MOTOR ACTIVITY DURING WALKING IN THE COCKROACH *PERIPLANETA AMERICANA*

I. FREE WALKING

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INTRODUCTION

In recent years increasing attention has been directed to the problem of the control of leg movement and co-ordination during locomotion in arthropods, especially at the behavioural level (cockroaches, Delcomyn, 1971*a*, *b*; locusts, Burns, 1973; stick insects, Graham, 1972; Wendler, 1966; crabs, Clarac & Coulmance, 1971; spiders, Wilson, 1967). However, only a few reports have appeared describing the patterns of motor activity which underlie leg movements during normal walking (Hoyle, 1964; Ewing & Manning, 1966; Usherwood, Runion & Campbell, 1968; Pearson, 1972). A detailed, quantitative description of such patterns during normal, unrestrained walking would be invaluable in helping us to understand how appropriate sequences of nerve impulses, and hence of leg movements, are generated, by providing quantitative data on which to base detailed models of the system. It would also provide important data to which patterns of neuromuscular activity in tethered or otherwise disturbed preparations might be compared, in order to elucidate mechanisms of neural control of walking.

The experiments described herein were undertaken in order to serve these functions through a study of the patterns of activity in selected metathoracic leg muscles during unrestrained walking in the American cockroach, *P. americana*. The principal results, which complement the work recently reported by Pearson (1972), support current models of mechanisms underlying stepping movements in individual legs (Pearson & Iles, 1970; Delcomyn, 1971*b*), and provide a base of data to which the patterns of neuromuscular activity in tethered cockroaches may be compared (Delcomyn, 1973).

MATERIAL AND METHODS

The preparation

Adult cockroaches, *Periplaneta americana*, of either sex, were used in these experiments. The recording methods were based on those described by Hoyle (1964) and Runion & Usherwood (1966), and were similar to those employed by Pearson (1972). Animals were first lightly anaesthetized with CO_2. Fine copper-wire electrodes (49 gauge, about 35·6 μm diameter), insulated except for the tip, were pushed through small holes in the cuticle on to or near the appropriate muscle. Muscle units which were

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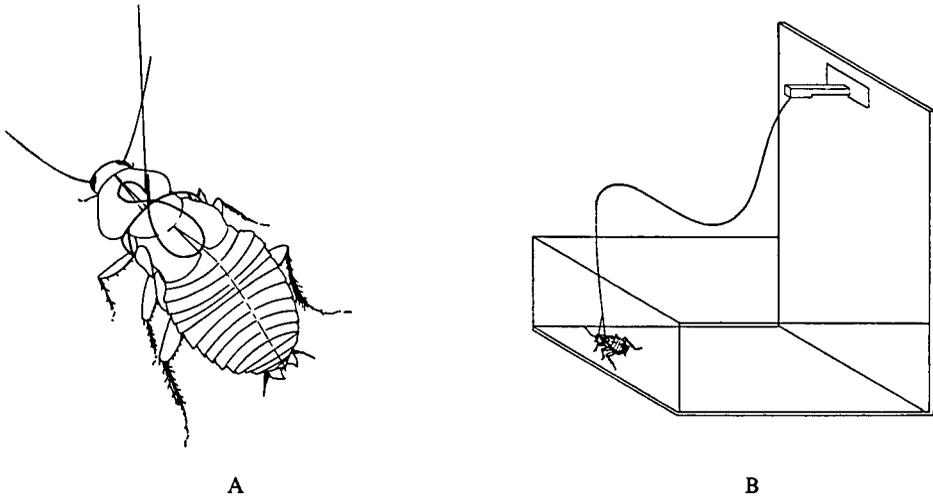<p style="text-align:center">A   B</p>

Fig. 1. The experimental arrangement. (A) A cockroach, wings removed, showing the metal framework in the shape of a horizontal figure eight and short vertical rod, attached to the dorsum of the animal to support the electrode wires. (B) The walking platform. The leads were sufficiently long to allow the animal to reach any spot on the platform. Petroleum jelly on the sides of the Lucite restraining wall prevented the escape of the animal.

continually active could be found repeatedly and reliably by keeping the preparation only partly anaesthetized during implantation and listening for the active unit on an audio monitor during implantation (M. D. Burns, personal communication). Each electrode was anchored at the point of passage through the cuticle by a small drop of melted wax. To increase strength, the wires were twisted together to form a cable, and anchored to a small wire frame fastened to the animal's back (Fig. 1A). The cable of electrodes (comprising 2 pairs from each rear leg) was further strengthened by the presence of a piece of thin monofilament fishing line, whose relative rigidity prevented excessive twisting of the wires as the animal moved about. When all electrodes had been implanted, the animal was placed on an earthed metal plate surrounded by a Lucite restraining wall (Fig. 1B). Recordings of muscle activity were taken as the insect walked about on the platform. Usable records could be obtained from animals prepared in this way for as long as three days in favourable preparations. Except for a slight deterioration in the quality of the recording there were no detectable differences between such records and records taken from freshly prepared cockroaches.

The recorded electrical signals were amplified and displayed on a Tektronix 565 oscilloscope. Permanent records were obtained by photographing the oscilloscope face with a Grass C4 camera. In addition, the movements of the animal were photographed simultaneously with a Bolex H-16 motion picture camera at a maximum filming rate of about 64 frames/sec. Timing pulses from the opening of the shutter for each frame were displayed on the oscilloscope with the records of muscle activity so that leg movements could be correlated with observed muscle activity (Burns, 1973).

<p style="text-align:center">Motor units</p>

Recordings were made from the main flexor (levator) and extensor (depressor) muscles in the coxae of the metathoracic legs. The main functional extensors are

muscles 178, 179, 177d, and 177e (Carbonell, 1947). Muscles 178 and 179 are innervated only by a single 'fast' axon shared with 177d and 177e (Pearson & Iles, 1971). The smaller muscles 177d and 177e receive, in addition to the 'fast' axon, a single 'slow' axon (D_s of Pearson & Iles, 1970) and three inhibitory fibres (Pearson & Iles, 1971). Muscle activity due to the 'slow' and 'fast' axons may easily be recorded with electrodes inserted near the medial edge of the ventral surface of the coxa. The activity of the two can readily be distinguished on the basis of differences in the relative rates of rise and decay and differences in amplitudes. Activity due to axon D_s rises and decays more slowly, and is of lower amplitude than that due to the 'fast' axon (Pearson & Iles, 1970). The muscle potentials due to D_s could usually be related directly to the activity of the axon on a one-to-one basis, since small nerve spikes could be seen preceding each muscle potential in most records. In such records neither nerve spikes nor muscle potentials were ever observed alone. It was therefore assumed that for records in which nerve spikes were not detectable, due presumably to an unfavourable position of the recording electrodes, each muscle potential nevertheless represented one spike in D_s.

The main functional flexors, according to Carbonell (1947), are the 181 group. The innervation of this group has never been studied in detail, but the work of Becht (1959) and Usherwood (1962) on the homologous muscles of the mesothoracic leg (m. 139) suggests that the innervation is complex, with at least one 'slow' and several 'fast' fibres. In addition, Pearson & Bergman (1969) report at least four 'fast' axons in m. 181. The source of the potentials obtained from muscle 181 could be classified as 'fast' or 'slow' through application of the same criteria as those used for extensor activity. Potentials in these flexor muscles could not be recorded with the same ease and degree of repeatability as those in the extensors. For this reason, and also because of the uncertainties of the innervation, no attempt was made to identify activity due to the individual axons beyond the 'slow' and 'fast' identification.

Analytical methods

Analysis of the results was carried out with the aid of a digital computer. Measurements were made of the distances of each muscle potential from an arbitrary origin point on the film record. These measurements were punched on to computer cards and submitted for analysis by computer. The computer program calculated interimpulse durations for each pair of impulses and generated a plot of interval duration against elapsed time (that is, a plot of sequential time intervals; e.g. Fig. 5). The times of occurrence of leg movements were also given to the program so that electrical activity could be related to leg movement. The program also searched the data for the occurrence of bursts of impulses. Bursts were identified in the following way: when any interval was found to be at least four times the average duration of the following two, the first impulse of the first short interval was taken as the first impulse of the burst. (By definition, then, no burst consisted of less than three impulses.) Successive intervals were then compared to a cumulative average of durations until one was found which exceeded the average by a factor of four. The first impulse of the pair forming this long interval was taken as the last impulse in the burst. In order
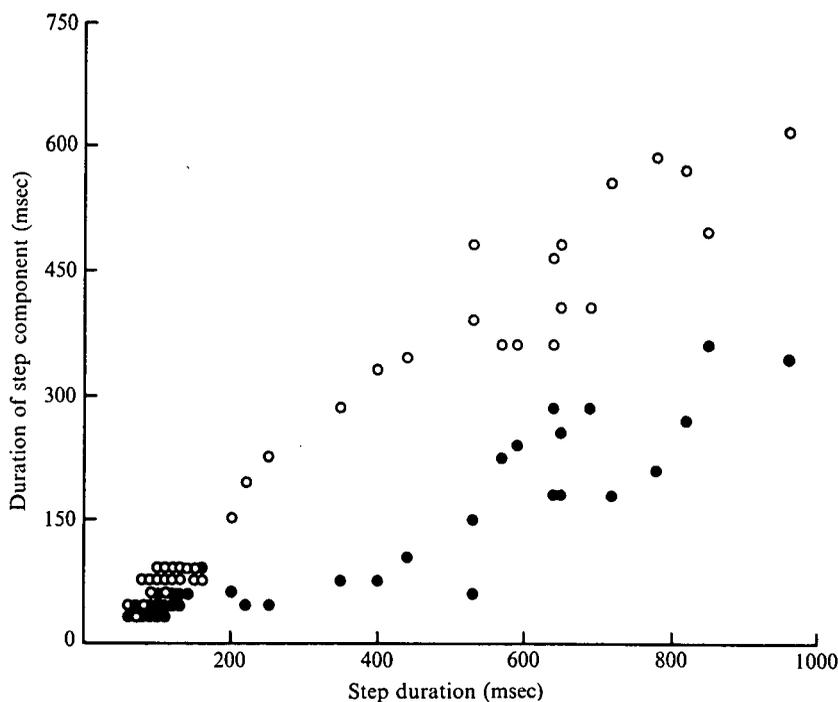
Fig. 2. The relationship between durations of protraction (filled circles) and retraction (open circles) and step duration for free-walking animals. In this and all subsequent plots over-lapping points are shown as one only. The slope of the best-fit regression line for each of the two groups of data ±S.E. of the mean is: retraction, 0·692±0·012; protraction, 0·308±0·012.

to ensure exclusion of bursts in which the duration of intervals gradually increased to values much larger than those with which the burst began, due to a rapid and steady reduction in speed of walking, a test for intervals between three and four times the duration of the running average was made. Groups of impulses for which this condition was met were excluded from computations of burst properties.

RESULTS

Observation of cockroaches as they moved about the recording platform gave no indication that the insects were in any way hampered by the recording electrodes or the metal support frame. Examination of filmed records of movements about the platform supported this impression. No parameter of stepping behaved in any way differently in these animals as compared with animals which had no frame or elec-trodes to carry. Fig. 2 shows the relationship between durations of protraction and retraction and step duration for the experimental animals. Similar relationships have been obtained for free, intact cockroaches (Delcomyn, 1971 a), locusts (Burns, 1973), and stick insects (Graham, 1972).

The muscles selected for study were the main functional extensors (depressors) and flexors (levators) of the femur (Carbonell, 1947). In the rear legs flexion of the coxo-trochanteral joint occurs exclusively during forward movement (protraction)
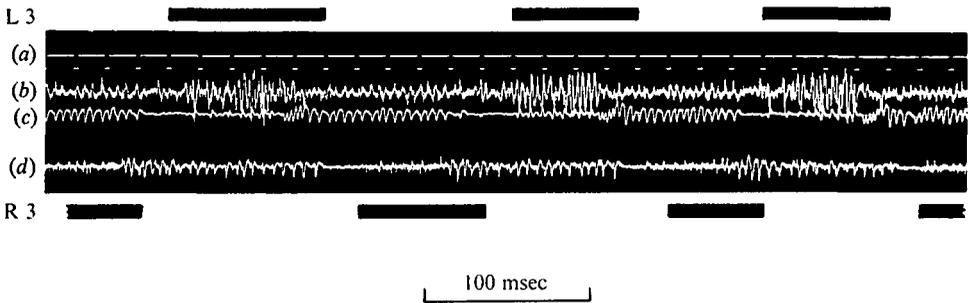
Fig. 3. Electrical activity in coxal muscles of rear legs during free walking. The black bars above and below the record represent the time during which (top) leg L3 and (bottom) leg R3 protract (flex). Traces: (a) ciné camera synchronization marks, signalling shutter open; (b) Activity of flexor muscles 181b, 181c, leg L3; (c) Activity of extensor muscles 177d, 177e, leg L3; (d) Activity of extensor muscles 177d, 177e, leg R3. Notice that at this speed of locomotion (about 5–7 steps per sec) leg movement lags behind muscle activity. (Muscle potentials retouched.)

of the leg, extension of the joint exclusively during rearward movement (retraction). When the insect is not moving the body weight is usually at least partly supported by the legs. In the rear legs much of the load is carried by the femoral extensor muscles. Records of muscle activity during standing substantiate this view. Muscle impulses due to the 'fast' extensor or 'fast' flexor motoneurones were never observed in stationary cockroaches and 'slow' flexor activity was usually associated only with visible shifts in posture by the animal. The 'slow' extensor motoneurone (axon D_s of Pearson & Iles, 1970), on the other hand, was continually active for long periods of time. The frequency of firing of the axon was quite variable, depending on what the cockroach had been doing just before the observation, but it usually fired at rates below 30 impulses/sec. As a period of inactivity after walking lengthened the frequency gradually fell, until after about 10–15 min activity often ceased altogether. Behaviourally the cockroach at this point was crouched down, apparently with its entire body resting on the walking surface. Disturbing the animal at such a time (for example, by tapping the running platform) usually caused it to lift its body off the platform as if in preparation for walking, and also caused immediate activity in D_s. Puffs of air or more vigorous disturbing stimuli initiated running.

The most prominent and consistent feature of the activity of the coxal leg muscles during walking was the occurrence of reciprocal bursts of activity in the flexor and extensor muscles (Fig. 3). This feature was completely independent of the speed of locomotion. Burst activity during walking has also been reported by Pearson (1972) and Ewing & Manning (1966) in cockroaches, by Hoyle (1964) in the grasshopper *Romalea*, and by Usherwood *et al.* (1968) in the locust *Schistocerca gregaria*. In agreement with Pearson's results, there was no sign of continuous activity in either flexor or extensor muscles, in contrast to the earlier reports of Ewing & Manning (1966) and Hoyle (1964). It should be noted, however, that in both of these latter studies only the activity of the extensor and flexor tibiae muscles were examined, and these may be controlled in a slightly different fashion from the coxal muscles under investigation in the present study.

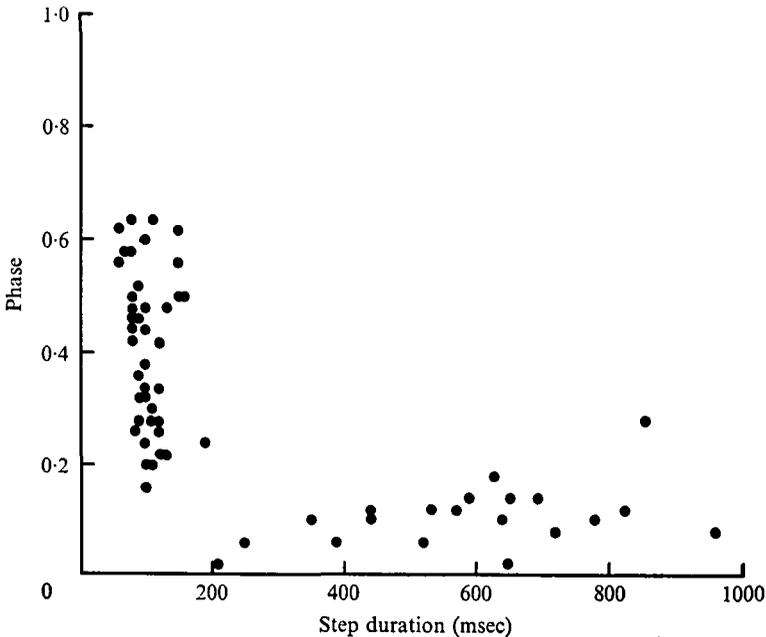Muscle activity due to the action of 'slow' extensor and flexor motoneurones was

Fig. 4. The overlap of the beginning of extensor bursts on the flexion movement of the femur as a function of the duration of the whole step. The overlap was determined by calculating the phase of the start of the burst relative to the flexion movement. The value of the phase signifies the extent of the overlap. The phase is zero if the extension burst began as flexion ended, 0·5 if the burst began half way through the flexion movement. Phase values greater than 0·65 have been omitted from the plot since they are reflexions of inaccuracies in determining the exact time of the start and end of flexion. The ciné film at best allowed resolution only to ±8 msec, while at high stepping speeds the duration of the flexion movement might be only 20–30 msec. Resulting errors could be as high as 50 %. Other methods of measuring leg movement always yielded phase values less than 0·65 and rarely over 0·45 (Delcomyn, 1973).

always grouped into bursts separated by silent periods, as was that due to 'fast' flexor motoneurones. The latter always showed activity synchronously with 'slow' flexor activity, but were recruited only at higher speeds of walking. At moderately low speeds of walking (approximately 5–8 steps per sec) only one or two impulses, if any, appeared, and at walking speeds below about 5 steps per sec, impulses due to the activity of a 'fast' flexor axon were extremely rare.

No activity due to the action of the single 'fast' extensor motoneurone was ever observed during walking. This axon, D_f of Pearson & Iles (1970), is the only axon innervating the large extensor muscles 178 and 179, and it also innervates parts of m. 177d and 177e (Pearson & Iles, 1971). Pearson (1972) reported activity of this axon during rapid walking. No explanation of the failure to confirm Pearson's results can be given.

The reciprocal bursting of the 'slow' extensor and flexor motoneurones was closely synchronized with leg movements during slow walking. That is, extension or flexion of the femur began as the corresponding muscles became active, or shortly thereafter, and ended as the muscles ceased their activity. However, at higher speeds of loco-motion, a clear lag between the onset and cessation of electrical activity and the onset and cessation of the appropriate movement developed. That is, the electrical activity
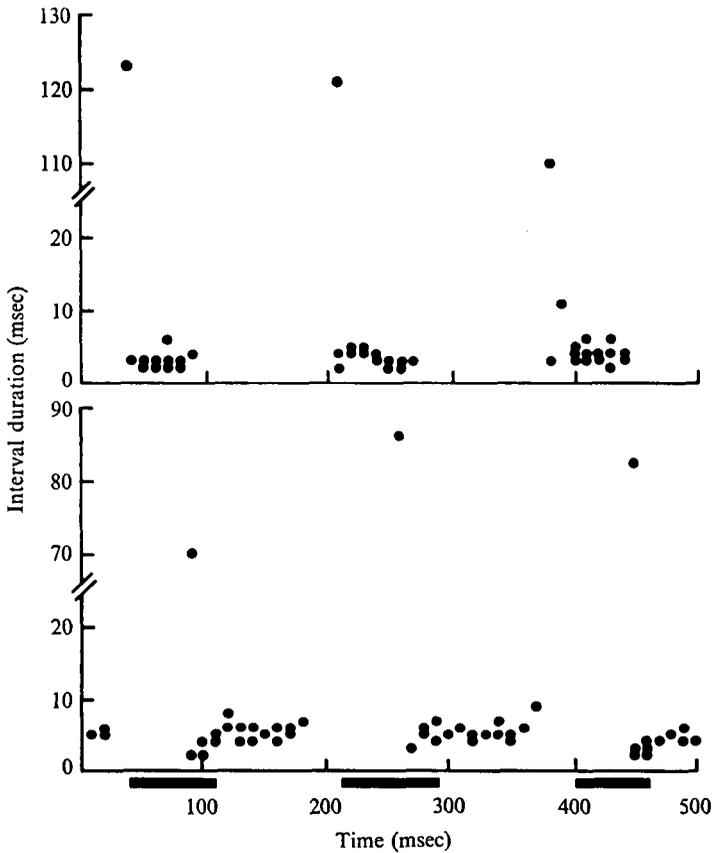
Fig. 5. Sequential time plot of intervals from leg L3. Record shown in Fig. 3. Top: Flexor intervals. Bottom: Extensor intervals. The solid bars under the abscissa represent the period of protraction of leg L3. Notice the groups of alternating bursts in both flexor and extensor.

in, for example, extensor muscles began before the preceding flexion movement was complete, and ended before extension was complete. The magnitude of the overlap between the start of the extensor burst and the flexion movement in progress was determined at different speeds of walking by calculating the phase of the beginning of the burst relative to the flexion movement of the femur; the phase would thus be zero if the burst began just as flexion ended (and extension began), and increasingly greater than zero as the burst began earlier relative to the flexion movement. The relationship is shown in Fig. 4. As step durations became shorter during faster walking, the phase increased, so that at the highest speeds of locomotion the electrical activity in the extensors sometimes began before the leg was half way through its flexion movement (phase greater than 0·5). Thus, at high speeds of leg movement much of the energy output of the muscle would seem to be expended in overcoming inertia in reversing the direction of leg movement.

Since the relative timing of flexor and extensor activity in a single leg, and of activity in other legs, is unaffected, the phenomenon has no direct bearing on problems of central generation of patterns of co-ordination. However, reflexes triggered by leg movements would occur at different stages of the muscle activity in slow walking

as compared with fast walking if the reflexes are phase-locked to the movement(
Wilson (1965) described such a phase-locked reflex. A similar reflex described by
Delcomyn (1971 c) exhibited a shifting phase of the response, but in the opposite
direction from the shift of the normal motor activity relative to leg movement. It
seems unlikely, therefore, that these leg reflexes contribute significantly to leg move-
ment during fast locomotion.

Sequential time plots such as that illustrated in Fig. 5 were examined for each
analysed record in order to determine whether there were any systematic non-uni-
formities in discharge rates within each burst. While flexor bursts usually had fairly
uniform discharge rates, one portion of extensor bursts often had a somewhat higher
or lower rate than the average in the whole burst. However, such variation in dis-
charge rate did not appear to be related to any other variable of burst activity; the
higher or lower rate seemed to occur as often at the beginning of the burst as at the
end or in the middle. Variations in discharge rates within a burst usually occurred
only during slower walking. Higher discharge rates at the end of the extension burst
during such slow walking (also reported by Pearson, 1972) could be a manifestation
of reflex activity (Delcomyn, 1971 c). Other variations may have been due to momen-
tary changes in the animal's speed of locomotion. If a cockroach suddenly slowed or
quickened its steps, an immediate change in the frequency of discharge in an ongoing
extensor burst was apparent. Severe changes of this sort were automatically excluded
from analysed data, but smaller changes were not, and these could account for some
of the observed variations in discharge rate.

Burst parameters

Muscle activity due to the 'slow' extensor motoneurone D_s and the 'fast' flexor
axon(s) were selected for detailed study in order to obtain quantitative data for a test
of a model of step generation proposed earlier (Delcomyn, 1971 b). Three parameters
of burst activity were chosen for examination: the duration of each burst, the number
of impulses in each burst, and the mean interval between impulses in each burst.

Extensor bursts. The relationship between each of the parameters and the duration
of the associated step for slow extensor bursts is shown in Fig. 6. In each case there
is a strong positive correlation between the parameter and step duration. That is,
when the animal walked slowly (long step durations) the duration of the extensor
burst, the number of impulses in it and the mean interval between them were all
greater than when the animal walked more rapidly. This held true for all animals
in which the relationships were examined in detail. In addition, however, in many
cases the relationships could be demonstrated to be non-linear. That is, the rate of
increase of the number of impulses per burst, and the mean interval per burst as step
duration increased, were greater over the range of step durations from 40 to about
250–333 msec than from 250–333 msec to the slowest steps (1–2 sec). The burst-duration
parameter was also often non-linear, but it had a lower rate of increase over the short
step durations than over the longer ones.

In general, the relationships shown in Fig. 6 held for all preparations, although
quantitatively there was sometimes some variation, such as small differences between
preparations in the rate of change of parameters. It may well be, therefore, that while
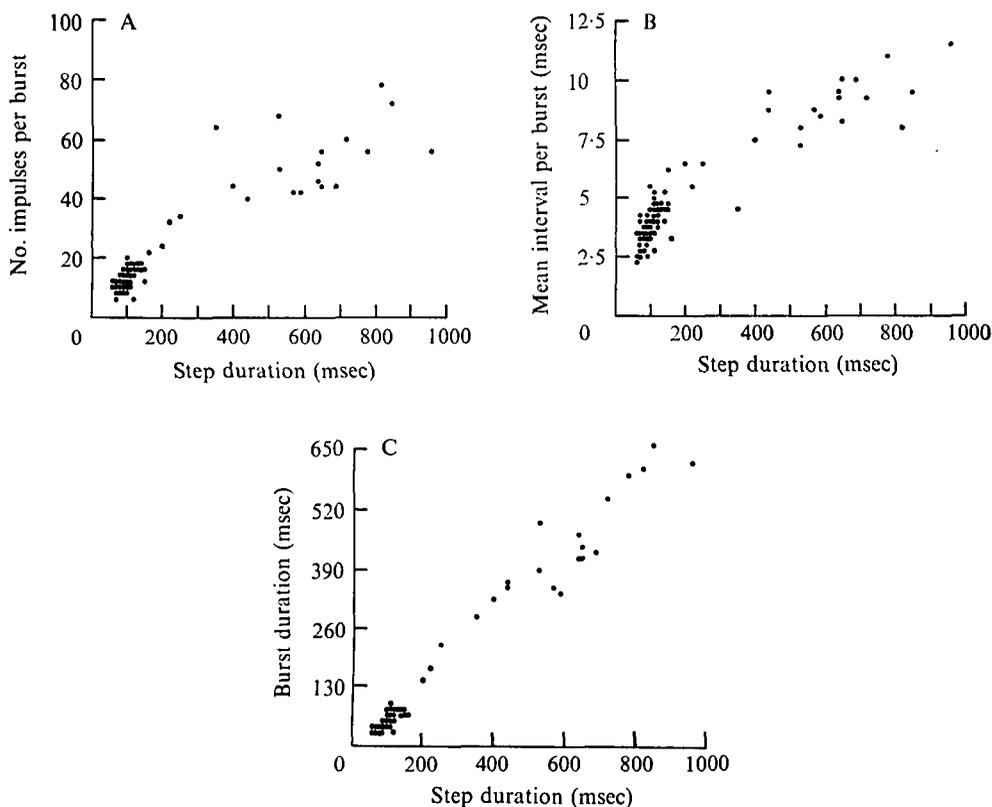
Fig. 6. Burst parameters as a function of step duration for 'slow' extensor bursts. (A) Number of impulses per burst. (B) Mean interval per burst. (C) Burst duration. Notice in A and B the clear reduction in rate of change at step durations of about 250–333 msec. The differences in the slopes of the regression lines fitted to the data above and below 300 msec were highly significant statistically ($P \ll 0.01$) for both plots.

qualitatively all cockroaches employ the same system of motor pattern generation, there are slight differences in the quantitative relationships between them in different individuals. Developmental differences could also exist, for although all experimental animals were adults, elapsed time since the last moult was not controlled.

Flexor bursts. Bursts of muscle activity due to the action of 'fast' flexor axon(s) showed some of the same relationships with the step duration as shown by 'slow' extensor bursts, but generally considerably less strongly, and in some cases not at all. For example, a weak positive correlation between mean interval per burst and step duration often could be demonstrated (Fig. 7A), but a correlation could not be demonstrated for the relationship between burst duration and step duration, or between number of impulses per burst and step duration. One factor influencing these relationships may have been a tendency for the number of impulses in a burst and the burst duration to be influenced by the duration of the preceding step. In several cases in which there was a clear decrease in step duration from one step to the next, there was also an unusually long burst of 'fast' flexor activity during protraction in the shorter (faster) step. Such an effect would clearly act to obscure any underlying positive correlation between number of impulses or
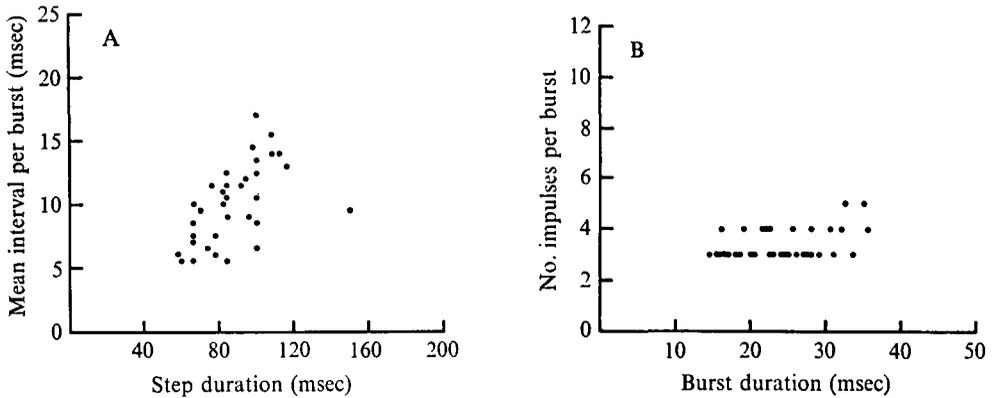
Fig. 7. (A) Mean interval per burst as a function of *step* duration for 'fast' flexor bursts. There is a weak ($r = 0.340$) but significant ($P < 0.05$) positive correlation between the two parameters. (B) Number of impulses per burst as a function of *burst* duration. Here as well there is a positive correlation ($r = 0.399$) which is statistically significant ($P < 0.025$).

burst duration and step duration. Other possible contributing factors are considered in the Discussion.

While the number of impulses per burst could not be correlated with step duration, a positive correlation between the former and burst duration could be demonstrated (Fig. 7B). This suggests that the parameters of 'fast' flexor bursts may depend on step duration in much the same way as do those of 'slow' extensor bursts, but that a weak relationship between burst duration and step duration, obscured by large variability, small sample size and limited sample range, and therefore undetectable by the statistical methods used in this study, also prevented a clear demonstration of the underlying relationship between these parameters, that is, mean interval and number of impulses per burst, and the step duration.

DISCUSSION

The results presented in this paper, together with the recent work of Pearson (1972) provide additional support for recent models of the mechanism of step generation in cockroaches (Pearson & Iles, 1970; Delcomyn, 1971b). All available evidence suggests that burst activity in metathoracic coxal muscles, at least, is always reciprocal in free-walking preparations. Modulated activity of one muscle acting against a continuous barrage in its antagonist, such as described for the tibialis muscles in the grasshopper (Hoyle, 1964) and several cockroaches (Ewing & Manning, 1966) has never been observed in coxal muscles of free-walking cockroach preparations. Thus, the gross features of the observed pattern of motor output are the same as those required by the model.

The qualitative details of the motor output are also the same. The basic mechanism of the model is that the frequency of a continuous central command sets the burst period and the duration and discharge rate of each burst, so that at higher command frequencies the burst period and duration are shorter (the discharge rate higher) than at lower frequencies of command. Thus, the model predicts a strong positive correlation between burst period (and thereby step period, or duration) and burst duration

▶nd mean interval per burst (the reciprocal of discharge rate). In general, this is just what one finds (see, for example, Fig. 6). The data thus support the model.

There are, however, two features of the results which warrant further considera-tion. The first of these is the apparent weak relationship between the parameters of the 'fast' flexor bursts and step duration. The model does not as it stands predict any qualitative difference between the properties of extensor or flexor bursts, or between bursts due to 'fast' or 'slow' axons.

However, there are several features of flexion and 'fast' activity which tend to obscure or weaken dependencies of 'fast' flexor burst parameters on step duration. Protraction duration (the flexion movement of the leg) increases as step duration increases, but considerably less rapidly than does retraction duration (Fig. 2). Thus, any changes in burst parameters which are dependent on protraction duration, such as burst duration, for example, would tend to be less strongly correlated with the duration of the entire step than would changes dependent on retraction duration, especially in the face of a background of natural variability. Compounding the prob-lem caused by these less obvious changes is the fact that the 'fast' flexor motoneurones are in general only recruited at step durations of less than about 200 msec. Thus, a large range of step durations, from 200 msec to over 1000 msec, is excluded from the data, again acting to make difficult the demonstration of any underlying relationships.

These factors tend passively to obscure positive correlations between step duration and burst parameters. Other factors actively operate against their expression. Be-cause the 'fast' axons are recruited only during the faster (i.e. shorter) steps, there is clearly a tendency for this threshold effect to *limit* 'fast' burst durations at steps near threshold, while the burst-generating mechanism tends to increase them. Any attempt to demonstrate one effect can only be hindered by the action of the other. The apparent tendency for the 'fast' burst duration to be influenced by the duration of the previous step as discussed in the Results also works against the expression of a simple positive correlation. In view of these factors, each tending in its own way to prevent the appearance of the same clear-cut correlations between step duration and burst parameters in 'fast' flexor bursts as appear in extensor bursts, it does not seem necessary to reject the model due to lack of close conformity by 'fast' flexor bursts.

The second unexpected feature of the data is more difficult to understand, yet also more interesting. Examination of Fig. 6 suggests that the rate of change of both mean interval per burst and number of impulses per burst as a function of step duration is greater for steps lasting less than about 300 msec than for those longer than this. Statistical tests of the independence of the slopes of the best-fit regression lines of the data above and below 300 msec steps showed highly significant differences. The phenomenon is not restricted to burst parameters. The dramatic change in slope of the phase plot shown in Fig. 4 also occurs at step durations of about 250–333 msec. It may be, therefore, that there is a subtle but fundamental difference in the function of the step-generating mechanism at stepping frequencies above and below 3–4 steps per sec. It is therefore of great interest that this frequency of stepping is the lowest at which the alternating triangle gait has been observed (Delcomyn, 1971*a*). At walking speeds lower than this the gait shifts to other patterns.

If the phenomenon of abrupt rate changes in the functions of some burst para-▶meters at stepping frequencies of 3–4/sec is of such general importance, its presence

ought to be observable elsewhere as well. Suspending a cockroach and allowing it to walk on a small Styrofoam ball does not abolish it (Delcomyn, 1973). The rate change still occurs at steps of approximately 250–333 msec, in both burst-parameter plots and phase-shift plots. The phenomenon can also be seen in the data presented by Pearson (1972), although he does not mention it and in fact draws continuous curved lines through his data. See especially his Figs. 5–7.

What might the functional significance of the phenomenon be? An especially appealing hypothesis is that it signals the switch from walking to what might be termed 'ambling'. While cockroaches have a wide range of walking speeds (Delcomyn, 1971*a*), it is generally difficult to obtain sequences of several steps at the very low speeds (less than 4 steps per sec). A very slowly walking cockroach is frequently exploring its environment, testing the walking surface with its antennae or maxillary or labial palps, turning from side to side, etc. It thus usually takes only one or two steps with any one leg before stopping again. Anthropomorphically speaking, it does not appear to want to go anywhere. During walking at higher speed, however, the insect usually takes many steps in succession before stopping, and appears to pay less regard to its environment. On a behavioural basis, therefore, very slow walking might better be termed ambling to distinguish it from the apparently more purposeful locomotion at higher speeds. A similar dichotomy between apparently purposeful walking and ambling has been described in first-instar stick insects (Graham, 1972).

The behavioural and physiological switch at 3–4 steps per sec could be due to the activation of central command fibres whose action results in, among other things, higher discharge rates in motoneurone bursts, and through their action on co-ordinating mechanisms, in a switch to the alternating triangle gait. These command fibres would operate in addition to the basic command which controls stepping of the leg, since the latter must operate even at low stepping rates.

Davis & Kennedy (1972) have demonstrated in the lobster swimmeret system the presence of command interneurones whose primary effect is on frequency within a burst, leaving the burst period unaffected. Similar interneurones may be present in the cockroach.

SUMMARY

1. The patterns of electrical activity of selected muscles of the rear legs were studied during locomotion in unrestrained, freely moving cockroaches.

2. During walking, muscle potentials in both extensor and flexor muscles were always grouped into bursts separated by periods of silence, with one burst occurring per step.

3. During very slow walking, the occurrence of flexor and extensor bursts was synchronized with, respectively, the flexion and extension movements of the leg. At increasingly greater speeds of locomotion, the movements of the leg lagged increasingly behind the muscle activity, so that during very fast walking the extensor or flexor burst often began while the preceding leg movement was not quite half completed.

4. 'Slow' extensor and 'fast' flexor bursts were studied in detail. The frequency of impulses within each extensor burst was usually steady, but sometimes declined in the middle or increased at the end of a burst. Frequency within 'fast' flexor bursts

was often more varied, but there was no systematic change in frequency with any other parameter which was examined.

5. For 'slow' extensor bursts, the duration of each burst, the number of impulses per burst and the mean interval between impulses in a burst each increased significantly as the duration of the associated step increased, i.e., there was a positive correlation between each pair of parameters. The rate at which the number of impulses per burst and mean interval per burst changed as a function of step duration was often significantly higher for steps shorter than about 300 msec than for longer ones.

6. For 'fast' flexor bursts, the duration of each burst, the number of impulses per burst and the mean interval per burst were each extremely variable; a weak correlation with step duration could only be demonstrated for the latter. However, both mean interval and the number of impulses per burst were positively correlated with the duration of the burst from which they were taken.

7. The data qualitatively support current models of step generation in insects, but also suggest that a useful distinction could be made between very slow walking (below 3–4 steps per sec), termed ambling, and faster walking.

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