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Dynamics of arthropod filiform hairs. V. The response of spider trichobothria to natural stimuli

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Trichobothria are cuticular filiform hairs of arachnids, which respond to air movements. In the wandering spider, *Cupiennius salei*, about 900 trichobothria form characteristic groups on the pedipalps and legs and are used to detect and localize flying insect prey. We analyse the response of the receptor cells of metatarsal trichobothria of different lengths (200–800 μm) to both natural and synthetic stimuli to understand what the single receptor can contribute to the detection of natural signals. (i) The receptor cells are not spontaneously active. Their response to hair deflection is strictly phasic. The airflow produced by a tethered flying fly (*Calliphora* sp.) elicits a physiological response up to a distance of 55 cm. The response strength, however, strongly depends on the orientation and position of the fly. The receptor cells encode a wide range of airflow velocities (1 mm s^{-1} to 1 m s^{-1}). The time-course and frequency content of the strongly fluctuating air movements characterizing a fly signal are well represented in the spiking pattern of the receptor cells. There is almost no adaptation to a broad-band noise stimulus but strong adaptation to monofrequency stimulation. The presence of a platform below the spider (corresponding to its dwelling plant) strongly enhances the response of the trichobothrium due to its 'amplifying' effect on flow velocity. Without the platform, the sensory space of the trichobothrium decreases from 55 cm to 15 cm. (ii) With the hair directly coupled to the stimulating device, threshold curves do not depend on hair length (200–800 μm). Physiologically and irrespective of their length, the trichobothria are all broadly tuned to a frequency range between about 50 and 100 Hz where threshold deflection angles are *ca.* 0.1° and sometimes as small as 0.01°. This contrasts the length dependence of the mechanical frequency tuning of trichobothria. Above threshold the bandpass characteristics of the cell reponse is much more pronounced than at threshold. (iii) Due to their low thresholds, their tuning and the highly phasic character of their response, the receptor cells of the trichobothria are well suited to detect and encode air particle movements produced by flying prey. Low-frequency background air movements (wind) are filtered by both the mechanical and the physiological properties of the trichobothria.

Keywords: air movement detection; spider trichobothria; sensory ecology; *Cupiennius salei*; mechanoreception; prey capture

1. INTRODUCTION

Adults of the tropical wandering spider, *Cupiennius salei*, have 936 trichobothria (±31 s.d.) on their walking legs and pedipalps. This is the largest number of filiform air movement detectors known of any spider. The trichobothria are arranged in groups of 2–30 hairs which increase in length towards the leg tip (Barth *et al.* 1993). Previous behavioural experiments showed that *Cupiennius* uses its trichobothria for the detection and localization of flying prey which it catches rather spectacularly with a precise jump into the air despite being blinded (Barth *et al.* 1995). The mechanical properties of the trichobothria of *Cupiennius salei* and the fluid mechanics of the hair–air interaction were described in detail (Barth *et al.* 1993; Humphrey *et al.* 1993, 1997) and found to be well adapted to receive medium vibration generated in the nearfield of flying insects. Hairs of different length (100–1400 μm) are mechanically tuned to different best frequencies, ranging from 40–600 Hz. Different hairs also differ in mechanical directionality.

The filter properties of such receptors, however, are only partly determined by the mechanical characteristics of the cuticular hair and its coupling to the medium. They are also determined by the stimulus transduction at the dendrite and the physiological characteristics of the sensory cell which encodes the stimulus into nervous activity.

The present study was undertaken to learn about the contribution of the receptors to *Cupiennius*'s remarkable capability to catch flying insects by using the information contained in air movement stimuli. We describe the response of single trichobothria receptor cells to both natural and synthetic stimuli and show that trichobothria are well adapted not only mechanically, but also physiologically, to respond to and localize a flying-prey signal and distinguish it from background noise such as wind.

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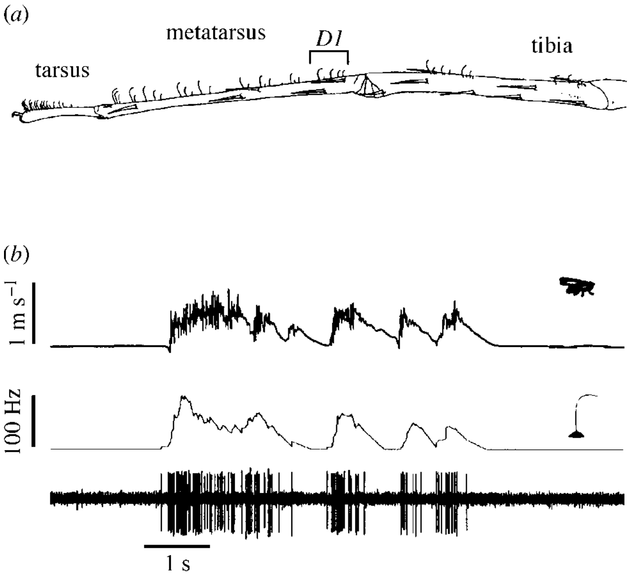

Figure 1. (*a*) Lateral view of a walking leg of an adult female of *Cupiennius salei* with its trichobothria (after Barth *et al*. 1993). Electrophysiological experiments were done with the hairs of the metatarsal group D1. (*b*) Response of a 500-μm long trichobothrium to the airflow produced by a tethered flying fly at a distance of 5 cm above the substrate and with its abdomen pointing towards the trichobothrium. Upper trace, velocity of the airflow recorded by hot wire anemometer; middle trace, mean spike rate (running average; window size 200 ms); lower trace, original recording of action potentials.

2. MATERIAL AND METHODS

(a) *Animal and preparation*

The electrophysiological experiments were performed on adult females of the Central American hunting spider, *Cupiennius salei* Keys., (Ctenidae; Lachmuth *et al.* 1981), from our laboratory stock in Vienna. The animals were kept in glass jars individually and fed once a week with flies and cockroaches. The temperature (22–28 °C) and humidity (80–95%) regime resembled natural conditions (Barth *et al.* 1988).

Recordings were made from the trichobothria of the group Dl on the dorsal side of the walking leg metatarsus close to the tibia–metatarsus joint (figure 1*a*). Group Dl consists of five hairs 250–750 μm long and all with preferred deflectability in a direction parallel to the long axis of the leg (Barth *et al.* 1993).

Before the experiment, the spiders were kept in the refrigerator at +4 °C for approximately 50 min, CO_2-anaesthetized and then fastened on to the preparation holder using a mixture of beeswax and colophony. All sensory hairs except the examined trichobothrium on the respective leg were removed with a razor blade.

(b) *Recording and stimulation*

Extracellular signals were recorded using electrolytically tapered tungsten electrodes. The recording electrode was inserted perpendicularly into the cuticle, approximately in the middle of the tibia. The main advantage of this particular site on the tibia was that it permitted the recording electrode to be kept far enough away from the metatarsal D1-trichobothria to allow proper stimulation. A grounded reference electrode was placed into the opisthosoma. Recording techniques were conventional.

A trichobothrium is innervated by four sensory cells in *Cupiennius* (Anton 1991) as in other spiders (Christian 1971). However, only one type of action potential was recorded at a time. Its origin was attributed to one of the four cells, following an analysis of action potential shape and considering the consistency of the response patterns. According to the available knowledge (Reißland & Görner 1985) it is typical of trichobothria (and indeed other arachnid hair sensilla) that responses can be recorded extracellularly from fewer cells differing in directional sensitivity (Görner 1965) than shown to be present histologically. It was not the goal of the present paper to study this problem, which can only be resolved properly by intracellular recording.

The natural stimulus used to deflect trichobothria was the air movement produced by a tethered stationary flying fly (*Calliphora* sp.). A small piece of paper glued dorsally on to the fly's thorax was used to attach the fly to a special fly holder, which allowed the exact adjustment of the position of the fly relative to the spider. To imitate the effect of a solid substrate, such as the dwelling plant of *Cupiennius*, the examined spider leg was mounted on a piece of cardboard (60 × 15.5 cm). The airflow produced by the stationary flying fly and stimulating a trichobothrium was recorded 35 mm behind the examined trichobothrium with a hot wire anemometer that had been calibrated with a laser-anemometer (velocimeter; POLYTEC LDV 380).

Synthetic sine wave stimuli generated by a function generator (Toellner TOE 7708) were applied with an electrodynamic vibrator (LING Mod. V 100) whose frequency response was linearized by means of an electronic feedback system. The vibrator was calibrated using a laser-Doppler vibrometer (POLYTEC OFV 2100 & 300). For ramp stimulation a motor driven micromanipulator was used. For sine wave stimulation the hair shaft was usually coupled with a tiny droplet of glue to the tip of a needle which in turn was fastened to the vibrator stylus. Due to the larger deflection amplitudes used, we did not couple the hair directly to the vibrator to avoid tension on the hair base when applying ramp stimuli. In this case coupling by electrostatic forces sufficed.

By rotating the vibrator around the spider on a turntable, the trichobothrium in its centre could be precisely deflected into the desired direction (parallel to the leg's dorsal surface). The threshold for impulse initiation was defined as the minimum stimulus strength necessary to elicit at least one impulse reproducibly. Thresholds were easy to determine because of the absence of spontaneous action potentials. Unwanted background air movement was not a problem; the experiments were carried out in a closed room. Except for threshold measurements the receptor cell responses were digitized (sampling rate 12.5 kHz) together with the respective stimulus and fed into a computer for further evaluation.

Throughout the text N refers to the number of preparations and n to the number of experiments.

3. RESULTS

(a) *Response to a natural stimulus*

The air particle movement produced by a tethered flying fly is a highly turbulent flow mainly directed obliquely downwards and backwards (see below). It was used as a quasi-natural stimulus to stimulate the trichobothrium.

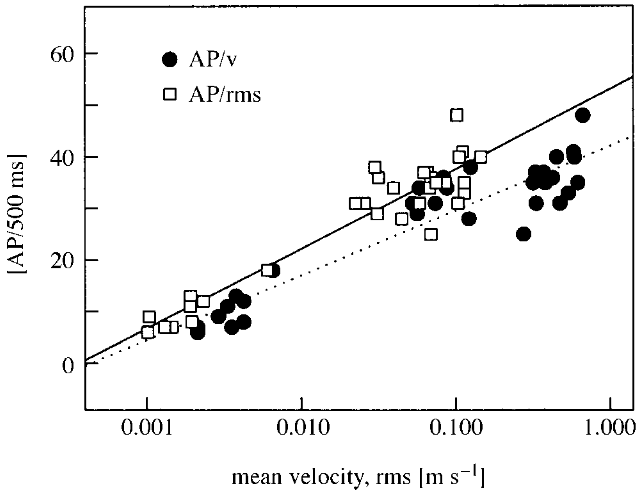

Figure 2. Representation of mean flow velocity (filled circles) and degree of fluctuation (rms) (open squares) of a fly signal by the AP rate of the receptor cells (for details refer to text). The lines are the first order regressions for the relations between action potential rate and the logarithm of flow velocity and its degree of fluctuation (rms). The steeper slope of the solid line suggests that the trichobothrium (length, $l=500\ \mu\text{m}$) is more sensitive to the degree of turbulence than to the mean velocity of a flow field. $N=1$, $n=31$.

The sensory cells are not spontaneously active; they generate spikes only in response to the deflection of the hair shaft.

Figure 1*b* shows a *typical response* of a trichobothrial sensory cell to the instantaneous airflow velocity representing the fly signal at the site of the trichobothrium and 5 cm away from the fly. After an initial phasic peak of the response, the time-course of the fly signal is well represented in the spiking pattern of the receptor cells. Both the mean velocity and the degree of turbulence (rms) of the flow field are represented logarithmically by the trichobothrium over a range from 1 mm s^{-1} to 1 m s^{-1} (figure 2). The steeper slope of the line representing the correlation between action potential rate and the logarithm of the rms (figure 2) suggests that the receptor is more sensitive to the degree of turbulence than to the mean flow velocity of the fly signal. This effect increases with increasing distance of the fly from the spider due to an increasing breakdown of the continuous nature of the air currents generated by the fly.

(i) *Sensory space*

How far away can a fly be detected by a single trichobothrium? To quantify the sensory space of a trichobothrium with respect to the air movement produced by a flying fly, we varied the position of the fly relative to the spider by changing the following parameters (figure 3*a*): absolute distance (x'), horizontal distance (x) and vertical distance (z) between the fly's prosoma and the trichobothrium, and the lateral distance (y) between the long axis of the spider leg and the long axis of the fly. The angle of the fly's position relative to the trichobothrium was defined as the angle (α). The long axis of the fly was always kept parallel to the long axis of the spider's leg and horizontal.

The presence of a *solid substrate* at the level of the spider leg (instead of the leg protruding freely into space), which entails an increase in flow velocity (Barth *et al.* 1995) dramatically increases the response of the trichobothria to the prey signal. With the plate present, a fly pointing away from the spider still elicits a physiological response of the examined trichobothrium at a distance of 55 cm. Without the spider platform this distance decreases to 15 cm (figure 3*b*). In contrast to a web spider, the presence of a solid substrate is typical for a hunting spider such as *Cupiennius salei*. All following experiments were therefore carried out with the platform present.

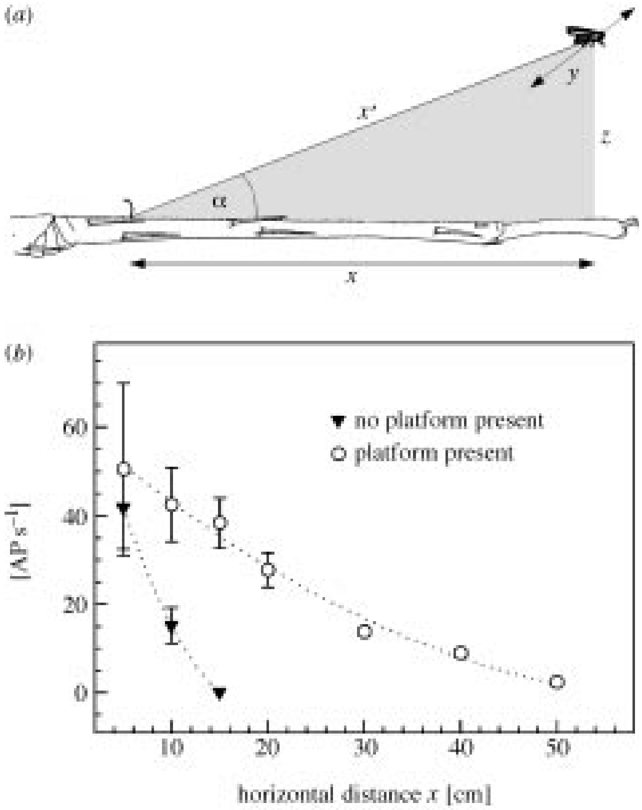

Figure 3. (*a*) Distance and position parameters varied in the experiments on the active space of a trichobothrium with respect to a tethered flying fly. (*b*) Influence of a solid substrate beneath the spider on the size of the active space of a trichobothrium ($l=500\ \mu\text{m}$). At a vertical distance z of 5 cm the horizontal distance x was varied between 5 cm and 50 cm. The presence of the plate beneath the spider leg strongly enhances the response of the trichobothrium. AP, action potentials; $N=2$, $n=9$; filled triangles, no platform present; open circles, platform present.

(ii) *Position of fly*

The main air movement signal produced by a fly is highly directional and contained in a cone-like region directed downwards from the fly at an angle of about 25–45° (Barth *et al.* 1995). Therefore, besides the absolute distance between the fly and the trichobothrium, the position of the trichobothrium relative to this cone of directed airflow determines the strength of the response.

Figure 4*a* shows the results of an experiment where the *horizontal distance* (x) was varied between 5 cm and 50 cm at two vertical distances (z). At a vertical distance of 2 cm the response is strongest at the nearest horizontal distance (5 cm). At a vertical distance of 9 cm, however, the response is strongest at a horizontal distance of 10 cm.

These results can be understood by considering the shape and position of the flow field generated by the fly (figure 4*a*). As the fly moves from position A ($x=5$ cm, $z=9$ cm) to position B ($x=10$ cm, $z=9$ cm), the trichobothrium becomes further embedded in the 'flow cone'. In figure 4*b* the angle α was kept constant and the *absolute distance of the fly* (x') varied between 5 and 35 cm. In this case, the trichobothrium stayed within the flow cone at all distances. The spiking rate decreased gradually with increasing distance following the decrease of average air particle velocity which measured $0.56\,\mathrm{m\,s^{-1}} \pm 0.08$ s.d., at $x' = 5$ cm, but only $0.08\,\mathrm{m\,s^{-1}} \pm 0.14$ s.d., at $x'=30$ cm ($N=2$, $n=8$). It should be noted here that in addition to the average air particle velocity, the spectrum of frequencies contained in the fly signal changes dramatically with distance. As seen by the example presented in figure 5, high-frequency components are disappearing rapidly. At a distance of 25 cm there are practically no frequencies above 50 Hz any more. By increasing the distance (y) between the long axis of the fly and the long axis of the spider leg from 0–11 cm, with the fly forming a constant angle (α) of 40°, the spiking rate again dramatically decreased (figure 4*c*) as the trichobothrium moved out of the flow cone.

All experiments described so far were carried out with the fly's abdomen pointing towards the trichobothrium. When the orientation of the fly was reversed, with the *flow field pointing away from the spider*, the response of the trichobothrium is much weaker and could only be elicited up to a distance of 10 cm. The action potential (AP) frequency measured $40\,\mathrm{AP\,s^{-1}}$ ($N=2$, $n=10$) and $5\,\mathrm{AP\,s^{-1}}$ ($N=1$, $n=6$) at 5 cm distance ($\alpha=40°$) with the fly abdomen pointing towards and away from the fly, respectively. For $x'=10$ cm the corresponding values were 23 and $1\,\mathrm{AP\,s^{-1}}$. We attribute these responses to the airflow towards the fly produced by the wingbeat.

With increasing horizontal distance of the fly, the air movement signal not only becomes weaker but also increasingly discontinuous. Figure 6*a* shows the air particle velocity measured at a distance (x) of 30 cm and the corresponding response of the trichobothrium. At large distances the fly signal consists of single gusts of air, thus diminishing the probability of the trichobothrium to be exposed to the stimulus. In figure 6*b* (same experiment as in figure 4*a*) the response of the trichobothrium is given as the highest spike rate that occurred. The percentages quantify the probability of a response to a stimulus resulting from 1 s of flight activity. At distances larger than 30 cm the instantaneous spike rate drops from several hundred to below 50 Hz and the response probability from 100% to 40%.

(b) *Response to synthetic stimuli*

Using the fly as a source of a natural stimulus, the stimulus parameters we could vary were distance, absolute position and relative orientation of the fly to the spider. To investigate further the response properties of the receptor we applied synthetic stimuli, which allowed us to control the single parameters of hair motion.

(i) *Ramp stimuli*

Does the trichobothrium 'measure' the position, the velocity or the acceleration of the hair shaft? Hairs were deflected in the direction of the long axis of the leg (i.e. in the direction of greatest mechanical sensitivity; Barth *et al.* 1993) with a constant velocity of $26.5°\,\mathrm{s^{-1}}$. The deflection angle was varied between 3.6 and 10.6° (figure 7). The receptor shows a phasic response. There is no spontaneous activity and no activity during steady deflection (hair at fixed angular location). The total number of action potentials increases with increasing deflection angle. The mean frequency of the response, however, decreases with increasing deflection angle, suggesting that the trichobothrium not only responds to the velocity, but also to the acceleration of hair deflection.

(ii) *Threshold curves*

The determination of stimulus thresholds at various frequencies might help to answer the question of whether a single trichobothrium preferentially responds to a relevant prey signal as opposed to background air movements which are known to be very low-frequency phenomena (<10 Hz; Barth *et al.* 1995).

To describe the threshold frequency response of trichobothria receptor cells without having to consider the mechanical air–hair interaction and boundary layer effects, measurements were made with the hairs directly coupled to the vibrator. Responses were recorded from all five hairs of the metatarsal group D1 between 10 and 750 Hz. The hairs were moved symmetrically around their resting position in the direction of the leg axis. The threshold decreases from 0.5°, at 10 Hz, to 0.1°, at 100 Hz, and then slowly rises again at higher frequencies (figure 8*a*). The smallest deflection angle found was 0.01° at a stimulus frequency of 100 Hz. With the hair directly coupled to the vibrator, threshold curves do not significantly change with hair length (figure 8*b*). When plotting peak velocity ($\mathrm{deg\,s^{-1}}$) at threshold instead of deflection angle, the trichobothria clearly present themselves as low-pass filters, with high sensitivity at frequencies up to *ca.* 100 Hz and steeply rising thresholds beyond.

Under natural conditions, however, trichobothria are deflected by air particle movements. For comparison with the values found with direct coupling of the hair shaft to the vibrator, threshold curves were therefore also determined for sinusoidal stimulation of the trichobothria in the nearfield of a loudspeaker. Here, because of the added influence of the mechanical properties of the hairs and the hair–air interaction (Barth *et al.* 1993; Humphrey *et al.* 1993), threshold curves do indeed depend on hair length (figure 9). At a stimulus frequency of 10 Hz a hair of 500 μm length is twice as sensitive as a hair 250 μm long. The longer hair is more sensitive in the low-frequency range, whereas the shorter hair is more sensitive in the high-frequency range. With nearfield stimulation all trichobothria investigated behave like strong high-pass filters for frequencies above *ca.* 25 Hz.

(iii) *Suprathreshold frequency response*

Most of the time trichobothria will not operate at threshold under natural conditions. To determine the suprathreshold frequency tuning for a trichobothrium directly coupled to the vibrator, the stimulation frequency was varied between 10 and 300 Hz at a constant stimulus amplitude of $2\,\mathrm{mm\,s^{-1}}$ (stimulus duration 1 s). When the response frequency is plotted against stimulation

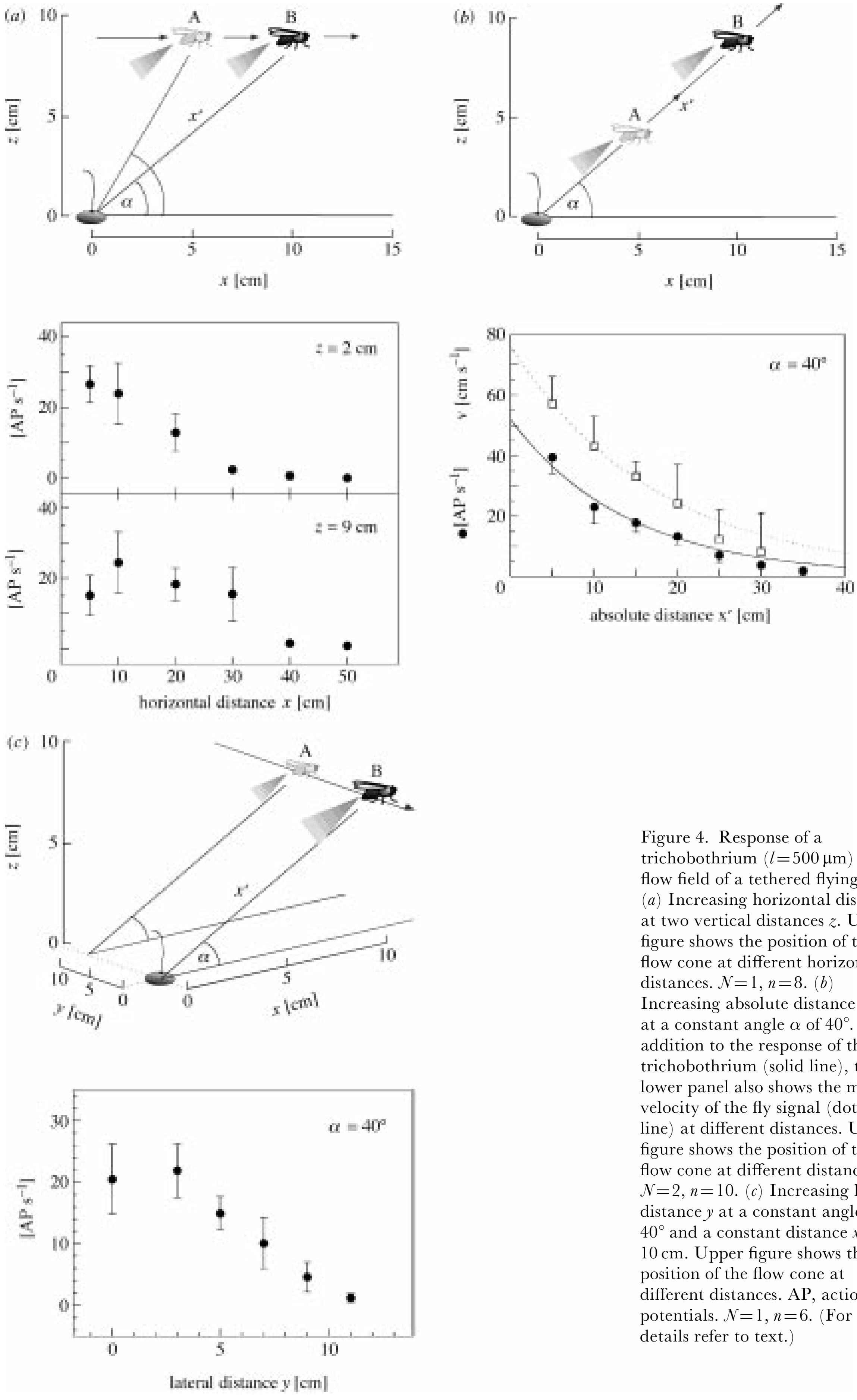

Figure 4. Response of a trichobothrium ($l = 500\ \mu m$) to the flow field of a tethered flying fly. (*a*) Increasing horizontal distance x at two vertical distances z. Upper figure shows the position of the flow cone at different horizontal distances. $N = 1$, $n = 8$. (*b*) Increasing absolute distance x' at a constant angle α of 40°. In addition to the response of the trichobothrium (solid line), the lower panel also shows the mean velocity of the fly signal (dotted line) at different distances. Upper figure shows the position of the flow cone at different distances. $N = 2$, $n = 10$. (*c*) Increasing lateral distance y at a constant angle α of 40° and a constant distance x of 10 cm. Upper figure shows the position of the flow cone at different distances. AP, action potentials. $N = 1$, $n = 6$. (For details refer to text.)

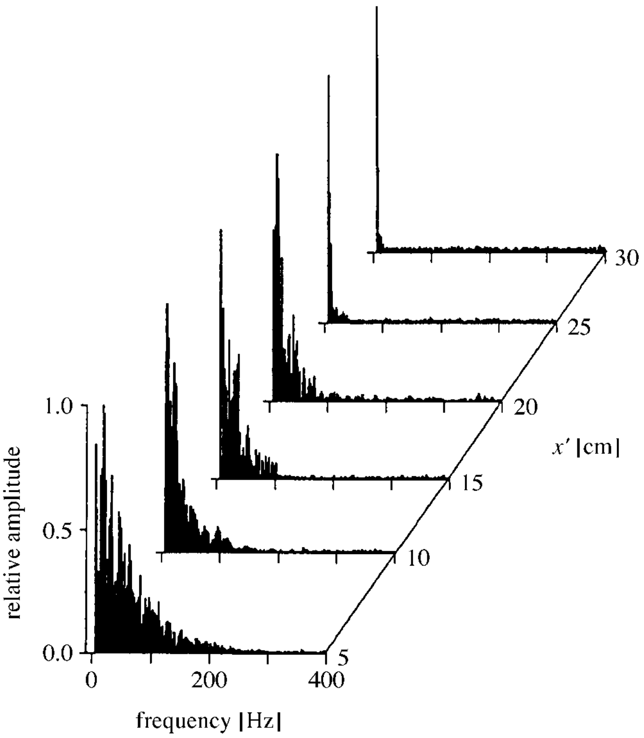

Figure 5. Frequency spectra of the air movement caused by a tethered flying fly and measured at increasing distance (x').

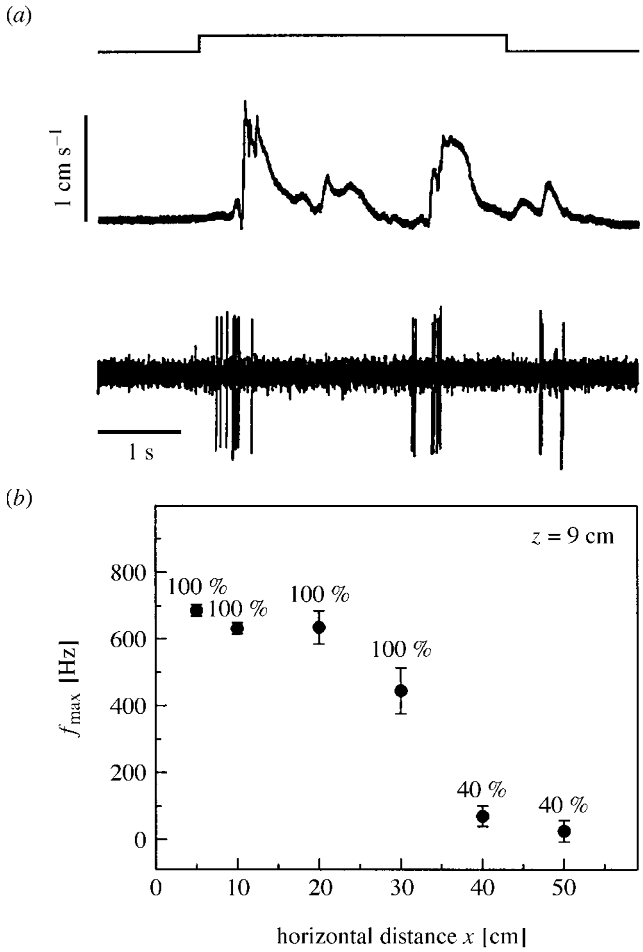

Figure 6. (*a*) Response of a trichobothrium ($l = 500$ μm) to the flow field of a tethered flying fly at a horizontal distance x of 30 cm. Upper trace, optically recorded duration of the flight; middle trace, velocity of the airflow, monitored by a hot wire anemometer; lower trace, APs. (*b*) Maximum action potential rate of a trichobothrium ($l = 500$ μm) in response to a tethered flying fly at increasing distance x. The percentage numbers show the response probability to a stimulus duration of 1 second. $N = 1$, $n = 9$.

frequency, the receptor behaves like a bandpass filter tuned to frequencies between 50 and 120 Hz (figure 10*a*).

The number of impulses per cycle decreases with increasing frequency (figure 10*b*), which would be expected from the decrease of cycle duration. At suprathreshold stimulation, for stimulus frequencies between 10 and 50 Hz, more than one impulse is generated per half sine wave; at frequencies above 150 Hz only one impulse per full sine wave occurs. At stimulus frequencies above 300 Hz impulses occur at irregular time intervals. For a given frequency the impulses of the sensory cells occur at a constant phase of the sine wave. At low frequencies, where spikes occur at both half waves the phase difference between both responses is exactly 180°.

(iv) *Representation of stimulus amplitude*

The experiments using a fly as a natural stimulus have shown that the mean velocity of the airflow is represented by the spiking rate of the trichobothrium (figure 2). To investigate amplitude representation at different frequencies we applied sinusoidal stimuli. The trichobothrium was moved around its resting position in the direction of the long axis of the leg. At stimulation frequencies below 150 Hz the stimulus amplitude is represented by the spiking rate of the receptor cells. Figure 11 shows a representative example at a stimulus frequency of 50 Hz. At stimulation frequencies above 150 Hz, however, there is always just one AP per cycle.

(v) *Adaptation*

Monofrequency stimulation results in receptor adaptation within a rather short time. On the other hand we have seen that the natural fly signal is unsteady and highly turbulent, especially close to the fly. In the following experiment the adaptation behaviour of trichobothria to monofrequency stimuli and to a 'noisy', unsteady stimulus were compared.

Adaptation speed increases with increasing stimulus frequency. At a stimulation frequency of 100 Hz the receptors completely adapt within 2 s, whereas at a frequency of 10 Hz the cells respond throughout the whole stimulation period of 5 s (constant stimulus amplitude). Stimulation with a broad-banded noise signal, however, leads to no adaptation even within a stimulation period of 90 s (figure 12).

4. DISCUSSION

(a) ***General properties of the receptor cells***

The lack of spontaneous activity and the pronounced phasic response characteristics of the trichobothria are not only typical of *C. salei* but of all spiders and scorpions so far studied (*Agelena*: Görner 1965; *Tegenaria*: Reißland & Görner 1985; *Ciniflo*: Harris & Mill 1977; *Euscorpius*: Hoffmann 1967). The trichobothria mainly function as

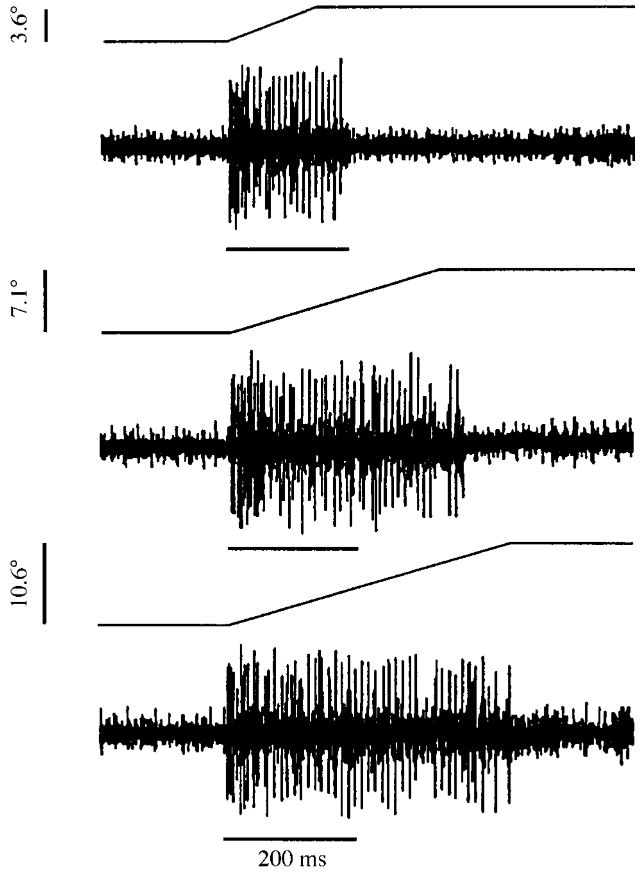

Figure 7. Response of a trichobothrium ($l = 500\ \mu m$) to linear deflection of the hair shaft from its resting position in proximal direction. Upper traces, deflection of the hair shaft; lower traces, APs.

velocity receivers. Accordingly, deflection of the hair shaft with constant velocity results in a rather constant spike rate (Görner 1965; Reißland 1978). A phasic response character is also typical of air movement-sensitive interneurons in the suboesophageal ganglionic mass of *C. salei* (Friedel & Barth 1997). It is suggested that this reflects the unsteadiness of biologically significant air movement stimuli (see below) and represents an important aspect of the sensory system's adaptation to such stimuli.

Ramp stimulation of the trichobothria of *C. salei* revealed that they are not only sensitive to stimulus velocity but also to acceleration. When considering the mere mechanics of the air–hair interaction, such mixed sensitivity was also found, short hairs being as good or better velocity sensors as long hairs, but more sensitive acceleration sensors (Barth *et al.* 1993). As our present data refer to experiments where the hair shaft was directly coupled to the vibrator, the source of this mixed sensitivity must be a different and additional one residing either in the mechanics of the dendrite coupling or in properties of the primary processes at the receptor membrane.

Threshold sensitivity of *Cupiennius* trichobothria is high (deflection by less than 1°) in the whole frequency range tested (10–500 Hz) and lowest (deflection angle *ca.* 0.1°) between *ca.* 50 and 100 Hz. The smallest threshold deflection angle observed (0.01° at 100 Hz) is considerably lower than the threshold deflection angles reported for other trichobothria (*Euscorpius* 2–3°, Hoffmann 1967; *Tegenaria* 3°, Reißland 1978). The trichobothria of *Cupiennius*, together with the filiform hairs on the cricket cercus (Shimozawa & Kanou 1984), are the most sensitive arthropod air movement detectors known.

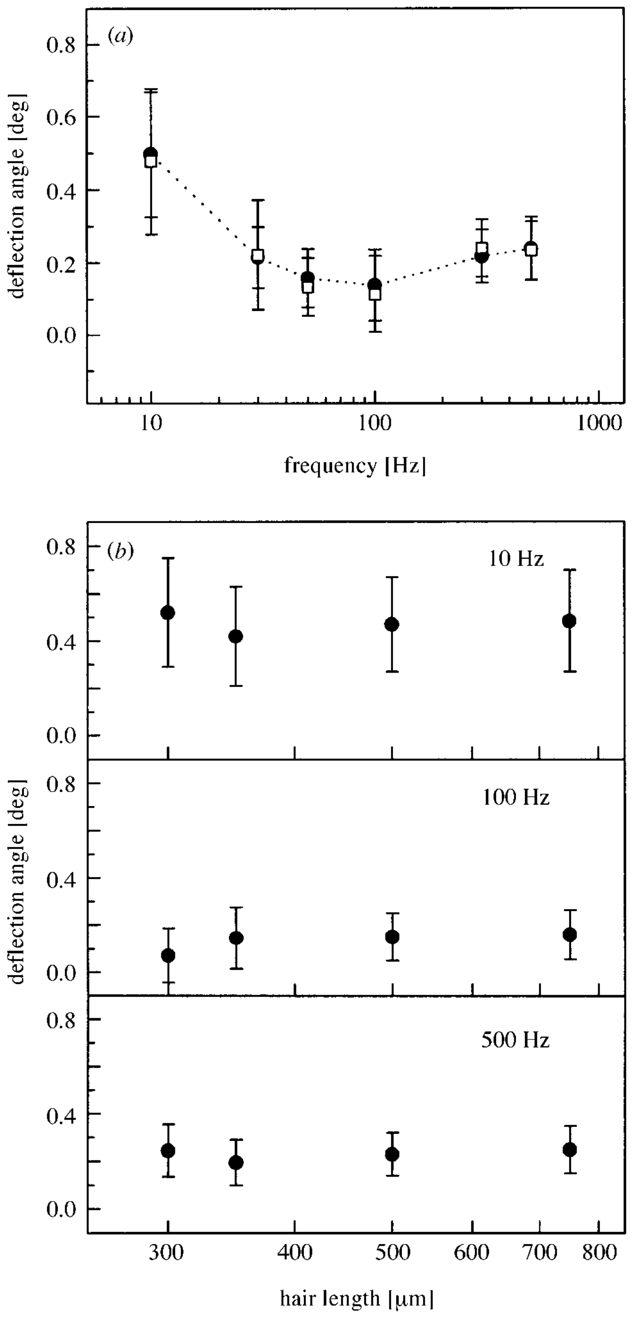

Figure 8. (*a*) Threshold curves for long ($l > 400\ \mu m$, filled circles) and short ($l < 400\ \mu m$, open squares) trichobothria directly coupled to the vibrator. $N = 6$, $n = 27$. (*b*) Threshold deflection angles for trichobothria directly coupled to the vibrator at three different stimulus frequencies in relation to hair length. $N = 6$, $n = 27$.

(b) *Detection of natural prey signals*

The large number of trichobothria on the legs of *C. salei* is exceptional among spiders (Barth *et al.* 1993) and suggests a particular behavioural significance of air movement detection in this species. *C. salei* is indeed able to catch flying insects from the air up to distances of

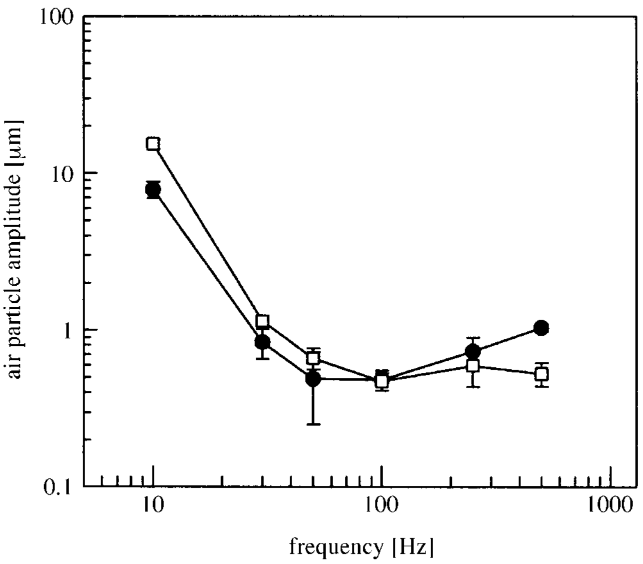

Figure 9. Threshold curves for a long ($l=500$ µm, filled circles) and a short ($l=250$ µm, open squares) trichobothrium stimulated by the nearfield air particle movement in front of the vibrator coil. $N=2$, $n=6$.

several centimetres. Behavioural experiments revealed that the trichobothria are responsible for the recognition and localization of such prey. After ablation of all trichobothria the capture of flying insects can no longer be elicited. After ablation of all trichobothria on one body side the ability to localize the stimulus source is impaired. The spider always turns to the intact side irrespective of stimulus position (Görner & Andrews 1969; Barth *et al.* 1995; Brittinger 1998). In addition to air movements produced by flying insects, those produced by insects walking close to the spider are behaviourally significant as well. For *Cupiennius,* insects not in flight are indeed the more common prey. The pulsed air movement produced by them and detected by the trichobothria at short distances (13 cm) adds to the effect of plant vibrations also produced by insects during locomotion (see discussion in Barth *et al.* 1995).

(i) *Sensory space*

A tethered flying fly elicits prey capture behaviour in *C. salei* up to a distance of 27 cm. The highest response probability is found at a fly–spider distance of *ca.* 10 cm (Barth *et al.* 1995). As seen from figure 4*a* for a fly–spider configuration very similar to that used in the behavioural experiments, the nervous response of the trichobothrium is largest in the same range of distances, reflecting the heterogenous structure and the directionality of the stimulus. In the present study we measured the active sensory space of single trichobothria by recording action potentials. The maximum distance at which a fly signal elicited a physiological response was 55 cm, with the spider leg resting on a solid substrate. Unlike web spiders, the hunting spider *C. salei* lives on broad-leaved monocotyledonous plants, such as bromeliads and banana plants. The presence of a solid substrate beneath the spider entails a significant increase in flow velocity above the surface (Barth *et al.* 1995). In the absence of such a substrate, single trichobothria detect the fly signal only up to a distance of 15 cm.

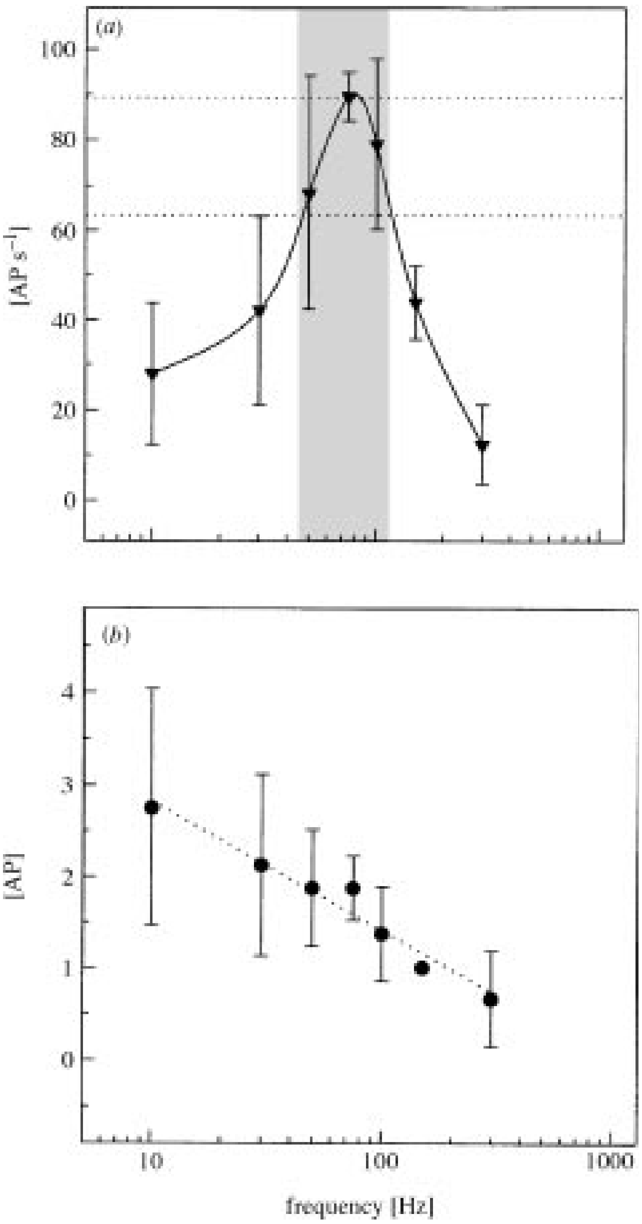

Figure 10. (*a*) Frequency response of a trichobothrium ($l=500$ µm) directly coupled to the vibrator shown as action potentials per second; stimulus amplitude constant at 2 mm s^{-1}. The shaded areas show the 3 dB range of maximum response. (*b*) Shows the number of APs per cycle. $N=4$, $n=11$.

The sensory space of a single trichobothrium of a spider sitting on its dwelling plant is roughly twice as large as that found for the whole animal in behavioural experiments. At distances greater than 30 cm the fly signal lacks the higher frequency components typical of prey insects and in addition is likely to be too low in amplitude and degree of fluctuation to be discriminated from biologically meaningless background airflow.

(ii) *Localization*

As the flow field generated by the fly is highly directional, not only the absolute distance between the fly and the spider but also the orientation of the fly determines the response of the trichobothrium. The flow generated by the fly is contained in a cone-like region behind the fly (Barth *et al.* 1995; Dickinson & Götz 1997). The response

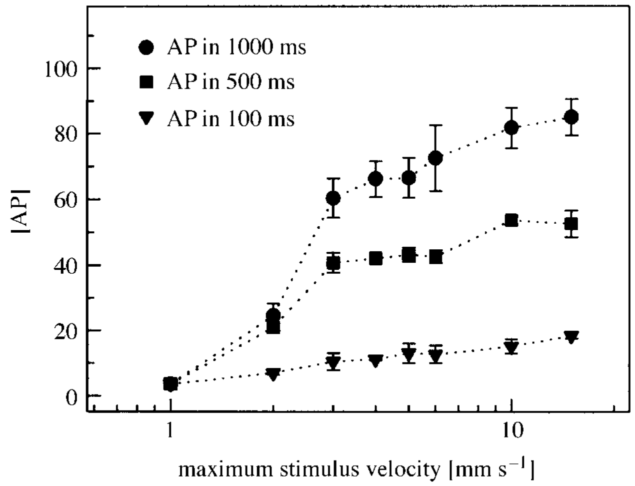

Figure 11. Representation of stimulus amplitude (deflection velocity) by a trichobothrium ($l = 500\,\mu m$) directly coupled to the vibrator. Stimulation frequency was kept constant at 50 Hz. $N = 1$, $n = 6$.

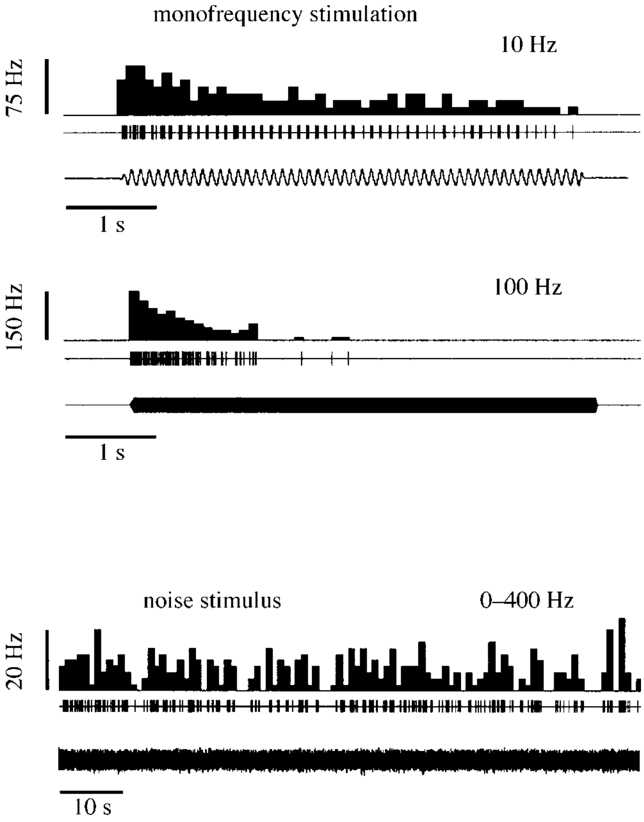

Figure 12. Adaptation of a trichobothrium directly coupled to the vibrator to different kinds of stimuli. Upper traces, AP rate histogram (bin width = 100 ms); middle traces, APs; lower traces, stimuli.

of the trichobothrium is strongest when it is in the centre of the cone. When the position of the fly is changed so that the trichobothrium falls out of the cone, the response immediately decreases. This effect is stronger than that of increasing absolute distance (x') between fly and trichobothrium. From behavioural observations we conclude that the spider is able to use the corresponding differences in the excitation pattern of its many trichobothria to exactly localize the fly.

When the fly's orientation is changed so that its head points towards the spider, a response of the trichobothrium can only be elicited up to a distance of 10 cm. This finding supports the view of trichobothria being air movement rather than sound pressure receivers.

(iii) *Recognition of fly*

How does the spider discriminate the fly signal from background wind? A closer look at the corresponding 'signals' seems to provide at least a partial answer.

The wingbeat of a flying insect produces sound waves (in addition to 'wind') that lead to periodic pressure variations and particle displacements in the vicinity of the insect. Because of their small size and their relatively low wingbeat frequencies flying insects are rather poor sound pressure radiators (Tautz 1979). Air particle displacements, however, can reach relatively large amplitudes close to a flying insect. A tethered flying fly produces airflow velocities of up to $1\,m\,s^{-1}$ with rms values of up to 25%. Background wind measured in the habitat of *Cupiennius* under biologically relevant conditions is characterized by velocities typically below $0.1\,m\,s^{-1}$ with rms values below 15% (Barth *et al.* 1995). In addition, the frequency content of the two 'signals' differs remarkably. Whereas the fly signal contains frequencies up to 150 Hz, the wind in the natural habitat is characterized by frequencies below 10 Hz. The experiments of the present study using synthetic stimuli revealed that the trains of APs sent to the central nervous system by a trichobothrium depend on the parameters mentioned above and contain the information needed for the discrimination task discussed. The threshold curves and, even more so, the response curves above threshold measured in the present study point to a tuning of the examined trichobothria to the frequency range relevant for prey capture behaviour. At distances of the fly greater than *ca.* 25 cm, however, the fly signal increasingly lacks its characteristic features, with all the high frequency components (>50 Hz) gone. Interestingly, behavioural reactions can no longer be elicited at such distances (Barth *et al.* 1995). Even if the spider recognized the air movement as that produced by a fly passing at some distance it would not make sense for the spider to try to catch the fly because of the time it would take it to approach the fly and because of the long delay in the fly signals reaching the spider to begin with (several seconds at distances of *ca.* 30 cm).

(iv) *Stimulus frequency*

Trichobothria of different length are mechanically tuned to different ranges of best frequencies. This finding can be understood by taking boundary layer phenomena into account (Barth *et al.* 1993; Humphrey *et al.* 1993). However, threshold curves do not depend on hair length when the hair is directly coupled to the vibrator. The 'physiological' tuning obviously does not add to the mechanical tuning in a hair length-specific way. The physiological threshold curves lack any sharp tuning. Similar to the mechanical tuning, the 3 dB range of maximum sensitivity is rather broad.

At suprathreshold stimulation the receptor cells show a pronounced tuning to a frequency range between 50 and 120 Hz. This is well within the range of the frequencies contained in the air movements close to flying insects. Low-frequency background air movements such as wind are effectively filtered already in the sensory periphery. Due to the different mechanical frequency tuning of trichobothria of different length, the spider might be able to detect the frequency content of an airborne signal.

(v) *Stimulus amplitude*

The amplitude of the airflow generated by a buzzing fly is encoded by the spiking rate of the trichobothria receptor cells over a wide range of velocities ($1\,\mathrm{mm\,s^{-1}}$ to $1\,\mathrm{m\,s^{-1}}$). With sine wave stimulation, increasing stimulus amplitude leads to a logarithmic increase of the AP rate at stimulus frequencies below 150 Hz. At stimulus frequencies above 150 Hz there is always just one spike per cycle regardless of stimulus amplitude. This frequency is high compared to that of the receptor cell of caterpillar filiform hairs (*Barathra*) where the frequency limit of amplitude representation is around 40 Hz (Tautz 1978). Since the natural fly signal contains frequencies typically below 200 Hz, the trichobothria receptor cells are well suited to represent accurately the velocity of natural air currents.

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