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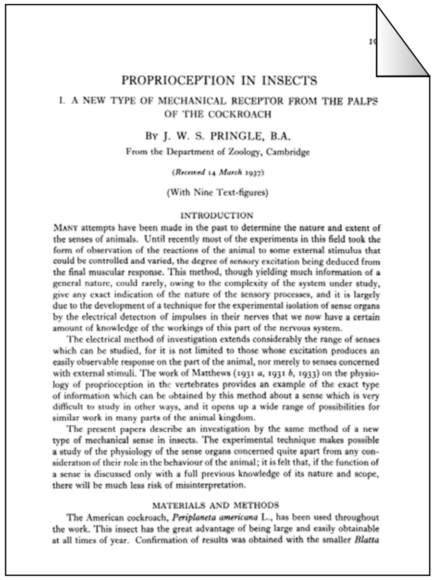
SMALL CUTICULAR DOMES ARE STRAIN RECEPTORS


PROPRIOCEPTION IN INSECTS

I. A NEW TYPE OF MECHANICAL RECEPTOR FROM THE PALPS OF THE COCKROACH

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(*Received 14 March 1937*)

(With Nine Text-figures)

INTRODUCTION

Many attempts have been made in the past to determine the nature and extent of the senses of animals. Until recently most of the experiments in this field took the form of observation of the reactions of the animal to some external stimulus that could be controlled and varied, the degree of sensory excitation being deduced from the final muscular response. This method, though yielding much information of a general nature, could rarely, owing to the complexity of the system under study, give any exact indication of the nature of the sensory processes, and it is largely due to the development of a technique for the experimental isolation of sense organs by the electrical detection of impulses in their nerves that we now have a certain amount of knowledge of the workings of this part of the nervous system.

The electrical method of investigation extends considerably the range of senses which can be studied, for it is not limited to those whose excitation produces an easily observable response on the part of the animal, nor merely to senses concerned with external stimuli. The work of Matthews (1931 *a*, 1931 *b*, 1933) on the physiology of proprioception in the vertebrates provides an example of the exact type of information which can be obtained by this method about a sense which is very difficult to study in other ways, and it opens up a wide range of possibilities for similar work in many parts of the animal kingdom.

The present papers describe an investigation by the same method of a new type of mechanical sense in insects. The experimental technique makes possible a study of the physiology of the sense organs concerned quite apart from any consideration of their role in the behaviour of the animal; it is felt that, if the function of a sense is discussed only with a full previous knowledge of its nature and scope, there will be much less risk of misinterpretation.

MATERIALS AND METHODS

The American cockroach, *Periplaneta americana* L., has been used throughout the work. This insect has the great advantage of being large and easily obtainable at all times of year. Confirmation of results was obtained with the smaller *Blatta*

Reinhold Hustert writes about J. W. S. Pringle's 1938 paper entitled 'Proprioception in insects. I. A new type of mechanical receptor from the palps of the cockroach'. A copy of the paper can be obtained from jeb.biologists.org

Proprioceptors are sense organs recording the relative position of body parts or internal tissues. The history of proprioceptor research is often characterized by long delays between a sensory structure's discovery and its functional characterization. A classic example of one such delay is the lengthy period between the anatomical indentification of vertebrate muscle spindles by A. Kölliker (Kölliker, 1862) and W. Kühne (Kühne, 1862) and the discovery of their proprioceptive role six decades later (Matthews, 1928). It was only in the 1960s that Ake B. Vallbo and Karl-Erik Hagbarth made heroic recordings from muscle spindle afferents in their own arm nerves (Vallbo and Hagbarth, 1967) to demonstrate the structures' natural function as tension receptors. In this JEB Classics article, I describe how research into the function of the small dome-shaped sensilla found on the insect cuticle followed a similarly lengthy but less tortured course, culminating in Pringle's classic 1938 paper describing the function of the campaniform sensilla (Pringle, 1938a).

First described by J. B. Hicks in the mid nineteenth century (Hicks, 1857) and termed 'sensilla campaniformia' in 1909 (Berlese, 1909), early speculation on their function centred around their possible chemosensory role. However, R. Vogel also suggested that the structures may have a mechanosensory function (Vogel, 1911). The conundrum was resolved in Pringle's groundbreaking paper on the maxillary palp campaniform sensilla in cockroaches, when he clearly showed that these intriguing structures respond to strain and are mechanosensory proprioceptors (Pringle, 1938a). These were the first proprioceptors to be described, both functionally and down to the level of single, or a few, sensory cells.

This remarkable breakthrough was made possible by the development of new electrophysiology technologies at the end of the 1920s, when physiologists studying sensory and motor systems in animals and humans first gained access to preamplifiers, oscilloscopes (Matthews, 1928) and audio-monitors, offering them the first opportunities to study nerve and muscle action potentials directly. By the early 1930s, after the publication of an increasing number of studies on vertebrate sensory and motor systems, the young J. W. S. Pringle noted that recordings from sensory nerves in vertebrates revealed both the characteristics of sensory signals and the information they encoded for the central nervous system (CNS). The first studies by Richard Julius Pumphrey of insect afferent action potentials directed towards the CNS from external receptors, such as mechanosensory spines and hairs (Pumphrey, 1936; Pumphrey and Rawdon-Smith, 1937), shed light on insect exoskeleton sensory responses and inspired Pringle's own studies.

However, Pringle's early attempts to apply these new techniques to insect chemoreceptors proved unsuccessful. Focusing on the cockroach mouthparts (palps), which in many insects continuously probe the chemical nature of possible food sources, Pringle may first have tried to find responses in ascending sensory nerves from chemoreceptors at the palps' tips. But it is still impossible, even today, to make nerve recordings with extracellular electrodes from the chemosensory cells' tiny axons. However, Pringle successfully obtained reliable neural responses whenever he physically disturbed the palps, especially when the joints between segments of the cuticle were moved. Able to distinguish these signals from the fast adapting responses of the palps' tactile hairs, which had been found on the insect's legs by Pumphrey a few years earlier (Pumphrey, 1936), Pringle made the groundbreaking discovery that the campaniform sensilla are mechanosensors. The results were published in 1938 (Pringle, 1938a); the paper also included the first full account of sensory function in a specific insect sensillum and established a new style of morphological and functional description in neural tissue, outlining the location and innervation of a specific sensillum type prior to analyzing the functional and electrophysiological properties of primary afferents.

Was it luck or insight that inspired Pringle to choose campaniform sensilla on cockroach palps as his first subject? Probably a mixture of both. The palp's campaniform sensilla are associated with the hinge-like articulations between the segments of the palps. Therefore, it is clear how compression of the cuticle, either by bending, release from bending or lengthwise strain on the palp's cuticle, affects the campaniform sensilla near the joint hinges causing their oval caps to bulge or flatten, which in turn produces strain in the underlying sensory neuron to generate afferent impulses directed to the CNS. This allowed Pringle to show that campaniform sensilla are exteroreceptors, which record strain due purely to external forces. Another fortunate property of Pringle's cockroach palpus preparation was that he could monitor the campaniform sensilla's responses to forces produced by the palp's own muscles, which also allowed him to show that campaniform sensilla function as proprioceptors (receptors that record internal strain caused by resistance to muscle tension). Furthermore, Pringle's palpus preparation allowed him to focus on responses from pairs or small groups of campaniform sensilla near single joints when he cut distal segments and recorded selectively from the remaining 1–3 campaniform sensilla. By selecting responses from small groups of the mechanosensors, he could identify their slowly adapting action potential frequency responses, which he selected by a primitive method of amplitude filtering: he simply turned down the monitoring loudspeaker to hear the largest impulses alone. But from here Pringle turned to very speculative thinking: unable to distinguish the uniform amplitude impulses measured simultaneously from two or three campaniform sensilla, he assumed that sensory axons can merge and form a single afferent fiber, which has never been found.

In summary, Pringle's paper (Pringle, 1938a) on proprioception in cockroach palps was the first to completely describe the function of single campaniform sensilla, and proved to be the benchmark for subsequent proprioceptor studies. Since then, whenever questions about campaniform sensilla function have been raised, the answer is usually prefaced with 'Pringle showed that'. Even Pringle's own companion paper on the trochanteral campaniform sensilla of legs, which includes a superb description and discussion of the campaniform sensilla's potential kinaesthetic function [allowing the insect to detect its own movement and position (Pringle, 1938b)], did not match the clarity of data that he derived in the palp study. He compensated for this in the leg study by developing a functional model of the limb's campaniform sensilla, which demonstrated that cuticle compression elevates the sensor's cuticular cap to stretch the attached dendrite and initiate an impulse. But even this model could not determine which axis of the oval-shaped campaniform sensilla provides the greatest mechanical sensitivity by deforming the most in response to compression – a problem that haunted most papers on campaniform sensilla until Stanley Spinola and Kent Chapman proved that compression perpendicular to the main axis in oval domed campaniform sensilla produces the most effective stimulation (Spinola and Chapman, 1975).

Having acknowledged that insect campaniform sensilla behave as strain sensitive proprioceptors, Pringle and his colleague, G. Fraenkel, were able to interpret the proprioceptive function of groups of campaniform sensilla at the halteres (Pringle and Fraenkel, 1938), oscillating club-shaped appendages that have replaced the hindwing structures in flies and had long been suspected of involvement in flight steering (Weinland, 1890). Much later, after the war, Pringle proved such a mechanism in detail by recording from nerves in freely moving halteres and found that specific campaniform sensilla groups associated with the oscillating halteres record path deviation parameters during axial movements of the fly's body. Much later this led to the detection of the most rapid neural pathway in insects ever identified, between the electrically coupled haltere afferents and the motoneurons of the fly's steering muscles (Fayyazuddin and Dickinson, 1996).

Detailed work on the functions of insect campaniform sensilla continued in the 1960s and 1970s, focussing initially on the functional morphology of different campaniform sensilla types in various locations (Chapman, 1965; Moran et al., 1971). The proprioceptive and kinaesthetic roles of campaniform sensilla were revisited even later in the 1980s from the perspective of their central neural connections, by tracing the neural connections from single insect receptors to the insect CNS (Hustert et al., 1981). Further locomotor studies dealt specifically with neural control in response to limb loading and unloading (Zill, 1981; Laurent and Hustert, 1988; Ridgel et al., 1999; Höltje and Hustert, 2003; Akay et al., 2004). To this day the question whether campaniform sensilla are the main source of gravitational information for the insect CNS remains unresolved. Although most insects appear to lack a specialized sense of gravity, campaniform sensilla are currently believed to be the possible seat of the gravitational sense in insects, but this has yet to be confirmed.

When Pringle initiated his study of cockroach palp campaniform sensilla in pre-war Europe, he had little idea of the legacy his paper would leave and the inspiration it would offer well into the 21st Century, making it a justifiable JEB Classic.

10.1242/jeb.02358

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