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PREY LOCALIZATION BY TRICHOBOTHRIA OF SCORPIONS

Summary Prey catching behaviour of scorpions (Buthidae: *Androctonus australis*, *Buthus occitanus*) was investigated in the laboratory. The scorpions locate nearby prey by accurately orienting to airborne vibrations produced either by live prey or by dummies. This performance is mediated by trichobothria, sensory hairs on the pedipalps of scorpions, being deflected by weak air currents generated e.g. by a whirring insect. One essential feature of these hairs is the distinct plane of oscillation. In most cases numbers and position of trichobothria are genus-specific and of taxonomic value. After plucking out all trichobothria, scorpions fail to orient towards a vibrating target any longer. Removal of all 39 trichobothria of one pedipalp influences the response of the animals if the stimulus source is directed to this extremity: in that case, predatory behaviour is elicited in only 25% of all trials (control: 84%). Unilateral removal of 8 trichobothria (with identical planes of oscillation) significantly influences the scorpions' behaviour: 1. the reaction times are longer, 2. the frequency of prey-capturing reactions decreases from 86% to 54%, 3. the accuracy of the orientation movements changes from r_S=0.99 (control) to 0.29 if the stimulus source vibrates in the plane of oscillation of the removed trichobothria. The experiments demonstrate a functional importance of scorpion trichobothria for the localization of prey.

Introduction

Studies on the behavioural physiology of prey-capturing in scorpions have mainly concentrated on the role of substrate vibrations in prey localization (Brownell & Farley 1979). Besides highly sensitive tarsal and basitarsal vibration detectors, scorpions possess trichobothria on their pedipalps. Often genus- or species-specific in number and spatial arrangement (Vachon 1973), and easily deflected by slight movements of the air, these hairs play an important role in the anemomenotactic orientation of desert scorpions (Linsenmair 1968). An important property of these sensilla is that they possess a preferential plane of oscillation.

This study aims at understanding the function of scorpion trichobothria in localizing airborne stimuli.

Materials and methods

The behavioural responses of *Androctonus australis* and *Buthus occitanus* (Buthidae) to airborne vibrations generated by live prey or dummies were tested. The standard stimulus was a vibrating cork ball (10 mm ϕ), driven by a Derritron Vibration Exciter 2MM, stimulus frequency about 20 Hz, stimulus amplitude 2 to 3 mm, and positioned at a distance of 10 to 30 mm to the scorpion's pedipalps. For evaluation, the orientation movements and other reactions of the animals to the stimulus were recorded with a video device. For ablation experiments trichobothria were plucked out with forceps. Orientation movements to the stimulus source and attempts to grasp it were counted as a (positive) response. For further details see Krapf (1986).

Results and discussion

Buthid scorpions are easily aroused by a crawling or flying insect. After a very quick orientation movement, the scorpion precisely seizes the prey in most cases. How is this behaviour elicited? When scorpions (N=4) are separated from a vibrating dummy by a vertical glass plate the proportion of capturing-responses decreases from 94% of n=316 (without glass plate) to 7% of n=160 (with glass plate). To investigate a possible role of optical cues, the median and lateral eyes of 2 *Buthus* were covered with black paint and the vibrating target was offered. This had no negative effect on eliciting prey capture (94%, n=54). Under the test conditions mechanical stimuli apparently were the decisive releasers for the scorpions' responses. As likely candidates the trichobothria were examined.

Touching a freely moving scorpion with a cricket releases prey capture in 90% (n=31). This is not significantly different (P>0.05, contingency table) from 70% (n=57) of positive responses following stimulation with the vibrating dummy. After removal of all trichobothria, direct contact with an insect was still a reliable releaser, while airborne vibrations lost their effectiveness (1%, n=87).

Are the sensory hairs of both pedipalps necessary for prey localization? To answer this question, all 39 trichobothria of the right extremity of 3 buthids were removed. Airborne vibrations of the dummy directed at this pedipalp from diverse directions evoked catching responses in only 25% of 192 trials. Additionally, the accuracy of the turns, calculated as the correlation between stimulus angle and turning angle of the animal, was significantly different from the control experiments where the stimulus source was directed at the intact (=left) pedipalp (r_S=0.27 vs 0.87; $P<0.001$, test for correl.coeff.). In the latter situation, the scorpions showed prey capture behaviour in 84% of 154 trials.

These experiments indicate that the trichobothria of only one pedipalp may provide a scorpion with sufficient information about the location of a vibrating target.

To evaluate the function of specific trichobothrial patterns, 8 trichobothria on the tibia of the right pedipalp of 3 *Androctonus* were plucked out. All of these sensilla were deflected in the same plane of oscillation (control: left pedipalp with complete set of trichobothria). It was assumed that the scorpions' response behaviour would be affected if the dummy vibrated within the plane of oscillation of those 8 hairs (◇ in Fig.1). Additionally, the dummy was perpendicularly directed at the finger tips, the chelae and the tibia of the pedipalps (● in Fig.1) from various directions. The positions of the stimulus source were randomly changed.

The following effects of this manipulation were observed (Fig.1): a) after stimulus onset, the scorpions responded significantly faster when stimulated at the intact pedipalp ($\bar{x}$=0.25s vs 0.37s; $P<0.01$, Kolmogorov-Smirnov-test), b) prey-capturing behaviour was drastically influenced: in contrast to 86% (n=51) positive responses (51% turning movements, 35% grasps) which followed stimulation of the intact pedipalp, stimulating the opposite extremity was successful in only 54% (17%+37%) of 59 trials ($P<0.001$, contingency table). Nevertheless, the disposition of the predators to catch prey was unchanged in both test situations - crickets touching a scorpion were seized at once, and c) airborne stimuli directed at the intact pedipalp from various directions elicited very

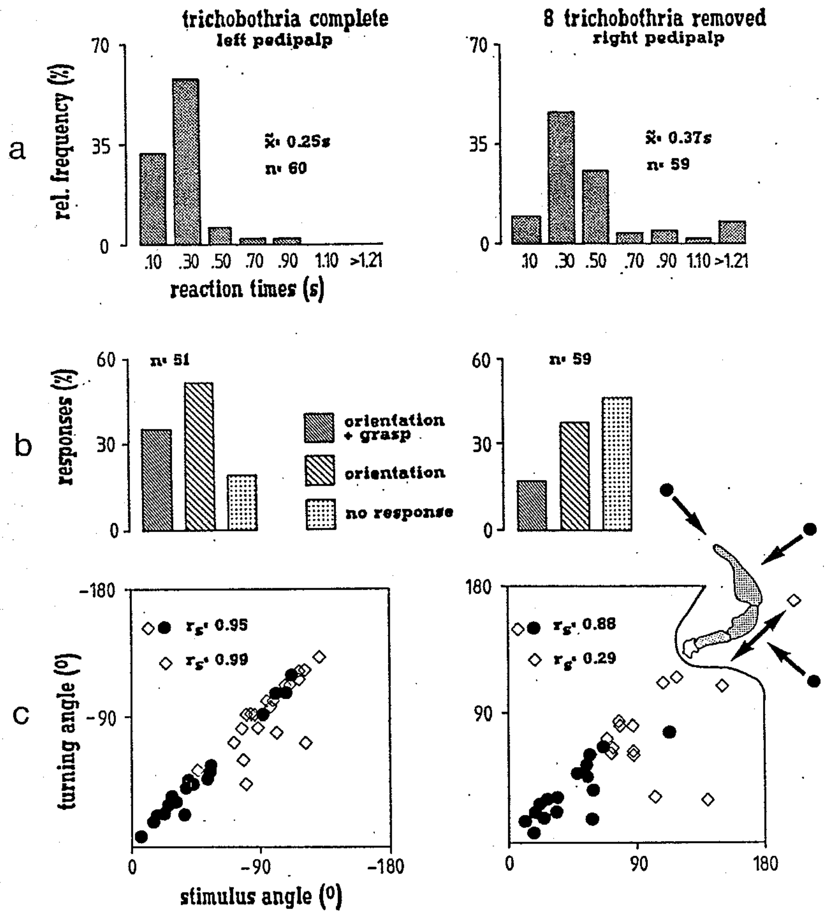

Fig.1: How is the prey localization behaviour of scorpions affected after removal of 8 trichobothria on the right pedipalp (control: intact left pedipalp)? 3 *Androctonus australis* were stimulated with airborne vibrations of a dummy.
a) reaction times (=time from stimulus onset to response),
b) behavioural responses following stimulation, c) accuracy of the orientation movements to the target (plot of turning angle vs stimulus angle).
The arrows indicate the directing of the dummy at the pedipalp:
◇ in the preferential plane of oscillation of the removed trichobothria (=parallel to the external surface of the tibia),
● perpendicular to the tips of chelae fingers, chelae and tibia. For further details see text.

accurate turns to the target (r_S=0.95); the accuracy reached even 0.99 if the dummy vibrated in the plane of the 8 trichobothria mentioned above. When stimulating the trichobothria of the right pedipalp, no significant difference in the overall correlation was observed (r_S=0.88; test for correl.coeff.). With 0.29, however, the correlation of the scorpions' turns was not significant, if the dummy vibrated in the plane of the removed trichobothria.

To summarize, the trichobothria are another effective sensory apparatus of scorpions for prey localization. The experiments demonstrate that the pattern of the trichobothria is highly adaptive: hairs with same preferential planes of deflection, often arranged in groups, act as sensors representing the receptive field for airborne stimuli of prey in that direction. A similar system is described by Camhi (1980): filiform cercal hairs mediate the escape behaviour of the cockroach *Periplaneta* - a common prey of many scorpion species.

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Schmidt: Are there differences in the behavioural pattern depending on the pattern of trichobothria in the different families of scorpions?

Krapf: Behavioural experiments, following ablation of trichobothria, were only performed with buthid scorpions. Comparing the responses of buthids and scorpionids (e.g. Scorpio maurus, Pandinus imperator) to airborne and substrate vibrations of prey showed that there are differences in scorpions: members of both families were sensitive to substrate vibrations, the buthids to airvibrations, too, and respond with catching actions. In contrast, in the scorpionids which often are burrow-inhabiting sit-and-wait-predators, airvibrations elicited escape and defense responses in most cases.