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# Danger detection and escape behaviour in wood crickets

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ABSTRACT

The wind-sensitive cercal system of Orthopteroid insects that mediates the detection of the approach of a predator is a very sensitive sensory system. It has been intensively analysed from a behavioural and neurobiological point of view, and constitutes a classical model system in neuroethology. The escape behaviour is triggered in orthopteroids by the detection of air-currents produced by approaching objects, allowing these insects to keep away from potential dangers. Nevertheless, escape behaviour has not been studied in terms of success. Moreover, an attacking predator is more than "air movement", it is also a visible moving entity. The sensory basis of predator detection is thus probably more complex than the perception of air movement by the cerci. We have used a piston mimicking an attacking running predator for a quantitative evaluation of the escape behaviour of wood crickets *Nemobius sylvestris*. The movement of the piston not only generates air movement, but it can be seen by the insect and can touch it as a natural predator. This procedure allowed us to study the escape behaviour in terms of detection and also in terms of success. Our results showed that 5–52% of crickets that detected the piston thrust were indeed touched. Crickets escaped to stimulation from behind better than to a stimulation from the front, even though they detected the approaching object similarly in both cases. After cerci ablation, 48% crickets were still able to detect a piston approaching from behind (compared with 79% of detection in intact insects) and 24% crickets escaped successfully (compared with 62% in the case of intact insects). So, cerci play a major role in the detection of an approaching object but other mechanoreceptors or sensory modalities are implicated in this detection. It is not possible to assure that other sensory modalities participate (in the case of intact animals) in the behaviour; rather, than in the absence of cerci other sensory modalities can partially mediate the behaviour. Nevertheless, neither antennae nor eyes seem to be used for detecting approaching objects, as their inactivation did not reduce their detection and escape abilities in the presence of cerci.

## 1. Introduction

Escaping from predators is essential for animal survival. The wind-sensitive cercal system of Dictyopteran and Orthopteran insects (e.g., cockroaches, crickets, and locusts) is one of the most sensitive systems for detecting an attacking predator (Camhi et al., 1978; Shimozawa et al., 2003). It is constituted by two antennae-like appendages located at the rear of the insects (i.e., the cerci), each bearing a high number of sensory structures, in particular, numerous filiform hairs, highly sensitive to air-movements (Shimozawa et al., 2003). The function of the cerci of crickets and cockroaches, as well as the neural elements carrying and processing mechanosensory information have been extensively studied since the early 70s. Since then the cercal sensory system has become a classical model in neuro-ethology of sensory integration and behavioural guidance (Jacobs et al., 2008; Ritzmann, 1993).

Crickets possess the most elaborate cerci (Jacobs, 1995), and their cercal mechanosensory system is the one that has been the most intensively analysed. Studies on these insects focused on the neural basis of wind-detection (Bacon and Murphey, 1984; Jacobs and Miller, 1985; Jacobs and Theunissen, 1996, 2000; Jacobs et al., 1986, 2008; Miller and Jacobs, 1984; Miller et al., 1991; Murphey, 1981; Paydar et al., 1999; Yono and Shimozawa, 2008), on the escape behaviour (Gras and Hörner, 1992; Kanou et al., 1999, 2006; Tauber and Camhi, 1995; Schrader, 2000), and on the plasticity and recovery after cercal ablation (Kanou and Kondoh, 2004; Kanou et al., 1999, 2001, 2002). To stimulate the cerci, most studies employed air-puffs directed towards them. However, an attacking predator is a source of multimodal signals, which are not limited to air movements. For instance, a predator is a visible and moving entity and may touch the insect before it can escape.

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Therefore, the sensory basis of predator detection is probably more complex than only the perception of air movements by the cerci, and thus we have only a partial understanding of predator perception in crickets. Furthermore, escaping permits crickets to keep away from the danger of predation. Nevertheless, escape success is frequently neglected. For instance, no evaluation of the escape success of crickets has been done, since the use of air puffs does not allow such an evaluation. The use of a stimulus closer to a natural attacking predator could reveal other characteristics of escape behaviour; particularly, the escape success and the implication of other sensory systems.

The aim of our study was to investigate the escape behaviour of wood crickets using stimuli which more closely resemble natural ones, i.e., the controlled approach of a piston.

In recent years, the wood-cricket, *Nemobius sylvestris*, started to be the subject of diverse studies focusing on prey–predator interactions, functional neuroanatomy, and modelling of the detection of a predator by the cercal sensory system (Dangles et al., 2005, 2006a; Insausti et al., 2008, 2011; Magal et al., 2006; Steinmann et al., 2006). The main predator of this cricket species in the area of Tours, France, where most of these studies were conducted, are wolf spiders of the genus *Pardosa* (Dangles et al., 2006a), whose aerodynamics of attack has also been characterized in detail (Casas et al., 2008). This knowledge of the signal produced by attacking predators allowed us to adjust the parameters of our piston in order to match a natural stimulus.

## 2. Methods

### 2.1. Insects

Wood-crickets were caught in the forest around the city of Tours, France (47°23′N, 0°41′E), two months or less before the experiments. Crickets were maintained in plastic boxes ($53 \times 30 \times 35$ cm) at room temperature (between 17 °C and 25 °C) and under a natural illumination regime. Water and dry cat food was provided *ad libitum*, supplemented from time to time with fresh fruits.

Three groups of crickets were used: J1, composed of juveniles of instars 1–3 (posterior femur length $< 2.24$ mm; Campan, 1965), J2, composed of juveniles of instars 7–9 (posterior femur length $> 3.85$ mm; Campan, 1965), and A, composed of adults.

### 2.2. Experimental device

The experimental device (Fig. 1A) used to analyse the escape behaviour was composed of a circular turning platform sur-

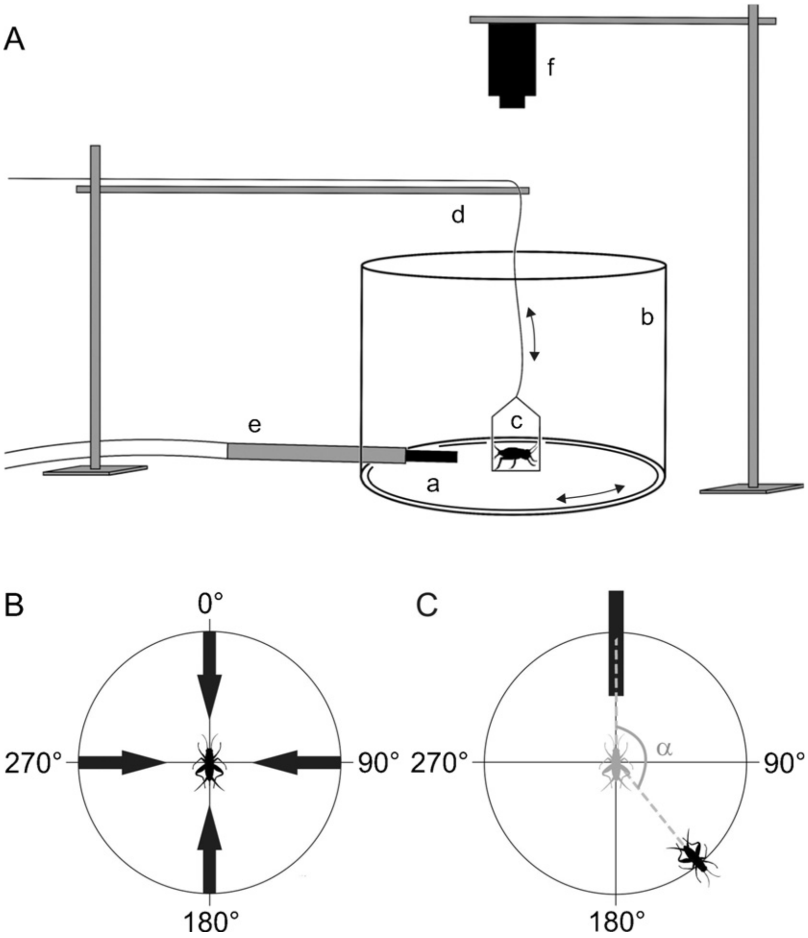

**Fig. 1.** (A) Set-up used to study escape behaviour. A circular turning platform covered with white paper (a) constitutes the experimental arena. A grey plastic cylinder (37 cm in diameter and 20.2 cm in height) (b) placed around the platform allowed us both to delimitate the experimental arena and to provide a homogeneous visual environment around the experimental individual. A transparent retention tube (2.8 cm in diameter) (c) was used to keep the cricket in place. A cricket was placed at the centre of the arena delimited by a cylinder (b). The base of the arena was a rotating area (a) allowing us to orientate the cricket according to the position of the piston (e). When the cricket was motionless, the tube (c) was removed gently by means of an articulated arm (d). If the cricket stayed immobile after the removal of the tube, the piston was activated and the cricket's behaviour was recorded by means of the high speed video camera (f). (B) Stimulation angles. Relative to the position of the cricket, it was stimulated at 0° (from the front), 90° or 270° (from the side) and 180° (from behind). (C) Escape angles correspond to the angle formed by the initial position of the cricket (at the beginning of the experience) (grey cricket) as related to the cricket longitudinal axis and the position of the cricket after escaping (black cricket).

rounded by a plastic cylinder, allowing both delimitation of the experimental arena and providing a homogeneous visual environment around the experimental individual. A transparent retention tube was used to keep the cricket in the centre of the arena until it was gently removed to release the cricket.

Spider attacks were simulated using a PC-controlled electromagnetic piston 0.8 cm in diameter (LAL35, Cedrat Technologies, Meylan, France) (Fig. 1A). The velocity and acceleration of the piston were accurately controlled using a computer (for more details see Dangles et al., 2006b, 2007). Two spot lights placed above the arena provide homogeneous illumination (2 spots of 230 V, 100 W white light). The cricket behaviour was recorded using one or the other of two high-speed video cameras (500 fps, res. 1280 × 1024 pixels. Gigaview from Southern Vision Systems, Inc. (SVSi), Madison, Alabama or 113 fps, res. 128 × 128 pixels. DALSA).

For stimulation, the piston was introduced into the arena through a hole at the base of the cylinder forming the arena wall. The piston was placed at a distance of around 4 cm from the cricket and moved at 25 cm/s over a distance of 4.5 cm. If a cricket did not escape, it was touched by the piston. In each trial, a cricket was placed at the centre of the arena, immobilized by the retention tube and then oriented according to the direction of the piston by rotating the platform. The tube was removed and the piston launched only when the cricket stayed immobile.

Crickets were stimulated from three directions: from the front (0°), from the side (90° or 270°) and from behind (180°), as represented in Fig. 1B. For the group J1, 22 crickets were stimulated from the front, 21 crickets from the side and 22 crickets from behind. For the group J2, 20 crickets were stimulated from the front, 20 crickets from the side and 21 crickets from behind. For the group A, 22 crickets were stimulated from the front, 21 crickets from the side, and 19 crickets from behind.

### 2.3. The involvement of different sensory organs

Crickets in the J1 group (i.e., instars 1–4) were divided into 4 subgroups. One of these subgroups ("intact") served as the normal control specimens, and received no surgical manipulation. Each of the other three subgroups was surgically altered to eliminate input from one of three sensory structures. Crickets in the subgroup "ablated antennae" were anesthetized by exposing them to a $CO_2$ atmosphere for 30 s, the antennae were cut and dental wax of low melting temperature was applied to seal the wound; ablations were performed at least 15 h before experiments. Crickets of the subgroup "ablated cerci" received the same procedure as before to remove their cerci. Crickets of the subgroup "covered eyes" were anesthetized by exposing them to a $CO_2$ atmosphere and their compound eyes were covered by black acrylic paint, at least 15 h before experiments.

### 2.4. Video and data analyses

Two different behavioural responses were quantified: "detection", defined as any evasive movement of the cricket, whether or not it was eventually touched by the piston, and "escape", defined as any evasive manoeuvre resulting in avoiding any contact with the piston.

The escape direction was measured and defined as the angle formed by the centre and longitudinal axis of the cricket's body at the beginning of the experience and the position of the centre of the body after escaping (Fig. 1C). We measured it with MB Ruler 3.3 software (Markus Bader – MB-Software solutions). The distance between the tip of the cerci and the piston was measured when the cricket started moving, but only for crickets that detected the piston movement coming from behind. Finally, the escape mode (jump, run, and turn) and the active movement of the antennae were noted for crickets that escaped successfully.

### 2.5. Statistical analyses

Two successive responses were analysed, i.e., piston detection and escape. These responses were studied on the three groups of crickets. Different directions of stimulation were presented to the cricket from the front, from the side and from behind.

Detection and escape rates for the different angles of stimulation and ages were compared using the binomial test (Hollander and Douglas, 1973). In case of multiple comparisons, the Bonferroni correction was applied. The escape direction angles were compared to the predicted direction using the *V* test or one to the other using the Williams *F* test (Zar, 2009). The detection distances were compared using the Kruskal–Wallis test.

## 3. Results

### 3.1. Escape behaviour and age

Fig. 2A shows the frequencies of occurrence of the two different responses, for the different age groups as a function of the piston directions. Crickets reacted more reliably to the approaching piston when it came from behind (i.e., 180°) or from the side than when it approached from the front (see Table 1 for the statistical analysis). In addition, the early juveniles (J1) performed better than the juveniles (J2) and adult (A) crickets (Table 2). All the early juveniles (J1) detected the piston when it approached from behind

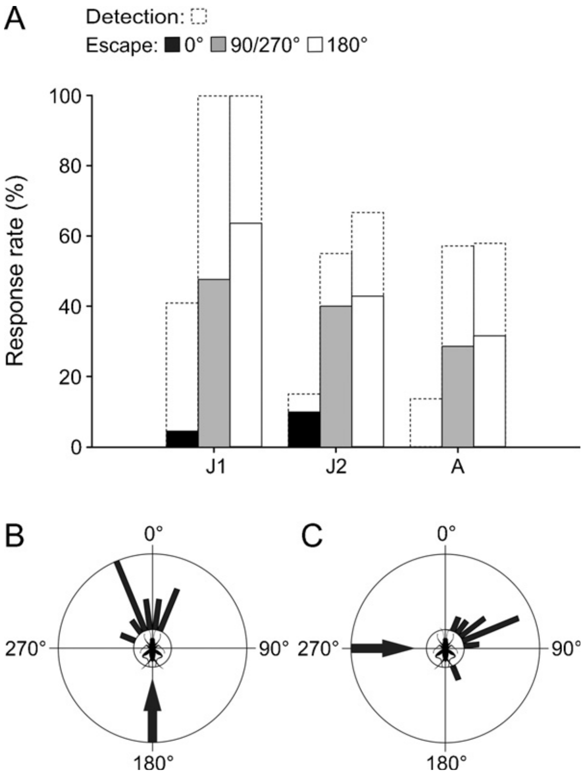

**Fig. 2.** (A) Response rates for the three groups of different developmental level J1 (1st to 3rd instars), J2 (7th to 9th instars), and A (adults), and the three directions of stimulation from behind (in black), from the side (in grey), and from the front (in white). Rates of two responses are represented; the detection of the stimulation (dashed lines) and the successful escape (full bars). (B) and (C) Distribution of escape angles of J1 crickets. Black arrows represent the stimulation direction. External circle corresponds to $N = 10$. (B) Results for a stimulation from behind. (C) Results for a stimulation from the side.

**Table 1**
Results of the statistical analysis (binomial tests) for comparisons between directions of stimulation (according to cricket). As multiple comparisons were done, a Bonferroni correction was applied and differences were considered as significant * for a $P < 0.016$ ($\alpha/3$, eq. $\alpha$ $P < 0.05$). ** correspond to $P < 0.003$ (eq. $\alpha$ $P < 0.01$) and *** to $P < 0.0003$ (eq. $\alpha$ $P < 0.001$). NS indicates non-significant statistical results, $P > 0.016$.

| | | Detection | Successful escape |
|---|---|---|---|
| Front vs behind | J1 | *** | *** |
| | J2 | *** | *** |
| | A | *** | *** |
| Front vs side | J1 | *** | *** |
| | J2 | ** | * |
| | A | *** | ** |
| Behind vs side | J1 | NS | NS |
| | J2 | NS | NS |
| | A | NS | NS |

**Table 2**
Results of the statistical analysis (binomial tests) for comparisons between cricket age groups. As multiple comparisons were done, a Bonferroni correction was applied and differences were considered as significant * for a $P < 0.016$ ($\alpha/3$). ** correspond to $P < 0.003$ and *** to $P < 0.0003$. NS indicates non-significant statistical results, $P > 0.016$.

| | | Detection | Successful escape |
|---|---|---|---|
| J1 vs J2 | Front | ** | NS |
| | Side | *** | NS |
| | Behind | *** | NS |
| J1 vs A | Front | ** | *** |
| | Side | *** | NS |
| | Behind | *** | ** |
| J2 vs A | Front | NS | *** |
| | Side | NS | NS |
| | Behind | NS | NS |

or the side. The success rate of J1 crickets was significantly better than that of A crickets for a stimulation from behind or from the front. The success rate of J2 was significantly higher than that of A crickets for a stimulation from the front. No difference was observed for other directions of stimulation or other groups. No significant difference was observed in the detection distance between J1 (detection at 8.5 ± 0.7 mm, mean ± S.E.M.), J2 (6.9 ± 1 mm) and A groups (8.3 ± 1.6 mm) (Kruskal–Wallis test: H = 2.93, 2 d.f., $P$ = NS). Crickets escaped by jumping or walking and, depending on the piston direction, they turned before escaping (stimulation from the front or the side) or did not (stimulation from behind, Table 3). For a piston approaching from the front or from the side, most crickets that successfully escaped first turned and then either jumped or walked.

**Table 3**
Escape behaviour of the three groups of different developmental stages for the different directions of stimulation. The escape is often constituted as a succession of different actions. Columns refer to the turn action and rows to the escape action. Percentages of crickets performing the action are indicated in the corresponding box.

| | | Turn | | | No turn | | |
|---|---|---|---|---|---|---|---|
| | | Front | Side | Behind | Front | Side | Behind |
| J1 | Only turn | 0 | 0 | 0 | – | – | – |
| | Jump | 100 | 70 | 7.14 | 0 | 10 | 85.71 |
| | Walk | 0 | 10 | 0 | 0 | 10 | 7.14 |
| J2 | Only turn | 50 | 12.5 | 0 | – | – | – |
| | Jump | 50 | 75 | 0 | 0 | 0 | 77.77 |
| | Walk | 0 | 12.5 | 0 | 0 | 0 | 22.22 |
| A | Only turn | 0 | 33.33 | 0 | – | – | – |
| | Jump | 0 | 50 | 0 | 0 | 0 | 33.33 |
| | Walk | 0 | 16.66 | 0 | 0 | 0 | 66.66 |

### 3.2. Escape performance

The proportion of crickets that perceived the approaching piston before it reached them was higher than the proportion of crickets that successfully escaped (for J1, from the front: $P < 0.001$; from the side: $P < 0.001$; from behind: $P < 0.001$). Indeed 5–52% of crickets that detected the stimulation were touched by the piston (all age groups and directions taken together) (Fig. 2A).

Because younger crickets showed better performances than older ones (Fig. 2A) particularly for the detection, and because younger crickets seem to be more predated by spiders (Dangles et al., 2006a), the subsequent analyses were conducted on crickets from group J1 only.

### 3.3. Escape direction

We also analysed the escape behaviour of group J1 as a function of the stimulation direction. Only the escape direction of crickets which escaped successfully was taken into account in this analysis. A very low proportion of crickets succeeded in escaping from stimulation from the front (1/22). Crickets mostly escaped in the direction opposite to the approach of the piston, but with a wide range of angles (Fig. 2B and C). For a stimulation from behind, crickets escaped at 169° ± 7° (mean ± S.E.M.) relative to the piston position (Fig. 2B) and for a stimulation from the side, they escaped at 156° ± 12° (mean ± S.E.M.) relative to the piston position (Fig. 2C). So, crickets escaped away from the stimulus in an opposite direction ($V$ test, theoretic angle = 180°: $V = 0.912$, $P < 0.001$ from behind and $V = 0.77$, $P < 0.001$ from the side). No difference was observed in the escape direction relative to the piston approach, to stimulation from behind and from the side (Watson–Williams $F$ test: $F_{1,22} = 1.324$, $P$ = NS).

### 3.4. Involvement of the different sensory organs in the escape

We conducted ablation experiments on J1 crickets to determine the relative contributions of the cerci and other sensory organs in the detection of air movement and escape behaviour. Either the antennae or the cerci were cut to eliminate sensory inputs from these organs, and we evaluated the performance of crickets responding to piston thrusts from the front and from behind.

Detection rate and escape success were significantly lower for crickets with ablated cerci than for intact crickets to stimulations coming from both directions (Fig. 3). Nevertheless, 48% of the crickets were still able to detect the approaching piston, and 24% were able to escape from stimulation from behind (Fig. 3).

Crickets lacking antennae showed detection and escape rates comparable to those of intact crickets when the piston approached from behind (Fig. 3). For a stimulation from the front, crickets with ablated antennae showed an apparently better detection ability than intact crickets, and no difference in successful escape rate was found between these two groups. Indeed, during stimulations from the front a majority of intact crickets were touched by the piston on the antennae; that was not possible in insects without antennae, giving the wrong impression that they were more successful in detecting the piston. We also observed that crickets tends to move their antennae towards approaching objects, a behaviour that was previously observed in crickets *Gryllus campestris* (Honegger, 1981). This behaviour was observed in 18% of the crickets stimulated from the front. The presence of these long antennae and this particular behaviour increase the probability of being

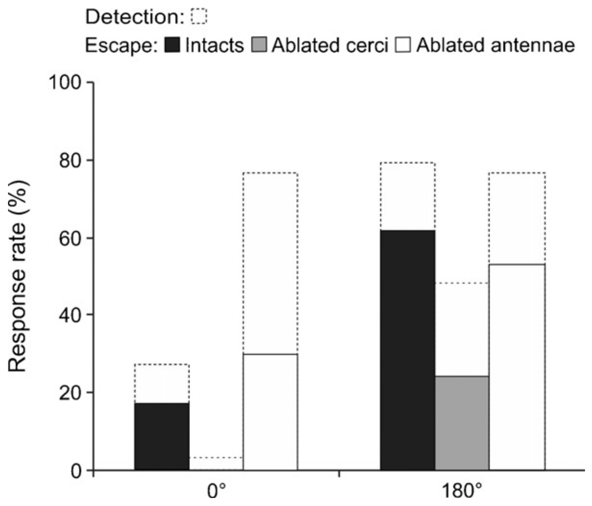

**Fig. 3.** Responses rates for the two directions of stimulation from the front and from behind and for intact crickets (black bars), crickets with ablated cerci (grey bars) and crickets with ablated antennae (white bars). Rates of detection of the stimulation (dashed lines) and of the successful escape (full bars) are represented.

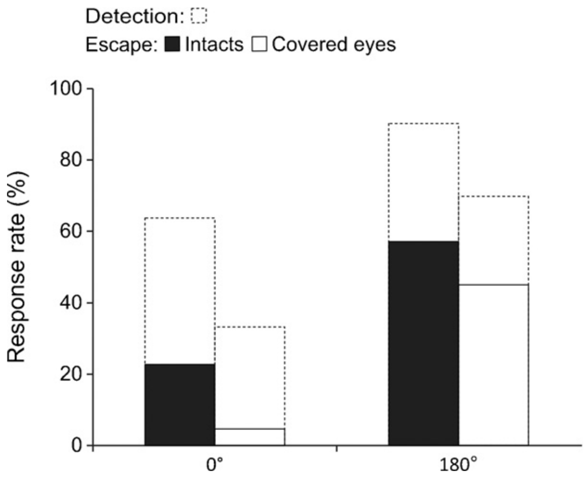

**Fig. 4.** Responses rates for two directions of stimulation from the front and from behind, for intact crickets (black bars), covered eyes crickets (white bars). Rates of two responses are represented; the detection of the stimulation (dashed lines) and the successful escape (full bars).

touched on the antennae by the piston. In this case, the increase of the detection rate does not correspond to better detection capabilities in antennectomized crickets.

To test this hypothesis we reanalysed the response of intact crickets. This time we did not take into account the antennae. So we considered that the cricket detected the piston when it moved before being touched by the piston somewhere on its body, except the antennae (i.e., if only their antennae where touched by the piston we considered that the cricket detected the piston). In this case, 69% of intact crickets could be considered as having detected the piston. This rate is not significantly different from the detection rate of the crickets with ablated antennae. Two other cases also yielded statistically equivalent detection rates: stimulation from the rear of crickets with intact cerci and antennae, and stimulation from the front of crickets with ablated antennae. Thus, the detection ability of crickets was similar to stimulation from the front and from behind (Table 4). So, depending on the evaluation criteria, the presence of the antennae extending forwards may influence our evaluation of the ability of crickets to detect an object approaching from the front, provided that they are easily touched by the piston.

Crickets with covered eyes showed a significant decrease in the detection rate as compared to intact crickets (Fig. 4) for a stimulation from the front (binomial test: $P < 0.01$) and for a stimulation from behind (binomial test $P < 0.01$). No effect from the elimination of visual inputs was observed on the success of escape for a stimulation from behind (binomial test: $P$ = NS). For a stimulation from the front the statistical result is close to the significance (binomial test: $P = 0.06$) indicating a small effect from the elimination of visual inputs.

**Table 4**
Results of the statistical analysis (binomial tests) for comparisons between different groups of crickets. As multiple comparisons were done, a Bonferroni correction was applied and differences were considered as significant * for a $P < 0.0125$ ($\alpha/4$). ** correspond to $P < 0.0025$ and *** to $P < 0.00025$. NS indicates non-significant statistical results, $P > 0.0125$.

| | Detection | Successful escape |
|---|---|---|
| Intacts vs ablated cerci | Front: **<br>Behind: *** | Front: *<br>Behind: *** |
| Intacts vs ablated antennae | Front: ***<br>Behind: NS | Front: NS<br>Behind: NS |
| Ablated cerci vs ablated antennae | Front: ***<br>Behind: ** | Front: ***<br>Behind: ** |
| Intacts stimulation from behind vs ablated antennae stimulation from the front | NS | ** |

## 4. Discussion

To escape from the attack of a predator, animals should be able, first, to detect the approaching danger as soon as possible and, second, to trigger the most appropriate motor pattern in terms of velocity and directionality. Most previous studies on the escape behaviour of crickets have been conducted by stimulating the crickets with air puffs (Kanou et al., 1999, 2006; Schrader, 2000; Tauber and Camhi, 1995). This type of stimulation, although easily controllable, neither distinguishes the different steps involved in escaping, nor evaluates the relative contribution of cerci in attack detection. In our experiments using the piston, it was possible to evaluate separately: (1) detection, as the number of crickets moving during the approach of the piston, i.e., before any contact and (2) escape, as the number of crickets that avoided being touched by the piston.

We found that the escape probability was always lower than the probability of detecting the approaching object, for all groups of crickets and for all stimulation directions. Indeed, the detection of the approaching piston was not always followed by successful escape and 5–52% of crickets that detected the stimulation were touched by the piston. This result emphasizes the importance of studying not only detection capabilities, but also escape capabilities. Younger crickets show better performance than older ones. This result, previously observed in field experiments (Dangles et al., 2005), is confirmed here under controlled laboratory conditions.

Concerning the direction of the stimulation, our results on intact crickets show significantly higher detection performances for the stimulation from behind than from the front. After ablation of antennae, or not taking into account if they are touched in intact crickets, we observed no difference between stimulations from the front or from behind concerning the ability to detect the approaching piston. However, differences still exist for the escape rate, i.e., significantly more crickets escaped successfully when stimulated from behind than from the front. The poor ability to escape from a frontal stimulation could be related to motor constraints rather than to a sensory inability to detect it, because crickets turn before jumping, adding a supplementary delay as compared to just jumping. It has been reported that *Troglophilus neglectus* crickets use a different sequence of movements to escape: they jump backward, away from the stimulus (Schrader, 2000), which could constitute a better strategy to quickly create distance between the cricket and objects approaching from any direction.

The ability to detect approaching objects was higher in our experiments than that observed in *Gryllus bimaculatus* (Kanou et al., 1999), or in *Gryllodes sigillatus* (Kanou et al., 2006). Our study was conducted using a piston approaching at 25 cm/s, a speed that seems to evoke the highest escape response of *N. sylvestris* (Dangles et al., 2006b). The air-speed stimulating the cerci was lower, since air-speed decreases with the distance from the piston (Casas et al., 2008; Kant and Humphrey, 2009) and crickets reacted before being touched. In other species, the air-speed employed to stimulate escape with air-puffs was much higher. For instance, a stimulation velocity of 90 and 300 cm/s were used in studies using *G. bimaculatus* and in *G. sigillatus* (Kanou et al., 1999, 2006). These velocities appear to be too high compared to that generated by an approaching predator (Casas et al., 2008; Magal et al., 2006). Moreover, a stimulation of 90 cm/s induces a low response in the crickets as only 1.3% and 10% of the crickets reacted respectively (Kanou et al., 1999, 2006), whereas in our experiments 43% of the adult crickets (and 80% of J1) responded to a stimulation of 25 cm/s.

Cerci ablation experiments confirmed the essential role played by these organs, since the rate of detection fell drastically in their absence. They also revealed, however, that cerci are not the sole organs involved in the detection of approaching objects in crickets. Indeed, in the absence of cerci, 48% of crickets still detected the piston movement and 24% escaped successfully. Residual capacity of detection after cerci ablation was also observed in *G. bimaculatus* (Kanou et al., 1999) and *G. sigillatus* (Kanou et al., 2006). Thus, crickets could perceive the air current produced by an approaching object by means of mechanoreceptors located on other parts of their body, as filiform hairs are distributed over almost the whole body surface, particularly on antennae, or by using other sensory modalities. We have partially analysed the contribution of the visual and antennal inputs. Surprisingly, ablation of antennae did not affect detection performances, even for stimulation from the front. It has been suggested for cockroaches that the "appropriate stimulus" for the antennae is probably touch, rather than wind (Comer and Leung, 2004; Comer et al., 1994; Stierle et al., 1994). The antennae may, nevertheless, offer the crucial function of redundancy for cases in which an animal would lose one or both cerci. Detection of the piston was also affected by the suppression of visual inputs, for the stimulation from the front and from behind, although no statistically significant effect on the rate of escape was observed. Because our measures of the visual field of *N. sylvestris* revealed that it does not extend enough to the rear to be able to see objects placed behind the insect, the decrease in the detection ability observed in crickets with covered eyes could be induced by a general decrease of the activity (kinetic effect) in the absence of light (Guillott, 2005).

Spiders are the main predators of *N. sylvestris* in the geographical area of this study. As we have shown, the escape success from an approaching object is strongly affected by the direction of approach. No data is, at present, available concerning the directionality of spiders' attack when trying to capture a cricket. Given the arms race usually established in evolutionary terms between predator and prey, it is possible that spiders had adapted their attacking strategy to exploit the low performance of crickets when attacked from certain directions, to increase their chances to succeed. Future work should focus on real attacks, in order to fully understand the actual functionality and performance of the sophisticated sensory system of the cerci.

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