

## LOCUSTS USE THE SAME BASIC MOTOR PATTERN IN SWIMMING AS IN JUMPING AND KICKING

BY HANS-JOACHIM PFLÜGER\* AND MALCOLM BURROWS

*Department of Zoology, University of Cambridge, Downing Street,  
Cambridge CB2 3EJ, England*

(Received 21 October 1977)

### SUMMARY

1. When on the surface of water, locusts (*Schistocerca* or *Locusta*) adopt a characteristic posture with the front legs pointing forwards and the middle and hind legs backwards.

2. Swimming is accomplished by the rapid extension of both hind tibiae. The legs move at the same time and not alternately as they do in walking. The swimming strokes are repeated at 2-3 Hz and give the locust a forward velocity of some 13 cm s<sup>-1</sup>.

3. The motor pattern that brings about the extension of the hind tibiae is described from extracellular recording in the tibial muscles during swimming. The tibia is first flexed and held flexed by spikes of the flexor motoneurones. Then the extensor motoneurones begin to spike so that there is a period when flexor and extensor motoneurones are both spiking. This leads to co-contraction of the muscles. The flexor motoneurones then stop, but the extensors continue, with the result that the tibia extends rapidly.

4. The same basic motor pattern for the movement of the tibia is used by the locust in jumping, kicking and swimming.

### INTRODUCTION

If a locust (*Schistocerca* or *Locusta*) is thrown into water it is able to swim well, by rapid and powerful extensions of its hind legs. Our interest in this behaviour was aroused by the apparent similarity of the movements of the hind tibiae during swimming and those used in kicking and jumping. It is the purpose of this paper to show by behavioural and electrophysiological analysis that the movements of the hind tibiae, used in the three diverse behaviours, are derived from the same basic motor pattern. It is shown in swimming, as in jumping and kicking (Heitler & Burrows, 1977*a, b*) that there is a co-contraction of extensor and flexor tibiae muscles, followed by a relaxation of the flexor, which allows the stored energy to produce the rapid movements of the tibiae.

At first sight, inducing swimming in what is a desert animal, might seem to be one of the more perverse delights of an experimentalist. In their normal habitat, however, locusts (usually *Locusta*) are sometimes forced to swim; marching bands of hoppers have been seen swimming across the river Danube in Rumania (Knechtel, 1938),

\* Present address: Fakultät für Biologie, Universität, Postfach 8640, D-4800 Bielefeld 1, Federal Republic of Germany.

across lakes in Russia (Nikol'skii, 1925) and across water channels in Ethiopia (Jannone, 1940), Persia and Kenya (Kennedy, 1945), and East Africa (Johnston & Buxton, 1949). There are also grasshoppers from South America (*Marellia remipes* and *Paulinia acuminata*) which live on broad floating leaves of aquatic plants and thus can be expected to occasionally fall into the water. The tibiae and tarsi of their hind legs are oar-like, enabling them to swim on the surface of the water, walk on the ground under water or climb upon submerged water plants (Carbonell, 1959). The East African Gryllid *Tridactylus madecassus*, when disturbed, jumps on to the water surface (Wickler, 1966) where it can swim actively (Miller, 1972). Mantids, *Sphodromantis lineola*, will also swim in the laboratory (Miller, 1972). The grasshopper *Melanoplus differentialis* swims well and the pattern of leg movements has been described (Franklin, Jander & Ele, 1977).

The ability of locusts to swim must indicate an evolutionary advantage and field observations give some indication of what this might be. In the Danube delta *Locusta migratoria* breeds on sandy islands, so that when all the grass is eaten, they are forced to find new feeding grounds. As the hoppers cannot fly the only way is to swim, but this involves a considerable journey in which heavy losses are likely. Knechtel (1938) saw one hopper band being carried 12 km downstream before reaching the other river bank. In Russia there are often fires in their natural habitat and escape can be effected only by entering lakes, where 5th-instar hoppers have survived for 13–28 h (Nikol'skii, 1925). Only one observation casts doubt on the ability of the locust to swim in what must have been their ultimate test (Exodus, x. 19): 'And the Lord turned a mighty strong west wind which took away the locusts and cast them into the Red Sea: there remained not one locust in all the coasts of Egypt'.

#### MATERIALS AND METHODS

Behavioural observations were made on 1st–5th instar and adult *Schistocerca gregaria* renamed *Schistocerca americana gregaria* by Dirsh (1974) of either sex, and on adult, male and female *Locusta migratoria*. High speed motion pictures, using a Hycam camera operating at 500 frames/s, were made of sustained swimming sequences of *Schistocerca* in a water container measuring 420 × 720 mm and 70 mm deep. Video-tape recordings were also made.

All electrophysiological recordings were made on *Schistocerca*. The electrical activity of the flexor and extensor tibiae muscles of a hind leg during swimming was recorded with pairs of 50  $\mu$ m copper wires, insulated but for the tips. The slow extensor tibiae motoneurone could be distinguished from the fast motoneurone by an additional pair of electrodes placed distally in the femur. The three pairs of wires were looped together and attached to a nylon rod glued with Scutan (Espe, West Germany) to the pronotum. With this arrangement of electrodes the locust could walk around freely, kick and jump, or could be held by the nylon rod upon the surface of the water to permit tethered swimming. Holding the locust rather than allowing it to swim freely thwarted the frequent attempts made by the locust to rid itself of its harness. Movements of a hind tibia were monitored by a 50  $\mu$ m wire which projected at right angles from the proximal end of the tibia, and which carried a 40 kHz 5 V peak-to-peak sine-wave signal. The leg moved between two submerged sensors 40 mm apart.

which gave a d.c. voltage proportional to the angular movement (Sandeman, 1968). All recordings were stored on FM magnetic tape for later analysis. All experiments were performed at an air and water temperature of 20–22 °C.

## RESULTS

### *Behavioural description of swimming*

Ten larval (1st instar–5th instar) and 30 adult *Schistocerca* were observed. *Locusta* was also observed but no differences from *Schistocerca* were found. When thrown into the water the initial behaviour of the locust takes four possible forms; first, all the legs make struggling or searching movements, each unsuccessfully attempting to grasp something; second, the legs are motionless and the insect merely floats; third, both pairs of wings are opened in a vain attempt to fly from the surface of the water; fourth, active swimming movements begin at once. After variable periods of time *all* the locusts begin to swim in a way that appears directed towards the nearest edge of the water container.

First and second instar locusts, which are no more than a few mm long, make co-ordinated swimming movements but the rapid extensions of their hind legs engender no forward progress against the surface tension of the water. When in their third instar and about 15 mm long, forward progress becomes possible. In one adult, the forward velocity of swimming was  $10.7 \text{ cm s}^{-1}$  140 ms after the first stroke and rose to  $13.8 \text{ cm s}^{-1}$  after the second. The attitude that the body adopts in the water is variable; the usual posture is for approximately half the height of thorax to be below the surface of the water. Successful swimming can nevertheless be accomplished even when the body is completely submerged, or rolled partially over on its long axis. In the usual posture, the abdominal spiracles are below the surface of the water and only those of the meso- and meta-thorax could permit gaseous exchange.

### *Posture of the legs*

When the locust is floating upon the water, its legs assume a characteristic posture (Fig. 1). *Front legs*: the anterior angle between the femur and the long axis of the body, as viewed from above, is small ( $50^\circ$ ), and the femoral tibial joint is partially flexed. The tibia is thus held protracted, almost parallel to the long axis of the body and with the tibia and the tarsus pointing forward. *Middle legs*: the angle between the femur and the body is large ( $100^\circ$ ) so that the whole leg is retracted. The femoral tibial joint is fully extended ( $170^\circ$ ). *Hind legs*: the angle between the femur and the body is large ( $100^\circ$ ) so that the femur is almost parallel with the long axis of the body. The femoral tibial joint can be either flexed or extended; it is movements of this joint that provide the major forward thrust in swimming. The posture is very similar to the landing posture adopted by locusts at the end of flight (Cooter, 1973).

### *The swimming stroke*

We define a swimming stroke of the hind legs as follows. The tibiae are first fully flexed and then they are rapidly extended through the water (Fig. 1). The whole cycle of movement is then repeated, typically at frequencies of 2–3 Hz. The duration of the flexion phase of the movement is more variable than the extension phase; the mean

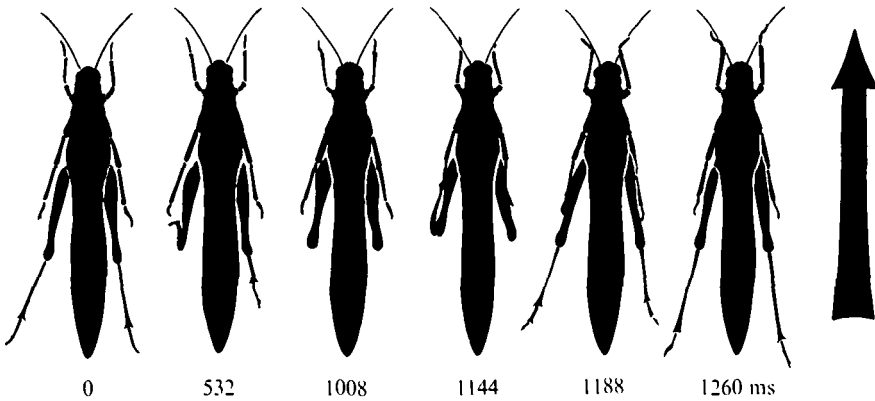


Fig. 1. Swimming in *Schistocerca* viewed from above. The tracings were made from film taken at 500 frames/s and show one complete swimming cycle lasting 1260 ms. The numbers indicate the time in ms between frames. The swimming was performed on the surface of the water, its direction being indicated by the arrow.

duration of flexion, as measured from 18 cycles on video-tape, is  $305.6 \pm 69.1$  ms (range 180–500 ms), that of extension, as measured from 31 cycles on high speed film, is  $50.5 \pm 15.4$  ms (range 39–90 ms). If the five long lasting extensions that started from incomplete flexions are excluded, the mean value of extension falls to  $44.9 \pm 7.9$  ms (range 30–56 ms). If the femoral–tibial joint is not fully flexed, reaching an angle of only  $20^\circ$ , then the extension that follows is not as rapid. During one sustained swimming sequence the durations of extensions may vary, but not in a predictable way: for example the first stroke may last 42 ms, the sixth 78 ms; in another, the duration may be quite constant with the first stroke lasting 45 ms, the twelfth 48 ms, while in another, the duration may decrease with the first stroke lasting 45 ms, the eighth 30 ms.

#### *Co-ordination of the legs during swimming*

Both hind legs normally participate in swimming: if only one hind leg is used repeatedly, the locust moves in a curve, there being no compensatory movements by the other legs. The two hind legs may move together, they may alternate or one leg may sometimes be used repeatedly for a few cycles (Figs. 1, 3). In 482 swimming strokes of eight locusts, 261 involved the use of one leg (114 the left, 107 the right) (Fig. 2a). In all strong swimming sequences the two hind legs were used together.

Only a few locusts consistently move their middle legs in swimming. When they do, the femoral tibial joint remains extended at about  $170^\circ$  with, perhaps, a slight flexion during protraction. The whole limb is thus protracted and retracted by a slight rotation of the coxa about the thorax, so that it acts like an oar (Fig. 3). Both middle legs usually move together but can provide little in the way of thrust. Their role is presumably to provide lateral stability to the body during the powerful thrusting of the hind legs.

The forward directed posture of the front legs, seen when the locust is floating, is maintained by most locusts during swimming (Figs. 1, 3). Occasionally there may be paddle-like movements similar to those of the middle legs.

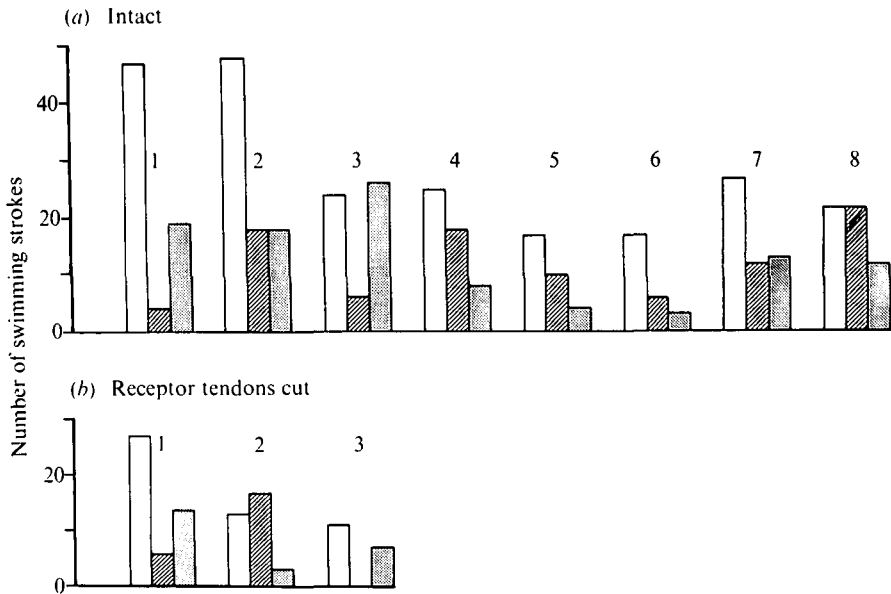


Fig. 2. Modes of co-ordination of the hind legs of *Schistocerca* during swimming. The open bars indicate that the two hind legs move together, the hatched bars that the left hind leg moves alone, and the stippled bars the right hind leg. (a) Eight intact locusts, in six of which there is a preference for the use of both hind legs together. (b) The receptor tendons of the chordotonal organs in both hind legs were cut but there is no effect upon the co-ordination.

A locust that is swimming by the use of all its legs moves them in a sequence that begins with the protraction of the front legs and ends with protraction of the hind legs. The onset of protraction in the two hind legs may vary but there is no consistent tendency for one leg to lead the other. The sequence of leg movements is quite different from that in walking where legs of one segment alternate, thereby setting up the typical alternating tripod gait. In swimming the legs of a segment usually move together.

To gain some insight into the mechanism of limb co-ordination during swimming, two surgical procedures were used. Decerebration does not abolish co-ordinated swimming movements, but the locust is now more likely to struggle than to perform powerful and synchronized movements of the hind legs. The characteristic posture is adopted when floating on water. Ablation of the chordotonal organ at the femoral tibial joint is reported to prevent jumping (Bässler, 1968) but not kicking (Heitler & Burrows, 1977*b*). To test whether ablation of this receptor could disrupt swimming, the receptor tendon was cut in both hind legs of three locusts. No differences were observed between the intact (Fig. 2*a*) or operated (Fig. 2*b*) locusts. In 98 swimming strokes of the operated locusts, 51 were by the two hind legs together and 47 by one leg alone (23 left and 24 right). In all the operated locusts swimming was as effective as in the normal ones.

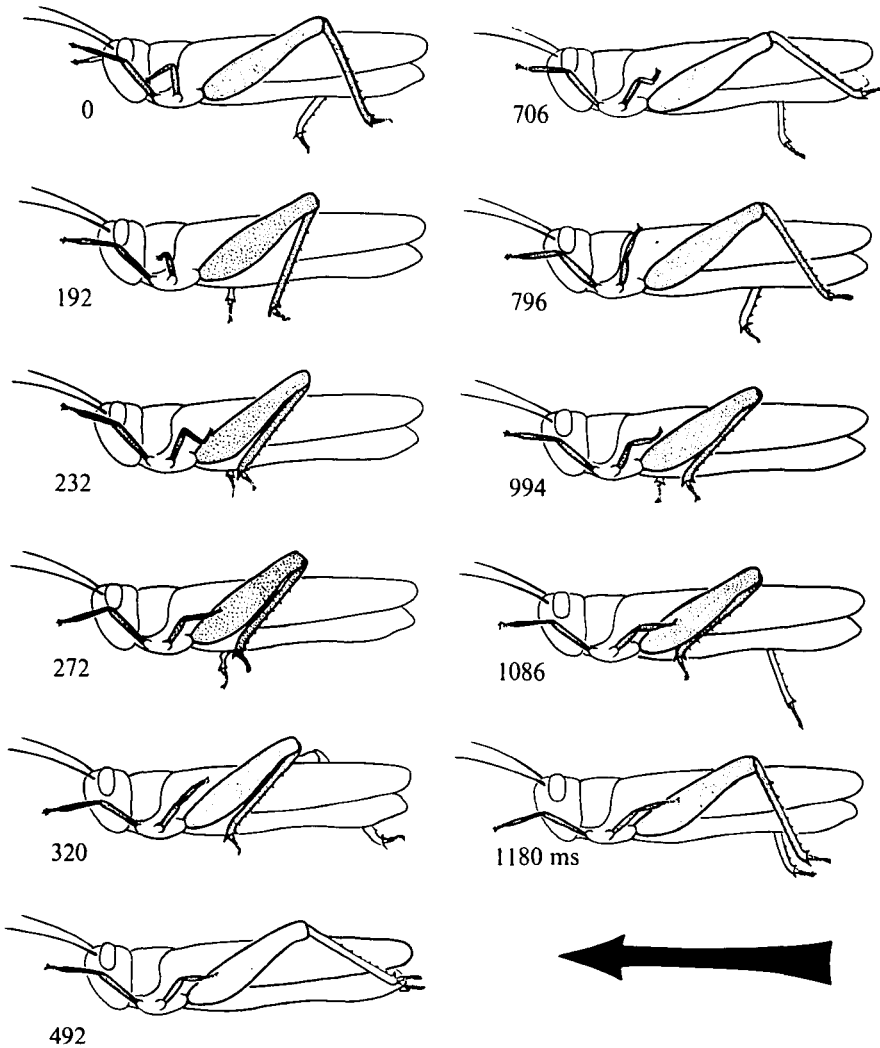


Fig. 3. Swimming in *Schistocerca* viewed from the side. This locust swam completely below the surface of the water which lessened the diffraction caused by the movements and thus allowed easier viewing of the individual legs. The tracings were selected from film taken at 500 frames/s and show two cycles of swimming lasting a total of 1180 ms. The frames are arranged in two vertical columns and the numbers indicate the time in ms. between each. The arrow indicates the direction of swimming.

#### *The motor pattern of the swimming stroke*

All recordings were made from the flexor and extensor tibiae muscles of the hind legs of *Schistocerca*. The sequence of activity that occurs in free (Fig. 4a) and tethered (Fig. 4b) swimming is remarkably similar in all swims by all adult locusts observed and takes the following general form. The tibia is flexed by the action of flexor motoneurones, which evoke facilitating synaptic potentials in the muscle. Presumed fast flexor motoneurones which evoke large non-facilitating synaptic potentials, are then recruited. The slow (SETi) and then the fast (FETi) extensor motoneurones

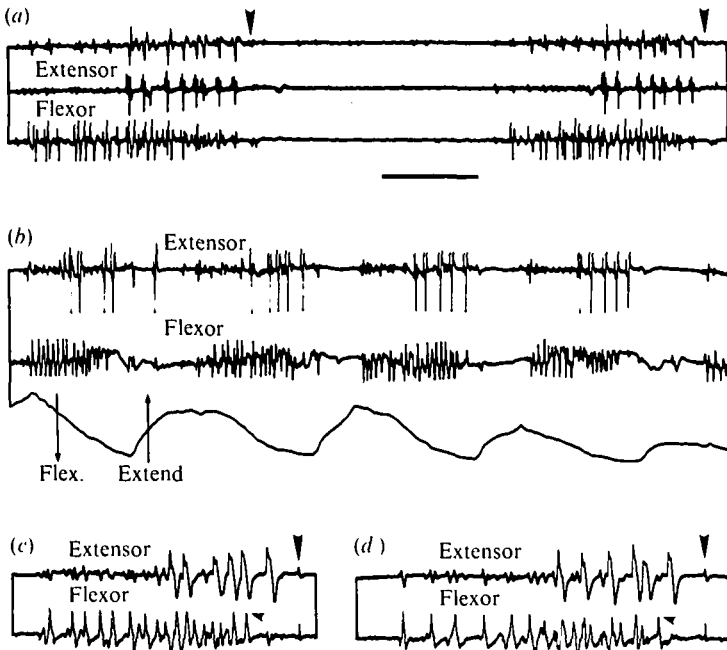


Fig. 4. Electrical activity in the extensor and flexor tibiae muscles of a hind leg during swimming. (a) Free swimming: flexor activity starts first (lower trace) to be followed by the slow extensor (upper trace) and then the fast extensor (middle trace). (b) Tethered swimming, in which the movements of the tibia are also monitored. (c, d) Expanded portions of two swimming cycles to show the cessation of flexor activity (small arrows) before the end of extensor activity and the commencement of the movement (vertical arrows). Time scale (a, b) 200 ms; (c, d) 100 ms.

begin to spike, so that there is a period when the flexor and extensor motoneurons are spiking at the same time. The flexor motoneurons then stop spiking but the extensor motoneurons continue, and rapid extension of the tibia follows.

#### *Flexor muscle*

The first action of the flexor muscle is to close the tibia tightly about the femur and thereby to engage the lock that exists at the femoral-tibial joint (Heitler, 1974). This gives the smaller flexor muscle an added mechanical advantage over the larger extensor muscle. The small potentials in the flexor muscle begin some 200 ms before the first FETi spike, and the large potentials appear some 110 ms later. During the flexion, there are always several motoneurons active and one in particular can often be distinguished by the height of its muscle potential (Fig. 4). The mean duration of the burst of flexor activity is  $233.2 \pm 115.3$  ms ( $n = 225$ ). The flexor activity always stops before the last FETi spike (Fig. 4c, d), the average time difference being  $57.1 \pm 23.0$  ms ( $n = 53$ ). There is thus a period of some 80 ms in which extensor and flexor motoneurons spike together.

*Extensor muscle*

There are only two excitatory motoneurons innervating the extensor muscle, but there is such an enormous discrepancy in the size of their synaptic potentials as recorded extracellularly that the large (from the fast motoneurone) usually swamps the small (from the slow). The SETi starts to spike first but the number of its spikes during one swimming cycle is difficult to determine. The better recordings reveal at least six spikes before they are masked by spikes of the FETi (Fig. 4*a*). In tethered swimming the FETi motoneurone usually spikes four times (s.e. =  $\pm 1.5$ , range 1–8,  $n = 219$ ) per stroke (Fig. 4*b*). In some free swimming sequences the number of FETi spikes is often higher (Fig. 4*a*). The mean duration of the burst of FETi spikes is  $106.7 \pm 56.4$  ms ( $n = 292$ ). The first FETi spike occurs about 90 ms (average  $92.1 \pm 51.9$  ms,  $n = 95$ ) after the first large flexor spike. The average frequency attained during the burst is 33 Hz and the highest 52.6 Hz. The average interval is  $30.1 \pm 9.7$  ms ( $n = 57$ ). Occasionally there may be an acceleration in the frequency throughout the burst but usually comparison of the first with the last interval reveals no significant difference.

In most swimming strokes, the last FETi spike occurs before the movement has been initiated, but in some it may occur after the movement (Fig. 4*b*). In recordings where the movement transducer was not used, the extension is marked by a movement artifact on the recordings from the muscles. The average time difference between the last FETi spike and the movement is  $24.1 \pm 34.8$  ms ( $n = 129$ ).

*Motor activity of both hind legs*

In each leg the number of FETi spikes is different even when both legs are moved at about the same time (Fig. 5*a*). The bursts of spikes may occur at the same time or there may be a considerable time difference, so that the asynchrony of the resulting tibial movements is visible to the eye (Fig. 5*c*). Occasionally one leg does not move and there is no electrical activity in the muscles (Fig. 5*b, c*). We have not recorded abortive activity in the muscles during swimming like that known to occur during jumping (Godden, 1975; Heitler & Burrows, 1977*a*). At other times a single FETi spike is recorded in one leg accompanying a full burst in the other (Fig. 5*b*). The leg is then slowly and weakly extended from an already partially extended position.

In the majority of swimming strokes the speed of flexion is the same on the two sides. Sometimes, and usually at the start of a swimming sequence, or during sporadic strokes, there may be a very slow flexion of one tibia and a more rapid flexion of the other which is followed by extension of both tibiae at about the same time (Fig. 5*d*).

## DISCUSSION

The results reveal that a locust that has never previously encountered water, has a very distinctive pattern of leg movements which enable it to swim successfully. The pattern is different from that used in walking in as much as the legs of one segment are moved together and not alternately. All locusts of any age that we tested were able to swim. Other land-dwelling insects that have been tested for their ability to swim



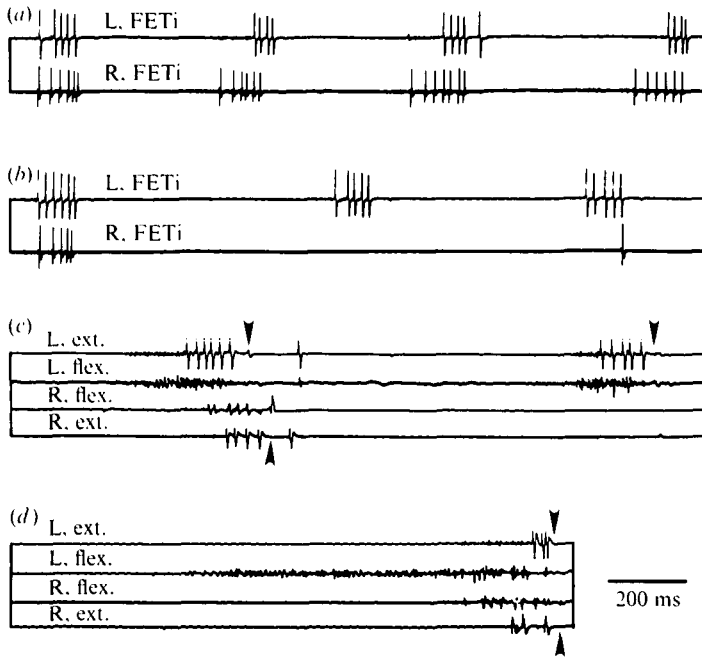


Fig. 5. The electrical activity in the femora of both hind legs during swimming. (a) The bursts of FETi spikes in the left and right legs are similar and the legs move at about the same time. (b) The legs first move together and then the left leg moves alone. This is followed by a weak extension of the right leg and a rapid movement of the left leg. (c, d) Flexor and extensor muscles of both legs. (c) There is first a movement of both legs together, then the left leg alone moves. (d) A slow flexion of the left leg is accompanied by a rapid flexion of the right, whereupon both legs extend at about the same time. Arrows in (c, d) indicate tibial extension.

are few. Mantids can swim well (Miller, 1972). The grasshopper *Melanoplus* has a swimming pattern very similar to that of *Schistocerca* (Franklin *et al.* 1977). We have tested several species of cockroaches and two species of crickets (Pflüger & Burrows, unpublished). *Periplaneta americana*, for example showed either a distinct swimming pattern in which the two legs of one segment moved together, or struggling movements that result in little forward progress. Crickets, *Gryllus campestris* or *Gryllus domesticus* by contrast, are excellent swimmers using all three pairs of legs in a stereotyped pattern.

Two questions about locust swimming remain unresolved. *First*, what triggers the adoption of the swimming posture (Fig. 1) and the commencement of swimming? The most obvious candidates are receptors such as those on the tarsi or abdomen that detect the water. While some sort of sensory signalling must be involved, some observations are difficult to reconcile with a simple picture. Locusts lifted from the water into the air will often not fly but continue for a short period with swimming movements of the hind legs. One locust that was held over the water so that only its tarsi and abdomen touched the water, showed vigorous swimming movements when raised clear of the water. Perhaps the persistent wetness of the tarsi and the reduction

of load upon them was a sufficient stimulus. We will show in the following paper (Pflüger & Burrows, 1978) that, after swimming, the locust grooms itself to rid its body of water.

*Second*, how is the locust able to breathe during swimming? Normally the pro- and meso-thoracic spiracles are above water but whether gaseous exchange through these alone is sufficient to explain the long survival in water observed by Nikol'skii (1925) seems doubtful. When all spiracles are completely submerged any explanation must involve either a role for the tracheae as a physical lung, or the synchronization of ventilation and leg movements. Since the thrust of the hind legs pushes the head and anterior part of the thorax above water at each stroke, this might allow sufficient time for the anterior spiracles to open.

#### *Comparison of swimming, kicking and jumping*

The most striking feature of swimming is the similarity in the movements of the tibiae of the hind legs with those used in kicking and jumping. From behavioural observations of leg movements, Franklin *et al.* (1977) concluded that there must be common features in the motor patterns underlying swimming and jumping. The available information on the three behaviours is summarized in Table 1. A revealing demonstration of the similarity in the underlying motor patterns is to record from one locust performing all three movements (Fig. 6). We describe only the typical performance of each behaviour. The jumps were elicited by movements of a hand in the visual field of the locust (Fig. 6*a, b*); the kick, from a standing position, was elicited by pricking the abdomen with a sharp pin (Fig. 6*c*); the swimming was tethered (Fig. 6*d*). The common features are the following. *First*, the motoneurones used are the same: the FETi, not used in walking, is active in each; many flexor motoneurones are active, but one, identified by the amplitude of its synaptic potential in the muscle, is active in all behaviours. *Second*, the sequence of action of the motoneurones is the same. The flexor motoneurones are always active first ensuring that the tibia is tightly flexed about the femur. The flexion is an essential prerequisite for a jump because there could not otherwise be a co-contraction of sufficient duration to achieve the energy required. If the leg is not fully flexed, weak swimming strokes or half-hearted kicks can still occur. Preventing full flexion of the leg with a mechanical stop does not prevent swimming (Franklin *et al.* 1977). Next the extensor motoneurones start to spike so that there is a period of co-contraction of the flexor and extensor muscles. The flexor muscles then relax while the extensor motoneurones continue to spike overcoming the lock at the femoral tibial joint (Heitler, 1974). The energy stored during the period of co-contraction is rapidly converted into the extension of the tibia. *Third*, in all three behaviours the hind legs may move together but the synchronization of the two is not absolute.

Jumping and kicking are very similar and differ only in degree as far as the movement of the tibiae is concerned. This is revealed quite clearly in the myograms (Fig. 6). Both jumps and kicks can vary in strength and this is reflected in the duration and frequency of the muscle activity, but not in its overall pattern. The greater force necessary in kicks and jumps is obtained by lengthening the period of co-contraction and increasing the number and frequency of FETi spikes. A typical duration for the

Table 1. Comparison of available data on jumping, kicking and swimming

The data are taken from this paper unless suffixed by a letter in parentheses indicating that they are from the following papers: (a) Heitler & Burrows (1977a); (b) Godden (1975); (c) Brown (1967); (d) Bennet-Clark (1975).

	Swimming		Kicking		Jumping	
	Flexor	Extensor	Flexor	Extensor	Flexor	Extensor
Number of spikes	Several unidentified units active	FETi 4.0 ± 1.5 (range: 1-8)	Fast: ~ 30 (a) Slow: ~ 100 (a)	FETi 19.1 ± 3.9 (a) (range: 13-25) 20	Several unidentified units active	FETi 10-20 (b) 17.2 ± 5.9 (range: 11-26)
Spike frequency (Hz). Inter-spike intervals (ms) and standard error in brackets	—	33.2 (30.1 ± 9.7)	Fast: ~ 60 (a) Slow: ~ 200 (a)	60-100 (a) First five spikes: 18.9 (53 ± 9.7) Last five spikes: 142.9 (7 ± 2.9)	—	First five spikes: 25.9 (38 ± 22.2) Last five spikes: 115.4 (8.7 ± 2.6)
Burst duration (ms)	233.2 ± 115.3 (range: 70-940)	106.7 ± 56.4 (range: 5-325)	Fast: 550 ± 50 (a) Slow: 615 ± 21.2 (a) 270 (b) 660	545.5 ± 170.5 (a) (range: 300-950) 250 (b) 600	409.9 ± 81.5 (range: 250-510)	~ 300 (b) 385.2 ± 116.2 (range: 210-690)
Delay (ms) between start of flexor and extensor bursts	169.5 ± 12.3 (first small flexor spike - first FETi spike) 92.1 ± 51.9 (first large flexor spike - first FETi spike)	57.1 ± 23.0	75 (first large flexor spike - first FETi spike)	75 (first large flexor spike - first FETi spike)	80 (first large flexor spike - first FETi spike)	80 (first large flexor spike - first FETi spike)
Delay (ms) between end of flexor and start of extensor burst	~ 80 (range: 20-130)	57.1 ± 23.0	30-60 (a) 20	30-60 (a) 20	34.7 ± 9.4	34.7 ± 9.4
Duration of co-contraction (ms)	—	—	~ 500	~ 500	~ 300 (range: 200-470)	~ 300 (range: 200-470)
Duration of tibial movement (ms)	305.6 ± 69.1 (range: 180-500)	50.5 ± 15.4 (range: 30-90) Without long duration: 44.9 ± 7.9 (range: 30-56)	—	—	—	Extension ~ 20 (c) 25-30 (d)

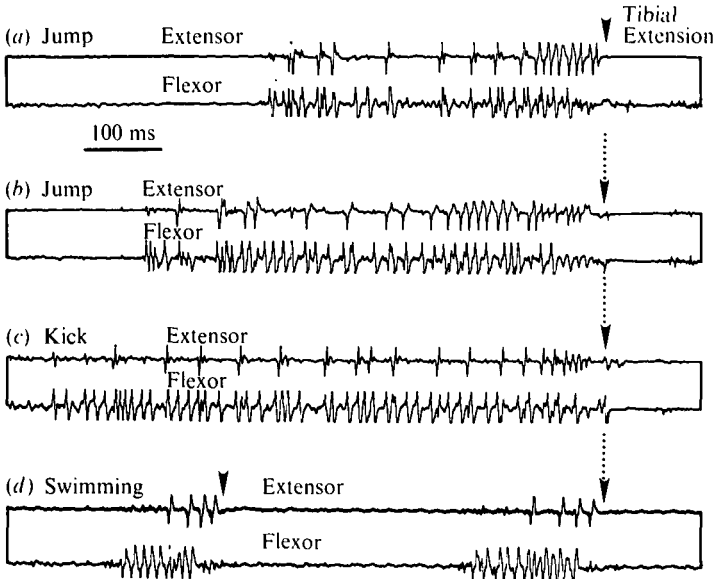


Fig. 6. Jumping, kicking and swimming. All recordings were made from the same locust within 1 h. (a, b) Jumps in response to visual stimuli. (c) A kick from the standing position in response to an abdominal prick. (d) Two cycles of tethered swimming. All records are aligned vertically at the moment of rapid tibial extension (vertical arrows). See text for detailed description.

co-contraction phase in a kick or in a jump is 500 ms, but in a swim is only 80 ms. In a kick or a jump there may be 10–20 FETi spikes which can sometimes reach a final instantaneous frequency of 200 Hz just before the movement. This is an extremely high frequency for a motoneurone that can produce a rapid and powerful muscle twitch even with a single spike. The high frequency of spikes leads to a diminution in the height of the muscle potentials, due either to antifacilitation, or movement of the wire electrodes. These high frequencies are never seen in a swimming locust. Typically in swimming there are 1–8 spikes which occur at a maximum frequency of 53 Hz. There is little difference in the delay between the end of flexor activity and the start of the tibial extension in any of the three behaviours. In jumping and kicking (Fig. 6a, b, c) a motor unit is recorded in the flexor muscle at the end of the spiking of the excitatory flexor motoneurons and before the tibial movement. This unit could be an inhibitory motoneurone, for it occurs at the time that these neurones are known from intracellular recordings to be active (Heitler & Burrows, 1977a). The same electrode placement during swimming fails to give convincing evidence that this unit is active.

The longer duration of the co-contraction before a jump leads to a more rapid movement of the tibia: extension is complete in 20–30 ms (Brown, 1967; Bennet-Clark, 1975). In swimming the extension lasts about 50 ms, perhaps being prolonged as well by the viscosity of the water. There are different requirements in the two behaviours. Jumping usually occurs just once so that the locust can escape, and a single kick usually suffices to warn-off an adversary; it is rare to observe more than a few repeated jumps or kicks. Swimming, by contrast, requires that the rapid extensions be repeated at 3–4 Hz for many cycles. We have often observed 14–20 strokes in one sequence.

It should be emphasized that there is not an absolute distinction between the movements of the hind tibiae in swimming, kicking and jumping. Rather the movements represent a spectrum in which a powerful jump represents one extreme and a weak kick or swimming stroke the other. For example, there may be little difference in the motor pattern underlying a weak kick and a powerful swimming stroke. The results of this paper suggest that each piece of behaviour may not require a separate motor pattern, but instead may be built from pre-existing patterns used for other movements. Our contention is that swimming, jumping and kicking all result from the same basic motor pattern. The complex movements of, for example, grasshoppers during courtship (Elsner, 1973), or the eclosion movements of crickets (Carlson & Bentley, 1977) are also built from the juxtaposition of pre-existing patterns used in other movements. What we need now to determine are the mechanisms that select and modify the basic patterns for the different behaviours.

This work was supported by S.R.C. and Nuffield Foundation grants to M.B. H.-J.P. was a European Science Exchange Programme Fellow supported by a grant from the D.F.G. (Pf 128/1).

## REFERENCES

- BÄSSLER, U. (1968). Zur Steuerung des Springens bei der Wanderheuschrecke, *Schistocerca gregaria*. *Kybernetik* **4**, 112.
- BENNET-CLARK, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. exp. Biol.* **63**, 58-83.
- BROWN, R. H. J. (1967). The mechanism of locust jumping. *Nature, Lond.* **214**, 939.
- CARBONELL, C. S. (1959). The external anatomy of the South American semiaquatic grasshopper *Marellia remipes* Uvarov (Acridoidea, Pauliniidae). *Smithson. misc. Collns* **137**, 61-97.
- CARLSON, J. R. & BENTLEY, D. (1977). Ecdysis: neural orchestration of a complex behavioural performance. *Science, N.Y.* **195**, 1006-1008.
- COOTER, R. J. (1973). Flight and landing posture in hoppers of *Schistocerca gregaria* (Forsk). *Acrida* **2**, 307-317.
- DIRSH, V. M. (1974). *Genus Schistocerca (Acridomorpha, Insecta)*. The Hague: Dr W. Junk, B.V.
- ELSNER, N. (1973). The central nervous control of courtship behaviour in the grasshopper *Gomphoceripus rufus* L. (Orthoptera: Acrididae). *Neurobiology of Invertebrates, Tihany 1971*, 261-287.
- FRANKLIN, R., JANDER, R. & ELE, K. (1977). The coordination, mechanics and evolution of swimming by a grasshopper, *Malanoplus differentialis* (Orthoptera: Acrididae). *J. Kansas Ent. Soc.* **50**, 189-199.
- GODDEN, D. H. (1975). The neural basis for locust jumping. *Comp. Biochem. Physiol.* **51A**, 351-360.
- HEITLER, W. J. (1974). The locust jump: specializations of the femoral-tibial joint. *J. comp. Physiol.* **89**, 93-104.
- HEITLER, W. J. & BURROWS, M. (1977a). The locust jump. I. The motor programme. *J. exp. Biol.* **66**, 203-219.
- HEITLER, W. J. & BURROWS, M. (1977b). The locust jump. II. Neural circuits of the motor programme. *J. exp. Biol.* **66**, 221-241.
- JANNONE, G. (1940). Relazioni fra corsi d'acqua e spostamenti delle larve e ninfe di cavallette in A.O.I. *Boll. Idrobiol. Cacc. Pesca. Afr. Orient. Ital.* **1**, 70-76.
- JOHNSTON, H. B. & BUXTON, D. R. (1949). Field observations on locusts in Eastern Africa. *Anti Locust Bull.* **5**, 73 pp.
- KENNEDY, J. S. (1945). Observations on the mass migration of desert locust hoppers. *Trans. R. ent. Soc. Lond.* **95**, 247-262.
- KNECHTEL, W. K. (1938). Ueber die Wanderheuschrecke in Rumänien. *Bull. ent. Res.* **29**, 175-183.
- MILLER, P. L. (1972). Swimming in mantids. *J. entomology.* **46**, 91-97.
- NIKOL'SKII, V. V. (1925). The asiatic locust *Locusta migratoria* L. A monograph. *Trudy Otd. prikl. Ent.* **12** (2), 1-332. (In Russian.)
- PFLÜGER, H.-J. & BURROWS, M. (1978). How the locust dries itself. *J. exp. Biol.* **75**, 95-100.
- SANDEMAN, D. C. (1968). A sensitive position measuring device for biological systems. *Comp. Biochem. Physiol.* **24**, 635-638.
- WICKLER, W. (1966). Freilandbeobachtungen an der Uferschrecke *Tridactylus madecassus* in Ostafrika. *Z. f. Tierpsychol.* **23**, 845-852.