Figs. 3, 5) and therefore do not initiate thoracic steering outputs.

3. Open- and closed-loop correctional steering do not differ in their behavioral components or temporal organization (Figs. 2, 6, Table 1).

4. In the absence of major disturbances, correctional steering under closed-loop conditions is performed with minimal ruddering (only a few degrees in amplitude), that probably produces little or no aerodynamic drag (Fig. 6).

5. Locusts prevented from moving their heads still stabilize their visual environment in the closed-loop situation. However, the precision of steering is affected by this constraint (Figs. 8, 9, 10, 12). Head immobilization also alters the temporal coordination of correctional steering (Figs. 7, 11).

6. These results show that head movements, in addition to their generally accepted role in vision improvement, also contribute to the precision and temporal coordination of correctional flight manoeuvres. The mechanism is partly via proprioceptive feedback.

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Introduction

A flying locust placed in an unstable visual environment engages in steering manoeuvres that tend to compensate for the perceived visual deviations. These correctional manoeuvres minimize unintended image motion over the retina and help to maintain a stable orientation with respect to the visual environment. This reaction is very important during flight; it helps to minimize instability due, for instance, to aerodynamical disturbances or motor imperfections (Wilson 1968).

The neural and behavioral organization responsible for visual correctional steering by insects in flight has received intense scientific attention, especially in flies and locusts (see Rowell 1988 for review). Compensatory steering in locusts involves ruddering with the abdomen and the hind legs (Dugard 1967; Camhi 1970a, b; Gewecke and Philippen 1978; Arbas 1986), and changes in wing kinematics (Wilson 1968; Zarnack and Möhl 1977; Thüring 1986; Schmidt and Zarnack 1987), both of which have obvious aerodynamic consequences. Head movements also occur (e.g. Goodman 1959; Taylor 1981a, b) but have no overt aerodynamic effect.

The functional role of these head movements in flight steering is still unclear. Two basic categories of explanations for head movements have been proposed, though these are not incompatible with one another.

a. Stabilization of the visual field. Stabilizing eye movements are common in animals with movable eyes. Eye movements are made to keep the visual system oriented with respect to the outside world or particular objects of interest. In locusts, as in all insects, the eyes have a fixed position relative to the head. Hence, head movements can be seen as eye movements. It is therefore assumed

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that head movements are primarily made to improve vision (see also Hengstenberg 1988 for a discussion of the problem in flies). A fundamental problem with this explanation is that head movements, though of the right direction to function in the postulated way, typically compensate for only a fraction of the real displacement of the visual image.

b. Proprioceptive input to the steering mechanism. Rotation of the head causes the eyes and the body to have different orientations. By measuring head and body misalignment, neck proprioceptors could contribute to the command sent to the aerodynamical effectors involved in flight steering (Mittelstaedt 1950; Goodman 1965). There is both physiological and behavioral evidence that in locusts proprioceptive information from the neck does participate in steering (Hensler 1988; Hensler and Robert 1990; Hensler, unpublished). Despite this, a recent behavioral study (Miall 1990) concluded that head movements are unlikely to play any functional role in correctional steering – as opposed to vision – in locusts.

Most experiments on flight steering have used tethered animals and open-loop conditions, both of which tend to exaggerate the steering manoeuvres. In free flight, by contrast, a visually-elicited correctional steering manoeuvre tends to minimize the perceived deviation that caused the manoeuvre. Correctional steering is a typical closed-loop behavior: stimuli and reactions are related through a circular chain of causality. The flight simulator used in the experiments reported below mimics the natural relation existing between self-motion and movement of the visual environment; by converting yaw torque produced by the animal into deviations of the panorama, it allows the locust to interact actively with its visual environment. This closed-loop paradigm was first applied by Reichardt and Wenking (1969), and adapted to the locust by Robert (1988) after Götz (1987). Although the insect is still tethered, the method allows questions concerning the organization of steering behavior to be addressed under more realistic conditions than usual. How are steering manoeuvres organized temporally? Do they have different time-courses under open- and closedloop conditions? How are head movements implicated in closed-loop flight steering?

In this paper, the behavior of locusts and the temporal organization of their correctional flight steering manoeuvres under open- and closed-loop conditions are analysed, compared and shown to be essentially similar. Locusts prevented from moving their heads while steering in the closed-loop paradigm are compared with unrestrained animals and shown to steer less well. It appears that head movements, through the visual reafference and proprioceptive signals which they cause, are functionally involved in course-corrections during flight.

Methods

Animals. Adult Locusta migratoria of either sex were taken from a crowded laboratory culture where the photoperiodic regime was 16:8 h light-dark. The animals were left intact and not submitted

to anaesthesia. The air temperature during experiments ranged from 26 to 28 $^\circ$ C.

Experimental setup. Tethered intact locusts were allowed to fly in the laminar air flow of a propulsion-type wind tunnel. Wind speed was adjusted to the usual flight velocity of 3 m/s (Gewecke and Philippen 1978). The locusts were tethered dorsally at the pronotum to a torque meter sensing the steering force produced around the vertical (yaw) axis (for details see Robert 1988). Steering was monitored as bending of the abdomen and outward rotation of the hindlegs (together referred to as ruddering) by means of capacitive position detectors (Forman and Brumbley 1980). Head rotations were recorded in the same way, using a vertical transmitting antenna glued to the frons. This antenna records both roll and yaw movements of the head.

In locusts, head movements made in response to yaw displacements of the visual field are primarily rotations around the roll rather than the yaw axis (Robert and Hensler, unpublished observations), due probably to the mechanical constraints of the neck joint and to the fact that in flight the animals bank during turns (Baker and Cooter 1979). In this study, we measured only the timing and amplitude of head movements, and not the extent to which the head movements actually compensate for movement of the visual field, a topic which is not the subject of this investigation. Consequently the technique of measuring a mixed yaw-plus-roll signal, as done here, is legitimate.

Behavioral tests were commenced only after 15 min of preparatory steady flight. In some experiments the animal's head was prevented from moving by waxing it to the anterior edge of the pronotum. This provokes a loss of major proprioceptive inputs that is sufficient to impair steering coordination (Goodman 1965; Taylor 1981b).

The experimental arrangement used for the open- and closedloop visual steering experiments has been described elsewhere (Robert 1988). The visual stimulus was composed of a vertical grating with a spatial frequency of 10.5° (average irradiance I: 1.4 mW/m²; contrast $\Delta I/I$: 0.4) or, of a single vertical black stripe of 30° width (I: 2.7 mW/m²; $\Delta I/I$: 0.5). The spatial characteristics of the grating stimulus were chosen according to the temporal resolution and the spatial acuity of the locust's movement detection system (Robert 1988). The visual stimulus was projected from beneath the animal onto the inner surface of a vertical and cylindrical white flight arena centered on the animal's flight position. The image presented to the locust was produced by illuminating a circular transparency, whose image was projected into the arena through a wide angle lens. The transparency was mounted on the shaft of a servomotor. Rotation of the transparency by the servomotor induced motion of the projected visual pattern. The inherent loop delay of the apparatus was 40 ms. The transparencies, the projection device and the electronics controlling the servomotor were generously lent by K.G. Götz of the Max-Planck-Institut für biologische Kybernetik, Tübingen, Germany.

Procedure. In the open-loop situation, the servomotor was driven by a wave-form generator, so that the motion of the visual stimulus occurred in a known manner (Fig. 1). The steering response of the locust had, in this case, no effect on the visual stimulus. Alternatively, under closed-loop conditions, the servomotor was activated by the unfiltered signals of the torque meter (Fig. 1). Thus, through the force it exerted on the torque meter, the animal could control both the speed and the direction of rotation of the panorama. The feedback loop was set so that torque produced in a given direction elicited rotation of the panorama in the opposite direction. This represents the natural negative feedback situation. The feedback signal was mixed with a constant bias voltage, which by itself resulted in rotation of the pattern at constant speed. In order to keep its visual environment stable, the locust therefore had also to compensate actively for the bias. Hence, any cessation of correctional steering would result in rotation of the pattern. The gain of the feedback loop was usually set at 55×10^5 °/Nms. However, other gain settings over the range of 12×10^5 to 14×10^6 °/Nms



Fig. 1. Principle of the open- and closed-loop experiments. In the closed-loop paradigm, the forces sensed by the torque meter are used to control the angular velocity of the visual environment of the flying locust. The feedback signal is mixed with a constant bias. In the open-loop situation, the waveform generator alone drives the visual environment. Detailed explanation in the text

could be used without affecting the stability of the whole feedback system, including the electronics and the animal. Control experiments made on 10 animals (each tested with several different gains) indicated that the size (and thus the strength) of individual locusts limits the range of usable gains. Within their individual ranges, however, locusts adapted the strength of their response (i.e. their internal gain) to that necessary to reach visual stability. This finding is important, for it shows that the results presented below are not an artifact of some unnatural feedback value. It also shows that the locusts are capable of adaptively altering the gain of their sensorymotor transfer function, as recently shown in connection with proprioceptive input to the flight system by Möhl (1988).

Extracellular muscle recordings. In some experiments, the activity of neck muscle M51 (Shepheard 1973) was recorded by inserting into it a single copper wire electrode ($40 \mu m$ diameter). The muscle was impaled near its apodeme in the pronotum. The ground electrode was inserted dorsally into the fourth or fifth abdominal segment. The electromyograms were stored on FM tape and subsequently fed into a window discriminator to transform each muscle potential into a pulse. Post-stimulus/time histograms were then constructed (Tracor Northern signal analyser) in which each dot represents a muscle action potential (ordinate: number of spikes per bin, bin width: 33 ms) (Fig. 4).

Time-course analysis. The time-course of open-loop reactions was assessed on unfiltered data that were fed into the signal averager, permitting delay measurements with an accuracy of 1.5 to 2.5 ms. Reaction times were measured at the 3 dB point of the first detectable deflection of the signal.

Under closed-loop conditions, the reaction time of the animal to visual stimuli cannot be directly measured. Under these conditions, causes and effects are not separable. Panorama deflections in closed-loop are simultaneously stimulus and response. To solve this problem, cross-correlation analyses between the variables pattern movement, ruddering and head movement were calculated for a range of time differences. These functions were temporally shifted relative to each other repeatedly and the coefficients of correlation recalculated for each shift. The resulting coefficients were then plotted against the time shifts (e.g. the correlograms in Fig. 7). The time value at maximum correlation is a measure of the actual time lag between the two functions (e.g. ruddering and head rotation). For the head rotation versus pattern movement and ruddering versus pattern movement correlations (Fig. 7b, c) the inherent loop delay of the apparatus (40 ± 5 ms, mean \pm sd) was subtracted.

Results

The behavioral components of correctional steering

Figure 2 shows that the rotation (trace 4) of a vertically striped pattern around the vertical axis (simulated yaw) of a flying locust evokes ruddering with the abdomen and the hindlegs (trace 3); these actions, in conjunction with alterations in the wing kinematics (Zarnack and Möhl 1977, and subsequent authors; not measured here) lead to the production of yaw torque (trace 1), which is developed in the same direction as the pattern rotation. The response also involves head movements (trace 2). Under these open-loop conditions, yaw torque, head and ruddering deflections are maintained after the cessation of the pattern rotation.

The time-course of open-loop correctional steering

From records similar to that shown in Fig. 2, the temporal organization of the open-loop optomotor response



Fig. 2. Open-loop optomotor response of a flying locust. The vertical grating (spatial frequency: 10.5° ; contrast frequency: 9 Hz; averaged irradiance: 1.4 mW/m^2 ; contrast: $\Delta I/I = 0.4$) can rotate around the yaw axis of the animal. The pattern trace shows the position of the vertical grating; a zero slope indicates a stable pattern. The horizontal line crossing the pattern trace corresponds to the longitudinal axis of the animal (0° deflection). This sequence is representative of similar tests performed with 40 locusts



Fig. 3. Temporal organization of the components of the correctional steering manoeuvre. The values in the bars are the delay of head, ruddering and yaw torque, averaged over 80 events. The delay of M51L stems from 16 consecutive events. Values are given with their standard deviations



Ruddering

Fig. 4a, b. Open-loop correctional steering in response to motion of vertical grating (same as in Fig. 2). M51L and M51R: post stimulus time histograms of the activity of the neck muscle M51 (Shepheard 1973). Each dot represents a muscle action potential. a Recording of the left muscle (5 averaged sweeps). b Recording of the right muscle (3 averaged sweeps)

has been analysed, and is represented graphically in Fig. 3. Ruddering and yaw torque begin respectively 59 ± 15 ms and 58 ± 16 ms (mean \pm sd, n = 80) after the start of the pattern rotation. Head movements begin 88 ± 23 ms (n = 80) after stimulus onset. The difference is



Fig. 5. Delay of head movements as a function of delay of ruddering. Data on 24 events, some overlap. Regression curve: r = 0.71; slope = + 0.75. The oblique line represents the plot that would be obtained were head turns and ruddering synchronous

highly significant ($P \ll 0.001$ by a two-sample *t*-test). In some experiments the activity of neck muscle M51 (Shepheard 1973), which is modulated during correctional steering, was monitored (Fig. 4a, b). The left M51 is activated exclusively during head movements to the left, and vice versa (Fig. 4a, b). The activity of M51 begins 47 ± 9 ms (mean \pm sd, n = 16) after stimulus onset (Fig. 3).

Further analysis shows that the delay of the head turn is strongly related to the onset time of the compensatory ruddering manoeuvre (Fig. 5). Any increase in the delay of ruddering correlates with a proportional increase in delay of head roll (supporting, incidentally, the view (see Discussion) that these behaviors are elicited by the same neural command). The line of the linear regression (r=0.71; slope = +0.75; n=24 steering events) is above the oblique line representing synchronous ruddering and head movements. This indicates that the delay between ruddering and head rotation is of constant sign and that head turns are temporally related to the start of compensatory steering. In this sample, compensatory head turns



Fig. 6. Closed-loop correctional steering with imposed perturbations. Downward arrows: reversal of the rotatory bias from the right to the left $(+74^{\circ}/s \text{ to } -74^{\circ}/s)$. Upward arrows: reversal from the left to the right. Open arrow: fine correctional manoeuvre compensating for a deviation to the right

performed under open-loop conditions begin 38 ± 12 ms (mean \pm sd; n = 24) after the onset of ruddering.

Closed-loop correctional steering

Locusts flying in a flight simulator converting yaw torque into deviations of the panorama actively stabilize their visual environment (Robert 1988; Hensler and Robert 1990). Further, they display this ability for long periods of time (up to more than one hour). Open- and closedloop correctional steering manoeuvres appear to be organized similarly. Yaw torque and ruddering are positively correlated with the imposed deflections of a vertical grating (Figs. 2, 6). Under closed-loop conditions, head turns, although more variable than in open-loop, are generally oriented in the direction of the visually perceived motion of the panorama (Fig. 6). In the 33 s sequence shown in Fig. 6, flight stability was challenged repeatedly by reversing the rotatory bias (74°/s, black arrows). Shortly after each inversion of the bias $(+74^{\circ})$ s to $-74^{\circ}/s$), the position of the panorama is stabilized again (overall zero slope of the pattern trace), and the animal adjusts its vaw torque to a suitable tonic value. In this record, coarse steering manoeuvres (directly following large perturbations) can readily be distinguished from small amplitude steering manoeuvres that occur during stable episodes (Fig. 6; plateaux between the arrows). Fine steering consists of small amplitude manoeuvres involving ruddering, yaw torque modulation, and also head movements (Fig. 6; the open arrow marks an obvious steering event).

The temporal organization of closed-loop steering

The time course of closed-loop manoeuvres was investigated by means of cross-correlation analysis. Figure 7 shows respectively the cross-correlation curves of ruddering : head movement, head movement : pattern movement and ruddering : pattern movement. The data are from a period of undisturbed closed-loop fine steering similar to that of Fig. 8a. For ruddering and head movements (Fig. 7a) the best correlation is obtained with a 40 ms forward shift of the ruddering function. Hence, ruddering precedes head movements by 40 ms. The best correlation of head and pattern movements is reached with a time lag of -95 ms (Fig. 7b), indicating that the visual stimuli lead head movements by 95 ms. The time lag between ruddering and pattern movements is 55 ms

Table 1.

	DELAYS [ms]	
	Open-loop (average \pm s.d.)	Closed-loop (from cross- correlation analysis)
Yaw torque Ruddering Head movement	$58 (\pm 16) (n=80) 59 (\pm 15) (n=80) 88 (\pm 23) (n=80)$	55 55 95



Fig. 7a-c. Cross-correlation plots. Data are from a 45 s long undisturbed flight sequence. a Correlation between ruddering and head movements. The best correlation is obtained for a 40 ms forward shift of the ruddering function. b Correlation between head movements and deflections of the pattern. Maximum of the correlogram occurs at a phase lag of 95 ms. c Correlation between ruddering and pattern movement. The best correlation is obtained for a 55 ms forward shift of the ruddering function

(Fig. 7c). Correlograms made on undisturbed flight episodes of three other locusts confirmed this result. Comparison of open- and closed-loop delays is shown in Table 1; they are virtually identical. The temporal organization of steering observed under open-loop con-



Fig. 9a, b. Frequency distribution of the pattern speed of rotation. The sequence is taken from a continuous flight episode of one animal. Sampling time: 40 s. Bin width is $2^{\circ}/s$. a The locust was free to move its head. b The head was waxed to the pronotum

ditions is essentially conserved during compensatory steering performed under closed-loop conditions.

Steering after the head is immobilized

a. The response to vertical gratings. Under open-loop conditions, the time-course of the compensatory response to a rotating vertical grating is not affected by fixing the head to the pronotum (data not shown). Ruddering begins after $57 \pm 11 \text{ ms}$ (sd, n = 20 events) with the the head free and $62 \pm 14 \text{ ms}$ (sd, n = 17) with the head fixed. (Camhi (1970a) previously showed that preventing head movements has no effect on the amplitude of abdominal ruddering in response to changes in the direction of the wind flowing over the head under open-loop conditions).

Under closed-loop conditions, locusts with their heads free are able to stabilize a vertical grating very well (Fig. 8a). Under the same conditions, locusts with their heads fixed still stabilize the visual environment, but the accuracy of their steering manoeuvres is reduced (Fig. 8b). Locusts with their head immobilized produce slightly overshooting reactions, as indicated by the larger oscillations of the pattern trace. The steering performance over 40 s of a locust with its head free to move is shown in Fig. 9a. (Due to the rotatory bias, an absence of all steering activity would have led to a constant rotation at

Correlation Ruddering-Pattern Movement



Fig. 10. Cross-correlation analysis between ruddering and pattern movement. Data are from 50 s long undisturbed flight sequences (closed-loop conditions). Head free and head fixed situations. When the head is fixed, ruddering occurs later and the correlation is lower

74°/s in this experiment). A locust with its head fixed still steers successfully (Fig. 9b); nevertheless, the equivalent frequency distribution is broader, indicating some degradation of steering control. Bartlett's test of homogeneity of variances (Sokal and Rohlf 1981) shows that the



Fig. 11a-c. Optomotor open-loop response to a single vertical black stripe (30° width) rotating around the vaw axis at 88°/s. a Head free situation. Averaged from 17 sweeps. b Head fixed situation. Averaged from 20 sweeps. c Time course of the openloop optomotor reaction to the single stripe. The measured parameter is the onset time of ruddering. Zero point on the time scale: time at which the stripe is aligned with the longitudinal axis of the animal. Oblique line: position of the stripe as a function of time. Speed of rotation: 100°/s. Onset time of ruddering with the head free: -79 ± 40 ms (sd), with the head fixed: $\pm 149 \pm 31$ ms (sd). Inset: stripe at the zero position. Arrow: direction of rotation. Broken lines: -90° and $+90^{\circ}$

variances of 8 independent samples are not homogeneous $(n=8; P \leq 0.05)$.

Cross-correlation analysis of flight sequences by 3 separate animals with the head free and the head fixed indicates that fixing the head to the pronotum influences the coordination of ruddering movements in two ways (Fig. 10). First, the correlation between pattern rotation and ruddering is weaker. Second, the maximal correlation is obtained with a time shift between ruddering and pattern position of -375 ms, compared with -79 ms with the head free. The effective response time is thus lengthened by nearly 300 ms, or a factor of about 5 times.

b. The response to a single stripe. A single vertical black stripe rotating around a flying locust evokes a corrective steering response only when it moves from front to back. The response under open-loop conditions and with the head free to move is shown in Fig. 11a. The compensatory manoeuvre starts when the stripe moves from the head-on position; ruddering and yaw torque are both in the direction of rotation of the stripe (here to the left), indicating a compensatory steering manoeuvre. Immediately after the onset of the stripe rotation, however, head turning and ruddering are transiently oriented toward the stimulus, i.e. to the right, as if the animal were "turning to look at" the moving stripe (Fig. 11a, open arrows). This transient flick is immediately followed by the "compensatory" head rotation and ruddering which are accompanied by torque production. The flick response starts 42 ms (for the ruddering component) and 96 ms (for the head rotation component) after the stripe begins to move (n = 17, sd values not available due to on-line averaging).

When head movements are prevented by waxing the head to the pronotum, the initial transient ruddering flick also disappears (Fig. 11b). We have no explanation for this fact, but the effect has also been seen in seven other animals. The compensatory ruddering and yaw torque still occur, but with a considerably longer latency. The latency of ruddering under the two conditions is shown diagrammatically in Fig. 11c. The stripe is assumed to be moving from 90° left to 90° right (at 100 °/s) as shown by the oblique line crossing the time axis at zero, at which point the stripe is head-on to the animal. The angular position of the stripe at a given time is given by the ordinate (minus is left, plus is right). The time at which the locust initiates corrective ruddering is represented by bars above the abscissa. In the head-free situation the animal reacts shortly before the stripe reaches the headа

head fixed

С



head free

Fig. 12a-d. Closed-loop visual steering in the presence a single vertical black stripe. The bias is constant $(40^{\circ}/s)$. a The head is free to move and the stripe is kept aligned with the longitudinal axis of the locust (zero position on the stripe trace). b Frequency distribution of the speed of the stripe (data from a 31 s continuous flight

on position (delay = $-79 \text{ ms} \pm 40 \text{ ms}$, mean $\pm \text{ sd}$, n = 17). A locust with the head fixed reacts 226 ms later (delay = $+147 \text{ ms} \pm 31 \text{ ms}$, mean $\pm \text{ sd}$, n = 20). Thus it appears that the initial flick of the head towards the stimulus results in an earlier alignment of the stripe with the visual midline and so shortens the latency of the optomotor part of the reaction.

Under closed-loop conditions this object-oriented optomotor response leads to a dynamic stabilization of the stripe in the locust's frontal field of view (Fig. 12a, b). Under these circumstances head movements are of very small amplitude (on the order of one degree) and not very strictly correlated with the oscillations of the stripe. The frequency distribution of the speed of rotation of the stripe is a good measure of the quality of long-term closed-loop steering. It can be seen in Fig. 12b (derived from a 31 s flight sequence) that the angular speed of the stripe is kept close to zero, not exceeding $\pm 15^{\circ}$ /s. (It will be recalled that simple cessation of steering would cause, because of the rotatory bias, a constant rotation, in this case at 40°/s.) Locusts (N=7) with fixed heads still manage to maintain the stripe frontally (Fig. 12c). However, the stripe is stabilized less accurately; the scatter of the frequency distribution is broader, extending to $\pm 25^{\circ}$ (Fig. 12d).

Summarizing, experiments using both the vertical grating (under closed-loop conditions) and the single



sequence). Bin width is 2 °/s. c The head is fixed to the pronotum. The stripe is still aligned frontally, though less precisely. d When the head is fixed, the rotation of the stripe is less well controlled by the locust; the scatter of the frequency distribution is broader

stripe (under open- and closed-loop conditions) show that immobilising the head reduces both the accuracy and the rapidity of compensatory steering manoeuvres. The reduction in response accuracy is small but significant, the reduction in response speed is considerable.

Discussion

Fine and coarse correctional steering

Open-loop correctional steering behavior (Fig. 2) involves at least 3 components: wing kinematics, ruddering with abdomen and hind legs, and head movements (for references see Introduction). It has been shown here that correctional steering performed under closed-loop conditions uses the same behavioral components and has the same temporal organization as under open-loop conditions. Experimentally it has been shown that closedloop steering leads to stabilization of the retinal image (Figs. 6, 8), fixation of a vertical stripe (Robert 1988, this paper, Fig. 12) or alignment to the horizon (Robert 1988; Hensler and Robert 1990); in the wild it is presumably responsible for straight or target-directed flight.

In the absence of major disturbances, however, correctional steering under closed-loop involves minimal ruddering of only a few degrees in amplitude, that would produce little or no aerodynamical drag according to the measurements of Gewecke and Philippen (1978). Consequently, fine steering probably involves mainly alterations of wing kinematics – it would be interesting to examine these under open- and closed-loop conditions too. In the presence of massive disturbances (e.g., as in Fig. 6, bias reversal resulting in a perceived yaw at 148°/s), steering with the wings alone may not be sufficient. Pronounced ruddering then contributes to the relatively violent manoeuvres needed for stabilization by modifying the aerodynamic drag and the center of mass of the animal.

Head movements during closed-loop steering, although adaptive, are highly variable (Figs. 8, 12). Contrary to the situation observed under open-loop conditions, head turns are not invariably compensatory and their gain may fluctuate rapidly as well (Hensler and Robert 1990). Normally they are smaller than those often encountered under open-loop conditions, though this probably represents mostly the tendency of experimenters to use large amplitude deviations in their open-loop experiments. The present work shows that it is precisely during small amplitude steering that head movements are critically important (Figs. 8, 12) for precision steering. This function is discussed below.

The time-course of correctional steering

In order to be effective, steering manoeuvres have to be of appropriate direction and amplitude. Even if these qualities are present, however, the success of a coursecorrection depends strongly on its speed of onset. The shorter the reaction time, the smaller the deviation to be corrected, the less the corrective behavior necessary, and the greater the overall precision of steering. The present results show that in the tethered locust course-correction starts within 50–60 ms (i.e., one wingbeat period). The latency of wing stroke modulation is also equivalent to one wingstroke (Zarnack and Möhl 1977, and subsequent authors). Our results indicate that the ability of the head to move freely during steering is important in keeping this reaction time short.

For comparison, the reaction time of hoverflies (Syritta) during the tracking of a visual target is 10 to 20 ms (Collett 1980), the wingbeat period being probably in the order of 4–6.6 ms (e.g. 150–250 Hz, common wingbeat frequencies for brachyceran flies (Sotavalta 1947)).

The role of head movements in steering

Though long known to occur, the role of head movements in flight steering by insects has been somewhat enigmatic. At least 3 hypotheses have been advanced: 1. Head turns, via neck proprioceptive inputs, initiate and control steering behavior (Goodman 1965). 2. Head turns are purely visual in function (i.e., they serve exclusively to reduce retinal slip) and either have no direct effect or even a deleterious effect on steering behavior (Miall 1990). 3. Head turns contribute proprioceptive information which, while not initiating steering, contributes to or modulates adaptively the steering commands proceeding to the thoracic motor centers. These hypotheses are discussed below. The latter seems most likely to be correct.

Head movements do not initiate steering manoeuvres. Mittelstaedt (1950) concluded from his experiments on dragonflies that visually perceived deviations from course first elicit compensatory head turns, causing a change in alignment between head and body. Subsequent alterations of the wingbeat were thought then to realign the body with the head. This simple and elegant model of compensatory steering has been generally adopted and head movements are often considered to initiate turns in flying insects. Goodman (1965) proposed effectively the Mittelstaedt model of compensatory steering for locusts. The present results do not however support Goodman's scheme. First, locusts are able to steer without information from the neck proprioceptors (Taylor 1981a; Hensler and Robert 1990; Miall 1990, see also the head-fixed situation of Fig. 8). Secondly, head movements begin after the start of the steering manoeuvre. During visually-evoked corrective steering, head movements begin about 90 ms after stimulus onset, some 30 ms after ruddering and torque production have already started (Fig. 3). Similarly, during yaw-correcting responses to alterations of the wind flow over the head, abdominal ruddering precedes head movements by 40-80 ms (Camhi 1970a). Hence, in Locusta, the steering manoeuvres cannot be initiated by head movements.

The evidence for head movements being irrelevant or deleterious to steering is flawed. The arguments which have been presented against a useful role of head movements in flight steering are the following. 1. Tethered locusts can perform correctional steering in flight after the head has been immobilised (Taylor 1981a; Hensler and Robert 1990; Miall 1990; this paper). This has also been shown for crickets (Tomioka and Yamaguchi 1980) and flies (Collett 1980; Götz 1987; Land 1975; Reichardt 1973). This however does not necessarily mean that the precision of their steering remained unchanged: in most of these studies this question was not addressed, and where it was (Land 1975: Fig. 21.2), steering precision was found to be reduced after immobilising the head. 2. Intact locusts thrown into the air after the head has been immobilized fly apparently normally (Miall 1990; Robert, personal observation). As in the case of the first argument, the observation is not disputed; it is however clear that the experimental situation is not appropriate either to elicit the most accurate steering or to demonstrate that its precision is unimpaired. 3. Tethered locusts flying under open-loop conditions increase the amplitude of their correctional steering after the head is fixed (Hensler and Robert 1990; Miall 1990). This is to be expected, because of the increased visual error caused by the absence of compensatory head movements. Miall (1989, 1990) interprets this result to mean that the reduction in the visual component of the eliciting stimulus caused by the rotation of the head is not adequately replaced by proprioceptive inputs, and that these are therefore unimportant to steering. An extension of this logic would lead to the rather bizarre prediction that the animal would actually steer better if other visual constraints did not require it to make compensatory head movements. There are a number of problems with this argument. First, the logic is based on the assumption that the larger steering response seen with the head fixed is somehow better ("more adequate" in Miall's phrase) because it more nearly aligns the head with the horizon, which Miall assumes to be the goal of the behavior. However, as the goal of the behavior is the subject of the investigation, it cannot be assumed. Such an assumption also ignores the fact that in Miall's experiments (and those of others) the locusts never compensate the visual error fully, even under maintained deflections under open-loop conditions; the maximum gain value which Miall reports is 55%. Second, the original result, even under open-loop conditions, only holds for very large amplitude $(>36^\circ)$ deflections. During the more realistic low amplitude steering manoeuvres the difference between head-free and head-fixed responses vanishes (Miall's Fig. 9a, b). Third, our results demonstrate that the amplitude of head movements under open-loop conditions is of little help in predicting what these will be under the more natural closed-loop circumstances.

There is substantial evidence that the proprioceptive signals generated by head movements are physiologically and behaviorally important in steering. 1. It has been known for a decade (Taylor 1981b; see also Hensler 1988; Miall 1990) that imposed head movements, in the absence of visual inputs, produce weak steering behavior of the wings.

2. All components of steering behavior (head, wing, abdomen and leg) can be elicited by stimulating intracellularly single neurons belonging to a population of descending interneurons conveying information from the head to the thorax and abdomen (Rowell 1989; Baader 1991; Hensler, unpublished). These descending neurons respond primarily to visual and/or wind hair inputs (Rowell and Pearson 1983; Reichert and Rowell 1985; Reichert et al. 1985; Rowell and Reichert 1986; Rowell 1989) and respond as a population to course deviation. Many, though not all of those tested, have been shown to get inhibitory or excitatory input from neck proprioceptors (Hensler 1988, 1989, and unpublished). This finding alone makes it virtually impossible that steering can be independent of proprioceptive input.

3. Hensler and Robert (1990) showed that under tethered conditions neck proprioception contributes some 20% to the steering response when the latter is measured as shift of the relative latencies of the first basalar flight muscle.

4. The present study shows that steering behavior is deleteriously affected by preventing head movements. In closed-loop conditions, especially, both the precision and the reaction time of steering are significantly reduced, and similar effects can be seen under open-loop conditions, given the more demanding circumstances of single-stripe fixation.

Finally, putative proprioceptive effects on steering can be demonstrated even in Miall's study (1990), which concluded that these did not exist. In darkness, head movements modulate the relative latencies of M97 by 1.5 ms (his Fig. 8a); this latency shift is what would be expected to be associated with small amplitude corrective steering, and can only be derived from proprioceptive information. Further, if neck proprioception has no effect on corrective steering, (a) the rotation of the horizon about a tethered animal prevented from moving its head (Miall, Fig. 9a) should provoke exactly the same response (in terms of relative latency shifts in the flight muscles) as (b) the forced rotation of the head relative to a stationary horizon (Miall Fig. 8b). This turns out not to be the case: (a) provokes a shift of 4 ms for a stimulus amplitude of 30° (Fig. 9a) and (b) elicits a 3 ms shift for 36° stimulus amplitude (Fig. 8b). The 33% difference in the shift can only be due to proprioceptive inputs from the neck receptors. It must be stressed that a 1 ms difference is important - steering often involves shifts in relative latency of the flight muscles of only one or a few milliseconds, even under open-loop conditions which tend to exaggerate manoeuvres (Zarnack and Möhl 1977; Taylor 1981b; Thüring 1986; Möhl 1988; Schmidt and Zarnack 1987; Hensler and Robert 1990).

What happens in corrective flight steering?

Deviation from course is known to be perceived by a variety of photo- and mechanoreceptors, and the processed signal transmitted to the thoracic motor centers by a population of descending interneurons (or ascending ones, in the case of information derived from the cerci (Fraser 1977; Boyan et al. 1986)). The first action potential arrives in the thorax some 25 ms after stimulus onset (Rowell and Reichert 1986). These interneurons synapse in the suboesophageal, thoracic and anterior abdominal neuromeres with the premotor interneurons and motor neurons responsible for steering movements. All these motor behaviors start at approximately the same time, some 60 ms after stimulus onset, except the head movements; it seems likely that the slower development of movement of the head (90 ms after stimulus onset) is due to the elasticity of its complex muscular suspension, as the muscles start firing at the expected time (Fig. 3). This sequence of events means that the compensatory turn is performed without reference to visual or proprioceptive feedback until the head starts to move, and that during approximately the first 100 ms following the deviation from course correctional steering must be conducted in an essentially open-loop mode. Thereafter, through compensatory head movements, visual reafference and neck receptor signals assist steering and minimize overshooting. This steering procedure is similar to the one proposed for flies (Musca and Calliphora) by Geiger and Poggio (1977; Fig. 4b), in which visual input controls in parallel head and steering motors.

Summarizing, course-control manoeuvres and head movements are initiated and primarily controlled by teloreceptor information (especially visual and wind hair inputs) and the former are additionally conditioned by both the visual reafference and proprioceptive information consequent on the head movements. The present work shows that head movements, in addition to their generally admitted role in improving vision (Collett 1980; Hengstenberg 1988), also contribute to the precision and temporal coordination of correctional flight manoeuvres. In our subsequent paper (Robert and Rowell 1992) their role in a non-correctional flight manoeuvre is investigated.

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