Muscle Receptor Organs in Grasshoppers and Locusts (Orthoptera, Acrididae)

By E. H. SLIFER AND L. H. FINLAYSON

(*From the Department of Zoology, State University of Iowa, and Department of Zoology and Comparative Physiology, University of Birmingham*)

With one plate (fig. 2)

SUMMARY

A pair of muscle receptor organs is present in each of the abdominal segments from the first to the tenth in the Acrididae. They are associated with the dorsal longitudinal muscles and each consists of a single, heavily encapsulated sensory neurone with numerous dendrites which end on a long, slender muscle-fibre which has its origin near the anterior end of the segment and is inserted on the anterior border of the segment next posterior to it.

PAIRED, segmentally arranged sensory structures which are associated with the dorsal longitudinal muscles of the thorax and abdomen have been described by Alexandrowicz (1934, 1951, 1952*a*, 1952*b*, 1954, 1956) for species of Crustacea belonging to several different orders. Alexandrowicz gave them the name of muscle receptor organs and suggested that they function as proprioceptors and are sensitive to alterations in the length of the body as it is extended or contracted. His suggestion concerning the function of these structures in Crustacea was confirmed by physiological experiments which were reported by Wiersma, Furshpan, and Florey in 1953. Florey and Florey (1955) made a detailed study of the anatomy of the muscle receptor organs of *Astacus*. In 1955 Finlayson and Lowenstein described similar structures in the larva, pupa, and adult of several species of silkworm moths. They examined the organs with the aid of an oscillograph and found that electrical impulses from the nerve increased in frequency when the organ was stretched and decreased again when the tension was released.

Muscle receptor organs have also been identified recently in the Acrididae and the present paper is concerned with a description of their major structural features.

MATERIALS AND METHODS

The species of Acrididae with which most of this work was done were *Locusta migratoria migratorioides* (Reiche and Fairmaire), *Romalea microptera* (Beauvois), and *Schistocerca gregaria* (Forskål), while *Dissosteira carolina* (Linnaeus), *Melanoplus mexicanus mexicanus* (Saussure), and *Phoetaliotes nebrascensis* (Thomas) were examined in less detail. Whole mounts of the dorsal body-wall, together with the dorsal vessel, dorsal muscles, and the principal nerves which innervate the abdominal terga, were fixed in Bouin's

[Quarterly Journal of Microscopical Science, Vol. 97, part 4, pp. 617–620, Dec. 1956.]

fluid and treated very briefly with Mallory's triple connective tissue stain so that only the outer layers of thick structures were coloured. These preparations proved helpful in locating the muscle receptor organs during the earlier stages of this investigation. Other specimens were vitally stained either by immersion of dissected parts in 0·5% methylene blue in Ringer's solution or by injection of the dye into the whole animal. Fixation was in ice-cold 8% ammonium molybdate to each 10 ml of which were added 5 drops of 2% osmium tetroxide. The material was left in the fixative in the refrigerator for at least 12 hours, then washed, dehydrated very rapidly with the higher alcohols and dioxan, cleared in xylene or toluene, and mounted in HSR synthetic resin. Sections were made of material which had been fixed in Bouin's fluid and these were stained with Mallory's triple connective tissue stain, picro-fuchsin, or Heidenhain's iron haematoxylin.

Results and Discussion

In the Acrididae a pair of muscle receptor organs is present in each of the abdominal segments from the first to the tenth. One member of a pair is located on each side of the dorsal mid-line. In the first to the eighth abdominal segments the receptor organ is attached to the medial edge of one of the longitudinal muscle bands which have their origin near the anterior edge of each segment and are inserted on the anterior border of the next segment behind. The particular dorsal longitudinal muscle band to which the organ is attached is usually the fourth, fifth, or sixth from the mid-line but there is some variation even within a single species. Since, however, the number of muscle bands is, itself, also subject to some variation, this is not surprising. In one exceptional case the muscle receptor organ on the left side of the fifth abdominal segment of a male *Romalea microptera* was found to be lying near the middle of a muscle band instead of at its edge. In the modified ninth and tenth segments at the posterior end of the abdomen the receptor organs are located near the centre of a muscle band. Each muscle receptor organ consists of a slender fibre and a single, large sensory neurone which is provided with a number of dendrites (figs. 1 and 2, A, C). The neurone, which is usually located somewhat posterior to the middle of the fibre, is surrounded by a thick capsule and a number of neurilemma cells are associated with it (fig. 2, B). Nothing corresponding to the 'ovoid sac filled with an unidentified substance which stains with some nuclear stains such as haematoxylin and celestin blue', which was described for the Lepidoptera by Finlayson and Lowenstein (1955), was found in the Acrididae. The axon of the sensory neurone passes anteriorly and laterally and then joins the ventral branch of the tergal abdominal nerve of the segment in which the receptor is located (figs. 1 and 2, A). The slender fibre with which the sensory neurone is associated is a modified muscle-fibre as Finlayson and Lowenstein found it to be in the silkworm moths. The striations of the fibre are distinct but less conspicuous than are those of the nearby muscle-fibres. Numerous, thick connective tissue-fibres are attached to this specialized muscle-fibre throughout its

length, and in some preparations they stain heavily with methylene blue (fig. 2, D). They are especially abundant close to and posterior to the neurone.

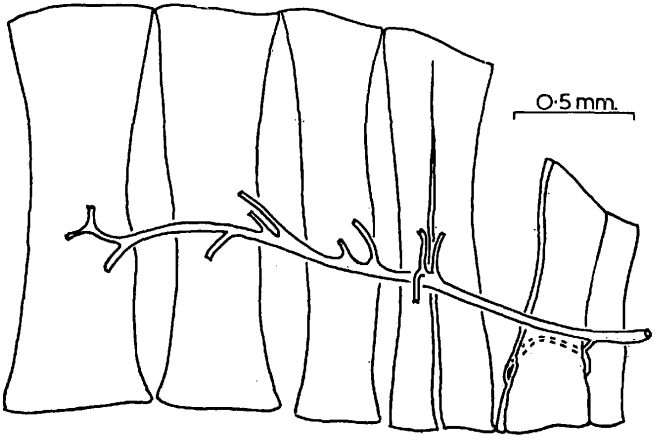

FIG. 1. Diagram showing relation of muscle receptor organ to dorsal longitudinal muscles of left side of second abdominal segment of a male adult *Locusta migratoria migratorioides*, as seen in ventral view. Mid-dorsal line at left. Slender muscle-fibre of receptor organ attached to medial edge of muscle band at extreme right. Encapsulated sensory neurone (darkened) posterior to middle of fibre. Nerve from receptor organ joins ventral branch of tergal abdominal nerve; other branches of tergal nerve, which provide a rich motor innervation for dorsal muscle bands, omitted except for short stubs.

Some of these connective tissue-fibres spread out over adjacent muscle-fibres and in this respect the receptor organ in the Acrididae differs from that of the Lepidoptera, where the connective fibres are confined to the modified

FIG. 2 (plate). A, posterior two-thirds of whole mount of a dorsal longitudinal muscle band with muscle receptor organ attached to its left edge from left side of second abdominal segment of a male adult *Locusta migratoria migratorioides*, as seen in ventral view. Sensory nerve from darkly stained neurone of receptor organ joins ventral branch of tergal abdominal nerve near right margin of muscle band. Methylene blue preparation.

B, part of whole mount of muscle receptor organ showing large, spherical nucleus of encapsulated sensory neurone surrounded by the nuclei of a number of smaller (neurilemma?) cells which are associated with it. Adult male *Romalea microptera*. Picro-fuchsin.

C, part of whole mount of muscle receptor organ from right side of third abdominal segment of a male *Romalea microptera*, showing sensory neurone with axon and dendrites. Methylene blue. The straight fibres in the upper (anterior) part are connective tissue fibres. The axon disappears out of focus for part of its way and reappears on the extreme right at the top of the photograph.

D, part of whole mount of dorsal longitudinal abdominal muscle band from right side of eighth segment of adult male *Locusta migratoria migratorioides* to show wavy, branched connective tissue fibres associated with muscle receptor organ. Compare with smooth edge of ordinary muscle band at right. Methylene blue.

muscle-strand. It seems probable that the muscle receptor organ of the Acrididae, since it is still intimately associated with the ordinary muscle adjacent to it, represents a more primitive condition than does that of the Lepidoptera, where separation from the dorsal longitudinal muscles is complete. Finlayson and Lowenstein found muscle receptor organs in the thorax as well as the abdomen of caterpillars but were unable to find receptor organs in the thorax of the pupa and the adult. It is possible that muscle receptor organs are present in the thorax of the Acrididae but as yet none have been found. The heavy and complex musculature of this region makes it difficult to locate such structures if they do occur, and a more intensive search may still disclose them.

As yet no satisfactory physiological data concerning the muscle receptor organs in the Acrididae have been obtained, but it seems probable that the receptors will eventually be found to respond in much the same way as do the very similar structures which are present in the abdomen of the Lepidoptera. Since the abdomen of the female grasshopper or locust is greatly elongated when filled with mature eggs and stretched even more drastically during the deposition of the eggs in the soil, it seems likely that receptors which are sensitive to muscular extension would have an especially important role to play at such times.

Note.—Dr. J. S. Alexandrowicz of the Marine Biological Laboratory at Plymouth was consulted during the early stages of the present investigation, and he very kindly made a series of methylene blue preparations of the stick insect, *Carausius morosus*, and sent them to the senior author. In this species muscle receptor organs are present not only in the abdomen but in the mesothorax and metathorax as well. (The prothorax was not present in any of these preparations, so the receptors may also occur there.) The muscle receptor organs in *Carausius* are similar to those described in this paper so far as their general features are concerned.

REFERENCES

ALEXANDROWICZ, J. S., 1934. 'The innervation of the heart of Crustacea. II. Stomatopoda.' Quart. J. micr. Sci., **76**, 511.

—— 1951. 'Muscle receptor organs in the abdomen of *Homarus vulgaris* and *Palinurus vulgaris*.' Ibid., **92**, 163.

—— 1952*a*. 'Receptor elements in the thoracic muscles of *Homarus vulgaris* and *Palinurus vulgaris*.' Ibid., **93**, 315.

—— 1952*b*. 'Muscle receptor organs in the Paguridae.' Jour. mar. biol. Assoc., **31**, 277.

—— 1954. 'Notes on the nervous system in the Stomatopoda. IV. Muscle receptor organs.' Pubbl. Staz. zool. Napoli, **25**, 94.

—— 1956. 'Receptor elements in the muscles of *Leander serratus*.' Jour. mar. biol. Assoc., **35**, 129.

FINLAYSON, L. H., and LOWENSTEIN, O., 1955. 'A proprioceptor in the body musculature of Lepidoptera.' Nature, **176**, 1031.

FLOREY, E., and FLOREY, E., 1955. 'Microanatomy of the abdominal stretch receptors of the crayfish (*Astacus fluviatilis* L.).' J. gen. Phys., **39**, 69.

WIERSMA, C. A. G., FURSHPAN, E., and FLOREY, E., 1953. 'Physiological and pharmacological observations on muscle receptor organs of the crayfish *Cambarus clarkii* Girard.' Jour. exp. Biol., **30**, 136.