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Material properties of photomechanical infrared receptors in pyrophilous *Melanophila* beetles and *Aradus* bugs

David Klocke *, Helmut Schmitz

Institute of Zoology, University of Bonn, Poppelsdorfer Schloss, 53115 Bonn, Germany

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ABSTRACT

Jewel beetles of the genus *Melanophila* and some pyrophilous species of the flat bugs genus *Aradus* show a pyrophilous behaviour and have developed so-called photomechanical infrared (IR) receptors. In a spherical photomechanical IR sensillum incoming IR radiation is converted into micromechanical action, finally stimulating the dendritic tip of a mechanosensitive sensory cell. The tip is located inside a tiny cuticular sphere with a diameter of about 12 μm. The material properties of the different cuticular components of this sphere are of great importance for stimulus generation. We measured the modulus and hardness of the outer exocuticular shell of the sphere and the mesocuticle inside the core. Measurements were made by nanoindentation at sensilla which were partly cut open under dry as well as under rewetted (i.e. quasi-natural) conditions. We found that in the rewetted sensilla the outer exocuticular shell of the sphere in the *Melanophila* sensillum is about 50% harder and 20% stiffer than reference exocuticle, and that in both species especially the rewetted mesocuticle of the inner core of the IR sensilla is significantly softer (about 80% in *Melanophila*) and more compliant (about 90% also in *Melanophila*) than the reference mesocuticle. The findings can be interpreted as special adaptations of the cuticular microdomains of photomechanical infrared sensilla to enhance thermomechanical performance and, thereby, sensitivity.

1. Introduction

Jewel beetles of the genus *Melanophila* belonging to the acuminata, or "flattened type", such as *M. consputa*, *M. notata*, *M. opaca*, *M. atropurpurea* and *M. acuminate*, are widely known to approach forest fires [1]. Similar pyrophilous behaviour has been observed in a few flat bug species of the genus *Aradus* (Heteroptera, Aradidae).

In both groups photomechanical infrared (IR) receptors have been found [2,3]. This unique type of sensillum is innervated by a mechanosensitive cell and is strikingly similar in beetles and bugs (see Fig. 1). In brief, the functional component of the photomechanical IR sensillum is a spherical IR-absorbing cuticular apparatus with a diameter of about 12–15 μm. The sphere consists of an outer shell made of hard exocuticle, which is reinforced by many layers of chitin fibres. Inside the sphere is a core of softer mesocuticle. In contrast to the solid shell, the mesocuticle has a spongy texture comprising a three-dimensional system of liquid-filled microlacunae and nanocanals (Fig. 1c and d). The tip of the mechanoreceptor enters the sphere through a pore in the shell and terminates inside the mesocuticular core (cf. Fig. 1c and d) [4,5].

According to the photomechanical model, IR radiation is absorbed by the organic molecules (i.e. proteins and chitin) as well as by the water inside the mesocuticular lacunae of the sphere. The corresponding increase in temperature mainly results in a thermal expansion of the core, consisting of mesocuticle and the liquid enclosed by the shell of the sphere. However, omnidirectional expansion is restrained by the outer shell. Thus the dendritic tip of the mechanoreceptor, as the only compliant element, is compressed. This is enough of a stimulus to activate the mechanosensitive neuron.

Electrophysiological experiments have shown that the IR receptors of *Melanophila* beetles rapidly transform IR radiation into a micromechanical event. Latencies were in the range of a few milliseconds [6,7]. Although the precise sensitivity of the photomechanical receptors is still unknown, there is some evidence that the IR receptors in *Melanophila* beetles may have a high sensitivity. One can postulate that *Melanophila* beetles and *Aradus* bugs use their IR sensilla for fire detection, as a number of anecdotal reports in the entomological literature suggest that *Melanophila* beetles can detect distant fires by IR radiation [8–10]. Large numbers of *Melanophila consputa* were observed at a large burning oil storage tank close to Coalinga in California [11]. Because Coalinga is situated in the arid San Joaquin Valley, it is unlikely that the majority of beetles had already been close to the tanks before the outbreak of the fire. Great numbers of beetles were also attracted by a large

* Corresponding author. Tel.: +49 228 73 5492; fax: +49 228 73 54 58.
E-mail address: dklocke@uni-bonn.de (D. Klocke).

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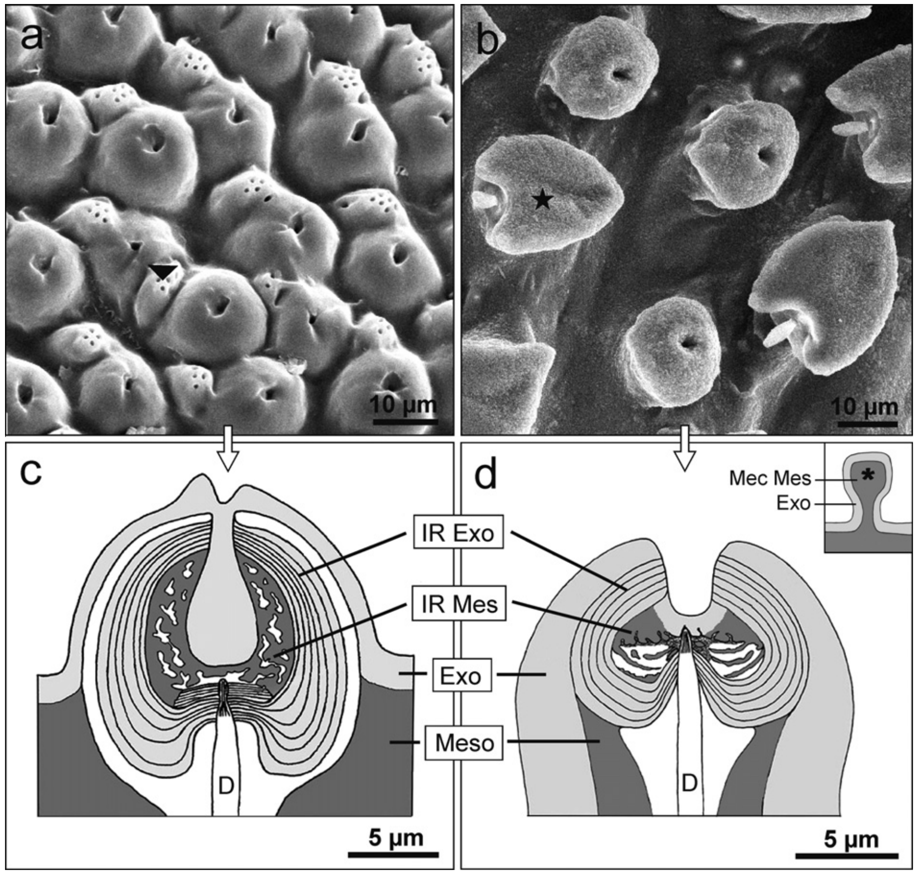

Fig. 1. (a) SEM image of dome-shaped IR receptors and associated wax glands (arrowhead) located at the bottom of the pit organ of *M. acuminata*. (b) IR receptors and hair mechanoreceptors (asterisk) of the propleural region of the prothorax of *A. albicornis*. Below: schematic drawings of single IR receptors of *Melanophila* (c) and *Aradus* (d) composed of different types of cuticle. The pressure chamber of the mesocuticular core is penetrated by the tip of a mechanosensory dendrite (D). Inset: schematic drawing of a contact mechanoreceptor of *Aradus*. Mec Mes in the marked region (*) was tested.

smelter plant [12], and several thousand *M. consputa* and *M. occidentalis* swarmed about two cement plants in southern California, where the beetles congregated near the kilns at high ambient temperatures. Beetles were especially numerous in the vicinity of the burning zone of the kilns [13]. These reports suggest that the beetles were lured by IR radiation from a considerable distance.

The cuticular sphere has to efficiently transform the IR radiation energy into mechanical displacement. Therefore, the thermomechanical properties of the spherical cuticular apparatus have to be optimized for this purpose. In an earlier paper, Müller et al. [14] measured the local modulus and hardness of the different cuticular components of the *Melanophila* IR sensillum. However, only dry material was investigated. As liquid is essential for the sensillum to function, we measured the mechanical properties as well as the water uptake behaviour (swelling properties) in dry and also fully hydrated (i.e. rewetted) sensilla of pyrophilous *Melanophila acuminata* and *Aradus albicornis*. The results are discussed with respect to the transduction process.

2. Material and methods

2.1. Animals

In summer 2010, adult *M. acuminata* hatched from burnt logs which were stored in the animal house of the Zoological Institute of Bonn University. The wood originated from Catalonia, Spain, and was burnt in the forest fires of summer 2009, during the reproduction period of *Melanophila*. The animals were kept for several weeks in plastic boxes and fed with raisins, peanuts and walnuts. Water was given ad libitum.

Adult *A. albicornis* were caught in burnt areas of eucalypt forests in Western Australia after fires in February 2011. The bugs were kept alive for several months in plastic boxes on burnt logs infested with post-fire fungi.

2.2. Scanning electron microscopy

Beetles and bugs fixed in 70% ethanol were cleaned by sonication in a mixture of chloroform and ethanol (2:1) for 2 min. After drying in air, specimens were glued onto holders with carbon glue (Leit-C, Fa. Neubauer), sputtered with gold and examined in a LEO 440i (Leica, Bensheim, Germany) scanning electron microscope (SEM).

2.3. Specimen preparation

Sensory IR pit organs were excised, together with about 0.5 mm of surrounding cuticle, from the metathorax of anaesthetized *M. acuminata.* Pieces of cuticle containing IR receptors were also excised from the propleural regions of the prothorax of anesthetized *A. albicornis*. After drying in air, specimens were embedded in Epoxy Resin L (Toolcraft) in a standard embedding form (Agar Aids Ltd.). Semi-thin cross-sections were cut from the embedded specimens using a Reichert Ultracut microtome with a diamond knife. The sections (1 μm) were stained with a 0.05% toluidine blue/borax solution and examined with a Leitz DM RBE light microscope.