

SHORT COMMUNICATION
MECHANORECEPTORS IN THE FINS OF THE
CUTTLEFISH, *SEPIA OFFICINALIS*

BY WILLIAM M. KIER*, JOHN B. MESSENGER† AND JALEEL A.
MIYAN

*Department of Zoology, University of Sheffield, Sheffield, S10 2TN and
The Plymouth Laboratory, The M.B.A., Citadel Hill, Plymouth*

Accepted 5 May 1985

Little is known about mechanoreceptors in cephalopods. The anatomical data are fragmentary; Graziadei (1964) described multipolar nerve cells in the arms of *Octopus* and the lips of *Sepia* and similar structures have been described in the mantle of *Octopus* (Sereni & Young, 1932) and *Eledone* (Alexandrowicz, 1960). While there is good physiological evidence for the existence of mechanoreceptors in the mantle of *Octopus* (Gray, 1960; Wilson, 1960; Boyle, 1976), mechanoreception in the mantle and fins of decapods has not been investigated. Here we present physiological evidence that there are receptors along the entire length of the cuttlefish fin that respond to mechanical stimuli. We also identify unusual structures in the fin whose distribution is consistent with their being these receptors.

The nerves to the fins of *Sepia officinalis* pass through a foramen in the mantle on each side and radiate out beneath the skin in a series of approximately fifteen bundles (Tompsett, 1939). The mantle foramen was exposed by cutting away the overlying skin under MgCl₂ anaesthesia (Messenger, Nixon & Ryan, 1985). Animals were held in a Perspex holder that clamped onto the mantle over the cuttlebone allowing free movement of the fins as well as normal respiratory movements. A suction electrode was attached to an intact fin nerve and its spontaneous activity was monitored using an Isleworth A103, or a Tektronix 122 preamplifier.

Regular, patterned bursts of potentials were recorded in each of the fifteen identifiable nerve bundles and were visually correlated to the beating of the fin itself (Fig. 1A). The nerve was then cut and each severed end attached to a suction electrode. The proximal end showed activity similar to that of the intact nerve while the distal end was silent. Stimulation of the animal induced more vigorous beating and increased the efferent activity recorded from the proximal cut end. During this fin beating we also recorded activity in the distal portion of the nerve at the bottom of the downstroke of that region of the fin innervated by the nerve (Fig. 1B).

Decapitated preparations ($N = 8$) were used to study this afferent activity in more detail. The mantle was secured with pins onto a Sylgard dish and the fin was spread flat and secured with pins on a raised platform of Sylgard. A suction electrode was

*Permanent address: Department of Biology, University of North Carolina, Chapel Hill, NC 27514, U.S.A.

†To whom reprint requests should be addressed.

Key words: Fin, mechanoreceptor, *Sepia*.

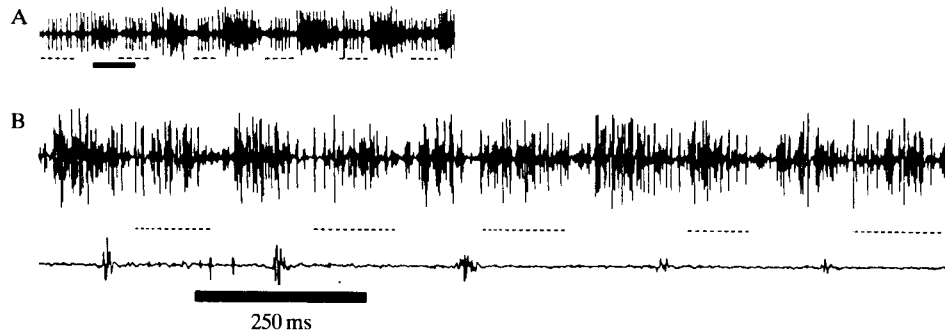


Fig. 1. Recordings of spontaneous activity in a fin nerve of *Sepia officinalis*. (A) Activity of an intact nerve. Bursts correlated with upward movement of the fin are marked with a dotted line. (B) Recordings from the proximal (upper) and distal (lower) cut ends of a fin nerve demonstrating the existence of afferent units being stimulated close to the bottom of the downstroke. Underlining as for A.

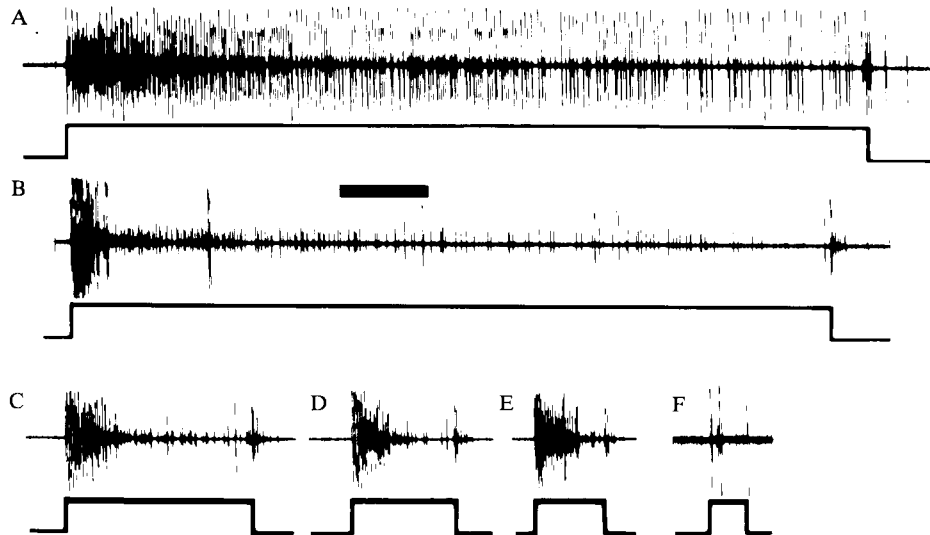


Fig. 2. Recordings of afferent activity from the distal cut ends of fin nerves in response to mechanical stimuli. (A) Three identifiable tonic units that all show a decay in response during stimulation. Two of the units appear to give an 'off' response. (B) shows a phasic unit with a short 'on' response, and a tonic unit with decaying response. (C)–(F) show four recordings of phasic units with varying responses to the stimulus. Most of the phasic units appear to show 'off' responses. Time bar is 0.5 s for A and B, and 0.25 s for C–F.

attached to the distal cut end of each fin nerve and recordings were made of the afferent units. Mechanical stimuli varying from a light touch or scratch to a strong downward pressure, repeated or sustained, were made to the fin surface by hand using a glass or wooden rod. These consistently evoked responses in the distal portion of the fin nerve, especially when applied to the lateral margin of the fin (see below). Subsequently we applied pressure to the fin *via* a plastic rod fixed to a speaker cone driven by a signal generator; no attempt was made to quantify the pressures applied.

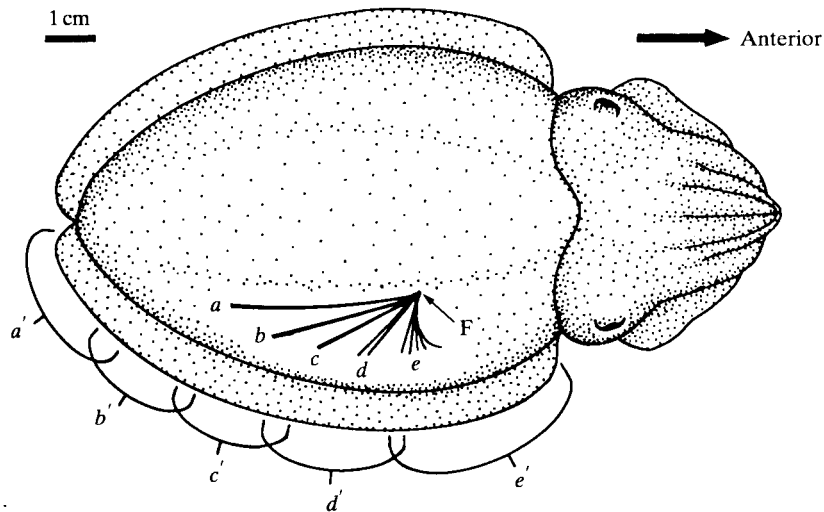


Fig. 3. Dorsal view of a cuttlefish showing a partial dissection of the fin nerves (*a-e*) at the right hand mantle foramen (F) and their receptive fields (*a'-e'*) as determined by simultaneous mechanical stimulation and recordings from the distal ends of cut nerves. Branching of nerve bundles was variable among the specimens examined; the general pattern of branching for one specimen is illustrated here. Subdivisions within each nerve bundle were also observed and could be mapped sequentially within each field. Note that some overlapping of fields was observed.

Three types of response were recorded (Fig. 2): (1) phasic bursts of potentials (from 5–20 different units) at the onset of the stimulus, (2) tonic bursts of potentials (from 10–15 different units) whose firing frequencies decayed slowly and (3) phasic bursts of potentials (from 1–6 different units) at the end of the stimulus. Similar response patterns were recorded from all the fin nerves. It was possible to map the receptive fields of each of the fin nerves and demonstrate that the entire length of the fin is represented in the afferent input to the CNS (Fig. 3). It needs emphasizing that all classes of response persist, apparently unaltered, when the overlying skin is stripped off, demonstrating that the receptors are not in the skin (cf. *Octopus* mantle, Gray, 1960) but in the fin musculature. Our recordings revealed little difference in the distribution of receptors along the length of the fin but an uneven distribution across it. By far the highest concentration of receptors is at the lateral margin; they are less numerous at the medial margin and scarcest of all centrally.

A preliminary histological investigation of the fin revealed none of the kind of multipolar nerve cells described previously (*loc. cit.*), but instead a large population of unusual structures embedded in, but distinct from, the fin musculature itself (Fig. 4). They are especially numerous along the lateral fin margin and are not present in the skin so that they are clearly candidates for the origin of the mechanoreceptor activity described here. Light-microscopic observations of sections stained with Milligan's trichrome (Humason, 1979) and by Palmgren's (1948) silver method (see Bone, 1972) show that these structures comprise sets of obliquely-striated muscle cells, some of which exhibit 'double-oblique striations' (Fig. 4), such as is often seen in isolated obliquely-striated muscle cells (Hanson & Lowy, 1957, 1960). They take up the same stains as the surrounding muscle, but much more intensely. They may,

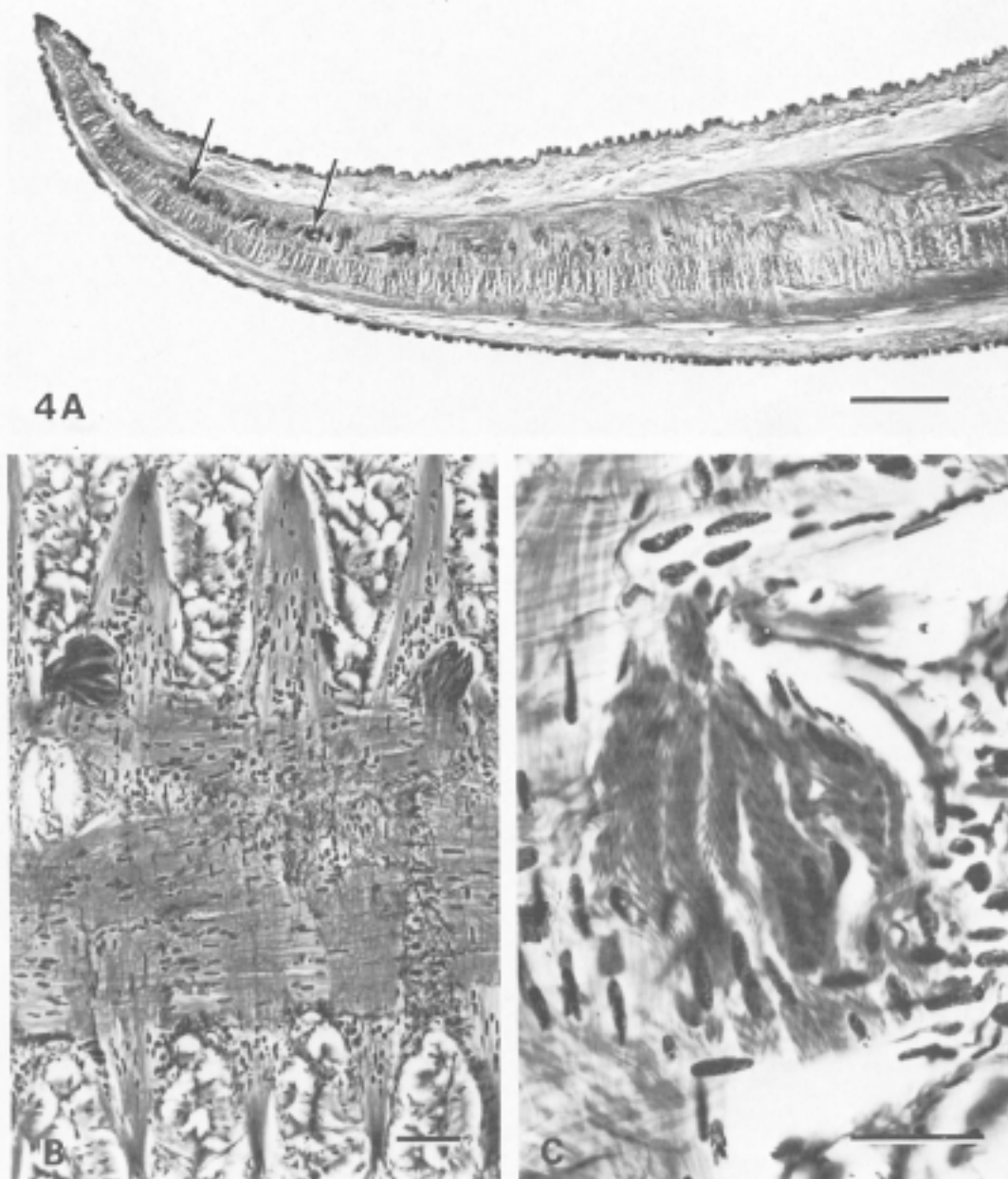


Fig. 4. Micrographs of transverse (A) and parasagittal (B, C) sections of cuttlefish fin showing the putative muscle receptor organs. (A) Intensely-staining receptors (arrows), visible in the musculature of the fin, are concentrated towards the lateral margin. Scale bar, 1 mm. (B) High power view of two receptors illustrating orientations both parallel, and perpendicular to the dorso-ventral muscles in which they lie. Scale bar, 100 μ m. (C) Single receptor at high power showing 'double oblique' pattern often observed in obliquely-striated muscle cells. Scale bar, 50 μ m. Palmgren's silver stain.

therefore, be analogous to the muscle receptor organs of crustaceans and other arthropods (see Mill, 1976) and vertebrates (see Matthews, 1972). It is striking that the long axes of these putative mechanoreceptors in the cuttlefish fin are oriented in three mutually perpendicular planes suggesting that deformation of the fin in any direction might be detected.

Although these structures occur in parts of the fin that are richly innervated, we have so far seen no trace of any nerve fibres unequivocally associated with them. It clearly remains to be established whether or not these are the receptors responsible for the physiological responses reported here. Their structure, as well as the neuromuscular organization of the fin and its behaviour during swimming are currently under investigation. At present we can only say that there are undoubtedly mechanoreceptors in the fin and that cuttlefish probably utilize peripheral mechanical information during swimming to regulate or control their fin beat.

It is a pleasure to thank the Director and staff of the MBA for the facilities provided during this study; and Dr Q. Bone and Mr A. D. Chubb for their generous help with histology. JBM and JAM were supported by SERC grant GR/C/92687. WMK was supported by grants from NATO, the Lerner-Gray Fund and The American Philosophical Society.

REFERENCES

- ALEXANDROWICZ, J. S. (1960). A muscle receptor in *Eledone cirrhosa*. *J. mar. biol. Ass. U.K.* **39**, 419–431.
- BONE, Q. (1972). Some notes on histological methods for peripheral nerves. *Med. Lab. Tech.* **29**, 319–324.
- BOYLE, P. R. (1976). Receptor units responding to movement in the octopus mantle. *J. exp. Biol.* **65**, 1–9.
- GRAY, J. A. B. (1960). Mechanically excitable receptor units in the mantle of the octopus and their connections. *J. Physiol., Lond.* **153**, 573–582.
- GRAZIADEI, P. (1964). Muscle receptors in cephalopods. *Proc. R. Soc. B* **161**, 392–402.
- HANSON, J. & LOWY, J. (1957). Structure of smooth muscles. *Nature, Lond.* **180**, 906–909.
- HANSON, J. & LOWY, J. (1960). Structure and function of the contractile apparatus in the muscles of invertebrate animals. In *Structure and Function of Muscle*, Vol. 7, (ed. G. H. Bourne), pp. 265–335. New York: Academic Press.
- HUMASON, G. L. (1979). *Animal Tissue Techniques*. Fourth edition. San Francisco: W. H. Freeman.
- MATTHEWS, P. B. C. (1972). *Mammalian Muscle Receptors and their Central Actions*. London: Arnold.
- MESENGER, J. B., NIXON, M. & RYAN, K. P. (1985). Magnesium chloride as an anaesthetic for cephalopods. *Comp. Biochem. Physiol.* **82**, 203–205.
- MILL, P. J. (ed.) (1976). *Structure and Function of Proprioceptors in the Invertebrates*. London: Chapman & Hall.
- PALMGREN, A. (1948). A rapid method for selective silver staining of nerve fibres and nerve endings in mounted paraffin sections. *Acta Zool., Stockh.* **29**, 377–392.
- SERENI, E. & YOUNG, J. Z. (1932). Nervous degeneration and regeneration in cephalopods. *Pubbl. Staz. zool. Napoli* **12**, 173–208.
- TOMPSETT, D. H. (1939). *Sepia*. L.M.B.C. Memoirs, no. 32. The University of Liverpool Press.
- WILSON, D. M. (1960). Nervous control of movement of cephalopods. *J. exp. Biol.* **37**, 57–72.