Seismic echolocation: do scorpions use this novel method of orientation to aid in locomotion?

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Summary

Relatively few species orient through echolocation. Bats, dolphins and whales, and a few species of cave-dwelling birds possess the ability to echolocate through a liquid or gaseous medium, but no animals have been shown to echolocate on a solid substrate. It has long been believed that the high velocity of acoustic signals through most solids prevents organisms from obtaining biologically useful information from sound waves. Sand, however, is an unusual solid that is physically capable of supporting echolocation as a means of orientation. Sand-dwelling scorpions have already been shown to be sensitive to sound waves transmitted over sand. They possess mechanoreceptors in their lower legs which can accurately detect prey movements using only substrate-borne vibrations. Since scorpions are so sensitive to vibrations in sand, perhaps they orient by seismic echolocation. In this study we remove all non-seismic cues and place *Paruroctonus utahensis,* a desert sand scorpion, in the center of a circular arena with one quadrant removed. The scorpions were then allowed to choose between the open area and the portion of the arena in contact with the sand. Control trials were also conducted with the arena suspended immediately above the sand. All movements in relation to magnetic North were random. Movements in experimental trials in relation to the open quadrant appeared biased but showed no statistical significance. However, control trials plotted in relation to the empty quadrant were statistically non-random. This indicates that scorpions can detect objects above the sand in the absence of all visual and chemical cues. We suggest that tricobothria, small hairs on the pedipalps of scorpions that are sensitive to slight air currents, may be responsible for this orientation behavior. We also suggest that our study does not effectively comment on seismic echolocation in scorpions due to our unexpected findings that scorpions can orient to objects suspended above the sand.

Introduction

Echolocation is a rare method of active orientation that involves an organism determining the position of objects around it through the emission (from the animal itself) of acoustic signals that return to the organism as echoes (Griffin 1986). Only four orders are known to contain animals that echolocate: Chiroptera (bats), Cetacea (dolphins and whales), Apodiformes (cave swiftlets) and Caprimulgiformes (oilbirds) (Norris & Evans 1986). Many invertebrates and even some mammals (rats, tenrecs, and shrews) have been shown to perform simple obstacle avoidance through passive echo detection, but this is not equivalent to active echolocation (Norris & Evans 1986; Ayrapet'yants 1974). Echolocation is thought to occur only through liquid and gaseous media because air and water possess homogenous and elastic properties which allow the efficient conduction of mechanical waves. Solids, in comparison, have long been believed to be incapable of transmitting sound in a biologically useful capacity due to the high speeds at which sound travels through most solid media (Brownell 1984). Sound waves traveling too fast will exceed the differentiating capacity of biological sensory systems and serve only as a warning of a general disturbance (Schwartzkopff 1974). Terrestrial organisms have thus seemed physically constrained from orienting to self-originated sounds transmitted through a solid substrate. Some types of sand, however, transmit sound at speeds of less than 150 m/s, less even than the speed

of sound in air (Brownell 1977). Organisms dwelling on sandy substrates are thus free of the physical constraints against echolocation imposed on most other terrestrial animals.

Sand-dwelling scorpions present an interesting model of a terrestrial animal that may echolocate on a solid medium. Sand scorpions have already been shown to be very sensitive to surface-borne sound waves. They possess the capacity to precisely determine prey location by detecting seismic vibrations that result from prey movements in the substrate (Brownell & Farley 1979b). Orientation to prey is dependent only on the sensation of substrate vibrations, and a scorpion can locate prey in the absence of all other sensory cues. Two sensory organs, the tarsal hairs and the basitarsal slit sensilla, are responsible for sensing seismic waves (Brownell & Farley 1979c). The basitarsal slit sensilla, located at the junction of the tarsus and basitarsus on the scorpion's lower leg, primarily detect surface, or Rayleigh waves, which allow the scorpion to orient to prey direction. The tarsal hairs, which are located on the tarsus and extend into the sand, respond to compressional waves and are most likely involved in determining distance of the disturbance (Brownell 1977). The range of a scorpion's accurate determination of direction and distance of cricket-sized prey is about 15 cm, and they can detect vibrations as far as 50 cm away (Brownell & Farley 1979b).

Since scorpions can accurately locate prey solely through substrate vibrations, we considered it possible that scorpions employ some form of seismic echolocation. That is, do scorpions detect and orient to substrate-borne vibrations, produced by themselves, which echo off of nearby objects in the sand? Since a scorpion can precisely detect the position of a disturbance made by prey much smaller than itself, perhaps it can detect and orient to reverberations from objects that originate from its own movements in the sand.

In this study we investigate the possibility that scorpions use seismic echolocation to during their orientation movements. *Paruroctonus utahensis* were subjected to dual experiments in a simulated natural habitat within the laboratory. All visual and chemical cues were removed. Scorpions are unable to detect light at IR wavelengths (Camp & Gaffin 1999; Machan 1968), so trials were recorded under IR light. We dropped the scorpions in a simple behavioral choice arena consisting of a circular ring with one quadrant removed. Experimental trials were conducted with the arena in contact with the sand while in the control trials the arena was suspended immediately above the sand surface. If scorpions use seismic echolocation to aid in orientation, we expect to see significantly non-random movement patterns (plotted in relation to the open quadrant) for experimental trials and random movements in control trials. While only the control trials showed significantly nonrandom movements in relation to the open quadrant, our experiments provide strong evidence that scorpions preferentially oriented to the arena in both control and experimental trials.

Methods

Animals

Twenty adult *Paruroctonus utahensis*, eight male and twelve female, were used in these experiments. The animals were collected from Monahans Sand Dunes State Park in Monahans, TX in early March 2000. Trials were begun one week after collection of scorpions to minimize behavioral effects due to sustained time under laboratory conditions. Animals were maintained in 3.8-L glass jars containing 250 mL of sand collected from the scorpions' natural habitat. Animals were neither fed nor watered during the trial period. The scorpions were maintained and experiments conducted in the University of Oklahoma animal laboratory facilities under constant temperature and humidity (22°C, RH 55-65%). The animals' normal light-dark phase was preserved as follows: 2000-0730 h dark and 0730-2000 h light.

Experimental apparatus

All experiments were conducted within a Diamond Head 22 gauge, 95 gallon galvanized metal (with zinc coating) stock tank measuring 91-cm in diameter by 61 cm deep. The tank was filled to a depth of 25 cm with sand from the animals' natural habitat to prevent echoes from the floor of the metal tank from interfering with the trials. The top 5-cm of sand was autoclaved to eliminate existing chemical cues. The tank was placed on a lazy susan, to allow free rotation, and on a Lewis Hyman rubber fatigue mat (1.9 cm thick, item #0515830) to reduce external vibrations. The tank was leveled using an Empire Unitek 18" aluminum level (model #580-18).

The experimental arena was a white plastic ring 25-cm in diameter by 5 cm tall. A sand scorpion's effective range of detection of vibrations is about 30-cm, thus we chose a ring with a radius of about 12.5-cm so that the walls of the arena might be near enough for the scorpion to detect. One quadrant of the bottom half of the ring was removed so that when the lower portion of the ring was set in the sand, three quarters of the arena would contact the sand and one-quarter would be open to the rest of the tank. The top half of the ring was left intact. Nine IR diodes (λ peak =940 nm; Tech America item # 900-1572) were embedded within and spaced equidistantly around the top of the ring and shaded with aluminum foil to direct the IR light onto the sand. The IR diodes were powered by a 3-5 Amp Samlex regulated DC power supply (output 13.8 V DC, item #RPS1203). The arena was suspended from a 3/4" plywood frame

constructed as follows: two main support beams 110-cm long by 10-cm wide were set on edge and connected in parallel by two pieces 30.5-cm long by 10-cm wide (placed 20-cm from each end of the parallel support beams). The support beams extended over and rested upon the top edge of the tank. Four sets of paired ridges (made from strips of sturdy adhesive tape) were raised at specific intervals around the top edge of the metal tank so that the frame could only rest in one of four positions. A semicircular wedge facing toward the outside edge of the support beams was attached to each of the connector pieces to allow the frame to fit securely within the metal tank yet still rotate freely. Attached to the support beams 15 cm from each of the connector pieces were two paired sets of descending arms measuring 25 cm by 10 cm. At the bottom of each descending arm was a metal plate through which a 41-cm screw was threaded. Each screw was affixed to its plate by two nuts, one above the plate and one below, that allowed the height of the screw to be adjusted. The two pairs of screws thus formed a square 30.5-cm on a side, and any of the screws could be adjusted up or down independent of the others. Two wooden blocks, set opposite each other and directed perpendicular to the length of the support beams, were each attached to two of the screws and placed in contact with a full quadrant of the lower ring of the plastic arena. The arena was wedged in between the two wooden blocks for the trials but remained removable. The arena was placed within the blocks with the open quadrant of the plastic arena facing away from the support beams (Fig. 1a).

A white plastic PVC tube was used to drop the scorpions in the center of the arena at the beginning of each trial (Fig. 1b). The tube measured 20 cm long by 5 cm in diameter and was 0.3 cm thick. The tube was attached to a circular piece of plywood 25 cm in diameter and 0.3 cm thick by an adjustable metal band that allowed the height of the wooden circle to be raised or lowered. This guide assured a consistent drop (starting) location among trials. Four small wooden dowels were placed at 90° increments around the edge of the circle to allow the plywood to rest on the edge of the experimental arena.

The trials were recorded on a Sony handheld Handycam Vision video camera recorder with NightShot (model #CCD-TRV16). The camera had both infrared emission and detection capabilities, but the IR light source also emitted some visible light. The viewfinder eyepiece and the IR light source on the camera were obscured with several plys of aluminum foil for the duration of the experiments. The camera was mounted on a tripod and aimed at a mirror (directed at 45° from the horizontal) placed 46 cm above the top of the metal tank. An external observer viewed the trials on a Panasonic color TV.
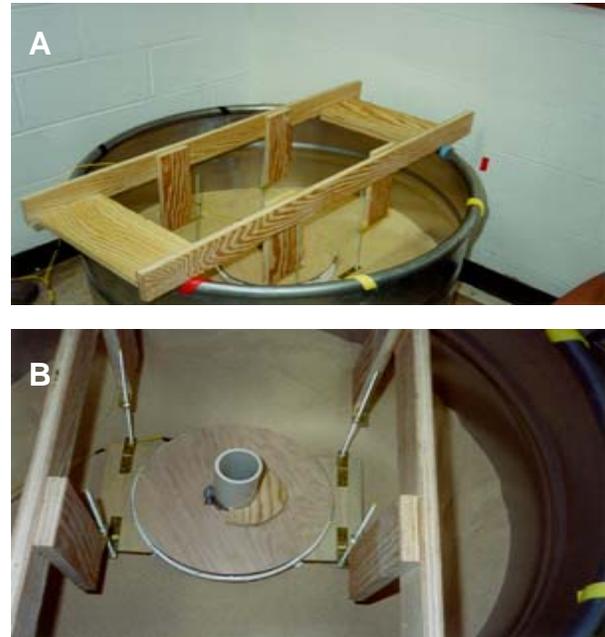

Fig 1: Photographs of experimental apparatus. Figure 1a (top). Plywood frame resting on metal tank (large arena). The colored pieces of tape mark boundaries for placement of the frame. Figure 1b (bottom). Circular arena (white) suspended from plywood frame. The drop tube is placed in the center of the arena.

Experimental protocol

Each of the *P. utahensis* was subjected to ten trials, five control and five experimental, for a total of 200 trials for twenty animals. Over a thirteen-day period in March 2000, twenty trials were conducted per night (only ten trials were conducted on the first and last nights of the experiments, and the scorpions were allowed to rest on the eighth and twelfth nights). Each scorpion was assigned a number, and the order of trials was randomly generated for each night. A set of ten consecutive control and experimental trials were conducted each night, but the order of sets was reversed for the next night. The arena was also adjusted and leveled in between sets of control and experimental trials. All experiments took place between 2000 h and 2400 h during the animals' normal period of activity. An observer in a separate room watched and timed the trials while another person remained in the room to carry out the experiments. During experimental trials the arena was placed in contact with the sand. In control trials the arena was suspended 0.4 cm above the sand. All other aspects of control and experimental trials, detailed in the following paragraphs, were identical.

Each night before trials began I sprinkled 750 mL of autoclaved sand onto the surface of the sand and leveled the arena floor. Between trials the sand substrate and experimental arena were prepared by leveling the

surface of the substrate and by wiping the sand clean with a piece of Plexiglas to break up any chemical trails laid down by the previous scorpion. The wooden frame holding the arena was rotated clockwise (to eliminate the possibility of learned behavior), and the metal tank was rotated counterclockwise (to eliminate the association of magnetic cues with arena orientation). The height of the sand was adjusted so that in the control trials the arena was suspended 0.4 cm above the sand, while in the experimental trials the arena sunk slightly into the sand to an equal distance along all sides of the circle. Care was taken to smooth the surface of the sand and to prevent excess ridges or furrows from forming in both control and experimental trials.

The drop tube was placed in the center of the arena and was allowed to sink slightly into the sand. (In preliminary trials, when the tube only barely contacted the sand, the scorpions would often dig their way underneath the tube and spoil the trial. Thus it was necessary to rest the tube on the sand, even though it left an impression.) The scorpion was then dropped in the tube and all light extinguished. The tube was raised and the scorpion was allowed to move freely. Each trial lasted one minute. Trials were deemed successful when the scorpion first touched the wall of the arena, or (in the case of the open quadrant) when the animal touched a position equivalent to a location on the wall. Only one data point, or successful trial, was gathered for each scorpion per night. A null trial was declared if the scorpion did not touch the wall within one minute, and the arena was prepared (sand swept clean and leveled, tank and arena rotated) and the scorpion immediately redropped. If the scorpion failed to reach the wall within one minute in the subsequent trial, it was also declared a null trial, and the scorpion was moved to the end of the night's trials to allow it to rest. Up to three more drops were conducted with scorpions participating in null trials so that no scorpion was dropped more than five times in one night. If a scorpion failed to move within five drops it was removed from trials for the evening and no data point was collected

Analysis

Videotapes of the trials were reviewed and data tabulated by a blind reviewer after the experiments were completed. The reviewer was unaware of the nature or purpose of the experiments. Scorpion movements were plotted on a polar coordinate system with two reference angles (magnetic North and the clockwise boundary of the open quadrant). Measurements were taken of a single initial and destination angle for each successful trial (rounded to the nearest 5° increment) based on magnetic North as the polar x-axis. Two destination angles were derived from the measurements. The derived angles corresponded to the location on the wall where the scorpion first touched. One angle described the

scorpions' contact position in relation to magnetic north, and the other described the contact position in relation to the clockwise side of the empty quadrant.

Results

There appeared to be no bias to the distribution of initial drop angles (Fig. 2a). Scorpions tended to move toward the direction that they initially faced, thus there was a distinctly limited range of variation (about 90° to either side) between starting and destination angles (Fig. 2b). Many scorpions chose a winding path, interrupted by one to three pauses of about one second each. Others moved immediately toward the wall with very little deviation from starting angle. One hundred ninety-seven successful trials were completed. About 20% (60 out of 257) of all drops were declared null, but a single scorpion accounted for 1/3 (18 total) of the redrops. We collected ten data points from all scorpions except one, for which we obtained only seven. Gross data from all successful trials (plotted relative to magnetic North and the open quadrant) is presented in Fig. 3.

Two classes of trials were observed. The first class we term "ballistic", and the second we term "deliberate".
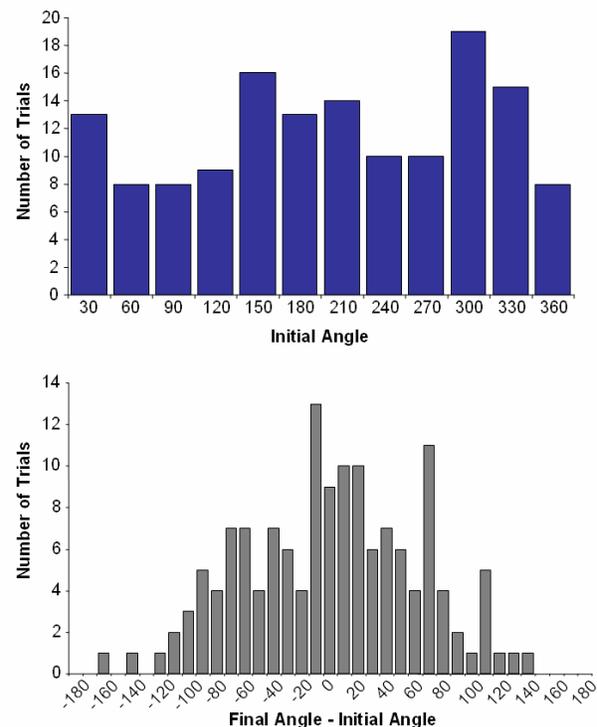

Fig 2: Illustration of scorpion behavior in relation to initial angle. Figure 2a (top). Starting angle in 30° increments for all trials (deliberate and ballistic). Note the broad distribution indicating random initial angle Figure 2b (bottom). Difference between final angle and initial angle for all deliberate trials. This demonstrates a general bias to move in the direction scorpions initially face.
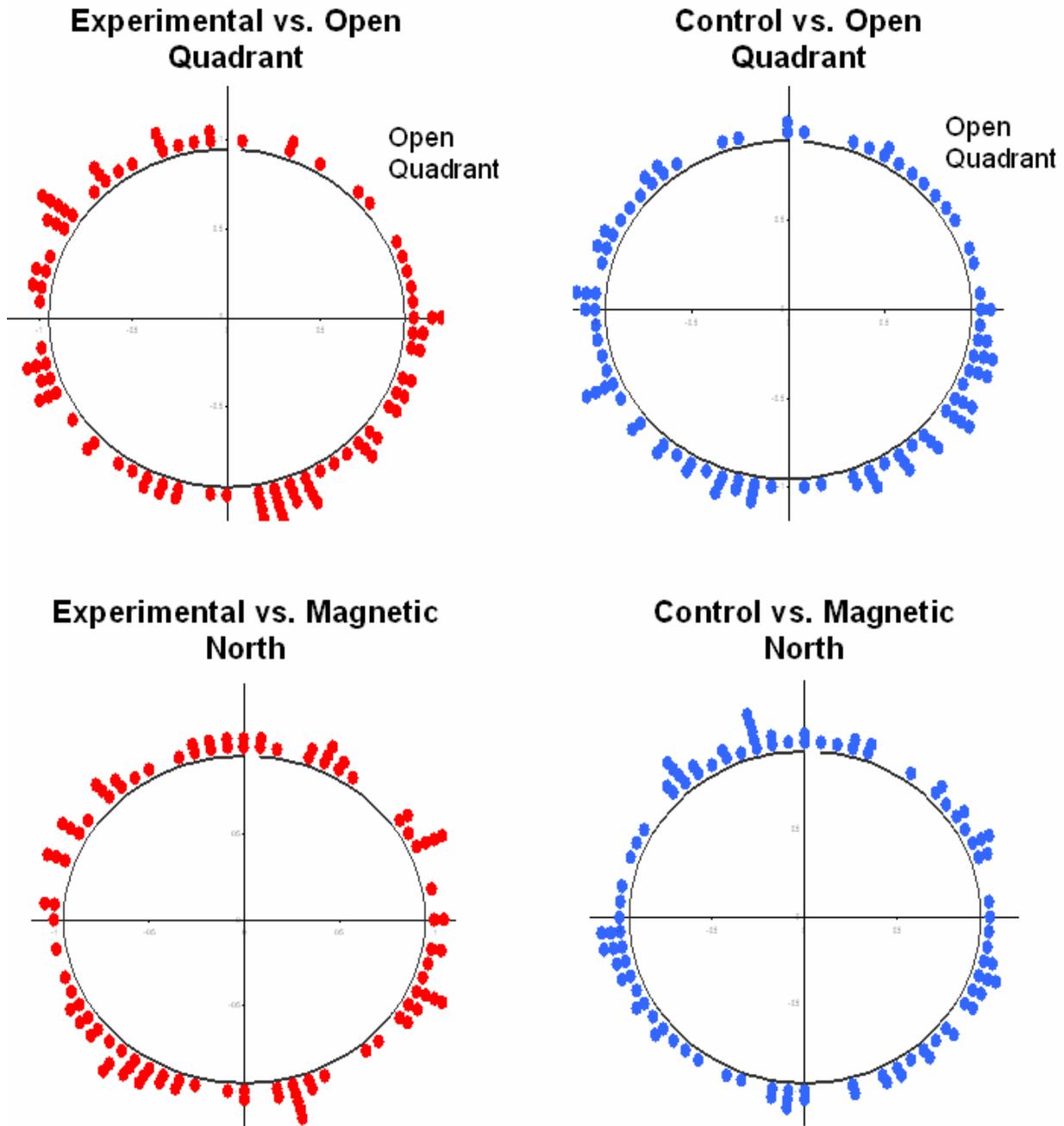
Fig. 3: Scorpion orientation behavior from all trials (total of 197) for both experimental and control groups. Animals' initial wall contacts have been plotted relative to the clockwise boundary of the open quadrant (top) and to magnetic north (bottom). Each dot represents a successful trial in which a scorpion touched first at that location (rounded to the nearest 5° increment). For clarity's sake, colors have been used to distinguish trial type: red = experimental, blue = control.

Ballistic trials were those in which scorpions touched the wall within two seconds of removal of the drop tube. We observed that scorpions moving immediately tended to touch the wall at angles very close (within about 10°) to their initial angle of orientation. This type of ballistic motion seemed to indicate reflexive escape response. We therefore excluded all trials (55 total; 28 experimental and 27 control) where scorpions exhibited this behavior. After removing ballistic trial data the number of data points remaining per scorpion varied between two and five per type of trial. The second class of trials, or deliberate trials, involved the scorpion
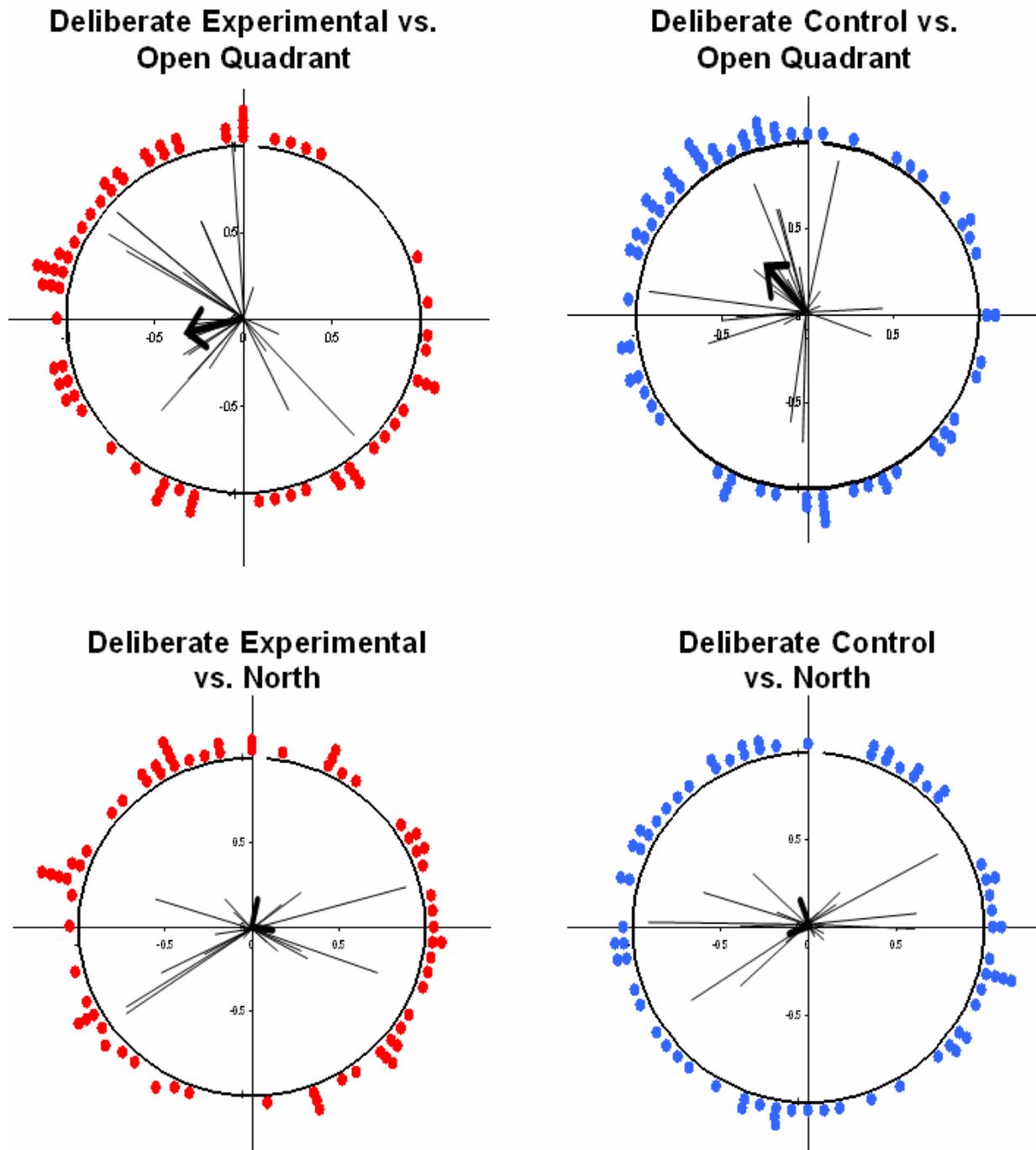
Fig. 4: Scorpion orientation behavior from deliberate trials (total of 142) for both experimental and control groups after eliminating data points from ballistic trials. Animals' initial wall contacts have been plotted relative to the clockwise boundary of the open quadrant (top) and to magnetic north (bottom). Each dot represents initial wall contact for one trial. The thin lines indicate the mean vector for each animal while the thick lines indicate the mean vector for each group. *Abbreviations:* r = mean length of vector, φ = mean angle of vector, and P = probability based on Rayleigh tests for randomness. For clarity's sake, colors have been used to distinguish trial type: red = experimental, blue = control.

remaining still for a few moments before beginning motion. Scorpions typically took a more winding or circuitous path to the wall in deliberate trials. All of the trials where scorpions exhibited this behavior (142 total;

72 control and 70 experimental) were considered valid and represented situations in which scorpions might orient to objects based on choice. Wall contact for all 142 deliberate trials are plotted against magnetic North and the clockwise boundary of the open quadrant (Fig. 4).

A mean vector was computed for each scorpion (Batschelet 1981) for each set of trials (n=20). After determining the mean vector for each animal within a group, we then calculated the mean vector for the entire group (Fig. 4). We used the Rayleigh test for randomness to determine statistical significance for the mean vector of each group (Batschelet 1981). Mean vector analysis shows that scorpions moved preferentially away from the empty quadrant in both control and experimental trials, but only the control trials showed a significant difference ($P < 0.05$) from random. The animals showed no preferential movement patterns in relation to compass direction.

Discussion

The animals show significantly nonrandom movement patterns ($P < 0.05$) in relation to the open quadrant with the arena off of the sand, but movement patterns remain random when plotted against magnetic North ($P > 0.900$). When the arena is in contact with the sand, it appears that the scorpions are able to detect and orient to objects, but in our trials their movement patterns were statistically insignificant ($P = 0.085$). Thus our study does not provide evidence that scorpions use echolocation to aid in orientation. However, there is unquestionably some orientation occurring in these trials.

Scorpions still appear to be capable of detecting cues from the arena under the conditions of our experiments. We have observed in the field that scorpions often move to hide under objects (such as leaves or small branches), which hang slightly above the sand but do not contact it. Scorpions may detect objects immediately above the sand using air currents that brush up against small hairs called tricobothria, which are located on their pedipalps. Little research has been performed on the tricobothrium, but it has been shown to be sensitive to the slightest air currents (Linsenmair 1968; Ignat'yev *et al.* 1976). Although scorpions may utilize the tricobothria to sense and orient to ambient air currents, the possibility also exists that scorpions can sense air currents that originate from their own movements and return to the scorpion from nearby objects. Under extreme low-light conditions this ability might aid the scorpion in locating objects under which they might hide from predators.

If scorpions use tricobothria to detect objects above the sand, this could also explain the patterns of behavior exhibited in the experimental trials. However, it seems likely that scorpions might use at least some information from seismic waves. Brownell has already shown that sand-dwelling scorpions use slit sensilla and tarsal sensory hairs to detect and orient on seismic vibrations emitted by the movements of their prey (1977). These tarsal sensory organs are extremely sensitive and can precisely locate the direction and distance of a disturbance in the sand within 15 cm, and can detect vibrations from prey-sized motions as far away as 50 cm (Brownell and Farley 1979a). This ability to detect and locate the source of seismic vibrations allows scorpions to find and capture prey in the absence of all other cues (such as cockroaches burrowing deep in the sand). Brownell showed that scorpions can receive and utilize seismic waves with as few as two of their feet in contact with the substrate (1979a). This seems to indicate that scorpions, even while moving, can detect seismic vibrations.

In light of the significance of the results in the control trials, we feel that our study was incapable of determining if scorpions seismically echolocate. Additional experiments are necessary to conclusively determine if seismic echolocation provides scorpions with orientation information. One simple set of trials could involve burying the arena within the sand so that it is positioned just level with the surface. This would remove the presence of an object above the sand from which air currents could return. If scorpion movements were still nonrandom in relation to the open quadrant, this would indicate that scorpions were using seismic echolocation to help locate the position of objects in contact with the sand. We could also conduct trials with scorpions whose tricobothria had been removed. This would determine if tricobothria were being used to collect information about nearby objects.

Our study presents strong evidence that *P. utahensis* use some form of mechanosensation to locate objects from a distance, but the experiments do not conclusively indicate the mechanism of that detection. In the absence of visible and chemical cues, scorpions show random movements in relation to magnetic north but significantly nonrandom movements in relation to the open quadrant when the arena is suspended above the sand. Further experiments need to be performed to isolate the precise mechanism by which scorpions detect the presence of nearby objects in the absence of visual and chemical cues.

Acknowledgments

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