ZOOLOGICAL SCIENCE 8: 187–191 (1991)

[COMMUNICATION]

Abdominal Stretch Receptor Organs of *Armadillidium vulgare* (Crustacea, Isopoda)

Akiyoshi Niida, Kouchi Sadakane and Tsuneo Yamaguchi

Department of Biology, Faculty of Science, Okayama University, Okayama 700, Japan

ABSTRACT—The body of the pill bug (Crustacea, Isopoda) is composed of a well-developed thorax and a greatly reduced abdomen. In spite of the small abdomen, a pair of stretch receptor organs comprising specialized muscles and receptor cells occur on the either side of the midline in the abdomen. All the abdominal stretch receptor organs show a slowly-adapting response to stretch stimuli. The output of an abdominal stretch receptor organ blocked impulse discharges from a thoracic stretch receptor organ evoked by an imposed stimulus, implying the presence of an inhibitory intersegmental reflex between them.

INTRODUCTION

Unlike the decapod with a well-developed carapace, the body of the pill bug, a terrestrial isopod, is predominantly occupied by freely movable thoracic segments. In this animal we have previously shown the occurrence of the thoracic stretch receptor organs which exclusively show slowly adapting responses to stretch stimuli [1]. The response characteristic of this sense organ is appropriate to detect sluggish movement of the thorax accompanying the conglobating behavior specific to this species.

Adjacent to the thorax, there exists the greatly reduced abdomen, which is composed of six abdominal segments. From such a segmental feature, on e would expect remnants of retrograding stretch receptor organs in the abdomen. In this paper it is reported that the abdominal stretch receptor organs exert an inhibitory action on the thoracic stretch receptor organ.

Accepted May 21, 1990
Received March 10, 1990

MATERIALS AND METHODS

Experiments were performed on male and female pill bugs (*Armadillidium vulgare*), 12–14 mm overall length. For morphological identification of the stretch receptor organs, conventional vital staining with methylene blue and axonal filling with nickel chloride were employed. In the latter staining technique, the cut distal stump from one of the four abdominal nerves (Fig. 1B), which arise from fused abdominal ganglia, was introduced into a glass capillary filled with 0.2 M $NiCl_2$. Electrical activities of each putative stretch receptor explored in this way were recorded from the abdominal nerve with the aid of a suction electrode.

RESULTS AND DISCUSSION

As shown in Figure 1B, the 8th thoracic ganglion is joined by several fused abdominal ganglia where four abdominal nerves occur on each side. Among these nerves the first contains (see also Ab.N. in Fig. 2B) not only the components of the 3rd nerve root of the 8th thoracic ganglion, but also the axons of the stretch receptor organs in the 1st abdominal segment. To avoid confusion with the description of the stretch receptor organs, the results will be described as from one side only. In the 1st to the 5th abdominal segments, identified

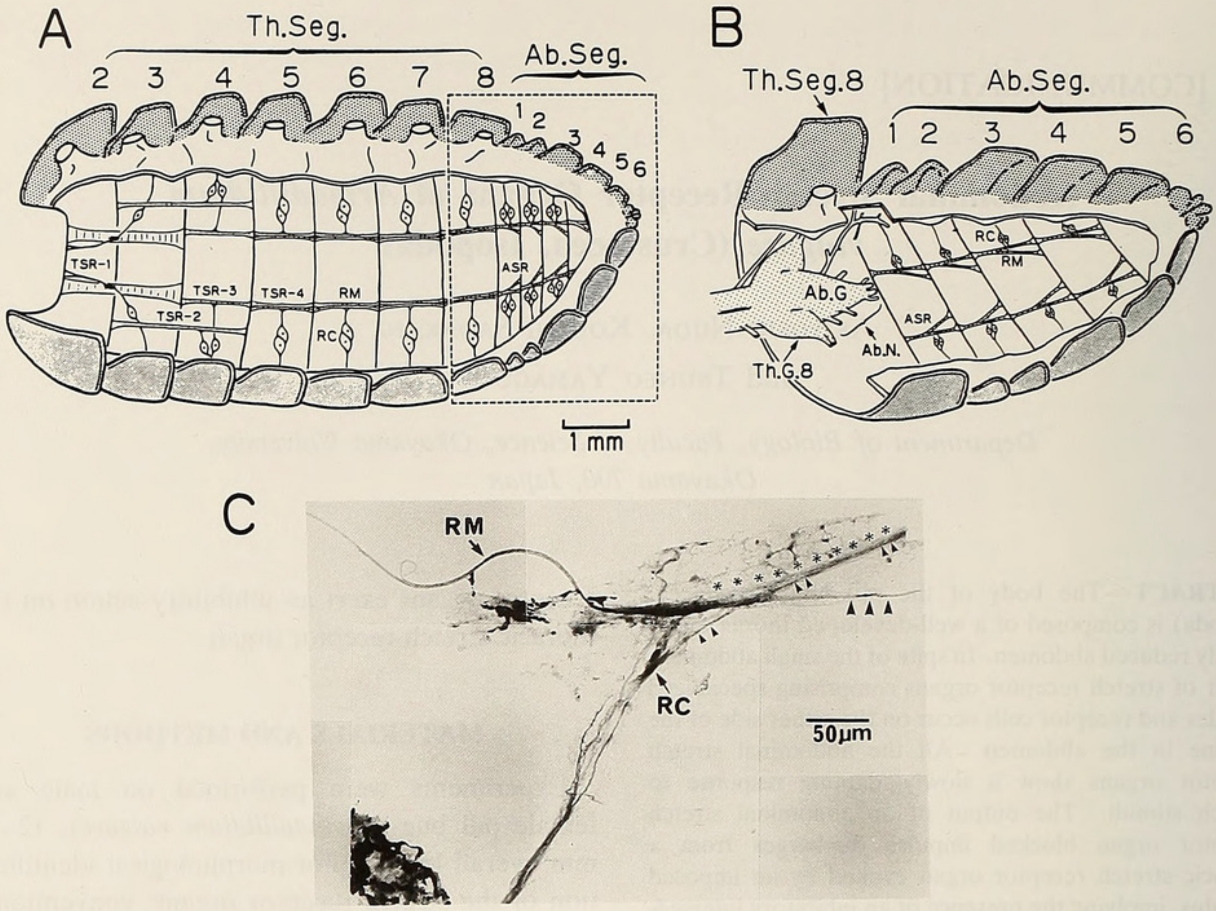

Fig. 1. (A, B) Schematic illustration of the organization of the thoracic and abdominal stretch receptor organs viewed from the ventral side, with head and legs removed. The relative size of receptor cells and muscles is exaggerated. Area enclosed by rectangle in A is shown in B, where the abdomen is depicted as being more elongated than actual size. Calibration bar in A is not available in B. Ab.G., abdominal ganglion; Ab.N., abdominal nerves; Ab.Seg., abdominal segments; ASR, abdominal stretch receptor organ; RC, receptor cell; RM, receptor muscle; Th.G.8, the 8th thoracic ganglion; Th.Seg, thoracic segment; TSR-1~TSR-4, 1st to 4th thoracic stretch receptor organs; (C) Photomicrograph of paired stretch receptor organs isolated from the 1st abdominal segment. This was obtained from a whole-mount preparation stained with methylene blue. The appearance of the waving receptor muscle (RM) in Figure 2C is an artifact which was caused in mounting a preparation on a slide. Asterisks, obliquely oriented receptor muscle; Thick arrow heads, horizontally arranged receptor muscle; Thin arrow heads, dendrite from a bipolar receptor cell.

stretch receptor organs are all similar in shape and are much smaller than those in the thorax (Fig. 1A). Each of the abdominal stretch receptor organs comprises a pair of receptor cells and differentiated receptor muscles (Fig. 1B, C). The receptor muscles, which lie in parallel and connect tightly with each other in the anterior part of the relevant tergum, run for some distance in the posterior direction, separating into two muscle components: one is arranged parallel to the antero-posterior axis of its own segment, while the other thickens and diverges obliquely (Fig. 1B, C). The former component forms a spindle-shaped structure and thins out towards posterior end. The posterior extremities of both components are located on the articular membrane of the anterior tergal ridge of the subsequent segment. In these receptor muscles, particular termination of dendrites from two receptor cells can be seen (Fig. 1C); one extends a long dendritic process along the obliquely oriented receptor muscle and this process presumably leads to the posterior extremity of the receptor muscle. The other has a short bulbous dendrite in the region of the spindle-shaped structure mentioned above.

Axons from a pair of receptor cells of the abdominal stretch receptor organs run centrally via an abdominal nerve. The axonal filling of the 2nd abdominal stretch receptor organs with nickel chloride reveals that two axons, of large and small caliber, project anteriorly into the brain and posteriorly into the fused abdominal ganglion. That is, they run medially through the connective closely parallel to each other. Short secondary branches of large caliber axon project extensively into every thoracic ganglion, while the small caliber axon usually lacks secondary branches. These modes of central projections of the axons of the abdominal stretch receptor organs are closely similar to that of the thoracic stretch receptor organs.

Figure 2A shows electrical activities from the 2nd abdominal stretch receptor organ. Experimental arrangement for recording and stimulation was similar to that illustrated in Figure 2B. In this arrangement a preparation was composed of the tergal slips of the 1st and 2nd segments containing the 2nd abdominal stretch receptor organs. The cut distal stump of the abdominal nerve was introduced into a suction electrode. A vibrator device providing stretch stimulus was driven by a ramp-and-hold pulse. As a result, two kind of impluse trains, differing in both amplitude and frequency were obtained (Fig. 2A1). These impulse trains were usually recorded separately through two window discriminators. The frequency plots from impulse trains discriminated in this way (Fig. 2A2) showed that each member of a pair of abdominal stretch receptor organs is undoubtedly of a slowly adapting type, since impulse discharge lasts as long as stretch stimulus is maintained. Thus, it may be inferred that in the

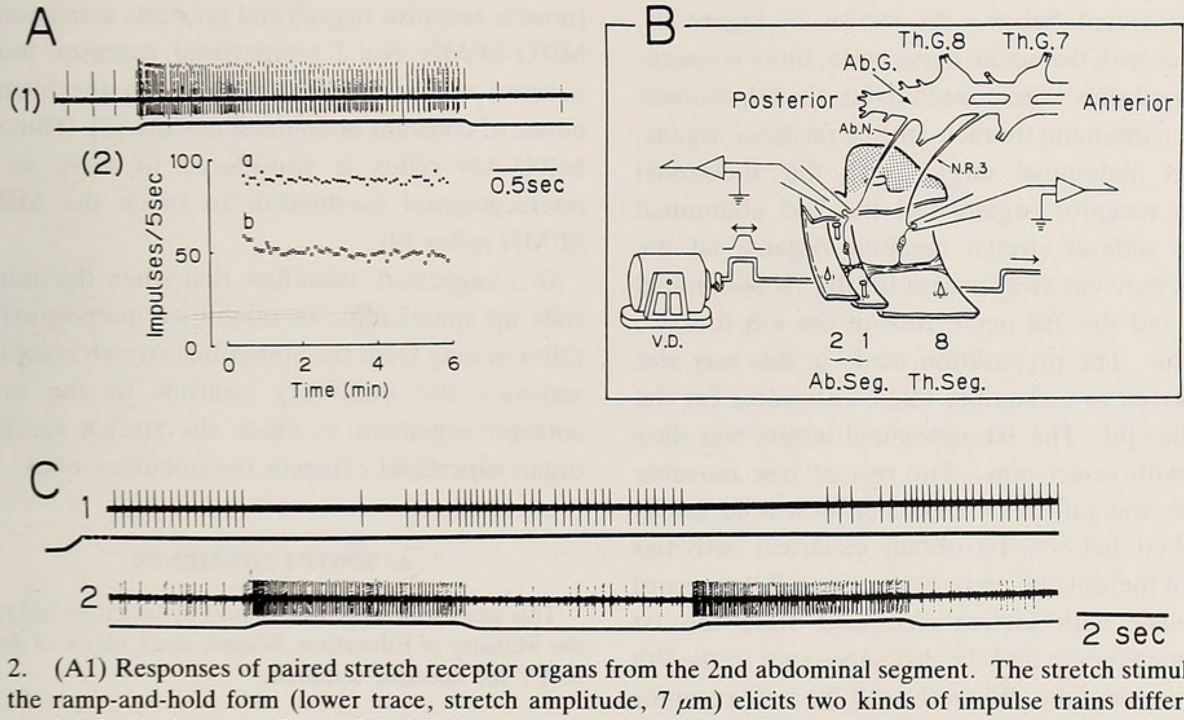

FIG. 2. (A1) Responses of paired stretch receptor organs from the 2nd abdominal segment. The stretch stimulus of the ramp-and-hold form (lower trace, stretch amplitude, 7 μm) elicits two kinds of impulse trains differed in amplitude: the largest spikes and slightly smaller ones of five potential sizes. (A2) Frequency plots from two kinds of impulse trains evoked by a stretch stimulus for a long period. Impulse trains were discriminated through two window discriminators. Dishcarges of high (a) and low (b) frequencies during the quasi-static phase continue at a constant rate for up to 6 min. Stretch amplitude, 7 μm. This was recorded from a separate sample.

(B) Experimental arrangement for showing inhibitory effect of an abdominal stretch receptor on a neighboring thoracic stretch receptor organ. Electrical activities were recorded en passant with suction electrodes from the 1st abdominal nerve and the 3rd nerve root in the 7th thoracic ganglion. N. R. 3, 3rd nerve root; V. D., vibration device. Explanation for other abbreviation: see Fig. 1.

(C1, C2) Records from stretch receptor organs of the 8th thoracic segment and those of the 1st abdominal segment in response to stretch stimuli, respectively. C1 shows inhibitory effects of the abdominal stretch receptor organ on the thoracic stretch receptor organ. In the lower trace of each record, upper deflection represents the application of stretch stimulus. Stretch amplitude: 50 μm in C1 and 3 μm in C2.

intact pill bug the tonic impulse discharges from a pair of abdominal stretch receptor organs change in proportion to the degree of flexion of the abdominal segment in a ventral direction.

Pharmacological application of GABA ($>10^{-5}$ M) to the thoracic stretch receptor organs suppressed impulsse discharges evoked by an imposed stimulus, though the experimental data are not shown. From available data concerning the GABA effect on the stretch receptor of the decapod crustacean [2–4], this suppression indicates that GABA is a putative inhibitory transmitter also in the pill bug, and that GABA inhibitory synapses [5] may exist on the receptor cells of the stretch receptor organs in this animal. On the other hand, Figure 2C shows an inhibitory effect of the output from an abdonimal stretch receptor organ on a thoracic stretch receptor organ. This inhibitory effect was demonstrated on a preparation as stated below. As shown in Figure 2B, together with the whole nerve code, three consecutive tergal slips were dissected out: the 8th thoracic tergite containing thoracic stretch receptor organs, the 1st abdominal tergite with the abdominal stretch receptor organs and the 2nd abdominal tergite without stretch receptor organs; all the nerves were cut away except for the 1st abdominal nerve and the 3rd nerve root of the 8th thoracic ganglion. The preparation made in this way was transferred to a chamber filled with saline for the woodlice [6]. The 1st abdominal tergite was then fixed with insect pins. The rest of free movable tergites was pulled in a manner as will be briefly described below. To obtain electrical activities evoked thereby, an en passant extracellular record was made with suction electrodes from the 1st abdominal nerve and the 3rd nerve root of the 7th thoracic ganglion. When the 8th thoracic receptor muscle was continuously stretched in a constant amplitude, a tonic impulse train appeared in the receptor cells of the 8th thoracic stretch receptor organ, as shown in Figure 2C, where the impulse train of another member of a pair of stretch receptors was eliminated through a window discriminator. Under this condition, when the 2nd abdominal tergite was pulled by driving the vibration device, there occurred impulse discharges in the 1st abdominal stretch receptor organs. These discharges resulted in the suppression of impulse discharges from the 8th thoracic stretch receptor organs.

These results indicate the presence of an inhibitory neuron innervating the receptor cell of the 8th thoracic stretch receptor organ. This type of inhibitory effect on the 8th thoracic stretch receptor organ may be mediated by an intersegmentally located inhibitory neuron which receives inputs from the ascending axon of the 1st abdominal stretch receptor neuron. A similar inhibitory effect has been already reported in the abdominal stretch receptor organs of the crayfish [7–9]. Page and Sokolove [9] observed that during voluntary tonic flexion of the abdomen, centrally originating excitatory input to the tonic extensor is removed and simultaneously high frequency discharge of AN (accessory nerve) occurs in the 2nd nerve root. This accessory discharge inhibits the tonic MRO (muscle receptor organ) and prevents activation of MRO-SEMN No. 2 (-superficial extensor motoneuron) reflex, which contributes to the maintenance of constant abdominal posture [8]. Thus the MRO-AN reflex is considered to serve as an intersegmental mechanism to block the MRO-SEMN reflex [9].

It is suggested, therefore that when the animal rolls up spherically, an inhibitory intersegmental reflex arising from the abdominal stretch receptors activates the inhibitory neurons in the more anterior segement to block the stretch receptor organ-superficial extensor motoneuron reflex.

ACKNOWLEDGMENTS

This work was supported in part by Grant in Aid from the Ministry of Education, Science and Culture of Japan to TY for scientific research.

REFERENCES

1 Niida, A., Sadakane, K. and Yamaguchi, T. (1990) J. exp. Biol., **149**: 515–519.

2 Kuffler, S. W. and Edwards, C. (1958) J. Neurophysiol., **21**: 589–610.

3 Hori, N., Ikeda, K. and Roberts, E. (1978) Brain Res., **141**: 364–370.

4 McGeer, E. G., McGeer, P. L. and McLennan, H. (1961) J. Neurochem., **8**: 36–49.

5 Elekes, K. and Florey, E. (1987) Neuroscience, **22**:

1111–1122.

6 Holley, A. and Delaleu, J. C. (1972) J. exp. Biol., **57**: 589–608.

7 Eckert, R. O. (1961) J. cell. comp. Physiol., **57**: 149–162.

8 Fields, H. L., Evoy, W. H. and Kennedy, D. (1967) J. Neurophysiol., **30**: 859–875.

9 Page, C. H. and Sokolove, P. G. (1972) Science, **175**: 647–650.