

THE CO-ORDINATION OF INSECT MOVEMENTS

III. SWIMMING IN *DYTISCUS*, *HYDROPHILUS*, AND A
DRAGONFLY NYMPH

BY G. M. HUGHES

Department of Zoology, Cambridge

(Received 27 February 1958)

Although many of the structural adaptations associated with the locomotion of aquatic insects are well known, there are few observations on the details of their propulsive mechanisms. In general, these may be subdivided into those which effect swimming by undulatory movements of the body (Kalmus, 1936; Gray, 1953), by oar-like movements of the legs or wings (e.g. *Polynema*, Hymenoptera), or by jet propulsion methods involving either the use of a surface active secretion (*Stenus*, Staphylinidae) or the active expulsion of water from the insect. Of these the use of legs as oars is the most common among adults. In this paper cinematographic analyses are given of two beetles which use this method and of the abdominal and leg movements involved in the jet propulsion of a dragonfly nymph. In addition, some observations are described on the effect of amputating legs on the swimming of *Dytiscus*. These differ significantly from the observations of Bethe & Woitas (1930) and support conclusions based on a study of cockroach movements (Hughes, 1957).

MATERIALS AND METHODS

The species used were the giant water-beetles, *Dytiscus marginalis* and *Hydrophilus piceus*, and late instar nymphs of *Anax imperator*. Swimming of the beetles was observed in a large sink containing water about 6 in. deep. Films were taken while the insects swam freely above a glass plate marked with a grid and placed in the field of the camera. Similar films were taken of the dragonfly nymphs but the results were not satisfactory for all purposes. Close-up films, either in side or in dorsal view, of nymphs freely suspended from the wing pads proved of much greater value in revealing the sequence of events in the swimming cycle. Spots of enamel paint placed on the abdominal segments and legs helped in plotting their position on successive frames. Sinclair 35 mm. and Zeiss Movikon 16 mm. cameras were used at speeds of 24–30 frames/sec. for the beetles, but much faster speeds (up to 60 frames/sec.) and briefer exposures were necessary to 'fix' the dragonfly movements. General lighting was provided by two Photofloods and in addition carefully placed Point-o-Lites were used for the close-up shots.

Additional information about the events during swimming of *Anax* was obtained from films and simultaneous recordings on an oscilloscope of the time course of pressure changes within the branchial chamber and/or the forces on the animal resulting from the jet. As these events are extremely rapid great care was taken in

the selection of recording apparatus and in the method of synchronizing films and oscillograph records. The wing pads of the insect were attached by a small paper clip to a short arm soldered to the anode of an RCA 5734 mechanotransducer valve. Although the natural frequency of the latter is 12 kcyc./sec. it was reduced considerably by these attachments. After suitable reductions in the length of the arm it was raised to 120 cyc./sec. which is sufficiently high to reproduce faithfully the true time course of the forces generated by the jet. Similarly, by using a Hansen condenser manometer (Hansen, 1949) with a natural frequency of nearly 100 cyc./sec., the time course of the pressure changes was accurately recorded even when fine (0.5 mm. outside diameter) hypodermic tubing was used. The following method of synchronization was suggested by Dr R. H. J. Brown, to whom I am grateful for advice on this and on other matters of technique. The point where a wire on a time marker, rotating $3\frac{1}{2}$ times/sec., touched a mercury drop was brought into focus in the camera field by a lens or mirror; this contact completed a circuit which modulated the intensity of the beams on the oscilloscope. It was thus possible not only to see which frame was related to the signal on the oscilloscope trace, but also to decide whether the frame was a fraction of a second before or after the signal by observing the actual position of the rotating contact on that frame.

RESULTS

(A) *The swimming of Dytiscus and Hydrophilus*

(1) *Morphological*

Dytiscus and *Hydrophilus* show many structural adaptations to their aquatic habitat some of which display striking convergences. On the whole, *Dytiscus* is better adapted to aquatic conditions than *Hydrophilus* which is correspondingly more efficient on land. The body is keel-shaped in both genera and offers little resistance to water flow, but it is in the legs that the most striking adaptations are found. The femur, tibia and tarsus of the meso- and metathoracic legs are all flattened. The hindlegs of swimming beetles are shorter relative to the body length than in terrestrial forms and the proportions of the segments are different. In Dytiscidae the tarsus is about twice the length of the tibia, whereas in terrestrial beetles they are nearly equal (Roth, 1909). Hairs are found on the tarsal joints of *Hydrophilus* and on both the tibia and tarsus of *Dytiscus*. In both genera these tarsal joints overlap one another on the surface which is anterior during retraction and thus increase the rigidity of the structure. They have a mechanism whereby the tarsi of the middle and hind pairs of legs can rotate, enabling them to 'feather' during the forward stroke. In *Dytiscus*, the articulation of the proximal segment with the tibia is similar to a ball-and-socket and facilitates a 100° rotation of the tarsus. This joint is fairly normal in *Hydrophilus*, but the articulation between the two proximal joints of the tarsus is very oblique and the rotation principally takes place about its axis. The other segments of the leg are also modified in both genera. Promotor-remotor movements of the coxae are completely excluded in *Dytiscus* as the coxae are fused to the sternum, while in *Hydrophilus* they are restricted by the coxae being sunk

into spaces in the sternum. This adaptation probably serves to lessen the drag of the insects in the water.

The coxo-trochanteral joints are dicondylic and determine the movement of the femur very rigidly. This movement is not in one plane, because of the shape of the trochanter, and has the result that the tip of the femur moves parallel to the ventral body surface throughout its stroke. The femur is flattened and curved so that it is almost flush with this surface throughout the arc of its movement, adaptations which will again decrease the resistance to forward movement.

(2) Cycle of hindleg movements

A series of diagrams (Fig. 1) showing the position of the hindlegs throughout the cycle has been constructed from the photographs of the swimming insect. At the completion of the effective stroke (ii), the hindleg of *Dytiscus* appears narrow in the

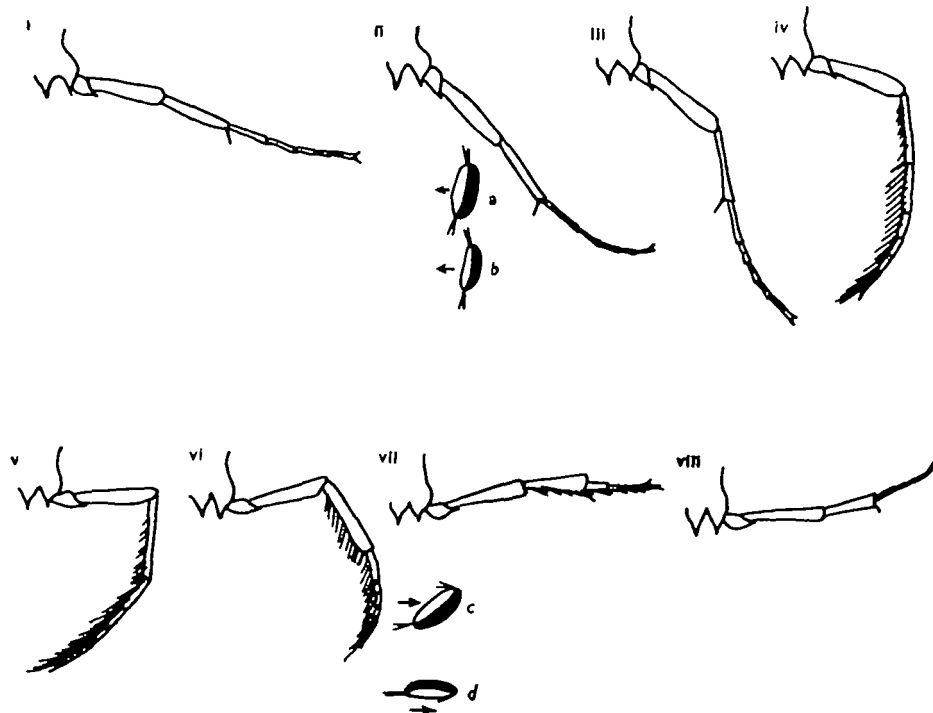


Fig. 1. *Dytiscus*. Diagrams (i)–(viii) show successive positions of the right hindleg during a typical cycle of swimming movements as seen in dorsal view. The rotation of the tibia (*a* and *c*) and tarsus (*b* and *d*) are indicated by diagrams of their cross-section at phases (ii) and (vi) of the cycle.

photographs because the flattened surfaces of the tibia (*a*) and tarsus (*b*) are pressing against the water and the hairs are spread out dorsally and ventrally to offer their maximum resistance. Protraction commences with flexion of the coxotrochanteral and femoro-tibial joints (iii). The tarsus rotates 100° (*b* to *d*) so that the edge which was anterior during retraction now becomes dorsal and the outline becomes blurred as the hairs are visible (iv). Roth (1909) described this tarsal rotation but

in the opposite direction. His account was shown to be wrong by filming insects with the tarsi painted white on one surface only. The anterior side during retraction becomes dorsal as the leg is drawn forwards and paint on its surface is only visible during protraction. The femur continues to protract and it forms the leading edge of the limb behind which trail the flexed tibia and tarsus (v). The tibia now begins to extend and takes up its fully protracted position (vi, vii). As Amans (1888) described, the rotation of the tibia (a to c) which occurs during the cycle is about 45° , but in the opposite direction to that of the tarsus. The femur is beginning to retract at this stage and as the tarsus rotates its tip passes dorsally to the rest of the limb. As the femur has already retracted by the time the tarsus is presenting its maximum surface to the water, it is probable that its extension and rotation are entirely passive. This may be partly true of the femoro-tibial joint also. The musculature agrees with this suggestion for, as Bauer (1910) pointed out, the extensor

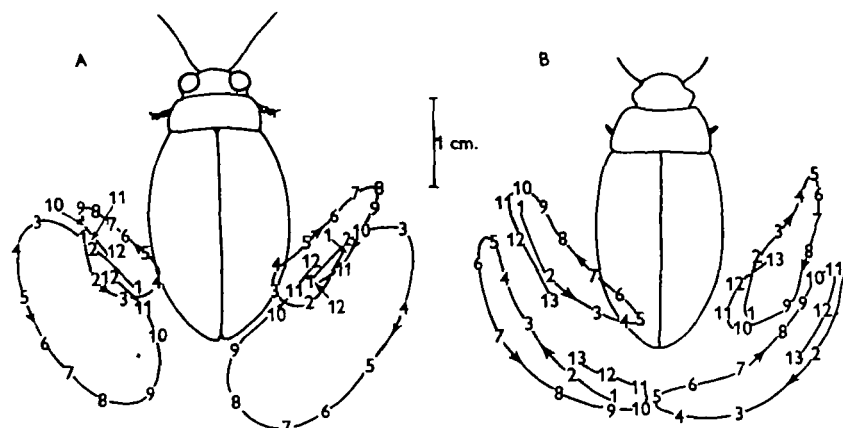


Fig. 2. Plots of the position of the tips of the hind- and middle legs on successive frames of a ciné film (30 frames/sec.) during normal swimming of *Dytiscus* (A) and *Hydrophilus* (B). In both cases the insect was turning slightly to the left.

tibiae is a much smaller muscle than its antagonist and there are no extensors of the tarsus. During retraction the tibia rotates progressively until it is inclined as shown in (a) at the end of the active stroke. The whole limb acts as an almost straight oar (i) and the tarsi are curved by the water pressure. The films of insects with painted tarsi showed that during retraction the posterior surface of the tarsus is inclined slightly upwards which will produce a force tending to move the insect downwards. Towards the end of the stroke, the tibia flexes while the tarsus is still exerting pressure (iii) and protraction begins once more.

This description indicates the principle underlying the 'rowing' movements of aquatic insects. It is highly developed in *Dytiscus* and the individual movements of the swimming legs of *Hydrophilus* conform to the same general plan. A comparison of the path followed by these legs illustrates the greater efficiency of *Dytiscus* in its swimming movements (Fig. 2A). During protraction of the legs in *Hydrophilus* (Fig. 2B) there is relatively little flexion of the femoro-tibial joint and the course

followed by the limb tip during protraction is consequently further away from the body and offers a greater resistance to forward movement of the body. On the other hand, the middle legs of *Hydrophilus* exert a more powerful thrust against the water than does this pair of legs in *Dytiscus*. In both insects the highly-developed extensor trochanteris is the most important muscle in propelling the body forwards.

These movements of the legs during the swimming of *Dytiscus* are obviously quite different from those employed by the insect when walking, but in *Hydrophilus* the differences are not so well marked. The greater activity of the flexor tibiae muscles and the increased promotor-remotor movements of the coxae, result in the path followed by the hindlegs being much closer to the body when the insect walks.

(3) *The rhythm of the swimming movements*

In *Dytiscus*, the rhythm in which the legs are retracted is completely different from that described for the walking insect (Hughes, 1952). The two legs of a limb pair retract simultaneously, ensuring that the body is subjected to only very slight turning moments (Fig. 3 A). When swimming along a path which is not perfectly straight the timing of a pair of legs may be altered. Fig. 2 A was plotted from such an insect and it will be noticed that the right legs are retracted a little in advance of the left legs and also with a greater amplitude. Both these features will tend to correct the slight turn to the right which was made in the previous stroke. More rapid turning takes place when one of the hindlegs is held outstretched in the protracted position, while the contralateral leg retracts actively (Fig. 4 B). The extended hindleg and also the middle leg on that side may make slight 'back-paddling' movements. The duration of protraction and retraction are usually equal in this insect, but sometimes protraction is shorter as in Fig. 4 A. The difference is slightly exaggerated here, however, because the legs appear to be in a protracted position for a longer period on account of the inclination of the body. Previous accounts of the rhythm hardly mention the middle pair of legs and suggest that they perform only occasional movements during turning and to preserve the balance. This is true when the insect is undisturbed and swims slowly but in more rapid swimming, these legs play a regular part and retract together but in opposite phase to the hind pair of legs (Figs. 3 A, 4). One function of the middle pair is to stabilize the body during the recovery stroke of the hindlegs. Their retractor movements are directed more ventrally than those of the hind pair, and this tends to raise slightly the front part of the body. For instance, in Fig. 4 A the apparent changes in length of the body are plotted beneath the leg movements. A decrease in length is due to the abdomen being raised relative to the head by the buoyancy of the air store. As the middle legs retract, the body becomes more level in the water and its apparent length increases. It is noticeable that the length starts to decrease before the hindlegs are completely retracted, suggesting that perhaps they do not play such a great part in regulating the horizontal position of the body. The middle legs also function to maintain a uniform speed of forward movement, since when they are amputated progression is somewhat jerky, especially when the insect is excited and the body does not keep on too even a keel.

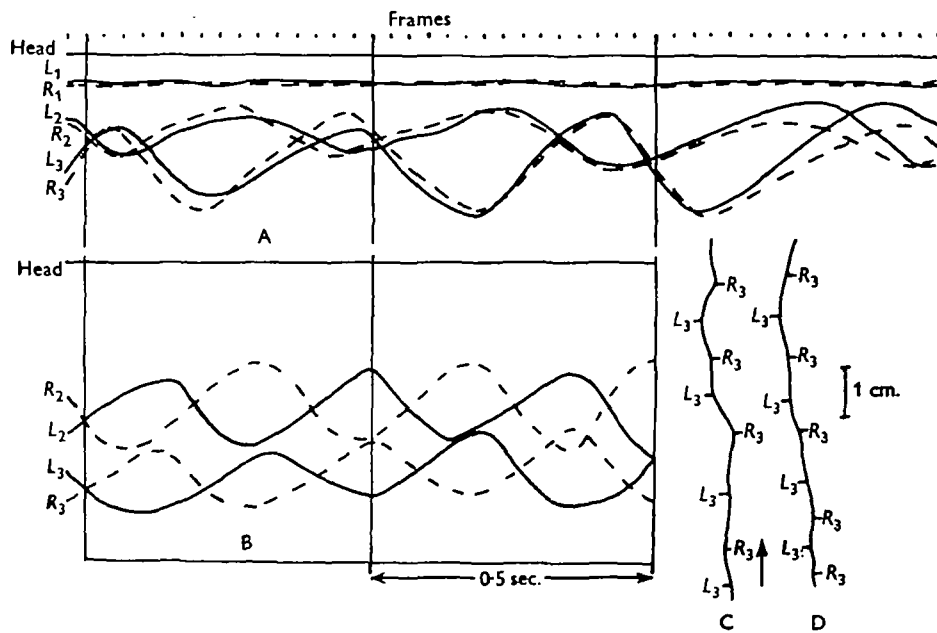


Fig. 3. The rhythm of leg movements during swimming plotted relative to the head in A *Dytiscus* and B *Hydrophilus*. C. The path of the head relative to the ground during B is shown, together with the instant when the hindlegs begin to retract. D. The same insect swimming along a straighter path.

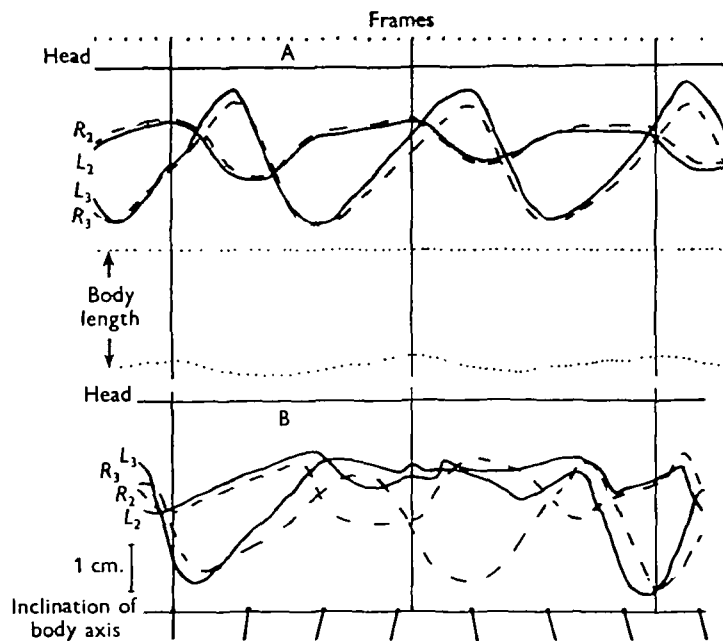


Fig. 4. *Dytiscus*. The rhythm of leg movements plotted relative to the head. In A the length of the body seen from above and in B the inclination of the body axis with respect to the grid are also plotted. The three vertical lines are separated by 0.5 sec.

The rhythm of leg movements in *Hydrophilus* differs from that of the Dytiscidae in that the two legs of a segment are in opposite phase. The middle and hind pairs are both employed and diagonal legs retract at exactly the same instant (Fig. 3 B). The fully retracted middle legs lie beneath the body so that it is difficult to determine whether this is also true at the beginning of protraction. The duration of protraction of the hindlegs tends to be longer than retraction by about a fifth of a cycle. The position of the head of this insect has also been plotted in Fig. 3 C, D and demonstrates that the path followed by *Hydrophilus* is much straighter than has been generally supposed. Deviations of the head to the right and left are associated with retraction of the hindleg on the opposite side. One of the reasons why these deviations are not so great is because the legs move simultaneously on the two sides. Synchronous retraction of diagonal legs is of further significance in that it distinguishes the swimming from the walking rhythm where there is always a slight delay between the instant at which R_2 and L_3 or L_2 and R_3 are retracted (Hughes, 1952).

(4) *The effects of limb removal in Dytiscus*

Bethe & Woitas (1930) described changes in the swimming movements which occur when one or more legs are amputated. The most striking changes take place when a single hindleg is removed. In such an insect they describe how the middle leg on the same side, previously inactive, became important in swimming and retracted simultaneously with the intact hindleg. However, analysis of films (Figs. 5, 6) taken in the present investigations has failed to confirm this and other details of their description. It can be readily observed that when the left hindleg (L_3) is amputated, the suddenly alarmed insect tends to circle to the left owing to the action of the right hindleg, but it soon swims along a straighter path because of the following modifications in leg movements:

(i) The intact hindleg (R_3) does not retract so far back as in the normal insect and during protraction it is not feathered so closely to the body nor does it move so far forwards. The movements of this leg do not have such a regular rhythm and give the impression of being constantly regulated. All these modifications tend to decrease the tendency for this leg to rotate the insect anticlockwise.

(ii) The left middle leg (L_2) continues in the normal rhythm so that it retracts as soon as R_3 has completed its effective stroke. The amplitude of its movements is increased both anteriorly and posteriorly.

(iii) Retraction is delayed in R_2 which therefore remains outstretched while L_3 retracts and, together with the protracting hindleg, acts as a fulcrum about which the body pivots.

Modifications (ii) and (iii) both increase the turning effect of L_2 and it has been noted already that similar changes occur in the normal insect when it turns (Figs. 2 A, 4 B). The net effect of the changes in rhythm and posture of the legs is that progression towards a given point is accompanied by oscillations which are due to an alternation of the turning moments produced by R_3 and L_2 . This is clearly shown by tracing the path of the head or centre of gravity (Fig. 5). The overall path is

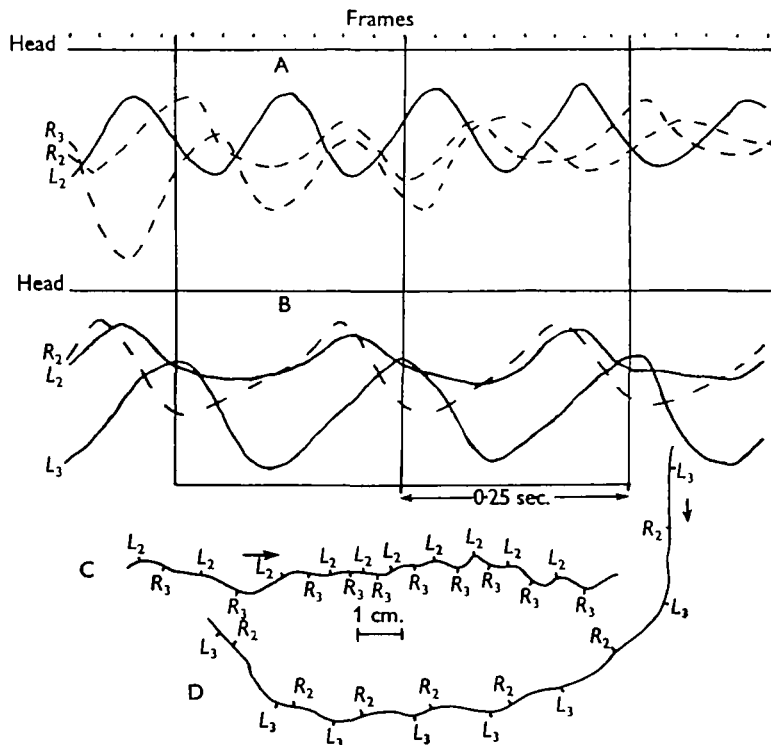


Fig. 5. *Dytiscus*. The rhythm of leg movements following the amputation of a single hindleg plotted relative to the head. In A the left hindleg (L_2) has been removed and the path of the head is shown in C. In B the right hindleg (R_3) was amputated and the insect was also blinded on the left side. This insect tends to circle more as is shown in D. In C and D the instants when the legs begin to retract are indicated.

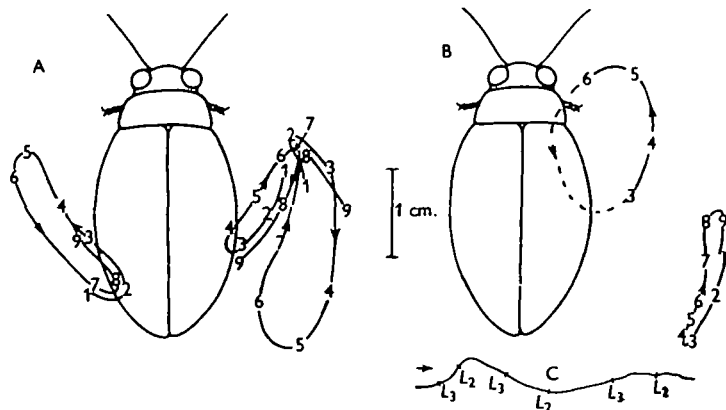


Fig. 6. *Dytiscus*. The position of the limb tips relative to the body on successive frames of ciné films (30 frames/sec.). The left hindleg has been removed in A which is the same insect shown in Fig. 5A, C. In B both the middle and hindleg on the left side have been removed. Its path through the water and the instants at which L_3 retracts and L_1 protracts are shown in C.

fairly straight, which would not be the case if these modifications had not taken place. Bethe & Woitas (1930) did not plot the movements of the legs from their photographs, which in fact clearly show that the intact hindleg and contralateral middle leg do *not* retract simultaneously. Most later illustrations of this phenomenon (e.g. Wigglesworth, 1953) reproduce Bethe's diagram and not the actual photographs.

Observations on the effects of amputating other legs differed slightly from those of Bethe & Woitas but will not be described here. Changes in posture of the remaining legs occur in addition to their taking over of the swimming function. One very striking example of this occurs if both the hind- and middle legs of one side (L_2 and L_3) are removed. As was to be expected the insect tended to move to the left, again especially when it was startled. But it was able to swim along a relatively straight path (Fig. 6C) surprisingly well when left undisturbed. In doing this the intact middle and hindleg both altered their normal movements a great deal although the rhythm remained relatively unaltered. The hindleg was held outstretched and scarcely feathered during protraction, which was longer than retraction. The middle leg, however, protracted very much farther forwards and during this phase was held away from the body. During retraction it moved ventrally and its active stroke was directed under the body and towards the left-hand side. This leg, therefore, moved in an anticlockwise direction (Fig. 6B) and tended to rotate the head towards the right. Progression was inevitably slow by this method which reminds one of the manoeuvres which can be made with a canoe paddle.

Several neurological mechanisms are involved in the production of these plasticity changes and while a complete analysis cannot be given some responses of intact *Dytiscus* are suggestive. It has already been noted how during a slightly 'wavy' course and when turning (Figs. 2A, 4B) the posture and rhythm of the legs are modified which is accentuated following amputation. Even more striking is the observation that when *Dytiscus* is held and moved through water in a circle of about 6 in. diameter, a characteristic compensatory response is invariably observed (Fig. 7). The outer hindleg is outstretched and shows little active retraction, but occasionally moves forwards in this stiff condition in a way very reminiscent of the single hind-leg of the insects described above. At the same time, the other hindleg retracts strongly and frequently, while the two middle legs show movements which would also produce rotation in the opposite direction to the imposed movement. The most important sensory structures involved in this response are the eyes, antennae, and receptors on the legs themselves. The response persists in red light,

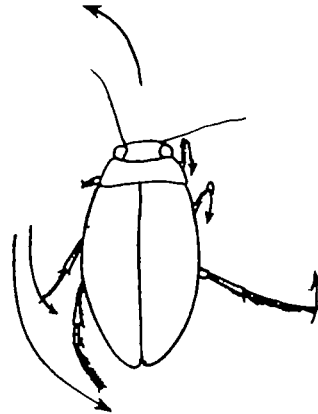


Fig. 7. *Dytiscus*. Diagram to illustrate the pattern of leg movements during the compensatory response produced when the insect is rotated in an anticlockwise direction.

but is not so marked after covering the eyes with wax containing lampblack, or when a striped environment is rotated at the same speed as the insect. If the antennae are also removed the response is sometimes absent and if it occurs is not very definite. During forced rotation of an insect there will, of course, be an asymmetric stimulation of the legs on the two sides because of the centrifugal force as is shown by the positions assumed by the legs when a dead insect is rotated.

It has not been possible to prove conclusively that any one of these receptors is solely responsible for this response. It seems likely that all three are able to produce it by themselves. The eyes are certainly involved a great deal in the orientation of this insect (Zeiser, 1934). They are probably the most important receptors as was concluded by Tonner (1938) in his study of similar compensatory responses of dragonfly nymphs. The importance of differential stimulation of antennae has not been discussed previously in *Dytiscus* but it must certainly occur even in normal swimming. The antennae are held forwards at an angle to the axis of progression and when the path deviates slightly a difference in their degree of bending is apparent on the films. The basal joints are profusely supplied with sensory structures which include Johnston's organ, a row of campaniform sensilla and several hair plates at the articulation. Both slowly and rapidly adapting responses to deflections of the antennae have been recorded from the antennal nerve. If a fine jet of water is directed at the antennae of a fixed *Dytiscus* from in front and to one side the contralateral hindleg usually kicks.

The above observations suggest that if the insect departs from a straight course the central nervous system will receive a changed pattern of sensory impulses from these sources and that the normal responses tend to restore the original orientation. As these responses have much in common with the alterations in motor activity which follow limb amputation, it is probable that these too are responses to the inevitable changes in peripheral inflow resulting from the tendency to circle. If insects with a single hindleg amputated are moved through the water in a straight path the remaining leg movements are almost normal. Correspondingly, the alterations in movements do not occur if the hindleg is removed from a blinded insect so that the insect circles for some time, particularly if the antennae are also removed. Insects which show almost rectilinear swimming after a hindleg has been amputated immediately circle when blinded. Some compensation does eventually take place in these insects, however, because of the proprioceptive inflow from the legs, but the majority of their movements are normal. Unilaterally blinded insects with a hindleg removed tend to circle, but may move fairly straight for short distances (Fig. 5 D). In this insect the intact hindleg moves normally and the two middle legs retract almost simultaneously (Fig. 5 B).

The supra- and suboesophageal ganglia must play a large part in the integration of the inputs from these different sources. Several lines of evidence suggest that they probably contain a mechanism which compares the inputs from the two sides of the body (cf. Kalmus, 1949) and controls the responses which occur when the insect departs from a given path. The latter need not necessarily be directly to or away from a given stimulus but can vary in its orientation. The factors controlling

the 'set' of this mechanism may involve central as well as peripheral patterns of stimulation, but once the 'set' has been established changes in peripheral inflow will be analysed with respect to it. Such a mechanism is essential otherwise the compensatory responses would prevent the insect from turning. Unilateral blinding or extirpation of a supraoesophageal ganglion so alters the balance of the co-ordinating mechanism that persistent circling results.

Faivre's (1857) observation that the direction of circling is away from the injured side has been substantiated by several workers and Baldus (1927) has established that alterations in the movements of the legs on both sides of the body are involved. His photographs show that they are strikingly similar to those reported above following unilateral amputation of legs or rotation of the insect. Circling away from the blinded or decerebrate side continued even when the middle and hindlegs were amputated on one side. If the legs removed were from the side opposite to that from which the supraoesophageal ganglion was extirpated, circling resulted from only slightly exaggerated movements of the remaining middle and hindlegs. If, however, the amputation and brain injury were on the same side the leg movements were very different. His description is almost identical to that given above when the two legs were amputated but there was no brain injury. Baldus mentions that he observed this activity but he holds quite the opposite view to Bethe & Woitas, i.e. that following limb amputation the remaining legs move quite normally and that these asymmetries occur only after unilateral brain injuries have also been performed.

It is evident that the brain has a large number of both homo-lateral and contra-lateral connexions with the lower motor centres, but their complexity makes any description at this stage not only inadequate but probably misleading. Nevertheless, the very striking similarities between the leg movements following the amputation of a single hindleg and those involved in the compensatory and circus movements strongly suggests the operation of a single co-ordination mechanism influenced by peripheral changes and is quite contrary to the plasticity theory of Bethe.

(B) *The swimming of the dragonfly nymph, Anax imperator*

Normally these predators creep extremely slowly among weeds and await their prey, but they can swim quite rapidly especially when disturbed. They usually swim when placed in a large volume of water particularly if there are few objects to which they can attach themselves. Nymphs also swim if the legs are free when they are suspended from their wing pads by a small paper clip fixed to a steel rod. Periods of swimming are often produced when the rod is struck or the insect touched with a brush.

Jet propulsion is achieved by an extremely rapid contraction of the abdominal musculature (Whedon, 1918; Tonner, 1936; Snodgrass, 1954) producing a pressure head within the enlarged hindgut which forms the branchial chamber. Water escapes as a fine jet at high velocity from the anal opening which is guarded by valves. The reaction from this jet propels the insect forwards at speeds which reach 30–50 cm./sec. during the first centimetre of propulsion. The frequency of the jets may be up to

3/sec. and they may continue for some time but in a fixed insect a pause usually occurs after ten to twenty of them. These features were conveniently recorded when the insect was fixed to the RCA 5734 transducer valve. The time course of the propulsive forces generated by the jet was also registered and as Figs. 9 and 11 show, a maximum value of 0.6 g. is reached within 0.03 sec. and the total duration is a little under 0.2 sec. The area beneath the curve is a measure of the impulse acting on the insect and is equal to the change of momentum which was about 52 dyne-sec. in an actual experiment. As the insect weighed 1 g. the expected velocity had the insect been free was 52 cm./sec. This figure, however, neglects the drag forces to which the free insect would be subjected, but, even so, it is in good agreement with speeds measured from films at the onset of swimming.

The precise sequence of muscular movements is difficult to establish as the total duration of the contraction is only about 0.1 sec. The most obvious movements are the longitudinal and dorso-ventral contractions of the abdomen, and the retraction

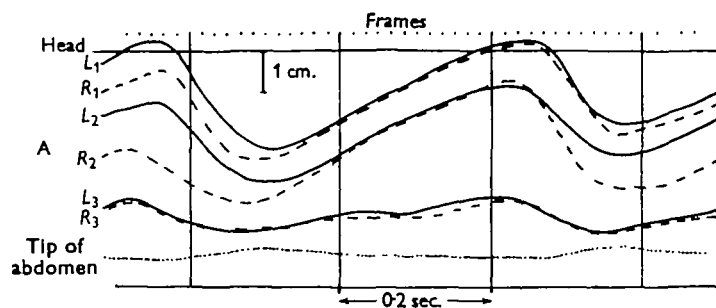


Fig. 8. *Anax*. Movements of the legs and tip of the abdomen relative to the head plotted from a film of the stationary insect.

of all six legs so that they lie alongside the body. When the insect is held stationary the legs come forwards again before the next jet (Figs. 8-10), but this does not occur normally because of an 'Angelegtbleiben' reflex (Tonner, 1935) elicited by water stimulating the antennae during motion. The two legs of a segment usually retract simultaneously, though cases have been observed where only the three legs on one side retracted. Some shots suggest that the order of retraction is hind, middle, fore, but the intervals separating these movements are extremely small, being at most 1/50 sec. (Fig. 8). One of the difficulties is to decide the exact phase at which retraction of a leg is associated with a given jet, but usually this is recognizable when a leg moves more rapidly backwards, regardless of its other activity.

The interval between the abdominal and leg movements is brief and in many cases they appear to be simultaneous. Most analyses suggest, however, that the hindlegs, at least, retract slightly before the abdomen shortens. Transducer records taken simultaneously tend to confirm this as there is a slight forward force synchronous with the leg movements and slightly preceding a rapid rise which coincides with shortening of the abdomen as the jet efflux occurs. The resulting propulsive

forces on the insect cease when the abdomen is maximally shortened (Fig. 9). Flattening of the sternum seems to occur a little before the abdomen shortens, but it does not reach a maximum until after the abdomen has partly extended again (Figs. 9, 10). Water probably begins to be drawn in when the abdomen lengthens and continues to do so as the sternum is depressed. The most striking

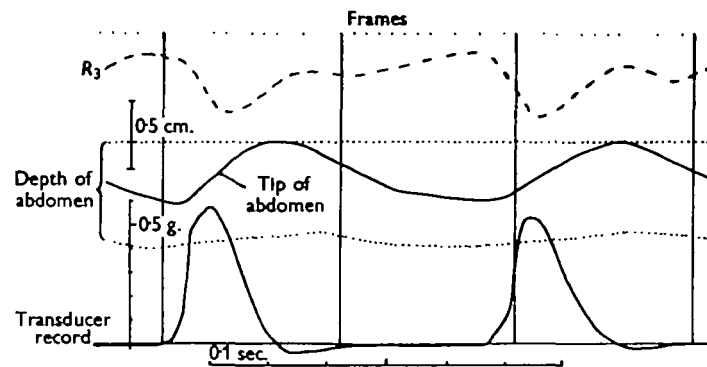


Fig. 9. *Anax*. The movements of the right hindleg and the tip of the abdomen plotted relative to the head. The depth of the 6th abdominal segment as seen in side view is also shown. A transducer record of the forces acting on the stationary insect as a result of these movements has been superimposed.

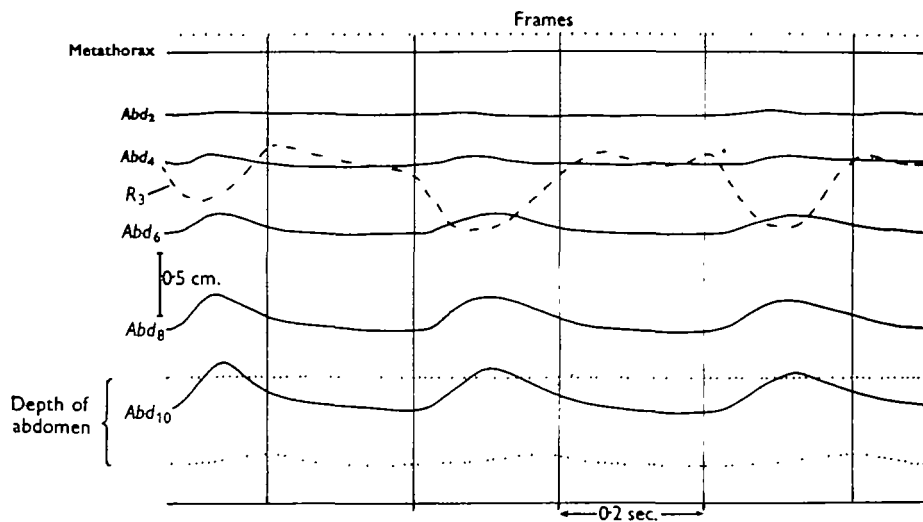


Fig. 10. *Anax*. The movements of different segments of the abdomen are plotted relative to the metathorax during swimming movements of a fixed insect. Movements of the right hindleg relative to the head and of the dorsal-ventral flattening movements of segment 6 are also shown.

feature of the whole response is the longitudinal contraction, however, which may cause the abdomen to shorten by 7–10% of its resting length. Most of this appears to take place in the posterior segments but plots of the positions of individual segments (Fig. 10) shows that all segments are involved to some extent. The largest

proportion (40%) occurs in segments 6–8 and this is also the region where flattening of the sternum is greatest. These observations correlate with the internal anatomy as the branchial chamber is situated in these segments which are therefore the region where the maximum decrease of volume would be expected when water is expelled. The segments do not all contract at exactly the same instant as can be seen particularly during some of the slower contractions. The hind segments contract first and the telescoping spreads forwards very rapidly. The very first part of the whole response appears to be the closing together of the three valves which guard the external opening. It has not been possible to obtain good films of the valves, but direct observation certainly suggests that the aperture is completely closed just before the longitudinal contraction commences. It then appears to open slightly as

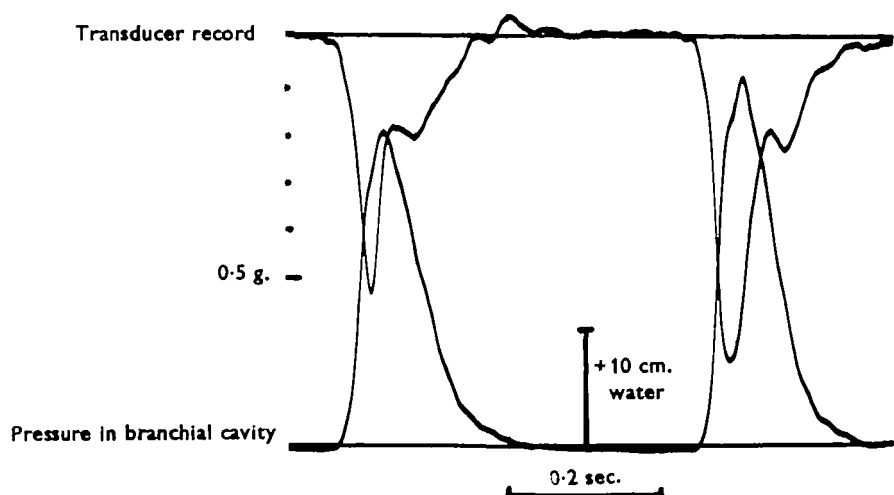


Fig. 11. *Anax*. A record of the pressure changes in the branchial chamber and the forces acting on the animal during swimming (upper trace).

water is expelled and later suddenly opens very widely and water is drawn in. The phase of valve closure is often associated with the slight apposition of the epiproct and two paraprocts. Opposite each of these terminal appendages is situated one of the three anal valves.

Analyses made so far of pressure changes in the chamber are in agreement with the account given above. Recordings taken when a fine needle was inserted through the anus into the branchial chamber show a rapid rise in pressure at the onset of the longitudinal contraction and may reach pressures of about 30 cm. water (Fig. 11). The pressure falls to that of the surrounding water (taken as zero) as the abdomen begins to elongate. This fall may be even more rapid than the rise in pressure especially during contraction at the end of a series. The opening wide of the valve is presumably associated with this rapid fall and is succeeded by a very small negative pressure as water is drawn in. The positive pressure occurs simultaneously with the impulse on the insect and has a similar time course. Some preliminary

attempts to record pressures in the body cavity suggest that the time course of these follows that of the longitudinal movements of the abdomen and not of the jet pressure or impulse records. Several other features of the pressure changes recorded during swimming as well as those occurring in respiration are of interest and will be considered in a later paper.

DISCUSSION

The importance of swimming in the life of these three insects varies. It is probable that *Dytiscus* swims the most and dragonfly nymphs the least. Both are carnivores but catch their prey in different ways. *Dytiscus* hunts actively in search of food (Tinbergen, 1951) but dragonfly nymphs lurk among weeds and await their prey. Swimming in the latter is mainly an escape mechanism for which rapid acceleration is of great importance. This is achieved by the expulsion of water at high speeds through a small aperture. The pressure and impulse records suggest that the jet velocity is about 250 cm./sec. and the aperture less than 0.01 mm.² in cross-section. The same volume of water is drawn in through the anal opening, but by increasing the cross-section the velocity of the water relative to the animal is low and the consequent change of momentum retarding progression will be considerably reduced. The use of the same aperture for both the expulsion and entry of water is probably unique among animals which use this method of propulsion. In Cephalopods, for instance, water is drawn in through the lateral openings of the mantle cavity. The extreme rapidity and synchronization of activities at the beginning of dragonfly flight was described as 'die Gesamtreflex' by von Uexküll (1908) and the same term might well be applied to the swimming insect. Its co-ordination probably involves nerve fibres which run the whole length of at least the abdominal nerve cord. Some of these are relatively large (Hughes, 1953) and provide rapidly conducting pathways such as are frequently found in escape mechanisms.

Hydrophilus is a vegetarian and is the least modified both structurally and functionally. This is apparent in the movements of pairs of limbs which alternate in *Hydrophilus* but retract together in *Dytiscus* and *Anax*. It has been shown, however, that these alternating movements are not exactly the same as in walking because of differences in their nature and of the timing between the middle and hind pairs. It is of interest to note that in the larval stages of the beetles the opposite is true, for *Dytiscus* larvae 'trample' along with the two legs of a segment alternating whereas it is reported that those of *Hydrophilus* move together as the body performs dorso-ventral undulatory movements.

All three insects are adapted to swim along a straight path and their resistance to progression is reduced. Deviations from this path are corrected by a number of compensatory responses of the animal. The observations reported on the effects of limb amputation on *Dytiscus* indicate the extent of these in the normal animal, how they operate under modified circumstances and within limits produce the same end result. Thus although a precise analysis of any so-called plasticity change is not possible at a neurophysiological level, sufficient is now known of the extensive

proprioceptive mechanisms of terrestrial insects to support the view that it is due to the altered stimulation of the proprioceptive mechanisms which occur when the mechanical conditions change (Hughes, 1957). The present work, while not ignoring such mechanisms, emphasizes the importance of extero-receptors in the orientation of aquatic animals where gravity does not have such a controlling influence. Of these the eyes are the most important, but there is some evidence that the antennae are important in detecting water currents as they are known to do in dragonfly nymphs (Tonner, 1935). The considerable importance of impulses reaching the central nervous system is shown in all these observations. The fineness of control which they exercise on motor responses probably involving extensive feed-back mechanisms, results in them often being taken for granted. The striking changes which occur following amputation, etc., show up their existence and give us some insight into their complexity. However, it must not be assumed that the original patterns of motor activity are completely discarded either in *Dytiscus* or in *Blatta*, for in both insects there remains a tendency for these to show up under 'stress'. Thus, if *Dytiscus* is dropped on water immediately after the amputation of a single hindleg, the remaining legs move rapidly and as a result the insect swims in small circles. But after a short time it slows up and makes a straighter path as described earlier. The same sequence is observed when the experiment is repeated on subsequent occasions even after a period of weeks.

SUMMARY

1. Movements of the legs during the swimming of adult *Dytiscus marginalis* and *Hydrophilus piceus* have been analysed from films. In both beetles the middle and hind pairs of legs play an active part and the front pair is held stationary beneath the thorax.
2. The two legs of a segment are retracted simultaneously in *Dytiscus*, the two limb pairs acting alternately. In *Hydrophilus* retraction of a hindleg is simultaneous with that of the contralateral middle leg. Movement is rectilinear in both insects, but the head of *Hydrophilus* rotates a little to the side opposite that on which the hindleg is retracting.
3. Following amputation of a single hindleg, *Dytiscus* swims along a relatively straight path as a result of modifications in the movements of the two middle legs and the remaining hindleg. Contrary to the description of Bethe & Woitas, the hindleg continues to alternate with the contralateral middle leg, the only change in rhythm being a delay in the retraction of the other middle leg. Some of the changes in action of these legs are similar to those used in turning of the normal insect and those which produce circling in unilaterally blinded insects.
4. Forced rotation of *Dytiscus* elicits compensatory movements which tend to produce circling in the opposite direction. The eyes, antennae and legs are the sites of receptors whose asymmetric stimulation produces this response. It is suggested that a similar asymmetry in the inflow from these sense organs is responsible for the modified movements following limb amputations.

5. In the swimming of nymphs of *Anax* the legs retract slightly before shortening of the abdomen takes place. Although all the segments take part, a large proportion of this shortening occurs in segments 6-8 which contain the branchial chamber. Water is ejected through a small aperture during this contraction but when water is drawn in the anal valves are open wide.

6. The pressure in the branchial chamber rises to about 30 cm. water within 0.03 sec. and the reaction from the jet enables the animal to attain speeds of 30-50 cm./sec. within the first centimetre of propulsion. The duration of this pressure and of the impulse on the animal correspond with the time during which the abdomen contracts longitudinally.

I wish to thank Dr Tybjaerg Hansen of the Rigshospitalet, Copenhagen, for allowing me the use of his electric manometers to measure pressure changes in the dragonfly nymph.

REFERENCES

- AMANS, P. C. (1888). Comparaisons des organes de la locomotion aquatique. *Ann. Sci. Nat. Zool.* (sér. 7), 6, 1-164.
- BALDUS, K. (1927). Untersuchungen zur Analyse der Zwangsbewegungen der Insekten. *Z. vergl. Physiol.* 6, 99-149.
- BAUER, A. (1910). Die Muskulatur von *Dytiscus marginalis*. *Z. wiss. Zool.* 95, 594-646.
- BETHE, A. & WOITAS, E. (1930). Studien über die Plastizität des Nervensystems. II. Mitteilung. Coleopteren, Käfer. *Pflüg. Arch. ges. Physiol.* 224, 821-35.
- FAIVRE, E. (1857). Du cerveau des Dytisques considéré dans ses rapports avec la locomotion. *Ann. Sci. Nat. Zool.* (sér. 4), 8, 245-74.
- GRAY, J. (1953). Undulatory propulsion. *Quart. J. micr. Sci.* 94, 551-78.
- HANSEN, A. TYBJAERG (1949). Pressure measurement in the human organism. *Acta physiol scand.* 19, suppl. 68.
- HUGHES, G. M. (1952). The co-ordination of insect movements. I. The walking movement of insects. *J. Exp. Biol.* 29, 267-84.
- HUGHES, G. M. (1953). 'Giant' fibres in dragonfly nymphs. *Nature, Lond.*, 171, 87.
- HUGHES, G. M. (1957). The co-ordination of insect movements. II. The effect of limb amputation and the cutting of commissures in the cockroach (*Blatta orientalis*). *J. Exp. Biol.* 34, 306-33.
- KALMUS, H. (1936). Über die dynamische Erhaltung der Höhenlage durch die Sprungbewegungen der Larven und Puppen von *Corethra*. *Z. vergl. Physiol.* 23, 651-62.
- KALMUS, H. (1949). Optomotor responses in *Drosophila* and *Musca*. *Physiol. comp.* 1, 127-47.
- ROTH, W. (1909). Studien über konvergente Formbildung auf den Extremitäten schwimmender Insekten. II. Teil: Coleoptera. *Int. Rev. Hydrobiol.* 2, 668-714.
- SNODGRASS, R. E. (1954). The dragonfly larva. *Smithson. Misc. Coll.* 123, 2, 1-38.
- TINBERGEN, N. (1951). *The Study of Instinct*. Clarendon Press, Oxford.
- TONNER, F. (1935). Schwimmreflexe und Zentrenfunktion bei *Aeschna*-Larven. *Z. vergl. Physiol.* 22, 517-23.
- TONNER, F. (1936). Mechanik und Koordination der Atem- und Schwimmbewegung bei Libellenlarven. *Z. wiss. Zool.* 147, 433-54.
- TONNER, F. (1938). Halsreflexe und Bewegungssehen bei Arthropoden. *Z. vergl. Physiol.* 25, 427-54.
- VON UEXKÜLL, J. (1908). Studien über den Tonus. V. *Die Libellen*, 50, 168-202.
- WHEDON, A. D. (1918). The comparative morphology and possible adaptations of the abdomen in the Odonata. *Trans. Amer. Ent. Soc.* 44, 373-437.
- WIGGLESWORTH, V. B. (1953). *The Principles of Insect Physiology*. London: Methuen.
- ZEISER, T. (1934). Die Aufhebung der Manegebewegung durch Photomenotaxis und negative Geotaxis beim Gelbrandschwimmkäfer *Dytiscus*. *Zool. Jb. Abt. (3)*, 53, 501-20.