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SHORT COMMUNICATION

STRETCH RECEPTOR ORGANS IN THE THORAX OF A TERRESTRIAL ISOPOD (*ARMADILLIDIUM VULGARE*)

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Little is known of the morphology and physiology of stretch receptors in isopods (Alexandrowicz, 1967; Alexander, 1971). The pill bug (*Armadillidium vulgare*), a terrestrial isopod, rolls up in a spherical shape in response to a noxious stimulus given to its body or to the removal of its substratum. In this study we show that stretch receptor organs which might detect the displacement of the tergites during this conglobating behaviour are present in the thorax, which forms a large part of the body. We describe the spatial organization of the receptors and their response to stretch stimuli.

Experiments were performed on male and female pill bugs, 12–14 mm in total length. For morphological identification of the stretch receptor organs, conventional vital staining with Methylene Blue and axonal filling with nickel chloride were used. In the latter staining technique, the cut distal stump of the dorsal branch of a third nerve root in a thoracic ganglion was introduced into a glass capillary filled with $0.2\,\mathrm{mol\,l^{-1}}$ $NiCl_2$ and the preparation was stored at 4°C for 12–24 h. For each putative stretch receptor explored in this way, electrical recordings were made by means of a suction electrode.

The organization of the four types of stretch receptor organs, termed TSR-1, TSR-2, TSR-3 and TSR-4, is shown in Fig. 1. The stretch receptors are bilateral and located dorsally in each thoracic segment from the second to the eighth thoracic segment. For simplicity, the results will be decribed as from one side only. The TSR-1 type has an extremely long dendritic process without a differentiated receptor muscle. This process extends from a bipolar receptor cell located in the third segment towards an extensor muscle lying medially between the second and the third segments, and forms a stout dendritic structure, part of which is firmly attached to the articular membrane in the anterior ridge of the third segment. Thereafter the dendrite regains a thin process, runs closely parallel with the extensor muscle, and attaches its extremity to the anterior ridge of the second segment. Thus, the entire length of the dendritic process from the receptor cell soma measures 1.5 mm.

Key words: stretch receptor, tonic response, isopod, Crustacea.

The TSR-2 and TSR-3 types are distinguished by their well-developed receptor muscles: the receptor muscle of TSR-2 spans anterolaterally over the third and fourth segments, and that of TSR-3 is located only in the fourth segment. These two receptor muscles lie in parallel about 300 μm apart. Although the function of such a topographical arrangement of the stretch receptors is difficult to conceive, it is noteworthy that, when the pill bug rolls up, the displacement of the fourth segment is much larger than that of any other segment.

The TSR-4 type is a paired structure, located in each of the fifth to eighth segments. The receptor muscles of each pair run closely together except for their extremities, and their sensory cells are also joined tightly by connective tissue (Fig. 1A,B). The dendritic process from each soma (about 20 μm in transverse diameter) spans about 300 μm and terminates in the central region of each receptor muscle. The receptor muscles are very thin (12–20 μm in diameter), but they could clearly be identified as muscles by observation of birefringence with polarization microscopy (Fig. 1C). The axons from both somata of the TSR-4s in each segment run *via* the third nerve root of each thoracic ganglion and project anteriorly into the brain and posteriorly into the fused abdominal ganglion; they run medially

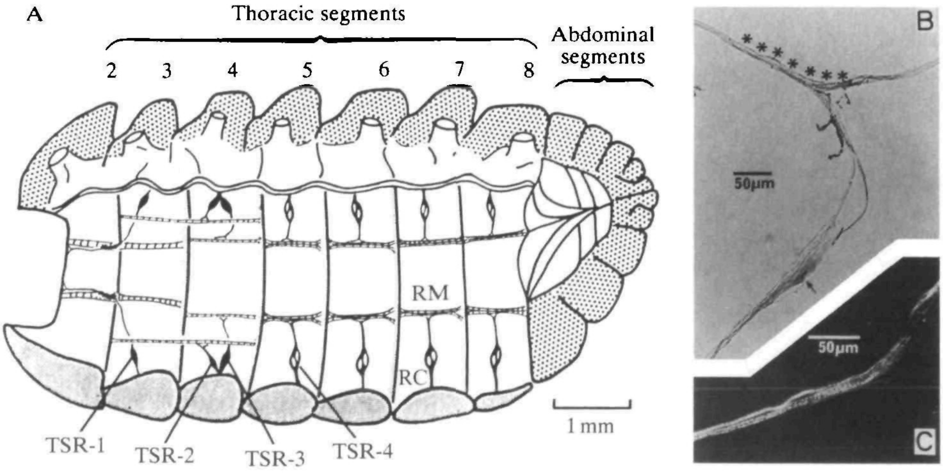

Fig. 1. (A) Schematic illustration of the organization of the thoracic stretch receptor organs viewed from the ventral side, with head and legs removed. The first thoracic segment is not depicted because it is fused with the head. The viscera are removed as well as all muscles except for those with which the stretch receptor organs are associated. The relative size of sensory cells and muscles is exaggerated. (B) Photomicrograph of isolated TSR-4 stretch receptor organs in the fifth segment. This was obtained from a whole-mount preparation filled with nickel which was precipitated by adding rubeanic acid. An arrow indicates the nucleus of a receptor cell soma. Another cell soma lies behind this soma (not seen here). Some connective tissue adheres to the distal part of the dendritic process, or on the muscle receptor (black debris). (C) Receptor muscle showing birefringence. The part marked with asterisks in B was observed under a polarization microscope. RC, receptor cell; RM, receptor muscle; TSR, thoracic stretch receptor organ.

through the connective closely parallel to each other and give off their short secondary branches in every ganglion. In the abdominal ganglion each axon makes a U-shaped turn before terminating in the contralateral hemiganglion. Thus, the fourth type of thoracic stretch receptor resembles the abdominal stretch receptor organs of higher crustaceans in its mode of projection (Bastiani and Mulloney, 1988).

Physiologically, all the stretch receptors described here were exclusively of the slowly adapting type, although there were slight differences among them in their responses to imposed stimuli. An example of a recording from a pair of TSR-4s in the fifth thoracic segment is presented in Fig. 2A, and was obtained as follows: the tergal slips composed of the fifth and sixth segments containing the TSR-4s were bisected along the midline and then one of the bisected slips was transferred to a chamber filled with saline for woodlice (Holley and Delaleu, 1972). The tergite of the sixth segment was fixed with insect pins, while the free movable tergite of the fifth segment was pierced by a hook-shaped needle, and then connected to a vibrator device (frequency response: d.c. to 200 Hz), which was driven by applying a ramp-and-hold pulse. By this means a controlled stretch stimulus was delivered to the receptor muscles in the fifth segment. The electrical activities of the pair of

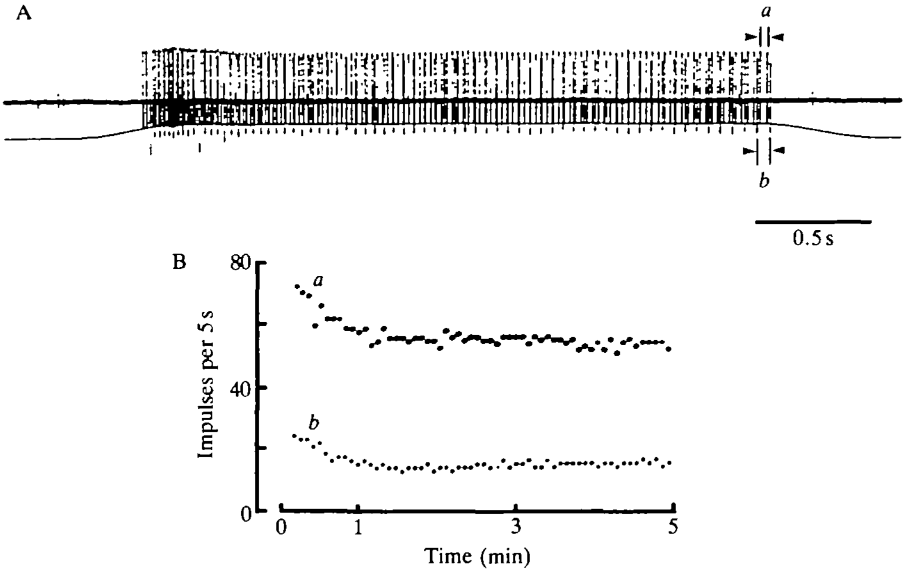

Fig. 2. Responses of stretch receptor organs of the fifth thoracic segment. (A) The stretch stimulus of the ramp-and-hold form (lower trace, stretch amplitude, 250 μm) elicits impulse trains with high (*a*) and low (*b*) frequencies (upper trace). This was recorded from the cut distal stump of the dorsal branch of the third nerve root, which contains two axons derived from their own segmental stretch receptors. (B) Adaptation of discharge frequency to a stretch stimulus maintained for a long period. The abscissa represents time after onset of the stretch stimulus. Discharges of high (*a*) and low (*b*) frequency during the static phase continue at a constant rate for up to 5 min. Stretch amplitude, 400 μm.

TSR-4s were recorded simultaneously from the dorsal branch of the third nerve root, whose cut distal stump was introduced into the suction electrode.

As shown in Fig. 2A, two kinds of impulse trains, which usually differed in both amplitude and frequency, were evoked by a ramp-and-hold stimulus given to the pair of receptor muscles. These impulse trains could be separately recorded through two window discriminators. The frequency plots obtained from the discriminated impulse trains (Fig. 2B) indicate that the relevant stretch receptor organs are undoubtedly of a tonic type similar to that described for the stretch receptors of higher crustaceans (Wiersma *et al.* 1953; Kuffler, 1954). From this result, it may be inferred that *in vivo* the tonic impulse discharges from a pair of TSR-4s in the fifth thoracic segment change in proportion to the degree of flexion of the body segment in a ventral direction. It was evident, however, that the member of a pair evoking the high-frequency discharge is less sensitive to flexion than the member evoking the low-frequency discharge. So far as we have examined, the response properties of the TSR-4s of other segments and also of the other types of thoracic stretch receptors were identical with those of the TSR-4s of the fifth segment. This indicates that each stretch receptor functions as a position detector as well as a flexion movement detector.

The present study has thus demonstrated the existence of stretch receptor organs both with differentiated receptor muscles and with undifferentiated ones. The latter type of stretch receptor is probably the equivalent of the so-called N-cells in the thorax of decapod crustaceans (Alexandrowicz, 1952; Wiersma and Pilgrim, 1961). The tonic responsiveness of the thoracic stretch receptors is not surprising if we take account of the gentle movement of the thorax accompanying the conglobating behaviour specific to this species. The absence of any fast-adapting stretch receptors, the function of which has been considered as being linked with fast muscle systems (Alexandrowicz, 1967), might correlate with such a slower degree of thoracic movement. The present results also lend support to the belief that the organization and response properties of the thoracic stretch receptors in large crustaceans are closely related to the mobility of the thorax, which is evidently associated with the development of the carapace (Alexandrowicz, 1967; Pilgrim, 1974; Bush and Laverack, 1982).

Further study on the functional properties of the thoracic and abdominal stretch receptors is now in progress, together with a study on the neural mechanism underlying the conglobating behaviour.

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