

## ORIGINAL PAPER

H. Schmitz · H. Bleckmann

**The photomechanic infrared receptor for the detection of forest fires in the beetle *Melanophila acuminata* (Coleoptera: Buprestidae)**

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**Abstract** We recorded from single units of individual sensilla of the thoracic infrared (IR) pit organs of *Melanophila acuminata*. When the organ was stimulated with a thermal radiator whose emission spectrum was similar to that of a typical forest fire, units responded phasically with up to seven spikes within 30–40 ms at a radiation power of  $24 \text{ mW cm}^{-2}$ . In the experiments all wavelengths shorter than  $1.6 \mu\text{m}$  were excluded by a longpass IR filter. Response latencies were about 4 ms and initial impulse frequencies were up to 250 impulses per second (ips). A single spike could be generated even when stimulus duration was only 2 ms. Reduction of total radiation power from  $24 \text{ mW cm}^{-2}$  to  $5 \text{ mW cm}^{-2}$  resulted in increased response latencies of 5–6 ms and the occurrence of only two to three spikes. Initial impulse frequencies decreased to 125 ips. According to our physiological results and calculations, *Melanophila* should be able to detect a 10-hectare fire from a distance of 12 km. Mechanical stimuli also evoked responses of the IR sensilla. All present morphological and physiological findings lead to the conclusion that the IR receptors of *Melanophila* must function by means of a hitherto undescribed photomechanic mechanism.

**Key words** Infrared receptor · Mechanoreceptor · Fire ecology · Insect cuticle · Photoacoustics · Remote sensing

**Abbreviations** ips impulses per second · IR infrared

**Introduction**

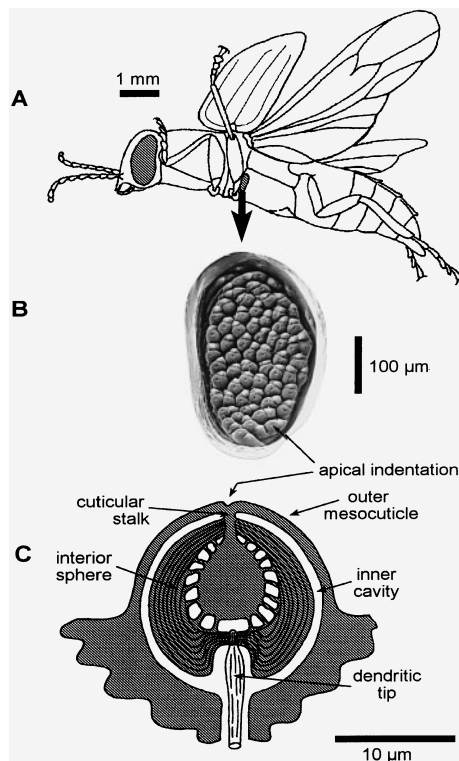
The beetle *Melanophila acuminata* (Coleoptera, Buprestidae) is the most well-known insect associated with

forest fires (Ricksecker 1885; Champion 1909; Manee 1913; Apel 1988; 1989). The larvae of *Melanophila* absolutely depend on wood of fresh fire-killed trees because they can not cope with the defence reactions of a living tree to insect feeding (Graham 1939; K-H Apel, personal communication). For this reason adult *Melanophila* approach forest fires in “sometimes unbelievable numbers” (Linsley 1943). Mating usually takes place while the fire is still burning and females deposit their eggs under the bark of burnt trees immediately after the flames have subsided. Under ordinary conditions the beetles are rarely encountered in nature (Linsley 1943). Therefore, *Melanophila* must be able to detect forest fires from great distances (Evans 1964) and approach distances up to 80 km have been reported (Van Dyke 1926).

Forest fires emit smoke, sound, visible light, and infrared (IR) radiation. A typical forest fire burns with a temperature between  $500 \text{ }^\circ\text{C}$  and more than  $1000 \text{ }^\circ\text{C}$  (a so-called full fire). According to the law of Wien which gives the emission of electromagnetic radiation of a surface as a function of temperature (Hecht 1989) those forest fires have a maximum emission in the wavelength range  $2.2\text{--}4 \mu\text{m}$ . IR radiation of this spectral composition is well transmitted through an atmospheric “window” ranging from  $3 \mu\text{m}$  to  $5 \mu\text{m}$  (Davis and Lettington 1988; Froehlich et al. 1992). Therefore, IR radiation provides an ideal means for the detection of forest fires (Hirsch 1969). Evans (1964) conducted behavioural experiments to elucidate how *Melanophila* detects a forest fire. In a first approach he found no indications that the beetle uses olfactory or acoustic cues. Because all species of the genus *Melanophila* are diurnal, it is unlikely that the beetles use their eyes for the detection of a fire from great distances (Linsley 1943). This assumption is in line with the observation that the beetles are also attracted by hot surfaces which do not emit visible light or smoke detectable by photoreceptors during the day.

All species of the genus *Melanophila* which are associated with forest fires possess two metathoracic pit organs situated directly next to the coxal cavities of the

H. Schmitz (✉) · H. Bleckmann  
Institut für Zoologie der Rheinischen  
Friedrich-Wilhelms-Universität Bonn,  
Poppelsdorfer Schloß, D-53115 Bonn, Germany  
Tel.: +49-228 735461; Fax: +49-228 7354580  
e-mail: hschmitz.zoology@t-online.de



**Fig. 1** **A** Schematic drawing of a flying *Melanophila*. Note that the mesothoracic legs are lifted in flight so that the infrared (IR) pit organs next to their coxae (vertical arrow pointing to **B**) are completely exposed. **B** Infrared pit organ at higher magnification. After removal of the wax filaments – normally filling the entire pit – 62 domed IR sensilla can be seen, each one accompanied by a wax gland appearing somewhat brighter because of the poor electrical grounding of wax residues. **C** Schematic drawing of the cuticular components (shaded areas) and the dendritic tip of the sensory cell of an IR sensillum; the enveloping cells are omitted (for further details see Vondran et al. 1995). From the apical indentation a small stalk originates which connects a large endocuticular sphere – situated within an inner cavity – to the outermost thin mesocuticle. Each sphere displays three different zones. Note that the middle zone shows many microlacunae. The sensory neuron innervates the sphere with the tip of the dendritic outer segment containing a tubular body. Expansion of the sphere due to absorption of IR radiation will cause a deformation of the dendritic tip containing the tubular body

mesothoracic legs (Sloop 1937; Fig. 1A). Evans (1966a) reported an unspecific and unquantified behavioural response of non-flying *Melanophila* to IR radiation (a twitch of the antenna ipsilateral to the IR source) when one of the pit organs was stimulated with IR radiation. In the most sensitive range (wavelengths 2.5–4 µm) an energy level of 60 µW cm<sup>-2</sup> was sufficient to cause a quick, back-and-forth lateral movement of the antennal flagellum even when the pit organs were irradiated for only 1/300 s. This unspecific behavioural response occurred only when the IR stimulus was focused on the pit organ. There was no response when the pit organ was covered with bronze paint or when such a weak IR stimulus was focused on other body parts (e.g. the antennae). These results led to the conclusion that *Melanophila* uses the pit organs for the detection of IR

radiation and thus for the detection of forest fires (Evans 1964, 1966a). There is a second observation which supports the idea that *Melanophila* uses the pit organs for the detection of forest fires: during flight the beetles lift their middle legs up to the elytrae (Fig. 1A), thus exposing the pit organs to a potential IR source.

Despite the above behavioural observations no one attempted a physiological study to learn whether the pit organs of *Melanophila* are indeed IR sensors. Evans speculated that the infrared sensilla may have originated from presumed thermoreceptors which he supposed to be distributed all over the body of the beetle (Evans 1966b). At the bottom of each pit – about 100 µm deep – there are between 50 and 100 sensilla bulging out with their upper hemispheres above the surface. Each sensillum is accompanied by a wax gland and therefore the entire pit is filled out by masses of wax filaments (Evans 1966b; Vondran et al. 1995; Schmitz and Bleckmann 1997; Fig. 1B). Recent ultrastructural studies of the sensilla at the bottom of the pits revealed that the cuticular apparatus consists of an endocuticular lens-like spherule bulging out with its upper hemisphere above the surface, covered only by a thin (1-µm) layer of unsclerotized mesocuticle (Evans 1966b; Fig. 1C). Each spherule is innervated by a single neuron which is anchored ventrally in the sphere with the distal tip – containing a tubular body – of its cylindrical and unbranched dendritic outer segment. The ultrastructure of the sensory cell is similar to that of a typical insect mechanoreceptor (Vondran et al. 1995; Schmitz 1996; Schmitz and Bleckmann 1997). We recorded the activity of single units of the pit organs of *Melanophila* and found them to be highly sensitive to IR radiation. In the wavelength range from 1.65 µm to far-IR, a stimulus intensity of 5 mW cm<sup>-2</sup> was sufficient to generate a neural response. First results of this study were published elsewhere (Schmitz et al. 1997).

## Materials and methods

### Experimental animals

Burnt pieces of wood (1–2 m long, diameter 0.05–0.2 m) infested with larvae of *M. acuminata* (Buprestidae) were stored in a room at 20–25 °C. The logs were frequently moistened to prevent desiccation. The wood originated from a forest fire north of Berlin in Brandenburg (Germany) which occurred in the middle of the year during the reproduction period of *Melanophila*. The beetles, which were collected from the white walls of a hatching room after having emerged from pupae, were kept in a terrarium. They were fed with raisins and unsalted peanuts. The photoperiod in the room was that of the external environment in Bonn. Under these conditions the beetles survived for about 3 months.

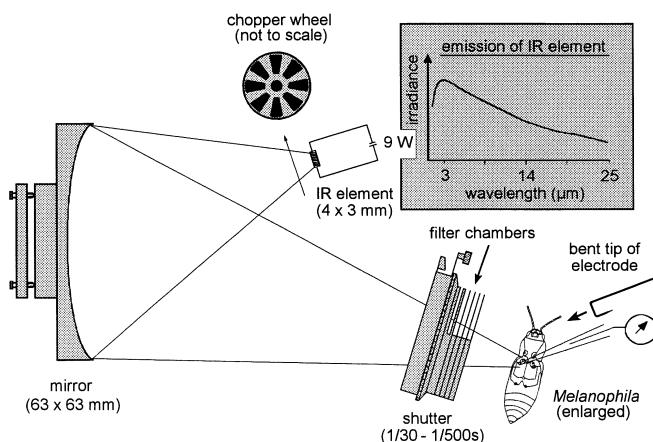
### Sensory recordings

For electrophysiological recordings the beetles were fastened ventral side up to an experimental platform with Bis-Acryl-Composite dental glue (Espe Dental-Medizin GmbH). In order to make the pit organs accessible, all legs were removed. The wax filaments in the pits were also carefully removed without touching the sensilla.

Preparations, which survived for up to 2 days, were tested at room temperature (20–25 °C). Single units were recorded with electrolytically sharpened tungsten electrodes (wire diameter 100 µm). In order to give IR radiation maximal access to the sensilla, the outermost tip of the electrode was bent in a hooklike manner by 180° and the electrode was drawn into the pit from the contralateral side with a micromanipulator (c.f. Fig. 2). The preparation was grounded using a reference electrode in the abdominal haemolymph. Neural activity was AC (1–3000 Hz or 300–3000 Hz) amplified (DAM 80, WPI), displayed on an oscilloscope (Hameg digital scope HM 205-3) and stored on a digital tape recorder (Biologic DTR 1200). For off-line data analysis spikes were AD converted. In some cases spikes were transformed to 5-V standard pulses of 0.5 ms duration prior to AD conversion. Spikes and standard pulses, respectively, were fed to a data acquisition system (GW Instruments, MacAdios II; Power Macintosh, Sampling rate 10 kHz) and further processed with the software SuperScope.

### Infrared stimulation

As a stimulus source we used the ORIEL IR element 6580 (size 4 mm × 3 mm) which, when supplied with 9W, has its maximum of emission at a wavelength of 3 µm (cf. inset Fig. 2). A concave mirror, positioned 13 cm away from the IR element and 25 cm away from the beetle, was used to reflect and focus the IR rays onto the pit organ (cf. Fig. 2). The angle between the axis IR element-mirror and mirror-beetle was 33°. A camera shutter (outer diameter 6 cm) was positioned 2 cm in front of the beetle. Prior to the experiments the above components and the beetle were adjusted using visible light. For this purpose the IR element was exchanged by the ending of a glass-fibre light guide (diameter 2 mm) and an image of the single glassfibres – visible at the cut end of the fibre bundle – was focused on the ventrolateral thorax of the beetle including the pit with the aid of a binocular microscope. Then the IR element was carefully replaced at the position of the fibrebundle ending. For the actual experiments germanium longpass IR filters (5% cut-on wavelength at 1.65 µm, or 2.4 µm, respectively, i.e. the filters start to transmit at the given wavelength) were inserted into one of the chambers at the camera shutter. The shutter was closed and set for speeds ranging between 1 s and 1/500 s. Stimulus intensity was reduced with a series of silicon and/or sapphire neutral density filters each of which reduced the IR intensity by about 10% (sapphire) or about 50% (silicon; in the following named reducing filters; specifications of percentage was given by the producers).



**Fig. 2** Experimental setup used for the electrophysiological recordings. The camera shutter was mounted to a support which was mechanically decoupled from the other components. The filter chambers at the shutter allowed introduction of a longwave filter and up to four reducing filters. *Inset*: emission characteristic of the ORIEL IR element when supplied with 9 W. Note that the maximum is at 3 µm; i.e. like that of a typical forest fire

Radiation power in the focus of the mirror was measured with a laser power and energymeter (Laserpoint, Mod. 3000) for the unfiltered radiation and for the filter combinations used. The diameter of the probe (10 mm) was larger than the IR spot focused on the thoracic pit organs and therefore all IR radiation was recorded. Stimulation time was monitored with a beam of visible light directed onto the shutter and a photocell positioned directly behind the shutter. Shutter opening gave rise to a fast 5-V TTL-signal recorded simultaneously with the neuronal activity indicating the onset and the end of the exposition of IR.

In a second series of experiments a chopper wheel was introduced into the beam 1 cm in front of the IR element (cf. Fig. 2). The turning speed of the wheel and thus stimulus repetition rate was adjusted with the aid of an oscilloscope. Wheel speeds were varied between 10 Hz (50 ms ON/50 ms OFF) and 100 Hz (5 ms ON/5 ms OFF).

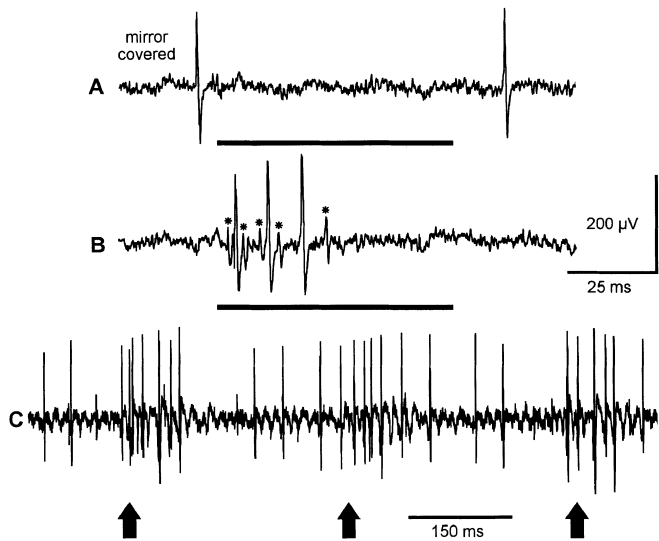
Reliable responses of a newly encountered receptor cell to IR radiation were always tested more than ten times. After that, the respective stimulus programme was performed. Under each stimulus regime (defined by the intensity of IR radiation and the IR exposition time) the receptor cell was tested 6–12 times. In this way on average three to four sensilla of an individual pit organ were examined. In general it was possible to record for more than 1 h from an individual sensillum.

If not otherwise stated, *N* refers to the number of experimental animals and *n* to the number of units recorded from. Mean values are given with their standard deviation.

## Results

### Physiology

While slowly advancing the recording electrode into the cuticle of a pit organ, we repeatedly interrupted the IR beam between the mirror and the open shutter with a piece of paper (= search stimulus). When the recording electrode was only slightly advanced in the cuticle the spikes which were encountered responded to the onset of the IR search stimulus but showed no ongoing activity. Units clearly responded to our IR stimulus but they never responded to a flash of visible light, to sound (voice or hand clapping), to smoke or to moderate air movements. When the electrode was pushed slightly deeper into the cuticle, the spikes, whose amplitudes now increased, started to show ongoing activity (Fig. 3A,C). This activity appeared to be positively correlated with the penetration depth of the electrode. Most likely the advancing electrode caused pressure on the cuticular components of nearby sensilla (especially the spheres) which in turn caused the cell to fire. When a sensillum which showed ongoing activity was excited by IR radiation, the number of spikes evoked was smaller than that evoked before electrode penetration depth caused ongoing spike activity (Fig. 3B). If the electrode was pushed even deeper into the cuticle, the IR stimulus was no longer effective. It was striking that IR sensitivity was negatively correlated with the penetration depth of the recording electrode. For the above reasons we decided that ongoing activity of units was artificial, i.e. was due to the mechanical stimulus caused by the electrode. To minimize mechanical artifacts, experiments were performed with the recording electrode barely penetrating the cuticle of the pit organs. In this

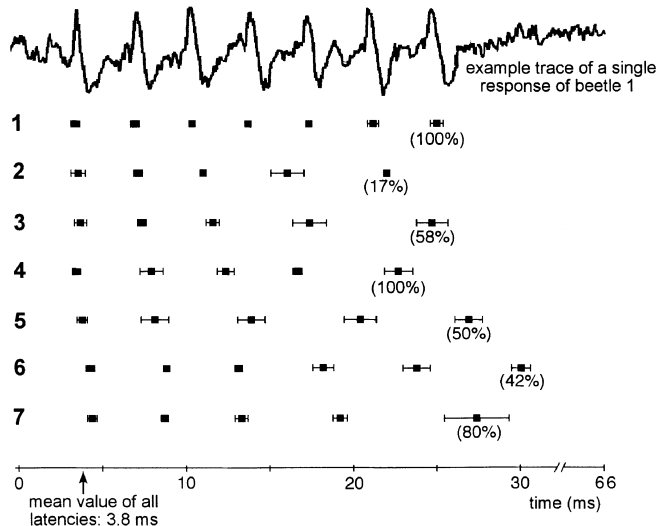


**Fig. 3** A–C Example of a single unit that displayed ongoing activity. In **A** and **B** IR radiation ( $24 \text{ mW cm}^{-2}$ ) lasted for 1/15 s (indicated by horizontal black bar). In **A**, however, the mirror was covered by a piece of paper, i.e. only ongoing activity, which was not correlated with shutter opening, is visible (as in **C**); in **B** three large spikes occurred during shutter opening. A second unit, apparently at a greater distance from the recording electrode and not visible in **A**, produced five small spikes (marked by asterisks). **C** Gentle tapping with the fingertip (arrows) on the metal plate of the setup caused the large unit to generate additional action potentials

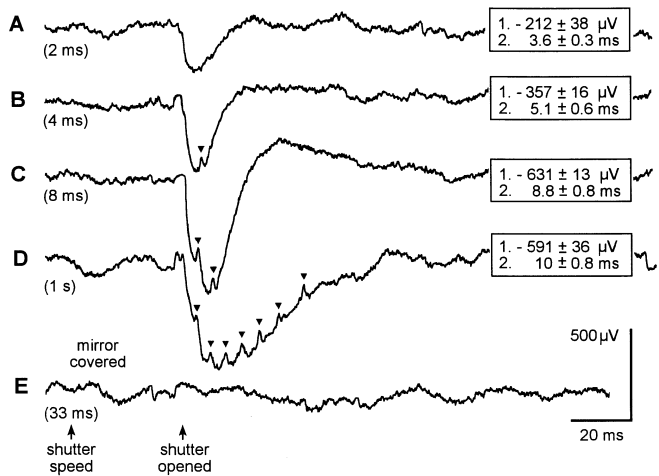
way, spike amplitudes usually were small (only two to three times the noise level), but the cells showed very little ongoing activity if any and remained very sensitive to the IR stimuli.

**Responses to IR radiation**

In a first set of experiments we stimulated the pit with unfiltered radiation from the IR element (Fig. 7A). To ensure that responses were caused by IR radiation and not by shorter wave-lengths which were also emitted by the IR source, we inserted a longpass IR filter (5% cut-on wavelength  $1.65 \mu\text{m}$ ) into the shutter opening. If not otherwise stated, this filter was used in all subsequent experiments. If shutter speed was set to 66 ms ( $=1/15 \text{ s}$ ), each IR stimulus (stimulus intensity at the level of the pit organ  $24 \text{ mW cm}^{-2}$ ) reliably caused a phasic ON response which consisted of five to seven action potentials within the first 30–40 ms after stimulus onset [corresponding to 200–250 impulses per second (ips), Figs. 4, 7B]. Mean latency of the first spike was 3.8 ms (Fig. 4); OFF responses were never observed. The number of spikes generated by a single sensillum in consecutive trials was not constant (Figs. 4, 6, 7). In some recordings the spikes were riding on a slow negative potential which may reflect the generator potential of the unit. Due to possible electrode polarization and the frequency response of tungsten electrodes, the shape of the receptor potentials (cf. Fig. 5) may be somewhat distorted. However, the amplitude and duration of these



**Fig. 4** Responses of single units recorded from seven beetles (1–7) to an IR stimulus (onset at 0 ms, duration 1/15 s,  $24 \text{ mW cm}^{-2}$ ). Each unit was irradiated six times in consecutive trials. In this figure and in Figs. 7 and 8, black squares indicate the mean point in time of occurrence of the first and following spikes. Horizontal bars indicate standard deviations. Note that in beetles 2, 3 and 4–6 the last spike was not always generated. Number in parentheses gives percentage of its occurrence

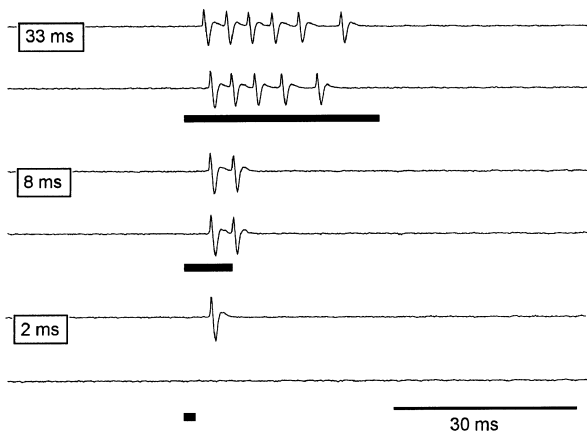


**Fig. 5** Receptor potentials and action potentials (indicated by arrowheads) recorded from an IR sensillum after exposure to IR stimuli of different durations (A–D). Stimulus onset is marked by arrow. Lowpass filter of the amplifier was set to 1 Hz. In order to elicit a maximal response, the longpass filter was not inserted in this trial ( $32 \text{ mW cm}^{-2}$ ; filter insertion resulted in a somewhat smaller amplitude). A downward deflection indicates a negative potential. Reduction of exposure time caused a reduction in the amplitude of the slow potential. Mean and SD of negative amplitude (1) and of appearance of the local minimum of the slow potential (2;  $n = 6$  exposures) are given in the boxes. When shutter speed was set to 1/500 s ( $=2 \text{ ms}$ , A) no spikes occurred but a distinct slow potential is still visible. Covering of the mirror yielded no response (E)

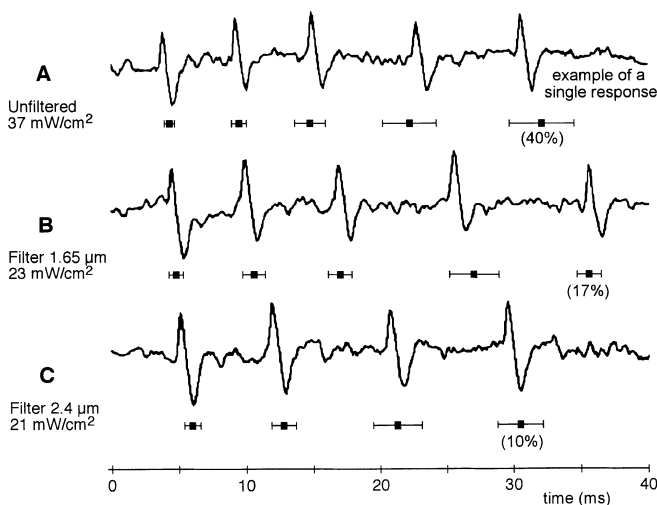
potentials clearly correlated with IR exposition time (Fig. 5). Controls showed that the responses to our IR stimuli were not due to convected heat from the IR

element nor to shutter vibrations which may have been transmitted to the preparation via the floor of the building. When we covered the mirror with a piece of paper we never got a response at any of the shutter speeds and IR intensities tested (see also Figs. 3A, 5E), even though the direct distance between the IR source and the beetle was smaller than the distance between the reflecting mirror and the beetle (cf. Fig. 2).

When IR exposure time was reduced below 66 ms the number of spikes decreased (Fig. 6). Even an exposure time of 2 ms was sufficient to generate one single spike



**Fig. 6** Reduction of exposure time (*horizontal bars* below responses) and its effect on the response of a single sensillum (stimulus intensity  $24 \text{ mW cm}^{-2}$ ). For each exposure time two consecutive trials are shown. Note that the number of spikes decreases with decreasing stimulus duration. A stimulus of 2 ms was sufficient to generate a single spike (*lower trace*)



**Fig. 7** Effect of longpass filter inserted into the camera shutter. Stimulus onset was at 0 ms and shutter speed was 66 ms in A, B and C. In A an unfiltered stimulus from the IR element was radiated onto the pit organ. In B and C longpass filters (1.65  $\mu\text{m}$  and 2.4  $\mu\text{m}$ , respectively) were inserted. *Black squares* indicate mean latencies of the first and following spikes ( $n = 15$ ). Reduction of radiation energy resulted in an increase of both latencies and interspike time intervals and in a decrease of spike number

after a latency of about 4 ms, i.e. about 2 ms after the shutter had already been closed, in about 70% of the sensilla tested ( $N = 9$ ; Fig. 6, lower trace).

In another set of experiments first an unfiltered stimulus was applied to a sensillum (Fig. 7A). Subsequently the 1.65- $\mu\text{m}$  longpass filter was inserted (Fig. 7B) and afterwards replaced by the 2.4- $\mu\text{m}$  longpass filter (Fig. 7C). When stimulus intensity was  $37 \text{ mW cm}^{-2}$  (Fig. 7A) the unit generated four to five spikes. If the 1.65- $\mu\text{m}$  filter was inserted, a considerable part of the wave-length spectrum was excluded and the radiation energy was reduced to  $23 \text{ mW cm}^{-2}$ . Nevertheless the number of action potentials elicited remained more or less constant (the fifth spike now occurred in only 18% of the events) and latencies of the first spikes and interspike time intervals were only slightly prolonged. Insertion of the 2.4- $\mu\text{m}$  longpass filter resulted in a further reduction of shorter wavelengths and in a reduction of radiation energy to  $21 \text{ mW cm}^{-2}$  but the effect on the number of spikes (decrease) and interspike-time-intervals (increase) was even more distinct (Fig. 7C).

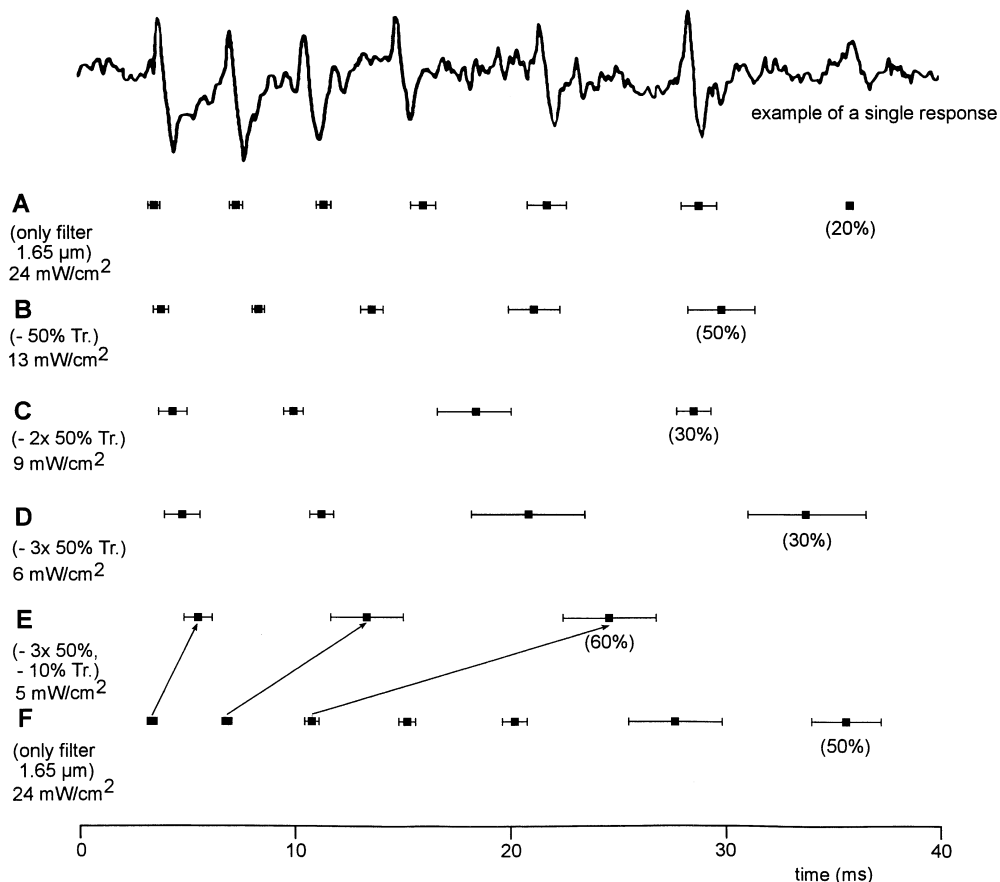
#### Responses as a function of stimulus intensity

In order to determine the threshold of the infrared sensilla we subjected the pit organs to decreasing stimulus intensities. For this purpose a unit was examined which generated up to seven spikes when irradiated with  $24 \text{ mW cm}^{-2}$  (Fig. 8A; longpass filter 1.65  $\mu\text{m}$  inserted; shutter speed 66 ms). In the consecutive trials up to four reducing filters were successively inserted into the filter chambers (B–E). As control all reducing filters were removed (F) at the end of the experiment. The control showed that the unit had not altered its responsiveness during the experiment. Especially the comparison between E (only two to three spikes generated) and F (six to seven spikes generated, see arrows) showed the marked difference in performance when radiation power was neutrally reduced by about 80%. Both response latencies and interspike time intervals decreased with increasing stimulus intensity. Average latencies of the respective first spike in A and F were 3.5 ms, whereas in E the mean latency significantly increased to 5.5 ms (Student's *t*-test,  $P < 0.001$ ). The reduction in stimulus intensity had an even greater effect on the interspike time intervals: In A and F the first interval had a mean duration of less than 4 ms, whereas it increased its mean duration significantly to 4.5 ms in B (Student's *t*-test,  $P < 0.001$ ). The mean of the first interval in E was 8 ms and of the second interval 11.2 ms.

#### Responses to repetitive stimulation

The phasic responses to the IR stimulus raised the question how the pit organs of *Melanophila* respond to a repetitive stimulus regime. In order to test this we placed

**Fig. 8** Effect of neutral density filters. Stimulus onset was at 0 ms and shutter speed was 66 ms in A–F. In A and F only the 1.65- $\mu\text{m}$  longpass filter was used. Beginning in B, up to four reducing filters were used which caused an increasing reduction of transmission. *Black squares* indicate mean latencies of the first and following spikes ( $n = 10$ ). Reduction of radiation energy resulted in an increase of latencies and interspike time intervals and in a decrease of the number of spikes

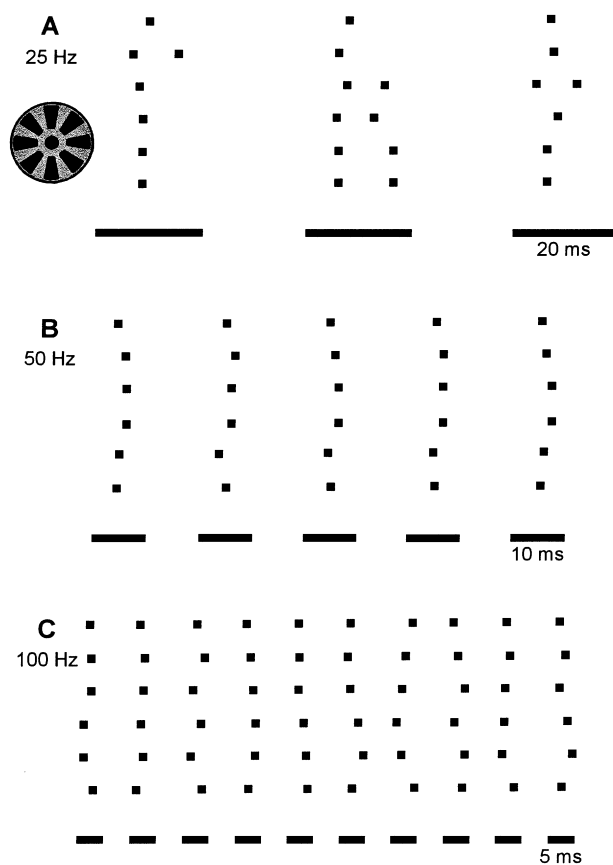


a chopper wheel, which had eight equally spaced openings, between the IR element and the mirror (cf. Fig. 2). Using a stimulus intensity of 37 mW cm<sup>-2</sup>, action potentials were reliably obtained up to a repetition rate of 50 Hz (in one case 100 Hz, Fig. 9). At low repetition rates (<20 Hz) each stimulus produced two to three action potentials. At higher repetition rates (30–75 Hz) each stimulus produced only one phase-locked action potential (Fig. 9B, C). If the repetition rate was further increased, phase-locked action potentials could still be recorded, but now failed to occur on some cycles. The physiological data strongly suggest that the pit organ of *Melanophila* is a fast, phasic IR receptor.

**Discussion**

Responses to IR and mechanical stimulation

Our experiments clearly show that IR radiation alone is sufficient to stimulate the pit organs of *Melanophila*:



**Fig. 9A–C** Raster plots of the responses of a unit recorded in a repetitive stimulus regime. Each trace shows one data collection sweep. *Dots* represent the time of occurrence of single action potentials. Stimulus repetition rate was 25 Hz **A**, 50 Hz **B** and 100 Hz **C**. Exposure time was 20 ms **A**, 10 ms **B**, and 5 ms **C**, respectively. *Horizontal bars* indicate IR exposure times. Note that the responses are phase locked to the stimulus

even if all visible light (wave length  $< 1 \mu\text{m}$ ) was filtered out, a stimulus intensity of  $5 \text{ mW cm}^{-2}$  still produced two to three action potentials. Single spikes could still be generated even at a stimulus duration of only 2 ms. Our physiological results are in line with the finding that an IR stimulus of 3.3 ms duration is sufficient to cause a behavioural response (a twitch of the ipsilateral antenna) in tethered *Melanophila* (Evans 1964, 1966a).

Our filters did not allow us to reduce the IR radiation power below  $5 \text{ mW cm}^{-2}$ . Linear extrapolation indicates that a radiation power of  $500 \mu\text{W cm}^{-2}$  may still cause one action potential. A physiological threshold of  $500 \mu\text{W cm}^{-2}$  comes close to the  $60\text{--}100 \mu\text{W cm}^{-2}$  threshold value found by Evans (1966a) in behavioural experiments. The lower behavioural threshold is not surprising for two reasons: First, the behavioural antennal responses of the beetles were probably based on the averaged input of many sensilla. This should improve the signal to noise ratio and thus IR sensitivity. Second, Evans (1966a) stimulated the animals with IR radiation of narrow bandwidth (about  $1 \mu\text{m}$ ). His threshold value of  $60 \mu\text{W cm}^{-2}$  was obtained at a wavelength of  $3 \mu\text{m}$  (bandwidth between  $0.6$  and  $1.2 \mu\text{m}$ ) where the animals showed maximal behavioural sensitivity (see Introduction). The extrapolated physiological threshold of  $500 \mu\text{W cm}^{-2}$  reported here is based on a broad-band IR stimulus, generated with a thermal radiator. We estimate that less than 10% of the total energy, i.e. less than  $50 \text{ mW cm}^{-2}$ , was in the wavelength range between  $2.5$  and  $4 \mu\text{m}$ . Compared to the behavioural study our physiological experiments have another disadvantage: There must have been some heat flow from the pit organ into the tip of the recording electrode. This heat flow may have decreased the sensitivity of the pit organ. For the above reasons we believe that the sensitivity of the pit organ of *Melanophila* can only be higher but not lower than the sensitivity found in our experiments.

The IR-sensilla of *Melanophila* not only responded to IR radiation but also to weak mechanical stimuli, i.e. those caused by relative movements between the tip of the recording electrode and the sensillum recorded from (Fig. 3C). This mechanical sensitivity is in line with ultrastructural findings: the sensory neurons innervating each sphere of a pit organ show all features of a typical insect mechanoreceptor of the ciliary type and there is strong evidence that the IR receptors may have evolved from hair mechanoreceptors (Vondran et al. 1995; Schmitz and Bleckmann 1997).

#### The new photomechanic mechanism

How does the IR receptor of *Melanophila* function? We probably can rule out a transduction mechanism based on specialized photopigments activated by the energy of absorbed photons, comparable to the photoelectrical transduction process in the eyes of both invertebrates and vertebrates. To our knowledge there are no

photopigments that are sensitive in the low wave-length range to which the pit organs of *Melanophila* respond. The range of vision in man and animals is generally between  $300 \text{ nm}$  and  $750 \text{ nm}$  and all known visual pigments have their absorption maxima within this range (Kirschfeld 1986; Stavenga 1995). In addition there are also no enlargements of the dendritic outer segment membrane resembling microvilli building a rhabdomere (see Vondran et al. 1995), a basic feature of all insect photoreceptors. Considering all morphological and physiological data, the following mechanism, which has never been suggested for any receptor before, seems most plausible: when heat is transferred from a warmer body to a cooler one by conduction and the bodies are in sufficient thermal contact (e.g. tightly pressed against each other), the temperature of the cooler body inevitably will rise. The material of the cooler body is of no importance for the process of heat transfer. If heat is intended to be transmitted by electromagnetic radiation it is of crucial importance that the radiation is maximally absorbed by the receiving (cooler) body. The absorption capacity highly depends on the material composition of the receiver. When the frequencies of vibration of a chemical bonding between two atoms and of the incoming radiation are identical, absorption will be 100%. It is well known that the mid-IR region between  $1 \mu\text{m}$  and  $10 \mu\text{m}$  is the spectral region where most organic molecules show vibrational absorption bands. The cuticular spherules of *Melanophila* (Evans 1966b; Vondran et al. 1995) like insect cuticle in general consist of a protein matrix in which long-chained chitin (*N*-acetylglucosamines) molecules are embedded, all having many C-H, N-H, and O-H groups (Weber 1974). Molecules with these atomic groups swing with a frequency of about  $100 \text{ THz}$  and therefore have stretch resonances at wavelengths in the range of  $3 \mu\text{m}$  (Herzberg and Huber 1950). A wavelength around  $3 \mu\text{m}$  not only coincides with the region of lowest transmission of the cuticle of *Melanophila* (Vondran et al. 1995) but also with the region of highest behavioural sensitivity (Evans 1964, 1966a). Molecules which have stretch resonances in the IR region convert the vibrational energy within fractions of a millisecond into translational energy, i.e. heat, by non-radiative de-excitation processes. Any heating must cause a change in spherule volume which finally must induce a deformation of the dendritic tip of the mechanosensory cell. We speculate that the sphere is designed to exert a maximal mechanical impact on the dendritic tip. For this reason it is possible that the coefficient of thermal expansion of the outer lamellated layer is greater than that of the interior components. Also the middle layer, showing many microlacunae, could help to enhance a displacement of the outer layer relative to the innermost layer. The eccentric position at the edge of the spherule is the location where strongest deformation is expected to occur (cf. Fig. 1C).

To estimate the deformation of a single spherule, we take  $5 \text{ mW cm}^{-2}$  – the lowest radiation power used in

our experiments – as a basis for the following calculation. The effective area, where absorption can take place, of a spherule of 15  $\mu\text{m}$  diameter (Vondran et al. 1995) exposed to IR radiation is  $A = 176 \mu\text{m}^2$ . Assuming a stimulus duration of 4 ms, and a supposed absorption of 80%, the energy absorbed by the spherule is about  $Q = 2.82 \times 10^{-11}$  J. The corresponding temperature increase is given by  $\Delta T = Q/(C_V \times V)$ , where  $V$  is the volume of the spherule, and  $C_V$  is the specific heat coefficient. Taking a volume of  $V = 1.8 \times 10^{-15}$   $\text{m}^3$ , corresponding to the volume of a sphere 15  $\mu\text{m}$  in diameter, and assuming a specific heat of  $1.5 \times 10^6$   $\text{J m}^{-3} \text{K}^{-1}$ , which is a typical value for solids of a lower hardness (e.g. hard rubber or resin; Kuchling 1985), the temperature increase in the spherule is  $\Delta T = 0.01$  K. The circumference  $L$  of a sphere of the above size changes due to the temperature change by  $\Delta L = \alpha \times L \times \Delta T$ , where  $\alpha$  is the thermal extension coefficient. Assuming  $\alpha = 200 \times 10^{-6}$   $\text{K}^{-1}$ , which again is a typical value for solids (Kuchling 1985), the deformation of the dendritic tip due to the change of the spherule circumference is  $\Delta L = 1 \times 10^{-10}$  m (0.1 nm). It is known that a displacement of this amplitude is sufficient to elicit a response from mechanoreceptors (French 1988, 1992; Thurm 1996). These minimal deformations are at the lower threshold range where an insect mechanoreceptor can work. Therefore, we speculate about the possibility that the thermal extension coefficient  $\alpha$  of the sphere is increased to a maximum by the design and composition of the endocuticular components. One reason for the missing sclerotization of the cuticle at the bottom of the pit (Evans 1966b) may be that softer material generally has a higher value of  $\alpha$ ; thus, the proposed mechanism is realistic and should work. It is worth noting that the suggested mechanism of transferring IR radiation to mechanical action is routinely used by photoacoustic spectroscopy (Bicanic 1992). In this ultrasensitive measuring technique a strong IR beam is used to thermally excite minimal amounts of absorbing matter (e.g. in gas phase) which in turn displaces the membrane of a loudspeaker. Obviously nature has reversed the principle, i.e. an optimized absorbing detector array equipped with highly sensitive mechanoreceptors is used to detect very weak IR radiation.

The finding of Evans that the IR pit organs show a maximum of sensitivity between wavelengths of 2.5  $\mu\text{m}$  and 4  $\mu\text{m}$  are consistent with our electrophysiological results. When we inserted the 1.65- $\mu\text{m}$  longpass filter, total radiation power was reduced by 38%. This considerable reduction in stimulus intensity only slightly altered the number of spikes, latencies and interspike time intervals in our recordings (Fig. 7A,B). When we replaced the 1.65- $\mu\text{m}$  filter by the 2.4- $\mu\text{m}$  longpass filter, the total radiation power declined by 43%. The reduction in comparison to the 1.65- $\mu\text{m}$  filter was only 2  $\text{mW cm}^{-2}$  (i.e. 8.7%). This further moderate reduction of total radiation power had the same or even a somewhat greater effect on the response (latency, number of spikes, and interspike time intervals) than the initial re-

duction of power (cf. Fig. 7B with Fig. 7C). This again demonstrates that the IR receptors of *Melanophila* are not sensitive to the visible range of the spectrum. The IR region between 2  $\mu\text{m}$  and 6  $\mu\text{m}$ , i.e. a region where Evans got reactions in his behavioural experiments, coincides with the specific spectral absorption bands of the sphere. Therefore, the spectral sensitivity of the IR-detecting system of *Melanophila* is apparently determined by the material of the sphere.

A tethered flying *Melanophila* lifts its mesothoracic legs and thus completely exposes its pit organs (Fig. 1A). In contrast, in a walking beetle the pit organs are covered by the coxae of the middle legs (Evans and Kuster 1980). Consequently, a walking beetle is unlikely to use the pit organs for the detection of IR radiation. The field of view of a pit organ extends mainly in a lateral and ventral direction (Evans and Kuster 1980) and hence a point source above the horizon, in front of or behind the insect could not be detected. If the beetle wants to detect a forest fire it has to carry out a few short circular search flights – ideally above tree-top level – each day and once a fire is detected the pit organ most likely guides the beetle tropotactically to the fire. To our surprise the pit organs of *Melanophila* responded only to stimulus onset. Therefore, the question arises: how can a phasic receptor be used to track a stationary IR source? We suggest the following explanation: whenever the beetle turns right or left the ipsilateral pit organ (with respect to the IR source) will be exposed to the stimulus and thus will respond with a brief train of action potentials. Assuming that these spikes influence flight motor neurons such that the beetle turns back in the direction of the IR source, this mechanism could lead the animal to the forest fire. If so, *Melanophila* approaches an IR source like a pilot approaches a runway: any deviation from the optimal landing course causes a signal (beep) in the headphones which is used by the pilot to correct the flight pass.

Why are there so many IR sensilla within each pit organ? As already mentioned one reason may be to increase the sensitivity of the system. Another possibility could be that the beetle gets a rough IR image of a heat source as already suggested by Evans and Kuster (1980). Because the IR sensilla respond in a strictly phasic manner to the onset of IR radiation, a permanent imaging of a fire seems unlikely, but perhaps the beetle can localize the relative position of a heat source with respect to its body with a single pit organ. When the source is in front of the flying beetle and it slightly swings off from the right course, the posterior sensilla will be first exposed to IR and become excited. This immediately induces a slight steering manoeuvre back to the correct destination, perhaps until the posterior sensilla of the contralateral IR pit organ become excited; therefore, the beetle has to take care immediately that no other sensilla of the pits become exposed to the heat source. On the other hand, when IR radiation strikes the beetle at an acute angle from behind, the anterior sensilla will be excited at first. In this case the beetle has to



enlarge the angle to the IR source (i.e. to bank) so that all the other sensilla of the pit will also become excited until the beetle is headed in the direction of the heat source. If this argument is true, a pit organ could do more than just signal whether there is a heat source within its field of view or not.

### Adaptation

The pit organs of *Melanophila* showed rapid adaptation (Figs. 4–8). This may result from filtering of the stimulus during its presumed (mechanical) transmission to the dendritic tip, from intrinsic properties of the dendritic membrane at the transduction site, or from both (e.g. Hamon and Guillet 1996). Adaptation may also occur during the encoding of the receptor current into action potentials. It is unlikely that the properties of the dendritic membrane and the spike generator, respectively, contribute much to the observed phasic response of the IR sensilla, however, since the firing of the sensilla caused by a constant mechanical stimulus (i.e. the pressure applied by the tip of the electrode) showed no obvious adaptation (Fig. 3A,C). Thus, the phasic response of the pit organ of *Melanophila* is most likely due to the thermal and/or mechanical properties of the stimulus transduction device.

Why are the IR receptors of *Melanophila* phasic and why do they follow stimulation frequencies up to 100 Hz? A beetle in tethered flight has a wing beat frequency of about 100 Hz (unpublished observation) suggesting that the beetle chops the IR radiation with its wings. We tried to stimulate the IR sensilla by introducing and removing an isolated wing of *Melanophila* just in front of the pit organ when the organ was exposed to IR; however, we did not get responses. Therefore, it remains unclear why the IR receptor of *Melanophila* is strongly phasic.

### Range of the IR receptor of *Melanophila*

The total radiation power output ( $\text{W m}^{-2}$ ) of a surface is given by the Stefan-Boltzmann law:  $W = \sigma \times \epsilon \times T^4$ , where  $T$  is the temperature of the surface in Kelvin,  $\epsilon$  is the emissivity of the radiating surface and  $\delta$  is the Boltzmann constant ( $\delta = 5.673 \times 10^{-8} \text{ W m}^{-2} \times \text{K}^{-4}$ ). Assuming a forest fire of 10 hectare (about  $320 \text{ m} \times 320 \text{ m}$ ) burning with a temperature of about  $700^\circ\text{C}$  and an emissivity close to 1 (i.e. close to a black body), the emitted total radiation power is  $5 \times 10^9 \text{ W}$ . The radiation is distributed into a hemisphere of  $2\pi r^2$  (where  $r$  is also the distance between the fire and the beetle) and the fire intensity decreases with the square of the distance to the fire. At a distance of 12 km, about  $500 \mu\text{W/cm}^{-2}$  would be predicted if we assume that the fire is a remote point source. The  $500 \mu\text{W cm}^{-2}$  correspond to the theoretical threshold value reported above. As mentioned in the Introduction there are reports in the literature which suggest that the beetles must be able to detect a fire from much greater distances. If so, the

threshold of the IR sensilla must be lower than the  $60 \mu\text{W cm}^{-2}$  reported by Evans (1966a).

### Infrared reception in animals

The only well-known IR receptors in the animal kingdom are those of crotalid and boid snakes. It is striking that the IR receptors of snakes have much in common with those of *Melanophila* beetles, but there are also marked differences. The most sensitive IR receptors among snakes are the pit organs of pit vipers (Crotalidae; Hartline 1974; Loftus 1978; de Cock Buning 1983). The IR-absorbing structures – in the case of the pit organs a thin membrane of  $15 \mu\text{m}$  thickness (Bullock and Fox 1957; Bleichmar and de Robertis 1962; Amemiya et al. 1995) and in the case of *Melanophila* a small sphere of the same diameter – can be expected to have an extremely low heat capacity thereby improving the sensitivity (de Cock Buning 1983). Consequently, the increase in temperature necessary to evoke a neural response is similar in both sensory systems. A temperature increase of  $0.003 \text{ K}$  is sufficient to evoke a generator potential in rattlesnakes if it is a rapid increase (Terashima et al. 1968), and in this study we came to the conclusion that in *Melanophila* less than  $0.01 \text{ K}$  must be sufficient to generate at least one action potential. Threshold energies necessary to induce these increases in temperature are  $10\text{--}100 \mu\text{W cm}^{-2}$  in snakes (Terashima et al. 1968; Loftus 1978; de Cock Buning 1983) and  $60\text{--}500 \mu\text{W cm}^{-2}$  in *Melanophila* (Evans 1966b; calculation in the present paper).

In general the response characteristics of the two IR receptors are also similar. The onset of an IR stimulus causes a transient burst of spikes. Impulse frequencies in snakes are about  $100\text{--}200$  impulses per second (ips) after stimulus onset (de Cock Buning et al. 1981; de Cock Buning 1983). The corresponding value for *Melanophila* is 250 ips, which has been measured within the first  $10\text{--}20 \text{ ms}$  following stimulus onset. When an IR stimulus of an adequate intensity persists (i.e. not causing a high-intensity depression in snakes, Bullock and Diecke 1956), a difference between the vertebrate and the invertebrate IR receptor system becomes obvious: whereas in snakes the initial high spike frequency gradually decreases to a lower rate during the following seconds (de Cock Buning et al. 1981), the response of the *Melanophila* receptor consisted of maximally seven spikes and after about  $40 \text{ ms}$  no further activity could be monitored. The receptors of snakes can thus be characterized as phasic-tonic, and those of *Melanophila* as strictly phasic. In *Melanophila* latencies are shorter and the peak of discharge rate is somewhat higher. In snakes an irregular static background discharge of about  $10\text{--}30$  ips can be observed (Bullock and Diecke 1956; Bullock and Barrett 1968).

The striking difference between these IR receptors is the fact that the absorbing structures in crotalid snakes are innervated by heat receptors (Bullock and Cowles

1952; Bullock and Diecke 1956; Goris and Nomoto 1967; Hensel 1974), whereas in *Melanophila* the spheres are innervated by a sensory cell displaying all fundamental morphological features typical for an insect mechanoreceptor. In snakes it has been ruled out by several authors that the thermosensitive endings of the trigeminal nerves innervating the membrane of snakes do also act as mechanoreceptors (Bullock and Diecke 1956; Hensel 1975; de Cock Buning 1981). Interestingly in *Python reticulatus*, which is considered to be a rather primitive snake, there are also bimodal receptors which respond to temperature rise and touch in the range between 0.1 g and 1 g (de Cock Buning et al. 1981). In pit vipers Bullock and Diecke (1956) found that mechanical deformation of the pit membrane was an effective stimulus. Recently, it was found that in the trigeminal ganglia of crotaline snakes bimodal thermo- and mechanosensitive neurons exist (Liang et al. 1995). These neurons have a threshold for mechanical stimuli at less than 10 mg. Because there are no structural differences between mechano- and thermoreceptors in the skin of vertebrates, some authors believe that the infrared receptors in snakes have evolved from mechanoreceptors as we suggest for the IR receptors of *Melanophila* (Vondran et al. 1995; Schmitz and Bleckmann 1997). The finding that *Melanophila* uses highly sensitive mechanoreceptors leads to the question of whether the IR receptors of snakes may accomplish transduction on the basis of a photomechanic principle – partially or additionally to pure thermoreception – with mechanoreceptors measuring the extension of the membranes after IR radiation has been absorbed.

We do not believe that the IR sensilla of *Melanophila* are the only IR receptors in insects. There are some reports in the literature which strongly suggest that some bloodsucking bugs use IR receptors to detect warm-blooded prey (Lazzari and Nunez 1989; H. Schmitz et al., unpublished results).

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