THE CO-ORDINATION OF INSECT MOVEMENTS

I. THE WALKING MOVEMENTS OF INSECTS

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(With Plate 12 and Eight Text-figures)

Though walking forms part of many insect behaviour patterns, the mechanism of insect walking has received relatively little attention in recent years. As a preliminary to a later investigation of neuromuscular co-ordination in insects, the normal pattern of walking movements in the cockroach and other insects has been studied. The results obtained and an account of the functional anatomy of the insect leg are given in this paper. The forces involved have not been measured, but a preliminary analysis of the mechanics of walking has been made with the help of 'stills' from cinematographic films. The use of cinematography greatly facilitates such an investigation.

Borelli (1680), in his *De motu animantium*, did not give a true picture of insect leg movements, but his suggestion concerning their order of protraction has been substantiated in the present research. In reviewing Borelli's account, Demoor (1890) was very critical of the supposition that it would be advantageous if the three ipsilateral legs of a hexapod were lifted in the order 'initium motus fieret a posteriori, cui succederet medius et ultimo anticus'. This suggestion was based not on observation but on the theoretical principle that the hindleg should move first in order to propel the centre of gravity forwards before the other legs were lifted. Demoor maintained that the foreleg of one side is lifted simultaneously with the middle leg of the opposite side while the ipsilateral hindleg is raised a little later, but all three legs of the triangle are placed on the ground instantaneously.

Paul Bert (1866) considered that the legs of *Carabus* are lifted in the order*: L3 and R2; R1; L2 and R3; L1 and R2; etc. This rhythm agrees with the principle of Borelli, but a study of films has shown that there is a short but definite delay between the lifting of the middle and contralateral hindleg. Bert was one of the few observers to recognize that insects have more than three legs on the ground during many phases of the locomotory cycle. Lloyd Morgan (1886) also drew attention to this fact when he wrote 'Much has been written on "the horse in motion". Can any readers of *Nature* supply me with references to published matter on the subject of hexapod progression?' In a reply, Wilkins (1887) stated: 'In general I found that the mode of projection in articulates does not differ essentially

* The convention adopted in distinguishing the different legs is as follows: R and L denote the right and left legs of each segment which are numbered from in front. Thus L2 is the left middle leg.
from what we see in vertebrates.’ This attitude resulted from the opinion then held by the majority of workers (E. Weiss, Müller, Bürmeister, Graber, Dahl, Carlet, etc.) that insect movement is accomplished by the alternation of two tripods of support, each composed of the foreleg and hindleg on one side, together with the middle leg of the opposite side. Thus, although having six legs the insect was envisaged as moving them in two alternating groups just as in a biped. Demoor extended this concept to include the majority of Arthropods, as he thought that they also used two alternating groups of diagonal legs. He concluded that the movement of insects, arachnids, and probably Crustacea, too, together with man and tetrapods, conforms to the general description that ‘La marche est une série de chutes successivement arrêtées’.

Cinematography discloses that many of these conclusions concerning the rhythm of leg movements in arthropods are oversimplified. The concept that movement is a series of checked falls seems to have little meaning except in the case of bipeds or tetrapods which are moving fast and thereby possess dynamic stability. The walking tetrapod may stop at any phase of the cycle and not fall over, as the centre of gravity always lies within the area of support. Paul Bert appears to have been the only worker to have denied this concept when applied to insects, an attitude which followed from his observation that there are often more than three legs on the ground at any one time.

There has been general agreement with regard to the roles fulfilled by the three pairs of legs during walking. The forelegs were considered to have a tractive function, and the hind pair to push while the middle legs act as fulcra. During the present century, the focus of research has moved from the mechanism of movement to a study of the role of the brain and different parts of the nervous system in the co-ordination of locomotory movements. Baldi (1921, 1922, 1924, 1938) made an extensive study of this aspect and also included an account of the leg movements of *Periplaneta* with which the following account is in substantial agreement. Baldi laid great stress on the lack of co-ordination in the movements which brought about any progression that followed removal of the suboesophageal ganglia. During the course of work on the importance of the higher centres in the locomotion of *Mantis*, Roeder (1937) made the interesting observation that the rhythm of leg movements might vary under different conditions. When the insect is quietly walking the order is L3, L2, R3, R2; when more excited the rhythm is L2–R2, L3–R3; when climbing L3–R1, L2–R3, L1–R2. Apart from this observation there has been no suggestion that the limb order might vary at different speeds, although Pringle (1939) considered that a distinction between running and walking was justifiable in the cockroach.

**MATERIALS AND METHODS**

Detailed studies were made on the cockroaches, *Periplaneta americana* and *Blatta orientalis*, and various beetles, *Dytiscus marginalis*, *Hydrophilus piceus*, *Carabus violaceus*, *Chrysomela orichalcea* and *Blaps mucronata*. The walking movements of other insects did not appear to differ from these in any essential feature. The insects
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I. Morphological

Before considering the morphology and movement of the legs it is necessary to define the terms to be used in this account.

*Protraction* is the complete movement forwards of the whole limb relative to its articulation with the body.

*Retraction*, similarly, describes the remaining half of the cycle between the instant when the leg is placed on the ground and the time when it is raised and protraction commences.

*Promotion* and *Remotion* refer to the corresponding anterior and posterior movements of the coxa with respect to the body.

*Adduction* and *Abduction* are likewise movements of the coxa brought about by extrinsic muscles. The former is a movement towards and the latter away from the body.

*Levation* and *Depression* describe parts of the protractor and retractor movements in which the leg is raised or lowered relative to the ground.

*Extension* and *Flexion* express the relationship between two adjacent segments of the legs; flexion occurring when the angle between them is reduced and extension when this is increased.

Cockroaches inhabit secluded crevices and show many modifications in relation to their mode of life. This is particularly evident in the structure and functioning of the thorax, and consequently an account of the locomotion of *Blatta* cannot be generalized for all insects. The leg articulations are placed more ventrally than in most insects, due to the extensive desclerotization of the sternum. These articulations are dicondylic, one episternal and the other trochantinal, in all the legs, and they limit the range of movements very closely. The axis of these articulations is inclined forwards at an angle of 60° to the ventral axis; a feature which enables the leg to obtain a more anterior *point d'appui* for any given degree of promotion than would be possible if the axis was at right angles to the mid-ventral line. The movement of the mesothoracic and metathoracic coxae is almost entirely restricted to the antero-posterior plane determined by this joint. A limited amount of adduction and abduction can take place, however, because of the flexibility of the ventral exoskeleton.
The range of movement of the prothoracic pair is much greater, and this is related to the nature of the coxal articulations. There are again episternal and trochantinal condyles which partially restrict the movement of the coxa to their axis. The greater mobility of the foreleg is to be attributed to the smaller size of the trochantin which is not wedged into the episternum and can move upon it (Text-fig. 1). Hence the axis of this joint is not so rigidly fixed as in the mesothoracic and metathoracic legs, because the trochantinal articulation can move relative to the episternal condyle.

Movement of the coxa is brought about by extrinsic muscles having their origin in the thorax and insertion on the proximal end of the coxa. Carbonell (1947) has given a detailed account of the many muscles involved, but for the present purpose it is more important to recognize the relationships of the main functional groups, and these are shown in Text-fig. 2. The remotors are the most powerful of these,
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particularly the tergal remotor coxa muscle which is inserted on the posterior rim of the coxa. Adduction is accomplished by muscles with their origin on the tergum lateral to that of the remotor, and their insertion on the inner edge of the trochantin near the coxo-trochantinal articulation. Abduction is chiefly brought about by the elasticity of the sclerites, but it is aided by the activity of a muscle originating on the epimeron and subalar plate, and inserted on the meron, i.e. lateral to the coxo-

episternal condyle. The promoters have their origin on the anterior edge of the episternum and are attached to the anterior coxal rim. In the prothoracic legs, however, the main promotor coxa muscle is absent and its function fulfilled by a muscle inserted near the coxo-episternal articulation and with its origin on the anterior part of the prothoracic shield. It is due to the upward component of this muscle's activity that a 'buckling' of the episternal-trochantinal hinge takes place during promotion.

Pringle (1938) has given an account of the functional morphology of the joints and the intrinsic musculature of the legs themselves which are typical of a running insect. The orientation of these appendages with respect to the body is not normal, however, as the middle and hind pairs always point obliquely backwards (Text-fig. 2 C), so that the extensor trochanteris muscles play a predominant role in the propulsive strokes of these legs.
II. The cycle of individual leg movements

The movements of the three pairs of legs were determined from simultaneous ventral and lateral photographs obtained by means of an inclined mirror. A series of diagrams was traced from these, and it shows the movements of the different limb segments throughout one complete cycle of walking (Text-fig. 3). The markings beneath each diagram are the footprints obtained when the insect was allowed to walk over smoked paper, a technique employed by many previous investigators.

In the fully protracted position of the foreleg, maximal promotion of the coxa is obtained by means of the episternal-trochantinal hinge. All the joints of the leg are extended so that the new point d'appui is in front of, and lateral to the head. During retraction the axis of the limb is moved backwards relative to the body, so
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that the angle of inclination ($\alpha$) of this axis gradually decreases. There is also a decrease in the angle ($\theta$) between the limb and transverse body axes as seen in ventral view (Text-fig. 4A). The activity of the remotor coxae, flexor trochanteris, and flexor tibia muscles produces these movements which draw the body forwards and towards the side of the active limb. When the limb axis has passed the vertical position, an extensor thrust is exerted along the axis by the contraction of the extensor trochanteris and extensor tibia muscles.

Protraction commences when the limb is levated from the ground as a result of the activity of the flexor trochanteris and flexor tibia muscles once again. Contraction of the promotor coxae muscles now swings the whole leg forwards and outwards while it extends as the result of increased activity by the extensor trochanteris and extensor tibia. Retraction commences the cycle once again as soon as the leg has obtained a new point d'appui.

The intrinsic leg muscles thus undergo four phases in the cycle, two of extension and two of flexion. The extrinsic muscles undergo one of promotion and one of remotion. When the leg is placed on the ground and starts to retract, the horizontal strut effect (Barclay, 1946) will tend to retard forward movement of the body, but, as a result of the activity of the remotor muscles, the horizontal lever effect is in the opposite direction and propels the body forwards. When the angle of inclination ($\alpha$) begins to increase again, after its reduction to zero during the earlier stage of retraction, the intrinsic muscles exert an extensor thrust along the axis of the limb. From Barclay's work on the patterns of extrinsic muscle-couples in the locomotion of toads, we should expect the promotor coxae muscles to be active during this latter phase of the cycle so that the horizontal strut and lever effects at the feet are again in opposite directions. If this is so, it can be seen that the change-over from retraction to protraction will be a smooth one because the contraction of the promotor muscles, which follows levation at the commencement of protraction, will have already begun at the end of retraction. This example serves to emphasize the impossibility of describing adequately any movement as a succession of discrete events, because the muscles contract and relax in a complex but more or less regular sequence of activities which grade one into another.

The coxae of the second pair never become perpendicular to the body during walking and hence the strut effect always assists forward movement. Protraction of these legs consists of promotion of the coxa, flexion of the trochanter and slight flexion of the tibia on the femur. The new point d'appui is obtained as the joints begin to extend, and at this instant the limb axis is at right angles to the body axis when viewed from above. Remotion of the coxa gives a lever action for a short time but the main propelling force on the body is produced by extension of the trochanter, and to a lesser extent of the tibia, towards the completion of retraction.

The promotor and remotor movements of the metathoracic coxae are even less than those of the middle pair of legs, and once again the extensor trochanteris and extensor tibia muscles are mainly responsible for the propulsive action of the legs. Evidently the legs of the cockroach can function as levers and inclined struts. The former activity being of greatest importance in the forelegs while the hindlegs are
functioning almost exclusively as inclined struts. This gradation is related to differences in the coxal articulations and musculature affecting the range of angular movements of the coxae (Text-fig. 2 C). This diagram was obtained from photographs of *Blatta* walking over glass and under such conditions of low friction it is

![Diagram](image)

**Text-fig. 4.** Diagrams indicating the forces operating when the insect legs are functioning as inclined struts. A, ventral view; B, side view to show the angle of inclination (α) of the fore limb axis. The force at the tarsi may be resolved into horizontal (H.S.E.) and vertical (V.S.E.) strut effects. C and D, diagrams to show the changes in the relative magnitudes of the lateral components (x, y, and z) of the horizontal strut effects at the *ponta d'appui* of the foreleg, middle and hind legs during the retraction of a triangle of support. Equal and opposite to these components are the forces exerted on the body (X, Y, and Z) which will produce turning-couples on the body. It can be seen that: x<sub>1</sub> < x<sub>2</sub>, y<sub>1</sub> > y<sub>2</sub>, z<sub>1</sub> > z<sub>2</sub> and hence X<sub>1</sub> < X<sub>2</sub>, Y<sub>1</sub> > Y<sub>2</sub> and Z<sub>1</sub> > Z<sub>2</sub>. The body axis will therefore tend to rotate in an anticlockwise direction during the retraction of this triangle of support.

interesting to notice that the legs were held a little more vertical than on rougher substrates.

Only the longitudinal components of the forces acting at the feet have been considered so far because these are concerned in propelling the body forwards.
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The transverse components \((x, y, z)\) are important, however, in determining the lateral displacement of the body (Text-fig. 4). Equal and opposite to these reactions at the feet are the transverse forces \((X, Y, Z)\) operating on the body, and these will produce turning couples which must balance one another if movement is to be rectilinear. This is very nearly so because the path followed by a walking cockroach is almost a straight line. There is a slight deviation, however, as the body axis rotates a little towards the side on which a foreleg is being placed on the ground and then it gradually rotates in the opposite direction during retraction of this leg. A simple hypothesis can be constructed to account for this observation.

If the legs are considered to function as rigid struts along their limb axes, the horizontal strut effects at the tarsi may be resolved into longitudinal and transverse \((x, y, z)\) components. The axial thrust of a limb when functioning as an inclined strut will exert a force on the body which will likewise have transverse \((X, Y, Z)\) and longitudinal components equal and opposite to those at the tarsi. There will be a change in the relative magnitudes of these components during the retraction of the three legs of a triangle which, for the present purpose, may be assumed to retract simultaneously. As the perpendicular distance of the articulations from the centre of gravity \((G)\) remains constant, such changes in the transverse components will determine the pattern of turning couples to which the body is subjected during progression. It can be seen from the geometrical relationships that the transverse component \((x)\) of the foreleg increases while that of the mesothoracic \((y)\) and meta-thoracic \((z)\) legs decreases during the retraction of a given triangle (Text-fig. 4 C). Such a pattern of couples will result in the observed rotation of the body axis away from the foreleg which is on the ground. When the other foreleg is placed on the ground it draws the anterior part of the body towards that side for a short time and then its strut effect brings about a contralateral movement as described above.

This hypothesis is an oversimplification for several obvious reasons. In the first place, the legs are not rigid struts, but can vary their axial thrusts by means of the intrinsic musculature. Secondly, the lever action of the legs which involves the extrinsic muscles has been neglected. And finally, the three legs of a triangle are not retracted synchronously but in the order \(R_1, L_2, R_3, L_1, R_2, L_3, R_1\). A consequence of this rhythm is that the middle leg will be placed on the ground and so exert its maximum turning moment on the body at an instant when the transverse component \((X)\) due to the first leg is increasing. Similarly, the component \(Z\) will be maximal when \(X\) is relatively large. It is apparent, therefore, that these factors will tend to reduce the net turning-moment on the body throughout the whole walking cycle.

Such considerations suggest that the delay between the instant at which the three legs of a tripod are protracted may have functional significance in that it will decrease the oscillations of the body along the direction of movement. It is certainly true that movement is much more rectilinear in insects, e.g. *Chrysomela*, in which the legs move at very nearly equal intervals after one another than those such as *Blaps*, in which the movement of the members of a tripod are only separated by very short intervals.
III. The rhythm of walking movements

The antero-posterior movements of the legs relative to the head can be plotted out from the films. The graphs obtained (Text-fig. 5) show the time relations of the protraction and retraction phases for each leg and the rhythm of the six legs relative to one another. The predominant order of protraction is R1, L2, R3, L1, R2, L3 (Pl. 12), in which the first three legs and the second three are protracted very soon after one another but not simultaneously. This delay between the protraction of the three legs of a triangle is true at all velocities, although it is only apparent at the
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faster ones if the camera speed is increased or flash cinematography employed. The same rhythm is present in films of *Chrysomela, Dytiscus* (Text-fig. 5), *Hydrophilus* and *Blaps*. The former beetle has a more regular distribution of the protractor phases of the different legs, but even here the distinction into two tripods is fairly definite (Text-fig. 5 A). Films also showed that *Carabus* uses this rhythm and that it moves along an almost straight line. The usual diagram (adapted from von Lengerken) given to illustrate insect walking is somewhat misleading, therefore, as it suggests that the path followed by *Carabus* is a very zig-zag one.

At the beginning of this paper it was indicated that the majority of workers have analysed the rhythm of insect and other arthropodan movements into two groups of legs moving alternately. Von Holst (1935) maintained that the following two rules are obeyed by nearly all insects, not only the normal ones but also those from which legs had been removed: (a) adjacent legs of a side alternate; (b) diagonal legs work synchronously. Analysis of films has shown that these rules are not strictly correct. The first is true in principle, but a more important relationship is that the wave of protraction passes forwards along the legs of each side, and in insects no leg is protracted until the one behind has taken up its supporting position. The second rule is plainly false, at least for insects and arachnids, and probably a closer investigation will confirm this in other arthropods.

It is generally possible to distinguish two groups of legs in which the three legs move very soon after one another, but this is not always the case. If a rigid alternation of tripods was employed, only three legs should be supporting the body at any one time during the locomotory cycle. But Text-fig. 3 clearly shows a complete cycle during which there are never less than four legs on the ground at any one instant. In fact, there is one phase (4) when all six legs are supporting the body. Furthermore, the legs of *Chrysomela* are often retracted at almost equal intervals of time after one another, and the distinction into tripods is not so evident, thus: L₃-3.4-R₁-2.7-L₂-2.8-R₃-3.2-L₁-3.1-2-R₂-3.2-L₃, etc. (the figures indicate the average number of frames which separate the protraction of the legs concerned).

Additional evidence is provided by the observation of rhythms which cannot be analysed into such a system of alternating tripods, and these indicate the possible basic units which make up the normal walking rhythm. The drawings in Text-fig. 6 show a cockroach in which the legs are protracted in the rhythm R₃, R₂, R₁, L₃, L₂, L₁, L₃, etc.

Such a rhythm is of rare occurrence especially beneath the photoflood lighting. It has been frequently observed in slowly-moving cockroaches, however, and in slowly moving insects such as aphids after they have been kept at low temperatures. A similar rhythm was also noted by Bert (1866) in dragonflies. In other parts of the film from which Text-fig. 6 was taken, the rhythm L₃, L₂, R₃, L₁, R₂, R₁, L₃, etc. was also found.

From these observations it is concluded that the rhythm of leg movements during normal walking obeys the following two rules:

(i) No fore or middle leg is protracted until the leg behind has taken up its supporting position.

(ii) Each leg alternates with the contralateral limb of the same segment.
It will be noted that the first rule is exactly the same as that which Borelli (1680) suggested would be most advantageous for a hexapod. The rhythm which Paul Bert described for *Carabus auratus* also agrees with this rule, but he was mistaken in supposing that the diagonal middle and hindlegs move simultaneously.

Text-fig. 6. Tracings of photographs from a film of *Periplaneta* walking at an exceptionally slow speed. The rhythm of protraction is R3, R2, R1, L3, L2, L1, etc. 16 frames/sec., every frame.

IV. The changes in limb movements associated with an increase in speed

The recognition of these two rules makes it easier to understand the relationship between the various rhythms discussed above. It can be shown (Text-fig. 7) that all of these rhythms may be obtained in a system obeying the two rules, and in which the ratio protraction time/retraction time \( p/r \) is varied. In Text-fig. 7, \( p/r \) is varied but \( p + r \) remains constant. During insect walking \( p + r \) tends to decrease with an increase in speed, but this does not alter the effect of the increase in \( p/r \). Thus, in the rhythm L3, L2, L1, R3, R3, R1, which is only found when the insects move very slowly, only one leg is off the ground at any one instant and \( p/r \) is about 0.2. If the insect moves faster as a result of a decrease in retraction time which is relatively greater than the decrease in the time for protraction, \( p/r \) will increase and a rhythm similar to that of *Chrysomela* will be followed. It can be seen that with an increase in speed the ratio tends towards unity when a rigid alternation of tripods would result and this was the system stressed by earlier workers. It has been pointed out, however, that a slight delay remains between the protraction of
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the three legs of a tripod even when the insect is moving very fast, and corre-
sponding to this $p/r$ is never quite unity.

An alternative to this system is one in which both $p$ and $r$ are shortened, but $p/r$
and hence the rhythm remains constant at all speeds. In tetrapods such as the newt
and in the cockroach, however, an increase in speed is always accompanied by
a relatively greater decrease in the duration of retraction than of protraction. The
energetics of the muscles involved may determine this feature as such a system is
probably the most efficient.

The rhythm $L_3$, $L_2$, $L_1$, etc., is rarely found, and then only at speeds below
1 cm./sec., but it is very important as it stresses the basic rules of the walking
rhythm. Cockroaches use very nearly the same rhythm ($R_1$, $L_2$, $R_3$, etc.) at all speeds
from 1 to 25 cm./sec., as was found by recording the rhythm for individual cock-
roaches moving at over a dozen different speeds. Graphs showing the rhythm at two
different speeds are shown in Text-fig. 5 B and C. The increase in speed is accom-
panied by a quickening of both the protraction and retraction phases of the cycle,
and $p/r$ increases (see Table 1). There is also a tendency for a decrease to occur in
the stride length, i.e. the movement of the limb tip relative to the head between
complete protraction and maximum retraction. The distance between successive
points d'appui was determined from the films, and by timing the insect walking
over a measured distance of smoked paper and then measuring the distance between successive 'footprints'.

From these observations it appears that the same basic rhythm of leg movements is found at all speeds of cockroach movement, although at the very slowest ones different rhythms may be observed. But these grade insensibly into the normal rhythm with an increase in speed, and no evidence has been found for a distinction between running and walking among insects. It is true that a slowly-moving cockroach immediately moves at a quicker speed when it is suddenly startled. From this observation it might be concluded that these insects are essentially two-speed mechanisms, but this cannot be maintained because many intermediate speeds are also found. This conclusion is contrary to that of Pringle (1939), who suggested that it was physiologically justifiable to distinguish walking and running. This suggestion was based on the description of a double innervation of insect muscle, but recent histological and physiological work (Hughes, 1952) suggests that several cockroach leg muscles are innervated by at least three motor nerve fibres.

**CONCLUSIONS**

The structure and movements of the legs of insects show considerable adaptive modifications so that a description based upon their condition in the cockroach cannot be extended to the whole class. It appears, however, that the rhythm of leg movements is remarkably constant for most orders of walking insects, and this feature strengthens the value of generalizations drawn largely from a study of cockroach movement. The constancy of the rhythm throughout insects, and the observation that the same rhythm is found in other Arthropods when these are rendered hexapodal suggests that it may possess advantages over the other possible sequences of leg movements. A constant pattern of walking movements is also found among Tetrapods, and here Gray (1944) has shown that the rhythm is determined by the mechanics of a four-legged system. He showed from theoretical considerations that it is the only one of the six possible rhythms in which stability is preserved throughout the cycle of leg movements. It is noteworthy that this same rhythm is found in insects which normally walk with four legs. For example, praying mantids use the rhythm L2, R3, R2, L3, L2, etc., when moving slowly with the front pair of prehensile legs off the ground. Similarly, some grasshoppers, and particularly the hopper stages of locusts, in walking adopt the rhythm L1, R2, R1, L2, L1, etc., while the hindlegs are lifted completely off the ground or move in
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a relatively independent rhythm, particularly when the insect is climbing (von Holst, 1943). The change in rhythm following the amputation of legs in the cockroach will be discussed in a subsequent paper, but it is relevant to point out here that the rhythm of a four-legged cockroach again conforms with that of walking Tetrapods.

A slowly-moving hexapod can move one leg at a time in many different sequences and retain stability throughout the cycle. It is evident that with an increase in speed either the rhythm may remain constant but be speeded up uniformly throughout the cycle, or the gait may change as a result of the unequal shortening of different parts of the cycle. Few workers have recognized different gaits in invertebrates, but Manton (1950) has recently given an account of many different gaits in Peripatus. She writes: 'Changes in speed of progression in Peripatus are carried out largely by an alteration in the gait, there being little change in the duration of each pace. In the Myriapoda, on the contrary, changes in speed are mainly effected by alterations in the pace duration, the gait remaining the same.' Insects conform to the myriapodan plan in so far as a shortening of the pace duration accompanies an increase in speed. It has been shown, however, that there are apparent changes in gait which merge into one another, and are the consequence of an increase in the ratio protraction time/retraction time at faster speeds, together with a close adherence to the two basic rules. In insects moving at faster speeds the legs move at almost equal intervals of time after one another. Such a rotary system produces a more uniform velocity than one of strictly alternating tripods, and it is probable that the muscles function more efficiently under the former conditions, particularly at the slower speeds. As in Peripatus, the gaits at faster speeds ensure fewer contacts with the ground at any one instant. The same is true of the horse in rapid motion, but the insect never has fewer than three legs on the ground, and hence even at the most rapid speeds it is mechanically stable should it stop at any instant during the cycle of movements. As this static stability cannot be achieved with fewer than three legs on the ground, it is apparent that in insects contacts with the ground have been reduced to the minimum number with which this is possible. This feature of their locomotory mechanism is no doubt responsible, in part, for the 'alertness' which we associate with all insects, as it enables them to stop suddenly or to change direction without needing to slow down.

This account has largely substantiated Borelli's view that the three ipsilateral legs should be lifted in the order hind, middle, fore. The only other possibility is one in which the wave of protraction moves backwards, and it can be shown that this has several disadvantages. If we assume that the order of protraction was fore, middle, hind, then it is evident that the rule would be that no leg should move before the leg in front had taken up its supporting position. This is obvious on considering the stage when the foreleg is off the ground, because otherwise the middle leg would also be lifted and the almost fully retracted hindleg would be quite insufficient to support the weight of the body on that side of the insect. The rhythm R3, L2, R1, L3, R2, L1, R3 obeys the rule, and is the reverse of the normal one. Such a rhythm would be stable at slow speeds, but it has the inherent disadvantage that the powerful propulsive stroke of the hindleg takes place before
the more anterior parts of the supporting base have been established, and for this reason it might be unstable at more rapid speeds. This is most clear if we again consider the instant at which R1 is lifted. At this moment L2 will be about to be placed on the ground and R3 will be exerting its maximum lateral thrust. In the other triangle L1 will be half retracted, R2 more retracted and L3 almost fully retracted as it would be the next leg to protract. The area of support is depicted in Text-fig. 8B, where it can be seen that the anterior edge of this is determined by L1 and R2, both of which are more than half retracted. Furthermore, R3 is exerting its maximum thrust, and there is no support in front of the centre of gravity on this side of the body where the need is probably greatest because of the turning moment resulting from the activity of the hindleg. Contrast this with the condition in the normal rhythm (Text-fig. 8A) where fore and middle legs of a given triangle have both commenced their active strokes and are in a supporting position before the hindleg exerts its maximum thrust. This system greatly lessens the danger of the centre of gravity falling outside the area of support even at the most rapid speeds and its advantage in bringing about a more rectilinear motion has already been considered.

From these considerations it appears that not only does the possession of six legs enable one pair to be adapted for another purpose, but also their rhythm is such that the animal can grade its speed, using presumably the same neuromuscular mechanism, and automatically reduce the number of contacts with the ground while retaining static stability at all speeds.
SUMMARY

1. An account is given of the functional morphology of the coxal articulations in the cockroach. The greater range of movements executed by the prothoracic legs is made possible by the mobility of the trochantinal condyle relative to the episternal condyle.

2. The movements of the individual legs were studied by means of films taken at speeds of 16-32 frames/sec. These show that more than three legs are in contact with the ground throughout the cycle of movements at normal speeds. Suggestions are also made concerning the mechanics of walking, but these require experimental verification.

3. The rhythm of walking movements in Periplaneta, Blatta, Dytiscus, Hydrophilus, Carabus, Blaps and Chrysomela obeys two rules: (i) no foreleg or middle leg is protracted until the leg behind has taken up its supporting position; (ii) each leg alternates with the contralateral one of the same segment. Other pterygote insects appeared not to differ from the species studied in any essential feature.

4. An increase in speed is accompanied by a decrease in the times of both protraction (p) and retraction (r), a shortening of the stride length, and an increase in the distance between the successive points d'appui. The range of speeds is continuous and no distinction could be recognized between walking and running.

5. Several gaits have been observed, the most common order of protraction being R₁, L₂, R₃, L₁, R₂, L₃, R₁, etc., but these grade into one another if the ratio p/r is altered and the two rules obeyed. A system of rigidly alternating tripods would result if the ratio p/r was unity, but this is never quite realized as there is always a delay, sometimes extremely short, between the protraction of the three legs of a triangle. At very slow speeds the rhythm R₃, R₂, R₁, L₃, L₂, L₁, R₃, etc., may be present.

6. It is concluded that insects are the end-product of a process of limb reduction among terrestrial Arthropoda in which p/r may be increased to nearly one and yet the animal retains static stability throughout the whole cycle. This is impossible with fewer than six legs.

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REFERENCES


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EXPLANATION OF PLATE 12

A series of photographs from a ciné film of Blatta during normal walking. The rhythm of protraction is R1, L2, R3, L1, R2, L3, R1, etc., 24 frames/sec., every frame.