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Afferent projections of infrared-sensitive sensilla in the beetle *Melanophila acuminata* (Coleoptera: Buprestidae)

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Abstract Beetles of the genus *Melanophila* are able to detect infrared radiation by using specialized sensilla in their metathoracic pit organs. We describe the afferent projections of the infrared-sensitive neurons in the central nervous system. The axons primarily terminate in the central neuropil of the fused second thoracic ganglia where they establish putative contacts with ascending interneurons. Only a few collaterals appear to be involved in local (uniganglionic) circuits. About half of the neurons send their axons further anterior to the prothoracic ganglion. A subset of these ascend to the subesophageal ganglion, and about 10% project to the brain. Anatomical similarities suggest that the infrared-sensitive neurons are derived from neurons supplying mechanosensory sensilla. The arborization pattern of the infrared afferents suggests that infrared information is processed and integrated upstream from the thoracic ganglia.

Key words Mechanoreceptor · Neuroanatomy · Thoracic ganglia · Brain · *Melanophila acuminata* (Insecta)

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Introduction

Unlike humans, some animals are able to detect infrared (IR) radiation. To locate their prospective prey, rattlesnakes, boid snakes, and some blood-sucking bugs make use of the long-wavelength radiation that warm-blooded animals emit (Bullock and Cowles 1952; Bullock and Barrett 1968; Lazarri and Nunez 1989). Among the insects, beetles of the genus *Melanophila* are the best-studied taxon with respect to IR radiation detection.

These beetles are peculiar in that they approach forest fires in order to deposit their eggs under the bark of freshly burnt trees immediately after the flames recede. *Melanophila* is well equipped to locate forest fires as they can detect IR radiation emitted by large fires over distances of up to 50 km (Linsley 1943). Such large forest fires have a peak emission at wavelengths between 2 and 4 µm, which are well transmitted through the atmosphere and can thus be perceived over long distances by the beetles (ecophysics reviewed by Schmitz and Bleckmann 1998). Behavioral thresholds for the detection of IR radiation by *Melanophila* have been established in laboratory experiments (Evans 1964, 1966a), and the IR receptors have been investigated in detail both morphologically (Evans 1964, 1966b; Schmitz and Bleckmann 1997; Vondran et al. 1995) and physiologically (Schmitz et al. 1997; Schmitz and Bleckmann 1998).

For physical reasons (high absorbtion by tissue and water, small energy content of the radiation), animals cannot make use of the "optic" qualities of the radiation. Whereas visible light up to a wavelength of about 800 nm directly evokes photochemical responses in all known photoreceptors, IR receptors use the thermal energy content of the radiation and hence function like thermoreceptors. The IR receptors of snakes are true thermoreceptors (Harris and Gamow 1971), whereas the IR receptors of *Melanophila* are modified mechanoreceptors (Vondran et al. 1995). In the beetle, 50–100 dome-shaped IR receptors reside in a pit organ located in the thorax wall close to the coxa of the middle legs. Each sensillum comprises a cuticular sphere that absorbs the

thermal energy of the IR radiation, heats up, and thus expands slightly. This expansion leads to a minute deformation of the tip of the dendrite of the sensory cell and thus adequately excites the cell according to a photomechanic mechanism (Schmitz and Bleckmann 1997, 1998). The sensory cells show phasic responses when stimulated with flashes of IR radiation and are able to follow stimulus frequencies up to at least 100 Hz (Schmitz and Bleckmann 1998).

Although the structure and function of the IR receptors has been well elucidated in recent studies, nothing is known about the processing of IR information in the nervous system of the beetle. As a first step toward understanding IR information processing, we describe the anatomy of the IR sensory pathway in the central nervous system and suggest how the flow of IR information may be organized in the nervous system of *Melanophila*.

Materials and methods

Burned wood containing the larvae of *Melanophila acuminata* was collected from forest fires in Brandenburg (Germany) and was stored at 20–25°C. Beetles eclosing from the wood were fed on raisins and peanuts and could be kept alive for up to 3 months (Schmitz and Bleckmann 1998). The external morphology of the IR sensilla and mechanosensitive hairs in their vicinity was examined by using scanning-electron microscopy (Zeiss DSM 962) of critical-point-dried specimens.

To visualize the sensory axons and their terminals in the central nervous system, beetles were first immobilized ventral side up and their middle legs fastened by using warm resin so as to obtain access to the IR pit organs at the mesothoracic coxae (Fig. 1a). The filamentous secretions of wax glands associated with the receptors were then removed, and some of the globular IR receptors in the pit organ were scraped off by using a broken glass capillary. Immediately afterwards, the pit was filled with a tiny droplet of fluorescent tracer (Lucifer yellow or the dextran tracer, Fluoro Ruby; Molecular Probes) dissolved in water. Alternatively, a tiny crystal of the dye was placed on the damaged sensilla and covered with a water droplet. The entire organ was then sealed with silicone (medium viscosity; Bayer) to prevent it from drying out.

To trace sensory afferents of "true" mechanosensory hairs, a rectangular part of the cuticle adjacent to the pit organ was cut on three sides and bent upward so as to expose the inner surface of the cuticle supporting the sensilla (cutting or scraping the sensilla shafts from the outside did not yield good results). The exposed region was then treated with fluorescent tracer and sealed with silicone. Likewise, a few motor neurons were stained by applying the dye to cut muscle stumps and sealing the operated site with silicone.

The animals were then left at ambient room conditions for diffusion times of 16–60 h. Afterwards, the animals were killed, and their thoraces and heads were processed according to standard routines, viz., paraformaldehyde fixation, ethanol dehydration, plastic embedding (Fluka Durcupan), horizontal or sagittal sectioning at 15–25 µm, and epifluorescence micrography (Gronenberg and Peeters 1993). Graphical reconstructions were made either from color slides (Kodak Elitechrome 400) or from monochrome videographs by means of a high-sensitivity digital storage camera (Kappa CF 8/1).

Results

The pit organ (Fig. 1a, c) comprises 50–100 dome-shaped sensilla (Fig. 1d) that can be discerned under the dissecting microscope. Under natural conditions, the organ is covered by wax filaments (Fig. 1b) secreted by multiporous ducts associated with each sensillum (Fig. 1d). By scraping the organ with a broken glass capillary, the cuticular apparatus of individual sensilla can be broken off. Light-microscopical thick sections of the dye-filled sensilla show that their outer part is not solid but contains a central spherical structure inside a cuticular hull (see arrow in Fig. 1f), as has been described in detail from ultrastructural studies (Vondran et al. 1995; Schmitz and Bleckmann 1997). In damaged sensilla, this globular structure is torn from the apical dendrite so that the dye is taken up by the dendrite. The tracer then diffuses through the cuticular canal (Fig. 1e, f) into the cell body and further along the axon.

The diameter of the axons as they originate from the IR cell somata is about 1–2 µm. These axons converge close to the pit organ to form a peripheral nerve that runs around the coxa of the middle leg where it joins other peripheral nerves supplying neighboring regions of the cuticle, dorso-ventral muscles, and leg muscles. This fused nerve (the metathoracic leg nerve) proceeds anterocentrally toward the fused second thoracic ganglion (Fig. 1e), which comprises the meso- and metathoracic neuromeres and part of the abdominal neuromeres (Figs. 1e, 2a). The nerve enters the ganglion through a posterior ventral root. The homologous mesothoracic nerve, which supplies the middle legs, also enters the fused ganglion ventrally, but more anteriorly than does the metathoracic nerve (Fig. 2a, d). Ventrally, the meso- and metathoracic neuromeres can clearly be discriminated in the fused ganglion (Fig. 2a, d). The sensory IR afferents terminate in this ventral region, whereas motor neurons (Fig. 2e, right) reside more dorsally where the meso- and metathoracic neuromeres are completely fused and indistinguishable. This dorsal part of the fused ganglion gives rise to a third pair of major nerves, the wing nerve, which is beyond the scope of the present account.

The afferents originating from the IR-sensitive pit organ have a characteristic arborization pattern (Figs. 1h, i, 2d). All axons enter the metathoracic neuromere ventrally and project as a thick diverging tract antero-centrally. In the ganglion, the axons are thin (1–1.5 µm). They traverse the neuromere at an angle of about 45° with respect to the long axis of the animal. The actual angle differs among different preparations as the axons fan out after entering the ganglion (compare left and right drawing in Fig. 2d).

The axons give rise to some blebbed collaterals (possibly presynaptic terminals) in the metathoracic neuromere. However, the majority of axons terminate directly (Fig. 2d) or feature most of their putative en-passent synapses (thick blebs along the thin axons; Fig. 1k, m). in the central area between the leg neuromeres, rather than in the neuromere proper. This central region is probably homologous to neuropil referred to as ventral association centers in the locust (Pflüger et al. 1988). Unstained thick profiles ("shadows" in the fluorescent image) reveal that this central neuropil is associated with central

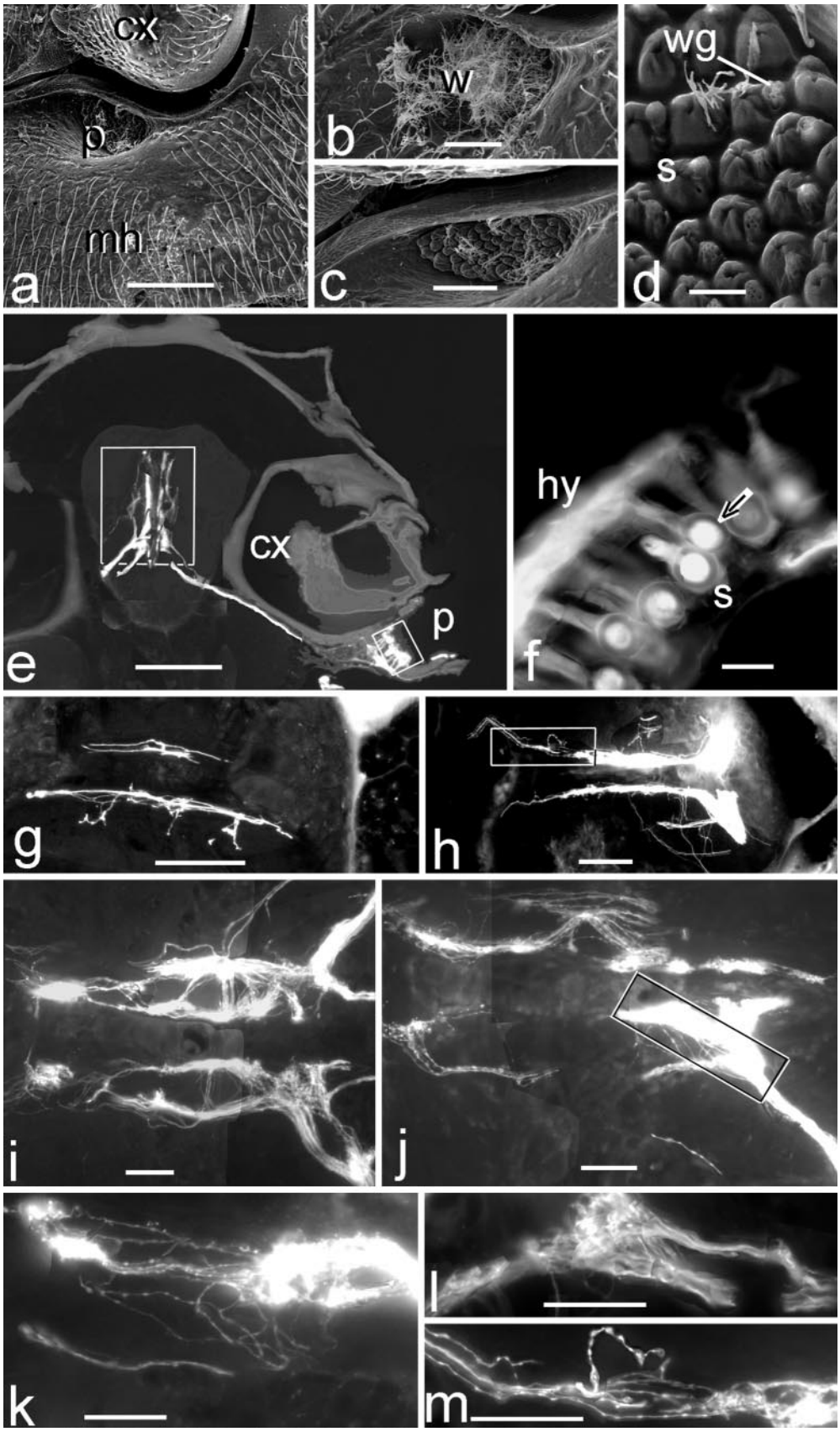

Fig. 1. Scanning electron micrographs of infrared sensilla (**a–d**) and videomicrographs (horizontal sections; **e–m**) of sensory afferents originating from the IR-sensitive pit organ and traced with Fluoro Ruby. **a** Pit organ (*p*) and "normal" mechanosensory hairs (*mh*) close to the mesothoracic coxa (*cx*). **b** Under natural conditions, the pit organ is covered by wax secretions (*w*). **c, d** Close-ups of the pit organ and its sensilla, respectively. Each sensillum (*s*) is associated with several ducts of a wax gland (*wg*). **e** Mesothorax with fused meso-metathoracic ganglion (*center*; *large box* indicates approximate position of sensory terminals shown for different preparations in **h–j**), the pit organ (*p*; *small boxed area* enlarged in **f**), and the mesothoracic coxa (*cx*). **f** Globular IR sensilla (*s*) with strongly fluorescing apical spheres (*arrow*) and hypodermis wall (*hy*) of the pit organ. **g, h–m** Central axon collaterals and terminals in the prothoracic and in the meso-metathoracic ganglion, respectively, at different magnifications; *box* in **h** enlarged in **m**, *box* in **j** indicates approximate area shown for a different preparation in **l.** *Bar* 250 µm (**a**, **e**), 100 µm (**b**, **c**, **g**, **h**), 50 µm (**i–m**), 25 µm (**d**, **f**). Anterior is *up* in **a**, **b, e** and to the *left* in **c, d, f–i.** Micrographs depict montages of several optical sections from one thick section (25 µm)

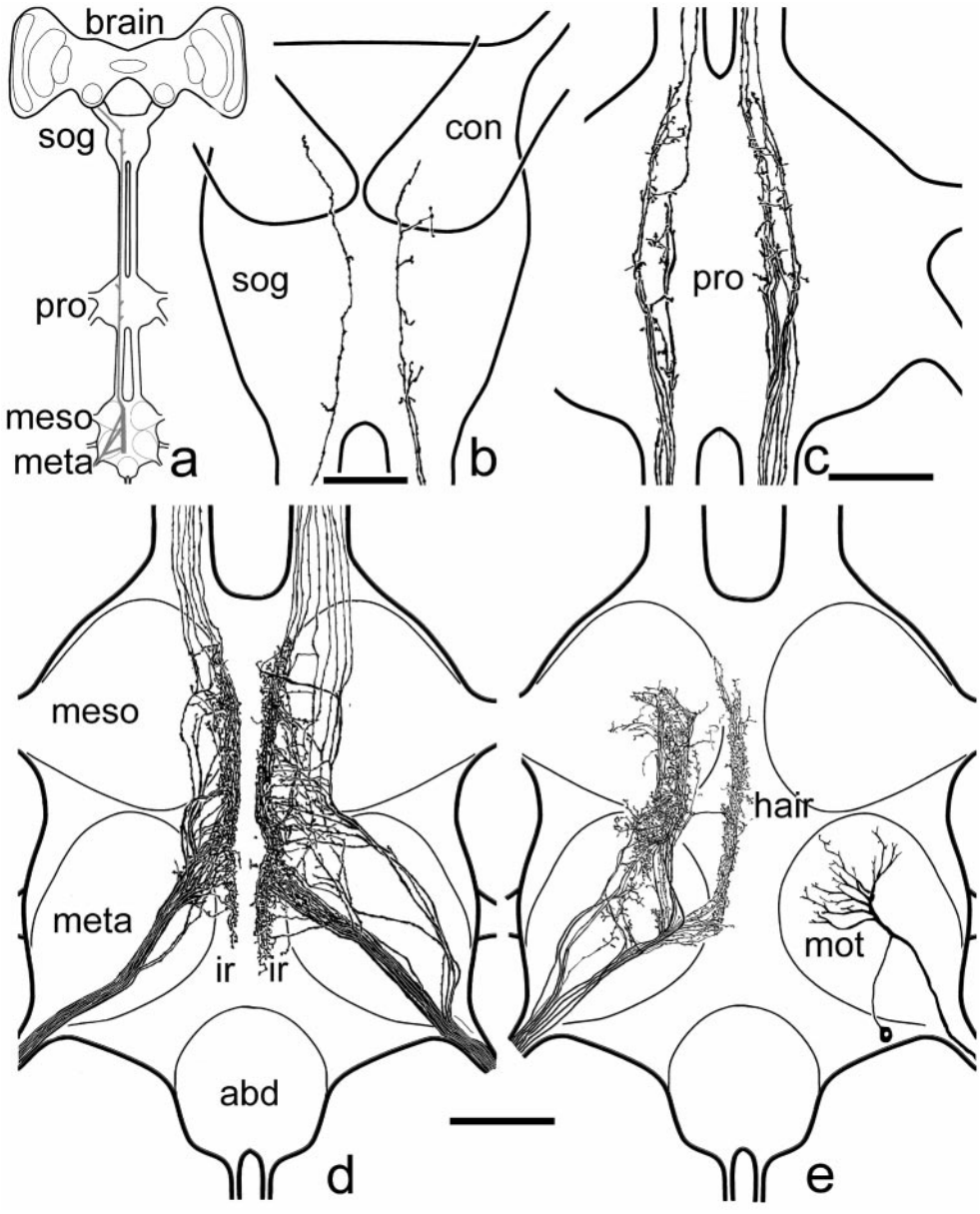

Fig. 2. a Schematized arborization pattern of IR-sensitive sensory afferents (*hatched*) in the nerve cord. **b–e** Graphical reconstruction of anterogradely labeled neurons. **b** Subesophageal ganglion (*sog*). **c** Prothoracic ganglion (*pro*). **d** Fused second thoracic ganglion comprising mesothoracic (*meso*) and metathoracic (*meta*) neuromeres and the nerve roots through which the IR-sensitive axons (*ir*) enter the nerve cord. **e** For comparison, afferents of hair sensilla (*hair*) homologous to and originating in the vicinity of the IR sense organ are shown, together with a leg motor neuron (*mot*) supplying a coxal muscle. (*abd* Abdominal neuromere, *con* esophageal connective). *Bar* 100 µm

tracts that ascend to and descend from the brain and anterior ganglia, indicating that the majority of IR-sensitive neurons interact with fibers of passage rather than with local pathways.

In Fig. 1i, it appears that the sensory axons occupy two central strata in each half ganglion; these are interconnected by fiber bundles that do not cross the midline. Depending on the actual number and position of sensilla stained in the pit organ, the two separate synaptic regions may be closer together (Fig. 2d), but the axons in the more lateral region always project anteriorly, giving rise to some short collaterals or to looping side branches (Fig. 1m). In contrast, the centralmost collaterals are much more intertwined and cannot be completely resolved from fluorescent staining (Fig. 1l), because the diameter of the finest profiles is very small (below 1 µm; note, however, that diameters of thin profiles cannot exactly be assessed from fluorescent material). In this central neuropil, the sensory axons form an almost lace-like entanglement of fine collaterals and terminals that extends almost throughout the ventrocentral ganglion in an antero-posterior direction (Fig. 2d). This region of fine arborizations is located slightly more ventrally than the more lateral collaterals that project anteriorly. Whereas the former are thought to contact central pathways exclusively, the latter probably connect to central ascending neurons and to some local neurons in the meso- and metathoracic neuromeres proper. However, no overlap has been found between IR receptor axons and leg motor neuron dendrites, which reside more dorsally in the neuromeres (Fig. 2e).

The axons straighten out toward the anterior end of the ganglion and proceed dorsally into and through the pro-mesothoracic connectives. In our preparations, about

half of all the IR sensory neurons entering the fused ganglion project through the connectives into the prothoracic ganglion (Fig. 2a, c). It is possible that this finding only reflects an artifact in that some of the neurons are filled incompletely. However, we consider that about half of the neurons are actually restricted to the fused ganglion, because this result does not depend on the diffusion time (diffusion times that are too short might cause incomplete filling). Although the actual number of neurons stained in each preparation varies (from 5–22, depending on the amount of damage inflicted to the pit organ), we have not found any axons thinning out in the connectives, which would indicate incomplete staining. Rather, the axons either stop before entering the connectives or can be traced up to the prothoracic ganglion or beyond.

The terminal arborizations of pit organ afferents are less complex in the prothoracic ganglion. Some axons terminate soon after entering the prothoracic ganglion within its posterior third. They feature only short stout side branches with pronounced swellings reminiscent of presynaptic terminals (Figs. 1g, 2c). Another group of axons runs straight through the ganglion anteriorly in central tracts and gives rise to short collaterals and en-passant connections that do not invade the prothoracic neuropil proper (as opposed to the central neuropil that comprises pluriganglionic tracts). We therefore suggest that information from IR receptors is not processed locally in the prothoracic ganglion but is fed into ascending pathways.

Only a fraction of axons entering the prothoracic ganglion proceed through the cervical connectives that connect to the subesophageal ganglion (SOG; Fig. 2a, b). In the SOG, the arborization pattern is similar to that found in the prothoracic ganglion: some of the axons terminate soon after entering the SOG (right hand side of Fig. 2b), whereas others project through the SOG centrally and give rise to a few short blebbed collaterals. We have found processes leaving the SOG through the esophageal connectives only in two out of 21 preparations. These axons could not be traced into the brain proper; they stopped in the region where the circumesophageal connectives fused with the brain. In these cases, we consider that the staining may not have been sufficient and that the axons may proceed a little further into the brain. These branches are very faint and eventually fade out completely. To summarize, the IR receptors mainly terminate in central neuropil of the ventral meso- and metathoracic ganglion where they engage in complex synaptic interactions. About half the neurons possess collaterals in the prothoracic ganglion, less than 20% reach the SOG, and probably less than 10% ascend directly to the brain.

The axons supplying mechanosensitive hairs in the vicinity of the pit organ are thought to be homologous to the IR receptors, run within the same nerve, and show an arborization pattern reminiscent of that of the latter. The mechanosensory neurons feature a similar region of fine intertwined terminal branches in the tracts of the fused thoracic ganglion (Fig. 2e); however, there are two distinct differences between the arborization pattern of mechanosensory hair afferents and IR-sensitive afferents. The more lateral region of arborization that supplies the meso- and metathoracic neuromeres proper is much more elaborate in the mechanosensory afferents than it is in the IR receptor neurons (Fig. 2e) and extends more laterally in the ganglion. Moreover, the mechanosensory hair afferents do not exhibit any axon collaterals proceeding anteriorly to the pro-mesothoracic connectives. A comparison between the afferents originating from IR sensilla and mechanosensory hairs thus suggests that the former are evolutionarily derived from the latter and that mechanosensory information is processed more locally than is IR information.

Discussion

Plurisegmental terminals in hair-like sensilla afferents

Two general classes of mechanoreceptor afferents exist in insects: their terminals are either restricted to the ipsilateral half of the corresponding ganglion or they terminate multisegmentally. Many tactile or wind-sensitive single hairs (as opposed to specialized hair fields) exclusively send their axons into the neuromere that corresponds to the respective body segment on which the sensillum resides. This has been documented for various types of sensilla on the legs of different insect species, e.g., locusts (Pflüger et al. 1981, 1988; Newland 1991), crickets (Eibl and Huber 1979; Hustert 1985), tettigoniid grasshoppers (Oldfield 1983), and the beetle *Tenebrio* (Breidbach 1990), and for afferents originating from the cerci (Murphey 1981). Most tactile or wind-sensitive hairs on the thorax also feature axonal projections that are restricted to a single neuromere (Pflüger 1980, Pflüger and Tautz 1982).

In contrast, many sensory structures related to insect wings and flight feature arborizations in more than one ganglion or neuromere. In locusts, sensory afferents originating from the wing tegula (Bräunig et al. 1983), from the wing-hinge stretch receptors (Altman and Tyrer 1977), or from the wing itself (Bräunig et al. 1983) terminate plurisegmentally, as do wing afferents in the beetle *Tenebrio* (Breidbach 1990) and in winged ants (Gronenberg and Peeters 1993). The same has been shown for the wing-homologous halteres of dipterans (Sandeman and Markl 1980; Palka and Ghysen 1982; Strausfeld and Seyan 1982; Hengstenberg 1984), some of whose afferents extend up to the brain. In addition, the afferents of some insect tympanal (hearing) organs, e.g., in parasitoid flies or in lacewings (Lakes-Harlan and Heller 1992, Robert et al. 1994, Miller 1984), and those insect mechanosensory neurons that serve proprioceptive functions (measuring changes within the body or movements, forces, accelerations, etc. between different body parts) have plurisegmental terminals. This is true for some hair plates in the locust, whose mechanosensory

neurons may arborize in two adjacent ganglia (Bräunig et al. 1983), and is generally found in chordotonal organs (Hustert 1978; Bräunig et al. 1981, 1983; Pflüger et al. 1988).

The sensory neurons that we describe in the current account correspond to the plurisegmental type found in flight-related, proprioceptive, and auditory neurons. Whereas they are not related to wings or ears, the hair-like sensilla surrounding the pit organ probably serve a proprioceptive function; they are located close to the base of the middle leg and are suited to measure the position of the femur with respect to the thorax. This might explain the complex arborization pattern of these seemingly "simple" hair-like sensilla. As the sensilla in the pit organ are probably homologous to these hair-like sensilla (Vondran et al. 1995), the afferents of the dome-shaped sensilla are likewise plurisegmental. In addition, plurisegmental terminals can be found in mechanosensory hair afferents that originate from specialized sensilla, such as wind-sensitive hairs involved in flight control (Tyrer et al. 1979) or specialized appendages involved in dominance interactions of a particular ant genus (Gronenberg and Peeters 1993). The IR-sensitive receptors of *Melanophila* are also specialized structures, even more so than wind-sensitive hairs on the wings. One might thus expect a plurisegmental arborization of IR-sensitive neurons to "match" their specialized function.

In evolutionary terms, it appears relatively simple to derive the more complex morphology of the IR-sensitive neurons from that of their putative mechanosensory ancestors. The number of axon terminals in the central neuropil of the fused thoracic ganglia has to be increased, and some of the axons have to grow further anteriorly up to the SOG or to the brain. It is much easier to imagine such a change in the arborization pattern of neurons than to comprehend the transformation of "simple" mechanosensory hairs into highly specialized, dome-shaped, IR-receptive sensilla (Vondran et al. 1995; Schmitz and Bleckmann 1997). To understand the latter transformation, one would ideally like to find intermediate stages, such as sensilla in beetles that have the ability to detect IR light but are not as specialized and dependent on this ability as are *Melanophila*. We assume that such "missing links" may exist, but so far nobody has looked for them. Indeed, if one does not expect such a sensory capacity, one would hardly notice it, since we do not perceive IR light ourselves. However, the pit organ of *Melanophila* actually comprises evidence for the transformation of hair-like sensilla into IR-sensitive structures: Schmitz and Bleckmann (1997) describe aberrant (probably non-functional) sensilla at the rim of the pit and other transitional forms that still bear setae (hair shafts), indicating that the IR-receptive sensilla may indeed be derived from hair-like sensilla. It would also be worthwhile to look at the development of these sensilla in pupae, as one would expect dome-shaped and hair-like sensilla at the leg base to share initial developmental steps.

The IR pathway

The functional aspect is important for understanding the evolution from standard mechanosensory axons to the more elaborate plurisegmental IR-sensitive axons. The mechanosensory hairs are probably involved in local reflexes (control of leg position) that rely on circuits within the same ganglion or, as is the case in the sensilla studied here, in the neighboring neuromere (upon movement, the femur of the middle legs may slide across and stimulate the hairs of the metathorax). This is reflected by a large number of sensory terminals in the meso- and metathoracic neuropil proper. In contrast, IR information is not involved in local (leg) reflexes, because it is of relevance only during flight, not during walking. This explains why IR afferents make most of their putative connections in the central neuropil, which is linked to the anterior ganglia and to the brain, and why part of the collaterals extend much further than those of the homologous hair afferents. Only a few other insect mechanosensory afferents feature comparable arborizations extending from the metathoracic ganglion up to the brain, viz., some haltere afferents in Diptera (Strausfeld and Seyan 1982; Hengstenberg 1984). Like the termination in central (as opposed to peripheral) thoracic neuropil, this indicates that IR information requires complex processing that involves input from various body regions.

Even though this information is ultimately used to guide the flight of the insect toward forest fires, its anatomy suggests that this flight control is not direct. Rather, we think that IR information is processed by the anterior ganglia, and the brain in particular, before changes in flight course are initiated. In the brain and/or SOG, IR information probably converges together with visual, olfactory, and various kinds of mechanosensory information onto descending neurons that connect to the flight motor.

The same central tracts in the thoracic ganglia in which the IR afferents terminate and which contain ascending neurons probably also carry descending neurons. It is thus possible that IR information might modulate descending signals, even in the thoracic ganglia. The descending neurons that control the flight motor are known to reside mainly in dorsal regions of the thoracic ganglia in other insects (Hensler and Rowell 1990; Strausfeld and Gronenberg 1990). Assuming that the same is true for beetles, the ventral IR-sensitive axon terminals are not likely to modulate flight performance directly. As IR information is only relevant during flight behavior, we assume that the IR afferents indeed contact ascending neurons in the ventral thoracic neuropil and not descending neurons, and that the final integration is carried out in the SOG and the brain, rather than in the meso-metathoracic ganglion. However, in the absence of physiological data and a comprehensive anatomical description of the central nervous system of the beetle, the actual connectivity of IR-sensitive afferents remains speculative.

Although stimuli such as (bat) ultrasound, wind, air turbulence, looming objects, etc. require that the flight parameters are altered very rapidly (hence directly in terms of neuronal processing), this is not the case in IR detection. Whether a heat source is miles or just meters away from the beetle, a couple of wing strokes (millseconds or even seconds) do not make a great difference to the overall performance of the beetle. Accordingly, the neurons do not need to be fast (hence thick and energetically expensive) as is required for an escape or collision-avoidance system. For this reason, the IR detection circuit is composed of very thin neurons. Whereas such a system cannot be fast, temporal resolution is not compromised: the receptors respond to stimuli as short as 2 ms and can resolve stimulus repetitions up to 50–100 Hz (Schmitz and Bleckmann 1998); the significance of this capacity is not yet fully understood. The sampling period is short (30–40 ms) because the IR receptors are strictly phasic, and stimulus amplitude is probably coded as interspike latency by each single neuron.

The small diameter of the IR afferents allows the animal to be equipped with many parallel channels, thus probably increasing the spatial resolution, without investing much metabolic energy in the construction and maintenance of the neuronal evaluation circuitry. Rather than building a fast dedicated pathway or labeled line system, IR information seems to be channelled into the "normal" ascending-descending pathways. Descending neurons are well equipped for the integration of different stimulus modalities and for the control of flight manoeuvres (Rowell 1989; Hensler and Rowell 1990; Strausfeld and Gronenberg 1990; Kanzaki et al. 1994).

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