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SHORT COMMUNICATION

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A new type of insect infrared organ of low thermal mass

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Abstract The Australian beetle *Acanthocnemus nigricans* is attracted by forest fires and has a pair of complex infrared (IR) receptor organs on the first thoracic segment. Each organ consists of a tiny sensory disc (diameter 120–130 μm) which serves as an absorbing structure for IR radiation. The disc is arranged above an air-filled cavity which is located just anteriorly to the coxae of the prothoracic legs. Inside the disc, about 30 multipolar thermoreceptors (warmth receptors) are tightly attached to the cuticle which is directed to the outside. The many dendrites of each multipolar neuron are tightly wrapped around the soma and contain a large number of mitochondria. Absorption of IR radiation by the disc causes an increase in temperature which is measured by the warmth receptors. Therefore, the IR receptors of *A. nigricans* can be classified as microbolometers with reduced thermal mass and in principle can be compared to the IR organs of pit vipers.

Introduction

Acanthocnemus nigricans (family Acanthocnemidae) is an inconspicuous black beetle with a body length between 3.5 and 5.5 mm. The beetle is widely distributed in Australia and has been introduced into various parts of Europe, Asia and Africa (Lawrence and Britton 1994). As a special behavioural feature, the beetle approaches forest fires (Champion 1922). After landing, the beetles start to run around quickly close to the flames (personal observation). The reason why *A. nigricans* approaches forest fires is not fully understood. Most probably the beetle and/or its larvae depend on food resources which become available after a fire. This food could be specialized ascomycete fungi, which start to grow on burnt wood or soil immediately after a fire (Wicklow 1988; Wikars 1992) or the cambium layer and wood of the burnt trees (Muona and Rutanen 1994). If the larvae depend on such food resources, it is quite possible that the area close to the fire serves as a meeting place for males and females. After copulation the females could deposit their eggs on the freshly burnt wood or soil. Pyrophilous buprestid beetles of the genera *Melanophila* and *Merimna* have metathoracic (*Melanophila*) (Evans 1964; Schmitz et al. 1997) or abdominal (*Merimna*) (Schmitz et al. 2000, 2001) infrared (IR) receptors, but nothing is known about heat receptors in *A. nigricans*. However, a pair of unusual hypomeral structures in front of the fore coxae have been described in *A. nigricans* (Lawrence and Britton 1994). We subjected these structures to morphological and physiological investigations with respect to a possible fire-relevant sensory function.

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Materials and methods

Animals

Adult *A. nigricans* beetles were collected during a field trip in Western Australia in January 2001. The beetles were kept for several weeks in small plastic boxes and fed on unsalted peanuts and raisins.

Light and electron microscopy

Three beetles were fixed in 70% ethanol for scanning electron microscope examination. The fixed insects were cleaned in a sonicator for 1 min and air-dried. Specimens were mounted with carbon glue (Leit-C) on holders, sputtered with gold and examined with a Hitachi SEM 2610-N. The prothoracic segments containing the IR organs of another three beetles were excised and fixed in 0.05 M cacodylate buffer with 3% glutaraldehyde (pH 7.2) for 2 h at 4°C. After 2 h post-fixation with 1.5% OsO_4 in the same buffer and rinsing in buffer solution, prothoracic pieces were dehydrated in ascending series of ethanol and embedded in Epon 812. Semi- and ultrathin sections were taken from four organs using a Reichert Ultracut microtome equipped with a diamond knive. Ultrathin sections were stained with uranyl-acetate and lead citrate and examined under a Zeiss EM 109.

Electrophysiology

Extracellular electrophysiological recordings were performed from prothoracic discs from four beetles by electrolytically sharpened tungsten electrodes which were gradually driven into the cuticle of the disc by a micromanipulator. To minimize damage to the disc by the electrode, penetration of the cuticle was stopped as soon as neuronal activity of the spontaneously active units was encountered. Signals were amplified ×1,000 and displayed on an oscilloscope. In order to mimic the natural stimulus (i.e. a forest fire), we stimulated the IR organ with a small thermal emitter which was mounted 40 mm away from the beetle and which could be heated to 400°C. The beetle was glued with its ventral side upwards onto a plate, and a shutter between the hot emitter and the beetle allowed defined exposure to the diffuse thermal radiation. The two-dimensional surface of the emitter, turned towards the beetle, was 0.7×2.5 cm. In a series of experiments, we irradiated the prothorax with the sensory disc for 1 s. To estimate the corresponding increase in cuticular temperature, we used a tiny thermocouple (Type K: Chromega/Alomega, diameter of the bead 33 µm). Because it was technically impossible to mount the bead under the outer cuticle of the intact sensory disc, we glued it with a minimal amount of Syndeticon to the inner surface of a piece of abdominal cuticle of an air-dried beetle. As the abdominal cuticle (about 15 µm) is twice as thick as cuticle from the outer side of the sensory disc (7–8 µm), temperature values might be slightly underestimated (but see below). The wires of the thermocouple were connected to an electronic thermometer (HH 202, Newport Omega, accuracy ±0.2°C) and the cuticle was exposed to the thermal emitter from a distance of 40 mm. Because the electronic thermometer needs 2 s for signal integration, and in order to compensate for the somewhat greater thickness of the abdominal cuticle, the shutter was held open for 3 s before the temperature was recorded. Mean temperature increase of the cuticle was 4.7±0.7°C (*n*=8 exposures).

Results

Morphology of the prothoracic IR receptors

The prothoracic structures consist of a pair of cuticular discs having a diameter of about 120 µm, which are located in hemispherical invaginations of the prothorax just anteriorly to the coxae of the prothoracic legs (Fig. 1A). Each disc is held in place by a small cuticular stalk (see arrow in Fig. 1A), which fixes the disc to the thorax just in front of the dorsal apex of the coxal cavity. Except for the stalk, a narrow crack surrounds the disc. Under the disc, an air-filled space, which we called the inner chamber, is situated (Fig. 1B). The air in the inner chamber communicates with the atmospheric air through the crack around the disc. At its deepest point, the inner chamber has a depth of about 100 µm measured from the outer surface of the disc. The disc has its greatest thickness (about 45 µm) at the caudal side, where the stalk inserts. From this point, the thickness of the disc gradually decreases towards the anterior rim. A series of semi-thin and ultrathin sections revealed that the disc is richly innervated by about 30 multipolar neurons, which are mainly situated directly under the outer cuticle of the disc (see Figs. 1B, 2). The neurons reveal a special arrangement of their dendrites; most of them branch all over from the soma and subdivide further into terminal subdendrites. As all dendrites are disposed in a tangled manner, the soma is enveloped almost completely by a mass of dendrites (Fig. 2). A striking feature of the neurons is the large number of mitochondria in the dendrites (see arrow in Fig. 2). Summarizing all features, the neurons can be classified as subepidermal multipolar receptors without accessory structures.

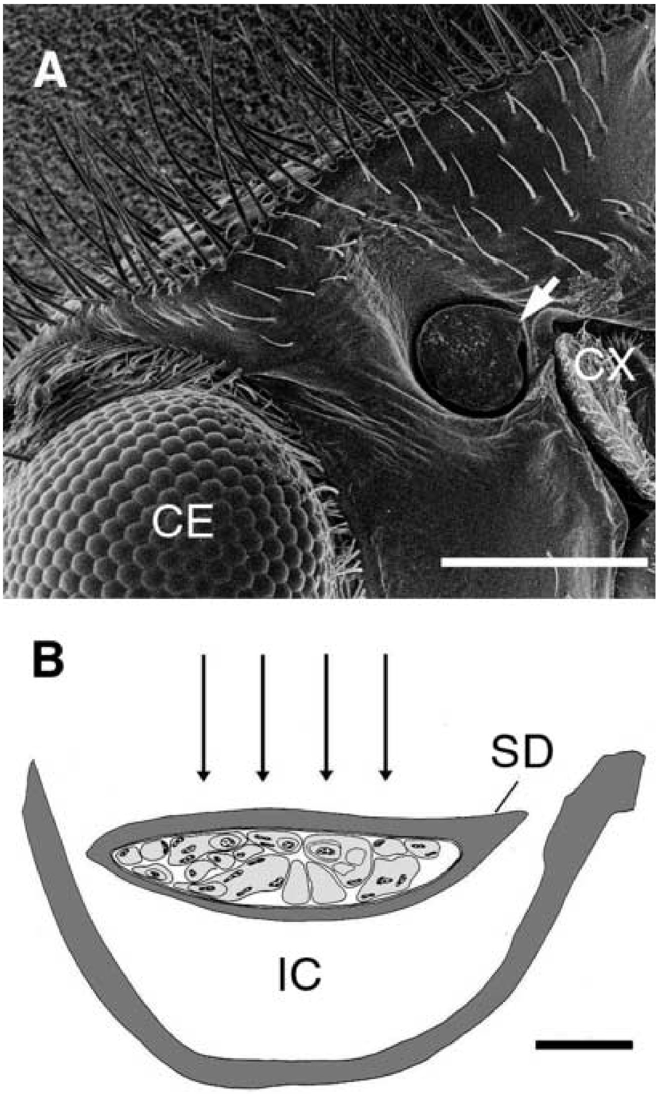

Fig. 1 **A** Scanning electron micrograph of the prothorax of *A. nigricans*. The infrared (*IR*) receptor organs are situated just in front of the fore coxae (*CX*). A little cuticular stalk (*arrow*) holds the sensory disc above an air-filled cavity. *CE* complex eye. *Bar* represents 200 µm. **B** Semischematic drawing based on a dorso-ventral section through an IR organ. The sensory disc (*SD*) is arranged over the inner chamber (*IC*). Exchange of air is accomplished by the crack around the disc. *Arrows* indicate the direction of incoming IR radiation. Multipolar neurons and their components (i.e. axon bundles and glial cells) in the haemocoelic space inside the sensory disc are *shaded in grey*. Epithelial cells, fat body, and trachea are not shown. *Bar* represents 30 µm

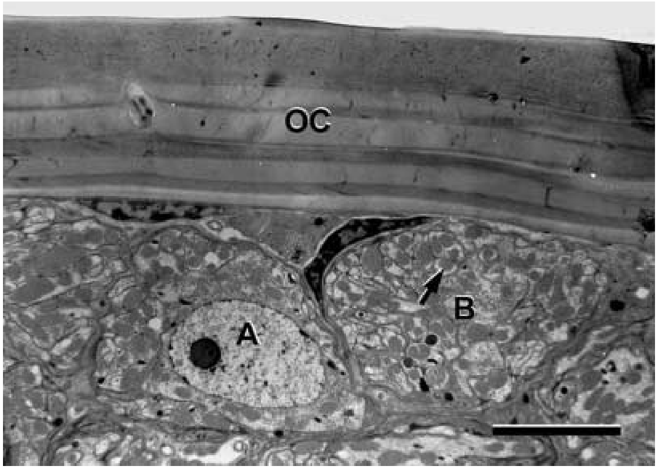

Fig. 2 Ultrathin section through the outer IR-absorbing cuticle (*OC*) of the sensory disc and two multipolar neurons (*A*, *B*) which are situated under the cuticle. In neuron *A* the nucleus is visible and also several dendrites which on the left are partly wrapped around the soma. In neuron *B* the dendritic region is shown, which consists of a tangled mass of numerous dendrites. Note the large number of mitochondria (*arrow*) in the dendrites. *Bar* represents 5 µm

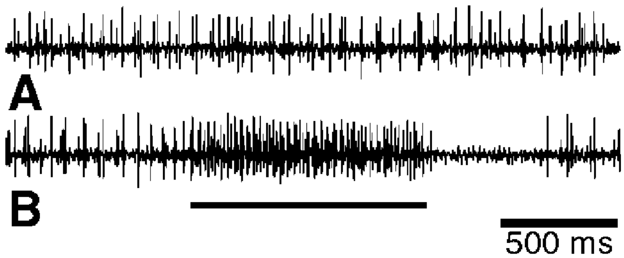

Fig. 3A, B Extracellular recording from the sensory disc. **A** Spontaneous activity from several units recorded at room temperature (20°C). **B** Example of an exposure to the heated thermal emitter for 1 s (indicated by *black bar*). The corresponding increase of a piece of cuticle from the abdomen of the beetle was 4.7°C±0.7°C. Spike frequencies increased in a phasic-tonic way. Cessation of the stimulus inhibited receptor activity for about 0.5 s

Electrophysiological recordings from the multipolar neurons inside the disc

The recordings from the sensory disc (*n*=4 beetles) showed that the multipolar neurons had ongoing activity at room temperature (Fig. 3A). The frequency of spontaneous activity of single units was between 5 and 10 Hz and was unaffected by sound (voice or hand clapping), moderate air movements or a gentle touch of the surrounding cuticle with a bristle. In contrast, exposition to the IR radiation from the thermal emitter increased firing frequency in a phasic-tonic way (Fig. 3B). We also stimulated the receptor with warm air and visible light from a red-light helium-neon laser, which had been used in previous studies to stimulate the IR organs of pit vipers (De Cock Buning et al. 1981). Independently of how the temperature was increased, an increased spike frequency resulted. In general, a higher steady-state temperature was coded by a higher discharge frequency of the units. Cessation of the stimulus inhibited the generation of action potentials.

Discussion

The electrophysiological recordings demonstrated that the multipolar neurons act as warmth receptors in the sensory disc. In our experiments the tip of the tungsten electrode which was inserted in the cuticle obviously sucked away a considerable amount of heat from the tiny disc. Therefore no determination of the sensitivity of the IR receptor could be made using this extracellular approach. It is known that insect cuticle itself absorbs IR radiation between 2.8 and 3.5 µm very well (Vondran et al. 1995). According to the law of Wien, this corresponds well to the maximum electromagnetic emission of a forest fire. Because the disc lies over an air-filled inner chamber, it can be classified as a thermally insulated microbolometer with decreased thermal mass. Therefore, the basic design of the IR receptor of *A. nigricans* is reminiscent of the IR organs of pit vipers (Crotalinae: Bullock and Fox 1957; Bleichmar and De Robertis 1962; Terashima et al. 1970; Amemiya et al. 1996). In pit vipers, such as rattlesnakes, a thin membrane absorbs the incoming IR radiation. The corresponding increase in temperature is measured by highly thermosensitive fibres of the trigeminal nerve (Bullock and Cowles 1952; Bullock and Diecke 1956; Goris and Nomoto 1967), which heavily innervate the membrane. A characteristic feature of the nerve endings is their large number of mitochondria. Thus Terashima et al. (1970) called the thermosensitive nerve endings innervating the IR-absorbing membrane in crotaline snakes “terminal nerve masses”. A large number of mitochondria were also found in the dendritic endings of the multipolar neurons in the sensory disc of *A. nigricans*. Another striking similarity between the IR organs of snake and beetle is the air-filled inner chamber and its connection with the atmospheric air. In the snake a small duct which runs from the inner chamber to the dorsal surface of the head represents this connection (Lynn 1931); in *A. nigricans* it is the crack around the sensory disc.

Looking at other IR receptors in insects, two different systems in two genera of buprestid beetles (Buprestidae) are known: (1) the metathoracic photomechanic IR sensilla in beetles of the genus *Melanophila* (Evans 1964; Schmitz et al. 1997; Schmitz and Bleckmann 1998), and (2) the abdominal IR receptors of the Australian “fire-beetle” *Merimna atrata* (Schmitz et al. 2000, 2001). Beetles of the genus *Melanophila* and *Merimna atrata* also approach forest fires and therefore most probably use their IR receptors for the same purpose as *A. nigricans*: for the detection of forest fires and for preventing them from harm caused by getting too close to the flames. Therefore, it is surprising that there are so many morphological and physiological differences between the IR receptors of *Melanophila* beetles, of *Merimna atrata* and of *A. nigricans*. In *Melanophila* beetles, a small pit is filled with about 70 cuticular IR sensilla (Evans 1966) which have evolved from ciliary hair mechanoreceptors (Vondran et al. 1995; Schmitz and Bleckmann 1997). The cuticular apparatus (mainly a small cuticular sphere) of an IR sensillum transduces IR radiation into a micromechanical event, which is measured by a mechanoreceptive sensory cell (a so-called photomechanic mechanism; Schmitz et al. 1997; Schmitz and Bleckmann 1998). Therefore, it can be seen that the *Melanophila* IR receptor is fundamentally different from the *A. nigricans* organ. The IR receptor of the Australian "fire-beetle" *Merimna atrata* is more similar to the *A. nigricans* receptor because it also functions as a microbolometer: each of the four abdominal receptors consists of a specialized round IR-absorbing area which is innervated by only one large multipolar neuron. This thermosensitive neuron has a highly branched terminal dendritic mass (TDM) which contains a large number of mitochondria (Schmitz et al. 2000, 2001). The dendrites of the multipolar neurons in the prothoracic discs of *A. nigricans* are also densely filled with mitochondria. However, the arrangement of the dendrites is different in *Merimna atrata* and *A. nigricans*: in *Merimna atrata* the TDM originates from the apical region of the soma and extends to the periphery of the IR-absorbing area, whereas in *A. nigricans* the dendrites are mainly concentrated around the soma. This special arrangement implies that each neuron measures the temperature in a small area restricted to the position of the soma region. Because there are about 30 neurons situated in a disc, it can be speculated that a mosaic of different temperatures can be perceived across the disc. For instance, such a mosaic can be generated when an IR source is moved around the beetle in a dorso-ventral or in a lateral manner.

Another fundamental difference between the IR organs of *Merimna atrata* and *A. nigricans* is that there is no air-filled inner chamber situated under the IR-absorbing cuticular surface in *Merimna atrata*. Although we have no data about threshold sensitivity of the IR receptor of *A. nigricans*, we speculate that the inner chamber serves to enhance the thermal insulation of the sensory disc and also to reduce the thermal mass, which together increase the sensitivity of the organ. This principle of a highly reduced thermal mass of the IR-absorbing structure to make the system more sensitive was found for the IR-absorbing membrane in pit vipers (for a review see Molenaar 1992). Therefore, the relatively simple IR organs of *Merimna atrata* can be compared with the lip organs of boid snakes, whereas the more complex *A. nigricans* IR organs show a number of striking analogies to those of pit vipers.

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