

INHERENT ASYMMETRY AND REFLEX MODULATION OF THE LOCUST FLIGHT MOTOR PATTERN

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In this paper I will present new data and ideas on two interrelated questions regarding the nervous control of insect flight. The answers to these two questions may be important for understanding other aspects of insect behaviour as well. The two problems are: (1) How perfect is the motor score which is built into the thoracic ganglia? (2) How is this motor score modified when anatomical damage makes the inherent score inappropriate? In addition to providing partial answers to these questions the results show that the phenomenon of adaptation of locomotory patterns to limb loss, called *Plasticität* by Bethe (1930), does not imply that locomotion is coordinated purely by proprioceptive reflexes. Although Bethe did not hold this view, later authors have often interpreted his work in this sense. They show also that two categories of possible central organization of locomotory behaviour, motor scores or sensory templates (the 'motor tapes' and 'sensory tapes' of Hoyle, 1964), are not mutually exclusive.

MATERIALS AND METHODS

Adult male *Schistocerca gregaria*, supplied by Anti-Locust Research Centre, London, were used in all experiments.

Electrical recording from the muscles was carried out according to the techniques described by Wilson & Weis-Fogh (1962). The wind tunnel was modified by the addition of an approximately cylindrical section which surrounded the flying animal. This section was divided longitudinally into an illuminated white translucent half and a black half (see Fig. 1). The section and illuminator could be rotated together and provided a controllable simulated horizon and sky for the flying animal. The animal was held in the wind stream on a mounting which allowed at most only one degree of freedom, namely freedom to roll. Wind speed was set at about 3.5 m./sec. The long, fine electrode wires wrapped around the mounting bar when the animal did roll. About five revolutions were possible before the wires interfered with the motion. By counting the turns of the wires an estimate of intensity of rolling behaviour could be made after brief flights in total darkness.

Observations on free-flight behaviour were made under two sets of conditions. The first was in a large normally illuminated lecture hall in which animals often made flights lasting 1 min. or more. The second was in a smaller room (about 12 × 4 × 3 m.) which could be darkened or illuminated with infra-red light only. Even in white light

* A portion of this work was performed at the Department of Molecular Biology, University of California, Berkeley.

the animals usually quickly flew into the black walls of this smaller room. But a few seconds of flight, enough to demonstrate stability, were possible. An infra-red viewing device (DetectIRscope) was available for observing flight in this room.

Animals were also blinded by removal of the retina or by painting over the cornea. Neither technique seemed fully satisfactory, the former because the animals seemed abnormal in unexpected ways, the latter because one could not be certain of the efficacy of the cover. The wind-receptive hairs on the head were incapacitated by covering them with a low melting-point wax. The wax was brittle and could be broken away in order to restore the reflex function of the hairs. Several applications of the wax were possible before reflex function was obviously damaged.

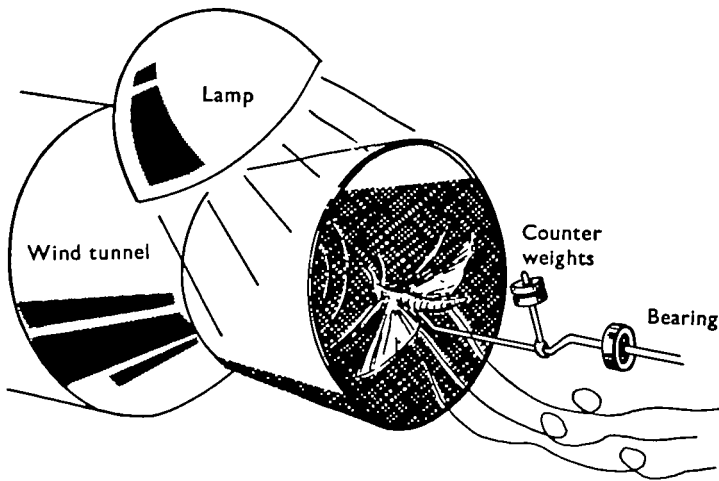


Fig. 1. Apparatus for observations on rolling behaviour. The lamp and horizon-simulating section of the wind tunnel can be rotated as a unit. After the animal is mounted, the balancing weight is adjusted so that there is no roll torque in any position when the animal is quiet. When the animal rolls the electrode wires twist around the roll bar, but four to five turns are possible before the wires limit the animal's ability to roll.

RESULTS

Asymmetrical motor command

In the early work on the flight motor command in locusts we had to discard the results of many experiments because we were equipped to study only straight flight, but the animals performed in an obviously asymmetrical fashion with respect to wing-stroke angle and posture of leg and abdomen (Wilson & Weis-Fogh, 1962). We did not try to explain these cases, but assumed them to be due to a stimulus-controlled turning tendency resulting from minor surgical damage or environmental cues. Animals showing strong asymmetry often persisted in doing so for 1 or 2 hr., when they were discarded.

If the locusts are flown on a mounting that allows roll, they usually fly with the dorsum upward. This posture depends upon exteroceptive input. Goodman (1965) showed that in the dark they might assume any orientation around the long axis. This is not too surprising, since locusts lack specialized gravity receptor organs, and when artificially suspended against gravity their natural aerodynamic stability cannot aid in orientation. Goodman also noticed that individual animals might spend considerable

time revolving about the long axis when deprived of visual cues. I have confirmed Goodman's conclusions and can add that the direction and speed of rotation of individual animals is not a random or even highly irregular variable as might be expected. Each animal shows some temporal variation in rolling tendency, but variation between individuals is much greater. One finds a whole spectrum of individual types, from animals with a strong tendency to counterclockwise rolling to those with clockwise rolling. Individuals with little rolling tendency are found, but in the dark even these do not orient in any regular way with respect to gravity. In the light all the

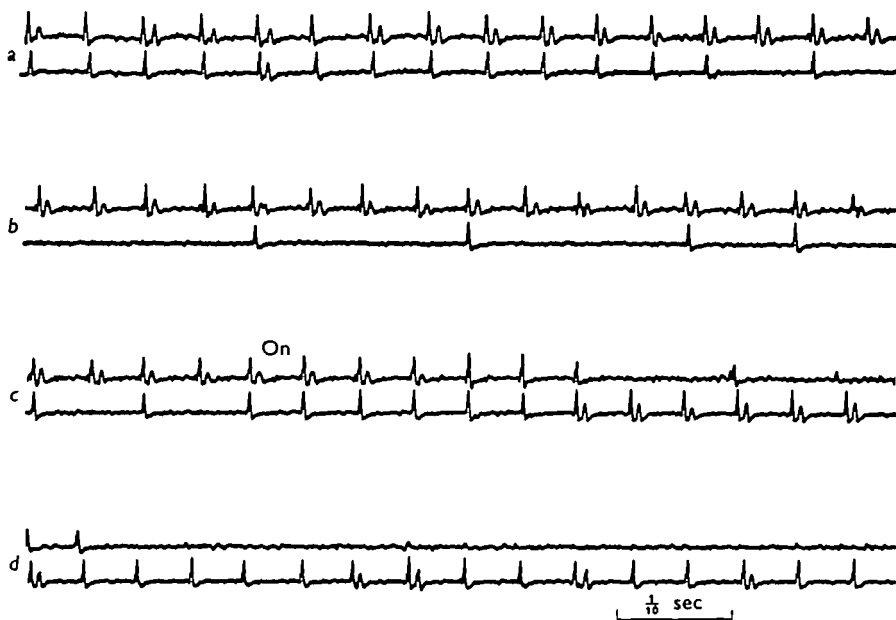


Fig. 2. Laterally biased motor output may occur in an intact animal in the dark. The right metathoracic subalar muscle (upper trace) is more active than the left. In line (c) the light was turned on and a strong, rapid compensatory reaction occurred which reversed the direction of roll.

animals orient stably with respect to the artificial horizon, no matter how the horizon is set. However, animals with an extreme rolling tendency may orient with a noticeable average error with respect to the horizon. A clockwise roller may hold a position with his frontal plane rotated 30° or more clockwise relative to the artificial horizon.

Electrical records from bilaterally homologous muscles show activity consistent with the biased behaviour (Fig. 2). Differences between the two sides are probably found in all the flight muscles, but I will report results on the metathoracic subalar muscles only. These muscles show the steadiest activity generally, and they seem to be good indicators of the functioning of the whole flight system.

Unequal levels of activity in these two muscles are found in two complementary circumstances. If the lights are on, but the roll bar is fixed so that the animal cannot roll (circumstance 1), in most animals, as expected, there are differences whenever the artificial horizon and the animal's frontal plane are not aligned. The subalar muscle on the side of the animal which is 'too low' is more active. Since the hind subalar muscle is a downstroke power muscle (Wilson & Weis-Fogh, 1962) its greater activity

indicates that lift on that side is greater. In a few preparations the output is asymmetrical even when the horizon and frontal plane are aligned and the light is on. This situation is comparable to that noted in the above mentioned study.

Many animals show asymmetrical motor discharge in the dark even if the roll bar is free (circumstance 2). Periodic observations show that the asymmetry can be quite persistent. In an extreme case, both units in one subalar muscle always fired twice per wing-stroke, while the other muscle had only one unit active once per wing-stroke most of the time. The same animal produced the same sort of pattern every time it was observed. Observations were made upon it several times a day for 5 days.

The rolling behaviour and asymmetrical motor discharge can occur in the dark and with the animal in any spatial orientation. It does not seem possible that they are due to asymmetrical exteroceptive sensation. That the asymmetrical motor pattern is not a function of differential interoception either will be shown in the next section.

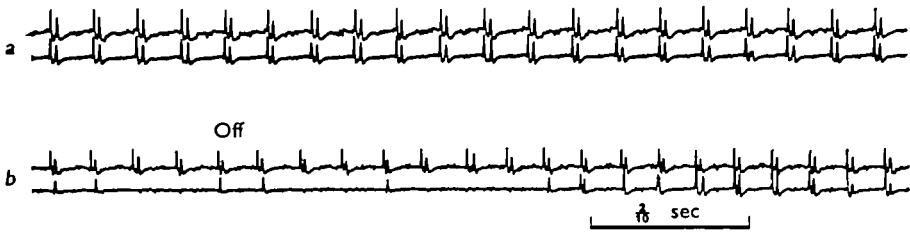


Fig. 3. Symmetrical output to the two hind subalar muscles may occur even after removing one of the hindwings. A symmetrically active animal was chosen. After the right hindwing was removed the record in line (a) was obtained. This sample is representative of minutes of record of flight in the dark. When the light was turned on the motor pattern changed so that the muscle of the intact wing was much less active than usual (b). Turning the light off (middle of (b)) resulted in a return to symmetrical output.

Motor patterns and gross anatomical asymmetry

Several years ago I attempted to demonstrate reflex modulation of the locust flight motor pattern after ablation of body parts, such as certain flight muscles or wing parts. The experiments were performed in the flight balance (in Weis-Fogh's Copenhagen laboratory) which gave the animal freedom in the lift and thrust directions and around the pitching axis. Surprising to me at the time was the observation that transecting one first basalar or subalar muscle of the forewing resulted in no conspicuous compensatory reaction in the other member of the antagonistic pair. I concluded that the flight system showed little of the motor plasticity seen in insect walking systems. Subsequently I have repeated the same type of experiment by recording from flight muscles of tethered animals before and after cutting off an entire wing. Little or no change in motor pattern in the muscles of the same or the remaining wings can be seen (Fig. 3). Similarly, if one wing is tied down so that it cannot flap (or if the fore- and hindwings are waxed together so that they *must* beat together, although this is abnormal (Wilson & Gettrup, 1963)) the motor pattern remains substantially unaltered. Surgical damage causing considerable anatomical asymmetry and considerably altered proprioceptive feedback does not result in conspicuous asymmetry of motor output pattern.

If, in an animal flying in the flight balance, removal of even a hindwing (which

normally produces 35% of the total aerodynamic power) does not result in a strongly altered motor output, then one would expect a strong turning force. If such animals are thrown in the air, on many trials they are completely unstable and tail-spin to the ground. In many other cases they fly successfully, however; and when flight is stable, it is also straight.* Removal of an entire wing does not result in circus movements in the range of flight behaviour over which compensation is possible at all. Flight is always slow, however, since a major power-producing member is missing. It seems that significant motor pattern adaptation would be required to allow straight flight after loss of one wing. Why was this not seen in the earlier electrical recordings? The answer lies in the fact that in the older experiments animals were always arranged so that asymmetrical forces could not be expressed as rotations of the whole animal; therefore, no exteroceptive error detection was possible.

If the animals are flown on the apparatus that allows free roll, then the result is different and reasonable. In the presence of exteroceptive cues such as the horizon there are changes in motor pattern when wings are ablated. If one hindwing is removed, and the animal flown in the dark, then the unchanged motor pattern virtually always results in rolling in the expected direction, that is, clockwise if the right wing is removed. With the lights on, the flight is usually stable, although there is often a significant error relative to the artificial horizon. With the lights on, compensatory changes in motor output pattern can be recorded (Fig. 3). Some animals are not able to compensate sufficiently and roll continuously even in the light. Their rate of roll is not constant, however; it slows over the range of angles which are near to normally stable positions. There are interesting but complex changes in motor pattern in the rolling animal associated with the fact that over part of the angular range it attempts to compensate by resisting the rolling tendency, while over other angles the roll force is temporarily exaggerated.

If an animal is rolling in the dark, either due to surgical or inherent neuro-motor asymmetry, and the horizon is illuminated, its motor pattern changes, but not in a simply predicted way (Figs. 2-4). There is nearly always a transient general increase in activity with the onset of illumination. Superimposed on this general transient are the roll compensation changes in motor pattern. These may be conspicuous within the first few wingbeats or may be considerably delayed. Sometimes they appear at first to be wrong in sign, only later to reverse. The delays and reversals are probably all correlated with its position at the time the light comes on. For example, depending on this position the animal may reverse its roll or accelerate it briefly.

Compensatory ability in free flight

Locusts with a few flight muscles cut or with one forewing or one hindwing incapacitated can often still fly quite well. It matters not whether the wing damage includes the main wing sense organs involved in flight (the campaniform sensilla Gettrup, 1966) or, in the case of the hindwing, whether the wing is cut off or merely tied down. (A forewing cannot be tied down without directly interfering with hindwing movement.) Not every flight is good. Tailspins or short flights veering rapidly

* It is fairly often true that, while the main flight path is straight, the body wobbles or oscillates noticeably in the yawing plane. The oscillation may be quite visible in slow flight and it has a frequency of about 3 cyc./sec. It appears that the correcting reflexes are underdamped under these conditions. This oscillation is the most rapid turning motion I have seen in free-flying *Schistocerca*.

laterally and downward are common. There seems to be a tendency toward all-or-nothingness. The same animal may make either good, but weak, flights, or tailspin badly. Even though the forewings have been thought to be the main control members, removal of a hindwing is more detrimental than removal of a forewing. This presumably is due to the fact that the hindwings produce much more power. Animals which were weak fliers before surgery often do not perform any stable flights afterwards. Very strong fliers may fly stably on all tests after one wing is removed.

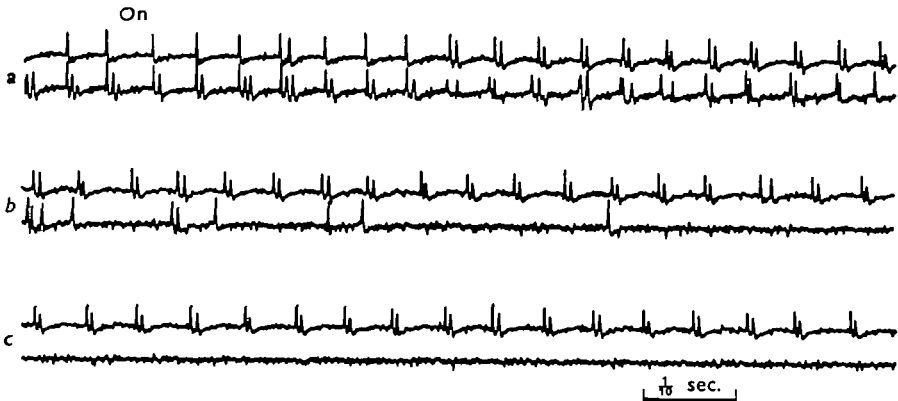


Fig. 4. A case opposite to that of Fig. 2. The light was turned on at the beginning of this sample of the record. Prior to that time the left hind subalar muscle had been more active than the right, and the animal was rolling clockwise. At the onset of illumination there was a relatively slow development of a compensating response.

Kamada & Kinoshita (1947) have reported that dragonflies can also fly after one wing is removed, and that their flight improves over the first several trials. I have noticed a few cases of apparent improvement in locusts, but these seem likely to be due only to thoracic warming associated with flight. In a tabulation of the first five flights of thirty animals with one wing removed I could find no correlation of flight ability with test number. Ten animals were observed for twenty consecutive flights, also without apparent improvement.

The sources of input which might aid in compensating for anatomical damage or central neuromotor asymmetry are the visual sense, wind direction sense, and proprioception. We have seen above that the visual input is effective in regulating orientation. The wind-direction sense, mediated by sensory hairs on the head, cannot by itself regulate orientation, since it can only report how the animal is moving (or rotating) relative to the air mass that it is in, and cannot report its orientation relative to the earth. However, if the animals have any aerodynamic stability of the sort built into aeroplanes and paper gliders, then this wind-sense feedback might be used only to help stop rapid turning away from the mechanically stable position. Or, if the animal were falling, the wind sense might give earth-related directional information. It is known that winds at an angle to the animal's long axis result in compensatory muscle actions (Dugard, 1967; Waldron, 1967). Proprioception might also help to correct transient deviations from normal orientation, but, judging from the results on the free-roll apparatus, it seems that proprioception probably cannot give a sufficient cue for long-term stable orientation.

It has been reported before that blind, but otherwise normal, locusts can fly stably (Haskell, 1960; Gettrup, 1966). This is easily confirmed. Animals with the head hairs covered can fly too. Ones with some of the wing proprioceptors damaged can also manage stable flight. If these sensory deprivations are made in combination, flight ability decreases more significantly. But I am not able to find a threshold condition under which stable flight is clearly impossible. Very strong fliers can tolerate much more damage to either the motor or sensory systems than I had expected.

If sensory and motor deprivations are combined, further disorder is noted. Animals which fly stably with one wing incapacitated may fail to do so under infra-red illumination, but not all do. Waxing over the wind-receptive head hairs may or may not prevent stable flight in animals lacking one wing. Within the set of my observations there are no sustained stable flights by animals with one hindwing removed and the head hairs covered while flying under infra-red illumination only. I have seen two very short well-oriented flights under these conditions, but I feel they may have been the fortuitous result of a particularly favourable launching attitude.

There seem to be no motor or sensory structures uniquely necessary for stable flight, and as one damages more and more of the whole flight control system, flight ability seems almost to disappear asymptotically.

DISCUSSION

What sources of input are involved in the regulation of stable flight in locusts? Only two kinds of cues seem possibly able to give precise enough information for orientation with respect to the earth. Visual input can and does aid in stability. The other likely reference system is gravity, but locusts do not have any special gravity receptors such as statocyst organs. They could measure differential effects of gravity on the body parts proprioceptively. For example, if the animal were tilted the head might twist relative to the thorax, or the abdomen might bend to the side. Goodman's (1965) and my results suggest that the locusts do not use such a source of input for orientation around the long axis, at least. Results on the roll bar are not adequate, however, to judge whether or not the animal has any ability to measure the direction of the gravitational force. Mounting the animal prevents the normal action of gravity on the whole body. If the locust were free to fall, then as it fell it would be subjected to a relative air current and, in principle, it could orient relative to that wind. This seems far-fetched as a possible explanation of the ability of blind animals to orient properly, since it would work only during vertical movement. The possibility of free fall would give a much more likely condition for stable orientation, however, which does not even depend upon sensory input. Under the normal action of gravitational force and air resistance many objects—and locusts are probably included in the category—have aerodynamic stability. The informational input for this kind of orientation in the locust comes via the genetic control of gross body structure. How much natural stability the locust has is unknown. In its gliding posture stability is good, as can be shown with dead specimens. Flapping probably results in lowered natural stability. However, natural stability plus correction of transients by means of wind direction or proprioceptive reflexes might account for stability in blind animals.

Some of the present results are relevant to the old argument about *Plasticität* and

the reflex control of locomotion. *Plasticität* in this context means the ability to make adaptive changes in the limb movements when one or more limbs are damaged (Bethe, 1930). The classic example is the one in which the mesothoracic legs of an insect are removed. Before the operation the animal usually walks on alternative tripods of support. After, he uses a limb pattern characteristic of normal tetrapods. No learning is involved. Proponents of the reflex hypothesis of locomotory control have used this phenomenon of *Plasticität* as one of their arguments (see Wilson (1966) for a review). The removal of one hindwing of a locust is a damage comparable in degree to the removal of one or two legs. The flying locust can make sufficient compensatory changes of its motor pattern to fully adapt to the damage, except that its power output capacity is reduced. Yet it has been shown that the locust flight control system consists in part of a non-reflex central nervous pattern generator (Wilson, 1961). This demonstration exemplifies the fact that the phenomenon of *Plasticität* is not incompatible with the presence of a central motor score.

Three significant differences between walking and flight should be mentioned, however. In walking the *Plasticität* consists of changes in the phasic pattern of leg movements as well as changes in amplitude. In the locust flight system there are no large changes in phase of the motor pattern to the different wings when one wing is removed. In the locust flight system the separate nervous control oscillators are very tightly coupled, whereas walking exhibits several features which suggest loose coupling between the control centres for each leg. Tight coupling in the flight system is necessary for mechanical reasons. A second difference between the walking and flight control systems is the nature of the most important inputs for compensatory changes in motor pattern. In the flight system exteroceptive sources seem to be necessary, whereas in walking, leg proprioception is probably sufficient. Thirdly, the flight and walking proprioceptive reflexes vary with respect to their speed of action. The leg reflexes are very fast and can affect a modulation of the leg movements cycle-by-cycle, whereas the known wing reflexes are all slow relative to the cycle duration of the wingbeat.

Related to the questions about reflexes and *Plasticität* is Hoyle's (1964) suggestion that there are two ways to build a command system into the central nervous system. One is to construct a 'motor tape' (I prefer the phrase *motor score*). That is, to provide the CNS with a neurone network which plays out a given pattern whenever it is sufficiently excited. The locust flight control system contains such a *motor score*. The other is to build in a 'sensory tape' (*sensory template*, Nottebohm, 1967) which contains information about the appropriate resulting feedback from a motor action. If the feedback does not match the template an adjustment of the output can be made. The same feedback could result from different outputs; therefore, the motor pattern is not fixed, but is instead capable of adaptation to changed conditions. The locust flight control system shows exactly the kind of motor adaptations due to sensory feedback that one expects of the *sensory template* control system. Hence finding adaptive motor phenomena does not show that there is no built-in *motor score*.

In the locust flight control system proprioceptive reflexes and exteroceptive inputs supplement and complement the information built into the CNS. Hence, even though the ganglia are pre-programmed to produce a nearly normal motor output pattern, that pattern can be modified to meet current needs. It seems to me that the CNS has

programmed into it through the genetic and developmental processes, nearly everything that it is possible for it to know before actual flight occurs. The sensory inputs supply only the genetically unanticipatable information such as wind direction and position of the horizon.

As we have seen, the central programme is not always perfect. It may produce asymmetrical output. Asymmetric behaviour has been noticed in some other insect behavioural control systems as well (Collett, 1967; Rowell, 1964; Wilson & Hoy, 1964; Chapple, 1966). Chapple showed that the leg nerve discharge in de-afferented bugs (*Oncopeltus*) can be asymmetrical, thus establishing the central origin of the bias. In the present study I have not worked with completely de-afferented preparations, but I have eliminated all reasonably likely sources of asymmetric input. The bias was shown not to be changed by surgical damage which is much greater than that associated with placing electrodes or mounting the animal. Since the direction and magnitude of the bias depends upon the individual animal, the experimental room and apparatus did not provide the relevant cues.

Exteroceptive reflexes are able to correct errors in the central motor score for locust flight. Thus the reflexes have a double role: to inform the CNS of peripheral conditions and to correct mistakes in its own programme.

Overall it appears that the flight control system is a very safe one, having a multiplicity of complementing mechanisms. It is centrally pre-programmed, perhaps to the fullest extent possible, but it also has a superimposed set of reflexes which can simultaneously relate the animal to its environment, compensate for bodily damage, and correct errors in its central programme. As a result it can tolerate a high degree of damage and still carry out a very demanding activity. No single component of the whole system seems to be necessary.

This discussion can be summarized in the following set of conclusions.

(1) For stable flight locusts utilize visual input (especially a horizon reaction) and probably their natural aerodynamic stability as primary references. Visual, wind direction, and proprioceptive senses all help to correct deviations away from the normal orientation.

(2) The locust flight control system exhibits Bethe's *Plasticität*. It also contains a reflex independent central nervous motor pattern generator. Therefore, the existence of *Plasticität* should not be used to argue that locomotion is primarily reflexly organized.

(3) The idealized concepts of *motor scores* and *sensory templates* as mechanisms of centrally built-in command systems are not mutually exclusive. The locust does contain the former, but it performs with the adaptive qualities attributable to the latter.

(4) Compensation for gross wing damage or other motor error is accomplished mainly through exteroceptive feedbacks in locust flight.

(5) Through genetic and developmental processes controlling the structure of the body and CNS much of the information necessary for flight control is built into the organism. In a sense the input has temporally remote origin. Sensory inputs supplement and complement the built-in information by providing current information about the body and environment which is not genetically anticipatable.

(6) The built-in motor score is not perfect. It often produces asymmetrical output. The exteroceptive reflexes help to compensate for built-in errors as well as provide information about the current state of the body and environment.

(7) Contrary to what might have been expected on the basis of earlier work, the locust flight control system is a very safe one in which almost any element can be removed without much impairing the whole.

A main theme of this paper, that apparently bilaterally symmetrical animals may have asymmetric behaviour, is not novel. There is an old and extensive, but apparently forgotten, literature on asymmetrical behaviour in structurally intact organisms of several phyla. One example is particularly worth noting. Schaeffer (1928) studied the spiralling tendency of blindfolded humans and concluded that 'The mechanism which produces the spiral path is not located in the locomotor organs, but in the central nervous system. . . ' and that straight walking, swimming, or driving depends upon orienting senses.

SUMMARY

1. Some aspects of the orientation and stability of flying locusts have been studied in free flight and with animals mounted so that they were free about the rolling axis only. Free flights were observed in white or infra-red light, with or without the wind-sensitive head hairs covered. Rolling behaviour was studied in light or darkness in front of a wind tunnel fitted with a movable simulated horizon while electrical recordings were made from flight control muscles. Flight muscles or single wings were removed in some experiments.

2. In the absence of visual feedback many intact animals roll consistently in one direction, and there is asymmetry in the motor output pattern. Removal of a wing causes a changed rolling torque in the absence of exteroceptive feedback.

3. In free flight, or in the presence of the illuminated simulated horizon, the centrally inherent or surgically induced asymmetrical behaviour is corrected by compensatory changes in the motor pattern.

4. Even though the locust flight control system contains a central motor score it exhibits the sort of adaptability called *Plasticität* in the case of insect walking. In locust flight the compensations depend mainly upon exteroceptive feedbacks.

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