light. Thus the reflected white light dilutes the reflected green light from the exocuticle so that, by contrast to the concentration of green light effected by the lenslike areas of the epicuticle, the light appears silver-white. However, when one avoids the perpendicular reflection, the greenish color is still very pale and so seems to be associated with the thickness of the epicuticle or merely the lack of intensification of the green light by lenslike structures.

The structures of the epicuticle and exocuticle were investigated further. Sections almost parallel to the surface were made in which some of the lens bottoms were truncated and cut, so that photographs of these showed the very clear spiral Bouligand pattern associated symmetrically with each lens as it acts as a negative "tubercle," which is Bouligand's term.

Figure 2 shows the arrangement of Bouligand patterns as they appear in a plane in the epicuticle parallel to the surface but below the convex lenses of the epicuticle. As indicated by the handedness of the patterns, the left-handedness indicates a right-handedness of the pitch of the oriented layers of parallel molecules, as one proceeds down from the outer surface (epicuticle) of the beetle. This comes from the depression instituted by the lenses of the epicuticle, as was expected by Bouligand. Figure 3 shows a second manifestation of the same Bouligand structure when the section is taken at a 45-degree angle to the layers of the fourth zone.

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Decremental Conduction over "Giant" Afferent Processes in an Arthropod

Abstract. *Four "giant" mechanoreceptive cells form part of a stretch receptor organ at the base of the uropod in the sand crab,* Emerita *(Crustacea, Anomura). Injection of the fluorescent dye Procion Yellow revealed that these sensory cells are monopolar with somata located in the central nervous system. No such cells have previously been described in arthropods. These neurons are also unusual in that they do not generate propagated action potentials; rather, they mediate stretch reflexes by transmission of graded, decremental potentials.*

Four "giant" mechanoreceptors (cells I–IV) form part of a stretch receptor organ in the sand crab, *Emerita* (Crustacea, Anomura) (Fig. 1A). These sensory cells are unusual not only because of the large size of their dendrites, but also because of the location of their somata within the central nervous system, in contrast to the peripheral location of most sensory cell bodies in arthropods. Furthermore, the dendrites do not sustain self-propagating, overshooting action potentials; they thus resemble certain thoracico-coxal receptors with which they are probably serially homologous, in other decapods (*1*).

At the base of the uropod [swimming appendage on sixth abdominal segment (*2*)], an elastic strand crosses the joint from the middorsal telson to the medioventral rim of the uropod coxopodite. The four sensory neurons send dendrites to this strand through the first ventral branch of the main root from the fifth (last) abdominal ganglion (Fig. 1A). Each dendrite maintains a diameter of 45 to 50 μm in the root and receptor nerve (in a crab of carapace length 2.5 to 3.0 cm), and divides dichotomously into several

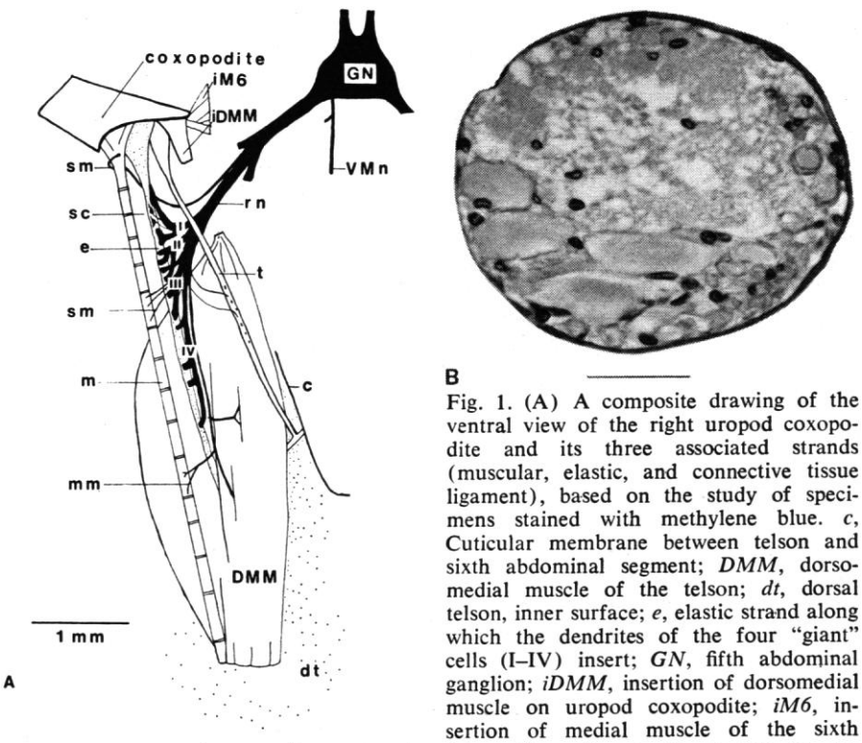

Fig. 1. (A) A composite drawing of the ventral view of the right uropod coxopodite and its three associated strands (muscular, elastic, and connective tissue ligament), based on the study of specimens stained with methylene blue. *c*, Cuticular membrane between telson and sixth abdominal segment; *DMM*, dorsomedial muscle of the telson; *dt*, dorsal telson, inner surface; *e*, elastic strand along which the dendrites of the four "giant" cells (I–IV) insert; *GN*, fifth abdominal ganglion; *iDMM*, insertion of dorsomedial muscle on uropod coxopodite; *iM6*, insertion of medial muscle of the sixth segment; *m*, muscular strand; *mm*, motor innervation of muscular strand; *rn*, receptor nerve branch of main root; *sc*, small cells of unknown function on elastic strand; *sm*, presumed sensory innervation of muscular strand; *t*, ligament between telson and uropod coxopodite; *VMn*, nerve to the ventromedial muscle, inserting on the uropod ventral to the dorsomedial muscle. (B) Cross section (silver-stained, 10 μm) of the fifth abdominal ganglion root within 1 mm of the ganglion (point of intracellular recordings). The four large profiles in the anterior-ventral quadrant are the "giant" dendritic processes; clockwise, cells IV, I, II, III, numbered according to their insertion from anterior (distal) to posterior (proximal) along the elastic strand. Marker, 40 μm.

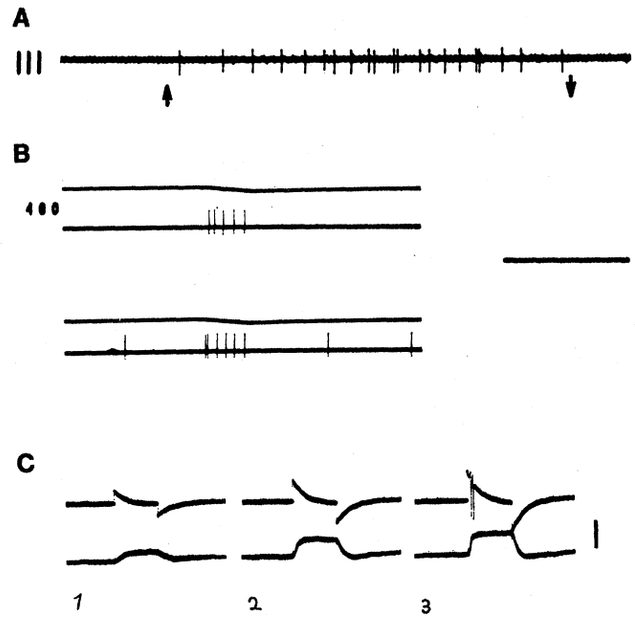

Fig. 2. (A) Reflex output in the nerve to the ventromedial muscle in response to stretch (between arrows) of the dendrite of "giant" cell III. Similar responses occurred after stretching of each of the other "giant" dendrites individually. (B) Reflex output to the ventromedial muscle (lower trace) in response to a 400-msec depolarizing pulse (10^{-7} amp) applied to cell II at its most distal end by an intracellular microelectrode. In the second record, slight tension on the whole strand increased the initial (phasic) part of the response to the depolarizing pulse. The upper trace of each recording is from a suction electrode applied to the root near the ganglion; it recorded a stimulus artifact, but no signs of afferent impulses in the "giant" dendrite. Similar results were obtained with depolarizations of each of the other three cells. (C) Intracellular microelectrode recordings from "giant" dendrite III of the sensory response in the root about 0.5 mm from the ganglion (lower trace), and of reflex motor output in the nerve to the ventromedial muscle (upper trace), in response to depolarizing pulses applied by a small suction electrode to the distal terminal of the cell at the level of the elastic strand. The dendrite, with a resting potential of −60 mv, was stimulated with pulses that were below threshold (*1, 2*) and above threshold (*3*). Markers, (A) 0.5 second; (B) 1 second; (C) 0.16 second, 20 mv.

branches which insert along the elastic strand. My experiments establish the sensory nature of these four "giant" processes by demonstrating reflex motor output in response to stretch, and to intracellular stimulation, and also present evidence of the graded nature of the afferent response. The somata of these sensory cells have been located, by dye injection, in the central nervous system.

The receptor organs and the fifth abdominal ganglion of *Emerita analoga* or *E. talpoida* females (collected from beaches of Monterey Bay, California, and Buzzards Bay, Massachusetts) were exposed (*2*). The temperature of the bath was maintained between 14° and 17°C for *E. analoga* and between 17° and 20°C for *E. talpoida* by continuously perfusing the chamber with chilled, filtered seawater. The receptor organ is anatomically associated with the dorsomedial muscle of the telson, which pronates the uropod (*2*) (Fig. 1A). The medial fragment of the coxopodite was isolated, leaving only the insertion of the elastic strand attached; this fragment of exoskeleton was gripped in a pair of forceps mounted on a micromanipulator in order to stretch the elastic strand. All nerves of the fifth ganglion, with the exception of the receptor nerve, were cut, and motor output in the nerve to the ventromedial muscle [a synergist of the main power-stroke muscle (*2*)] was recorded with a suction electrode. The individual dendrites were then cut so that only one remained inserted on the elastic strand. Motor reflexes were recorded after stretch was applied separately to the dendrites of each of the four cells (Fig. 2A). Reflex activity was also recorded while individual dendrites were depolarized by long current pulses passed through a microelectrode that penetrated the peripheral portion of the dendrite (Fig. 2B). These experiments showed that each neuron senses the return stroke of the uropod and, in turn, causes a motor discharge to a synergist of the power-stroke muscle.

Initial observations suggested that the "giant" sensory processes in *Emerita* do not generate propagating action potentials in response to stretch or to electrical stimulation; first, no evidence of afferent spikes in the receptor nerve or root accompany either mechanical stretching or electrical depolarization of the dendrites (Fig. 2B, top recording); second, long depolarizations ($\geqslant 15$ msec) were required to elicit reflex output; and, third, these receptors closely resemble the thoracico-coxal receptors (*3*) known to exhibit decremental peripheral conduction (*1*) in other decapods. In confirmatory experiments, the fifth ganglion and both receptor organs were excised and pinned on a translucent resin sheet to allow transillumination; the connective sheath was stripped from the proximal root, and a KCl-filled microelectrode (20 to 30 megohms) was inserted into one of the dendrites. Usually cell I or II was penetrated, less often III, and rarely IV (Fig. 1B).

Resting potentials ranged from −30 to −65 mv (about 25 penetrations). A similar range of values for resting potentials of the coxal receptors has been reported (*1*). Figure 2C is a record of electrical activity in one giant dendrite, taken near the point of entry of the dendrite into the ganglion, when the individual sensory process was electrically stimulated peripherally; the graded potential, and the lack of regenerative spikes, are evident. The depolarizations were maintained during the 50- or 100-msec stimulus pulses, and there were no signs of regenerative membrane responses (*4*). When *Emerita* swim, the dendrites would normally be stretched for 40 to 60 msec with each uropod stroke (*2*). Thus, these afferent processes with diameters of 40 to 50 μm carry depolarizations that are graded according to stimulus intensity over a distance of up to 3 mm into the ganglion; once there, they excite or inhibit motoneurons of the uropod muscles (*2*).

Staining of freshly dissected specimens (methylene blue) and serial sections of the receptor nerve and root (silver) failed to reveal any peripheral somata associated with these four "giant" sensory neurons. Therefore, the fluorescent dye Procion Yellow M4RS (*5*) was injected into the distal end of the dendrites in order to locate the cell bodies. This technique has been used to study neuronal architecture in other arthropods (*5, 6*), mollusks (*7*), and annelids (*8*).

The unusual features of "giant" sensory cells (Fig. 3) are: (i) the

central location of the sensory cell soma; (ii) the large diameter of the dendrite, which is maintained for several millimeters from the elastic strand into the ganglion; (iii) the corresponding large size of the soma (100 to 140 μm in longest dimension); and (iv) the unipolar nature of these mechanoreceptive cells. With the exception of the size of the somata and peripheral processes, the cell geometry resembles that described for interneurons and motoneurons in other decapods (*6*).

Sensory neurons with central somata occur in annelids (*9*). In addition, other mechanoreceptive cell bodies in arthropods occur close to the central nervous system (*10*) or must be presumed to lie within it (*11*), and a central location has been inferred for the somata of large, stretch receptor cells that do not normally produce overshooting nerve impulses (nonspiking cells) in other decapods (*1, 3*). However, the results presented here demonstrate for the first time the occurrence of monopolar sensory cells with somata in the central nervous system in arthropods.

Synaptic connections in the central nervous system are often rather inaccessible and have generally not been examined in other systems where nonspiking neurons have been found (*1, 12*); rather, sensory coding or ionic mechanisms have been studied. The significance of graded, electronic transmission may lie in the possibility of its providing a continuous monitor of the input (stimulus). Such graded nonregenerative responses may occur normally in short-axon cells in the central nervous system (*13*). The reflex connections of the nonspiking mechanoreceptors in *Emerita* are more complex than those described for any other resistance reflex; they involve coordinated excitation and inhibition of both sets of excitatory and inhibitory motoneurons of the antagonistic swimming muscles in the telson (*2*). Thus, the system of "giant" sensory cells and motoneurons involved with swimming may be a useful model for studying graded, decremental transmission in nervous function, because of the fact that the target neurons are known, and the neuropil is readily accessible for physiological recording.

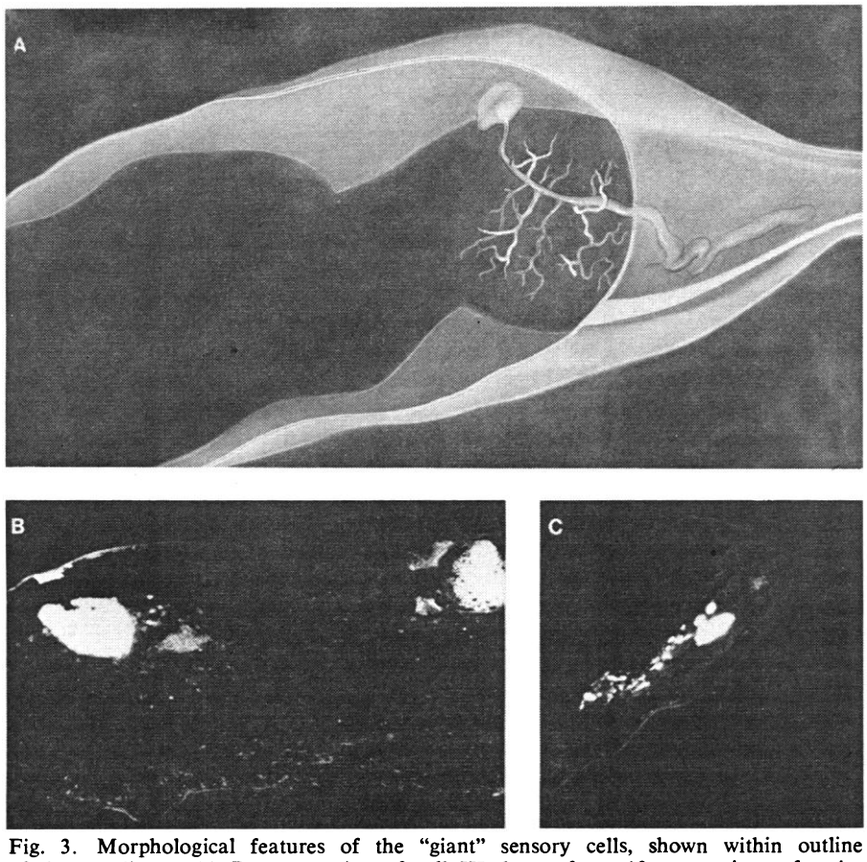

Fig. 3. Morphological features of the "giant" sensory cells, shown within outline of the ganglion. (A) Reconstruction of cell III drawn from 10-μm sections after injection of Procion Yellow into the distal end of the dendrite. Only the posterior half of the ganglion is shown as viewed from the anterior. Distinguishing features include the large dendrite exiting through the left root and the extensive branching in the ipsilateral posterior neuropil. (B) and (C) are photomicrographs of 10-μm cross sections showing profiles of injected cells within the last abdominal ganglion. (B) A section through both "giant" cells II (the pair of bilateral homologs) near the dorsal surface, approximately midway through the ganglion. (C) Section through the main dendrite of cell III in the posterior part of the ganglion; a number of small branches spread from it horizontally toward the midline. None of the branches of any of the four cells has been observed to cross the midline. Markers (B, C,), 40 μm.

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