

MOTOR ACTIVITY DURING WALKING IN THE COCKROACH *PERIPLANETA AMERICANA*

II. TETHERED WALKING

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INTRODUCTION

Reasonably detailed knowledge concerning the mechanisms of regulation of simple behaviour in insects is now available for a number of systems (see Hoyle, 1970, for review). Generally speaking, this knowledge has been accumulated through studies at several organizational levels: the behavioural, the neuromuscular, and the central neuronal, often for both intact animals and those subjected to various experimental manipulations. Some of the systems of which we now have some understanding include locust flight (Wilson & Weis-Fogh, 1962; Wilson, 1961; see also review by Wilson, 1968), grasshopper courtship (Elsner, 1968; Elsner & Huber, 1969) and cricket singing (Ewing & Hoyle, 1965; Bentley & Kutsch, 1966; Bentley, 1969). Walking is a form of behaviour which until recently has received attention primarily on the behavioural level (e.g., Hughes, 1952, 1957; Delcomyn, 1971*a, b*; Burns, 1973; see also review by Wilson, 1966). Pearson & Iles (1970) have provided information on the patterns of motor output in partly de-afferented cockroach preparations, but until very recently no studies had been made on the patterns of motor activity in intact animals free to move about (Hoyle, 1964; Ewing & Manning, 1966; Usherwood, Runion & Campbell, 1968; Burns & Usherwood, 1973; Delcomyn & Usherwood, 1973) or in free animals subjected to any kind of experimental manipulation (Usherwood *et al.* 1968; Pearson, 1972).

The experiments described in this paper were undertaken in order to provide detailed, quantitative information concerning the effect on motor output patterns of allowing cockroaches to walk by holding a small ball while suspended in the air (tethered). This information, when compared with similar studies on free cockroaches (Delcomyn & Usherwood, 1973; Pearson, 1972) can provide important clues regarding the possible roles of central and peripheral mechanisms of control of leg movement.

The results support the hypothesis that some aspects of the motor output, such as discharge rate in a burst, are strongly influenced by sensory information delivered from the legs, while others, such as the duration of the burst, are not. The lack of influence of the experimental procedure on the major parameters of motor activity suggest that this preparation may be suitable for more technically sophisticated studies on CNS function in animals which can nevertheless still walk.

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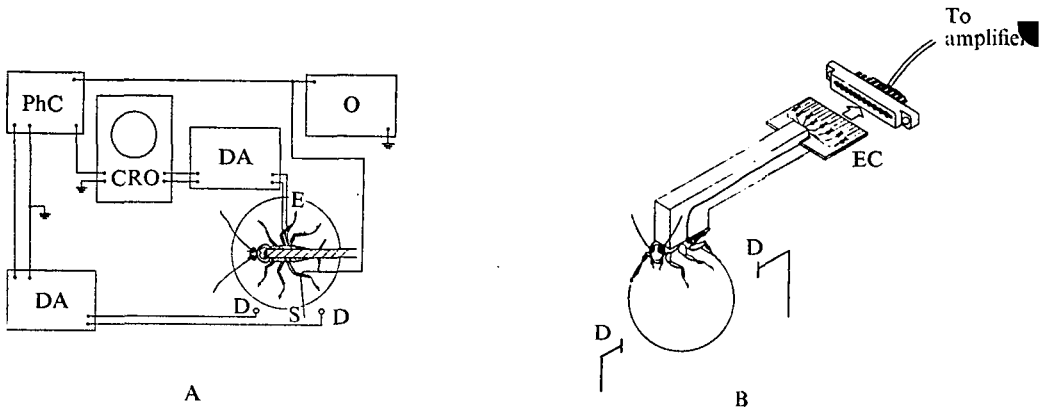


Fig. 1. The experimental arrangement. A. A diagrammatic representation of the preparation and recording equipment. Symbols: PhC, phase-detecting circuit (Sandeman, 1968); CRO, oscilloscope; DA, differential amplifier; O, oscillator; E, recording electrodes; S, sensing wire; D, detecting knobs. See text for operational details. B. A diagram of the animal, holder and ball. The edge connector (EC) plugs into a receptacle connected to AC amplifiers. A sensing wire (not shown here) attached to a leg moves between the detecting knobs (D) as the animal walks. See text.

MATERIAL AND METHODS

The preparation

Adult male or female American cockroaches, *Periplaneta americana*, were used in all experiments. Animals were prepared for electromyography in the following way. The insect was lightly anaesthetized with carbon dioxide and its wings were removed. It was then fastened to a supporting stick with melted wax which hardened so that the dorsum of the animal from the pronotum to the last few abdominal segments was firmly fixed to the support. Small holes were made in the cuticle over or near selected muscles, and fine copper-wire electrodes (48 gauge, 40 μm), insulated except for the tips, were pushed through the cuticle on to or near the desired muscles, as described in the preceding paper (Delcomyn & Usherwood, 1973). Recordings were made from the main extensor (depressor, m. 178, 179, 177d, 177e) and flexor (levator, m. 181b, 181c) muscles in the coxa (notation of Carbonell, 1947). The sources of the potentials which were recorded were identified on the basis of the size, shape and gross pattern of impulses, considering also the position of the electrodes and the innervation of the muscle from which the recordings were taken. The recording electrodes were terminated on an edge connector (to which the supporting stick was also fastened) so that the entire arrangement was completely portable. When the wire electrodes had been inserted, the edge connector was plugged into a socket, which was in turn connected to the appropriate pre-amplifiers (Fig. 1B). Subsequent amplification and recording were conventional.

As the animal recovered from anaesthesia, it was given a lightweight Styrofoam ball to hold, so that when it made walking movements, the ball rotated freely beneath it. Recordings of muscle potentials were taken as the animal walked on the ball, and simultaneously the movements of a selected leg were monitored, with the aid of a device described by Sandeman (1968). The salient features of this device are as follows. A 40–50 kHz signal is fed from an oscillator to a lightweight wire fastened to

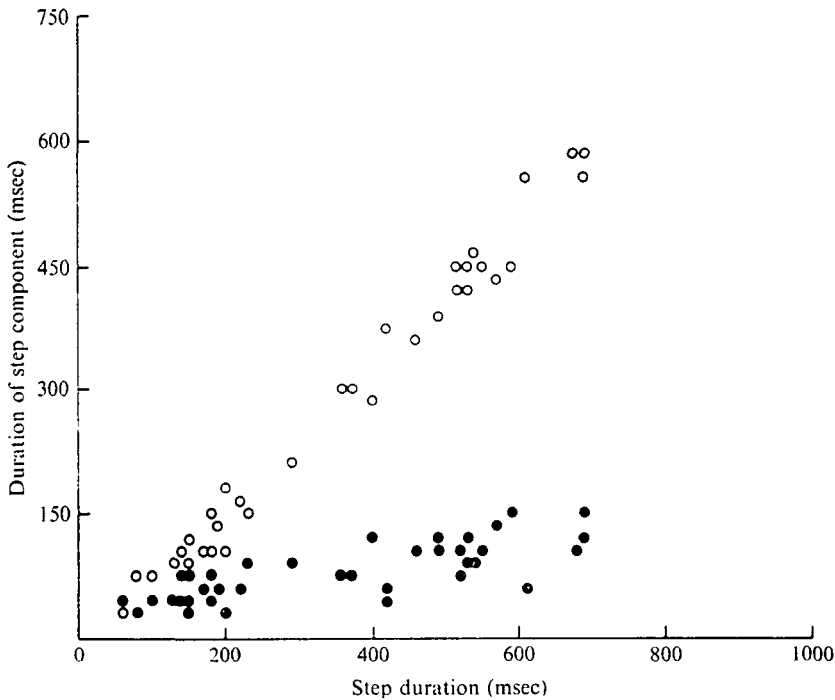


Fig. 2. A plot of the durations of protraction (forward movement, filled circles) and retraction (rearward movement, open circles) as a function of step duration in tethered cockroaches. In this and all subsequent plots coincident points are shown as one only. The slope of the best-fit regression line for each of the two groups of data \pm S.E. of the mean is: retraction, 0.872 ± 0.016 ; protraction 0.118 ± 0.114 .

the proximal portion of the insect's tibia (or to a small plastic peg fastened to the tibia) in such a fashion that it lay approximately mid-way between two metal detecting knobs (Fig. 1 A). A comparison of the differentially amplified signal from the two knobs with the original signal in the phase-detecting circuit yielded a d.c. voltage whose magnitude was directly proportional to the physical distance between the signal wire and the detecting knobs. Thus, as the leg bearing the wire moved back and forth during walking, the concomitant movement of the wire resulted in an alternating increase, then decrease in voltage representing the leg movement (e.g. Fig. 3). A brief description of this approach as applied to the cockroach has appeared previously (Burns & Delcomyn, 1970).

Analytical methods

Recordings of muscle potentials were analysed as described in the preceding paper (Delcomyn & Usherwood, 1973). Briefly, measurements were made of the distance of each muscle potential and each change-of-direction of leg movement from an arbitrary origin on the film record. These measurements were punched on to computer cards and submitted for analysis to a computer program which calculated certain parameters of motor activity. Bursts were defined as groups of at least three impulses which were separated from nearby impulses by intervals at least four times the duration of the first or average interval in the burst. These criteria were written into the program.

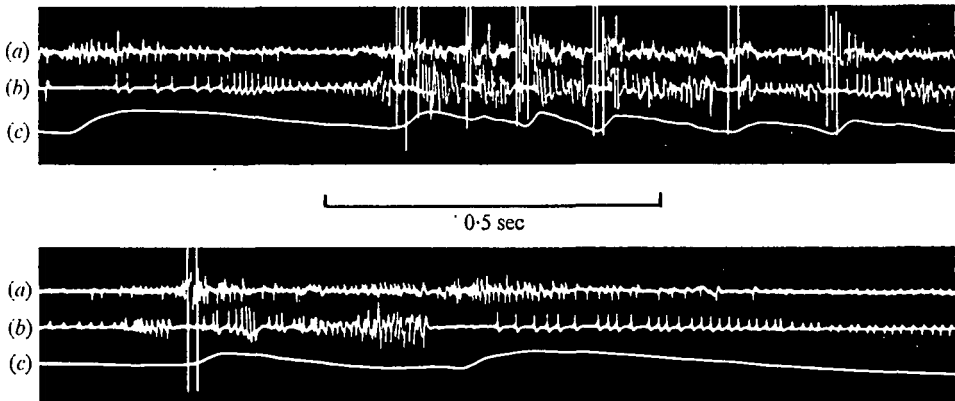


Fig. 3. Electrical activity in coxal muscles of leg L₃ during tethered walking. Traces: (a) Activity of flexor muscles 181b, 181c; (b) activity of extensor muscles 177d, 177e; (c) monitor of leg movement. Upward deflection is leg flexion. Notice that 'fast' flexor impulses (the largest potentials) occurring during the faster steps are grouped into discrete bursts which alternate with the extensor bursts, while 'slow' flexor activity continues even during leg extension. Top and bottom records not continuous. (Muscle impulses retouched.)

RESULTS

A tethered cockroach prepared as described above will remain alive and healthy for many days. Examination of the pattern of leg movements during walking on the ball with the aid of a high-speed motion picture camera did not reveal any qualitative differences in patterns of stepping as compared to an intact free-walking cockroach. As an example, the increase in both protraction (forward) and retraction (rearward) movements of the two rear legs as step durations increase is shown in Fig. 2. The relationship is essentially the same as that observed in free preparations (Delcomyn & Usherwood, 1973).

The activity of motor axons in a stationary tethered cockroach was no different from that in a free one. Neither 'fast' flexor nor extensor axons were active when the animal was not walking on the ball. Activity due to 'slow' flexor axons was usually absent, except when the animal moved the ball slightly (presumably equivalent to shifting posture in a free insect). During periods of inactivity support for the ball is provided not by flexors in the coxa which move the femur but by the combined action of the flexor tibialis and the retractor unguis muscle, whose action is to flex the tarsal claws, allowing them to dig into the soft surface of the ball. Somewhat surprisingly, the single 'slow' extensor axon (D_s of Pearson & Iles, 1970), was often active continually for long periods of time. As in free preparations, the level of activity was usually greatest just after walking had occurred, and gradually declined as the time since the last step increased. After many minutes of inactivity (i.e. not walking), D_s was usually shut off altogether. Such a pattern of activity in a motoneuron possibly reflects the level of the central excitatory state in the insect.

During *free* walking, the major feature of the activity of the coxal motor axons is the occurrence of reciprocal bursts of activity in extensor and flexor motoneurons (Pearson, 1972; Delcomyn & Usherwood, 1973). Models of the mechanism of control of leg muscles during stepping have incorporated this reciprocal burst feature as an

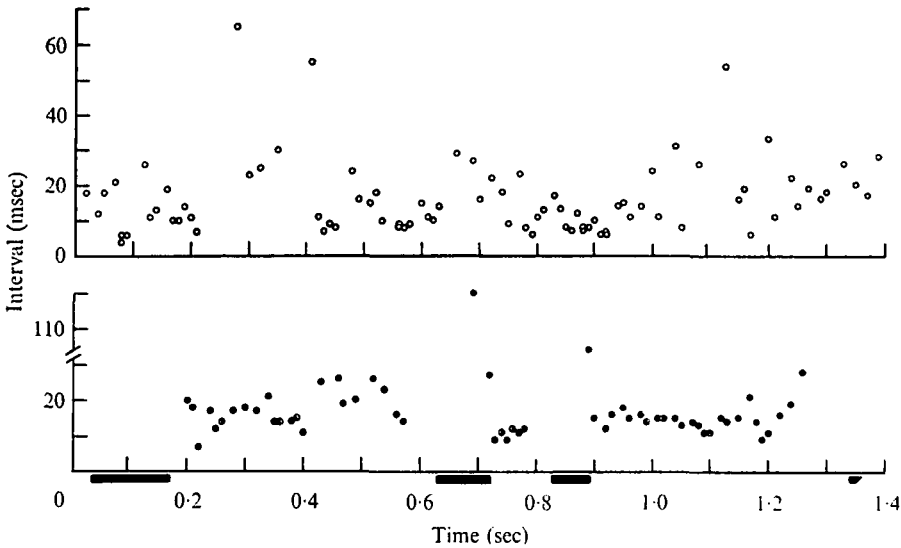


Fig. 4. Sequential time plot of intervals of a portion of the top record, Fig. 3. Top: 'slow' flexor intervals. Bottom: extensor intervals. The solid bars under the abscissa represent the period of protraction of the leg. Notice the continuous, modulated activity of the flexors, the bursts of the extensors.

intrinsic component (Pearson & Iles, 1970; Delcomyn, 1971b). It was therefore unexpected to find that 'slow' flexor activity in the tethered cockroach was rarely grouped into distinct bursts but was instead more or less continuous. Fig. 3 illustrates two typical records.

None of the other muscle units studied in the tethered cockroach had patterns of activity qualitatively different from those which have been described in free-walking cockroaches (Pearson, 1972; Delcomyn & Usherwood, 1973). This includes activity in the 'fast' flexors, which occurs exclusively in short bursts when they are recruited in leg flexion during faster steps (Fig. 3). The 'slow' extensor (axon D_s of Pearson & Iles, 1970) was active in bursts which reciprocated with 'fast' flexor activity. There was no sign of any activity in the single 'fast' extensor axon D_f . Pearson (1972) has reported recruitment of this axon during fast walking, but Delcomyn & Usherwood (1973) found no such activity in their animals.

The striking difference between the patterns of activity of 'slow' flexor and extensor muscles is well shown in a plot of sequential intervals against real time (Fig. 4). While potentials recorded from the extensor muscles are clearly grouped into bursts separated by long intervals, the potentials recorded from the flexors are not grouped in this way. Nevertheless, flexor-unit activity is not totally independent of stepping. Instead, the activity of the flexor muscles is modulated so that frequency is highest during leg flexion, lowest during extension. This modulated activity, and the difference between it and bursting, may be illustrated especially well in plots of interval duration as a function of the phase of individual muscle potentials relative to the whole step (Fig. 5). While intervals between extensor muscle impulses are relatively uniform in duration and fall in the extension cycle of the step (Fig. 5A), intervals between flexor muscle impulses are not uniform in duration, and fall throughout

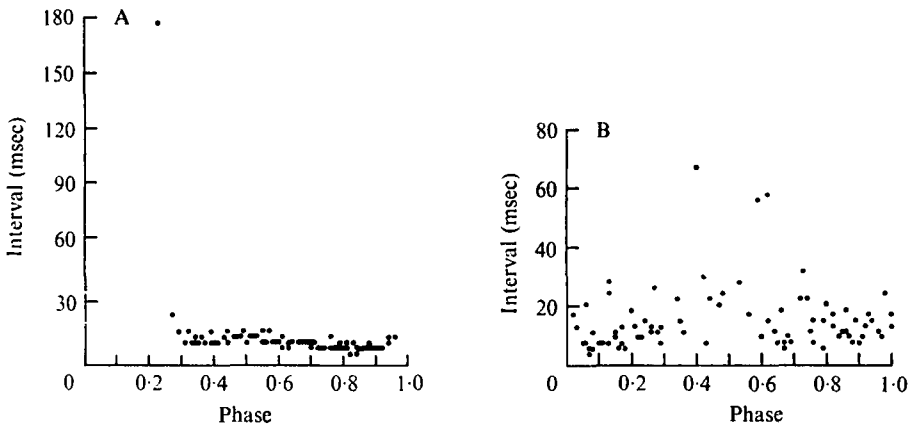


Fig. 5. Inter-impulse interval duration as a function of the phase of the interval relative to the whole step for muscle potentials of extensor (A) and flexor (B). The phase of an interval was defined as the time from the beginning of the step (the start of protraction) to the occurrence of the second impulse defining the interval, divided by the duration of the whole step. In these plots flexion ends and extension begins at a phase of approximately 0.3 (the exact value varies from one step to the next). Note that while the extensor muscle is silent during flexion, the flexor muscle continues to show activity during extension, although at a lower average frequency (longer intervals).

the step (Fig. 5B). However, the shortest intervals are grouped at the beginning (during leg flexion) and the end (just preceding flexion) of the step.

The phasing of the start of each extensor burst relative to the flexion and extension movements of the leg was dependent on the duration of the step. At very low speeds of walking each burst began as the leg completed its flexion and began its extension movement. During increasingly shorter (i.e. faster) steps, the movement lagged increasingly behind the burst, so that the burst started well before flexion was complete and ended before extension had finished. At the very highest walking speeds the flexion movement was only half completed before the extensor burst began. Such a lag between muscle activity and leg movement occurs in free-walking preparations as well (Delcomyn & Usherwood, 1973) and has important implications for the potential role of reflex feedback from the legs (see Discussion).

The bursts of D_s and the 'fast' flexors were selected for examination in greater detail in order to determine whether there were any significant departures from the course of events in free cockroaches. The results are discussed below.

The effect on the burst activity of D_s of variations in step duration may be seen in Fig. 6. The same relationships seen in free preparations (Pearson, 1972; Delcomyn & Usherwood, 1973) may be observed here. The duration of the burst increased as the duration of the step itself increased (Fig. 6C). Simultaneously, the number of impulses in the burst increased (Fig. 6A), as did the mean interval between impulses in it (Fig. 6B). In addition, the rate of increase of each of these parameters was usually significantly greater at step durations below approximately 250–333 msec than during steps longer than this. As discussed by Delcomyn & Usherwood (1973), this phenomenon may possibly be evidence of the recruitment of command fibres in the locomotor control system which are not employed when stepping is slower than 3–4/s.

Quantitative comparisons between data from free and tethered insects revealed

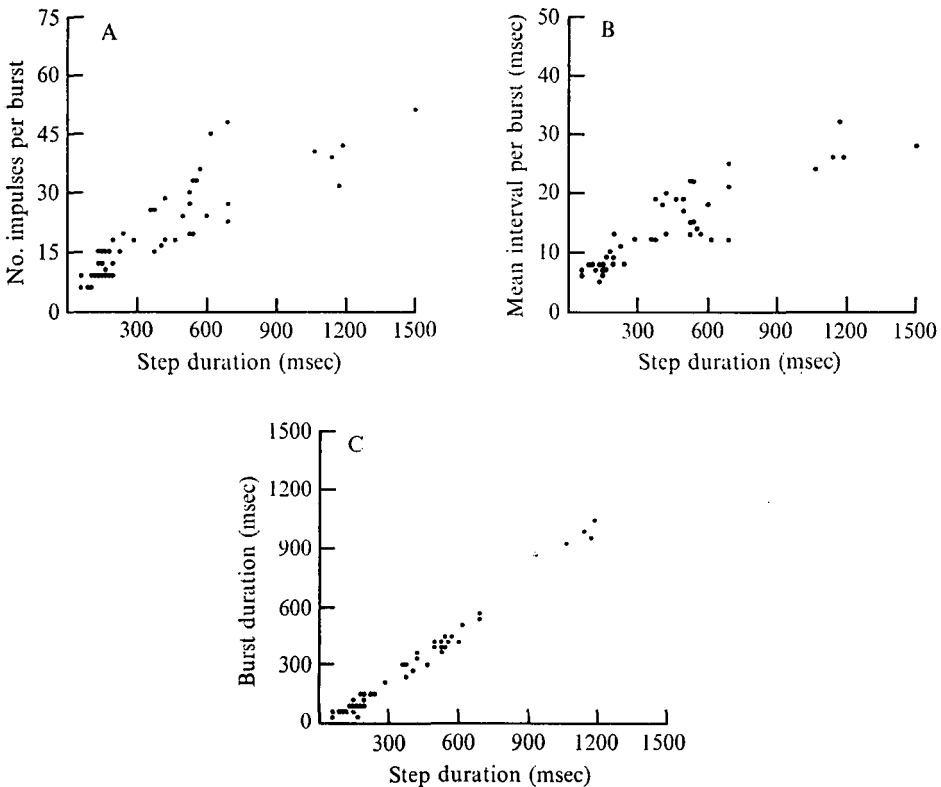


Fig. 6. Burst parameters as a function of step duration for 'slow' extensor bursts. (A) Number of impulses per burst. (B) Mean interval per burst. (C) Burst duration. The slopes of the best-fit regression lines independently fitted to the data above and below about 300 msec steps in plots A and B were significantly different ($P \ll 0.01$).

several interesting features. The most obvious of these was that in D_s (extensor) bursts, while there was no effect of tethering on burst duration, for steps of any given duration the number of impulses in the associated burst was in a tethered insect about half that in a free one. The mean interval per burst was about twice normal, reflecting this lower discharge rate. The tethered insect must carry the ball, and is not required to support its own weight, a function normally assumed partly by the extensor muscles in the coxa. One may interpret this result, at least during slow walking, as the effect of a reflex decrease in output to a muscle in response to a decrease in effective load on that muscle. The result very nicely complements the finding of Pearson (1972) that an increase in load resulted in an increase in discharge rate.

There was no change in burst duration when load was reduced. Pearson (1972) reported an increase in this parameter when load was increased. Apparently the neural mechanism responsible for regulating burst duration is not sensitive, or not nearly as sensitive, to the sensory signals which carry information about leg loading as is the mechanism which regulates the discharge rate within each burst.

As is the case in free-walking cockroaches the effect on 'fast' flexor bursts of variations of step duration is not as clear as the effects on D_s bursts. Nevertheless, some relationships emerge on close study. Perhaps surprisingly, there was no

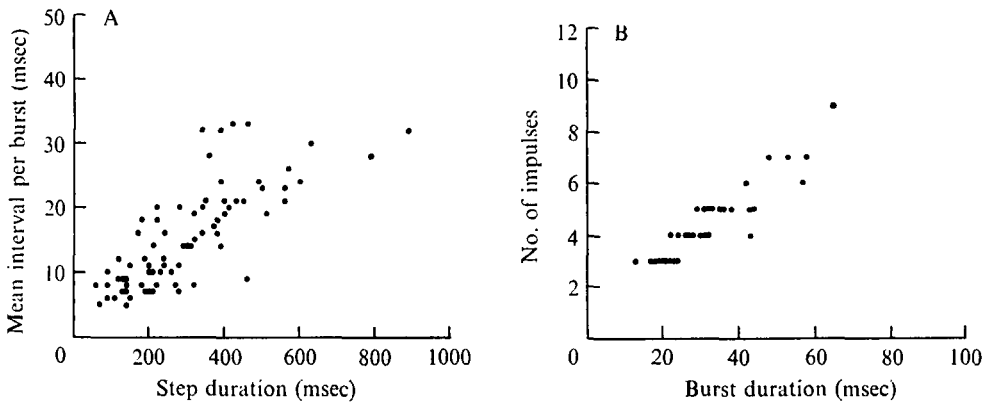


Fig. 7. (A) Mean interval per burst as a function of step duration for 'fast' flexor bursts. The correlation coefficient (r) between the two variables is 0.9257. (B) Number of impulses per burst as a function of *burst* duration. $r = 0.7695$.

detectable quantitative or qualitative difference between the behaviour of 'fast' flexor bursts in free and tethered preparations. Formal, statistically significant variations of the burst parameters as a function of step duration were often difficult to demonstrate. As in free-walking cockroaches, however, this apparent lack of close dependencies is probably due to the influence of a number of factors, such as a small sample range of step durations, low rates of change of protraction relative to step duration (Fig. 2), negative influence of high thresholds, interaction with events in previous steps, etc., as discussed previously (Delcomyn & Usherwood, 1973), each of which acts to obscure or counteract the expression of a close dependency of 'fast' flexor burst parameters on step duration. This view is supported by the occasional clear finding of such dependencies, such as the dependence of mean interval per burst (Fig. 7A) and burst duration, upon step duration. In addition, there was usually a very strong correlation between burst parameters (mean interval per burst and number of impulses per burst, Fig. 7B) and burst duration.

DISCUSSION

During free walking in cockroaches, coxal extensor and flexor muscles are active in reciprocal bursts, and there is an increase in burst length, number of impulses per burst, and mean interval per burst as step durations increase (Pearson, 1972; Delcomyn & Usherwood, 1973). If a cockroach is tethered and made to walk by rotating a small, lightweight ball that it holds, the animal is no longer required to support its own weight, but instead supports the ball, primarily through the action of tibial flexors and the retractor unguis muscles. In addition, since the ball is approximately the same size as the insect, the legs are of necessity positioned slightly differently from normal, primarily in that they tend to be more extended than in a free-standing or walking cockroach.

The results described in this paper have shown that when a cockroach prepared as described above walks on the ball, 'slow' flexor units, which in free-walking insects are active in bursts, become active continually, while 'fast' flexor units retain their

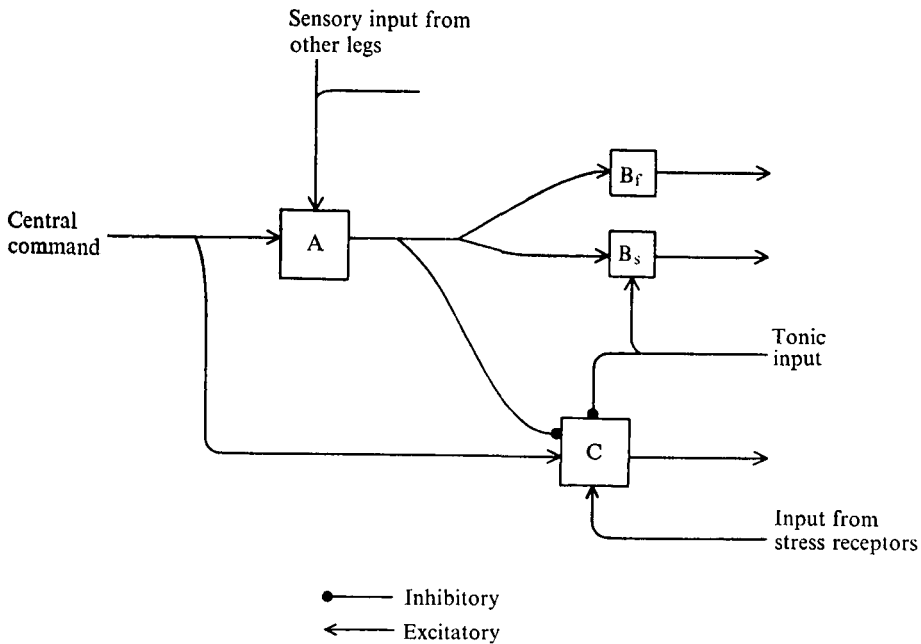


Fig. 8. A hypothetical model of a possible mechanism to produce observed patterns of motor output to leg muscles during walking. The boxes are only intended to represent functional elements of the system. Each element may or may not be represented by single neurones in the animal. See text for explanation.

burst activity; and that the discharge rate in 'slow' extensor bursts, and the number of impulses in each burst, drop to about half normal at any given step duration, but without any effect on the duration of the bursts themselves.

Clearly, the change in the physical arrangement of the animal was responsible for the change in motor output pattern. The change was most probably a direct result of the altered sensory input from the legs. (Painting over the eyes had no apparent additional effect, so the lack of a moving visual stimulus did not seem important.) A model of the generation of motor impulse pattern in leg muscles which was derived from behavioural studies (Delcomyn, 1971*b*) was adequate to account for the motor patterns observed during free walking (Pearson, 1972; Delcomyn & Usherwood, 1973). This model was composed of three elements (see Fig. 8); A, which converted a steady frequency central nervous command to a sinusoidally modulated one; B, driven by A, with a threshold which resulted in a discrete burst output (representing output to the flexor muscles of the coxa); and C, inhibited by bursts from B so that output exactly out of phase with the flexor bursts were produced (representing output to the extensor muscles). Can this model be modified to account for the new results?

One possible modification is illustrated in Fig. 8. For clarity, element B is divided into separate components for 'fast' and 'slow' flexor output, since these are not affected in the same way by tethering the animal. In addition, the inhibitory impulses which determine the burst pattern of C now are set to come from A rather than B, as proposed by Pearson & Iles (1970) in their similar model, since extensor bursts

continue unchanged even though 'slow' flexor bursts have been abolished. A new tonic excitatory input to the 'slow' flexor output is postulated. It is suggested that the level of activity of this input would be set by the state of flexion or extension of the appropriate leg, so that if the leg were more extended than normal, the frequency of firing of this channel would be greater than normal. On the ball, then, there must be sufficient input to the 'slow' flexor motoneurons (or to the neurons which directly drive them) so that their excitability is high enough to allow expression of the sinusoidal input from A throughout the entire cycle of leg movement, and not just during leg flexion. Such a system would be of functional use to the animal in its normal habitat since cockroaches often walk upside down (e.g. on ceilings) and would therefore presumably find it useful to regulate the activity of flexor motoneurons on the basis of how extended the leg was. This hypothesis could readily be tested.

The reduction in burst discharge rate in the 'slow' extensor muscles could be accounted for in several ways. One would be a tonic *inhibitory* input to the extensor motoneurons which would also originate from more extended leg positions. Additionally, or perhaps alternatively, one can postulate the presence of excitatory input to the 'slow' extensors originating from load-detecting receptors in the leg, so that during walking on the ball, when load on the legs is reduced, the reduced input from these receptors would result in a reduction in the level of output to the extensor muscles. The presence and action of such receptors was suggested by Pringle (1961) and confirmed by Pearson (1972), who found an increase in discharge rate in the extensor muscles when increasing loads were put on the leg during walking. Pearson showed that the campaniform sensilla in the trochanter, which give barrages of output when the cuticle in which they lie is stressed (for example, when the leg takes up part of the weight of the body), were probably the sense organs responsible for this effect.

There is, however, a problem with this interpretation. The system would work perfectly well as long as the muscle activity was synchronized with the leg movements, but in tethered as in free-walking preparations (Delcomyn & Usherwood, 1973) leg movements tend to lag behind muscle activity at higher speeds of locomotion. At very high speeds of locomotion, extensor activity begins well before the leg touches the ground for the extension phase of the step; yet there is not any detectable change in the discharge rate. It is possible that there is sufficient stress in the trochanteral cuticle when the extensor begins to brake the ongoing flexor movement than there is very little additional output from the receptors when the leg actually touches the ground, and thus no change in discharge rate is visible. The point is one that can and ought to be tested, and one that reveals the importance of simultaneous behavioural observations during investigations of the physiological basis of movements.

SUMMARY

1. The patterns of electrical activity in selected muscles of the rear legs were studied during locomotion in tethered cockroaches.
2. Stepping movements did not appear significantly different in a tethered insect compared to one which was freely moving.
3. During walking, the muscle potentials due to 'fast' flexor and 'slow' extensor

motoneurons were always grouped into alternating bursts separated by periods of silence, but those due to 'slow' flexor motoneurons were not usually grouped in this way.

4. Muscle potentials due to 'slow' flexor activity were usually modulated in frequency such that the highest frequencies occurred when in the free-walking insect one would have expected a burst to occur.

5. 'Slow' extensor and 'fast' flexor bursts were studied in detail. Minor fluctuations of the frequency of impulses within each burst were not related to any other parameter of activity which was measured.

6. For 'slow' extensor bursts, the duration of the bursts, 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. As in free-walking animals, the rate at which the latter two changed as a function of step duration was often significantly higher for steps shorter than about 300 msec. than for longer ones. However, the absolute value of these two parameters in tethered preparations was about half that at corresponding step durations in free-walking preparations.

7. For 'fast' flexor bursts, weak positive correlations between step duration and burst duration, number of impulses per burst and mean interval per burst could be demonstrated only in a few preparations. The relationships were not significantly different from those seen in free-walking preparations.

8. The results suggest that reflex feedback loops can strongly affect some parameters of motor output, such as discharge rate within a burst, but affect others, such as burst duration, only very slightly if at all. A model of the mechanism by which steps may be generated is modified accordingly.

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