Leg Co-Ordination during Walking in the Crab,
*Uca pugnax*

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Summary. 1. Cine films of fiddler crabs (*Uca pugnax*) walking sideways on land were analysed frame by frame in order to study the co-ordination of the legs both during normal walking and following amputation (induced autotomy) of one of the 3rd pair of legs.

2. Although the average gait of unoperated animals approximates to an alternating tetrapod rhythm, equivalent to the alternating tripod gait of insects (Figs. 3–7), the stepping order of legs on leading and trailing sides of the animal is different. The dominant sequence on the leading side is 2435 (legs numbered from front to rear), that on the trailing side 2534 (Table 1), the chelae (leg 1) being usually held off the ground.

3. Stepping parameters also change with walking speed (Figs. 8, 10), the most clear-cut of these changes being the reduced relative duration of the power stroke at high walking speeds. At low walking speeds, clear-cut metachronal co-ordination is sometimes seen in trailing legs (Fig. 9), but the data nevertheless do not fit Wilson’s 1966 metachronal model for insect locomotion.

4. Amputation of one of the 3rd pair of legs causes adaptive changes in the gait. The most obvious of these changes are that the chelae are now frequently used in walking and legs 4 and 2 on the operated side of the animal now alternate whereas before they moved together (Figs. 11–13, Table 2). Evidence is presented to show that these changes are brought about by the changed sensory input and are not due either to the effects of axon section on motorneurone electrical excitability, or to the animal walking more slowly and using a different but normally occurring gait.

Introduction

The plasticity of walking in decapod crustaceans makes it an interesting subject for studying behaviour in terms of the nervous system. Compared to, for example, song production in Orthoptera (e.g. Elsner, 1973) or insect flight (review: Wilson, 1968) the decapod locomotor pattern exhibits considerable variability and adaptability. The motor output pattern is not constant from cycle to cycle even when an animal is walking on a treadmill (Barnes, Spirito and Evoy, 1972) and gross changes occur when the animal is walking up a gradient or when one leg is prevented from playing its normal role in locomotion (Clarac and Coulmance, 1971; Evoy and Fourtner, 1973). It is clear that central and peripheral influences interact to produce a pattern of behaviour that is modifiable according to the situation faced by the animal. The locomotion of crabs is particularly intriguing because of the problems posed by sideways walking. The action of the legs on the two sides of the body is necessarily quite different. Leading legs pull by flexing, trailing ones push by extending. Indeed, as the results described here show, this asymmetry extends even to the way in which the legs are co-ordinated.
A description of the behaviour itself provides the framework essential to any such neuroethological study. In the analysis of leg co-ordination during walking, the following parameters have been shown to be important: the gait which is the stepping order of the legs; phase relationship between legs, the relative timing of pairs of legs with respect to each other; and some measure of the relative duration of power and return strokes. It is also important to know how all these parameters vary with walking speed, and how much variation they show at any one speed. Hardly surprisingly, most early work on crustacean walking (e.g. List, 1895; Bethe, 1897, 1930; Voelkel, 1922; Köhler, 1931; Herter, 1932; Baldi, 1936) does not provide adequate information on all these subjects. Indeed, there is considerable disagreement even about the dominant gaits. More recently, Parrack (1964) has studied stepping sequences in the crayfish, and, concurrently with this study, MacMillan (in preparation) has carried out an analysis of walking in the lobster, Homarus americanus, but no recent data is available for crabs.

In this study of sideways walking carried out on the fiddler crab, Uca pugnax, I have considered the findings with regard to the two main models of arthropod locomotion. The first of these models is based upon metachronal co-ordination of the legs. Metachronal sequences are particularly obvious in centipedes and millipedes and have been shown to occur in several crustaceans with more than about 10 legs including the isopod, Ligia (Alexander, 1972) and the brine shrimp, Artemia (Lent, 1971). Although in animals with fewer legs such metachronal rhythms are not obvious, there is no a priori reason why the mechanism of co-ordination should not be the same. Indeed, Wilson (1966a) has put forward a descriptive model for insect walking based on metachronal rhythms with stepping patterns varying with frequency. Fig. 1A shows Wilson’s model, which was itself based to some extent on the data and ideas of Hughes (1952) and Wendler (1964), adapted for decapod crustaceans. The walking legs on one side of the animal, numbered from front to rear, move in the basic metachronal sequence 5432. The chelae (leg 1) are not often used in walking, at least in Uca, and so are not considered. Legs on opposite sides of the body alternate with each other. For simplicity, only those on one side are illustrated. At low speeds a complete metachronal sequence is completed before the next one begins (Fig. 1A I), but as the stepping speed increases there is progressive overlap of the metachronal waves (Figs. 1A II–IV), resulting in changes in gait, phase relationships between legs and relative duration of power and return strokes. Although metachronal waves passing up the body are by far the most common, posteriorly moving metachronal waves are also known, for example, in the myriapod, Cryptops (Manton, 1953), so an equivalent model based on the basic sequence 2345 could also apply. Indeed the data which follow suggest that this latter pattern is the more appropriate one.

The second model is presented in Fig. 1B. It is based on the classical observation that most insects, most of the time, use an alternating tripod gait in which legs L1, R2 and L3 (left prothoracic, right mesothoracic and left metathoracic) move together and alternate with legs R1, L2 and R3, which also move together. Recently, detailed analyses have been made of locomotion in cockroaches and stick insects. Cockroaches almost always fit this alternating tripod pattern (Delcomyn, 1971a), and 1st instar, but not adult, stick insects use it much of the