

MUSCLE RECEPTOR ORGANS IN SOME DECAPOD CRUSTACEA

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Abstract—The presence of muscle receptor organs was determined in the abdomen of ten species of decapod Crustacea. These were *Pandalus danae*, *Paracrangon echinata*, *Crago franciscorum*, *Eualus* sp. (tribe Caridea) belonging to the Natantia, and *Munida quadrispina* (tribe Galatheidea), *Upogebia pugettensis*, *Callinassa gigas* (tribe Thalassinidea), *Pagurus aleuticus*, *P. alaskensis*, *P. kennerlyi* (tribe Paguridea) belonging to the Reptantia. Responses of the sensory neurons were obtained by flexion of the joints of isolated abdomens, and in some cases by stretching the organs themselves or by the use of acetylcholine. All species yielded slowly-adapting responses and some gave also fast-adapting responses. Anatomical examination was used to confirm the existence of the organs in a number of species. In one species of true crab, *Cancer magister* (tribe Brachygnatha), no evidence was obtained, either physiologically or anatomically, for the presence of muscle receptor organs. The known distribution of muscle receptor organs in higher Crustacea is tabulated and the possible widespread occurrence of such organs in the Crustacea as a whole is discussed.

INTRODUCTION

SINCE the discovery and description by Alexandrowicz (1951) of the muscle receptor organs (MRO) in the abdomen of *Homarus vulgaris* and *Palinurus vulgaris*, considerable progress has been made in elucidating the microanatomy and function of the structures in these and other Crustacea. Most, if not all, segments of the abdomen in the Crustacea examined possess two pairs of MRO lying a little apart from the mid-dorsal line and more or less closely associated with the superficial extensor musculature. They are situated towards the posterior end of the segments and bridge the joint between successive terga so that they become stretched when the abdomen is flexed. Each MRO comprises a receptor muscle (RM) with a closely-associated, peripheral, sensory neuron and the afferent axon of this cell. The muscle is also supplied with a number of efferent axons which run with the afferent axon in the second root of the ganglion lying in the segment in front of that containing the MRO (Hughes & Wiersma, 1960). Of the two receptor muscles of a pair, one (RM₁), usually lying more laterally, is

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commonly shorter and has coarser cross-striation and longitudinal sub-division of its muscle elements. Wiersma, Furshpan & Florey (1953) showed that the sensory neurons are sensitive to stretching of the receptor muscle and that RM₁ with its neuron is a slowly-adapting sense organ, while the other (RM₂) with its

TABLE 1—CRUSTACEA IN WHICH ABDOMINAL MUSCLE RECEPTOR ORGANS HAVE BEEN DETERMINED. SYMBOLS IN THE THIRD COLUMN INDICATE THAT THE PAPER REFERRED TO INCLUDES EXAMINATION WHICH IS PHYSIOLOGICAL (p), ANATOMICAL (a), OR HISTOLOGICAL (h)

Species	Type of organ	Method of examination	Reference
EUCARIDA—DECAPODA			
Natantia			
Caridea			
Pandalidae:			
<i>Pandalus danae</i> Stimpson	RM ₁ RM ₂	(p) (a)	This paper
<i>Pandalopsis dispar</i> Rathbun	RM ₁ RM ₂	(p) (a)	Florey (personal communication)
Cragonidae:			
<i>Paracrangon echinata</i> Dana	RM ₁ RM ₂	(p) (a)	This paper
<i>Crago franciscorum</i>	RM ₁	(p)	This paper
Hippolytidae:			
<i>Eualus</i> sp. (Stimpson)	RM ₁	(p)	This paper
Palaemonidae:			
<i>Leander serratus</i> (Pennant)	RM ₁ RM ₂	(a) (h)	Alexandrowicz, 1956
Reptantia—Palinura			
Scyllaridea			
Palinuridae:			
<i>Palinurus vulgaris</i> L.	RM ₁ RM ₂	(a) (h)	Alexandrowicz, 1951
<i>Panulirus interruptus</i> Randall	RM ₁ RM ₂	(p) (a)	Wiersma, Furshpan & Florey, 1953
Astacura			
Nephropsidea			
Astacidae:			
<i>Astacus fluviatilis</i> L.	RM ₁ RM ₂	(p) (a) (h)	Florey, 1955; Florey & Florey, 1955
<i>A. leptodactylus</i> Eschscholtz	RM ₁ RM ₂	(p)	Burkhardt, 1959
<i>A. trowbridgei</i> Stimpson	RM ₁	(p)	Giese & Furshpan, 1954
<i>Procambarus clarkii</i> (Girard)	RM ₁ RM ₂	(p) (a)	Wiersma, Furshpan & Florey, 1953
		(p)	Kuffler & Eyzaguirre, 1955
<i>P. alleni</i> (Faxon)	RM ₁ RM ₂	(p) (a)	Kuffler, 1954; Eyzaguirre & Kuffler, 1955
<i>Orconectes virilis</i> (Hagen)	RM ₁ RM ₂	(p)	Eyzaguirre & Kuffler, 1955; Kuffler & Eyzaguirre, 1955
Nephropsidae:			
<i>Homarus vulgaris</i> L.	RM ₁ RM ₂	(a) (h)	Alexandrowicz, 1951
<i>H. americanus</i> M—Edwards	RM ₁ RM ₂	(p) (a)	Kuffler, 1954

Cont.—

TABLE 1—cont.

Species	Type of organ	Method of examination	Reference
Anomura			
Galatheidea			
Galatheidae:			
<i>Munida quadrispina</i>	RM ₁ RM ₂	(p) (a)	This paper
Benedict			
Thalassinidea			
Callianassidae:			
<i>Upogebia pugettensis</i>	RM ₁ RM ₂	(p) (a)	This paper
(Dana)			
<i>Callianassa gigas</i> Dana	RM ₁ RM ₂	(p) (a)	This paper
Paguridea			
Paguridae:			
<i>Pagurus aleuticus</i>	RM ₁ RM ₂	(p) (a)	This paper
(Benedict)			
<i>P. alaskensis</i> (Benedict)	RM ₁ RM ₂	(p) (a)	This paper
<i>P. kennerlyi</i> (Stimpson)	RM ₁ RM ₂	(p) (a)	This paper
<i>P. calidus</i> (Risso)	RM ₁ RM ₂	(a) (h)	Alexandrowicz, 1952a
<i>P. striatus</i> (de Latreille)	RM ₁ RM ₂	(a) (h)	Alexandrowicz, 1952a
<i>Eupagurus prideauxi</i>	RM ₁ RM ₂	(a)	Alexandrowicz, 1952a
(Leach)			
Brachyura-Brachygnatha			
Canceridae:			
<i>Cancer magister</i> Dana	Absent	(p) (a)	This paper
HOPLOCARIDA—			
STOMATOPODA			
Squillidae:			
<i>Squilla mantis</i> (Rondel)	RM ₁ RM ₂	(a) (h)	Alexandrowicz, 1954

neuron is, relatively speaking, a fast-adapting organ. They also showed that stimulation of the motor nerve to the organ caused contraction of both RM₁ and RM₂ and that sensory discharges in both afferent neurons resulted. These observations were extended in a series of papers (Kuffler, 1954; Eyzaguirre & Kuffler, 1955; Kuffler & Eyzaguirre, 1955) in which it was demonstrated, *inter alia*, that each RM₁ and RM₂ is innervated by at least one motor axon and a common inhibitory axon. These workers confirmed that motor nerve stimulation as well as stretch excitation of the RM led to the production of sensory nerve discharges and further showed that inhibitory nerve stimulation acted to reduce or prevent the sensory responses.

The occurrence of such organs in the abdomen in several groups of Crustacea, as recorded in the literature and as found in the present investigation, is shown in Table 1. Among the Decapoda, good anatomical and histological data are available so far for the Palinura, Astacura and Anomura, and in one species of the Natantia (for details see especially Alexandrowicz, 1951, 1952a, 1956; Florey & Florey, 1955), while physiological examination has been reported only for the

Palinura and Astacura. The present work was carried out to examine other groups of Decapoda for the presence or absence of these organs.

METHODS

The organs were searched for by a physiological technique based on that used by Wiersma *et al.* (1953) for *Procambarus clarkii*. Isolated abdomens, either a dorsal strip only in the larger forms, or the entire abdomen in the smaller forms, were pinned out in a waxed dish by their anterior segments, and a thread attached to the telson was used to flex the preparation. In this way the inter-tergal joints could be flexed either slowly or rapidly and the degree of flexion held constant by fixation of the thread. Sensory discharges were picked up from the nerve close to the organ by a Ag/AgCl electrode and passed to both an oscilloscope and a speaker. Sea-water proved satisfactory as a bathing medium for the preparations from marine organisms. Crayfish Ringer (Van Harreveld, 1936) was used for experiments on *Procambarus*. After the experiments an examination of the region from which the impulses originated was carried out in several species, using Rongalit-methylene blue staining.

OBSERVATIONS

(a) *Decapoda Natantia*

Preparations from *Pandalus danae* Stimpson, *Paracrangon echinata* Dana, *Crago franciscorum* (Stimpson), and an unidentified species of *Eualus* all gave slowly-adapting responses to flexing the abdomen in a manner which would cause stretching of the MRO. Attempts to record from an exposed nerve of the dorsal strip of the abdomen were not very successful in these small animals. This may be due to the high proportion of damaged muscle causing the preparations to

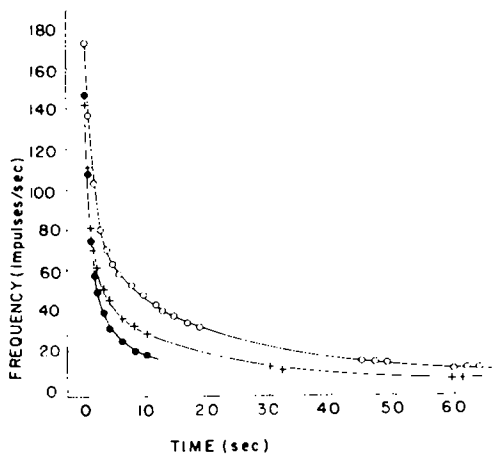


FIG. 1. Frequency response curves of slow-adapting stretch receptors (RM_1) from three separate preparations of *Paracrangon echinata*. In all figures, frequency in impulses/sec is plotted against time from point of peak frequency following stimulus.

deteriorate rapidly, possibly by the release of potassium. Excellent results were obtained by slitting the ventral side of the abdomen medially and exposing the nerve cord. The second nerve root was then cut from its ganglion, in one or more segments, and prepared free from muscles, connective tissue and integument to above the mid-lateral line, the nerve branches to those structures being cut. Beyond this point there were no further branches giving sensory discharges so that uncontaminated recordings of the MRO discharges were readily obtained. In the case of *P. echinata* and *P. danae*, the nerve was further dissected at the conclusion of the experiment to check its connections and it was found to comprise efferent fibres to the dorsal extensor muscles as well as fibres belonging to the MRO. In all four species, oscillographic records showed long-lasting slowly-adapting responses indicating the presence of RM₁ (see Fig. 1 for an analysis of the response in *P. echinata*). Occasionally in the latter species there was observed in addition a fast-adapting response such as would be expected from RM₂; the adaptation rate was very rapid, the response decaying almost linearly with time to cease between 2.5 and 2.6 sec after the time of peak frequency. The existence of both sense organs in this species was confirmed by subsequent examination with methylene blue. In *P. danae* such examination also showed the presence of two sense organs though no clear double responses were obtained from this species.

(b) *Decapoda Reptantia*

1. *Anomura. Munida quadrispina* Benedict was prepared in the same manner as the natant forms above; its abdomen is similarly transparent and mid-ventral dissection can be carried out readily without damage to the nerve roots. Responses from RM₁ only were obtained from several segments. Subsequent dissection and staining showed that both RM₁ and RM₂ were present; presumably the flexion applied during the experiments was inadequate to stimulate the fast-adapting component in this species, as was probably the case in three of the four species of Natantia.

The specimens of *Upogebia pugettensis* (Dana) which were available were considerably larger than the preceding forms and were dissected as described by Wiersma *et al.* (1953) for *Procambarus*. The preparation proved to be the most hardy in the present series and several segments in turn could be easily investigated in a single specimen. Responses were found from RM₁ of each segment from the first to the fifth on many occasions, and from RM₂ in several segments. The response of RM₁ was more readily obtained in any one preparation than that of RM₂, but both could be elicited by flexing the abdomen, by stretching the MRO with a needle, or by administration of ACh at 10^{-6} to 10^{-5} . The sensory discharge of RM₁ to a constant stretch was maintained for 45 min or longer and many preparations lasted in good condition all day. The peak frequency recorded for RM₁ discharge varied clearly with the amount of flexion provided, for example from 133/sec for a nearly maximum flexion to about 50/sec for slight flexion. The rates of adaptation following these different peak values are remarkably parallel (Fig. 2). Following slight flexion the discharge rate often became steady for many

minutes at a very low value, e.g. 1.96–2.77 impulses/sec at 16.3°C, and 2.26–2.33/sec at 16.0°C. These compare with the rate of “about 2/sec” found by Wiersma *et al.* in *Procambarus*. After still further adaptation in *Upogebia* irregularity set in and, at approximately one impulse/sec to one/two sec the discharges were grouped with intervals of several seconds but still persisted for some minutes.

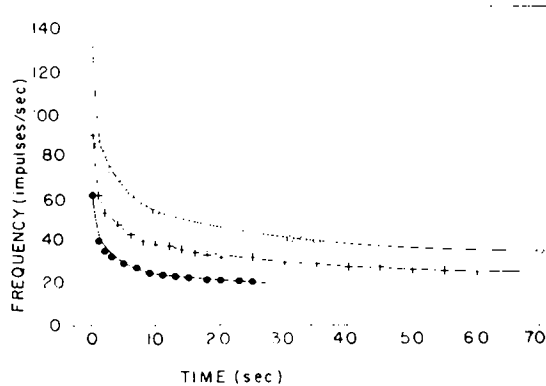


FIG. 2. Frequency response curves of slow-adapting stretch receptors (RM_1) from three separate preparations of *Upogebia pugettensis*.

Staining revealed that the MRO were placed somewhat more laterally than in *Procambarus*. The receptor muscles were shorter in the more posterior segments; in the fifth segment they were less than half the length of the tergum and were oriented at an angle of about 20° with the longitudinal axis. The cell-body of the sensory neuron of RM_1 was, in appearance, scarcely more than a swollen portion of the axon with the nucleus lying in its thickest region and often with a dendrite arising from the side central to the nucleus. This peculiarity is also shown by RM_1 in the Paguridae (Alexandrowicz, 1952a). The neuron as a whole much more closely resembled that figured by Florey & Florey (1955, Fig. 4) in *Astacus* than those of *Homarus* and *Palinurus* illustrated by Alexandrowicz (1951).

Callinassa gigas Dana gave responses similar to those of *Upogebia*, but the animal is much more difficult to keep under laboratory conditions, as it tends to shed its limbs with resultant loss of blood. The loose nature of its intersegmental articulations also made the preparations from this animal too fragile for consistent results. It was therefore not possible to make quantitative measurements, but discharges of both types of sense organ were obtained, and the presence of both RM_1 and RM_2 was confirmed anatomically.

Three species of hermit-crabs, *Pagurus aleuticus* (Benedict), *P. alaskensis* (Benedict), and *P. kennerlyi* (Stimpson), were used. They were removed from their shells, the abdomen cut off and opened mid-ventrally. The ventral nerve cord was located and the segmental nerves dissected out to the dorso-lateral side, the main ventral muscle mass and the soft tissues being removed at this time. The

entire abdominal wall was then pinned out as flat as practicable. Although responses were obtained from RM_1 of several of the anterior segments of the abdomen, consistent results were not readily forthcoming. The difficulties involved are the softness of the cuticle and the consequent inability to determine readily the limits of the segments internally. This meant that stimulation of the receptors by stretching individual segments was not simple and too easily led to damage of the MRO. Flexing the entire dorsal wall without mechanical interference with the leads was also not convenient owing to the spiral form of the abdomen. Good results were, however, obtained from the MRO in the sixth segment which responds to flexion of the telson with respect to this segment. Satisfactory manipulation of the telson could be achieved with the remainder of the abdomen pinned down. In all three species both RM_1 and RM_2 were detected by recording their responses to flexion of this joint, to stretching the organ with a needle, and to ACh at ca. 10^{-5} . Confirmation of the presence of the MRO was made in all species with methylene blue and both RM_1 and RM_2 were shown to be present. In agreement with the findings of Alexandrowicz (1952a) in other species of hermit-crabs, there was a comparatively large amount of connective tissue in the neighbourhood of the sensory cells, tending to bind them together.

2. *Brachyura*. Large female specimens (carapace width ca. 12-16 cm) of *Cancer magister* Dana were prepared by removing the ventral surface of the isolated abdomen. Each of the numerous nerve trunks was then placed in turn on the recording electrode. Though flexion of each of the freely-movable joints readily gave responses, all of these could be attributed to sense organs of surface hairs and none could be identified as originating from muscle receptor organs.

Microscopic examination following staining showed no sign of any structure which could be regarded as a MRO. It is therefore concluded that these organs are absent, at least from the abdomen, in the higher true crabs.

(c) *Comparison between species*

In order to compare the above results with those of a species already described in the literature, experiments were conducted on isolated abdomens of *Procambarus clarkii*. In general, it appears that the properties of the RM_1 and RM_2 discharges in all the species reported on here are quite comparable. However, certain interesting differences were noted and these may be of functional significance. As mentioned, the RM_2 discharges of the shrimp *Paracrangon* decline very abruptly under experimental conditions, whereas those of *Procambarus* do so much more gradually. With respect to RM_1 responses, a comparison is shown in Fig. 3 of the frequency response curves from three decapods widely separated systematically, the curves being plotted from experiments conducted in comparable conditions. Although the peak frequencies were similar (*Upogebia* 133/sec, *Procambarus* 148/sec, *Paracrangon* 143/sec), the initial rates of decline are markedly different in the three species. They all reach a very slowly falling plateau in ca. 1 min, but the maintained frequencies there differ considerably, being respectively about 30, 20 and 5/sec.

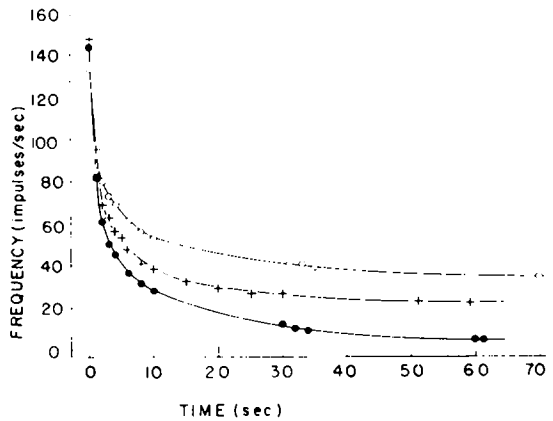


FIG. 3. Comparison of frequency response curves of RM_1 of three species from preparations in which peak frequencies were similar. $\circ-\circ$, *Upogebia*; $-\cdot-\cdot-$, *Procambarus*; $\bullet-\bullet$, *Paracrangon*.

DISCUSSION

From an inspection of the results illustrated in Fig. 3, it is evident that there is considerable quantitative variation in the responses of RM_1 among species of different groups of Decapoda. The variation in RM_2 responses has also been referred to above. These variations are largely in respect to the rate of decline of the discharge frequency and to the frequency of the sustained response in isolated preparations, but it should be noted that they reflect only the properties of the receptor organs themselves. No work has been reported yet on the central connections of the afferent fibres from the MRO, except that one or two interneurons in the sixth abdominal ganglion appear to integrate the impulses from all RM_1 (Wiersma, 1958; Hughes & Wiersma, 1960). Nothing is known, however, about the integration of their responses with those of other sensory modalities. Both of these factors may well vary between species, but until they are determined and the appropriate reflex reactions discovered it will not be profitable to extrapolate from the physiological differences in isolated MRO to the functional meaning of the intact organs *in vivo*. Their significance at present lies in peripheral phenomena and may indicate species differences in the production of generator potentials or in the subsequent transformation of these into action potentials.

As can be seen from the accompanying list of species (Table 1), muscle receptor organs have now been found in animals from a wide range of higher Crustacea. There can be little doubt that they will be found in several of the remaining groups of Decapoda, viz. Penaeidea, Stenopidea, Eryonidea, Hippidea; indeed a major reason why they are not yet recorded is probably the relative unavailability of large specimens of these forms in the living state for experimental work. The question of the possession of MRO by the Brachyura remains an interesting problem; their probable absence in the higher forms may be related to the very reduced nature of the abdomen and the fact that it is functionless in locomotion.

An examination of the more primitive members of this group (Oxystomata and Dromiacea) might throw light on the way in which they have become reduced or eliminated in the Brachygnatha.

The presence of stretch receptor organs is also recorded in the thorax by Alexandrowicz (1952b, 1956). In each of the seventh and eighth segments in *Homarus* and *Palinurus* are two pairs of organs anatomically very similar to those in the abdomen. Eyzaguirre & Kuffler (1955) have shown that the similarity also holds physiologically, in that the median MRO of these segments respond as fast-adapting organs, while the lateral MRO behave as slowly-adapting ones. Alexandrowicz's comparison of median with an RM_2 and lateral with an RM_1 is thus well substantiated. Further, Wiersma (1958) reports central responses from the RM_1 of the eighth segment in *Procambarus* when recording in the circum-oesophageal "commissure". These responses are similar to those recorded centrally from the RM_1 in the abdominal segments.

The occurrence of thoracic MRO is reported in other groups of Crustacea, though there are some interesting variations in morphology. In *Leander serratus* (Alexandrowicz, 1956), there is only one pair of organs on each side of the thorax. Of these the lateral MRO appears similar to the above, but the median MRO bears four nerve cells on a single muscle unit. Alexandrowicz postulates that the latter organ represents the partial fusion of four separate segmented organs. In the Stomatopoda (*Squilla mantis*, Alexandrowicz, 1954), the posterior four thoracic segments possess each two pairs of normally-appearing MRO, but in the fourth segment two cells occur on a single muscle while in the third segment there is only one, normally-appearing, MRO. Alexandrowicz draws attention to the fact that there is an overall correlation in the higher Crustacea between the number of segments containing MRO and the number of segments between which mobility is present. The correlation is striking and may well be significant.

In several species Alexandrowicz reports the presence of "N-cells", nerve cells apparently loosely associated with the thoracic muscles, and considers them either as a more primitive type of receptor (1952b) or as a somewhat vestigial MRO (1956) which has lost its specialized muscle along with the reduction in motility of the corresponding thoracic region. Evidence as to the function of these N-cells in *Procambarus* will be presented in a later paper.

Since organs functionally comparable to the MRO are described for insects (Finlayson & Lowenstein, 1958) it may well be that the Arthropoda are basically endowed with receptor organs in the muscles of their axial joints. Some species of several crustacean groups outside the Decapoda and Stomatopoda would be large enough for experimental work and should be investigated where available. Microanatomical examination could be carried out in almost every major group and should produce significant results for a comparative survey.

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