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# Sensory modalities underlying the escape response of the cricket, *Acheta domesticus*, to looming stimuli

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Sensory Modalities Underlying the Escape Response of the Cricket, *Acheta domesticus*, to  
Looming Stimuli

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An Honors Program Project Presented to  
the Faculty of the Undergraduate  
College of Science and Mathematics  
James Madison University

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by Ariel Miranda Childs

May 2016

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Accepted by the faculty of the Department of Biology, James Madison University, in partial fulfillment of the requirements for the Honors Program.

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## **II. Acknowledgements**

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### **III. Abstract**

In order to prevent injury or capture by a predator, animals have evolved escape behavior. Despite offering a more realistic, multimodal, approximation of an approaching predator, looming stimuli have rarely been used to evoke escape behavior in crickets. Wind stimuli, however, have been used on a variety of insects, including crickets where it has been found that direction of escape is directly correlated to the angle of incoming wind stimuli. Wind stimuli are detected by sensilla trichodea, small filiform hairs covering the cerci of crickets, locusts and cockroaches. Despite having other complex sensory systems, such as antennae and vision, little is known concerning utilization of these systems in evoking escape behavior. In this two part study, a looming stimulus was used to determine if angle of approach affects angle of escape in the cricket, *Acheta domestica*. Subsequently, ablation experiments were used to determine which sensory modalities, vision, antennae and cerci, are necessary or sufficient for evoking an escape response. To the looming stimulus, the angle of escape was directly correlated to angle of stimulus approach, with crickets escaping directly away from the stimuli ( $r^2 = 0.87$ ;  $p < 0.001$ ). When escape response frequency was analyzed based on angle of approach, vision was necessary and sufficient to evoke an escape response at anterior angles only ( $p < 0.0005$ ). At posterior and midline angles, cerci were necessary and sufficient to elicit escape response and angle of escape was directly correlated to angle of stimulus approach ( $p < 0.0005$ ).

### **IV. Introduction**

Invertebrates, insects especially, provide a model organism with which to study the effect of aversive stimuli on escape behavior. Insects provide a simplified insight into the underlying systems involved in stereotypic behavior elicited by more complex organisms. Experimental models using insects simplify methodology, lessen time and lower cost simplifying experimental

protocols in comparison to more complex animals. Certain insects, such as locusts, cockroaches and crickets also employ the use of specialized sensory systems not present in mammalian counterparts, such as antennae and cerci. The cercal system, in particular its role in eliciting escape behavior, has been studied in a variety of insects using diverse stimuli (Kanou et al. 2014, Camhi and Tom, 1978, Dupuy et al. 2011). Other than that of locusts, there is little information regarding an insect's behavior in response to multi-directional looming stimuli, and its utilization of other sensory mechanisms (Santer et al. 2006). In order to fully understand an escape behavior one must first understand the components from which it is derived. The response of an organism to a stimulus can be broken down into three main questions addressing: stereotypic behavior, factors influencing escape response directionality and underlying sensory mechanisms.

## **A. Behavior**

Escape behavior is the natural response of many animals to deter injurious or mortal wounds that may be inflicted by an advancing predator, thus maximizing their chance of survival and increasing reproductive potential (Dominici, 2011). Experimental stimuli, such as auditory, visual or wind stimuli, looming objects and live toads, have been utilized to mimic the natural stimuli elicited by an advancing predator (Camhi and Tom, 1978; Kanou et al. 2006; Dupuy et al. 2011; Santer et al. 2005). For example, when an aversive noise stimulus is presented to goldfish (*Carassius auratus*) they respond by quickly C-bending their bodies away from the stimulus (Preuss and Faber, 2003). In response to visual stimuli, such as video recordings representing shadows of aerial predators, lizards (male Jacky dragons) will either startle and flee to cover or startle and remain immobile (Carlile et al. 2005).

In response to a wind stimulus, cockroaches turn away from the wind and run or walk away (Camhi and Tom, 1978). Even when faced with the relatively low air displacement



produced by a live, natural predator, such as a bullfrog, cockroaches display similar escape behavior: an initial pivot away from the source of stimuli and run, or, in this specific case, gets captured (Camhi et al. 1978).

Crickets respond to experimental wind stimuli in one of three ways: 1) turning, arising from a pivot about the rear of the animal 2) jumping, without taking any steps or 3) first turning and then jumping (Tauber and Camhi, 1995). In addition to turning, crickets utilize jumping as a means of escape and tend to jump when the stimulus is produced from approximately behind and at angles more toward the posterior end (Tauber and Camhi, 1995). Overall, crickets turned in 16 out of 46 trials, jumped 6 of 46 trials and turned and jumped 24 of 46 trials, demonstrating a preference for turning and jumping (Tauber and Camhi, 1995).

Locusts primarily use jumping to escape in response to looming stimuli, which offer both visual and wind cues. The locusts cock their hind-legs and either remain jump-ready or jump (50% of trials) consistently away from the side in which the stimuli presented (Santer, 2005). Due to the high likelihood of locust jumping away from a stimulus, escape directionality is ascertained by a locust's ability to land on a specific location. In comparing voluntary jumps to those elicited by a stimulus, locusts tend not to land at a designated spot, when eliciting stereotypical jumps, as urgency and last-minute trajectory adjustments are crucial for escape (Santer et al. 2005).

To looming stimuli, whether produced using a computer display, characteristic predatory shadow or circular ball on a piston, animals will elicit similar escape behavior. When confronted with an expanding small black circle on a computer display that gets larger in diameter with time, goldfish were observed to execute a c-shaped bend of the head and tail and a subsequent flip for forward propulsion (Preuss et al. 2006). To similar representations of looming objects,

Jacky dragons initially startle and then flee to cover or orient themselves to the location of the stimulus (Carlile et al. 2006).

Looming objects, which better emulate an attacking predator, also elicit escape behavior in insects. Locusts will alter their flight pattern and stereotypically glide and dive in response to a looming object represented by a black disc on a video screen (Santer et al. 2006). When confronted with a cylinder piston rod projected at them, crickets will turn and walk or jump away (Dupuy et al. 2011).

## **B. Directionality**

Escape behavior can be quantified by the direction in which an animal turns or moves. Zebrafish (*Brachydanio rerio*) and goldfish (*Carassius auratus*) were observed to typically turn to the right, away from a stimulus, after an initial C-bend (Domenici, 2011; Heuts, 1999). Lizards (*Podarcis muralis*) also typically turn to the right, when the stimulus approaches from behind (Domenici, 2011; Bonati et al. 2010). Frogs, (*Hyla regilla*) on the other hand tend to jump, or otherwise escape, to the left, when stimulated on the right or rear and more forward when stimulated on the left (Domenici, 2011; Dill, 1977).

In insects such as locusts, the dependence of angle of escape on angle of stimulus approach has not been found to be strongly correlative; however, they tend to favor escaping away from the side in which the stimulus approached (Santer et al. 2005). Unlike locusts, many other insects, including cockroaches and crickets, have shown strong correlation between escape trajectory and stimulus laterality (Santer et al. 2005; Domenici et al, 2005; Kanou et al, 1999 and 2006; Tauber and Camhi, 1995; Dupuy et al. 2011). For example, when faced with a wind stimulus, intact crickets are not only able to discriminate right/left wind direction but the angle of

approach on each side, turning between 162-180 degrees away from the stimulus (Kanou et al. 1999).

## **C. Physiological Mechanism of Insect Sensory Modalities**

In order to be able to detect minute changes in the environment through a thick exoskeleton, insects have evolved extremely small pores with sensitive receptors on a few key surfaces, such as the cerci and antennae (with a small number on the mouthparts). In combination with the eyes, these modalities provide the sensory basis for escape (Klowden, 2007).

### **a. Cercal System**

When a predator advances towards prey it can produce wind currents and many invertebrates have benefitted by evolving sensory systems to detect even minute wind currents and react accordingly. A variety of insects, including crickets, utilize a specialized neural mechanism comprised of appendages called cerci, covered in hundreds of thin, hollow, filiform hairs or sensilla trichodea, attached posterior to the abdomen (Dethier, 1963). The filiform hairs covering the cerci are a relatively long and extremely delicate form of mechanoreceptor that can detect small changes in air currents associated with approaching predators (Dethier, 1963; Olsen et al. 2014). Interestingly, cercal hairs exhibit characteristics similar to that of mammalian cochlear receptors, including synchronization with stimulus action potentials at low stimulus frequencies (Dethier, 1963). On the cerci, at the base of each sensilla trichodea, is an axon attached to the terminal abdominal ganglion, within which are wind-sensitive interneurons that carry information to the thoracic ganglia which contains motor regions (premotor and motor neurons) that generate escape responses (Olsen et al. 2014).

The cercal system has proven an integral sensory system in eliciting escape behavior in insects. When the cerci were ablated in crickets, response rates to wind stimuli decreased from

95% to 4.1% (Kanou et al. 2006). Cerci are also crucial for insects to determine their degree of turn. When cerci were covered unilaterally, cockroaches were misoriented in turning responses and often turned towards the stimuli (Camhi et al. 1978).

## **b. Eyes**

An attacking predator is a source of multimodal signals, which are not limited to air movements detected by the cerci or antennae. For example, a predator elicits wind from movement but is also a visual entity (Dupuy et al. 2011). Crickets, and many other insects, have developed complex, compound eyes to obtain visual information from their surroundings. Compound eyes are comprised of groups of individual optical units called ommatidia, each with its own lens and light receptors (Zufall et al. 1989; Klowden, 2007). Each species of insect has its own unique number of ommatidia. Cockroaches (*Periplaneta americana*), for instance, have around 2,000 ommatidia and dragonflies can have as many as 30,000 (Klowden, 2007). Each ommatidia can vary in size, shape and functionality, based upon the area in which it is located on the eye, and produces its own image which is integrated, in combination with images produced by other optical units, in the insect's central nervous system. Depending on the radius of the eye, insects can have markedly large fields of vision with a panoramic view of their surroundings (Klowden, 2007). Crickets, in particular, have relatively large fields of vision for their size, from 6 to 67 degrees along the x-axis and 6 to 37 degrees along the y-axis (Blum and Labhart, 2000). Within each section of ommatidian lie photoreceptors that can register different wavelengths of light (Zufall et al. 1989). In crickets (*Gryllus bimaculatus*) blue light receptors (wavelength 445nm) were found only in the dorsal rim area, UV light (wavelength 332 nm) receptors were found in the dorsal region of the pigmented area, and green receptors (wavelength 515 nm) were found in the dorsal, ventral and frontal regions of the eye (Zufall et al. 1989).

When a group of crickets had only their eyes covered with a non-toxic, thick black nail lacquer there was a significant decrease in frontal detection rate of a looming object represented by a piston ( $p < 0.01$ ) as compared to that of their intact counterparts (Dupuy et al. 2011). These findings indicate that vision plays a role in the detection and escape from looming objects (Dupuy et al 2011).

Vision has also been shown to aid in the directionality of escape. When presented with a wind or tactile stimulus, crickets (*Gryllus bimaculatus*), escaped to a “shelter”, an area enshrouded in a dark background, rather than escaping to a white or lighter background region, almost 100% of the time (tactile-98% between 30 to 200 seconds after stimulation; wind puff-98.3%; Kanou, et al. 2014). Vision has also been shown to aid other sensory modalities in information gathering (Yoshifumi et al. 2014).

### **c. Antennae**

Insect antennae are comprised of a variety of sensory receptors, including mechanoreceptors, chemoreceptors and even olfactory receptors, which aid in a plethora of functions. For example, sensilla trichodea, the mechanoreceptors that also comprise the cercal system for wind detection in certain insects, are also found on the antennae (Dethier, 1963). While crickets and other insects are afforded complex visual systems, visual stimulation alone has not been shown sufficient to produce an escape response (Yoshifumi et al. 2014; Ye et. al. 2003). Vision, can however, aid the antennae of crickets and cockroaches in discerning predator from non-predator and male competition from viable females (Leonard and Hedrick, 2009; Okada and Akamine, 2012; Yoshifumi et. al. 2014; Dupuy et al. 2011; Ye et al. 2003).

Concerning initial escape behavior, it is clear the antennae are not involved in evoking a response. When a group of crickets' antennae were ablated and presented with a looming stimulus in the form of a piston, there was no significant difference in detection between those ablated and intact trials (Dupuy et. al. 2011). These findings may reinforce the observation that antennae are utilized primarily for gathering further information about a stimulus.

Although antennae are not necessary for eliciting an escape response in insects, they have been shown to aid in gathering other sensory information (Yamawaki et al. 2014). Cockroaches will point their antennae towards white-tipped rods entering their field of vision (Ye et. al, 2003). Similarly, when supplied with a different visual cue in the peripheral field of view, such as a small styrofoam ball, crickets tend to point their antennas towards the incoming looming object (Yamawaki et al. 2014). In both cases, the antennal positioning was correlated with turn angle ( $p < 0.005$ ), a crucial second element of overall escape behavior (Ye et al. 2003).

Previous literature does not mention the influence of sensilla trichodea located on other parts of the body, such as the legs, on escape behavior. According to Klowden, these mechanoreceptors are only located on a few key surfaces, such as the antennae, mouthparts and cerci and likely do not aid in escape behavior (Klowden, 2007).

## **V. Specific Aims**

In the common house cricket, *Acheta Domesticus*, there is little information regarding the escape behavior in response to a looming stimulus and if the horizontal angle of stimulus approach influences escape direction. In order to determine how crickets respond to looming stimuli and if the angle of approach affects escape, crickets were presented with a looming stimulus, comprised of a 2" ball on a piston cylinder, projected at 45 degree incremental angles lateral to the cricket. I

predicted that the angle of stimulus approach would affect cricket escape trajectory due to previous research on wind stimulus in which direction of escape trajectory correlated with the angle of approach.

There is also a deficit in information regarding which modality, such as the cerci, eyes or antennae, offers the primary source of input at various lateral angles. I investigated the role of vision, antennae and cerci were investigated by ablating individual sensory modalities and presenting a looming stimulus at various lateral angles. I predicted that the sensory modalities utilized would be determined by stimulus laterality; specifically, visual information would elicit an escape response when an incoming stimulus presents at anterior angles only, while cercal information would be used for posterior angles. Crickets have a complex visual system with a large visual range. With cerci located at the posterior of the cricket, it follows that a sensitive sensory system would be necessary for escape, in the case of stimuli presented anteriorly.

## **VI. Methods:**

### **A. Crickets**

Nymph (adolescents that have not completed their final molt) male and female house crickets (*Acheta Domesticus*) were obtained from a local pet store (PetSmart, Harrisonburg, Virginia). Although most previous studies have used common field crickets (not commonly available commercially in the U.S), *Acheta domesticus* was used by Stabel et al. in 1985 to test escape response and Olberg and Miller in 1991 to explore the sensory information of the cricket cercal system. Crickets were fed an unrestricted diet of cricket food (Polyacrylamide copolymer with added calcium by Gutload™) and water. Crickets were typically tested between 10am and 5pm in a temperature-controlled room that varied between 20-22 degrees Celsius.

## **B. Set-up**

The experimental set-up included an eight-inch circular “stage” comprised of white, paint-coated canvas (to minimize slippage) layered on thin pine wood and mounted on three felt pads to decrease noise and friction during movement. The stage was encircled by a three-inch high barrier comprised of white poster paper taped into a circle and fitting flush around the stage (Figures 1 and 2). While acclimating to the stage, the cricket was housed in acrylic tubing (2” in diameter and 3.5” high) wrapped in tape to allow some light but limited visual cues. Similar staging areas were used in several previous studies including Kanou et al. in 2006, however, they encircled this “arena” in wire mesh, whereas we used a matte white poster board and a non-transparent cup so as to prevent unintentional visual cues from the environment (Kanou et al. 2006).

## **C. Looming Stimulus**

The looming object stimulus was comprised of a 2.5” black polystyrene ball attached to the end of a piston arm of a 12” air-cylinder angled 45 degrees from the surface of the experimental stage and placed on its own table to eliminate vibrational coupling to the stage that could be detected by cricket mechanoreceptors. Compressed nitrogen at 11 psi was used to power the air cylinder resulting in a ball-speed of 1.0 m/s toward the cricket. Fully extended, the ball remained 2 cm from the midline of the cricket and care was taken to ensure physical contact with the cricket, especially the antennae and cerci, did not occur. The piston was triggered using a custom made switch which also simultaneously triggered the camera to begin video acquisition (Fig. 1 and 2).

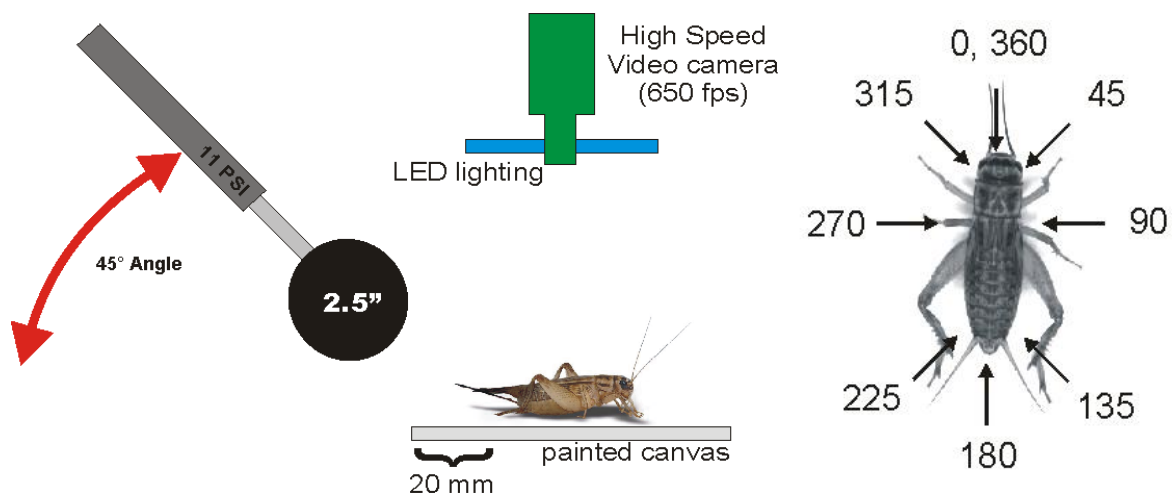


## D. Video Recording

A circular, low-heat LED light was placed directly over the staging area surrounding a high-speed camera (IDT/Redlake Pasadena, CA) that recorded at 650 frames per second, which was located directly over and pointed straight down over the staging area. The camera was triggered simultaneously with the stimulus trigger mechanism to ensure capturing the full response.

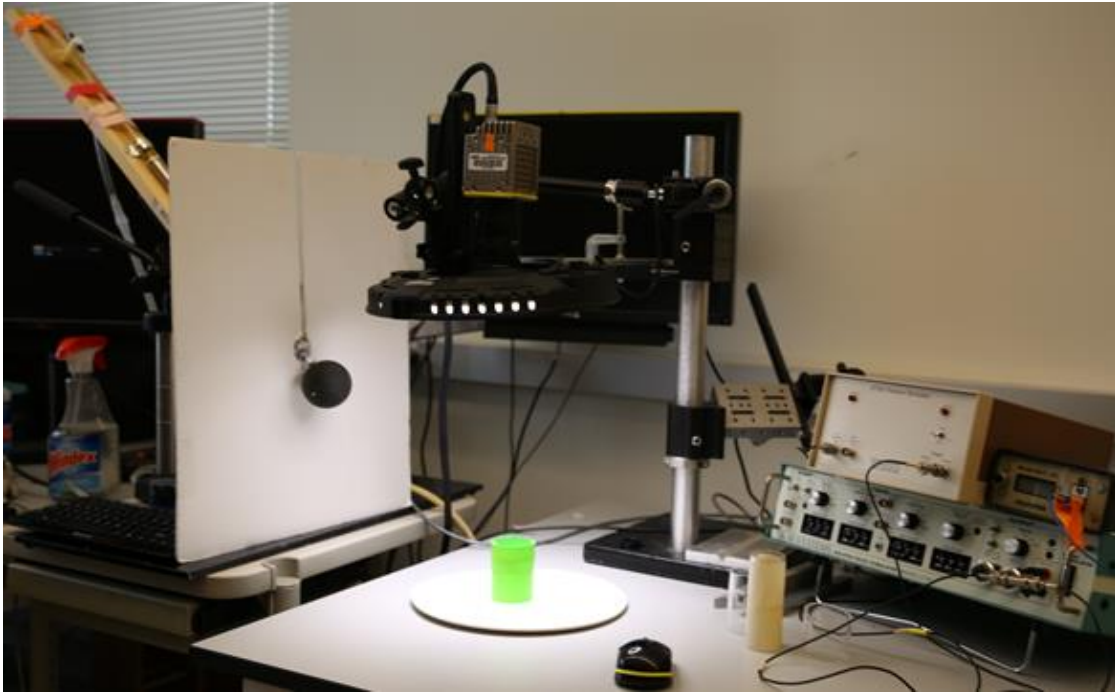
## E. Protocol

Before each trial, crickets were allowed to become acclimatized for approximately 15 minutes. Only trials in which the cricket did not move before presentation of the stimulus were analyzed. The angle of approach (Figure 1) of the looming stimulus in the horizontal plane was defined relative to the midline of the cricket and was accomplished by gently turning the circular stage. For example, 0 degrees corresponded to stimulus approaching the cricket directly anterior. The sequence of angle approach (0, 45, 90, 135, 180, 225, 270 and 315 degrees) was randomized for each cricket and a 4 minute resting-period between each trial was instituted to balance any inter-stimuli affects. The cricket was manually turned to each angle, the acrylic tube removed and the looming stimulus delivered.



**Figure 1: Diagram of Experimental Setup.** (left) Experimental setup showing the looming stimulus, a black, 2.5" polystyrene ball, which approached at 1.0 m/s, 45 degrees from the horizontal plane. Movements were captured by an overhead, high-speed camera, (IDS Redlake,

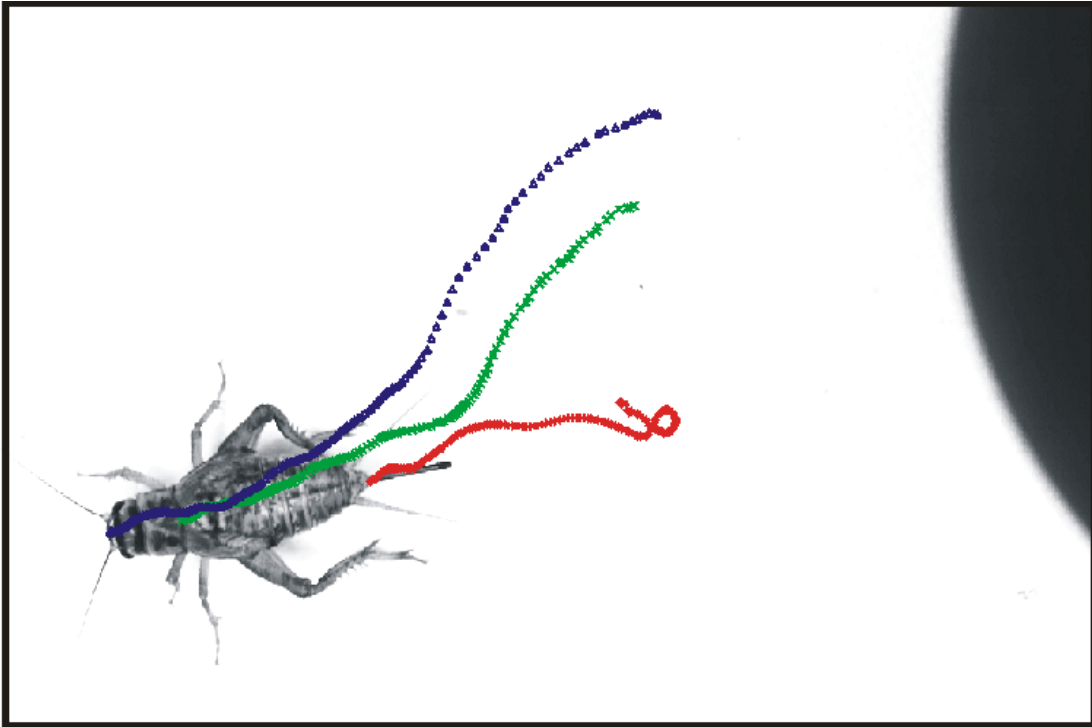
650 fps). Lighting was provided by an overhead, low-heat LED ring light. The stage was comprised of a circular piece of thin pine covered in painted white canvas for traction, which was manually turned for each stimulus angle. Crickets were positioned 20 mm from the stimulus end-point to ensure they were not touched by the ball, including the antennae. Looming stimuli were projected at lateral angles 0, 45, 90, 135, 180, 225, 270, and 315 (right). The angular coordinate system also describes the movement and direction of cricket response (right).



**Figure 2: Photograph Depicting Experimental Setup.** Setup included piston cylinder (left) with attached polystyrene ball and white backdrop. Also shown: two-inch green tube for pretrial acclimatization on circular stage (center) and the combined stimulus/camera controller (right).

## F. Analysis

The recorded video frames were tracked using ProAnalyst (Xcitex Woburn, MA) analysis software. Three specific anatomical locations were tracked: the head anterior to the eyes, the abdomen-thorax juncture, and the posterior of the cricket. The posterior tracked location was used as the (0,0) reference point. Tracking was done from five frames before movement of the cricket to the end of movement (Figure 3). Frames spaced 2-10 frames apart were tracked and intervening locations were determined by polynomial interpolation. The data was transferred to Matlab for Chi<sup>2</sup> and T-Test analyses using custom routines.



**Figure 3: Tracking Movement of Cricket in Response to Looming Stimuli:** Example of a trial tracked using ProAnayst software showing lateral movement of cricket in relation to its starting point 90 degrees relative to the stimulus.

### **G. Sensory Ablation**

Each cricket was anaesthetized using gaseous CO<sub>2</sub> from AlkaSeltzer tablets direct fed by a rubber hose into a closed-system beaker (using parafilm) housing each individual cricket.

Ablations were carried out in congruence with methods utilized in previous research (Triblehorn et al. 2014, Dupuy et al. 2011). Following ablation, each animal was removed to a recovery area comprised of a 5-inch long acrylic tube with black velvet covering half of the outer surface on one end. This recovery area was used as a means to casually detect the light sensing capabilities of visually ablated crickets. As crickets prefer the dark, a cricket not fully visually ablated would migrate toward the dark end of the tube. Each cricket, regardless of ablation, was housed in the same recovery area prior to the experiment for approximately an hour to acclimate.

**a. Visual Injury:** Crickets were positioned laterally under a dissecting microscope and black nail polish (lacquer nitrocellulose) was applied with a small paintbrush to completely cover both eyes. The animals were gently immobilized using forceps and bent dissecting pins in order to prevent the coating of any tissue other than the eyes. Care was taken to avoid sticking either antennae or forelegs to the tacky lacquer while moving the animal to the recovery area. Crickets are unable to see wavelengths greater than approximately 600nm (Zufall et al, 1989). This fact was useful when determining a way to provide a non-invasive visual knock-out model for experiments involving vision. With this in mind, red light was used and all other light sources, such as natural light from windows, were removed or blocked using heavy cloth.

**b. Cercal Lesion:** Using forceps, animals were moved to the lateral position and adjusted to the angle necessary to lesion the cerci nearest to the abdomen. To control the cut, micro spring scissors were used to ablate each cercus in a single cut. Any liquid discharge was quickly wicked with a Kimwipe, and the entire wound, in addition to any surviving cercal hairs located at the base of the cerci, was coated with a thick layer of petroleum jelly using a small brush. Coating the lesioned area with petroleum jelly decreased the possibility of any remaining proximal sensilla being unintentionally stimulated by an air current. A thick glass panel, placed between the looming stimuli and the cricket was also used as a non-invasive means of removing cercal stimuli.

**c. Antennae Lesion:** Forceps were used to keep the head steady while the micro spring scissors lesioned the antennae at their base, as close to the head as possible. Infrequently, there was liquid discharge, which was wicked with a Kimwipe and lightly covered with a thin coat of petroleum jelly using a small brush.

**d. Knock-Out Model**

A knock-out model was used to determine the sufficiency of filiform hairs, located on the body, in eliciting an escape response. The knock-out model was produced by ablation of cerci, antennae and covering of eyes (see ablation procedures above). Three trials were conducted to assess escape response in knock-out models.

**H. Ablation Protocol**

Two approaches were used for ablation, individual modalities to determine necessity and all but one modality to determine sufficiency. The necessity and sufficiency model is used to determine if the sensory modality is necessary for an escape response or sufficient to elicit a response by itself. In order to ensure the viability of the crickets, each was tested using the standard laterality protocol before being ablated and all responded stereotypically (Table 1).

**Table 1: Table Showing Ablation Treatments and Number of Crickets per Treatment.** The ablation treatment combinations show where only one sensory system is ablated (left) and where all sensory systems but one is ablated (right). Intact with glass was a non-invasive means of “ablating” stimulation of cerci and/or antennae.

<b>One Sensory System Blocked (no. crickets)</b>	<b>All but One Sensory System Blocked (no. crickets)</b>
<b>Vision</b>	<b>Vision</b>
Black Lacquer-Covered Eyes- 7	Only Eyes Remain (Antennae and Cerci cut)- 7
Red light- 2	
<b>Cerci</b>	<b>Cerci</b>
Only Cerci Cut- 6	Only Cerci Remain (Antennae Cut, Eyes Covered)- 5
Intact with Glass- 6	
<b>Antennae</b>	<b>Antennae</b>
Only Antennae Cut- 1	Only Antennae Remain (eyes covered, cerci cut) -3

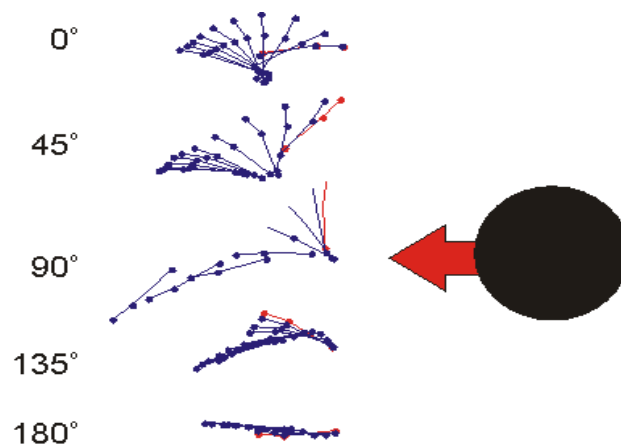
## VII. Results

### A. Laterality

#### a. Looming Stimuli evoke Escape Behavior

Crickets (n=30 crickets, 221 trials) reliably responded to a looming stimulus, presented at each of 8 lateral angles, by turning and walking or turning and jumping (with the exception of 180 degrees posterior, in which crickets typically did not turn but walked forward, see Figure 4).

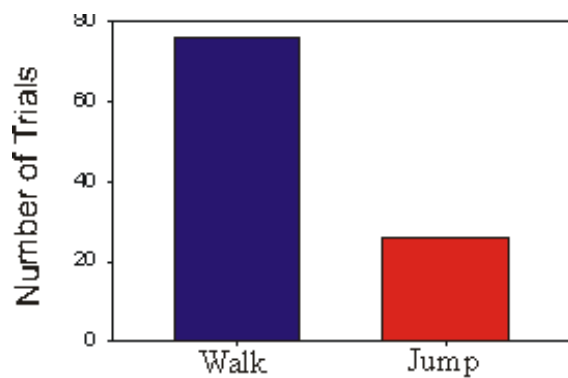
When the stimulus was approached from 0 degrees anterior, crickets turned and escaped away from the looming stimulus (see Figure 4).



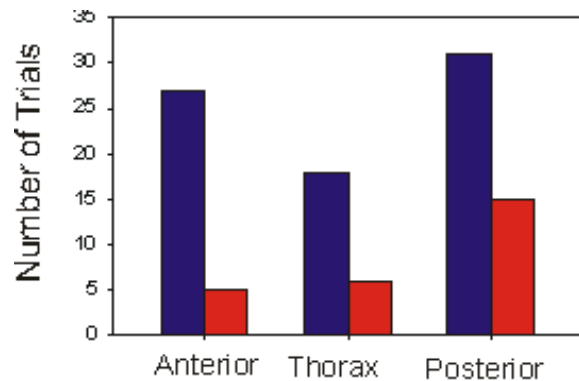
**Figure 4: Crickets Turn Away From Looming Stimuli.** Whether from anterior angles (0 degrees or 45 degrees) or lateral angles (90 degrees on either side) crickets turn and escape. From directly behind, 180 degrees, crickets escape forward either by walking or jumping. Red lines/dots denote each body location tracked at the initial position of the cricket in relation to the incoming stimulus and blue lines/dots denote each body location tracked as the cricket turned away from the stimulus.

## b. Crickets Walk Rather than Jump

In order to determine preference for walking or jumping in cricket escape behavior, the number of trials in which crickets responded by jumping, as opposed to walking, were counted and graphed both overall and in relation to stimulus location (Figure 5). Crickets showed a significant ( $p < 0.0001$ ,  $\chi^2$ ) preference for walking rather than jumping (Figure 5A). When responses were grouped according to stimulus location, we found that the proportion of walk versus jump responses did not vary over stimulus location, however a trend was observed that when crickets do jump they do so more frequently in response to stimuli approaching at posterior angles ( $p = 0.2$ ,  $\chi^2$ ).



A.

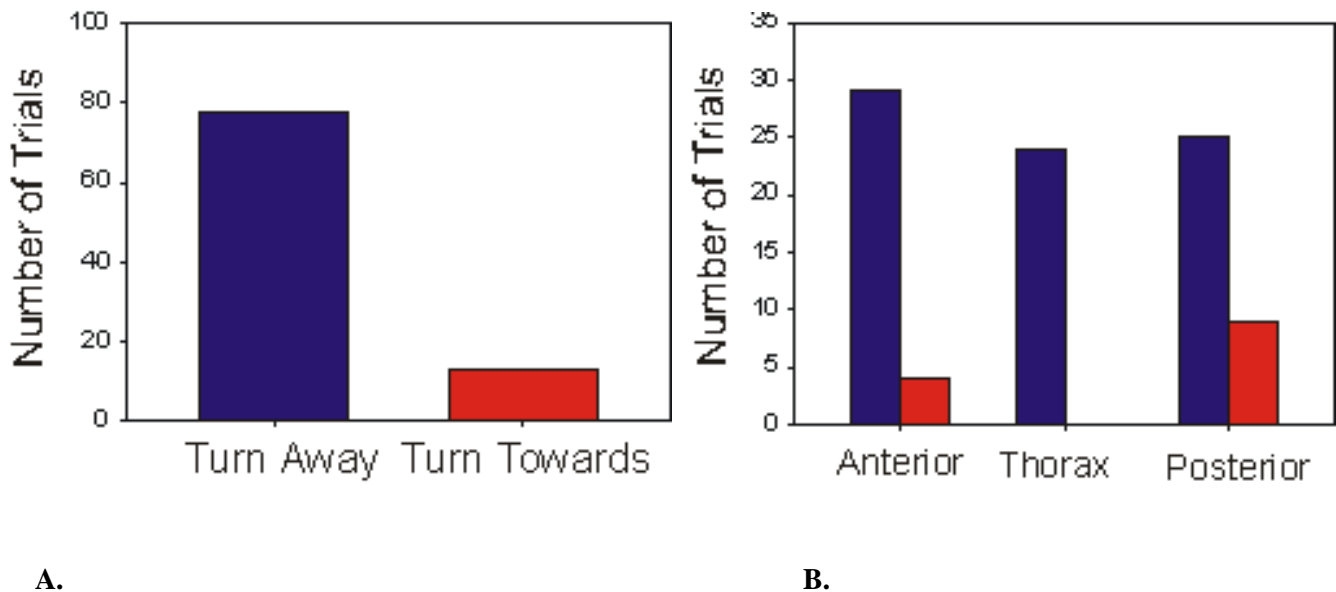


B.

**Figure 5: Crickets Walk Rather Than Jump.** The red bars indicate trials in which the cricket jumped; blue bars indicate trials in which the crickets walked after the looming ball was projected towards it. A. Overall, crickets showed a significant ( $p < 0.001$ ,  $\chi^2$ ,  $n = 221$ ) preference for walking rather than jumping. B. When responses were grouped according to stimulus directions (anterior, thoracic and posterior angles), we found that the crickets tended to walk rather than jump similarly for all three groups of directions ( $p = 0.2$ ,  $\chi^2$ ,  $n = 221$ ).

### c. Crickets Turn Away From the Looming Object

In order to determine whether crickets showed a preference for turning toward or away from a looming stimulus, the number of towards and away responses were counted and graphed both overall and according to stimulus location (Figure 6). Crickets turned consistently away from the stimulus ( $n=221$ ,  $p<0.0001$ ,  $\chi^2$ ; Figure 6A). When responses were grouped according to stimulus location (anterior-0, 45 and 315 degrees, thoracic-90 and 270 degrees and posterior angles-135, 180 and 225 degrees) significant preference was shown to turn away and not towards a stimulus at angles on either side of the thorax, as there were no responses of towards at midline angles. When comparing towards and away responses at anterior and posterior angles, there was a significant increase in towards responses at posterior angles ( $p=0.008$ ,  $\chi^2$ ; Figure 6B).

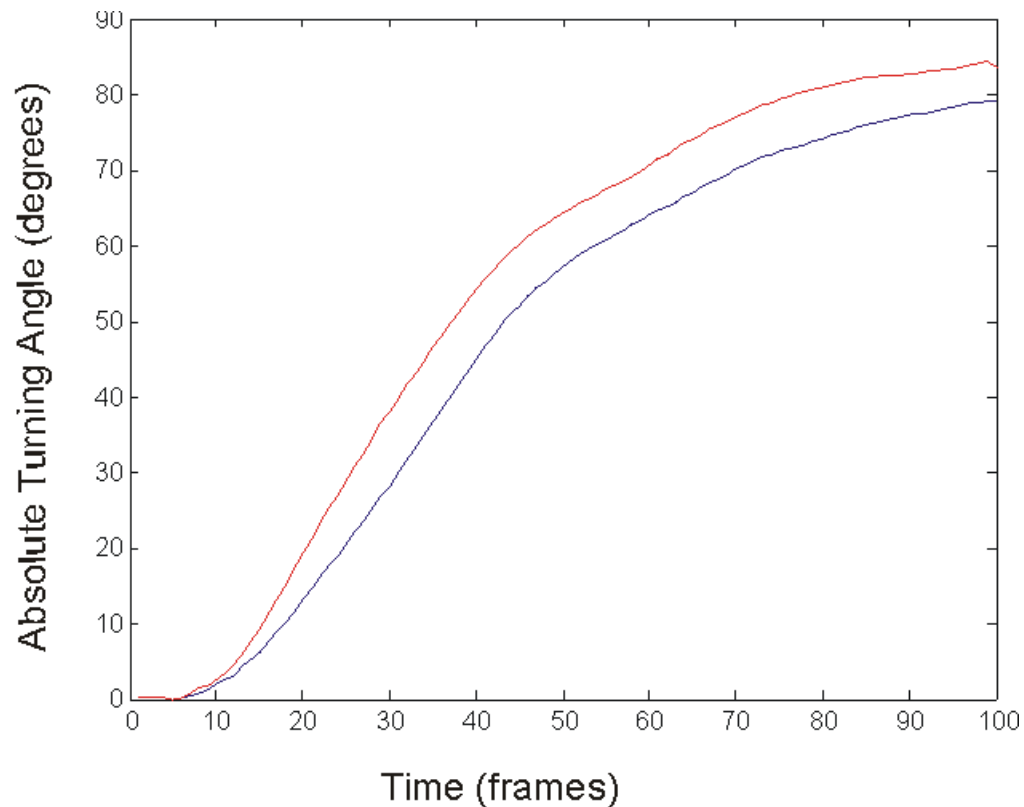


**Figure 6: Crickets Turn Away from Looming Stimuli.** The red bars indicated the trials where the cricket turned towards the projected stimulus and the blue bars indicate the trials in which the crickets turned away from the stimulus. In most trials, crickets turned consistently away from the stimulus ( $p<0.0001$ ,  $\chi^2$ ,  $n=221$ ). When responses were grouped according to stimulus location (anterior, thoracic and posterior angles) significant preference was shown to turn away and not towards a stimulus at angles on either side of the thorax, when compared to that of posterior angles ( $p=0.008$ ,  $\chi^2$ ).



#### d. The Head Leads the Turning Response

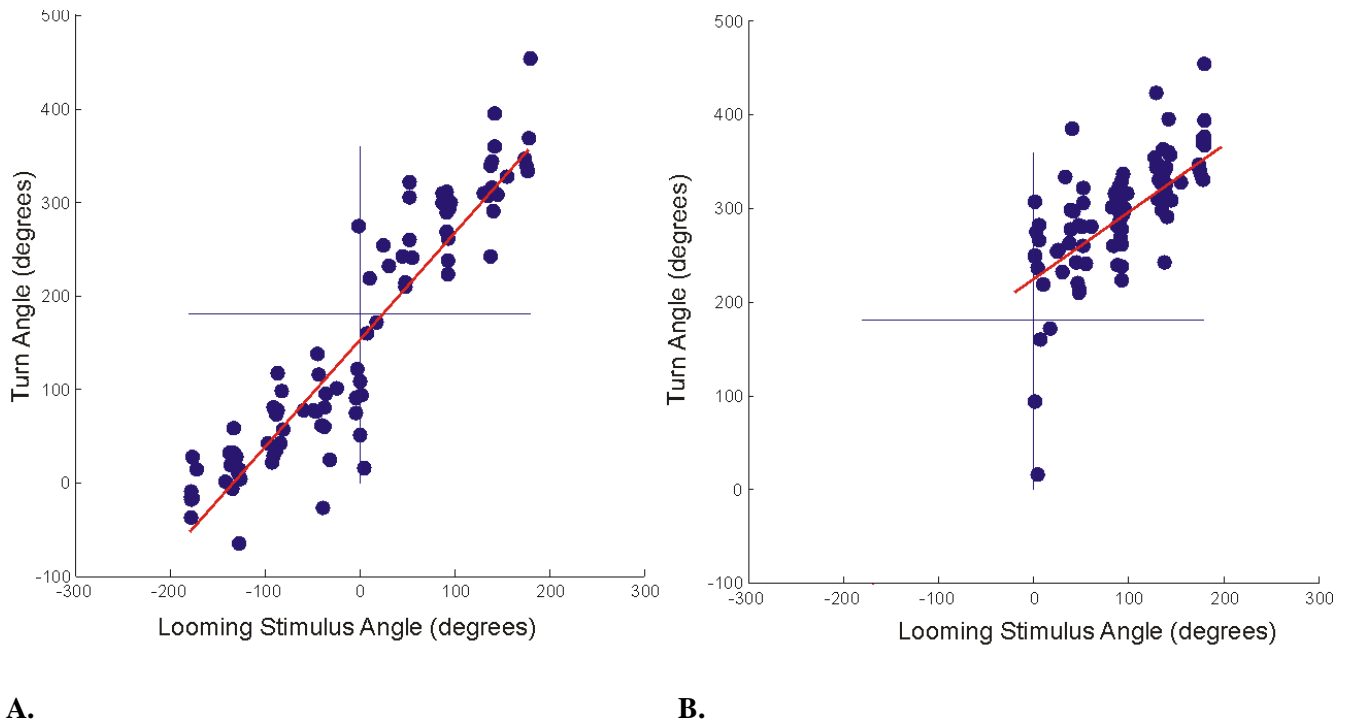
To determine whether the head or abdomen led the turning response, turn angle of the head and body were separately graphed in relation to time (Figure 7). The head is shown to lead the turning response, followed closely (approximately 5 frames = 5.1/650s) by the abdomen.



**Figure 7: Head Leads the Turning Response.** The turning angle of the head (red line) leads the turning angle of the abdomen (blue line). This graph was created by averaging the relative, absolute change in angle of both the head and abdomen at each timepoint (frame= 1/650s) over all trials (n=92).

### e. Response Angle Depends on Looming Laterality

In order to determine the degree to which angle of stimulus approach affects the angle of escape, the angle of turn in relation to the angle of approaching stimulus were compared and a positive correlation ( $r^2=0.87$ ;  $m=1.12$ ,  $p<0.000001$ ,  $n=221$ ) was found (Figure 8A). In order to more accurately determine if laterality *per se* of the stimulus direction influenced response direction, the response and stimulus angles were reflected and again graphed (Figure 8B) to reveal a significant ( $m=0.92$ ;  $p<0.00001$ ;  $n=221$ ,  $\chi^2$ ) linear relationship. Slopes were close to 1 (1.12 and 0.92) indicating crickets will escape approximately 180 degrees from the angle of stimulus approach.

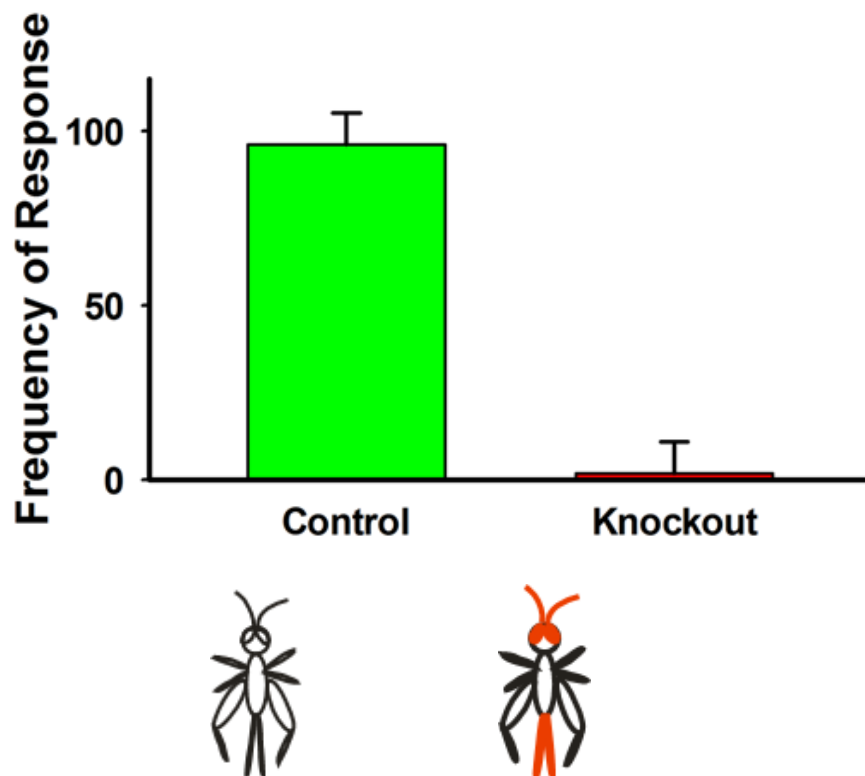


**Figure 8: Response Angle Depends on Looming Direction.** A. The plot shows a positive correlation ( $r^2 = 0.87$ ;  $m=1.14$ ;  $p<0.000001$ ;  $n=221, \chi^2$ ) between angle of turn and angle of looming stimulus approach. B. In order to determine if laterality in the absence of left-right side of the stimulus angle influenced the response direction, the response and stimulus angles were reflected and graphed as shown. The significant ( $m=0.92$ ;  $p<0.00001$ ;  $n=221, \chi^2$ ) linear relationship demonstrates that response depends on the laterality of the stimulus.

## B. Sensory Modalities

### a. Body Hairs Are neither Sufficient nor Necessary to Evoke an Escape Response

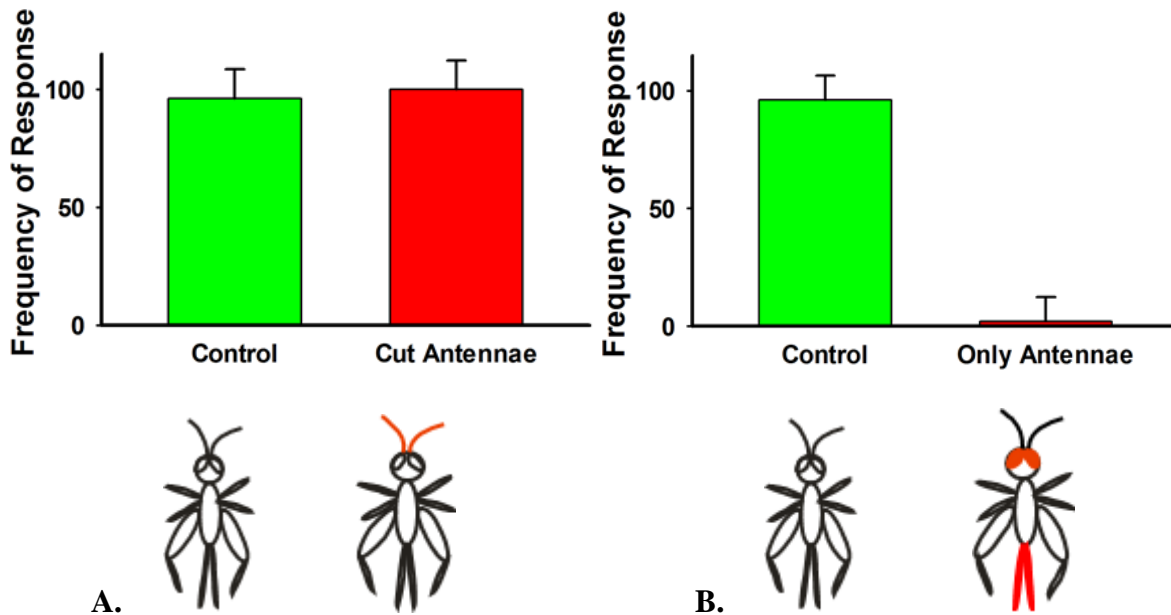
To determine if any other wind-sensitive mechanoreceptors, such as those located on legs or other parts of the body, could aid in evoking an escape behavior, the eyes were covered and both antennae and cerci were ablated. Crickets never responded when provided with a looming stimulus (n=221 control, n=24 full ablation,  $p < 0.0005$ ,  $\chi^2$ ).



**Figure 9: Body hairs not sufficient to evoke an escape response.** When eyes were covered and both antennae and cerci ablated, no escape responses were evoked at any angles, which demonstrated a significant difference when compared to that of intact, control trials (n=221 control, n=24 full ablation,  $p < 0.0005$ ,  $\chi^2$ ).

### b. Antennae are neither necessary nor sufficient to evoke an Escape Response

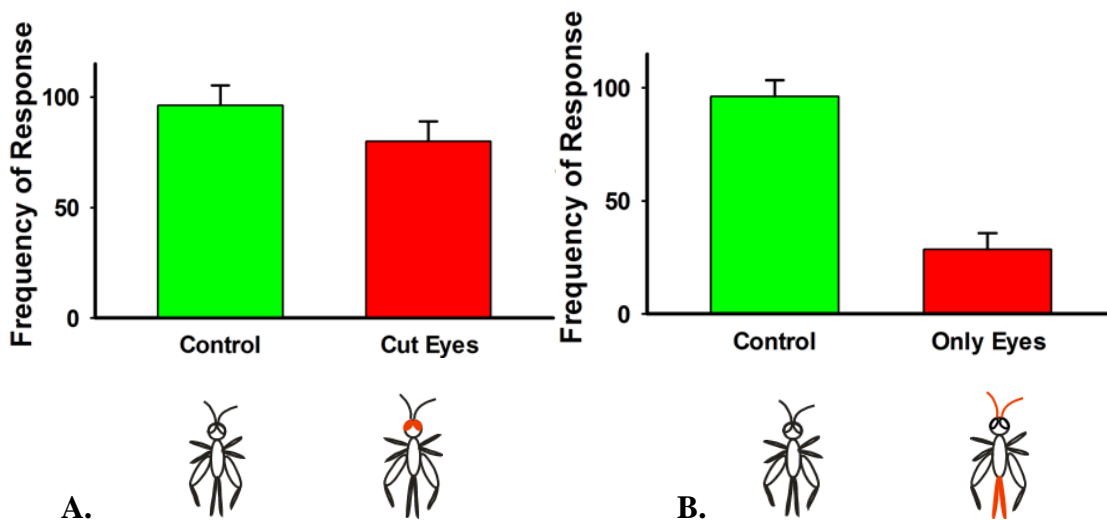
To determine whether antennae were necessary and/or sufficient to evoke escape behavior, antennae were ablated or only the antennae were left intact (vision and cerci were ablated; body mechanoreceptors were already shown to be ineffective; Figure 9). When only antennae were ablated (Figure 10A) the overall frequency of escape response was unchanged from intact, control, crickets, ( $n=221$  control,  $n=8$  ablated,  $p=1.0$ ,  $\chi^2$ ), which showed that antennae are not necessary for the escape response. When only the antenna were available, (Fig. 10B), no escape responses were evoked, which showed the sensory information from the antennae alone was not sufficient to evoke an escape response ( $n=221$  control,  $n=24$  only antennae,  $p<0.0005$ ,  $\chi^2$ ).



**Figure 10: A and B: To Looming Stimuli Antennae are neither necessary nor sufficient for the escape response.** A. When only antennae were ablated, the frequency of escape response was not changed from control at any angle of stimulus approach ( $n=221$  control,  $n=8$ , ablated,  $p=1.0$ ,  $\chi^2$ ). B. When eyes and cerci were ablated, with only antennae remaining, no escape responses were evoked ( $n=221$  control,  $n=24$  only antennae,  $p<0.0005$ ,  $\chi^2$ ).

### c. Vision Aids in the Escape Response

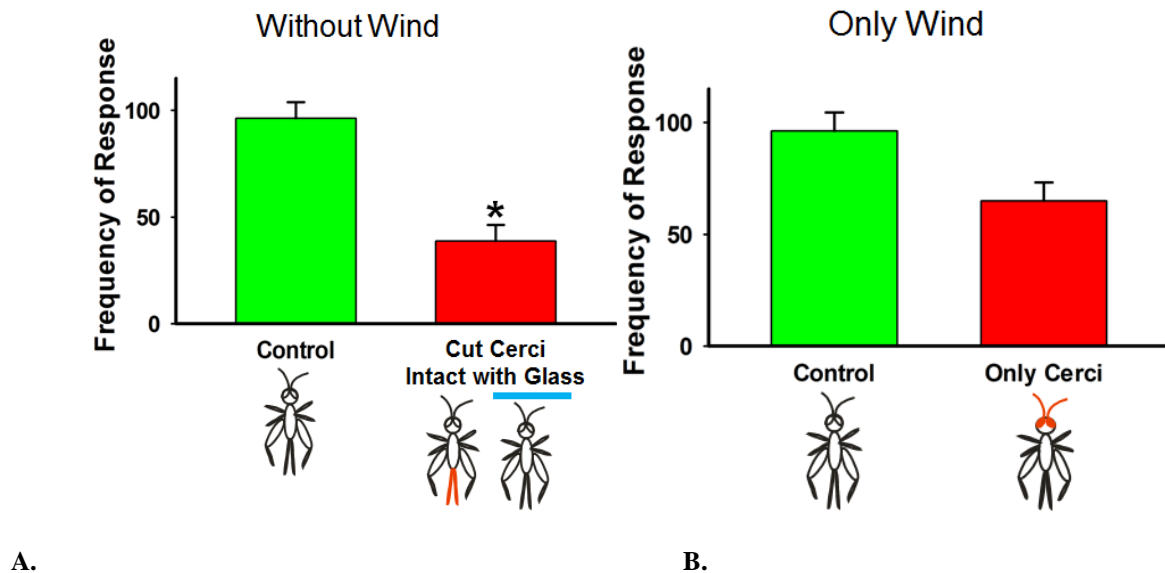
To determine whether vision was necessary to evoke escape behavior, vision was ablated by covering the eyes with paint or conducting trials in red (660nm) light only which crickets cannot sense (Zufall et al. 1989). Although there was a significant decrease in the frequency of escape response ( $n=221$  control,  $n=80$  ablated,  $p=0.03$ ,  $\chi^2$ ; Figure 11A), a 75% response rate persisted, demonstrating that vision contributes but is not necessary. To determine if vision was sufficient to evoke an escape response, only eyes were left intact and the antennae and cerci were ablated (body mechanoreceptor were previously shown to be insufficient). With only vision available (Figure 11B), there was a significant decrease in escape frequency as compared to intact trials, which showed that vision alone was not sufficient to evoke an escape response overall, but could still produce escape responses (28.6%) in some trials ( $p<0.0005$ ,  $\chi^2$ ; Figure 11B). These results are consistent with vision, although neither necessary nor sufficient, contributing to the escape response.



**Figure 11: Vision aids in the escape response** **A.** When only eyes were covered or red light was used, the frequency of escape was slightly decreased from control ( $n=221$  Control,  $n=80$  vision ablated,  $p=0.032$ ,  $\chi^2$ ). **B.** When both antennae and cerci were ablated, leaving only eyes, there was a significant difference between control trials and vision only trials ( $n=221$  Control,  $n=56$  only vision,  $p<0.0005$ ,  $\chi^2$ ). The escape response frequency was higher, at 28.6% on average, than that observed in antennae-only crickets at 0%.

#### d. Cerci are Necessary and Sufficient to evoke an Escape Response in Most Trials

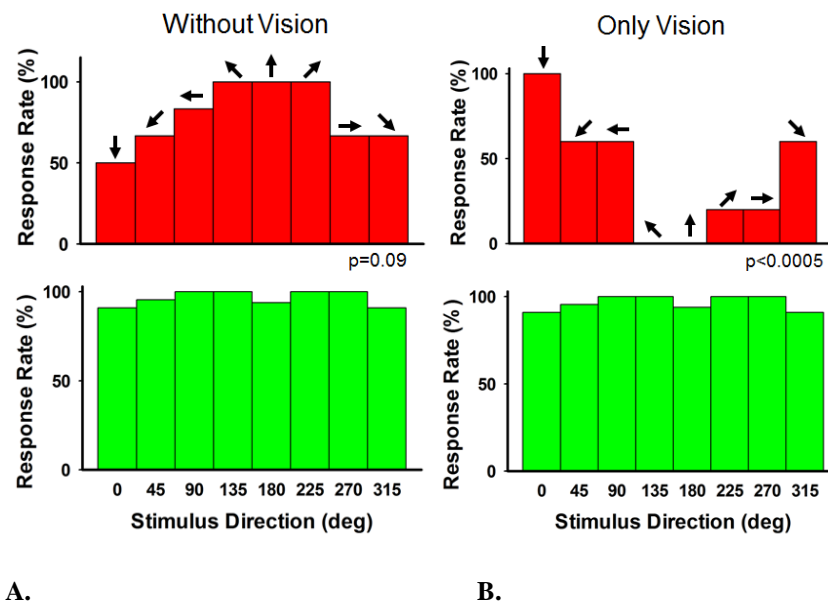
To determine whether cerci are necessary to evoke an escape response, cerci were ablated, or a windscreen was used, and to determine sufficiency, only cerci were left intact. When only cerci were cut, or a glass windscreen was in place (Figure 12A), escape response rates significantly decreased compared to control (n=221 control, n=96 cerci ablated or blocked with glass,  $p < 0.0005$ ,  $\chi^2$ ), which showed that cerci were necessary to evoke an escape response in most trials. When eyes and antennae were ablated (Figure 12B), leaving only the cerci intact, there was a significant decrease in escape responses compared to control trials ( $p = 0.004$ ,  $\chi^2$ ). However, cerci were sufficient to evoke an escape response in most trials (65% response frequency; Figure 12B).



**Figure 12. Cerci are necessary and sufficient for the escape response in most trials** **A.** When only cerci were cut, or a glass windscreen was in place, escape response rates significantly decreased compared to control (n=221 Control, n=96 cut cerci,  $p < 0.0005$ ,  $\chi^2$ ). **B.** When eyes and antennae were ablated, with only cerci remaining, there was a significant difference compared to escape response frequencies of intact, control crickets (n=221 Control, n=40 only cerci,  $p = 0.004$ ,  $\chi^2$ ). With only cerci remaining, escape responses were evoked in 65% of trials.

### e. Vision Aids in Escape Response at Anterior but not Posterior Angles

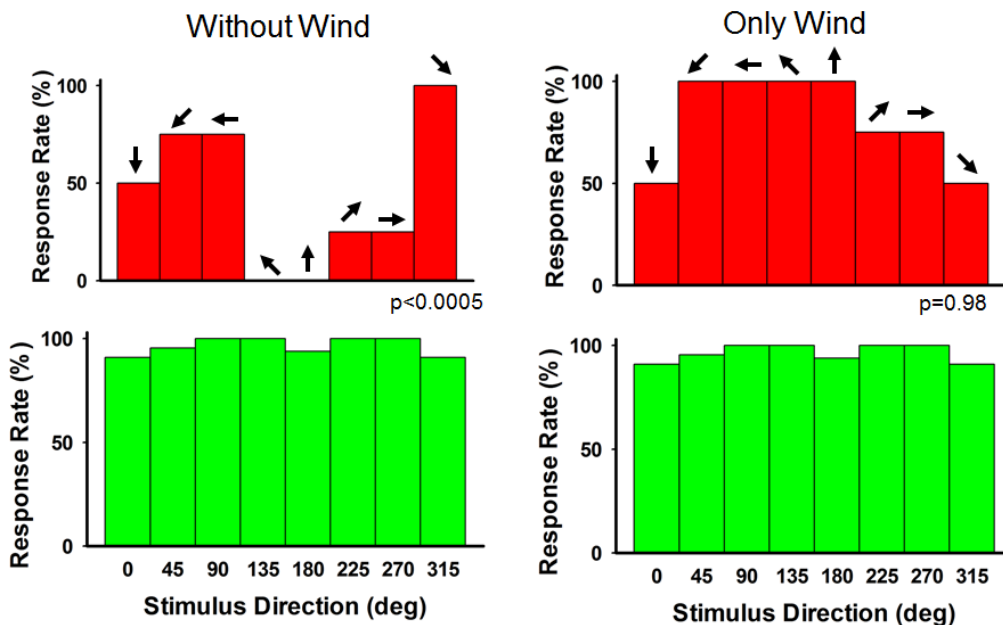
The above results demonstrate that both cerci and eyes contribute to the escape response, raising the question whether they contribute preferentially to looming stimuli approaching from different directions. To determine if vision contributed to escape behavior at anterior angles, response rates were compared to control crickets separately for each of the eight different looming directions. When only vision was ablated (Figure 13A, upper panel) there was a decrease in response rates in vision ablated crickets with stimuli approaching at anterior angles, compared to that of intact trials (n=221 control, n=80 ablated, p=0.09; Figure 13A, lower panel). When only vision remained (Figure 13B), escape responses were elicited at only anterior angles, with no responses elicited at posterior angles, which showed a significant difference in frequency response, when compared to that of intact, control crickets (n=221 control, n=56 vision only, p< 0.0005,  $\chi^2$ , Figure 13A).



**Figure 13. Vision aids in escape response at anterior but not posterior angles.** A. When only vision was ablated, response rates decreased at anterior angles but not at posterior angles, as compared to that of the control (n=221 control, n=80 vision ablated, p=0.09,  $\chi^2$ ). When only vision remained, escape response was elicited at only anterior angles, with no responses elicited at posterior angles, compared to that of intact cricket responses. (n=221 control, n=56 vision only, p< 0.0005,  $\chi^2$ ).

### f. Cerci Aid in Escape Response at Posterior but not Anterior Angles

To determine if the cerci contributed to escape behavior at posterior angles, response rates were compared to control for each of the eight different looming directions. When only cerci were ablated (Figure 14A, upper panel) there was a significant decrease in response rates in cerci ablated crickets with stimuli approaching at posterior and midline angles, compared to that of intact trials (n=221 control, n=96 ablated,  $p < 0.0005$ ,  $\chi^2$ ). When only cerci remained (Figure 14B), escape responses were elicited at posterior and midline angles similar to that of control, however response rates at anterior angles were decreased as compared to control (n=221 control, n=40 only cerci,  $p = 0.98$ ,  $\chi^2$ ).



A.

B.

**Figure 14. Cerci aid in escape response at posterior but not anterior angles.** A. When only cerci were ablated, response rates decreased significantly at posterior angles but not at anterior angles, as compared to that of the control (n=221 control, n=96 ablated,  $p < 0.0005$ ,  $\chi^2$ ). When only cerci remained, escape response was elicited at midline and posterior angles, with a decreased response to anterior angle stimulation, though not significant when compared to control (n=221 control, n=40 only cerci,  $p = 0.98$ ,  $\chi^2$ ).



## **VIII. Discussion**

Although there has been a plethora of research conducted involving a cricket's response to a wind stimulus, there is little information on how a cricket will behave when presented with a looming stimulus. Concurrently, there is also little known about the involvement of different sensory modalities in eliciting escape response and if stimulus laterality influences which modalities are utilized. In a two part study, escape behavior in crickets was elicited using a looming stimuli at various lateral angles, in both sensory intact and sensory ablated crickets. Most intact crickets responded by turning and walking, with the head leading the turn, rather than by jumping. Stimulus laterality had a direct, correlative relationship with angle of escape, with most crickets escaping directly away from the stimulus. In ablated crickets, vision was found to aid in evoking an escape response to stimuli at anterior angles and cerci at posterior angles, as predicted. The antennae and body mechanoreceptors were found to be ineffective in evoking escape responses, as previous literature had suggested.

### **A. Dependence on Looming Direction**

In previous studies using looming objects, crickets were found to escape directly away from the stimuli at around 169 degrees (+/- 7 degrees) if stimulated from posterior angles and 156 degrees (+/- 12 degrees) if stimulated from the side (Dupuy et. al. 2011). When we analyzed the angle of turn in relation to the laterality of the angle of the approaching stimulus we found a positive correlative relationship, which agreed with that of Dupuy et. al (2011) for looming stimuli and Tauber and Camhi (1995) for wind stimuli. Crickets consistently turned approximately 180 degrees away from a wind stimulus, similar to 162-180 degrees that Camhi and Tauber (1995) found, though higher than that of Dupuy et al. (2011), possibly due to the larger size of our stimuli in comparison (2.5" diameter ball, compared to a cylinder of 0.8 cm, diameter). This

indicated that crickets have the ability to discern the angle in which a looming stimulus approaches and turn accordingly, rather than follow a unilateral, right or left, side bias as seen in vertebrates such as goldfish (Preuss, 2003) and lizards (Carlile et. al. 2006).

In most of our trials, crickets showed a significant preference for walking after an initial turn, with the head initiating the turn, rather than jumping, contrary to previous findings by Tauber and Camhi (1995), who used wind puffs to elicit escape behavior (Tauber and Camhi, 1995). The looming stimulus used in our study provided a smaller, more dispersed amount of wind stimulus compared to that of Tauber and Camhi who used localized wind puffs with speeds of up to 0.23 meters per second (Tauber and Camhi, 1995). Delivering a relatively strong wind stimulus to sensitive wind receptors resulted in most of their crickets jumping, as a larger, faster predator would cause a greater wind stimulus and the need for a cricket to launch an immediate, stereotypical behavior. Walking away from a stimulus is energetically less costly, so it would be beneficial for crickets to utilize this escape behavior when the stimulus is not perceived as an immediate, or possibly large enough, threat.

## **B. Sensory Modalities**

In previous studies, ablation has been used to determine the necessity or sufficiency of specific sensory modalities in eliciting an escape response (Camhi et. al. 1978, Dupuy et. al, 2011, Kanou et. al, 2006). Vision has been shown to aid in directionality of escape but has not been shown to be necessary nor sufficient to elicit escape behavior on its own, except from anterior angles (Dupuy et. al, 2011, Kanou et.al, 2014). Our results concur with both findings in that vision was neither significantly necessary nor sufficient to elicit escape behavior when response rates for lateral angles were combined, but once response rates were determined for each lateral angle it became clear that vision contributed to escape behavior for anterior angles, which concurred with

Dupuy's findings (Dupuy et. al 2014). Due to the location of eyes on the anterior of the cricket, and cerci on the posterior, it follows that stimuli directed at anterior angles of the cricket would be perceived by the eyes more than cerci, and vice-versa. However, it was clear that cerci are more relied upon for escape response, as demonstrated by a higher overall response rate with cerci-only trials and a significantly low response rate in cercal-ablated crickets.

Previously, the antennae have been shown to aid in sensing stimuli but are not sufficient to evoke an escape response by itself (Dupuy et. al, 2011). Our results concur that there was no significant difference between response rates in ablated and intact crickets nor were any escape behaviors produced when the antennae were the only sensory modality remaining. This may be due to the variable sensory nature of antennae, which contain mechanoreceptors, olfactory and chemoreceptors and are not as specialized for wind-stimuli as the cerci. Interestingly, in all of the trials when antennae were ablated, crickets were observed to use their mouthparts to feel around their surroundings, as surrogate, albeit limited, antennae, possibly due to the presence of a density of sensilla trichodea located on the mouthparts (Klowden, 2007).

## **IX. Conclusion**

Crickets clearly have complex systems of sensing and understanding their environments, which they use as a basis of response. In understanding the complexities of one of the humblest of organisms, our interpretation of the natural world we inhabit advances, giving us a more comprehensive understanding.

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