Statocysts in Crabs: Short-Term Control of Locomotion and Long-Term Monitoring of Hydrostatic Pressure

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Abstract. Crabs show well-coordinated locomotion. They have proprioceptors similar to those of lobsters, but they differ in terms of their balancing systems and their condensed nervous system, which allows rapid interganglionic conduction. Typically they exhibit dynamically stable locomotion with a highly developed semicircular canal system that codes angular acceleration in each of three orthogonal planes (horizontal and vertical at 45° and 135° to the pitching plane). Left and right interneurons each code one direction of angular acceleration, carrying information between the brain and the thoracic ganglia. Cell A codes head-up vertical plane angular accelerations. Cell B codes rotations in the horizontal plane. Interneurons C and D code head-down vertical plane information, carrying it ipsilaterally and contralaterally respectively. These interneurons have a central role in locomotion. They are activated and have their responsiveness to angular acceleration enhanced before and during locomotion. Such simple activation pathways point to how an angular-acceleration-controlled robot (CRABOT) could be constructed. Hydrostatic pressure information carried by the thread hairs, which also sense angular acceleration, is filtered out from direct pathways onto the interneurons, but spectral analysis shows that it still has an influence via central pathways. Long-term recordings from equilibrium interneurons in free-walking crabs taken from the wild into constant conditions show tidally changing frequencies of bouts of activity, with peaks that correspond to times of high tide.

Introduction

Brachyuran crabs are conspicuous animals that occupy a variety of habitats and show well-coordinated locomotor ability while walking, crawling, climbing, swimming, or burrowing under a variety of hydrostatic pressure conditions. Compared with the ladder-like nerve cord of macrurans (crayfish and lobsters), their nervous system shows condensation and fusion of thoracic ganglia, allowing rapid interganglionic conduction of impulses. The abdomen has been much reduced and, in contrast to that of macrurans, is little used in normal or escape swimming. These crabs can survive leg autotomy: 13%–43% of individual Carcinus sampled from the wild have missing legs (McVean, 1982). Typically they exhibit dynamically stable locomotion, with statocyst (or balancing organ) interneurons having a central role (Fig. 1; Fraser, 1982; Fraser et al., 1987). Thread hair receptors, which respond to fluid displacements in the statocyst, have been shown to have their spontaneous activity and sensitivity to angular acceleration modulated by small changes in hydrostatic pressure (Fraser and Macdonald, 1994; Macdonald and Fraser, 1999). Clearly, elucidating the simplifying principles underlying such versatility and diversification of function is an important aim. One approach to dissecting such complexity is to concentrate on a fundamental difference between crabs and lobsters—that is, the elaboration in crabs of the statocyst and its central pathways.

Statocysts and Leg Proprioceptors Involved in Locomotion

The statocyst contains a statolith and angular acceleration receptors. In the crab, the crescent of statolith hairs (Sand-
eman and Okajima, 1972) is much smaller than the macruran crescent (see Lemmnitz and Wolff, 1990). The fluid-filled sac has been shaped from a simple cavity in the macruran statocyst into two orthogonal semicircular canals. Angular accelerations in the planes of the horizontal or vertical canals are monitored by a row of long, slender thread hairs (Fig. 1C; Sandeman and Okajima, 1972; Fraser and Takahata, 2001). Typically the response of thread hairs to an angular acceleration is unidirectional, with two oppositely responding directional classes. Analogous to those of vertebrates, the receptors integrate angular acceleration and code angular velocity in the horizontal plane or in vertical planes either at 45° or at 135° to the median line. Thread hairs are the main sensory component involved in a variety of statocyst-driven behaviors ranging from walking to eye-stalk movement, with free hook hairs and statolith hairs playing a lesser role (Cohen and Dijkgraaf, 1961; Fraser, 1989). Leg proprioceptors are used in the fine motor control to produce coordinated behavior, but during rhythmic behavior, sensory information does not vary much on each cycle unless a leg hits an obstacle. A variety of receptors include muscle receptor organs, which measure muscle stretch (Bush, 1977); chordotonal organs, which are articular (joint rotation) receptors measuring stretch around joints; and apodeme receptors and cuticular stress receptors, which record muscular tension via tendons and cuticle respectively (Wales et al., 1971). The funnel canal organs at the ends of the dactylopodites must be silent for the animal to swim, whereas their rhythmic firing in walking is used for step regulation (Libersat et al., 1987). Although it is not possible here to do justice to the complexity of information relayed by these proprioceptors, in general their role in locomotion in crabs is broadly similar to that in lobsters and crayfish.

Equilibrium Interneurons Involved in Locomotion

The angular acceleration sensors, the thread hairs, project onto a small set of eight large interneurons that link the brain to the fused thoracic and abdominal ganglia (Fig. 1; Fraser, 1974, 1990). These fire in the short term during angular accelerations caused by locomotion (Fig. 2A, B; Fraser, 1982), but are also activated centrally before and during bouts of walking or swimming (Fig. 2B; Fraser et al., 1987; Fraser, 1975, 1989). Their activity long term consists of quiescent periods with short bouts of extremely elevated activity. Cells are not coupled and are more likely to act in anti-phase during short-term oscillations that form part of the locomotion. Over a longer time scale, on the order of minutes, their overall activity is well synchronized. Vector information is hence preserved (Fraser et al., 1997, 2001). During these bouts of firing, the gain in the statocyst pathways alters greatly so that perturbations of angular acceleration have a large effect (Fig. 3).

In the context of discussing the role of the interneurons in
locomotion, Fraser (1982) points out that "where a behavior involves vectorial output in more than one dimension, or where feedback loops are involved, then the output measured by displacement of appendages or by muscle activity is no longer an adequate measure of the behavior... in terms of understanding the underlying neural activity, locomotion in crabs may be better described in terms of components of force and torque in the planes used by the equilibrium cells rather than in terms of the gaits employed." The angular displacements of crabs have been monitored in orthogonal planes with a miniature triaxial accelerometer.

Although proprioceptor input affects the activity of the interneurons, their outputs in free-walking animals are not particularly complicated (Fraser, unpubl. data; Fraser, 1995). Interestingly, Cruse et al. (1998) and Schmitz (2001) state that in the stick insect there is little evidence for a central pattern generator. Instead sensory information derived from leg position and ground contact, together with six different coupling mechanisms, allows selection between swing networks and stance networks. Lobster walking has been successfully modeled with five main classes of components: central pattern generators, command systems, coordinating systems, proprioceptive and exteroceptive sensors, and phase- and amplitude-modulating sensory feedback (Ayers et al., 1998). Stepping rates for such models are low. It may be that the crab has more similarities to the stick insect model than to the lobster model in terms of its reliance on sensory control, and an orthogonal command set based on the equilibrium interneurons may be sufficient to control a large part of its locomotion.

The finding that the statocyst thread hair receptors alter their activity under the influence of hydrostatic pressure makes understanding of their role more complicated (Fraser and Macdonald, 1994; Fraser et al., 1996; Macdonald and Fraser, 1999). Positive-going and negative-going modulation of thread hair spike frequency is thought to arise from activation of the two directional classes of mechanoreceptors via the linking chorda because of the slight volume changes associated with differential compressibility of the cuticle and other tissue components. Although thread hairs respond directly to alterations in hydrostatic pressure, thread hair interneurons do not seem to do so. Tidal period rhythms of firing pattern in equilibrium interneurons occur and match those found for general locomotor activity (Naylor and Atkinson, 1972; Fraser and Takahata, 2001). These are affected by hydrostatic pressure pulses or cycles, and spectral analyses of long sequences show that some of the
pressure information is getting through, presumably via higher order inputs (Fraser et al., 2001).

CRABOTS in the Future

Crabs show well-coordinated but highly variable walking patterns and easy transitions between walking and swimming. Activation patterns of equilibrium interneurons during such movement are simple and should be easily copied. This points the way to how an angular acceleration controlled walking robot (CRABOT) could be constructed, which would advance maneuverability of such robots and should save energy. Optimism for the success of this approach comes from early experiments showing circling movements in crabs when one esophageal connective was cut and reversal of this circling behavior with stimulation of the cut connective. This circling may be explained in terms of the effects on equilibrium cells (Fig. 2B; Bethe, 1897; Fraser, 1982). At present, a major limitation regarding realistic robotic modeling is the stepping frequency of artificial limbs and activators.

![Figure 3. Long-term recording from equilibrium interneurons (spike frequency measured every 100 s) in a free-walking crab, Carcinus maenas, taken into constant conditions in an aquarium after capture at low tide. The recording starts 6 h after capture. Arrows mark the occurrence of high tides. High bouts of activity in the cells correspond to locomotor behavior in the crab, and there is clear tidal rhythmicity. (Redrawn from Fraser and Takahata, 2001).](image-url)

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