Proprioceptive reflex interactions with central motor rhythms in the isolated thoracic ganglion of the shore crab

Steward I. Head* and Brian M.H. Bush
Department of Physiology, University of Bristol, Park Row, Bristol BS1 5LS, England
Accepted January 29, 1991

Summary. Experiments were carried out on an isolated central nervous system preparation of the shore crab, *Carcinus maenas*, comprising the fused thoracic ganglion complex with two proprioceptors of one back leg still attached. These, the thoracic-coxal muscle receptor organ and the coxo-basal chordotonal organ, monitor movement and position of the first and second joints, respectively. Motor activity was recorded extracellularly from the central cut ends of the nerves innervating the promotor and remotor muscles of the thoracic-coxal joint, and the levator and depressor muscles of the coxo-basal joint of the same leg. Simultaneous intracellular recordings were made from central processes of individual motoneurones of each muscle.

In the absence of any sensory input, the isolated ganglion exhibited rhythmic bursting in the motor nerve roots, with a slow, usually irregular cycle period of 5–50 s.

Both receptor organs had both intra-joint and inter-joint effects on the rhythmically active preparation. In most cases the coxo-basal receptor organ had the greater effect.

Resistance reflexes initiated by each of the joint proprioceptors were modulated by the rhythmic activity.

It may be concluded that, while the isolated thoracic ganglion of the crab is capable of generating rhythmic motor output, proprioceptive feedback from the two basal joints is important in shaping the motor patterns underlying locomotion. Inappropriate reflexes which would impede active movements about these joints are modulated or reversed so as to permit and even reinforce intended locomotory movements.

Key words: Proprioceptors – Motoneurones – Reflexes – Central nervous rhythms – Crab leg

Introduction

It is now generally recognised that central neural networks are available that enable rhythmic motor outputs similar to those underlying locomotion and other rhythmic behaviours to be centrally generated without reafference (Delcomyn 1980; Grillner and Wallén 1985). However the degree to which these central rhythms correspond to the motor patterns recorded from intact animals varies greatly. Some central rhythms are almost totally patterned and do not appear to require any sensory feedback, e.g. the swimmeret beating of the crayfish (Hughes and Wiersma 1960; Heitler 1981) and the ventilatory movements of the crab scaphognathite (Simmers and Bush 1983). In other behaviours sensory input plays a major role in patterning the motor output, and may even in some cases be regarded as an integral part of the pattern generating system (Pearson 1985, 1987). In locust flight, for example, deafferentation has the effect of doubling the cycle period of the rhythm and changing it from a phase-constant to a latency-constant pattern, and alters the recruitment order and number of spikes generated in each cycle (Pearson 1985). Further, cyclical mechanosensory input in the wing nerves can entrain the rhythm generator and greatly modify the patterns of membrane potential oscillations in identified motoneurones (Pearson et al. 1983; Wolf and Pearson 1987).

In the walking system, too, deafferented or isolated thoracic ganglia of cockroach, stick insect and crayfish can produce sustained motor rhythms, but these are usually slower and lack the spatio-temporal patterning seen in normal walking (Pearson 1985; Bässler and Wegner 1983; Sillar and Skorupski 1986). For instance, there may be little or no correlation between the durations or cycle times of motor bursts in antagonistic muscle
nerves. Again, in both arthropods and mammals, proprioceptive input can profoundly influence the centrally generated activity of walking leg motoneurons (e.g. Bässler 1985, 1988; Pearson 1985, 1987; Zill 1985; Rossignol et al. 1988). The slow and irregular motor rhythms observed in the isolated thoracic ganglia of the crayfish can be entrained by regular movement stimulation of the single muscle receptor organ (TCMRO) at the base of the leg (Sillar et al. 1986).

In addition to such peripheral regulation of the central rhythm generating system, there is growing evidence for the opposite form of interaction, namely central modulation of reflex pathways. Examples include the rock lobster antenna (Vedel 1982) and stick insect and mammalian, including human, limbs (Bässler 1986; Rossignol and Drew 1986). Crayfish walking leg reflexes mediated by the TCMRO in the isolated ganglion preparation reverse in a phase-dependent manner during the central rhythm (Skorupski and Sillar 1986).

The present study had 3 main aims: (1) to see if the crab’s isolated thoracic nervous system could spontaneously generate any rhythmic activity in the motoneurons innervating the proximal leg muscles, and whether this could be correlated with any known motor behaviour in intact animals, in particular walking; (2) to assess the effects of input from two identified proprioceptors, the muscle receptor organ (TCMRO) of the first (thoracic-coxal) joint and the coxo-basal chordotonal organ (CBCO) of the second joint of a walking leg, individually and in combination, upon any recorded motor rhythm; and (3) to determine how, conversely, the intra- and inter-joint reflexes evoked by these proprioceptors in quiescent or tonically active, non-rhythmic preparations (see Head and Bush 1990a) are influenced by any spontaneous centrally generated rhythmic activity.

Materials and methods

For a detailed description of the materials and methods see Head and Bush (1990a). Briefly, the complete fused thoracic ganglion complex of the shore crab, together with the two main proprioceptors of the first two basal joints of the rear right leg, were totally isolated from the animal, and pinned out under crab saline in the experimental chamber. The TCMRO, which monitors movement of the first, thoracic-coxal, joint of the leg and is stretched by remotion of the leg, was attached to an electromechanical puller at its distal end to apply controlled stretch-release stimuli. The CBCO, which spans the next, coxo-basal, joint of the leg and is stretched by depression of the leg, was attached to a second puller.

Polyethylene suction electrodes were used to record extracellularly from the cut ends of the 4 motor nerve roots. Glass microelectrodes (30–100 Ω when filled with 5% Lucifer yellow in 1 M LiCl) were used to record from central processes of motoneurons. The data from each experiment were stored on a FM tape recorder for subsequent analysis. Lucifer yellow was iontophoresed into selected motoneurons for subsequent viewing, drawing or photography in whole ganglion preparations with a fluorescence microscope.

The criteria for identifying a cell as a motoneuron were similar to those used in the previous paper, namely 1:1 correlation of intra- and extra-cellularly recorded spikes; constant latency and threshold intracellular spikes in response to peripheral nerve stimulation; and the presence of a stained axon in the appropriate nerve following Lucifer yellow injection into the cell centrally. At least two of these criteria had to be met before the cell was considered positively identified as innervating a particular muscle.

Results

The spontaneous motor rhythm

The totally isolated thoracic ganglion of the shore crab produced a rhythmic motor output in the promotor, remotor, depressor and levator motor nerve roots of the back leg in approximately one out of every 10 experiments (Fig. 1). The results presented in this paper are based on a total of 24 preparations which produced a rhythmic motor output. Although the TCMRO and CBCO were still attached, the rhythmic motor output occurred in the total absence of any sensory input, or of any other stimulations which have been shown in the crayfish to evoke rhythmic behaviour (Sillar and Skorupski 1986).

As can be seen from Fig. 1A–D, the motor rhythm was irregular and variable, both within and between preparations. Nevertheless there is generally a clear reciprocity between antagonistic motor bursts. For example, when promotor and depressor nerves are active, the levator and remotor nerves are largely silent, and then the latter motor nerves become active while promotor and depressor nerves fall silent.

It can be concluded, therefore, that in the totally isolated and deafferented thoracic ganglion of the crab there exists some mechanism by which a rudimentary rhythm can be generated centrally. However, due to its very slow cycle time (10–50 s) and the lack of spatial and temporal patterning, the spontaneous rhythm could not readily be related to any motor pattern which has been recorded from intact decapod crustaceans undergoing specific behaviours (Clarac 1985; Clarac and Barnes 1985). Despite this, the motor output in these rhythmically active preparations clearly differs from that seen in the purely reflex and tonic states of the isolated ganglion preparations considered in our previous paper (Head and Bush 1990a).

Effects of TCMRO input on the spontaneous rhythm

To see what effect the proprioceptive input could have on patterning the very crude motor output from the thoracic ganglion, each receptor was stimulated in turn. In some of the preparations showing rhythmic activity, sensory input from the TCMRO altered the timing and duration of the bursting in the promotor roots (Fig. 2). In the spontaneous control recording (of which only a small part is shown in Fig. 2A), the average cycle periods of the levator and remotor bursts were 13.5 seconds (SD ± 6.3 s) and 25.0 seconds (SD ± 15.0 s), respectively. The TCMRO was then stimulated with a ramp-and-hold stretch stimulus of 1 s duration every 5 s (Fig. 2B). The bursting in both levator and remotor nerves now became loosely locked onto this stimulus, and the subsequent