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Analysis of the direction of escape response of crickets to looming-object stimulation

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Analysis of the Direction of Escape Response of Crickets to Looming-Object Stimulation

A Project Presented to
the Faculty of the Undergraduate
College of Science and Mathematics
James Madison University

in Partial Fulfillment of the Requirements
for the Degree of Bachelor of Science

by Kate Louise Reiman

May 2014

Accepted by the faculty of the Department of Biology, James Madison University, in partial fulfillment of the requirements for the Degree of Bachelor of Science.

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II. Abstract

Arthropods such as cockroaches, locusts, and crickets exhibit various escape strategies in response to wind, tactile, and looming stimulation. Cockroaches typically run from aversive stimuli, while locusts execute large jumps away from stimulation, and crickets display a combination of both walking and jumping techniques in response to stimulation. Looming object stimulation is perhaps the best type of stimulation to obtain information about how arthropods would respond to aversive stimuli in a natural setting, as it most accurately represents the complexity of multimodal inputs received by arthropods from external sources of stimulation while being preyed upon in the wild.

Previous studies regarding looming object stimulation have centered mainly upon the response direction of locusts to the aversive stimuli, while not much research has been done with crickets. Further, the few studies regarding the response of crickets to looming stimulation focused on the type of escape strategy executed by crickets as well as whether or not their escape was successful, while the escape direction of the cricket in response to looming stimulation has not been as widely studied. As a result, the specific aim of this study was to determine whether the escape direction of the cricket was dependent upon the angle of approach of the looming stimulus.

In response to looming stimulation, crickets displayed a combination of turning and either walking or jumping away from the incoming stimulus (a black

ball). The degree of turn of the cricket's body was significantly dependent upon the angle of the incoming stimulus, and crickets almost always moved away from the direction of the looming object.

III. Introduction

The relationship between predator attack and prey response has been evolutionarily established. There are typically two outcomes to this relationship: either the predator makes a successful capture, or its prey achieves a successful escape. As a result, prey animals have had to develop escape strategies that enable them to successfully outrun their predators. There are several types of responses to predators that arthropods have evolved, which include offensive reactions, attacking the predator, doing nothing, and escaping or attempting to escape (Baba and Shimozawa, 1997; Okada and Akamine, 2012).

Previous studies of arthropods have endeavored to determine both the search strategies of predators (Dangles et al., 2006) and the resulting escape strategies of their prey (Morice et al., 2013). While many experiments have attempted to study the response of arthropods to wind puff stimuli, with the exception of locusts (Rind and Simmons, 1992; Gabbiani et al., 1999; Gabbiani et al., 2004; Simmons et al., 2010; Heitler and Burrows, 1977), there have been few studies on the response of arthropods to looming-object stimulation, which presents the animal with a complexity of multimodal sensory information that represents an incoming predator much more accurately than a mere puff of wind, touch, or visual stimulus. Typically, looming-object stimulation is represented by a ball or a piston approaching the animal to simulate an incoming predator. In particular, crickets present an interesting study for looming object stimulation because they can both

run and jump, while the cockroach and the locust are confined to only one type of movement.

Sensory Structures Enable Escape Responses

Escape responses produced by arthropods, such as orthopteroid insects (cockroaches, locusts, and crickets), are often governed by their sensory structures in reaction to a stimulus. Sensory modalities that arthropods may use to obtain information about incoming stimuli include their wind-sensitive cercal systems, their antennae, and their visual systems (Despommier et al., 2005).

Cercal System

The cercal system of arthropods is made up of wind-sensitive hairs on the hind legs that detect changes in air current. It is important to arthropods for detecting sensory information in the surrounding environment and conveying that information to interneurons in order to respond to stimulation. There are three groups of neurons that are sensitive to the direction and dynamics of stimuli such as air currents and work together to compute an escape response: mechanoreceptor-coupled sensory neurons, local interneurons, and projection interneurons (Jacobs et al., 2008).

Cockroaches (*Periplaneta americana*) have hundreds of filiform hairs containing wind-receptive sensory cells located on the ventral surface of their cerci that stimulate giant interneurons, which can process information from and produce

an escape response to an incoming stimulus (Camhi and Tom, 1978; Westin et. al, 1977). It is thought that the seven bilateral pairs of giant interneurons that are excited by these wind-receptive cells play a role in the evasive behavior of the cockroach, helping it to determine its corresponding escape direction to an incoming stimulus (Ritzmann and Camhi, 1978).

In order to determine the importance of the cerci in generating an escape response to wind puff stimuli, the filiform hairs located on the ventral surface of the cerci were covered with adhesive tape to prevent exposure to wind. As a result, cockroaches with covered cerci were not sensitive to wind stimuli compared to the control group (Camhi and Tom, 1978). In addition, no escape response was generated among cockroaches that were exposed to visual, auditory, vibrational, and olfactory cues from a predatory toad in the absence of wind, further suggesting that wind serves as the primary modality for detecting incoming predators in cockroaches (Camhi et al., 1978). However, it is possible that covering the cerci rendered the cockroaches desensitized to other modes of stimulation as they could have been distracted by the sensation of the tape. It has also been hypothesized that the cerci are involved in determining the turning direction of the escape response, as the direction of the cockroach's turn and the direction of the leg movements correlate with the angle of the incoming stimulus relative to the cerci rather than the cockroach's body (Camhi and Tom, 1978).

The cercal system of locusts communicates with merely four giant interneurons compared to the seven found in cockroaches and crickets (Boyan et al., 1986). Their cerci are covered with approximately 200 microfiliform hairs that enable them to detect the direction and magnitude of an incoming threat by sending information to the terminal ganglion of the CNS via the cercal nerve (Boyan, 1988). The signals generated by these filiform hairs are induced by air displacements such as those caused by wind or low-frequency sounds (Rozhkova et al., 1984).

Of the three types of arthropods, crickets appear to have the most wind-sensitive cercal system. Like cockroaches, crickets have at least seven pairs of giant interneurons that are used to detect and generate responses to external stimuli (Boyan et al., 1986). These giant interneurons receive input from cercal receptors which are excited by filiform hairs on the cerci in response to wind stimuli, generating a response to stimulation (Kloppenburger and Horner, 1998).

Due to their highly sensitive cercal system, which can detect an incoming predator from far away distances based on air flow, crickets are one of the most difficult species of prey to catch; in most cases even mild stimulation to the cerci results in an escape response produced by crickets that are being preyed upon (Morice et al., 2013). Crickets are prey to a variety of predators, the most notable of which are birds and spiders (Dangles et al., 2006). Their abdominal cerci can have up to 3400 hairs used to detect air displacement, contributing to a highly sensitive mode of predator detection (Edwards and Palka, 1973). To counter this selective

advantage of crickets, it would be expected that their primary predators adopt a cautionary sit-and-wait attack strategy, since directly attacking the cricket may result in a successful escape after stimulation of receptors on the cerci. This is in fact observed in the wolf spider when it is preying upon the wood cricket *Nemobius sylvestrus* (Dangles et. al, 2006). The wolf spiders either opted to sit and wait for the crickets to come close enough for a successful attack, or attacked the crickets at high speeds that did not give the crickets time to escape.

The importance of the cerci in detecting wind stimuli was confirmed when crickets that underwent cercal ablation did not respond to air-puffs or attempt to escape up to 19 days (when the experiment ended) after the removal of their cerci (Kanou et al., 2006). In the absence of their cerci, crickets may have to rely upon tactile or visual cues to determine the appropriate escape response to incoming stimuli.

Antennae

The antennae of arthropods may also help to obtain information regarding aversive stimuli in their surrounding environment. There is evidence that cockroaches use their antennae to allow them to navigate around and away from obstacles. For example, cockroaches with intact antennae were able to judge their distance from a glass shelf as well as how high the shelf was from the ground, allowing them to successfully climb up onto the shelf with apparent ease (Knight, 2009). Cockroaches that had their antennae removed in this study often used brute

force to ram themselves up onto the shelf, or waved their legs around wildly until they were able to scramble up onto the shelf, suggesting that antennae may be necessary to gain sensory information useful to navigate obstacles.

Antennae might also be useful in processing sensory information obtained by an incoming predator, as the cockroach can determine the distance and height of an incoming predator based upon information obtained by its antennae. Indeed, an incoming stimulus that deflected one antenna of the cockroach elicited an escape response away from the direction of antennal displacement caused by the stimulus (Ye et al., 2003).

Locusts' antennae are also sensitive to the direction of incoming stimuli. Air displacement has been found to deflect the antennae of locusts, alerting a field of sensory receptors to the direction of an incoming stimulus (Gewecke and Heinzel, 1980). Avoidance reflex circuits exist to protect the antennae from damage by removing the antennae from the stimulus source (Saager and Gewecke, 1989). This typically results in the locust responding to an external stimulus either by removing its antennae or its entire body from the site of stimulation.

The antennae of crickets also respond to external stimulation, allowing the cricket to both detect incoming predators and produce a necessary response to avoid predation. When field crickets (*Gryllus bimaculatus*) were stimulated by using tactile stimulation to their antennae, they displayed four types of responses: aversion, aggression, antennal search, and no response (Okada and Akamine, 2012).

This information, coupled with the antennae being used to track visual targets, suggests that antennae may play a role in escape strategies produced by crickets in response to external stimulation. However, crickets with ablated antennae that were exposed to an incoming piston showed no significant difference in the rate of detection from that of intact crickets, both when the stimulus approached from the front and from behind (Dupuy et al., 2011). This provides contradictory evidence that antennae may not play a key role in helping crickets to detect and avoid aversive stimuli.

Vision

In addition to the cerci and antennae, vision is thought to play a role in escape responses performed by cockroaches, locusts, and crickets. While vision is not essential for cockroaches to produce an escape response, it has been found to influence the positioning of the antennae as the stimulus approaches (Ye et al., 2003). Therefore, cockroach vision has an indirect effect on the direction of the cockroach escape, as cockroaches may use the information obtained by their antennae to determine the direction of their response away from the stimulus.

Several studies have focused on the visual system of locusts (Rind and Simmons, 1992; Gabbiani et al., 1999; Gabbiani et al., 2004; Simmons et al., 2010) to determine its role in their detection and escape from incoming stimuli. Birds are one of the major predators of locusts, and they provide them with dynamic visual stimulation when making their predatory attack (Simmons et al., 2010). The

descending contralateral movement detector (DCMD) is a visual neuron that responds to objects moving towards or away from the eye, although it responds more vigorously to stimuli approaching the eye than going away from it (Rind and Simmons, 1992). The lobula giant movement detector (LGMD) is an accompanying visual neuron which serves as the major source of synaptic input to the DCMD and responds vigorously to objects approaching the animal on a collision course (Rind and Simmons, 1992; Gabbiani et al., 1999).

Both the DCMD and LGMD neurons enable locusts to process visual sensory information to help produce escape responses to a looming threat (Rosner and Homberg, 2013). While the LGMD provides synaptic input to the DCMD, the DCMD gives directional responses to images of approaching versus receding objects; thus, locusts can tell the difference visually between an approaching object and a receding one (Rind and Simmons, 1992). The LGMD was found to be more selective to looming stimuli than receding objects due to several different mechanisms of action, including both lateral inhibition among presynaptic elements and intrinsic membrane properties (Simmons et al., 2010). This enabled locusts to determine the direction of an incoming looming stimulus based upon visual cues that were processed by the LGMD. The DCMD, which is acted upon by the LGMD, displayed peak activity at a fixed time after the size of the looming object reached an angular threshold (Gabbiani et al., 1999). Therefore, the visual information processed by the LGMD and DCMD may be used to elicit an escape response in locusts when an incoming visual stimulus appears to be an imminent threat.

While cricket vision has not been extensively studied, it is thought to also play a role in evading capture by a predator. Crickets with covered eyes had a significantly lower detection rate as compared to intact crickets when a piston was approaching from the front and from behind (Dupuy et al., 2011). Crickets that were exposed to large black disks in front of a white background tracked them with their antennae as they moved in front of the crickets in a visual angle of up to 48 degrees (Huber et al., 1989). This suggests that crickets are capable of visualizing a target that is moving in front of them, and also supports the idea that they use their antennae to keep track of incoming stimuli when they can see it.

To summarize, there are three main sensory modalities that arthropods use to obtain information about and respond to stimuli in their environment: the cerci, the antennae, and vision. The cerci play a major role in detecting air displacement on the animal's body, whereupon they send information regarding the stimulus to giant interneurons, allowing the animal to produce an escape response (Ritzmann and Camhi, 1978; Camhi and Tom, 1978; Boyan et al., 1986; Morice et. al, 2013). In comparison, the antennae are not essential for determining an appropriate escape response, but arthropods can use them to obtain information about their surrounding environment and incoming stimuli (Knight, 2009; Gewecke and Heinzel, 1980; Okada and Akamine, 2012). Vision can affect antennal placement in cockroaches (Ye et al., 2003) and crickets (Huber et al., 1989), and also in the case of locusts helps alert the animal to a looming threat (Rosner and Homberg, 2013).

Escape Strategies in Response to Stimulation

Predators in the wild often present arthropods with a combination of multimodal sensory information as they carry out their attack. Not only do they present visual targets, but they cause air displacement and have the ability to touch their prey if it does not escape successfully. Arthropods have developed different escape strategies to various types of stimulation, which can be used independently or in conjunction with one another in response to stimuli (Dupuy et al., 2011). Resulting escape responses often allow the prey to avoid injury or predation.

Wind puff stimuli

Escape responses in arthropods, as well as their underlying mechanisms and escape trajectories, have been studied extensively with regards to wind-puff stimulation. Wind-puff stimulation usually involves a puff of air being directed at the insect from various angles and distances and is thought to imitate the quick puff of air created by an incoming predator as it launches an attack on its prey.

Cockroaches, in response to wind-puff stimulation, turn away from the incoming stimulus and run away rapidly (Camhi and Tom, 1978). Cockroaches that were exposed to the predatory strike of a toad in a lab setting were most successful at avoiding capture when they made an initial pivot away from the toad, whereas those that pivoted towards the toad were most often captured by the projectile tongue (Camhi et al., 1978). This data suggests that pivoting away from the stimulus is actually a highly adaptive escape movement. The pivot occurred around

the posterior end of the animal to move its head away from the incoming wind source. In most cases, the angle of turn of the cockroach was not a full 180 degrees, although it did point them in a direction away from the incoming stimulus.

Therefore, cockroaches may turn at an angle to achieve a successful escape from the incoming stimulus without having to make a full 180 degree turn away from the stimulus.

Although cockroaches initially pivot away from the direction of the incoming stimulus, there is variability in the overall direction of the escape. Cockroaches have been found to keep their escape direction unpredictable by running along a preferred set of escape trajectories at fixed angles away from the direction of the incoming wind puff stimulus after the initial pivot (Domenici et. al, 2008). This could ensure that, while their initial pivot may be in response to the angle of the incoming stimulus, there is necessary variation in the direction of their overall escape to avoid injury or predation.

In comparison to the running technique of cockroaches, locusts exhibit large jumps away from approaching stimuli, possibly because they cannot run away quickly in response to an external threat due to biomechanical constraints of their powerful hind legs (Tauber and Camhi, 1995). Few studies have examined the escape response of locusts to wind-puff stimuli. One study, which directed a fine air jet at *Schistocerca gregaria* locusts, found that there were wind-indicator and wind-direction cells associated with interneurons that govern the locusts' response to

wind-puff stimulation (Camhi, 1970). The information obtained by these cells allows for locusts to reposition themselves appropriately away from the incoming stimuli by rolling and yawing their bodies in order to direct their escape jumps up to 50 degrees either side of a straight ahead trajectory in relation to their body axis (Santer et. al, 2005). The rapid movements of their forelegs allow for the escape trajectory of locusts to be determined at the last minute as the escape jump is triggered. Further, wind-puffs directed at both the head and the cerci of intact tethered locusts produced identical flight responses, suggesting not only that the neurons of the cercal system are directed to the flight motor, but the same motor circuit is activated by the two different pathways (Boyan et al., 1986).

Crickets, which can walk and jump, exhibit both walking and jumping techniques in response to an incoming wind-puff stimulus, sometimes in combination with each other (Tauber and Camhi, 1995). Often, crickets that were exposed to the predatory strike of a wolf spider under experimental conditions would pivot away from the stimulus before walking or jumping, similar to the escape response demonstrated by the cockroach (Dangles et al., 2007). In a similar experiment, crickets that were exposed to an air-puff stimulus exhibited oriented or directional walking responses (Oe and Ogawa, 2013). This walking behavior often followed an initial turn or pivot in a direction away from the incoming stimulus angle. While this initial pivot seems time consuming, it may aid the cricket in escaping from natural predators, instead of just allowing it to escape in a straight line trajectory relative to the incoming stimulus. Indeed, while many crickets escape

in a direction away from an external wind stimulus, the direction that they escape in is not typically 180 degrees away from the incoming stimulus source, as was the case with cockroaches (Kanou et al., 2006).

Tactile stimuli

While wind puff stimulation induces escape responses in arthropods, tactile stimulation provides an additional source of sensory information to be processed by the animal as the stimulus has the ability to touch the animal of interest in addition to causing air displacement. Tactile stimulation therefore typically produces similar escape responses in animals as wind puff stimuli, although the mechanisms for producing these escape responses may be slightly more complex.

Cockroaches obtain sensory information via tactile cues using their antennae to avoid predation. However, cockroaches must be able to interpret this information to distinguish between predation, in which they escape away from the stimulus, and wall-following, which involves a continuous adjustment of movement towards the stimulus (Chapman and Webb, 2006). Tactile stimulation produces directional escape responses in the cockroach similar to those produced in response to stimulation by wind puffs (Comer et al., 1993). In one study, an incoming stimulus that deflected one antenna of the cockroach resulted in an escape response away from the direction of antennal displacement caused by the stimulus (Ye et al., 2003). Similar to wind-puff stimulation, cockroaches that were exposed to tactile stimuli

tended to escape in a direction away from the incoming stimulus. This raises the question of whether the underlying neural circuits that are operating during both wind and tactile stimulation converge.

Recent studies have indicated that the escape responses to tactile stimuli in cockroaches are potentially a result of convergence between wind and tactile stimulation, as the thoracic interneurons that receive input from the giant interneurons during wind-puff stimulation are also excited independently during tactile stimulation (Ritzmann and Pollack, 1994). Based upon the results obtained in one study that the cockroaches' responses to stimuli coming from different directions were the same for both tactile- and wind-evoked escape behaviors, it has been suggested that the same control circuit is operating regardless of the sensory modality to which it is responding (Schaefer et al., 1994).

Locusts also demonstrate evasive behavior in response to tactile stimulation when it is applied to their hind legs and antennae (Siegler and Burrows, 1986). According to one study, motor neurons that innervate the muscles in a hind leg are stimulated by tactile sensors on particular parts of the leg (Siegler and Burrows, 1986). When the hairs on the hind leg are touched by an outside force, the motor neurons are excited and the locust can move in response to the tactile stimulation. In this study, the movements of the locust were aimed at avoiding or escaping from the tactile stimuli; when touched, the hind leg would move away from the direction of the incoming stimulus.

Crickets displayed four types of responses to antennal tactile stimulation: aversion, aggression, antennal search, and no response (Okada and Akamine, 2012). When crickets were exposed to two successive tactile stimuli in one study, the first one gentle and the second much stronger, they mostly exhibited antennal search and aversion, respectively (Okada and Akamine, 2012). When mechanical tactile stimulation was applied to the wings of crickets, it induced an escape response in the crickets consisting of an initial jump followed by running away to avoid the stimulus (Hiraguchi et al., 2002). Among three types of tactile stimulation applied to the wings of the crickets (bending, touching with a paintbrush, and pinching with forceps), pinching evoked the most effective escape response, although the system responsible for detecting and responding to this type of stimulation remains unknown.

Looming stimuli

Looming-object stimulation is perhaps the most complex form of stimulation applied to arthropods, as it may combine wind-puff, tactile, and visual stimulation. This often presents the animal with a combination of wind-receptive, visual, and mechanical cues to aid in forming an escape response. This stimulation is most representative of a natural predatory attack as the insect can both see and feel the incoming stimuli if they allow it to get too close.

When the escape behavior of cockroaches was studied in response to the predatory strike of a toad under semi-natural conditions, it was similar to the

aversive escape behavior produced in response to wind-puff stimuli (Camhi et al., 1978). The toad presented the cockroaches with a looming stimulus as it moved towards them, also generating a rush of air current past the cockroaches from the approaching direction of the toad. As a result, cockroaches exhibited the same turn and run technique along a set of fixed trajectories away from the toad in response to this looming threat.

In response to looming object stimuli, locusts often perform a series of postural changes in preparation for a jump away from the incoming stimuli (Heitler and Burrows, 1977). The postural adjustments are quickly followed by three hind leg actions (flexion, co-contraction, and triggering) that serve to store energy in the hind legs before quickly releasing it to jump away from the looming object.

Similar to locusts, fruit flies (*Drosophila melanogaster*) used visual information obtained from a looming object stimulus to position themselves in a way that allowed them to escape in a direction away from the incoming stimulus (Card and Dickinson, 2008). To do this, they performed a series of postural adjustments that allowed for them to shift their centers of mass and push off with their legs away from the approaching stimulus. These postural adjustments occurred even in instances when the flies chose not to jump. In addition, it was found that the motor adjustments to reposition the legs were sufficient enough to control the direction of escape without help from the wings, as flies who had their wings removed still jumped away from the incoming stimulus.

Researchers designed an experiment to evaluate the escape response in crickets to looming-object stimulation by using the controlled approach of a piston (Dupuy et al., 2011). This design enabled the researchers to look at the crickets' escape responses based upon both wind-generated and visual detection of the stimulus, and also allowed them to determine the success of the overall escape response. A significant amount of crickets showed signs of detecting the piston, but the proportion of crickets that detected the piston was higher than the proportion of crickets that successfully escaped. The escape success from the approaching piston was strongly affected by the direction of the approach, with more crickets successfully escaping when the piston approached from behind, suggesting that the cerci were more useful than the visual system in detecting the stimulus. Comparable to wind-puff stimulation experiments, crickets tended to escape in a direction away from the incoming looming stimulus.

A separate study found that crickets tracked the looming stimulus with their antennae, which may have helped to determine the direction of the escape response (Yamawaki and Ishibashi, 2013). Antennal pointing occurred more when the stimulus (a ball) was approaching from the front of the cricket, and also when a larger ball was used, supporting the previously mentioned theory stating that visual cues allowed for the antennae to track the incoming stimulus. Indeed, when the eyes of crickets that were exposed to a looming stimulus were covered, it resulted in a reduced rate of detection of the stimulus approaching from the front

despite having intact antennae, whereas ablation of the antennae alone did not reduce the rate of detection or successful escape (Dupuy et al., 2011).

To summarize, the three different types of stimulation used in the lab setting - wind, tactile, and looming - induce escape responses in arthropods that take them away from the direction of the incoming stimuli. However, the mode by which the cockroach, locust, and cricket escape differs. While cockroaches initially turn away and then run from an approaching stimulus, locusts typically jump away, while crickets display a combination of turning, walking, and jumping away. Of the three types of stimulation used in the laboratory, looming object stimulation best represents the sensory complexity that would accompany an attack by an actual predator, as it combines sensory effects of both wind and tactile stimulation with an additional visual input.

A New Approach to Looming Stimuli

While extensive research has been performed surrounding wind puff stimulation, with the exception of locusts (Rind and Simmons, 1992; Gabbiani et al., 1999; Gabbiani et al., 2004; Simmons et al., 2010; Heitler and Burrows, 1977), few studies have been done regarding the escape responses of arthropods to looming object stimulation. However, looming object stimulation, as previously noted, best represents the complexity of sensory information conveyed during an attack by a predator. Further, studying the escape strategies of crickets to looming object stimuli possibly can provide more information regarding underlying motor

programs than studying the response of cockroaches because the cricket can both walk and jump, whereas the cockroach does not jump.

While the few studies regarding the escape responses of crickets to a looming-object stimulus focused on the escape strategy and success of the crickets as a function of angle of stimulus approach (Dupuy et al., 2011), no work has been done to examine the angle of escape of the cricket in response to change in the angle of stimulus approach.

The specific aim of this study was to use high speed video analysis to determine the relation between the angle of approach of a looming object (black ball) and angle of the resulting turn executed by the cricket.

IV. Methodology

Animal Care

Crickets were obtained from two different local pet stores (PetSmart and Petco). All crickets were kept in a covered plastic tub (dimensions 38.1x29.2x29.8 cm) with constant access to food and water. Both male and female crickets were used for the experiment, with 2 male and 5 female crickets being used. Sub-adult (instar 8-9) crickets were used because full wings (adults) would interfere with tracking points on the body during data analysis. After each experiment, the crickets were euthanized by placing them in sealed bags and exposing them to the interior of a freezer.

Experimental Setup

Crickets were placed on a primed canvas glued to a wooden circular platform (diameter 25 cm) which was designed to provide traction so that they could move and not slip in response to stimulation. The platform was white to provide contrast against each cricket's body during video recording. For each trial, one cricket was placed on the platform and exposed to the looming stimulus (Figure 1). A white cardboard square was cut out and placed behind the stimulus to provide contrast so that the cricket could detect the incoming stimulus. Each cricket was confined within a plastic tube up until the stimulus was released to ensure that it was in the desired location on the platform immediately before stimulation. A high-speed (650

fps) video camera (IDT/Redlake) using a wide angle lens (25 mm) was positioned above the platform at a 90 degree angle. The camera was 22 cm above the platform and was connected to a computer so that the images of the cricket's movement could be digitally stored.

The temperature was measured using a standard thermometer before each experiment. The average temperature for all experiments was 21.6 °C. An LED ring light was used to illuminate the cricket while minimizing heating from an external light source.

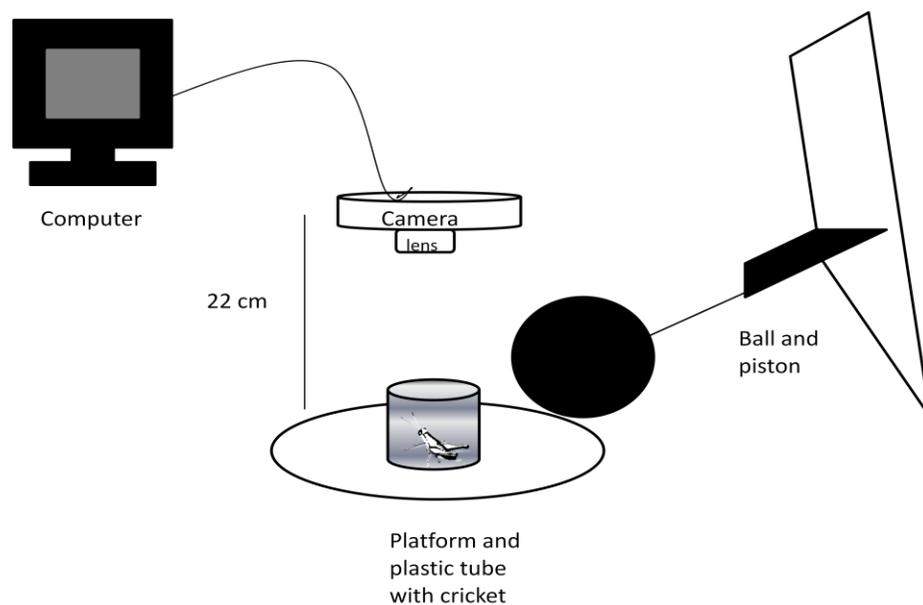


Figure 1. Diagram of experimental setup. The camera was positioned above and perpendicular to the platform bearing the cricket at a distance of 22 cm from the platform. The ball approached the cricket at an approximately 45 degree angle and an average speed of 94.1 mm/s. Video recordings were captured by the high speed (650 fps) video camera (IDT/Redlake) using a wide angle lens (25 mm). The camera was connected to a computer so that digital images of the cricket's movement could be saved and used for analysis. An LED ring light was used to illuminate the cricket.

Stimulation and Movement Recording

A black polyurethane ball (diameter 2.5 inches) was attached to the piston of an air cylinder (12 inch travel) that was driven by a solenoid controlled pressure source (nitrogen tank). Upon triggering the solenoid valve, the ball traveled towards the cricket at an approximately 45 degree angle and an average speed of 94.1 mm/s. This setup exemplified the concept of a looming-object stimulus (Figure 1).

The movement of the ball and resulting escape response of the cricket were recorded using Motion Studio x64 software (IDT). A trigger was used to capture recordings of the 5 frames before the stimulus and up to 3 seconds (1950 frames) after the stimulus was initiated. The resulting images were digitally saved to a computer for later tracking and analysis purposes.

Protocol

Crickets were stimulated by the ball facing the cricket from eight different initial directions: 0, 45, 90, 135, 180, 225, 270, and 315 degrees (Figure 2). The sequence of angles was randomized. If no response or a jump response was obtained during a trial, the initial angle of stimulation was repeated at the end of the other trials until an appropriate walk was obtained that could be tracked.

Each cricket was placed just out of reach of the ball when the piston was fully extended (20 mm) so that it could not contact them if they did not attempt to escape

sufficiently quickly. Once the cricket was positioned correctly, the ball was released and the response was recorded.

After stimulation, the cricket was quickly captured again using the plastic tube and allowed 2 minutes to recover before being positioned in preparation for the next trial. The tube was not removed until the cricket was stationary. When all eight initial stimulation angles had been successfully tested with the looming stimulus, the cricket was disposed of in the manner previously mentioned.

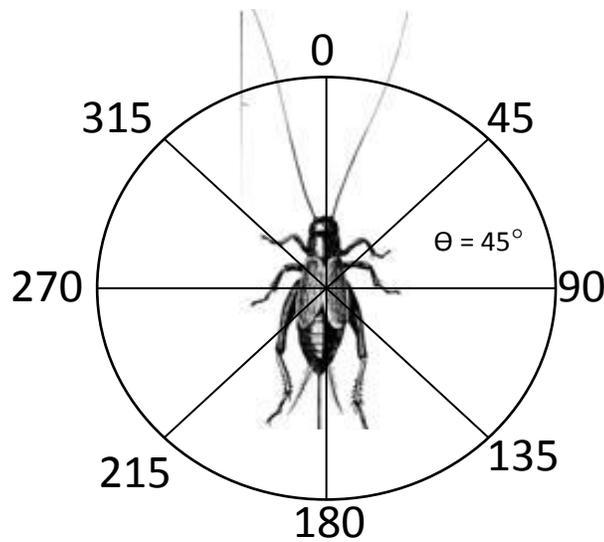


Figure 2. The angle of stimulation with respect to the cricket. Each cricket was stimulated with a looming object (black ball) at angles 0, 45, 90, 135, 180, 215, 270, and 315 degrees. The order of angles of stimulation was randomized for each cricket.

Movement Data Tracking and Analysis

Digitally saved videos of the crickets' movement were tracked using ProAnalyst computer software (ProAnalyst, Xcitex, Boston). Three separate points of each cricket's body were tracked manually using ProAnalyst: the tail, the middle, and the head. In order to do this, video data from one trial was uploaded, converted from pixel to mm, and tracked individually for each cricket. Tracking occurred from five frames before the start of movement to the final frame or when the cricket stopped moving.

Analysis of the movement of the three body parts was completed using Matlab, Microsoft Excel, and Sigmaplot. In custom programs written in Matlab, the angles of the cricket's abdomen and head were calculated over time (Figure 6). Graphing and statistics were conducted in Sigmaplot, Oriana, and Matlab.

V. Results

The results are divided into two different sections. The first section addresses the dependence of the change in angle of the cricket's body on the angle of the approaching stimulus. The second examines whether the head and the body move independently of one another in response to stimulation. The occurrence of jumps versus walks for each angle of stimulation was also noted.

A. Dependence of Movement on Stimulus Location

When exposed to the looming object stimulus, crickets displayed one of three behaviors: either no response, a response involving a turn and walk, or a response involving a turn and jump. Clips from video recordings of these responses are shown in Figure 3, with the exception of no response. The cricket responded by turning away from the stimulus and either walking (Figure 3A) or jumping (Figure 3B). In Figure 3A, the cricket turns approximately 45 degrees counterclockwise before walking away from the ball. In Figure 3B, the cricket turns approximately 30 degrees counterclockwise before jumping away from the ball. Figure 4 shows the movement of three features of the body over time in response to various angles of stimulation: the tail, the middle, and the head. It is clear from these images that the cricket begins by making an initial turn away from the stimulus before either walking or jumping away.

Cricket typically produced escape responses to all eight angles of stimulation, raising the question of whether the response of the cricket was dependent upon the stimulus angle. Representative initial and final positions of the cricket are shown to illustrate the movement of the cricket in response to the ball when it approached from angles 0, 45, 90, 135, and 180 degrees (Figure 5). The cricket typically turned or moved in a direction away from the ball when it approached from all angles; there was only one instance where one individual cricket turned towards the ball when stimulated at 45 degrees, indicative of an aggressive response (Figure 5). However, video analysis showed that, while the cricket turned towards the ball, it shifted its apparent center of mass away from the ball to avoid contact.

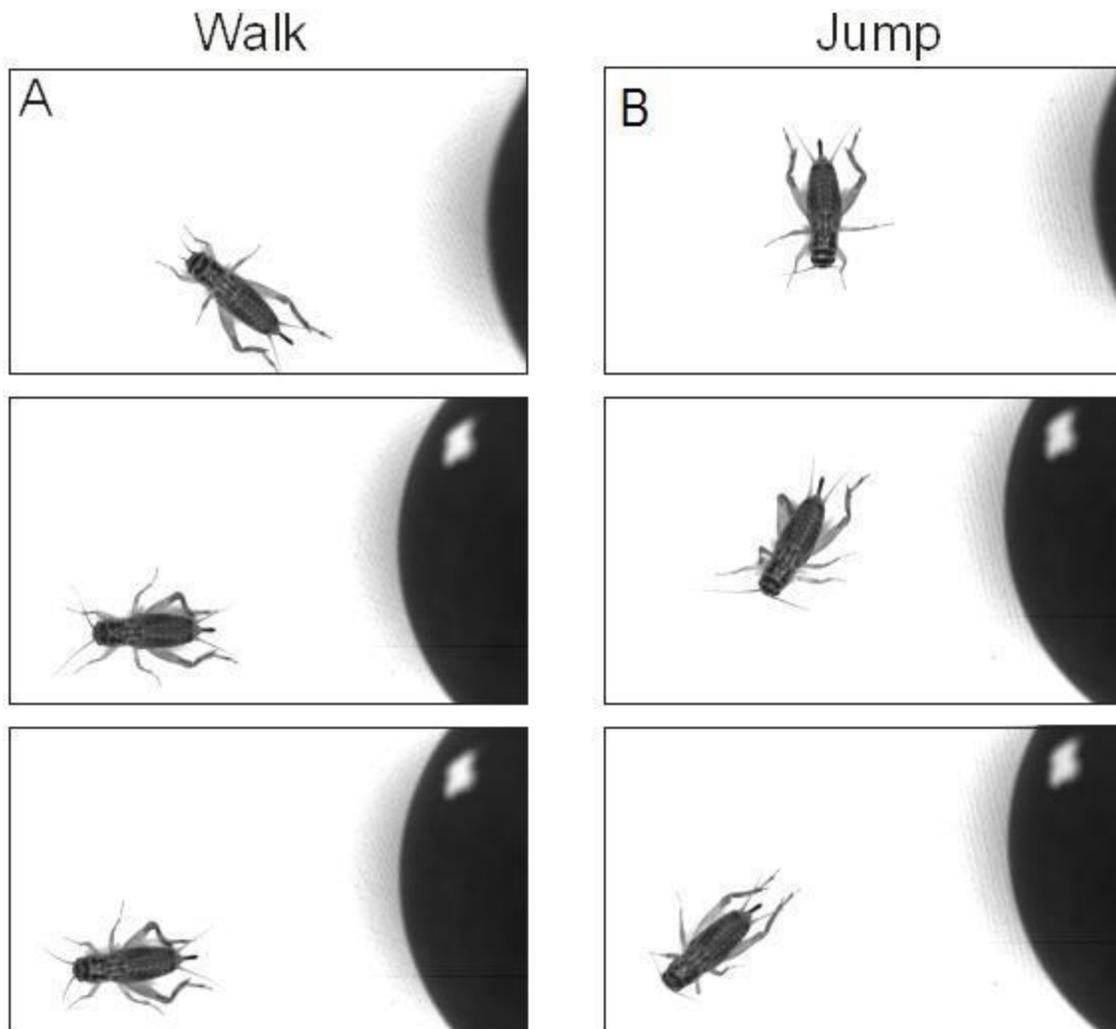


Figure 3. Representative example of a walk and a jump response in a cricket. Single select sequential frames from video recordings of a cricket responding to the stimulus (coming from the right) by walking (3A) and jumping (3B) are shown. Crickets typically turned before walking or jumping in a direction that took them away from the incoming looming stimulus. The images show the change in position of the cricket over time in response to stimulation.

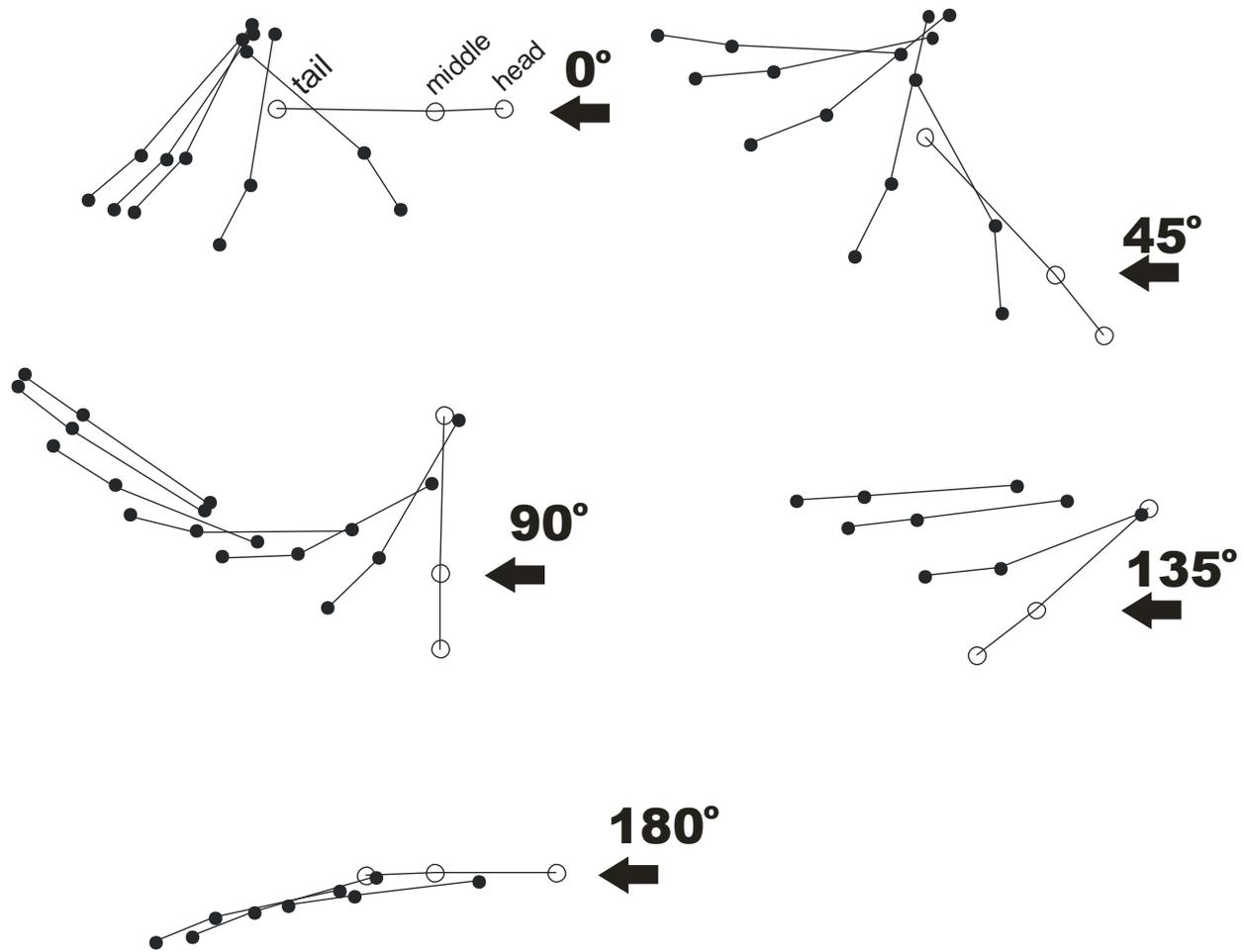


Figure 4. Representative examples showing the movement of the cricket in response to stimulation. The crickets were stimulated from 0, 45, 90, 135, and 180 degrees by the looming object (black ball). The lines with clear circles indicate the head, middle, and tail of the cricket before stimulation. The lines with the filled in circles represent the movement of the cricket over sequential 20 frame increments ($20 \times 1/650$ s). Arrows show the direction of the incoming stimulus while the numbers above the arrows indicate the degree of the approaching stimulus angle. Crickets appear to turn away from the stimulus before moving in a direction that takes them away from the stimulus.

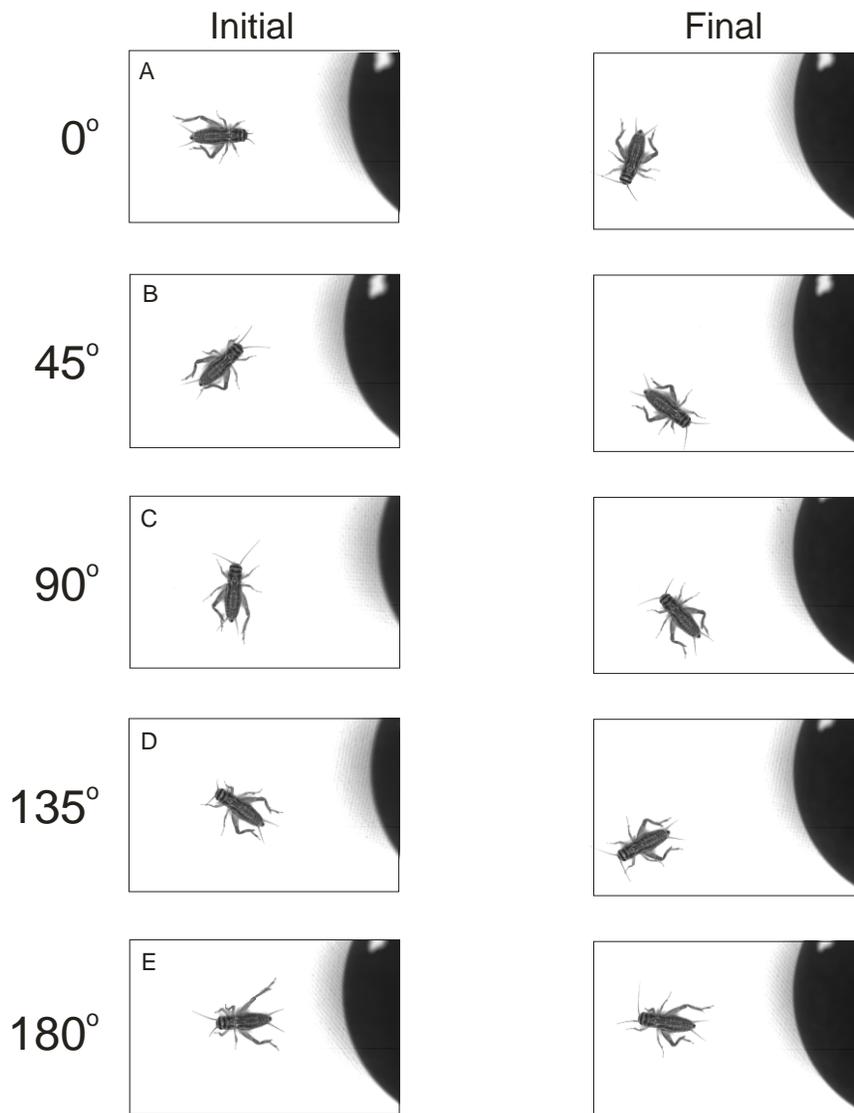


Figure 5. Representative examples of the initial and final position of a cricket to lateralized angles of stimulation. Crickets were exposed to the looming stimulus at 0, 45, 90, 135, and 180 degrees. The initial and final positions of a cricket are shown here for all angles of stimulus approach to show how the animal moved in response to stimulation. Crickets typically ended up facing away from the direction of the incoming stimulus. When stimulated at 45 degrees, the cricket appears to turn towards the ball (5B).

The degree of turn of the cricket's body in response to stimulation was quantified by measuring the change in body and head angles. Figure 6 shows the change in angle over time for the body and head. The beginning of the plateau on the resulting graph, which illustrated the point at which there was no further change in angle of the body or the head over time, was used to measure turn angle.

To determine whether the angle of resulting escape depended upon the angle of incoming stimulation, the stimulus angle was plotted in relation to the angle of body response (Figure 7). The graph shows that turn angle of the cricket depended upon the stimulus angle. Most points show that the animal is turning away from the incoming stimulus. For example, when stimulated at 180 degrees (from behind), the cricket has a turn angle of 0 degrees (moves directly forward) as it is already facing away from the stimulus, while a stimulation angle of 90 degrees resulted in a turn angle of -90 degrees away from the stimulus. However, in a few cases the cricket appears to turn towards the stimulus (seven points in the top right and bottom left quadrants). While there is a correlation between stimulus angle and turn angle based upon the graph as a whole, the relationship is less clear within each quadrant. This is important because each quadrant represents the response of the cricket to the stimulus when approaching from the front (0 degrees) through the side of the cricket (90 degrees) to the rear of the cricket (180 degrees). The top left quadrant represents the stimulus approaching from the right side of the cricket, while the bottom right quadrant represents the stimulus approaching from the left side.

There appears to be left/right symmetry between the angle of stimulation and the turn angle of the cricket when stimulated from each side. Although the response direction depends on whether the stimulus approached from the left or the right, it is unclear whether the laterality of the incoming stimulus angle has an effect upon the turn angle of the cricket. To determine whether the angle of response depended upon the laterality of the stimulus angle, the response of the cricket's body was plotted against stimulus angles reflected to the right hand side of the cricket's body (Figure 8). The cricket still appears to turn slightly away from the angle of stimulation, without making a full 180 degree turn away. For example, when stimulated at 0 degrees (from the front), the average turn of the cricket was 90 degrees, while a stimulation angle of 135 degrees resulted in a response turn of approximately 45 degrees away from stimulation. A linear regression was performed to determine the correlation between lateral stimulus angle and the angle of the cricket's escape (slope=-0.57, $R^2=0.47$). The plotted data had a slope of -0.57, indicating that the cricket did not turn directly away from the stimulus each time. The angle of turn of the cricket is dependent on the laterality of the incoming stimulus angle ($p<0.0005$). Figure 8 also shows the occurrence of jump (black circles) versus walk (grey circles) responses to each angle of stimulation. It appears that there was a greater tendency for the cricket to jump when stimulated from the rear.

The occurrence of jump and walk responses were counted with respect to stimulation angle (Figure 9). It appears that the cricket has a tendency to jump

instead of walk away from the looming stimulus when stimulated from the rear.

However, there is no significant effect to support this data, possibly due to the small number of jumps ($n=6$).

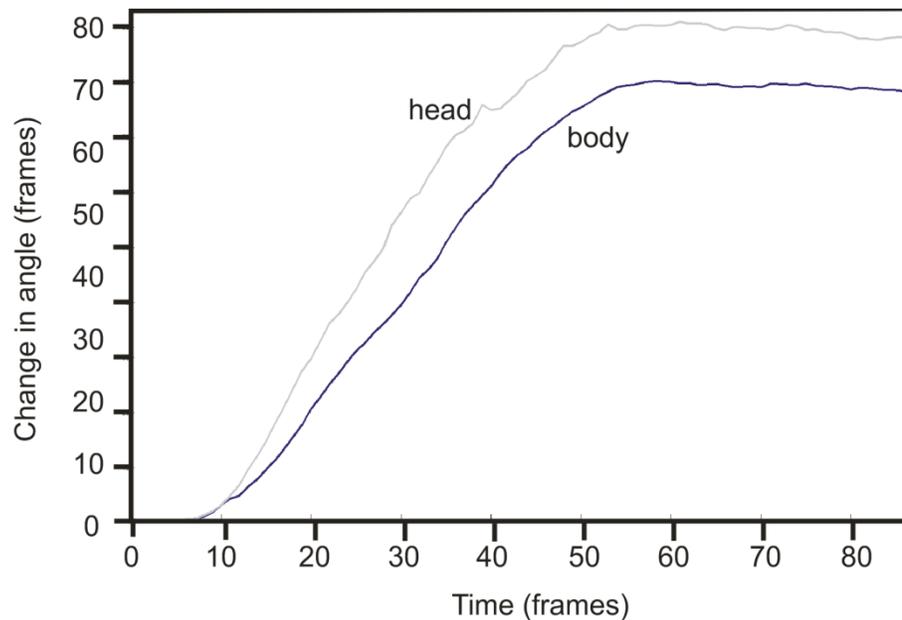


Figure 6. Representative example of the cricket's turn over time in response to stimulation. The change in angle of the cricket's body and head were plotted against frame number. The graph shows how the cricket turned in response to stimulation, as well as how long it took the cricket to complete the initial turn. The dark grey line represents the angle of the body, while the light grey line represents the angle of the head. The point that the cricket stopped turning occurs at the beginning of the plateau, as there is no change in angle over time at this point.

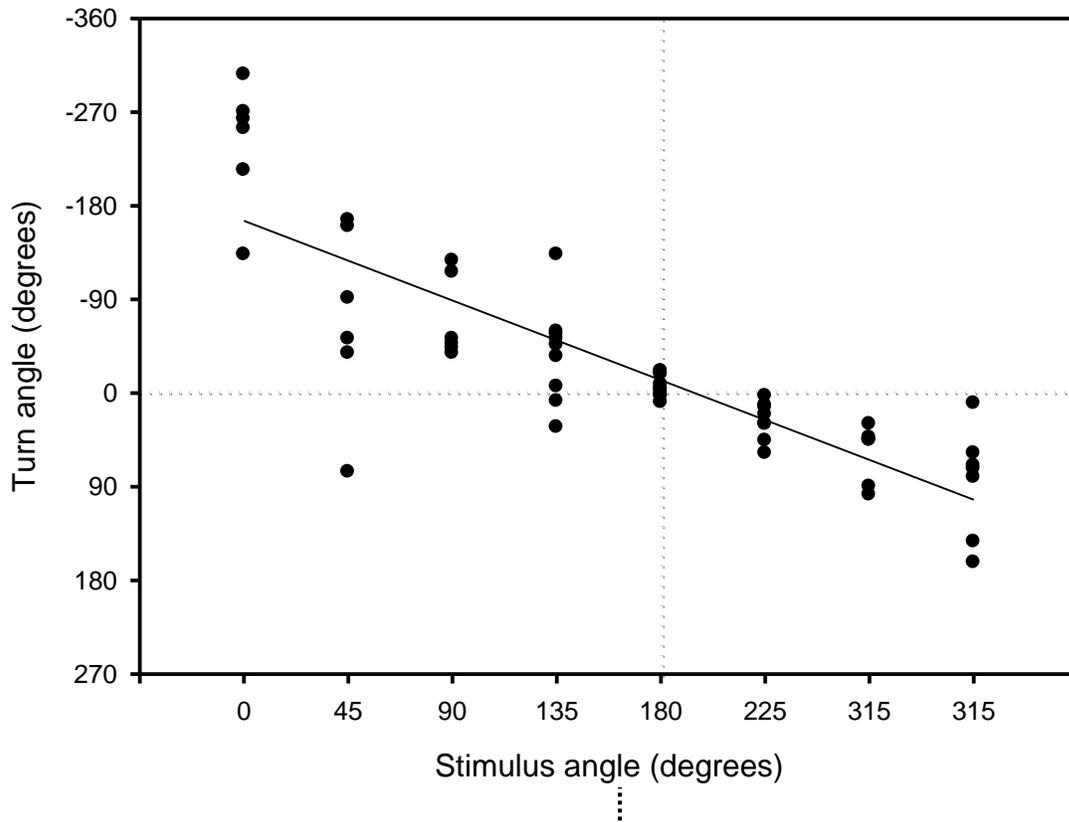


Figure 7. The angle of the cricket’s turn versus the angle of incoming stimulus. The change in body angle was measured against the incoming stimulus angle to determine the relationship. For each experiment, the cricket was stimulated at 45 degree increments between 0 and 315 degrees. The order of the angle of stimulation was randomized for each experiment. The cricket appears to turn away from the incoming stimulus, although there are a few points where the cricket appears to turn towards the looming ball. The response direction also appears to be dependent upon the incoming stimulus angle.

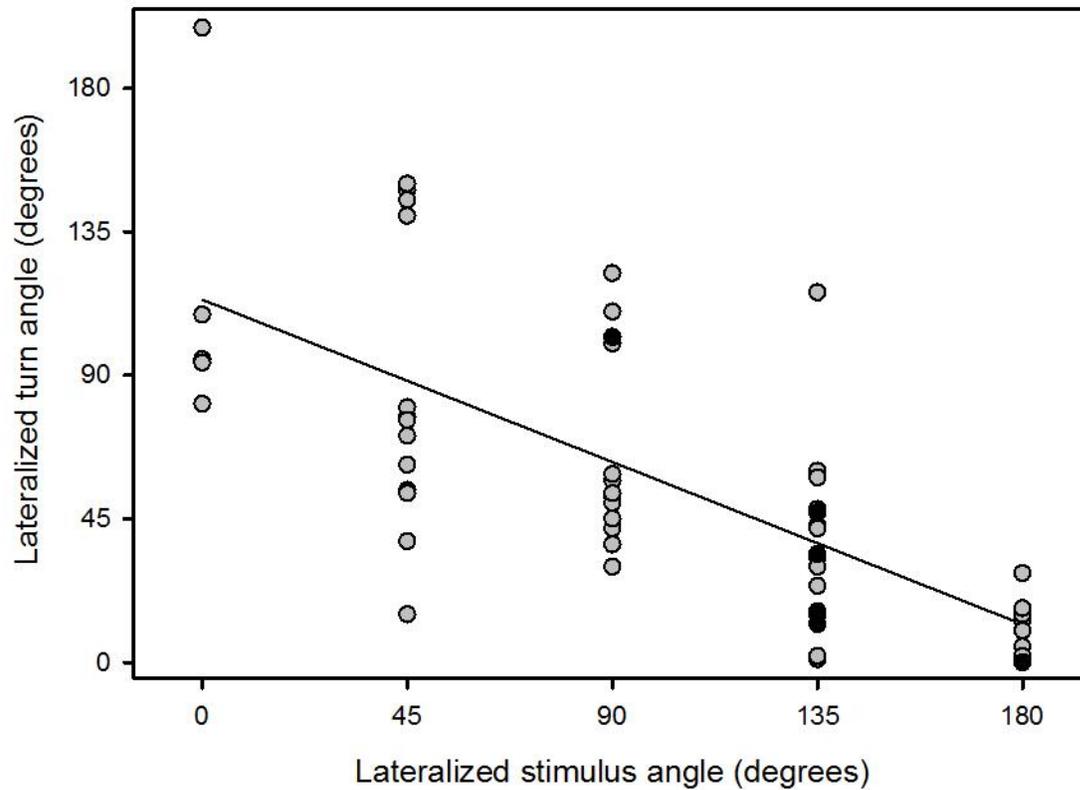


Figure 8. The absolute change in angle of the cricket’s body in response to lateralized stimulus angles. The change in angle of the cricket’s body was measured in response to stimulation from the lateralized stimulus angles. A linear regression was performed, indicating that the angle of turn was correlated with the angle of incoming stimulation (slope=-0.57, $R^2=0.47$). The angle of stimulation has a significant effect on the angle of turn of the cricket ($p<0.0005$). Responses in which the cricket walked are shown in gray, while jump responses are shown in black. Crickets appear to jump when the stimulus is approaching from near the rear. There is no apparent difference in turn angle between walk responses and jump responses.

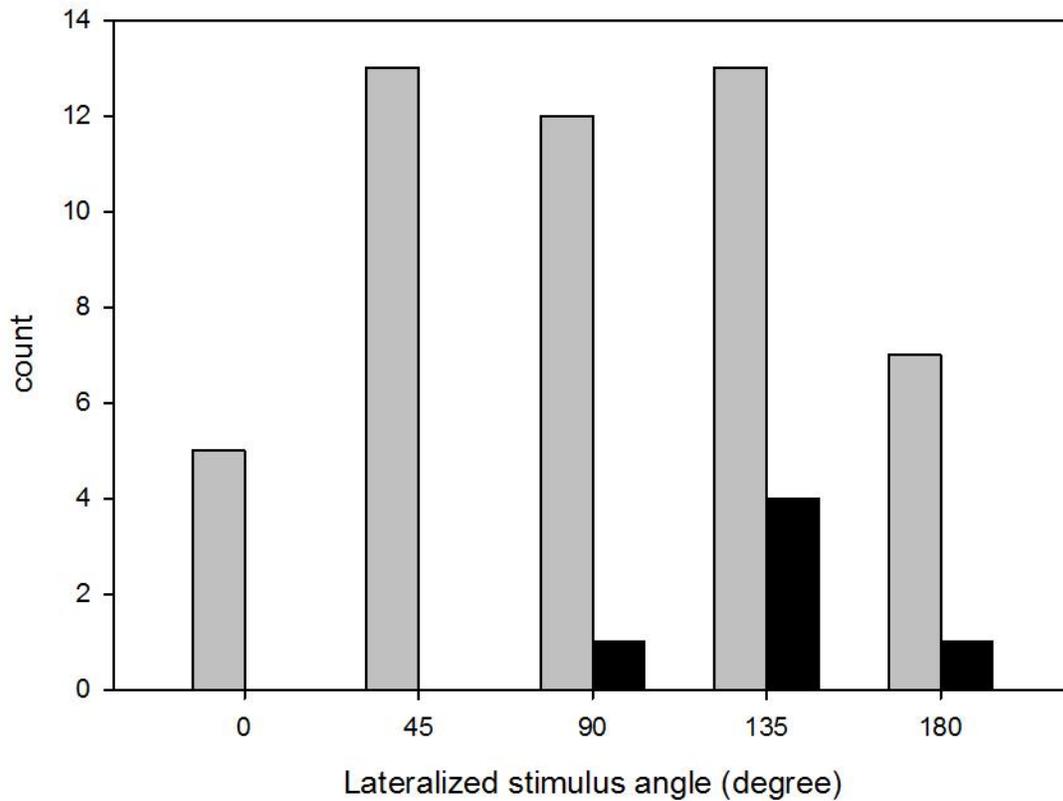


Figure 9. Counts of Jump and Walk Responses for all Reflected Stimulus Angles. The occurrence of jump and walk responses were counted with respect to all reflected stimulus angles. Walk responses are shown in grey, while jumps are shown in black. There appears to be a tendency for the cricket to jump when stimulated from behind, but there is no significant effect of stimulus angle on jump responses. This could be because an insignificant number of jumps were obtained (n=6).

B. Dependence of the head movement on body movement.

The segmentation of the cricket's body raised the question of whether the cricket turned its head and body as one unit, or whether one feature moved separately from the other. In order to determine whether there was a difference in the angle of turn between the head and the body, these two features were plotted against one another (Figure 10). A linear regression was performed to determine the degree of correlation between the angle of turn of the head and the body. The angle of turn of the head was found to be significantly correlated with the angle of turn of the body (slope=0.94, $R^2=0.99$, $p<0.001$), meaning that the change in body angle and change in head angle were similar.

Interestingly, it appears that, while the head and the body turn the same amount of degrees in response to stimulation, the cricket often turns with its head leading the body (Figure 6). This can be seen in representative examples of the movement of the cricket in response to stimulation (Figure 4). Before the initiation of stimulation at 0, 45, 90, 135, and 180 degrees, the head and body of the cricket were collinear (aligned). In the following sequences, representing the position of the cricket 20 frames (0.031 seconds) later, the head is bent away from the direction of stimulation with respect to the body. However, in the final frame, the head and the body are aligned once more.

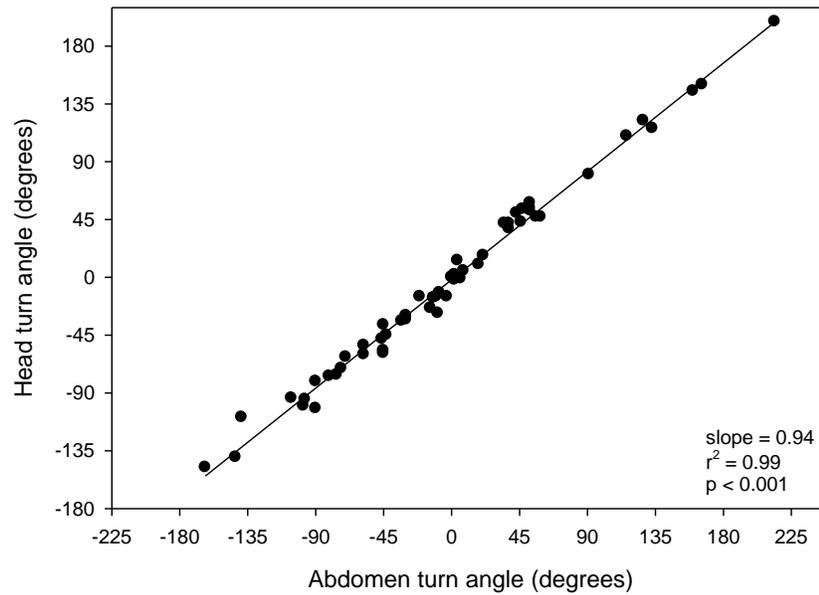


Figure 10. The relationship between the degree of turn of the cricket's body and the degree of turn of the cricket's head. The degree of turn of the cricket's body and head were plotted against each other to determine if there was any correlation between the angles of turn of the two features. Based upon the results of a linear regression (slope=0.94, $R^2=0.99$), there is a significant correlation between the degree of turn of the head and the body ($p<0.0001$).

VI. Discussion

Summary

The results of this study indicate that the angle of escape of a cricket is dependent upon the angle of approach of a looming object stimulus. Crickets turned their bodies away from the stimulus before either jumping or walking away from the direction of stimulation. Crickets usually walked away, but had a tendency to jump instead of walk when stimulated from behind, although this tendency was not significant. While, as expected, the angle of turn of the head is significantly correlated with the angle of turn of the body, the head appears to lead into the turn as the cricket turns away from the direction of stimulation.

Comparison to Previous Results

The specific aim of this study was to use high speed video analysis to determine the relationship between the angle of approach of a looming object and the angle of the resulting turn executed by a cricket. Previous studies regarding looming object stimulation have mainly focused on the response of locusts (Rind and Simmons, 1992; Gabbiani et al., 1999; Gabbiani et al., 2004; Simmons et al., 2010; Heitler and Burrows, 1977; Santer et al., 2005) and fruit flies (Card and Dickinson, 2008), while exposure of crickets to looming stimuli has been minimal (Dupuy et al., 2011; Yamawaki and Ishibashi, 2013).

Locusts that were stimulated with a black ball being rolled down a ramp towards them at 0, 45, 90, 135, and 180 degrees often exhibited escape responses that took them in a direction away from the looming stimulus (Santer et al., 2005). When stimulated from the rear at stimulus angles greater than 120 degrees, locusts displayed a 0 degree trajectory movement away from the stimulus, meaning that they did not turn but instead jumped directly ahead and away from the incoming ball. However, no precise correlation was found between the angle of escape and the angle of approach of the looming stimulus when it approached from the side.

Fruit flies, when stimulated by a falling black disk, tended to jump away from the looming object and initiate a flight response (Card and Dickinson, 2008). When the stimulus approached from directly in front (0 degrees) or directly behind (180 degrees), the flies jumped directly backward or forward away from the looming object, respectively. However, when the disk approached from the side of the fly, the fly jumped in a direction that was halfway between directly away from the stimulus and directly forward (slope=0.44, $36 < \Theta < 72$ and $72 < \Theta < 108$). These values were significantly different from the fly jumping either directly forward or directly backward in response to stimulation ($p=0.05$).

In this study, crickets displayed a similar direction of escape in response to the looming stimulus as the fruit flies and the locusts did to looming stimuli, as they did not move directly away from the black ball at all times, instead turning at an angle that was somewhere between 0 and 180 degrees away from the angle of

stimulation (slope=-0.57). The slopes obtained from the graphs of escape direction of the fly (0.44) and cricket (-0.57) in response to stimulus angle, which provide information about how much the animal turns, are comparable, further suggesting that the two types of arthropods escape from a looming stimulus in a similar manner that is partially away from the direction of the incoming stimulus.

The few studies regarding the response of crickets to incoming stimulation have centered upon the type of escape response, as well as the success of the cricket in escaping away from the stimulus. In this study, most escape strategies involved a turn away from the looming stimulus before a walk or a jump was executed, which is consistent with previous findings suggesting that crickets turn, turn and walk, or turn and jump in response to stimulation (Dupuy et al., 2011; Camhi et al., 1978). Dupuy et al. (2011) qualified the escape of the cricket as being successful if the cricket did not get hit by the looming piston. For successful escapes, Dupuy et al. looked at the angle of escape response compared to the stimulus angle, and found that it spanned a wide range of angles when stimulated from behind ($169^{\circ} \pm 7^{\circ}$) and from the side ($156^{\circ} \pm 12^{\circ}$) relative to the piston. These values indicate that the crickets moved away from the direction of incoming stimulation, which is consistent with the findings of this study, although the escape responses were not classified as being successful versus unsuccessful. The escape success of crickets could not be determined in the same manner in this experiment, as crickets were placed 20 mm away from the ball when the piston was fully extended, so that the ball could not touch them if they failed to execute an escape response.

Previous studies using aversive stimuli have never mentioned any separation between the movement of the head and the body of the cricket or other arthropods. Although the head and the body turned the same amount of degrees in response to stimulation in this study, the head appeared to lead the body into the turn for most trials. While the head began the turn earlier in most trials, the cricket ultimately ended up with its head and body aligned (Figure 4), suggesting that the body turned just as much as the head of the cricket, only more slowly.

Mechanisms

Sensory structures that arthropods use to obtain information about their local environment include the cercal system, vision, and the antennae. In this study, the large surface area of the ball probably creates a substantial amount of wind as it moves towards the cricket. This movement of air most likely stimulated the wind-sensitive receptors on the cricket's cerci, especially when the ball was approaching from the rear where the cerci are located, alerting the cricket to a potential threat and thus generating an escape response.

In addition, vision probably plays a role in producing an escape response in the cricket upon stimulation with the ball. The ball was large (diameter 2.5 inches) and black, and was placed in front of a white square canvas to provide contrast so that the cricket could see it. Visual information obtained by the cricket as the ball was looming towards it could be used to direct the escape response away from the

angle of stimulation in conjunction with information regarding air displacement obtained by the cerci.

Functional Implications

It is necessary to evaluate the escape strategy of the cricket in response to the looming stimulus to assess the functional implications of the escape. Although several crickets (n=6) turned and jumped away from the ball, the majority of the escape responses typically consisted of the cricket taking an initial turn away from the ball, walking a few steps, and stopping. This escape strategy did not take the cricket far away from the ball. However, it is important to note that once the ball was 20 mm away from the cricket, it stopped moving. The cricket might continue to walk or even produce a greater number of jumps away from the ball if the ball was allowed to get closer to the cricket.

The occurrence of walking versus jumping escape responses has some functional significance. Jumping is a time consuming escape mechanism that is energetically costly, while walking away from an incoming stimulus does not exhaust the cricket so quickly and enables it to travel a short distance away from a potential threat. Therefore, it would be expected that crickets walk more often than they jump away from a threatening stimulus. The frequency of jump responses was greater when crickets were stimulated from the rear. This could be because the wind-sensitive cerci are located towards the rear of the cricket, and thus can better detect wind displacement, alerting the cricket to a threat and allowing it to jump

away from the stimulus. Another potential explanation could be that, when the stimulus is approaching the cricket from the rear, the cricket does not need to turn away from the direction of the incoming stimulus, which can be time consuming, and therefore can use this extra time to prepare for a jump away from the incoming stimulus.

While the degree of turn of the cricket's body was significantly correlated with the degree of incoming stimulus angle, crickets did not turn directly away from the incoming stimulus every time they were stimulated (Figure 8, slope=-0.57). Instead, crickets turned their bodies at an angle that seemed to point them away from the incoming stimulus angle before walking or jumping away from the direction of stimulation. The degree of turn might point the cricket in a direction sufficient to avoid being touched by the stimulus, without wasting unnecessary energy on executing a 180 degree turn away from the direction of stimulation.

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