PRESSURE RECEPTORS IN THE FINS OF THE DOGFISH
SCYLLIORHINUS CANICULA

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INTRODUCTION

In 1908 Wunderer described 'terminal nerve corpuscles' (Terminalkorperchen) in the fins of five species of elasmobranch fish, *Mustelus canis*, *Scyllium (Scylliorhinus) canicula*, *Acanthias vulgaris*, *Centrina salviani* and *Squatina angelus*, and he believed these organs to represent the only sensory structures of this type found in the Anamnia. The organs are situated in the loose connective tissue surrounding the radii and horny rods of the fin skeleton. The horny rods are arranged in two layers, and are separated from the corium of the skin and from each other by connective tissue. Between the two layers of horny rods the connective tissue forms a gelatinous wedge-shaped mass tapering towards the margin of the fin where the two layers of horny threads meet. The fin nerves form a plexus just distal of the end of the cartilaginous skeleton. The plexus gives rise to axially running nerve stems with numerous side branches embedded in the gelatinous connective tissue. The majority of the side branches end in what Wunderer believed to be an encapsulated skein of nerve fibres, myelinated for part of their course through the skein. Dr A. Barets, of the Laboratoire de Biologie Animale of the University of Paris, while working at Plymouth, made methylene-blue preparations of dogfish fins and was able to confirm all essential points of Wunderer's description of the organs. He has kindly let me have one of his preparations, and has given me permission to include a drawing of it in this paper (Fig. 1). The only point in Wunderer's description so far lacking confirmation is the presence of a thin sheath-like capsule surrounding the nerve coil.

The shape and arrangement of the organs point to their functioning as pressure receptors, and their presence in the fins only, and not, according to Wunderer,
under the skin of head and trunk, made it appear likely that they might act as proprioceptors in the widest sense of the term. The results of the experiments to be described confirm this assumption.

METHODS

Most of the experiments were carried out on the pectoral fin of medium-size dogfish, but identical results were obtained from all the other fins. The fish were killed by decapitation and pithing, and the fins severed from the body. The dorsal and ventral skin was then removed either by stripping it from the muscular part of the fin only, or from the entire surface. Fig. 2 shows a longitudinal section of the

![Diagram of a fin showing position of terminal corpuscle, access to nerve, and mode of application of pressure.](image)

fin, and the site at which access was gained to the sensory nerves. A sufficiently long stretch of nerve was isolated in the region distal to the fin musculature and connected to a silver forceps electrode for oscillographic recording; the second electrode was a silver wire making contact with inert tissues of the fin. The fin was mounted flat on a Perspex plate for stimulation by pressure, which was effected by lowering metal disks of various diameters on to the surface of the fin by means of a vertical screw device. Alternatively, only the proximal region of the fin was clamped down to the plate, and the distal portion projecting freely from the holder could be deformed by dorso-ventral bending.

RESULTS

When the preparation is mounted for recording, a certain amount of irregular discharge activity is picked up. This usually consists of spike potentials of a considerable range of amplitude, obviously derived from fibres of a similarly large range of diameters. Fig. 3A shows a representative record of this kind. It would be wrong, of course, to describe all this as spontaneous activity. As will be seen presently, the adaptation of the terminal corpuscles is slow, and there are bound to be lasting stresses in the mounted fin which may well be responsible for much of the continuous activity of the preparation. It is relatively easy to isolate the impulse discharge from a single functional unit by careful selection of the site of stimulation. The 'adaptation' of a single unit to continued pressure is shown in Fig. 4. The discharge frequency, after having reached its maximum during the application of pressure, falls fairly rapidly to about a third of its maximum value, and then declines more slowly.
Fig. 5 shows a series of single-unit responses to a step-by-step increase in pressure interrupted by periods of 'adaptation'. The higher level of discharge activity at the end of the experiment was recorded for a period of over 40 sec., and was observed to go on unaltered for a number of minutes after the end of the recording. The 'adaptive' behaviour shows a considerable latitude, and this is the case even among unit discharges of the same amplitude and speed of propagation. Probably a considerable part of the decline in discharge frequency, especially the initial rapid fall,
may be caused by mechanical accommodation connected very likely with the viscous flow of the gelatinous tissues in which the end-organs are embedded, and it would appear safe to assume that neurologically the organs are of the slowly adapting type. The existence of mechanical accommodation would also explain the observation that successive applications of identical pressures do not as a rule yield quantitatively identical responses, a fact which made a study of the quantitative stimulus/response relationship impossible.

DISCUSSION

Wunderer quite rightly diagnosed the sensory nature of the terminal corpuscles, and also correctly described them as pressure receptors. They are by their distribution and behaviour admirably suited to signal the spatio-temporal patterns of pressure changes arising in the course of active and passive deformation of the fins. This is well illustrated by the record of the effect of repeated ventral deflexion of the fin (Fig. 3 B). It may thus be legitimate to consider the organs as proprioceptors in the widest sense of the term.

Muscle receptors of the type described in Raja by Polonmordwinoff (1898) and functionally analysed by Fessard & Sand (1937) do not appear to be present in the fins of the dogfish (Barets, personal communication). However, diffuse nerve endings are found in the muscle fasciae, and they are the only sensory structures connected with the fin musculature to which a possible proprioceptive function could be attributed. The fact that the responses described in this paper were picked up far distal of the muscle layer makes it certain that they were definitely not derived.
Pressure receptors in the fins of the dogfish

from the latter endings. The degree of contribution of the less highly organized nerve endings in the skin to the control of posture and steering movements of the fin is difficult to assess. On recording from parts of the fin covered with skin, it was found that the discharge activity in any given nerve twig was more complex. Responses from the skin of the clasper, where the absence of terminal corpuscles makes possible the study of skin receptors in isolation, showed that there is a sufficient overlap in impulse characteristics between the impulses from skin receptors and those from Wunderer's organs, to make it difficult to discriminate between them in preparations of the fin covered by intact skin.

SUMMARY

1. The presence of so-called terminal corpuscles in the connective tissues of the fins of Scylliorhinus canicula, first described by Wunderer in 1908, is confirmed.
2. It is demonstrated that they are pressure receptors with a slow rate of adaptation.
3. From their topographic distribution and from their mode of response to mechanical stimulation, it is postulated that the terminal corpuscles serve as proprioceptors in the widest sense of the term by signalling the spatio-temporal patterns of active or passive deformation of the fin.
4. Their topographic distribution makes it possible to distinguish their responses from those of sense endings associated with the muscles or tendons of the fin.

REFERENCES