

THE AIR FLOW GENERATED BY A FLYING PREY INSECT AROUND A WANDERING SPIDER AND ITS MOTION SENSING HAIR SENSILLA

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ABSTRACT

Spiders use cuticular filiform hairs (trichobothria) to detect air motions generated by flying prey and predators. The wandering spider *Cupiennius salei* has about 900 such hairs on its pedipalps and legs. Their length and base diameters range from 100 μm to 1400 μm and 5 μm to 10 μm , respectively, and hairs of different length are arranged in characteristic clusters. Using an optically transparent test section for digital particle image velocimetry measurements, we analyzed the flow field generated by a flying prey (*Calliphora erythrocephala*) around *Cupiennius salei*. The humming fly was placed in biologically important positions with respect to the spider. The flow fields ahead of the fly showed velocities detectable by the trichobothria from a distance of at least 13.2 cm. Since their frequency content differs significantly from that of background flow they may well be used by the spider as signals indicating the fly's approach. Flow patterns change with the fly in different positions. The closer the fly was to the spider the more the absolute values for peak velocity and turbulence intensity increased. The peak velocity and the turbulence intensity above the fourth walking leg (WL4) changed from 5.11 mm/s and 29 % with the fly approaching the spider and 10 cm away from its center to 13.84 mm/s and 97 % (only 5 cm away). As the trichobothria do not respond to constant air velocity but to its fluctuations (Barth and Höller 1999), the rms values and the turbulence intensity are of major interest. The increasing turbulence intensity may well indicate to the spider that a fly is approaching. When comparing the peak velocities and the turbulence intensity right above the tarsi of each walking leg the highest values were measured above the walking leg closest to the fly (see WL4). The values decreased for the walking legs further away. Thus above WL1 and with the fly approaching the

spider from behind and 5 cm away from its center the values for peak velocity and turbulence intensity were only 2.68 mm/s and 63 %. Considering the differences at the eight legs of the spider these may well be used as indicators of the azimuthal direction towards the prey.

BIOLOGICAL CONSIDERATIONS AND OBJECTIVES OF THIS INVESTIGATION

Arthropods such as crustaceans, insects and arachnids possess a wide range of specialized sensory organs by means of which they perceive and interact with their environments. These include sensors sensitive to light, odor, touch, substrate vibration and air or water medium displacement. The sensors responding to air flow in spiders are used to detect prey and predators. Individual sensilla usually form arrays. These have evolved under natural selection pressures over millions of years to perform adequately. As a consequence, they often display extreme sensitivity and selectivity with regard to the behaviorally relevant signals they detect.

Here we report on experimental work with the wind-sensing filiform hairs, or trichobothria, of spiders, in particular those of the wandering spider *Cupiennius salei*. Fig. 1 shows such hair sensilla on the tarsal segment of a spider leg (Barth 2002). Each of the spider's eight legs has about 100 filiform hairs; in addition there are ca. 50 trichobothria on each of the two pedipalps. The total of 900 hairs is arranged in specific clusters or arrays. Different clusters contain between 2 and 24 hairs which range in diameter from 10 μm at the base to 2 μm at the tip and are from 100 to 1400 μm long, depending on their location on the leg. Earlier work (Barth et al. 1993) showed that the range of hair lengths in a cluster works to extend the

effective frequency range as compared to that of an individual hair. According to theoretical studies (Humphrey et al. 1993, 1998, 2003) and experiments using controlled laboratory flows (Barth et al. 1993, 1995; Barth and Höller 1999) the trichobothria of *Cupiennius* respond to extremely low velocity oscillations (p-p amplitudes as small as 0.15 mm/s) and are mechanically tuned to stimulus frequencies between 40 Hz and 600 Hz. Using natural stimuli like the turbulent air flow generated by a flying insect, prey capture behavior is elicited in the spider (Barth et al. 1995, Brittinger 1998).

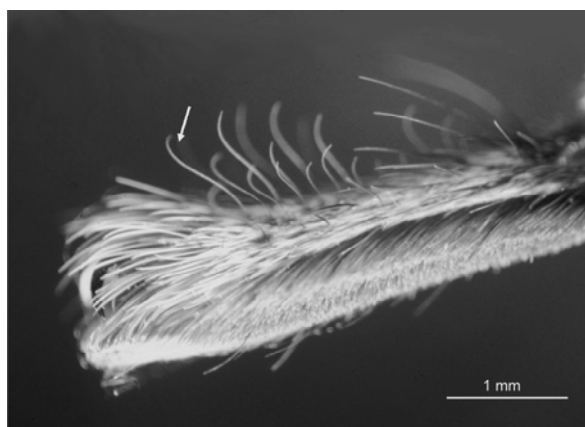


Fig. 1: Tarsal segment of a *Cupiennius salei* leg showing an array of long, slightly curved wind-sensing filiform hairs or trichobothria (arrow) (Barth 2002).

The flow in the wake of a fly is highly three dimensional, unsteady and vortical and, as a result, it is very rich in its spectral content (Barth and Höller 1999). In the present study we have extended our work by the application of the Digital Particle Image Velocimetry (DPIV) technique to determine the spatial and temporal structure of the flow generated by a fly above a spider and inducing oscillations of its trichobothria.

The wandering spider *Cupiennius salei* is able to catch flying insect prey like flies by jumping towards them. This behavior is a remarkable achievement which relies on the detection, recognition and orientation towards an airborne moving object. It is guided by information provided by air flow stimuli. The main objectives of this investigation are to measure and analyze the flow patterns used by the spider (i) to detect the flying object, (ii) to recognize it as prey and (iii) to orient towards it when catching it.

THE EXPERIMENT

Test Section and Equipment

A box made of Perspex ($55 \times 30 \times 30 \text{ cm}^3$) contains the fly-spider system. It serves to shield the flow generated by the fly from external perturbations while keeping the DPIV seeding agent confined to the measurement volume. The seed particles are introduced through a re-sealable hole in the box (Fig. 2).

A small strip of paper is glued to the dorsal thorax of the fly with a mixture of beeswax and colophony. The paper strip is then clamped to the fly support which consists of two rotatable units, the holder itself and a small plate used to provide contact for the legs of the fly. The fly starts flying when this plate is rotated away and thus the tarsal contact of the fly removed. The fly support can also be displaced vertically allowing the effects of biologically important fly-spider positions and orientations to be measured. The spider rests on a horizontal Perspex plate ($15 \times 30 \text{ cm}^2$). The origin of the three dimensional (x, y, z) coordinate system is defined to be on the Perspex substrate in the center of a circle which touches all of the spider tarsi. The x-axis points towards the spider's anterior end, the y-axis normal to it in the same plane, and the z axis vertically upwards (Fig. 3).

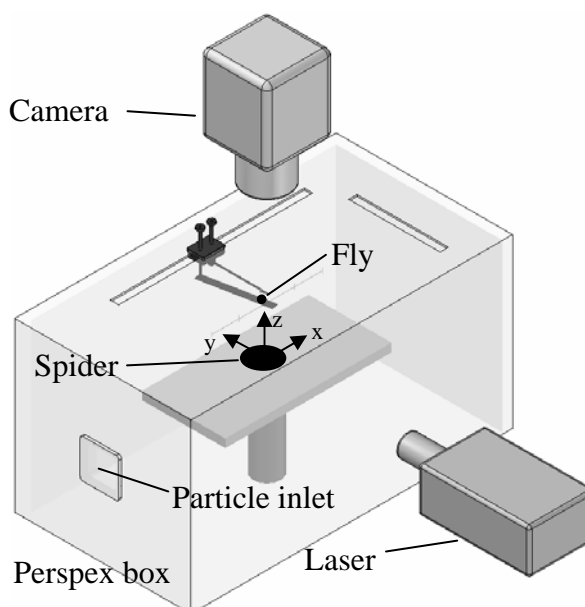


Fig. 2: Test section showing the location of the spider on a horizontal Perspex substrate. The fly is tethered by means of a clamp support that can be moved relative to the spider. The camera and the laser of the DPIV system are arranged as shown.

A Dantec DPIV system is used to measure the air flow velocity. The system consists of two New Wave Mercury Nd:YAG lasers (4 W/532 nm wavelength) coupled to a dual laser unit. The laser optics (Dantec 80 × 60 series) generates a pulsed light sheet of 2 mm waist thickness at its focal point. The repetition rate between two laser pulses is up to 100 kHz. An IDT iNanoSense TR camera with a CMOS chip and equipped with a special light intensifier allows high quality measurements with reduced laser power so as not to damage the animals. A Nikon AF Nikkor 85 mm f/1.8D lens is used with a Soligor spacer ring (12 mm). Data acquisition and post processing are performed using the Dantec Dynamic Studio software (Version 1.30).

When the fly has started to fly, the DPIV system is triggered using a Constant Temperature Anemometer (Dantec Multichannel CTA 54N81) with a one dimensional fiber film probe (Dantec 55R01). When flight is induced,

the signal rises above threshold. Due to online measurement ten pictures taken prior to threshold are saved in addition. The trigger delay is 0.01 s.

Seed particles of a nominal diameter of 2 μm are produced by means of a fog generator (Dantec Flow Tracker 700 CE) using a special fog fluid (Safex Inside Fog Fluid Super). The particles do not affect the performance of the CTA.

Measurement Procedure und Uncertainties

A dead spider is positioned in the center of the flat rectangular Perspex substrate with its legs and pedipalps in their natural position. The fly (*Calliphora erythrocephala*) is located 10 cm above the substrate and in the spider's symmetry plane. Measurements are taken at five different x-positions (-10 cm, -5 cm, 0 cm, +5 cm, +10 cm) (Fig. 3). The laser sheet is aligned as shown in Fig. 3, its vertical position being such that it grazes the tarsi where the highest concentration and the largest group of trichobothria (up to 30 on each leg) occur. The front and side edges of the spider support are sufficiently removed that they do not interfere with the flow over it. Likewise, the flow approaching the spider from the fly is not affected by the front edge of the plate.

The DPIV image size is 1280 x 630 pixels and large enough to photograph the flow around half of the spider ($9.8 \times 7.8 \text{ cm}^2$). At positions $x = -10 \text{ cm}$ and -5 cm single frames are recorded at a rate of 25 Hz whereas the frame rate at position $x = 0 \text{ cm}$ has to be 100 Hz taking into account the higher velocities with the fly at this position. Adaptive Correlation (Cross Correlation with Moving Average Validation and Interrogation Area Offset) is used to create the velocity vector plots. The interrogation area is 32 by 32 pixels with 50% overlap. The origin of the DPIV (x-y/u-v) system of coordinates is at the bottom, left-hand corner of the image. The size and the overlap of the interrogation areas are chosen to render uncertainties due to out-of-plane particle displacement negligible.

The maximum frequency contained in the air motion caused by a tethered flying fly is less than 600 Hz (Barth and Höller 1999). At 600 Hz the velocity amplitude of a 2 μm seed particle is at least 99.9 % of that of the air motion it tracks, and its phase lag with respect to the air is 0.09° , approximately (Dring 1982). Therefore, possible errors due to the seeding agent not tracking the air flow are negligible.

RESULTS AND DISCUSSION

Flow in the Wake of the Fly

We first take a look at the flow around the fly itself. Fig. 4a shows a snapshot of a tethered fly during a measurement.

Figs. 4b-d present the means of various parameters measured over ten wing beats and with the laser sheet 5 mm below the wing plane. The big vortex behind the left wing (Fig. 4b) rotates counter clockwise with a maximum vorticity of -167 s^{-1} whereas the one behind the right wing turns clockwise with a maximum of $+165 \text{ s}^{-1}$. The velocity magnitude (Fig. 4c) defined as $V_{\text{mag}} = (U_x^2 + U_z^2)^{1/2}$ goes

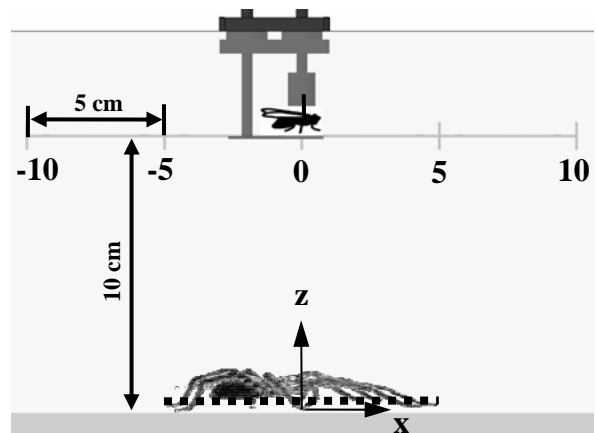


Fig. 3: Setup with the spider and fly in one of many possible relative orientations. The laser sheet (dotted line) of 2 mm waist thickness is aligned immediately above the tarsi of the spider (3 mm above the spider substrate).

up to 65 cm/s in the wake of the humming fly. Due to conservation of mass, the air in front of the fly is sucked with a velocity magnitude of up to 23 cm/s towards the wings. The highest values of the rms velocity in x direction (47 cm/s) are seen directly in front of each wing and in the wake (Fig. 4d).

Flow over the Spider

$X = -10 \text{ cm}$: Simulates the situation when a fly approaches the spider from behind. In this case a uniform flow is found above the spider that moves towards the fly (Fig. 5a). At low frequency flows (10 Hz) the physiological threshold is ca. 0.7 mm/s (Barth and Höller 1999). The mean velocity magnitudes here range from $1.74 \pm 0.13 \text{ mm/s}$ above walking leg 1 (WL1) to $2.94 \pm 0.29 \text{ mm/s}$ above WL4 so that action potentials are generated (frequencies at around 11 Hz). The angular variation of the velocity vectors ranges from $148^\circ/\text{s}$ to $505^\circ/\text{s}$.

$X = -5 \text{ cm}$: With the fly still behind but closer to the spider, the flow is much more irregular (Fig. 5b). Immediately behind the spider, especially, the instantaneous velocity vectors vary significantly both in terms of magnitude (range from 0 to 22 mm/s) and direction (angular variation per second up to $1400^\circ/\text{s}$). The fly generates a highly turbulent flow signal that is directed downwards from the fly at an angle of about 25° - 45° in a cone like region (Barth and Höller 1999). The redirection of this flow by the Perspex substrate is thought to be the reason for the increased turbulence intensity for this case (Figs. 5b and 6a). This effect also is to be expected under natural conditions with *Cupiennius salei* sitting on large and mechanically strong leaves like those of a bromeliad.

Above the tarsi of walking legs WL3 and WL4 the instantaneous velocity magnitudes are not as constant as at $x = -10 \text{ cm}$ (Figs. 5a and b). The mean rms values over WL4 are 2.82 mm/s with the fly at $x = -5 \text{ cm}$ as compared to 0.84 mm/s at $x = -10 \text{ cm}$. In addition the peak velocities are higher. The averaged peak velocity above WL4 is 13.84 mm/s at $x = -5 \text{ cm}$ and 5.11 mm/s at $x = -10 \text{ cm}$.

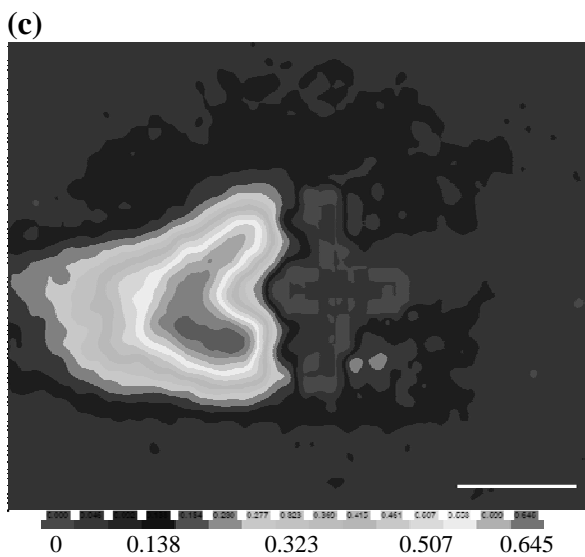
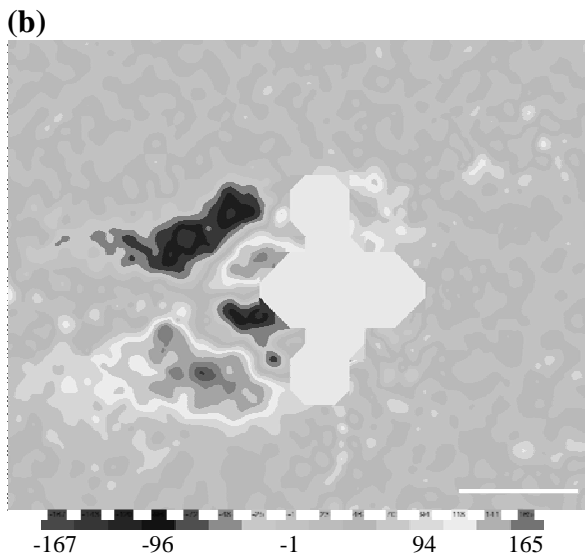
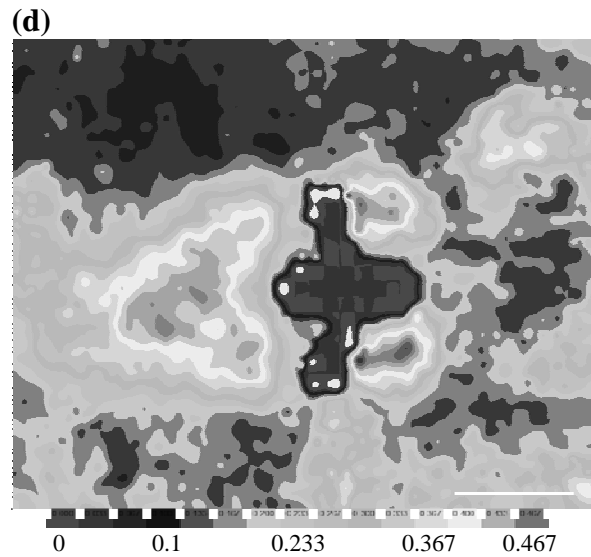
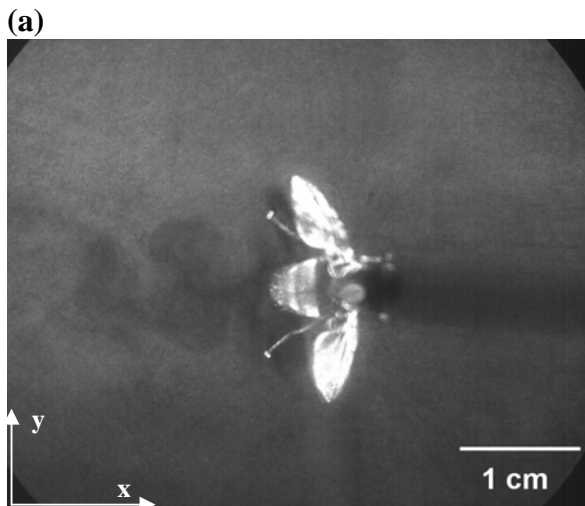


Fig. 4(a): Top view snapshot of the seeding agent flowing around a tethered fly due to the flapping wings (laser sheet in wing plane). (b) Vorticity (s^{-1}) around the wings. (c) Mean values of velocity magnitude ($m s^{-1}$). (d) rms of the U_x velocity component ($m s^{-1}$). Plots (b), (c) and (d) refer to a plane 5 mm below the wing plane.

There are no significant differences among the mean velocity magnitudes of different walking legs at the same position of the fly (Fig. 6b). Furthermore the mean velocity magnitudes are also similar above the same walking leg comparing the two positions ($x = -10$ cm and $x = -5$ cm).

Because the trichobothria do not respond with action potentials to the velocity magnitude but to the velocity fluctuations (Barth and Höller 1999) rms values and turbulence intensity are of major interest. The mean rms velocity magnitudes at WL3 and WL4 are much higher (1.45 mm/s and 2.82 mm/s) at $x = -5$ cm than at $x = -10$ cm (0.72 mm/s and 0.86 mm/s). This also results in a higher turbulence intensity ($V_{mag,rms} / V_{mag,mean}$) $\times 100$, especially at WL3 and WL4 (77 % and 97 %) at $x = -5$ cm and may indicate to the spider that the fly is close enough to be caught. In comparison at $x = -10$ cm the turbulence intensities are 23 % at WL3 and 29 % at WL4 (Fig. 7). The difference between $x = -5$ cm and $x = -10$ cm is significant for all walking legs (Wilcoxon signed ranks: $p = 0.043$ for all legs). Furthermore the leg with the highest rms velocity (WL4) points towards the fly suggesting a mechanism by means of which the spider may be able to detect from which direction the fly is approaching.

$X = 0$ cm: When the fly is directly above the spider the turbulent flow field is displaced further towards the spider and is also more immediately above it (Fig 5c).

$X = +5$ cm: This effect is even more pronounced with the fly in this position. Averaged streamlines (Fig. 5d) provide an impression of the complex character of the flow generated by the fly, as intercepted and affected by the spider. The mean velocity magnitudes increase to values of up to 40 mm/s and the mean vorticity ranges from $-18.9 s^{-1}$ to $5.6 s^{-1}$.

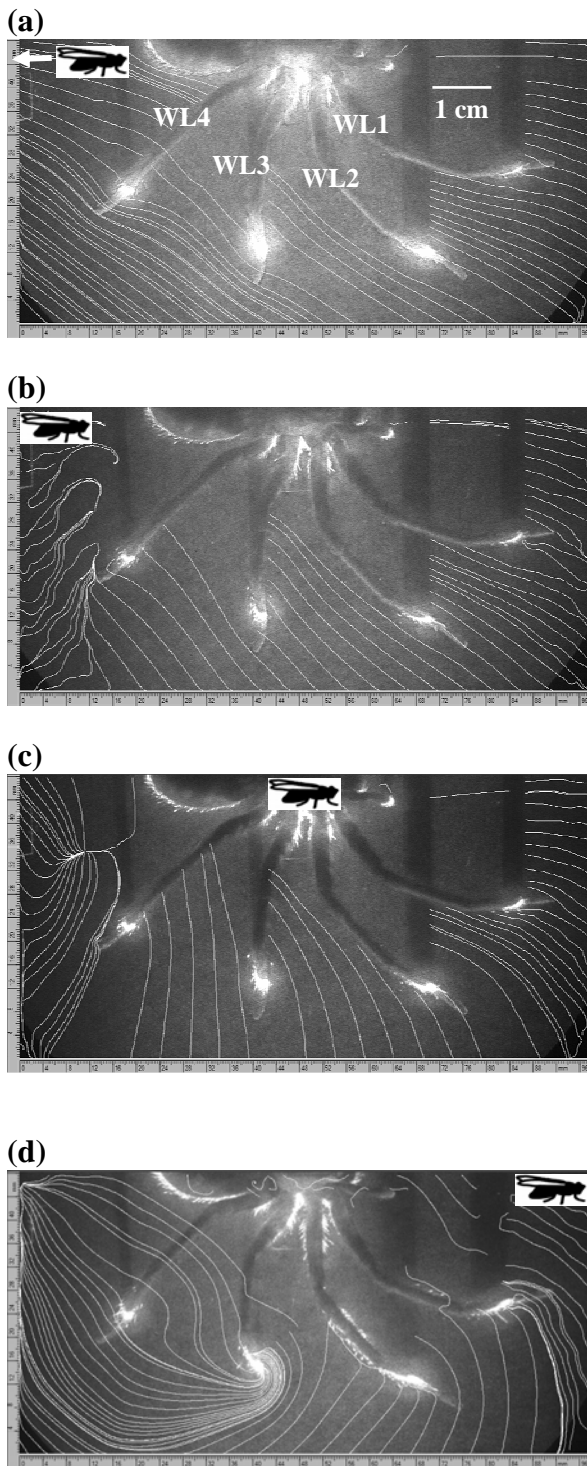


Fig. 5: Streamline plots of mean velocity magnitude for the spider placed at $x = -10$ cm (a), $x = -5$ cm (b), $x = 0$ cm (c) and $x = +5$ cm (d) with the laser sheet immediately above the tarsi.

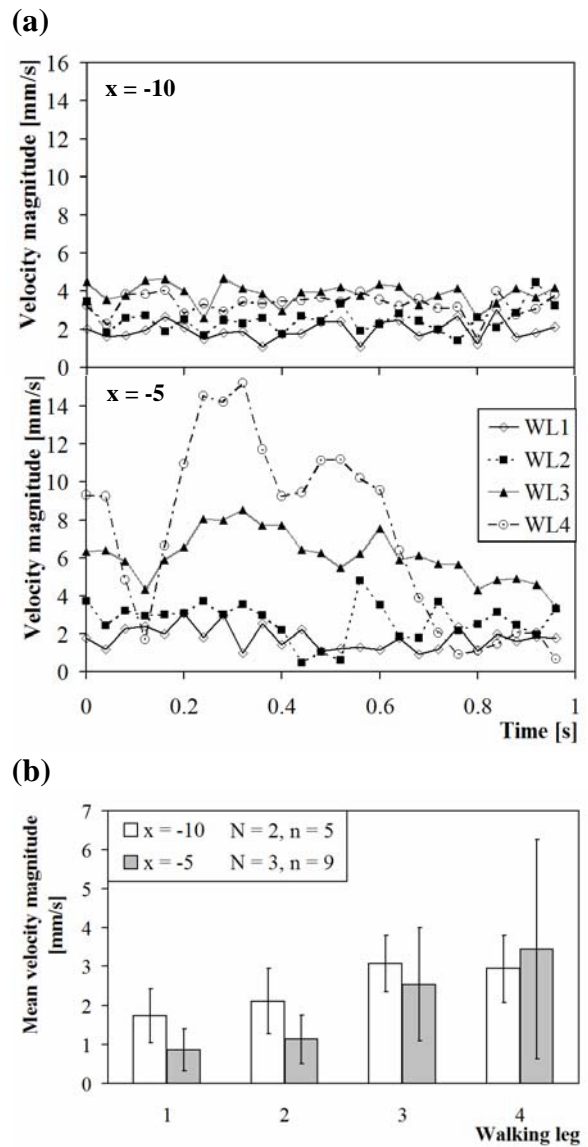


Fig. 6(a): Velocity magnitude plotted as a function of real time at locations immediately above the tarsi of each walking leg for a fly at positions $x = -10$ cm (top) and $x = -5$ cm (bottom) and 10 cm above the spider platform. (b) Mean velocity magnitude and mean rms values for the cases shown in (a). N and n represent the number of different flies and the number of measurements, respectively.

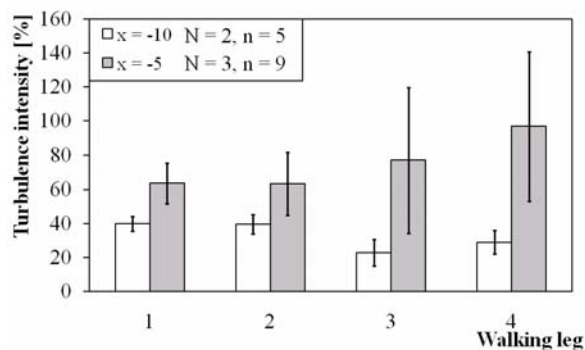


Fig. 7: Turbulence intensity over each walking leg with the fly at positions $x = -10$ cm and $x = -5$ cm.

CONCLUSIONS

Our measurements suggest that a fly approaching a spider from behind and from as far as $x = -10$ cm away generates enough air motion to deflect the spider's extremely sensitive trichobothria in a way leading to action potentials.

The largest distance where measurements could be taken was at $x = -13.2$ cm. For this case, the velocities above the spider's tarsi are as large as 2.65 mm/s above WL4 and decrease to 1.5 mm/s above WL1. This suggests that the spider can not only detect very well a fly approaching from behind at that distance but also from even further away.

The air velocity signal changes when the fly is nearer to a position where it can be caught ($x = -5$ cm). At this location, the increased peak velocity and turbulence intensity may serve to inform the spider that it is time to jump. The proper direction may be derived from a comparison between the air flows at the different legs.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the financial support provided by DARPA BioSenSE AFOSR Grant # FA9550-05-1-0459 in support of this study. JACH expresses his sincere thanks to the University of Vienna where part of the work was performed while on sabbatical as a Guestprofessor in the Department of Neurobiology and Cognition Research. The comments of Clemens Schaber on the manuscript and the competent technical assistance of Karina Jorke are highly appreciated.

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