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*ESCAPE BEHAVIOUR OF NEMOBIUS SYLVESTRIS*

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## 1. EXECUTIVE SUMMARY

Wood crickets *Nemobius sylvestris* constitute an appropriate model system to study both, the escape behaviour and the associated mechanosensory system, in an ecological context. In this report, we describe and analyse the escape behaviour of these crickets under controlled laboratory conditions. We measured the ability of crickets to escape, when exposed to defined mechanical stimuli. We also tested the implication of different sensory system (antennal and cercal mechanosensory receptors, eyes) in this behaviour. We used a set-up with controlled environment and a computed-controlled piston to stimulate the cricket. Crickets showed a rate of escape that reached about 67%. Performance was decreased when the piston came from the front ( $0^\circ$ ) as opposed to other stimulus directions. Younger crickets obtained better scores than older ones when the piston came from the rear ( $180^\circ$ ). Crickets of different age groups escaped in the direction opposite to the direction of stimulation. There was a strong correlation between escape angle and stimulation angle (J1:  $r=0.91$ , J2:  $r=0.96$ ). The ablation of the cerci drastically affected the success rate for both stimulations at  $180^\circ$  and at  $0^\circ$ . Crickets with ablated antennae exhibited a higher variance in escape angles than other tested groups (for a stimulation at  $180^\circ$ ). In the case of stimulation at  $0^\circ$ , the increase of variance was significant only when compared to intact crickets.



## 2. ESCAPE BEHAVIOUR OF *NEMOBIUS SYLVESTRIS*

### 2.1. INTRODUCTION

Escape behaviour has been studied for several decades in different invertebrates like copepods, crayfish, and insects. It is particularly well studied in insects in which the escape is initiated by the perception of wind by mechanosensory organs (Camhi et al, 1978a). Studies of this behaviour allowed to analyse the mechanism that underlie the perception of air flow. Insects, particularly orthopteroids, have two appendices at the end of the abdomen, called cerci, covered by several kind of receptors. Some of these receptors are filiform hairs. These hairs are deflected by air flow and this deflection activates a sensory neuron. This mechanism is the basis of air flow perception by orthopteroid insects. The escape behaviour can also be elicited by air flow generated by an attacking predator, i.e., the mechanosensory system of cerci allows orthopteroid to detect attacks of natural predators (Camhi et al, 1978b).

Behavioral studies on cockroach show that a minimal wind velocity averaging 12 mm.s<sup>-1</sup> and a minimal wind acceleration averaging 600 mm.s<sup>-2</sup> can evoke an escape (Camhi, 1984). Using air-puff on the crickets *Grillus bimaculatus* and *Grillus sigillatus*, it was observed that by increasing the air-puff peak velocity, the response rate increases. Moreover, it was observed in this same experiment that crickets escape in a direction opposite to the air-puff direction. Different cricket species use different strategies in wind-evoked escape, e.g., *Grillus sigillatus* exhibits higher sensitivity to air motion, and *Grillus bimaculatus* shows a greater accuracy of escape direction. (Kanou et al, 2006; Kanou et al, 1999). Other differences in escape behaviour were observed; *Grillus bimaculatus* turns its body away from the air-puff before jumping and *Troglophilus neglectus* Krauss jumps directly away from the air-puff (Schrader, 2000). Many studies were carried out to analyse the nervous system



involved in the escape behaviour, including studies of the nervous structures implicated in the perception of the air movement, and the structures generating the motor escape activity. They show that each filiform hair is associated to sensory neurons projecting their axons in the terminal abdominal ganglion (TAG). In this structure, the sensory neurons connect to two kinds of interneurons, local interneurons or giant interneurons. The sensory information is processed and leaves the TAG to reach the thoracic ganglion (Edwards and Palka, 1974; Insausti et al in press,).

Since some years ago, the wood cricket *Nemobius sylvestris* has become a model to study escape behaviour and the mechanosensory system that triggers this behaviour. These crickets present numerous advantages: they are present in huge quantity in forests near to the laboratory, and their natural environment is easy to access and allows us to conduct experiments in the field, that can also be focused on the ecology of this species. We know the principal ecological needs of these crickets: they live in the litter of forest, and their principal predators are wolf spiders of the genus *Pardosa*. We developed a piston that simulates the attack of a spider. The characteristics of the stimulus produced by the piston and its efficiency to evoke the escape behaviour in crickets were already studied (Dangles, et al 2006). However, we have little information about the characteristics of the escape behaviour of this cricket under controlled conditions. Only one experiment was done in the laboratory, showing the performance of the crickets for a velocity range between 5 and 50  $\text{cm}\cdot\text{s}^{-1}$ . Here, we describe and analyse the escape behaviour of the cricket *Nemobius sylvestris* under controlled conditions, we used a controlled laboratory environment and a computer-controlled piston to stimulate the cricket. The aim of our study was to describe the performance of the cricket when confronted with defined stimuli and to study the implication of different sensory systems (mechanosensory receptors localised on cerci and antennae, and vision) in this behaviour. Our test consisted in presenting a black square in an otherwise



homogeneous (grey) visual environment. The rationale for such biotest is to offer a potential hiding place to the escaping cricket.

## 2.2. MATERIAL AND METHODS

### 2.2.1. Experimental insects

Experiments were realised on wood crickets (*Nemobius sylvestris* Bosc) of three different age classes: J1, composed by juveniles of instars 1, 2, 3 and 4 (length of posterior femur < 2.73 mm), J2, juveniles of instars 7, 8 and 9 (length of posterior femur > to 3.85 mm without wing), and adults (Campan, 1965). Crickets were collected less than two month before the experiments and they were maintained in plastic boxes (70cm x 40cm) with food (cat food and fresh fruit) and water *ad libitum*. Each cricket was used only once.

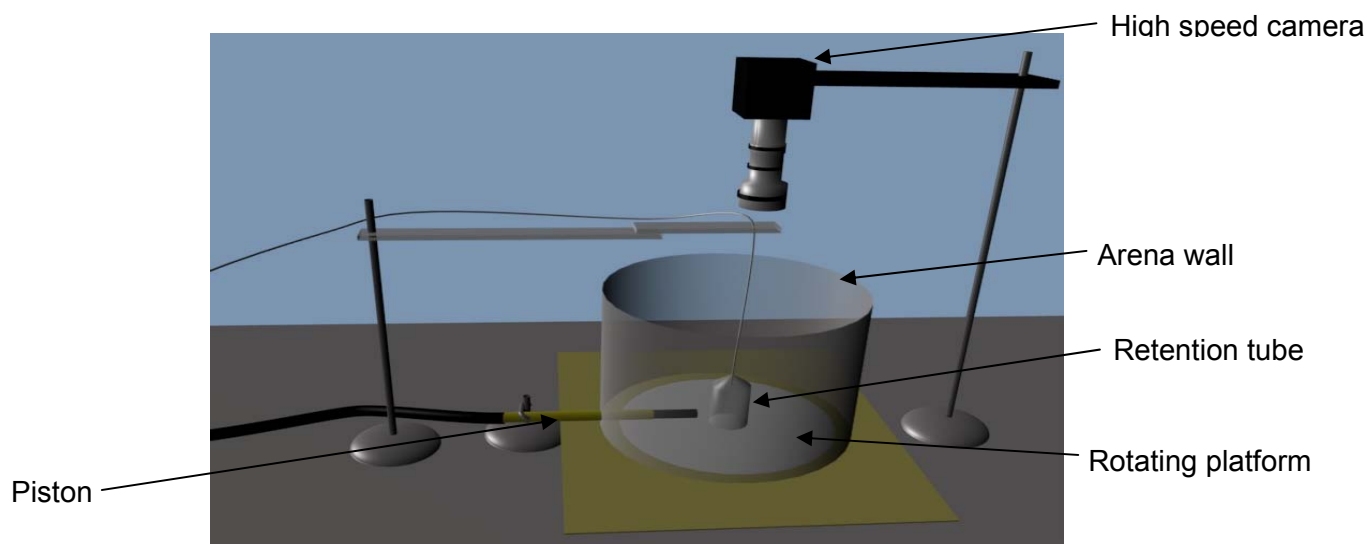
To test for the implication of sensory structures in the escape behaviour, we carried out experiment on 4 groups, namely intact crickets (G1), crickets lacking both cerci (G2), crickets lacking both antennae (G3) and intact crickets considered as touched by the piston when any part of their body except the antennae were touched (G4). To realise ablation of cerci and antennae crickets were anaesthetised with CO<sub>2</sub> for about 30 sec. Both cerci or antennae were cut at their base and a drop of low-temperature melting dental wax was applied over the base to avoid bleeding. This procedure took place at least 15 hours before an experiment. During this time, the insects were kept in individual tubes.

### 2.2.2. Experimental set-up

A cylinder (37 cm of diameter) was placed over a rotating platform and illuminated by a homogenous white light (11.70  $\mu\text{W}\cdot\text{cm}^{-2}$ ) generated by two light-spots on each side of the arena) (Figure 1). The cricket was placed at the centre of the arena and kept immobile in a transparent retention tube (2.8 cm of diameter). A circular piston (LAL35, Cedrat



technologies, Meylan, France) was used to stimulate the cricket. The piston was placed at a distance of about 4 cm from the cricket. It moved with a velocity of  $25 \text{ cm}\cdot\text{s}^{-1}$  over a distance of 4.5 cm, potentially touching the resting cricket. The ability of the piston to trigger the cricket's escape was already demonstrated (Dangles et al, 2006). The retention tube was gently removed and the piston actuated. The response of the cricket was recorded with a camera (High-speed video camera Gigaview from Southern Vision Systems, Inc. (SVSi), Madison, Alabama, (first experiment) or with DALSA CCD,  $113 \text{ f}\cdot\text{s}^{-1}$ ,  $128\times 128$  pixels (second experiment)).



**Figure 1** : Experimental set-up

For multimodality experiments a black square paper (10 cm side) was attached to the arena wall. This visual information was placed at  $90^\circ$  for one group of crickets and at  $270^\circ$  (according to the cricket position) for the other group. The data were pooled. Air-wind stimulation was applied at  $180^\circ$ .



### 2.2.3. Analysis

To quantify the cricket's response to the approaching piston, we analysed in the video records for each cricket whether: 1- it moved before being touched (interpreted as perception of air flow) 2- it escaped, avoiding being touched by the piston. We consider this event as a "successful escape". We measured "the angle to initial position" (Figure 2, angle  $\alpha$ ) corresponding to the angle formed by the initial position of the cricket (at the beginning of the experiment) as related to the cricket longitudinal axes and the position of the cricket after escape and "the angle to piston" (Figure 2, angle  $\beta$ ) corresponding to the angle formed by the initial position of the cricket (at the beginning of the experience) as related to the piston longitudinal axis and the position of the cricket after escaping.

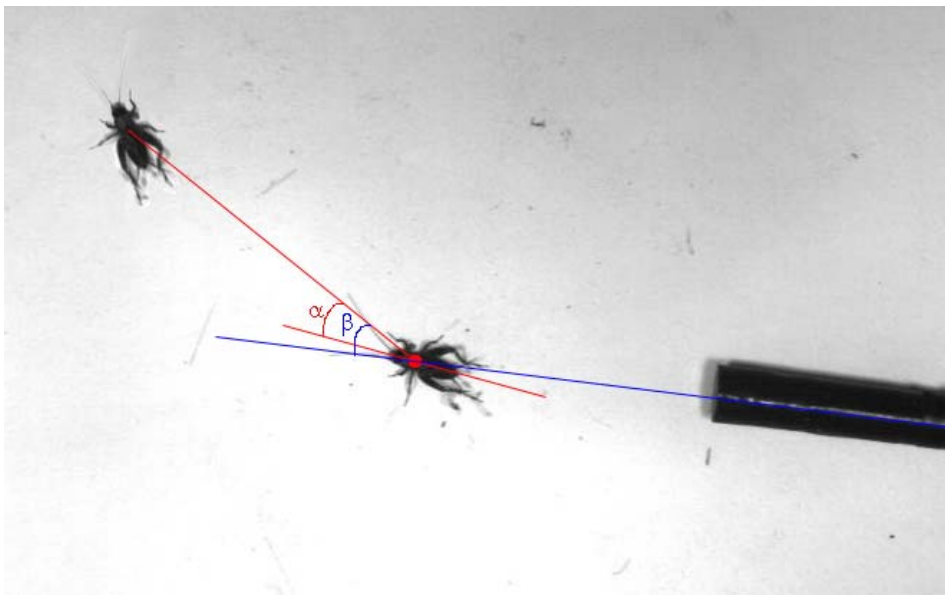


Figure 2: Angles measured for analysis: "the angle to initial position" ( $\alpha$ ) corresponding to the angle formed by the initial position of the cricket (at the beginning of the experiment as related to the cricket longitudinal axes and the position of the cricket after escape. "The angle to piston" ( $\beta$ ) corresponding to the angle formed by the initial position of the cricket (at the beginning of the experience) as related to the piston longitudinal axis and the position of the cricket after escaping.



## Statistical analysis

The statistical analysis was performed using R 2.7.0 software. The Binomial test was used, followed by the Bonferroni correction, to compare the escape success among groups. The correlations between escape and stimulation angles were performed by using a circular correlation. The variance of angles were compared using the Kappa test (Mardia et al, 1999). The escape direction angles were compared using the 'aov' circular test (Mardia et al, 1999).

## 2.3. RESULTS

### 2.3.1. Normal escape behaviour and ontogeny

When the stimulation was from an angle of 180° (piston arriving from the rear), 100% of J1 crickets moved before being touched, showing that they had perceived the air movement, but only 67% escaped successfully. In the case of the group J2, 60% of the animals perceived the air movement and all escaped successfully. Finally, 60% of the tested adults reacted to the air movement and 20% escaped successfully. Thus, the perception of air movement seems not to be sufficient to induce a successful escape.

All crickets showed a higher escape success for the piston coming from the rear (180°) than from the front (0°) (binomial test and Bonferroni correction J1:  $P < 0.001$ , J2:  $P < 0.001$ , A:  $P < 0.05$ ) (Figure 3). Crickets from group J2 and adults obtained significantly better scores for a piston coming from the side (90°) than from front (0°) (binomial test and Bonferroni correction J2:  $P < 0.01$ , A:  $P < 0.001$ ). The escape success of young crickets (J1) when the piston came from the side was intermediate between the two other directions of stimulation, but didn't show significant differences. Using data of all groups, we observed that crickets started to escape when the piston was at a distance of  $5.8 \pm 0.7$  mm for a stimulus at 180°.

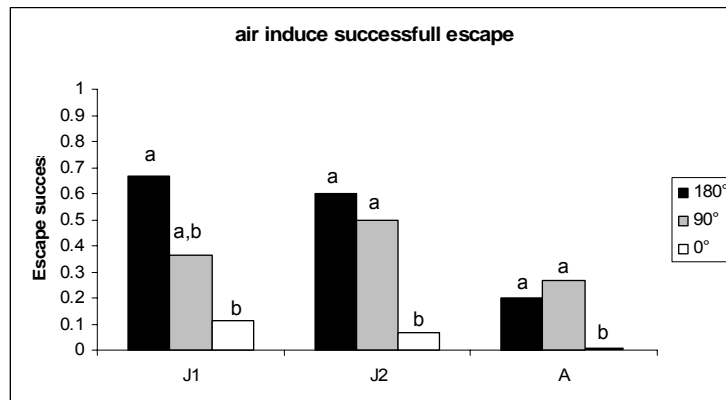


Figure 3: Rate of successful escapes for the different directions of mechanosensory stimulation and for the three different groups of crickets. Statistical comparisons were made between angles of stimulation. Different letters (a, b) indicates significant differences (binomial test with Bonferroni correction, significant differences are considered for a  $P < 0.016$ )

Young crickets (J1) showed a significantly better performance than older ones for stimulation from the rear ( $180^\circ$ ) (binomial test and Bonferroni correction  $180^\circ$  J1/A:  $P < 0.01$ ) (Figure 4). Crickets from group J2 showed a rate of escape which was intermediate between the other groups, but didn't present significant differences with them. When the piston arrived from the front ( $0^\circ$ ) or from the side ( $90^\circ$ ), no difference between animals of different age was observed.

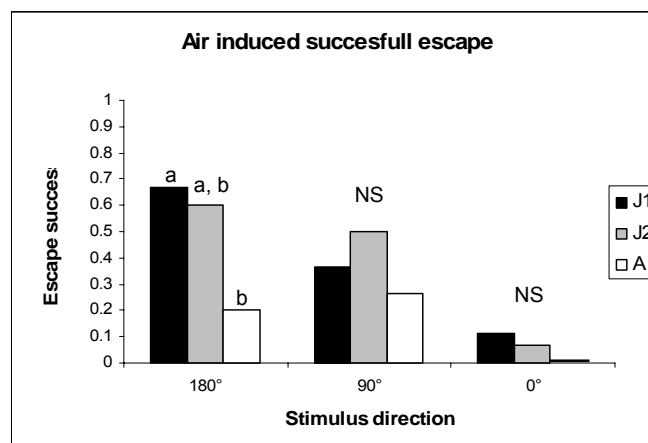


Figure 4 : Rate of successful escapes for the different directions of mechanosensory stimulation and for the three different groups of crickets. Statistical comparisons were made between groups of crickets. Different letters (a, b) indicates significant differences (binomial test and Bonferroni correction, significant differences are considered for a  $P < 0.016$ ).



In general, crickets of each group escaped in a direction opposite to the stimulation angle (Figure 5). We calculated the correlation between the angle of escape of the cricket (“angle to initial position” Figure 2, angle  $\alpha$ ) and the angle of stimulation. In crickets of all groups there were comparably strong correlations between these two angles (circular correlation J1 :  $r=0.91$ ,  $test=2.97$ ,  $P=0.0030$ ; J2 :  $r=0.96$ ,  $test=3.03$ ,  $P=0.0025$ ; A :  $r=0.92$ ,  $P=NS$ ). Thus, when data from all groups were pooled, the correlation was very strong (circular correlation  $r=0.96$ ,  $test=5.16$ ,  $P=2.45.10^{-7}$ ).

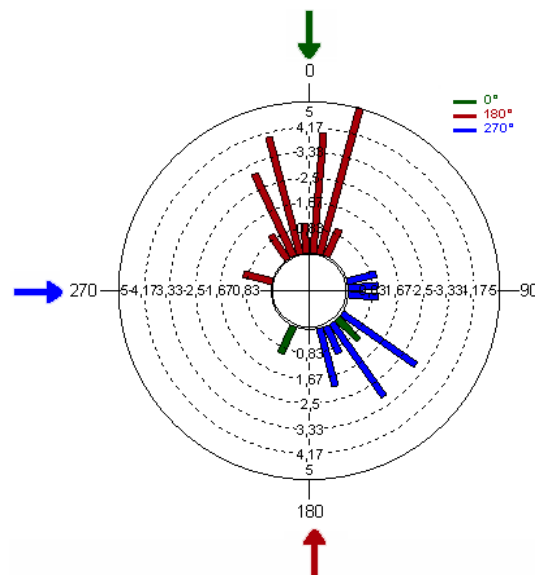


Figure 5 : Escape directions (“angle to initial position” Figure 2, angle  $\alpha$ ) of the crickets as a function of the stimulus direction ( $0^\circ$  in green,  $180^\circ$  in red,  $270^\circ$  in blue) indicated by an arrow.

For a piston coming from the front ( $0^\circ$ ), 11% of J1 crickets, 40% of J2 crickets and 27% of adults moved actively their antenna toward the moving piston. Very few, if any, crickets moved the antennae in a similar fashion for the other stimulation angles.

### 2.3.2. Implication of sensory structures in the escape behaviour

These experiments were carried out with cricket of the group J1. The ablation of the cerci evoked a strong reduction of the escape success, 63% of reduction for stimulation from  $180^\circ$  and 100% of reduction for a stimulation at  $0^\circ$ . Crickets lacking cerci (G2) exhibited a



significant reduction in their escape success as compared to intact crickets (G1) (for both a stimulation from 180°; Binomial test  $P=1.12 \cdot 10^{-5}$  and 0°; Binomial test  $P=0.006$ ).

For a stimulation at 180° the ablation of antennae didn't affect the escape success (Binomial test  $P=NS$ ). For a stimulation at 0°, many crickets were defined as touched and therefore unsuccessful in their escape. Normally, crickets moved their antennae in the direction of the approaching piston but this behaviour was no longer possible for cricket with ablated antennae. This partially explains the higher escape success recorded for antennectomized crickets (Figure 6 G3). We re-analysed thus the video records of intact crickets considering a cricket as touched by the piston when any part of their body except the antennae were touched (G4). The results (G4 in green in Figure 6) show a higher escape rate than previously considered (in black in Figure 6). Using the data of intact crickets without considering the antennae (G4) we didn't observe any effect of the ablation of the antennae (Binomial test  $P=Ns$ ).

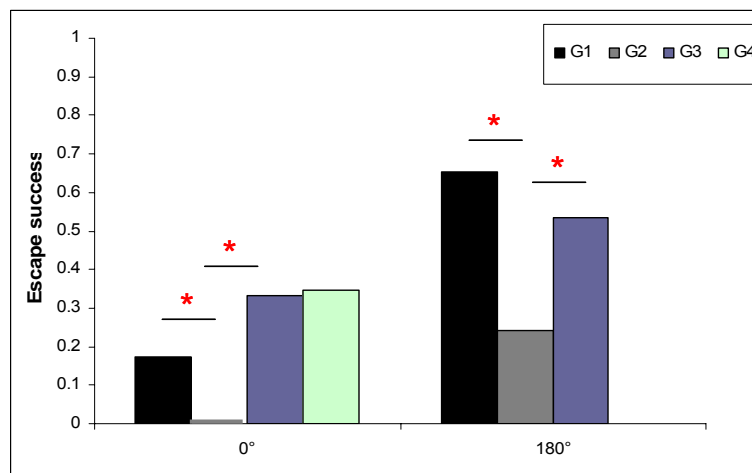


Figure 6 : Rate of successful escapes for intact crickets (G1, black), crickets without cerci (G2, grey), crickets without antennae (G3, purple), intact crickets defined as touched by piston for contact between the piston and any part of the cricket body except the antennae (G4, green). \* indicate a difference with  $P<0.016$ . Binomial test with Bonferonni correction.



Thus, antennae do not seem to influence the escape success. We compared the dispersion of the escape angles (“The angle to piston” Figure 2. angle  $\beta$ ) of the different groups. The crickets with ablated antennae showed a higher variance of the escape angle than intact crickets (Figure 7) for a stimulation at  $180^\circ$  (equal kappa test:  $\text{ChiSq}=7.24$   $P=0.007$ ) (Mardia *et al*, 1999). For a stimulation at  $0^\circ$ , the variance of escape angles was not significantly different from that of intact crickets (equal kappa test:  $\text{ChiSq}=2.1$   $P=\text{NS}$ ). Nevertheless the antennae seem to be implicated in the precision of the escape.

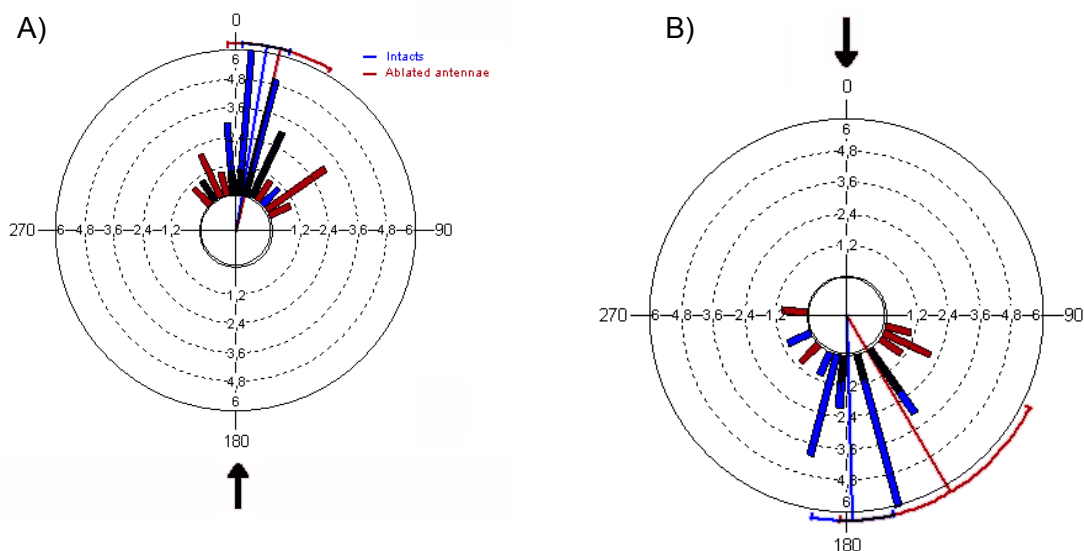


Figure 7: “The angle to piston” (Figure 2. angle  $\beta$ ) for 3 groups: intact crickets (in blue), crickets with ablated cerci (in red) and for crickets with ablated antennae (in orange). A) Representation of escape direction for stimulation at  $180^\circ$ . B) Representation of escape direction for stimulation at  $0^\circ$ .

Crickets lacking cerci (G2) showed a significant reduction in their escape success as compared to crickets with ablated antennae (G3) for a stimulation at  $180^\circ$  (Binomial test  $P=0.002$ ) and at  $0^\circ$  (Binomial test  $P=6.69 \cdot 10^{-6}$ ) (Figure 6). The variance of escape angles of intact and ablated crickets, once pooled, was higher for a stimulation at  $0^\circ$  than for a



stimulation at 180° (equal kappa test:  $\text{ChiSq}=5.55$   $P=0.018$ ) that can be easily explained by the rotation (that add variability) realised during an escape for a stimulation at 0°.

### 2.3.3. Effect of visual information in the escape behaviour

These experiments were carried out with cricket of the group J1. The crickets escape direction (“The angle to piston” Figure 2. angle  $\beta$ ) wasn’t different in the presence of visual information from the escape direction compared to that observed in a homogenous environment (aov.circular test,  $F=2,95$ ,  $P=NS$ ) (Figure 8). Nevertheless, the variance was wider in the presence of visual information than in homogenous environment (equal kappa test,  $\text{ChiSq}=3.89$ ,  $P=0.048$ ) (Figure 8).

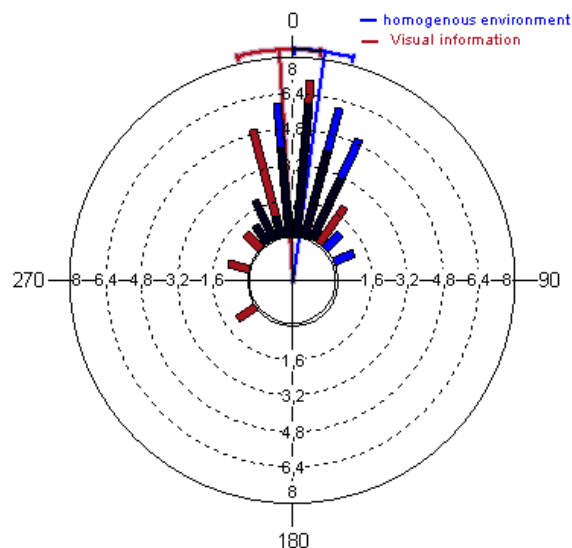


Figure 8: Escape direction (“The angle to piston” Figure 2. angle  $\beta$ ) of crickets in visually homogenous environment (in blue) or in presence of a visual information (black square) (in red) on the arena wall at 90° (according to the cricket orientation).



## 2.4. DISCUSSION

Crickets show a good rate of successful escape to a piston stimulus, reaching up to 67%. They show decreased performance when the piston came from the front ( $0^\circ$ ) compared to other stimulation angles. Younger crickets of group J1 performed better than older ones when the piston came from the rear ( $180^\circ$ ). Crickets of all groups escaped in the direction opposite to the stimulation direction with a very good correlation between escape and stimulation angles. The ablation of cerci affected drastically the rate of successful escape, both for a stimulation of  $180^\circ$  and for a stimulation of  $0^\circ$ . For a stimulation of  $180^\circ$ , crickets with ablated antennae showed a higher dispersion of escape angles than crickets from the other groups. For a stimulation of  $0^\circ$ , crickets from the ablated groups behave similarly, but statistically differently from the intact crickets.

Younger crickets showed better escape behaviour capabilities than older ones. The rate of successful escape was higher for juvenile than for adults. These results are in agreement with previous results obtained in the field (Dangles et al, 2007) and with the observation that early stage juveniles are more predated by spider than older ones (Dangles et al 2006b). All these observations are supported by the life history theory for crickets (Ydenberg and Dill, 1986, Dangles et al, 2006). We considered only air detection, thus all crickets touched by the piston were considered as not responding. The studies of Dangles (Dangles et al, 2007) showed however that touch perception by cerci plays an important role in the escape behaviour.

In our experiments, we obtained a rate of successful escape of 67% for a velocity of  $25\text{cm}\cdot\text{s}^{-1}$  which corresponds to the attack velocity of their natural predators, spiders of the genus *Pardosa* (Dangles et al. 2006a). In *Gryllus bimaculatus*, the rate of successful escape was 56% for a velocity of  $390\text{ cm}\cdot\text{s}^{-1}$ . To a stimulus velocity of  $10\text{ cm}\cdot\text{s}^{-1}$ , *Gryllus bimaculatus*



responded at a rate of 0.7% and *Grylloides sigillatus* at a rate of around 10%. For in *Grylloides sigillatus*, it was 94.4% for the same velocity. However, these experiments were performed with an air puff stimulus. Thus, using stimuli generated by the piston lead to better responses than simple air puffs, which have no natural counterparts. Moreover, in the experiments with air puffs the distinction between air flow perception and successful escape was not made. By contrast, all J1 crickets had moved before being touched by the piston, for a stimulation at 180° and 90°. Thus, the capability to escape was higher than expected on the basis of the previous experiments, run with other cricket species. To distinguish between the effect of the stimulus used and the crickets species, it will be necessary to realise the same experiments with the other species, using the piston to generate air movement. Furthermore our own experiments and the experiments realised in the field (Dangles et al. 2006) demonstrated that early instars of crickets *Nemobius sylvestris* are better at escaping than older ones. This is not clear for other species, since previous both behavioural and neurobiological experiments were performed exclusively on adults of *G. bimaculatus*, *A. domestica*.

Ablation experiments showed the importance of cerci in the escape behaviour. Nevertheless 24% of the crickets were able to escape the piston without cerci. This demonstrates that cerci are not the only one organ allowing the perception of an attacking predator. Ablation of antennae increased the dispersion of the escape angle, suggesting an implication of the antennae during escape. Moreover active movement on antennae was observed, particularly when the piston came from the front. An implication of the antennal system for perceiving and identifying potential predators was previously described in cockroach (Ye et al, 2003. Comer et al, 2003). Our experiments show the importance to use adequate stimulus and insects to study this natural behaviour.



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