

## CONTRIBUTION OF COMPOUND EYES AND OCELLI TO STEERING OF LOCUSTS IN FLIGHT

### II. TIMING CHANGES IN FLIGHT MOTOR UNITS

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#### SUMMARY

Locusts (Orthoptera, Acrididae) were induced to fly while tethered within a simulated horizon display. Rotation of the horizon about the animal's long axis caused changes in the relative timing of the spikes of homologous flight muscles of either side. Changes in relative timing paralleled the pattern of head motions (Taylor, 1981) elicited by horizon rotation. Systematic changes in relative spike timing were also seen after the compound eyes were surgically disconnected and in response to forced head rotation. These results are discussed in relation to the functions of the compound eyes, the ocelli, and the cervical proprioceptive hairs for visual flight stabilization.

#### INTRODUCTION

There are several mechanisms by which flying insects change course during flight. They use body appendages as rudders (Camhi, 1970), they alter the mechanical properties of the thoracic box and wing hinge by the contraction of accessory flight muscles (Pringle, 1957; Pfau, 1977), and they change the timing and strength of contraction of the flight power muscles. This report concerns the third mechanism.

Locusts are a well-studied example of neurogenic flight control in which muscle contractions are timed by impulses from the central nervous system. Each motoneurone spike is followed closely by a muscle spike and twitch.

The stereotyped rhythmical pattern of motoneurone firing which characterizes locust flight was found to occur in the absence of reflex sensory inputs (D. Wilson, 1961), and was therefore attributed to a pattern generator located within the central nervous system. Some aspects of the neural network involved in the pattern generator have been studied previously (Kendig, 1967; Burrows, 1973).

Several previous studies have investigated responses of the wings or wing muscles of locusts to stimuli which cause steering behaviour (Dugard, 1967; Waldron, 1967; Zarnack & Möhl, 1977; Koch, 1978; Möhl & Zarnack, 1978; Cooter, 1979; Baker, 1979*a, b*). Controversy surrounds the exact manner by which changes in muscle

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firing cause changes in motion of the wings and the manner that wing motions elicit aerodynamic forces which change the body orientation (see Discussion). This is complicated by the variety of stimulus configurations, methods of tethering animals, and methods of data analysis. However, there is little doubt that changes in the timing of muscle spikes occur during attempted flight steering behaviour, and that the changes are consistent for different animals in the same situation.

The experiments reported here were undertaken to quantify changes in the output of the flight motor pattern in response to visual and proprioceptive stimuli which would be expected to affect the direction of flight. A method of quantifying changes in the output of the motor pattern generator was devised (similar to that used by Zarnack & Möhl, 1977 and Baker, 1979*b*), and the resulting data were compared to the stimulus and to the optomotor output of head turning. This approach was taken in the hope that eventually the physiology of individual identifiable neurones which receive visual and/or proprioceptive input and whose output affects the flight motor pattern generator could be described (see Discussion).

Some of the results presented here have appeared in preliminary form (Taylor, 1979).

#### METHODS

Useful data were obtained from 23 mature male locusts (*Schistocerca gregaria* (Forsk.)) which were obtained from culture at the University of British Columbia. Animals were kept in an environment of alternating temperature (day 38 °C, night 21 °C) and low relative humidity (*ca.* 20%) which hastened their maturation and made them more active than animals kept at a constant temperature (Albrecht, Michel & Casanova, 1978).

Experiments were performed at 32–35 °C, and flight was stimulated with a small diameter wind jet directed at the cephalic wind hairs. The spike activity of individual flight muscles was monitored by inserting single (50 µm diameter) silver wires (insulated except for ½ mm at the tip) through small holes drilled in the cuticle at the ventral insertion of individual flight muscles. These wires were held in place with wax. Recordings were made with reference to an indifferent electrode placed in the animal's abdomen.

The visual stimulation apparatus has been previously described (Taylor, 1981). An artificial horizon (light above, dark below) was displayed to animals tethered by their pterothoracic sternum. The horizon could be displaced manually about the animal's long axis. Continuous records of horizon position and head position about the animal's long axis were obtained as before (Taylor, 1981). All visual experiments described here were performed with the lighted hemisphere of the horizon illuminating the locust at approximately 1000 lux. Muscle spikes and head position were recorded on an FM tape recorder. (Since the tape recorder had only three channels, horizon position was recorded with an oscilloscope camera. In some experiments horizon position was not recorded; in figures made from these experiments, the approximate horizon position is indicated by a dashed line.)

In all experiments, the time of the first spike in the right-side muscle was measured in relation to the time of the first spike in the homologous left-side muscle within each

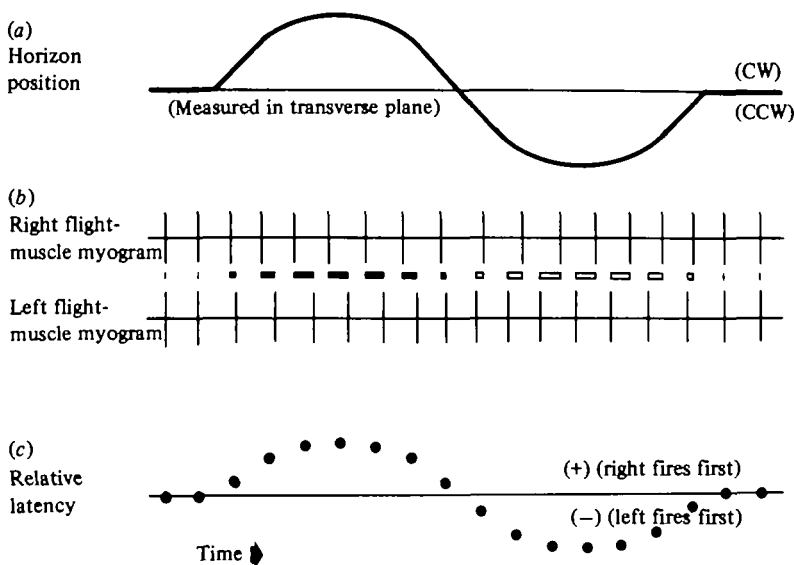


Fig. 1. Schematic diagram demonstrating method of spike train analysis. (a) Horizon position was registered by a potentiometer attached to the horizon display: downward deflexion of trace signifies counterclockwise rotation with respect to the animal. The horizon was manually rotated about the animal's long axis. (b) Myograms from the right and left forewing first basalar (direct pronator-depressor of forewing) were recorded in most experiments. During analysis of each wingbeat cycle, the time between the first spike of the right muscle and the first spike of the left muscle was termed *relative latency* (solid bars). If the left muscle fired first, the relative latency was defined as negative (unfilled bars). (c) Relative latency was plotted for each wingbeat cycle, allowing trends to be compared with the visual stimuli.

wingbeat cycle (Fig. 1). This value, henceforth called *relative latency*, was defined as positive if the right muscle fired first, zero if the spikes were simultaneous, and negative if the left muscle fired first. The relative latency was determined for each wingbeat cycle with the exception of cycles in which one of the muscle units failed to fire.

Often, and especially after extensive surgical manipulation, animals could not be induced to fly steadily for long periods. In these cases, the relative latency usually showed a shift toward positive or negative values which steadily increased until the end of a flight (e.g. Fig. 6a). In some of these cases, the data were corrected for the change (which was apparently unrelated to the visual stimuli applied) by the following method. A straight line which best described the overall trend in relative latency over the course of the entire flight was fitted by eye. This line was then subtracted from the raw data, approximately eliminating any trend. Whenever this correction was applied, the maximum correction (in ms) subtracted from the data is stated beside an asterisk alongside the corrected data.

A consequence of the method of data analysis is that the wingbeat cycle number bears only an approximate relationship to time. For this reason, elapsed time for each flight is shown by 1 s hatch marks below each figure.

All surgical manipulations and electrode placements were verified by post-mortem dissection. In some cases, electrode position was verified by staining the silver deposited iontophoretically from the recording electrode.

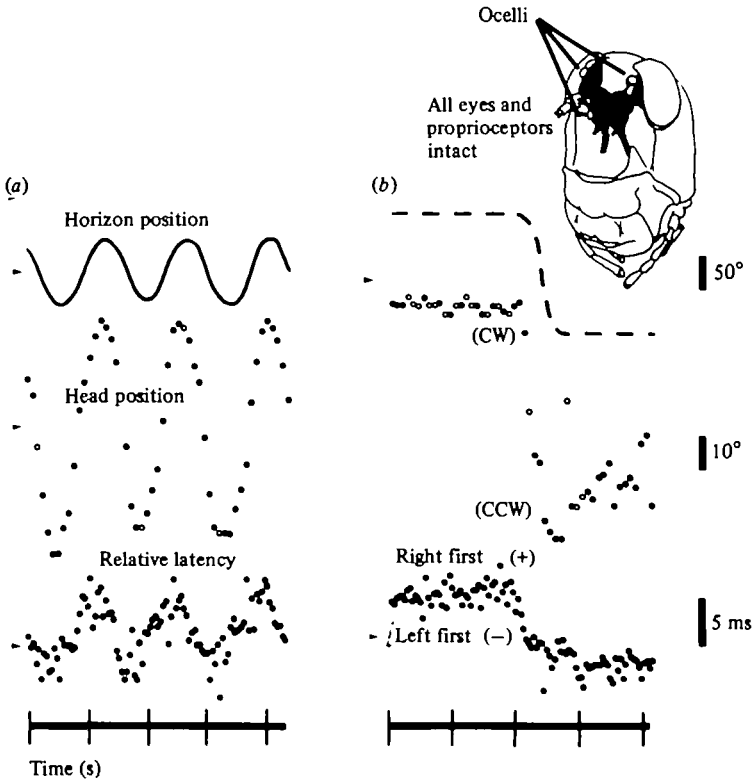


Fig. 2. Changes in head position (○) and in the relative latency of forewing first basalar muscles (●) in response to changes in horizon position. Animals with all eyes and cervical proprioceptors intact (inset). In this and following figures, small arrowheads to the left of each trace indicate neutral horizon position (i.e. dark below, illuminated above), resting head position, and zero relative latency (i.e. simultaneous right and left muscle spikes). (a) Horizon describes approximately 90° peak-to-peak sinusoidal rotation about the animal's long axis. (b) Stepwise rotation of horizon from a position which darkens the left side of the animal (upward deflexion) to a position which darkens the right side (downward deflexion). Dashed line indicates that horizon position was not recorded on tape (see Methods).

For one experiment, the locust's head was forcibly displaced about the roll axis. A small steel rod was attached to the axis of a pen motor and waxed to the front of the animal's head. This experiment was performed in darkness.

## RESULTS

Intact flying locusts followed horizon displacement about the animal's long axis with motions of their head and also made rudder-like motions with the abdomen and legs (Taylor, 1981). In addition, the relative latency of forewing first basalar muscle spikes of either side changed in a characteristic manner (Fig. 2a). When the right side of the horizon was rotated 50° downwards (i.e. clockwise, as seen by the animal), the relative latency changed from approximately zero (before rotation) to a positive value of 3–5 ms (6–10% of wingbeat period). For horizon rotation which alternated from 90° on one side to 90° on the other, shifts of relative latency as large as 25 ms (50% of wingbeat period) were observed.

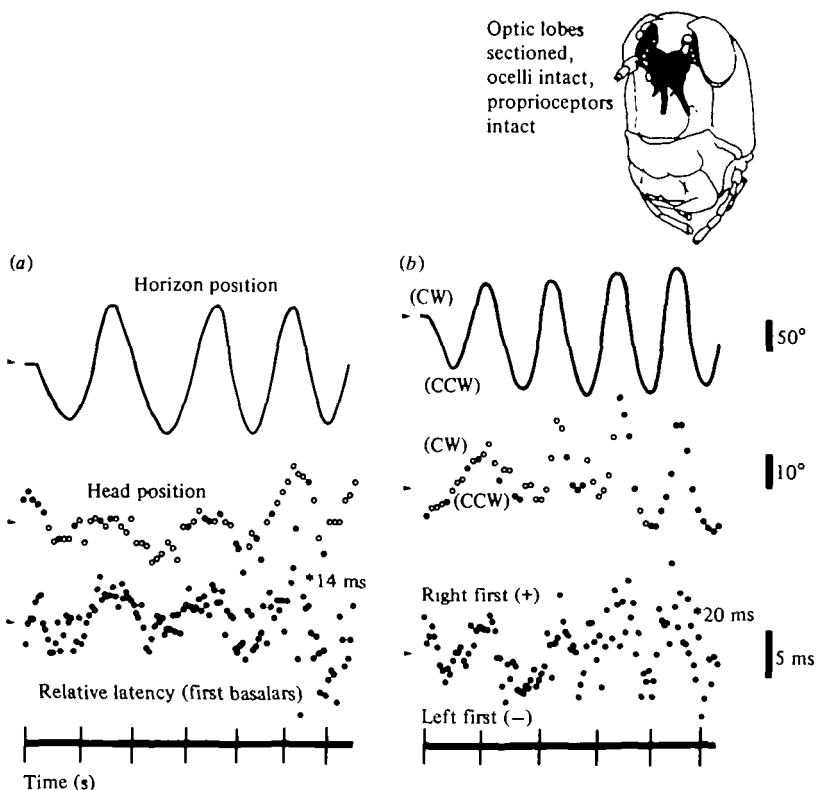


Fig. 3. Changes in head position and relative latency in response to horizon motion. Compound eyes were disconnected by sectioning optic lobes, leaving the ocelli intact (inset). In both panels, flight begins shortly before the beginning of records. Values following asterisks are the maximum correction which was applied to these data (see Methods). (a) Relative latency of forewing first basalar muscles. (b) Relative latency of forewing tergosternal (indirect elevator) muscles.

The changes in relative latency produced by different patterns of horizon rotation were paralleled by head motions: sudden changes in relative latency were accompanied by sudden changes in head position; maintained changes in relative latency were accompanied by maintained displacements of head position; and slow sinusoidal horizon motion produced head motion and changes in relative latency which paralleled each other (Fig. 2*a, b*). The quiescent period between a sudden horizon displacement and the resulting change in relative latency was difficult to estimate because of scatter in the baseline relative latency, and because of limits upon the maximum rate that the horizon could be moved manually. However, from a number of experiments, the quiescent period was estimated as being no greater than two wingbeat periods (100 ms). This is similar to the quiescent period of the head motion response (Taylor, 1981).

#### *Responses with compound eyes disconnected*

After the compound eyes were surgically disconnected from the central nervous system by cutting through the optic lobes distal to the optic peduncles (Taylor, 1981),

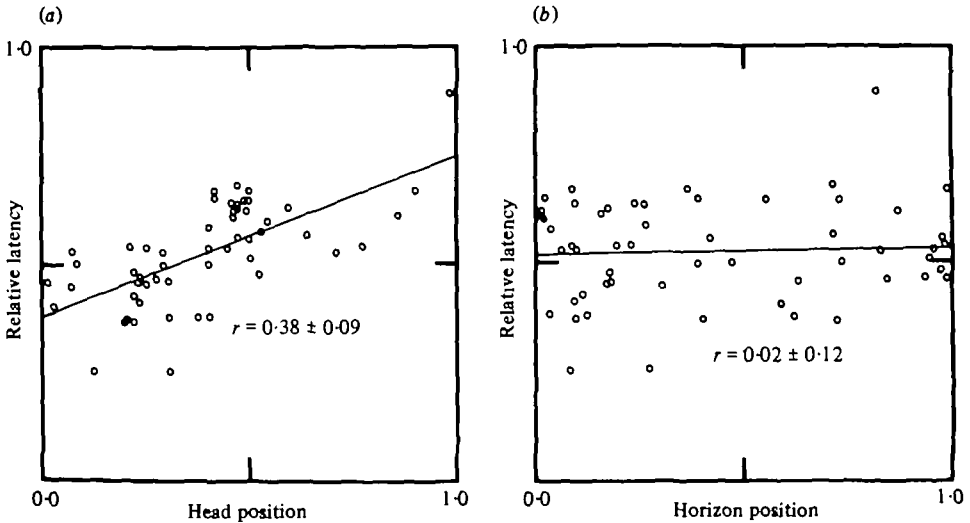


Fig. 4. The same data displayed in Fig. 3*a* (head position and relative latency during horizon rotation, compound eyes disconnected) are used. Relative latency and head position raw data were normalized and averaged in consecutive groups of two (see text). (a) Relative latency treated as a function of head position. The linear regression line derived from these data is shown; slope ( $r$ ) is 6.6 standard errors from zero. (b) Relative latency treated as a function of horizon position. Although the linear regression line has a slightly positive slope, the slope is not significantly different from zero. For the data shown, relative latency is predicted by head position significantly better than by horizon position ( $P < 0.025$ , single-tailed test).

shifts in the relative latency between homologous first basalar muscles were still observed in response to horizon displacement (Fig. 3). However, larger displacements of the horizon were required to elicit unambiguous results, and usually vigorous flight could only be maintained for a short time, with greater variation in relative latency.

In all experiments in which steady flight was obtained, horizon displacement changed the relative latency in the same direction as observed with intact animals; clockwise horizon displacement always caused a positive shift in relative latency, and the changes in relative latency closely paralleled changes in head position. However, when the compound eyes were disconnected, head position and relative latency had a rather constant relationship to each other even when head position did not follow the horizon position closely (e.g. Fig. 3*a*, Fig. 7).

Linear regressions were performed on the data presented in Fig. 3*a* to determine whether relative latency is best described as a function of horizon position or of head position. Head position, horizon position, and relative latency were each measured once during each wingbeat, at the time of firing of the forewing first basalar muscles. Each set of data (head position, horizon position, relative latency) was normalized so that its range was between 0.0 and 1.0. Each set of data was then averaged in consecutive groups of two wingbeat cycles in order to reduce scatter (this procedure was done with the assumption that little significant change occurred during the 50 ms separating consecutive data points.) The resulting normalized values of relative latency were plotted as a function of normalized head position (Fig. 4*a*) and a

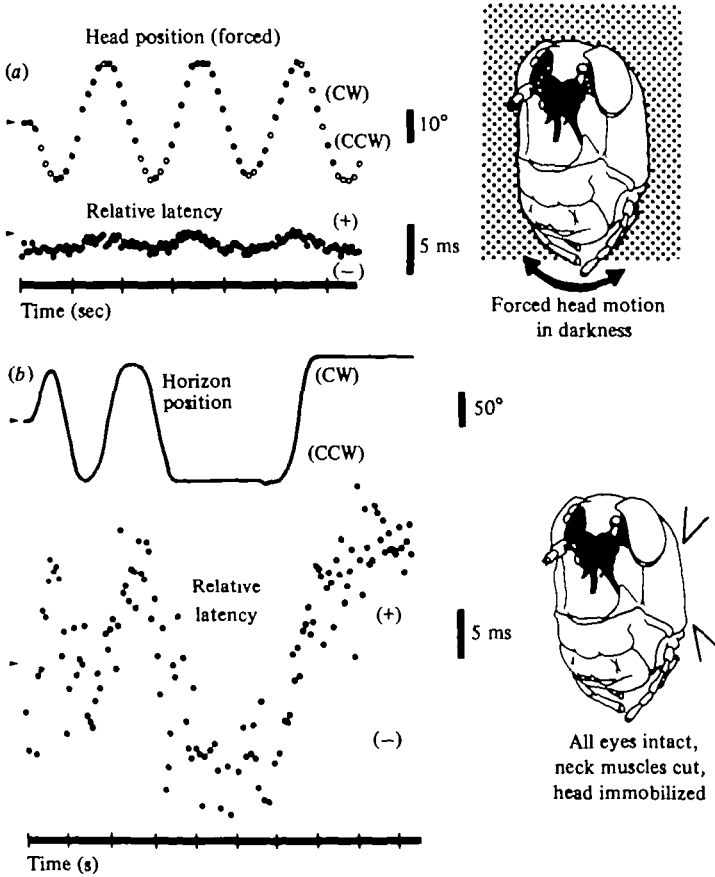


Fig. 5. (a) Changes in relative latency of forewing first basilar muscles (●) in response to forced rotation of the head about the animal's long axis (○). Visual stimuli were prevented by sectioning the compound eye optic lobes and darkening the apparatus (inset). (b) Changes in relative latency of forewing first basilar muscles (●) in response to horizon motion. Neck tissues except for ventral nerve cord and gut were sectioned and the head immobilized, all eyes were intact.

a function of normalized horizon position (Fig. 4b). The linear regressions of each of these relations are shown.

The slope of the line relating relative latency to head position (Fig. 4a) was 6.6 standard errors from zero, which indicates a highly significant relation. However, a similar analysis of relative latency treated as a function of horizon position (Fig. 4b) revealed a regression line whose slope was not significantly different from zero. Thus, relative latency is predicted significantly better by head position than by the visual stimulus ( $P < 0.025$ ).

The only other muscle pair investigated extensively was the right-side and left-side tergo-sternal muscles of the forewing. The relative latency of these muscles followed the same pattern of response as the first basalars: clockwise horizon rotation shifted the relative latency to more positive values (Fig. 3b). The same pattern was also observed from the tergo-sternal muscles in response to horizon displacement in animals with all eyes intact (data not shown).

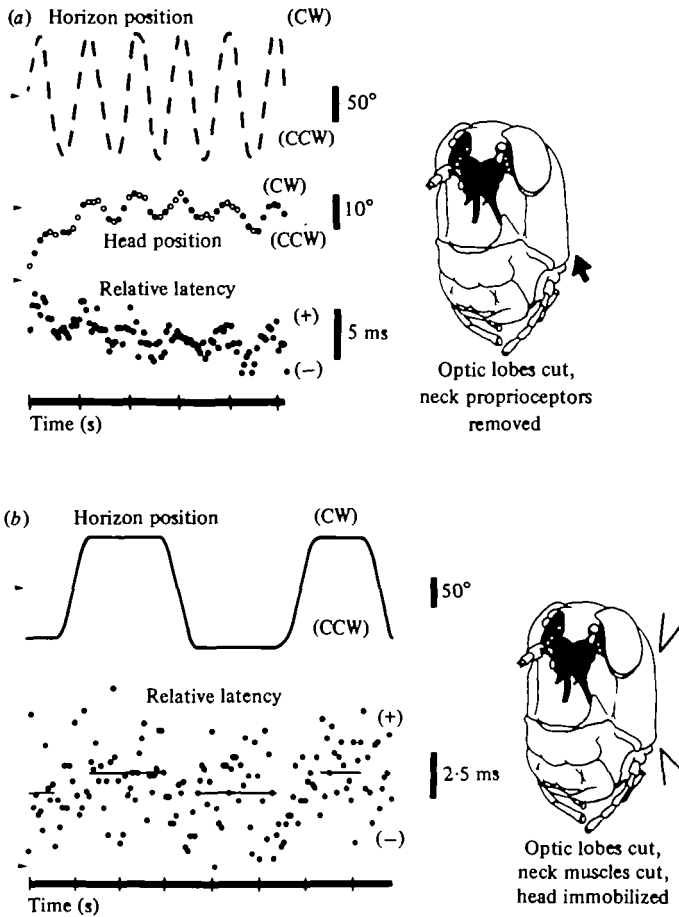


Fig. 6. Changes in relative latency of forewing first basalars (●) in response to horizon rotation, compound eyes disconnected. (a) Neck proprioceptive hairs of the cervical sclerites and nearby pronotal shield were surgically removed, head was free to move (○). (b) Neck tissues except for gut and ventral nerve cord were sectioned and the head immobilized. The mean latency during horizon rotation which darkened the left side of the animal is represented by the thin upper lines; during rotation which darkened the right, by the thin lower lines. The two means are significantly different ( $P < 0.005$ , single-tailed test,  $N = 97$ ).

### *The cervical proprioceptors*

The relative latency of forewing first basalars was analysed in response to forced rotation of the head in darkness (see Methods). The response of an animal stimulated in this manner is shown in Fig. 5*a*. Rotation of the head clockwise (in relation to the animal) resulted in earlier firing of the right first basalar, but less shift was seen than that associated with head movement elicited visually (cf. Figs. 2, 3). The same experiment in the absence of wind (data not shown) indicated that the observed response was not caused by changes in the angle of wind incidence to the head.

In order to investigate the role of the cervical proprioceptors further, animals which had their head immobilized were observed for responses to horizon rotation. All tissues of the neck except the gut and ventral nerve cord were severed, and the head was secured to the thorax with wax. Although the trauma of surgery made flight mor-



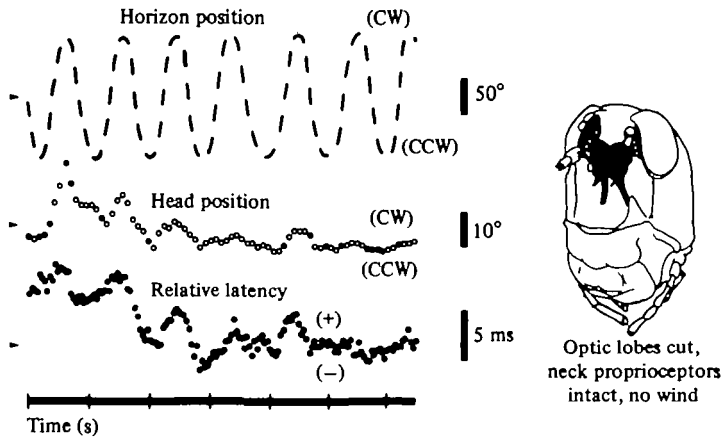


Fig. 7. Changes in relative latency of forewing first basalars (●) and in head position (○) in response to sinusoidal horizon rotation; compound eyes disconnected at optic lobes. Wind to the cephalic wind-receptive hairs was interrupted just before the beginning of the record.

irregular than in intact animals, thus causing larger scatter in relative latency, there was little if any effect on the delay from visual stimulus or the length of time that a response was maintained (stimuli were maintained for only about 3 s) (Fig. 5*b*). In this experiment and in others (not shown), there was a larger maximum shift in relative latency than was seen in intact animals. This was in spite of the fact that the head was fixed to the body, and no proprioceptors could be functioning.

Other experiments investigated whether changes in relative latency caused by ocellar stimuli (with the compound eyes ablated) can also be elicited without neck proprioception. In one animal, the sensory hairs of the cervical sclerites and nearby pronotal shield were cut off just beneath the cuticular surface with a fine scalpel and the optic lobes were sectioned. The responses of this animal are shown in Fig. 6*a*. Finally, the neck tissue (except for the gut and ventral nerve cord) of the same animal was sectioned and the head immobilized. In this highly dissected animal, flight was difficult to maintain. Nevertheless, Fig. 6*b* shows changes in relative latency in response to horizon rotation. For these data, the mean of relative latencies while the horizon was at the clockwise extreme of rotation ( $n = 49$ ) was significantly greater than the mean of relative latencies while the horizon was at the counterclockwise extreme ( $n = 48$ ) ( $P < 0.005$ , single-tailed test).

#### *Ocellar response with no wind*

An experiment was performed to investigate whether wind applied to the cephalic wind-receptive hairs was necessary for the ocelli to cause changes in relative latency.

An animal whose compound eyes had been disconnected was placed in the apparatus and induced to fly with the wind jet. Fig. 7 illustrates such an experiment in which the wind jet was extinguished just prior to the beginning of the record. This animal continued to fly steadily for about 2 min after the wind jet was turned off. The magnitudes of head motion and of changes in relative latency were increased for a few seconds after the wind was turned off, and then they gradually decreased to lower level than during continuous wind.

## DISCUSSION

It has long been known that the compound eyes of insects are important for steering during flight. However, the results presented here extend the findings of the previous report (Taylor, 1981) in suggesting that the ocelli of locusts can independently elicit co-ordinated behaviour which tends to stabilize flying animals to an artificial horizon.

Visual stimuli which would be expected to be highly relevant to a freely flying animal cause stereotyped changes in the timing of certain flight muscle spikes. These changes in timing serve as a reliable monitor of changes in the excitability of neurones which are involved in flight steering.

Finally, the current study indicates that in contrast to the conclusions of earlier studies (Mittelstaedt, 1950; L. Goodman, 1965), changes in the flight motor pattern produced by visual stimuli can be elicited in the absence of proprioceptive information concerning head position. Purely proprioceptive stimulation independently produces similar, though quantitatively smaller responses, and the two effects normally summate.

*Visual flight steering mechanisms*

The type of visual stimulus used here (a cylinder with half the circumference illuminated, half dark) was shown (L. Goodman, 1965; D. Wilson, 1968) to elicit a dorsal light reaction during flight. Locusts tethered so that they were free to roll during flight actively oriented their bodies so that their dorsal side faced the illuminated half of the cylinder.

Waldron (1967) showed that flying locusts with fixed body position responded by producing torque about the roll axis which would tend to realign their body with the horizon. Therefore, it is assumed here that displacement of the artificial horizon elicited changes in the flight pattern which would have caused a dorsal light reaction if the animals had been free to roll.

The changes in relative latency of forewing muscle spikes reported here agree with the results of other recent studies of locust flight steering. Zarnack & Möhl (1977) found that when locusts were subjected to a forced counterclockwise roll of the body, all the forewing direct depressor muscles fired earlier on the right and later on the left. In the present study, the analogous situation of clockwise horizon rotation caused the first basalar and tergo-sternal muscles of the forewing to fire earlier on the right side. (It is interesting to note that although Zarnack & Möhl illuminated their animals with a stationary overhead light, they stated that 'visual stimuli can probably be disregarded' (Zarnack & Möhl, 1977). The present study suggests that overhead illumination would on the contrary be significant.)

Other studies by Koch (1978) and Möhl & Zarnack (1978) suggested that earlier spiking of the forewing first basalar of one side (with respect to the peak of the upstroke) is consistently associated with earlier and greater pronation of that wing during the following downstroke.

Baker (1979*a, b*) and Cooter (1979) have indicated that yaw and lateral translational flight turns are always accompanied by a roll of the body which rotates the animal

that the side toward the turn rotates downwards (i.e. producing a banked turn similar to that of an aeroplane). During banked turns the relative latency of forewing first basalar and tergothoracic muscles was shifted so that muscles on the side which rolled downward fired earlier (Baker, 1979b).

Thus, the changes in wingstroke (Taylor, 1981) and changes in relative latency reported here are the changes which would be predicted if a dorsal light response was caused by the artificial horizon.

*Simplified model for mechanism of flight steering.* A simple model can predict changes in unilateral lift for a forewing which undergoes changes in muscle spike timing. A roll to one side is partially caused by changes in the relative latency between the homologous right and left first basalar muscles of the forewing. Changes in latency and frequency of firing of this *pronator-depressor* muscle cause an earlier and greater pronation during the downstroke on that side. Earlier and larger pronation would *reduce* lift on that side and perhaps increase thrust (depending on the activity of other muscles).

#### *Neural mechanisms*

The visual stimuli which affect the ocelli during steering responses seem to be well modelled by simple changes in ocellar illumination (Taylor, 1981; M. Wilson, 1978; Stange & Howard, 1979). One could reasonably expect all of the neural elements involved in conveying information from the ocelli to neurones involved in flight to function in a partly dissected animal, such as the preparations used to study intracellular responses of neurones to behaviourally relevant stimuli.

Simmons (1980) has already completed preliminary studies of a large identifiable neurone (O<sub>3</sub> of Williams, 1975 and C. Goodman, 1976) which appears to be part of a neural pathway from the median ocellus to flight motoneurones. Spikes in O<sub>3</sub> (in response to reduced illumination of the median ocellus) caused EPSPs in identified flight motoneurones. Simmons reasoned that a tonic barrage of EPSPs would cause increased firing of the motoneurones, and that the resulting changes in wing movement might compensate for an orientation error. Very recently, Rowell & Pearson (in preparation) have found that a large number of flight motoneurones (and also local interneurones of the thoracic ganglia) receive neural input from the ocelli; both excitatory and inhibitory synaptic potentials were recorded. These recent results suggest that visual stimuli may affect the timing of muscle spikes by affecting interneuronal elements of the central pattern generator as well as motoneurones.

Some of the present results suggest the possibility that neurones which roll the head and those of the flight system receive common input from visual neurones. Fig. 4 shows that in some cases relative latency is predicted better by head position than by the visual stimulus. However, Figs. 5 and 6 suggest that head motion and resultant proprioception are not the major cause of changes in relative latency. These results would be expected if visual 'steering' neurones project in parallel to neck motoneurones and to those of the flight system.

*The role of neck proprioception*

The results of Figs. 5 and 6, which show large visually elicited changes in relative latency after cervical proprioceptors were disabled, and the results of Taylor (1981), seem to conflict with those of earlier studies (Mittelstaedt, 1950; L. Goodman, 1965). However, it is probable that removal of proprioceptive hairs in the earlier studies did not eliminate visually evoked flight steering behaviour, but instead reduced its effect so that animals which were previously capable of visually stabilizing themselves (and the apparatus) were no longer able to do so. A hypothesis for the function of neck proprioception which takes these factors into account is stated below.

A sudden stepwise horizon displacement elicits head motion which quickly realigns the head with respect to the (displaced) horizon. Thus, the horizon displacement would be seen by the eyes as a sudden change in horizon position which is rapidly compensated (i.e. retinal slip would initially be large, but would be small after the compensatory head movement). On the other hand, the body of the animal, due to its larger mass, would require a longer time to be stabilized with respect to the horizon than would the head. The body would be only partly realigned to the horizon when the head motion is complete (this was actually the case for the locusts in L. Goodman's (1965) experiment). At this point there would be no additional visual stimulus perceived by the eyes, and the body would remain somewhat misaligned to the horizon. In intact animals, the body misalignment would be remedied by the neck proprioceptors; although there would be no visual signal from the eyes to realign the body, the cervical proprioceptors would signal misalignment of the body with the head, and steering behaviour would continue until the body as well as the head was realigned to the horizon. Thus, an important function of the neck proprioceptors may be to ensure that the animal's *body* as well as its head remains in equilibrium with the horizon.

Other hypotheses for the function of neck proprioception have been stated (Liske, 1977, 1979; Olberg, 1978). These authors proposed that neck proprioception of head position would *counteract* visual stimuli received by the eyes during optomotor head movement (Liske) or during 'voluntary' head turning, e.g. pursuit of prey (Olberg). Additional carefully designed experiments will be required in order to prove or disprove these various hypotheses.

*Wind and the ocellar response*

The results of Fig. 7 suggest that although continuous wind onto the cephalic wind hairs is not necessary for ocellar stimuli to elicit changes in relative latency or head position, wind affects the amplitude of responses caused by changes in ocellar illumination (see also Taylor, 1981). This would be expected if some of the neurones which are involved in conveying information from the ocelli to the motor output systems receive input from both the cephalic wind hairs and the ocelli. One neurone with these characteristics has been investigated by Simmons (1980).

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