

Table 3. Response of *G. morsitans* males to female extract on cork decoys

Extract	Quantity of extract (female equivalents)	No. of tests	Male reactions (%)			
			0	1	2	3
Intact females more than 1 week old	2	69	7.24	2.89	23.18	66.66
Legs of ready to emerge females	12	20	10	50	40	-
Ready to emerge females without legs	12	20	70	30	-	-

cuticle between shaft and spike. Many canaliculi of other gland cells open at the lateral margins of the base of the spike (figure, b). Structures similar to those of *Musca* were also observed in *Stomoxys calcitrans*, which has also been reported to secrete a sex recognition pheromone<sup>13</sup>. The proximity of spike and seta (in *Musca*) directs the flow of material excreted through the slit upwards, as described here for the specialized spines in the tsetse. Preening spreads the material on the body surface.

The location of these cuticular structures on the upper part of the lower tarsi and outer parts of the tibia affords maximum tactile contacts with other flies. Although direct experimental evidence is still lacking, the distribution of the glands, combined with the evidence presented here that the legs are the source of sex pheromone in housefly and in tsetse flies makes it plausible to infer that the source of the pheromone is the gland cell at the base of the cuticular seta or spine.

In an elegant set of experiments, Lang<sup>14</sup> demonstrated the site of contact sex pheromones in the mosquito *Culiseta inornata* as the legs, but, unlike the flies, the sex pheromone remains restricted to the legs and is not spread over the body surface of the mosquito. With our finding in *Glossina* and *Musca*, presented here, it appears that the release of contact sex pheromones from the legs may be common in Diptera.

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Stretch receptors in the eye muscles of a teleost fish

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**Summary.** Extraocular muscles of a teleost fish, *Girella tricuspidata*, contain a predominantly phasic stretch receptor, which consists of fine beaded nerve terminals within the red portion of the muscle.

Muscle stretch receptors are well known in mammals, where they typically form part of the muscle spindle complex, and have also been described from all other gnathostomous vertebrate classes except the bony fishes. The complete absence of this type of receptor from a whole vertebrate class would be surprising, and its apparent

absence may only result from the difficulties of obtaining suitable nerve-muscle preparations in fish. A possible proprioceptive feedback of eye velocity information during induced vestibulo-ocular reflex<sup>2</sup> could indicate the presence of stretch receptors in extraocular muscles. In addition to this, the discrete straplike nature of extraocular muscles,



Fig. 1. Response of the receptor to an applied stretch. Upper trace: en passant electrical recording of the spike discharge; spike amplitude approximately 40  $\mu$ V. Lower trace: stimulus monitor; stimulus intensity 0.13 N, duration 3 sec.

their accessible innervation and small size all provide considerable advantages over other fish muscles in an electrophysiological and histological search for receptor endings.

Specimens of the New Zealand parore (*Girella tricuspidata*) were caught in set nets and maintained in aquaria for several days before use. Fish were killed by decapitation and the orbit exposed from a ventral approach. All studies were made on the inferior oblique muscle.

For electrophysiological studies the preparation was placed in an organ bath at room temperature (approximately 22 °C), and the oculomotor nerve branch supplying the muscle was placed over a bipolar recording electrode. For most recordings, central connections of the nerve remained intact. Unitary spike activity was amplified and photographed directly from the oscilloscope, or recorded onto magnetic tape for later analysis. A thread was attached to the orbit close to the insertion of the muscle, which was stretched by the application of weights via a smooth pulley, or by activation of a calibrated solenoid. Throughout the experiment, the preparation was irrigated with fresh physiological solution (231 mM NaCl, 8 mM KCl, 2.25 mM CaCl<sub>2</sub>, 3.67 mM MgCl<sub>2</sub>, 10 mM Tris-HCl, pH 7.7). With care, the preparation could be maintained for 4–5 h with no obvious deterioration. Experiments were performed on preparations from 5 fish.

Spontaneous spike activity was not observed in the nerve when the eye was in its resting position and the muscle

unstretched. The presence of a stretch receptor was revealed by stretching the muscle, which resulted in a unitary spike discharge (figure 1).

The response was obtained with or without an intact CNS connection of the nerve. On no occasion was more than a single unit response obtained, which implies that there must be only a very limited number, perhaps only one, receptor per muscle. The conduction velocity of the unit, measured over 6–8 mm lengths of nerve in 2 preparations, varied between 8 and 13 m·sec<sup>-1</sup>, which in fish would correspond to a medium diameter myelinated fibre. Fukuda<sup>3</sup> established that goldfish lateral line fibres with similar conduction velocities had mean total diameters of 4–7 µm. Contraction of the muscle by topical application of 0.1% acetylcholine caused only a very brief response (1–7 spikes) from the receptor. The brevity of the response due to contraction is consistent with a stretch receptor in parallel with the contractile elements, probably located in the body of the muscle, but slightly removed from the site of acetylcholine application, so that any initial tension due to contraction of distant fibres is rapidly relieved by propagation of contraction to the vicinity of the receptor.

The muscle was stretched by a range of applied forces from 0.05 N to 0.2 N (force applied by a mass of 5–20 g). Well defined phasic-tonic responses were observed to stimuli in the range 0.1–0.2 N. Spike frequency rose rapidly to a maximum (about 80 Hz for a 0.2-N stimulus), and then declined to about 25% of the initial response after 2 sec. The predominantly phasic response, with a degree of maintained tonic firing, resembles the stretch receptor in urodeles<sup>4</sup> and rays<sup>5</sup>. The velocity sensing characteristic of the eye muscle receptor would be suitable to provide the proprioceptive feedback postulated by Allum and Graf<sup>2</sup>. Terminations of the oculomotor nerve in the inferior oblique muscle were examined in silver impregnated (Palmgren's method)<sup>6</sup>, and in methylene blue preparations. Motor terminations were similar to those found in myotomal muscle in some fish<sup>7</sup>. Both staining procedures also revealed occasional examples of a 2nd type of nerve ending, consisting of a series of ovoid swellings along the course of a fine nerve filament closely associated with muscle fibres (figure 2). The inferior oblique muscle of parore is divided into red and white fibre regions; where endings of the 2nd type could be localized, they occurred amongst the red fibres. Identification of the nerve ending illustrated in figure 2 as the stretch receptor is based on a comparison of the form of this ending with the much more common motor nerve terminals. This fine beaded nerve terminal is also very similar in form to that described in urodele amphibia<sup>4</sup>, where its identification as a receptor ending has been convincingly demonstrated. It also resembles a varicose nerve ending in the fin ray of another teleost, *Aspitrigla*, which is thought to be sensory<sup>8</sup>.



Fig. 2. Photomicrograph of the presumed receptor ending (25 µm Palmgren stained section).

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