7-2007

Sensory modulation of crustacean non-giant tailflipping

Sandra Y. Espinoza
The University of Texas Rio Grande Valley

Zen Faulkes
The University of Texas Rio Grande Valley, zen.faulkes@utrgv.edu

Sensory modulation of crustacean non-giant tailflipping

Sandra Y. Espinoza and Zen Faulkes

Department of Biology, The University of Texas-Pan American, 1201 W. University Drive, Edinburg, TX 78539, U.S.A.

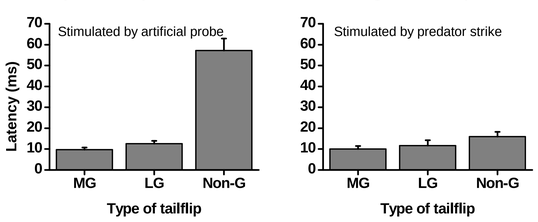
Email: beluhua@aol.com, zfaulkes@utpa.edu

Louisiana red swamp crayfish, *Procambarus clarkii* (Girard, 1852).

Introduction

Many crustaceans swim by tailflipping, but the behaviour has been best studied in Louisiana red swamp crayfish (*Procambarus clarkii*). Although crayfish tailflipping appears to be a single behaviour at first glance, it is actually three distinct behaviours. Two tailflips are mediated by sets of giant neurons. These are short latency, stereotyped, single tailflips. The third form of tailflipping is controlled by an as yet undescribed set of non-giant neurons. Non-giant tailflips have a significantly longer long latency than giant-mediated tailflips, and are variable and repetitive. Some decapods, such as spiny lobsters, lack giant neurons associated with tailflipping and are only capable of non-giant tailflipping (Espinoza et al., 2006; Faulkes, 2004). This suggests that non-giant tailflips may have a more significant survival value than previously thought.

Originally, non-giant tailflips have been considered to have response latencies that are not merely significantly longer (in the statistical sense), but *dramatically* longer than the response latencies of giant tailflips (Reichert and Wine, 1983). More recent work showed that the latency of non-giant tailflips was significantly reduced depending on whether the initiating stimulus was an artificial probe or an actual predator (Herberholz et al., 2004). Although still significantly longer in the statistical sense, the latency of these predator-initiated non-giant tailflips are much closer to the giant-mediated tailflips. This may explain a report of short latency tailflips in spiny lobsters (Newland et al., 1992), which do not have escape-related giant interneurons (Espinoza et al., 2006). How these non-giant tailflips have a latency nearly as short as those generated by giant neurons is unknown. Presumably, sensory cues modulate the non-giant tailflip circuit.



Latency of crayfish non-giant tailflips changes with type of stimulus. MG = medial giant interneuron mediated tailflips; LG = lateral giant interneurons mediated tailflips; Non-G = non-giant interneuron mediated tailflips. Redrawn from Herberholz et al. (2004).

As a first step in re-examining the modulation of non-giant tailflipping, we further investigate how the presence of weapons affects non-giant tailflipping. Removing both claws significantly changes the threshold for tailflipping (Krasne and Wine, 1975; Lang et al., 1977). Claw removal affects several variables at once, however; e.g., the animal's mass; visual stimuli associated with having claws; tactile and proprioceptive cues. For example, a crayfish with claws that are present but useless might "bluff," and may not tailflip away from a stimuli more than an intact animal.

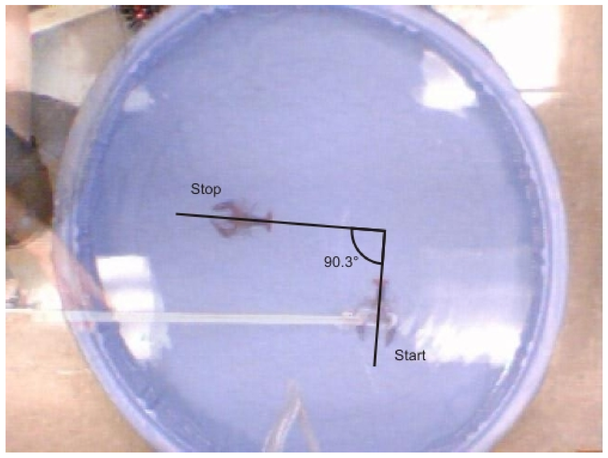
Methods

Crayfish of both sexes, ranging in size from 26-57 mm, were bought from a commercial supplier (Carolina Biological Supply Co.; *Procambarus clarkii*) or collected locally (*Procambarus* spp.) and housed individually in small tanks at The University of Texas-Pan American.

Crayfish were anaesthetized by chilling before surgery. Claws were deafferented by making an incision at the coxa-basis joint and cutting the claw nerve with fine scissors. Surgery was tested by placing an object in the claw and seeing whether the crayfish would grab it. The same animals were measured in all three conditions (i.e., intact, 1 claw deafferented, 2 claws deafferented).

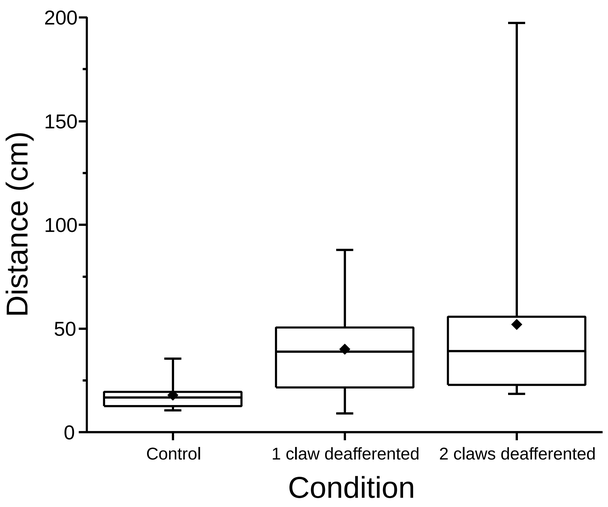
Behavioural trials were carried out in a wading pool filled with water. Tailflips were initiated by tapping the animal with a "yabby whacker." Behaviour was recorded by a web cam (Logitech QuickCam) placed 2.3 m directly over the top of the pool, and video was recorded directly to a PC.

Single video frames of various points of the tailflip were grabbed from the file using Media Player Classic v.6.4, and imported into Image-Pro Plus v. 4.5 (Media Cybernetics) for measurement and analysis. The distance travelled and the change in the angle of body orientation were measured.



Sample image composed of two merged video frames, showing how the angle of a crayfish's change in orientation was measured.

Data were plotted in Origin 7 (OriginLab Corporation). Distance data had skewed distributions in all groups and unequal variances between groups. To solve this, the data were log transformed. Distance data were analyzed using SPSS 12; angular data were analyzed by hand following Batschelet (1981).

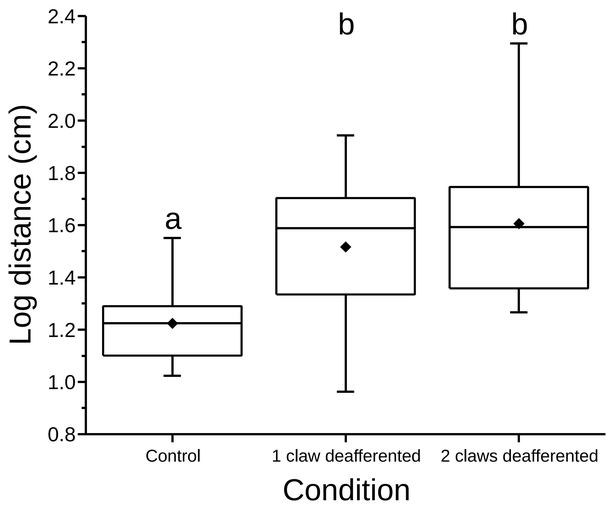


Raw (non-transformed) distance data, showing skewed data and wide variance in different experimental conditions. Diamond = mean; box = 50% of data; horizontal line in box = median; whiskers = minimum and maximum.

Results

Distance tailflipped

Sensory input from claws significantly alters the distance crayfish tailflip when tapped (one way ANOVA, $F(2,36) = 7.538$, $p = 0.002$; n = 13). Intact crayfish (control) tailflipped for significantly greater distances after deafferenting one or both claws, although there was no significant difference in distance between one claw being deafferented versus both claws being deafferented (post hoc LSD test).



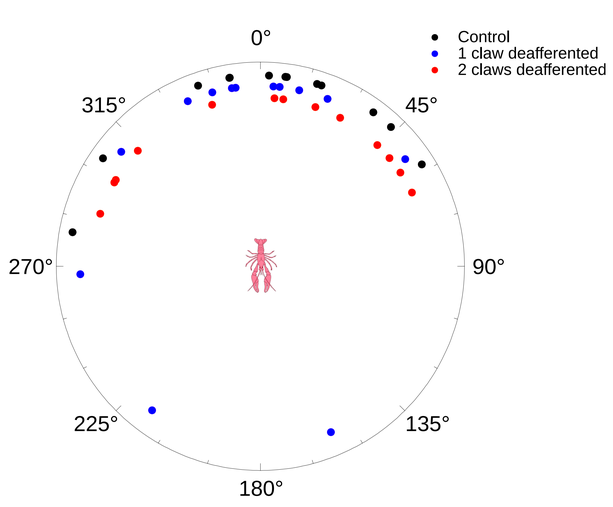
Log transformed distance data. Treatments sharing a letter (e.g., b) do not differ significantly from each other. Diamond = mean; box = 50% of data; horizontal line in box = median; whiskers = minimum and maximum.

Conditions contrasted		Mean difference	Standard error	Significance
Control	1 claw deafferented	-.29261(*)	0.10286	0.007
Control	2 claws deafferented	-.38170(*)	0.10286	0.001
1 claw deafferented	2 claws deafferented	-0.08909	0.10286	0.392

Post-hoc comparison of means (LSD test).

Direction tailflipped

The orientation that crayfish assumed once they finished tailflipping did not differ significantly in either mean angle or amount of dispersion (i.e., variation) with claw deafferentation (Mardia-Watson-Wheeler test, $W = 2.9$, $df = 4$, $p > 0.22$).



Orientation of crayfish relative to initial position after they completed tailflipping. 0° indicates the animal moved directly backwards; 90° indicates a turn to the right, 270° indicates a turn to the left.

Discussion and future directions

Removing sensory input from even one claw significantly increases the distance that a crayfish tailflips. The results are consistent with previous studies and emphasize the importance of claws in anti-predator behaviour and agonistic interactions with conspecifics.

Future experiments will be aimed at finding the sensory cues that reduce the latency of non-giant tailflipping to be almost as rapid as those of giant mediated responses. Electromyograms (EMGs) of abdominal muscle activity will be used to measure response latency.

This project is also planned as the first step in comparative studies examining modulation of tailflipping in other decapod crustacean species. For example, spiny lobsters use antennae instead of claws as weapons; their sensory input to the non-giant tailflipping pattern generator would be substantially different than the claws of crayfish. We predict that deafferentation of the antennae in spiny lobster will also significantly increase the distance they tailflip in response to threats.

Acknowledgements

We thank David Macmillan and Blair Patullo (Department of Zoology, University of Melbourne) for providing plans of the original yabby whacker, and Tom Eubanks (Department of Biology, The University of Texas-Pan American) for building the new yabby whacker used in this project.

References

Batschelet E. 1981. *Circular Statistics in Biology*. Academic Press: London.

Espinoza SY, Breen L, Varghese N, Faulkes Z. 2006. Loss of escape-related giant neurons in a spiny lobster, *Panulirus argus*. *The Biological Bulletin* **211**: 223-231.

Faulkes Z. 2004. Loss of escape responses and giant neurons in the tailflipping circuits of slipper lobsters, *Ibacus* spp. (Decapoda, Palinura, Scyllaridae). *Arthropod Structure & Development* **33**: 113-123.

Herberholz J, Sen MM, Edwards DH. (2004). Escape behavior and escape circuit activation in juvenile crayfish during prey–predator interactions. *The Journal of Experimental Biology* **207**: 1855-1863.

Krasne FB, Wine JJ. 1975. Extrinsic modulation of crayfish escape behaviour. *The Journal of Experimental Biology* **63**: 433-450.

Lang F, Govind CK, Costello WJ, Greene SI. 1977. Developmental neuroethology: changes in escape and defensive behavior during growth of the lobster. *Science* **197**: 682-684.

Newland PL, Cattaert D, Neil DM, Clarac F. 1992. Steering reactions as adaptive components of the tail-flip in the spiny lobster *Jasus lalandii*. *The Journal of Experimental Biology* **164**: 261-282.

Reichert H, Wine JJ. 1983. Coordination of lateral giant and non-giant systems in crayfish escape behavior. *Journal of Comparative Physiology A* **153**: 3-15.