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STEPPING PATTERNS IN THE COCKROACH, *PERIPLANETA AMERICANA*

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In free-walking *Periplaneta americana* coordination of the legs (i.e. the gait) has been shown to vary with speed. During free-walking (which occurs over a flat, horizontal surface) gait changes with speed during slow walking ($<3-4$ steps s^{-1}) and is constant during fast walking ($>3-4$ steps s^{-1}) (Hughes, 1952; Delcomyn, 1971). The change in gait has been said to 'grade insensibly' from the former to the latter as walking speed increases (Hughes, 1952). Delcomyn & Usherwood (1973) recorded electromyogram (EMG) activity from the third leg extensors of *P. americana* during free walking. They found that the slope of the curve, relating the number of spikes in an EMG burst to the step cycle duration associated with the burst, displayed an inflexion point. This inflexion point coincided with the step frequency at which the gait transition was seen. The occurence of this discontinuity in the EMG record, plus their observation that a slow-walking animal seldom takes more than a few consecutive steps in any one direction, lead Delcomyn and Usherwood to suggest that this slow walking represented a behaviour that differed from 'purposeful walking' (Delcomyn & Usherwood, 1973). Work presented here indicates that continuous, orientated walking does occur at stepping frequencies below 3–4 steps s^{-1}. There is also a strong indication that there are two types of behaviour which determine the range of observed walking speeds in this cockroach.

Adult animals of either sex were used. Following anesthetization with CO_2, animals had their wings removed and were restrained on a Tackiwax platform during attachment of the electrodes. Electrodes consisted of joined pairs of insulated 25 μm copper wire. The ends of the joined pairs of wire were stripped, inserted superficially into specific muscles (see below) and held in place with Eastman 910 adhesive. A fine cotton thread attached to the animal's pronotum served as a tether.

The origins of the femur extensor 7trMEi in legs 1, 2 and 3 and the femur flexor $7tr_2$, PFi in legs 2 and 3 (notation of Alsop, 1978) were the sites of electrode placement. These muscles are the main flexors and extensors of the leg (Carbonell, 1947), have segmentally homologous innervation (Pipa & Cook, 1959), and are segmentally homologous with respect to their anatomy (Alsop, 1978). An animal carried three electrodes simultaneously. These were placed in either the 1st leg extensor and the 2nd leg extensor and flexor (preparation 1), or the 2nd leg extensor and the 3rd leg extensor and flexor (preparation 2).

Output from the electrodes was differentially amplified (Grass p15 or p511) and photographed (Grass C4 camera) from the screen of an oscilloscope (Tektronix D44).

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Fig. 1. Records from two different animals. Top record: high-film-speed record of activity in (from top to bottom) mesothoracic flexor, mesothoracic extensor and metathoracic extensor. Burst-cycle duration (BCD) indicates *ca.* 4 steps s^{-1}. Bottom record, low-film-speed record of activity in (from top to bottom) mesothoracic flexor, mesothoracic extensor, metathoracic flexor. BCD indicates *ca.* 3 steps s^{-1}. Time scales are accurate, potential scales are approximate.

The film speed (100 mm s^{-1}) measured to the nearest millimeter (= ±5 ms), gave records with resolution equivalent to cinema filming of 100 frames s^{-1}. An example of film records is given in Fig. 1.

Recordings were made within 2 h following release of the animal from its restraints. When walking was not spontaneous, one of two stimuli was provided to elicit walking; a sharp tap on the dorsum of the abdomen or a gentle touch to a tarsus or cercus. The response to the former was usually, but not always, running. The reponse to the latter stimulus was variable. A gentle touch could elicit running, walking, or change in posture with no associated locomotion. Only straight-line walking was recorded. EMG records were collected from 12 adult animals: 7 in preparation no. 1 and 5 in preparation no. 2. Over 350 bursts were recorded from approximately 50 bouts of walking in each preparation. Thus, the average bout of walking consisted of 7 steps. Bouts of less than 4 steps were not used.

Delcomyn & Usherwood (1973) indicated that the duration of an EMG burst cycle reflected the duration of a step cycle. Thus, I have here considered step cycle duration and burst cycle duration (BCD) to be equivalent. A histogram (relating the time from the beginning of one burst to the beginning of the next (i.e. the BCD) to the frequency of occurence) revealed that there were certain burst cycle durations which occurred more frequently than others (see Fig. 2). The distribution is distinctly bimodal with a virtual absence of activity at BCD's of 200 ms duration. The range of the short BCD mode is much narrower than that of the long BCD mode (190 ms *v.* 600 ms). Thus, frequency of stepping in the cockroach, as indicated by the duration of EMG burst cycles, is organized into two discrete modes. The high-speed (short duration) mode has a mean of approximately 13 steps s^{-1} (75 ms duration) and exhibits a range between 5 and 25 steps s^{-1} (200–40 ms duration). The low-speed (long duration) mode has a mean of approximately 2 steps s^{-1} (400 ms duration) and a range between 1·5 and 5 steps s^{-1} (700–200 ms duration).

These findings indicate that free-walking in the cockroach, which occurs over a flat horizontal surface, occurs either as fast or slow walking. They suggest that slo

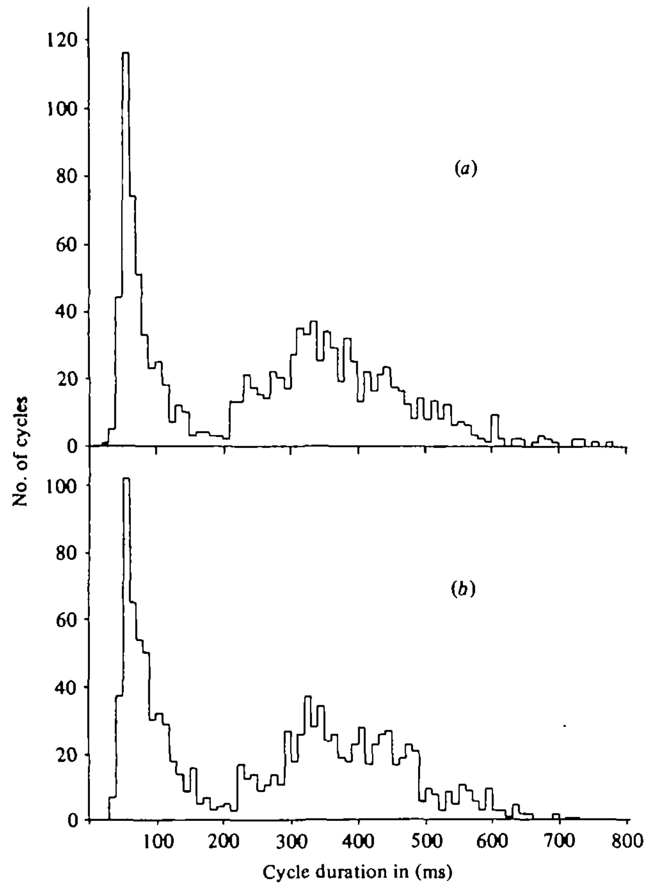

Fig. 2. Histograms of frequency distributions of burst cycle durations. (*a*) A composite of all-burst-cycle durations from preparation 1. (*b*) A composite of all-burst-cycle durations from preparation 2.

walking coincides with the speed-dependent gait and fast walking coincides with the speed-independent gait. However, Spirito & Mushrush (1979) recorded with cinema film the use of the speed-independent gait at step frequencies as low as 2 steps $^{-1}$. This finding, taken with Hughes's observation (1952) that the transition from one gait to another is not pronounced, can be used to argue that the mode (fast or slow) of walking changes with the behaviour (escape or non-escape) of the animal and that gait may vary due to some causation other than step frequency.

Based on these findings, future descriptions of walking, or explanations of the generation of walking, should specify which mode of walking the animal is using.

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