Investigating the potential for image forming vision in *Strongylocentrotus droebachiensis*

Adrian Shaw

ABSTRACT

Sea urchins have no eyes or eyespots, and yet studies have shown that they are capable of photosensitivity and image forming vision. While the mechanisms that underlie this are not yet clear, visual resolutions of urchins can be determined behaviorally by their orientation towards static targets on the edge of circular tanks. I gathered twenty *Strongylocentrotus droebachiensis* individuals and exposed them to three different isoreflectant stimuli – a uniform control as well as 70° and 38° targets. While there was a slight trend in the direction of the 70° target, the urchins did not show significant orientation towards any of the stimuli. This suggests that if *S. droebachiensis* are capable of image forming vision, it is very low resolution. Additionally, this study suggests the potential that dark stimuli commonly used to study urchin vision may be less effective at distinguishing between directional photosensitivity and image forming vision than thought.

INTRODUCTION

Sea urchins have no eyes or eyespots. Despite this, they have been shown to be capable of detecting light. Much of the body surface of urchins is light-sensitive, and can continue to react to shadows even when the body has been cut into multiple pieces with viscera removed (Millott & Yoshida 1960). More complex behaviors such as phototaxis have also been long observed, but require the oral nerve ring to be possible (Holmes 1912). While more simple photosensitivity has been well documented in urchins, there is also increasing evidence that urchins are capable of image forming vision (Sumner-Rooney & Ullrich-Lüter 2023).

In order for directional photoreception and more complex forms of vision to be possible, photoreceptors need some form of screening to limit the angle at which light can be received (Nilsson 2009). This is commonly achieved with shading pigment cells with screening pigments that shade the photoreceptor cells (Arendt et al. 2009). While photoreceptor cells have been observed in the tube feet pores of *Strongylocentrotus purpuratus*, associated screening pigments could not be identified (Ullrich-Lüter et al. 2011). Due to the apparent lack of screening pigments, it is unclear how urchins achieve directional vision, and there are currently several proposed mechanisms for how screening may be achieved in urchins.

Chromatophores have been observed in some urchins which expand and contract in reaction to light (Dambach 1969; Yoshida 1956). While this has not been investigated in urchins, in the fellow class of echinoderms Ophiuroidea, expanded chromatophores have been shown to shade photoreceptor cells (Sumner-Rooney et al. 2020). Alternatively, there is evidence that photoreceptor cells in tube foot pores could be shaded by the urchin's test, as well as that the spines of urchins could provide the necessary screening. Kirwan et al. (2018) found that theoretical visual resolutions for *Diadema africanum* calculated according to the test screening and spine screening hypotheses were both compatible with behaviorally determined resolutions. Multiple other studies have also found theoretical visual resolution via spine screening to match behaviorally demonstrated visual resolutions in other species, as well (Blevins & Johnsen 2004; Yerramilli & Johnsen 2010).

Angular resolutions for vision have only been studied in a small number of urchin species. Of those, the majority place the urchins in a circular arena and track what size of stimulus they will move towards, though there has been research done looking at defensive reactions to a suddenly appearing stimulus as well (Sumner-Rooney & Ullrich-Lüter 2023). Across the species that have been studied, proposed angular resolutions range as low as 9.35º and as high as 72º (Al-Wahaibi and Claereboudt 2017; Woodley 1982). Similar methods with colored stimuli have been used to investigate color vision in urchins, with *Diadema setosum* being shown to respond to red targets but not green or blue ones (Al-Wahaibi and Claereboudt 2017). However, almost all studies of urchin vision use a dark stimulus against a light background (Sumner-Rooney & Ullrich-Lüter 2023). It is theoretically possible that in those tests the urchins are simply detecting a broad, slightly darker region, and lack the ability to resolve an image of the target. Isoreflectant stimuli provide a stricter test of visual ability, as the stimuli should even out to be the same brightness if the target is too small for the urchin to see (Kirwan et al. 2018; Kirwan et al. 2024).

In order to gain a broader knowledge of the visual abilities of sea urchins, I used isoreflectant stimuli of various angular widths to try to estimate the angular resolution for *Strongyloentrotus droebachiensis* vision.

MATERIALS & METHODS

Urchins

Twenty *Strongylocentrotus droebachiensis* urchins were collected for the experiment. Fourteen were acquired from a series of dredges roughly one week before the start of testing at Iceberg Point and Rock Point, near Lopez Island in the San Juan Islands. Six additional urchins were already present in sea tables, having been captured during a previous quarter, and as such did not have records of where they were captured. Urchins varied in size from 5 cm in diameter to 10 cm in diameter. Prior to the trials, all of the urchins were kept together in an indoor flow through sea table with natural seawater at Friday Harbor Labs, and fed algae (*Costaria costata*) collected off the Friday Harbor Labs dock.

Experimental setup

A Tuff Stuff Products 70 quart black bucket was used as a circular arena for trials. The base had a diameter of approximately 39 cm, and as the walls of the bucket slanted out slightly to have a wider mouth, all measurements were taken using the dimensions of the base. Stimuli were printed on sheets of paper and placed in transparent plastic sheet protectors to provide waterproofing, and were attached to the walls of the bucket in a ring around the base. Three stimuli were used – a control stimulus, which was entirely covered in a black and white checkerboard pattern with squares roughly 1mm on each side, one stimulus with a black stripe with an angular width of 70º from the center of the tank bordered with white stripes on either side 35º in width and the rest of the wall of the tank covered in the checkerboard pattern, and the last stimulus similar to the 70º stimulus, but with a 38º black stripe bordered by two 19º white stripes (Fig. 1). A checkerboard pattern was used over a plain gray coloring to ensure that it would be isoreflectant with the larger stripes due to being exactly 50% white and 50% black. The size of the squares in the checkerboard pattern were much smaller than the visual resolution determined for any urchin species, and so should be functionally the same as a gray background of the same average shade. A ring of sheets with the checkerboard pattern were placed around the walls of the bucket above the stimuli to cover the tops of the sheet protectors and the tape, to ensure that the view in all directions was consistent besides the stimuli.

The bucket was filled with natural seawater approximately 10 cm deep. A board of transparent plastic was laid across the top of the bucket, on top of which was placed a cellphone which was used to record video of the trials. The cellphone was rectangular but roughly centered over the tank. The video was also streamed to a viewing area some distance away so that the progress of each trial could be monitored without leaning over the arena and potentially disrupting or influencing the trial by providing an additional stimulus (Fig. 2).

Trials

Trials were held outside on the Friday Harbor Labs campus, away from any buildings to ensure that the view of the sky was uniform and consistent. Urchins were placed one at a time into the center of the arena and allowed to explore undisturbed until reaching the outer wall, at which point they were removed from the arena and placed into a holding space separate from the urchins that had not been tested yet. Approximate final positions were recorded during the trials, and precise final positions were determined after the trials from video recordings. After each trial, the floor of the arena was scrubbed to remove any trails, and any objects (dropped spines, leaves) present were removed. Every five trials, the water in the arena was replaced and the stimuli were rotated 90 degrees from their previous position, in order to control for any influence from the arena, the filming setup, or the surrounding environment on the behavior of the urchins. Trials were performed during overcast weather or in the early evening while it was still bright, in order to reduce harsh shadows that might influence behavior. During trials, urchins were kept in one indoor sea table and one outdoor tank, both filled with natural sea water. The same individuals were used for all trials. Typically individuals would only be used for one trial in a day, but on occasions where an individual would be used for two trials, they were allowed to rest for at least 30 minutes in between trials.

Analysis

Angles of each urchin’s final position on reaching the wall of the arena were determined from videos of the trials using the Tracker Video Analysis and Modeling Tool.

(0,0) on the axes was always set to the center of the tank, and for tests besides the control, 0º was always aligned to be center of the dark stripe. These positions were plotted and analyzed in R using the circular and knitr packages. A Rayleigh Test of Uniformity was used to check for significant unimodal orientation in each group.

RESULTS

20 trials – one with each urchin – were performed with each stimulus, for a total of 60 trials. Trials were typically 2-6 minutes, with two trials taking 9 minutes each. Each trial was successfully completed with the urchin reaching the edge of the tank. Final positions of each urchin were plotted and mean directions for each group were calculated (Fig. 3). The mean orientations relative to the stimulus were 62.2177º for the control trials, 18.1704º for the 70º stimulus trials, and 176.7336º for the 38º stimulus trials. No set of trials showed significant unimodal orientation (Rayleigh test, control $p=0.6164$, 70º stimulus $p=0.2611$, 38º stimulus $p=0.4945$).

DISCUSSION

Although the urchins showed a slight trend towards the 70º stimulus, they did not orient significantly in any direction in any of the sets of trials. While it is possible that with a larger sample size and more trials the pattern could become significant, it's not certain and it would be unlikely to be a strong trend. If *S. droebachiensis* have image forming vision, it is likely very low resolution and potentially not a sense that they rely on much.

It is worth noting that the majority of the urchins in these trials were collected from a subtidal habitat through dredging, and observationally appeared to have relatively sparse spines for their species. Both of these factors could have contributed to worse vision for the urchins. As the urchins were from a subtidal habitat with limited light, it is possible that holding the visual trials in daylight was too bright, and that the urchins were blinded. Additionally, if the spine shading hypothesis for urchin vision is correct, then the density of spines directly correlates to the resolution of the urchin's vision, and lower density of spines would impair vision. The closely related urchin *Strongylocentrotus purpuratus* has been shown in studies to have a visual resolution of either 10º or 42º (Yerramilli & Johnsen 2010; Notar 2016). Visual ability in that range would be more than enough to be able to see a shape with a 70º angular width, so it is interesting that the *S. droebachiensis* had so little reaction.

However, both of those studies on *S. purpuratus* were using a dark stimulus against a light background. It is possible that the difference in results was not due to a difference in visual ability, but rather due to the use of an isoreflectant stimulus in this study. While some urchin species have demonstrated visual abilities in tests with isoreflectant stimuli (Kirwan et al. 2018; Kirwan et al. 2024), most – including *S. purpuratus* – have not. This raises questions as to how effective dark stimuli are for determining visual resolution, and whether trials that were thought to be tests of vision could not potentially be testing photosensitivity.

Further research utilizing isoreflectant stimuli could help delineate between directional photosensitivity and image forming vision in urchins, and studies with isoreflectant stimuli on urchin species that have already been studied with dark stimuli could provide important comparisons to help determine how effective tests with dark stimuli actually are at demonstrating visual resolution. Additionally, while spine density between

species does not seem to correlate with environments where vision would be more helpful (Notar et al. 2022), it could be worth investigating whether visual ability within a single species of urchin is influenced by the environment.

The primary theory for the reason urchins move towards stationary dark targets is that they are seeking shelter and places to hide, though *S. purpuratus* has shown a bimodal response towards and away from a stimulus that could demonstrate vision or photosensitivity being used for predator avoidance as well (Yerramilli & Johnsen 2010). Additionally, urchins in the genus *Diadema* have been shown to react with defensive spine movement to shadows (Millott & Takahashi 1963). Understanding how urchins perceive their environment, as well as what they are capable of perceiving in their environment, could provide important insights into their ecology and how they experience the world around them.

ACKNOWLEDGEMENTS

I would like to thank everyone who assisted me with this project, including the teaching team for the 2026 Zoobot program, Dr. Megan Dethier, Dr. Miranda Roethler, Dr. Hazel Havens, Jennifer Ortiz, and Emily Bews, as well as Dr. Julia Notar for the advice and expertise and Dr. Erik Sperling for helping to collect the urchins for the study. Thank you as well to every member of the FHL staff and community, without whom none of this would have been possible.

LITERATURE CITED

Al-Wahaibi, M. K., & Claereboudt, M. R. (2017). Extraocular vision in the sea urchin Diadema setosum. *Marine and Freshwater Behaviour and Physiology, 50*(1), 31–40. https://doi.org/10.1080/10236244.2016.1265206

Arendt, D., Hausen, H., & Purschke, G. (2009). The 'division of labour' model of eye evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1531), 2809–2817. https://doi.org/10.1098/rstb.2009.0104

Blevins, E., & Johnsen, S. (2004). Spatial vision in the echinoid genus Echinometra. *Journal of Experimental Biology, 207*(24), 4249–4253. https://doi.org/10.1242/jeb.01286

Dambach, M. (1969). Die Reaktion der Chromatophoren des Seeigels Centrostephanus longispinus auf Licht. *Zeitschrift für vergleichende Physiologie, 64*(4), 400–406. https://doi.org/10.1007/BF00340434

Holmes, S. J. (1912). Phototaxis in the sea urchin, Arbacia punctulata. *Journal of Animal Behavior, 2*(2), 126–136. https://doi.org/10.1037/h0076037

Kirwan, J. D., Bok, M. J., Smolka, J., Foster, J. J., Hernández, J. C., & Nilsson, D.-E. (2018). The sea urchin Diadema africanum uses low resolution vision to find shelter and deter enemies. *Journal of Experimental Biology, 221*(14), jeb176271. https://doi.org/10.1242/jeb.176271

Kirwan, J. D., Li, T., Ullrich-Lüter, J., Camera, G. L., Nilsson, D.-E., & Arnone, M. I. (2024). The sea urchin Paracentrotus lividus orients to visual stimuli (p. 2024.01.05.574409). bioRxiv. https://doi.org/10.1101/2024.01.05.574409

Millott, N., & Takahashi, K. (1963). The shadow reaction of Diadema antillarum Philippi. IV. Spine movements and their implications. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 246*(736), 437–469. https://doi.org/10.1098/rstb.1963.0011

Millott, N., & Yoshida, M. (1960). The Shadow Reaction of Diadema Antillarum Philippi: I. The Spine Response and Its Relation to the Stimulus. *Journal of Experimental*

Biology, *37*(2), 363–375. https://doi.org/10.1242/jeb.37.2.363

Nilsson, D.-E. (2009). The evolution of eyes and visually guided behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1531), 2833–2847. https://doi.org/10.1098/rstb.2009.0083

Notar, J. C. (2016). A comparative study of Sea Urchin Visual ecology. Masters thesis, University of California, Los Angeles.

Notar, J. C., Meja, B., & Johnsen, S. (2022). Testing Mechanisms of Vision: Sea Urchin Spine Density Does Not Correlate with Vision-Related Environmental Characteristics. *Integrative and Comparative Biology*, *62*(3), 509–520. https://doi.org/10.1093/icb/icac119

Sumner-Rooney, L., Kirwan, J. D., Lowe, E., & Ullrich-Lüter, E. (2020). Extraocular Vision in a Brittle Star Is Mediated by Chromatophore Movement in Response to Ambient Light. *Current Biology*, *30*(2), 319-327.e4. https://doi.org/10.1016/j.cub.2019.11.042

Sumner-Rooney, L., & Ullrich-Lüter, J. (2023). Extraocular Vision in Echinoderms. In: Buschbeck, E., Bok, M. (eds) *Distributed Vision.* Springer Series in Vision Research. Springer, Cham. https://doi.org/10.1007/978-3-031-23216-9_3

Ullrich-Lüter, E. M., Dupont, S., Arboleda, E., Hausen, H., & Arnone, M. I. (2011). Unique system of photoreceptors in sea urchin tube feet. *Proceedings of the National Academy of Sciences*, *108*(20), 8367–8372. https://doi.org/10.1073/pnas.1018495108

Woodley, J. D. (1982). Photosensitivity in Diadema antillarum: does it show scototaxis? In: Lawrence JM (ed) *Echinoderms: Tampa Bay: proceedings of the international echinoderm conference.* Balkema and NH Salem, Rotterdam, p 61

Yerramilli, D., & Johnsen, S. (2010). Spatial vision in the purple sea urchin Strongylocentrotus purpuratus (Echinoidea). *Journal of Experimental Biology*, *213*(2), 249–255. https://doi.org/10.1242/jeb.033159

Yoshida, M. (1956). On the Light Response of the Chromatophore of the Sea-Urchin, Diadema Setosum (Leske). *Journal of Experimental Biology*, *33*(1), 119–123. https://doi.org/10.1242/jeb.33.1.119

FIGURES

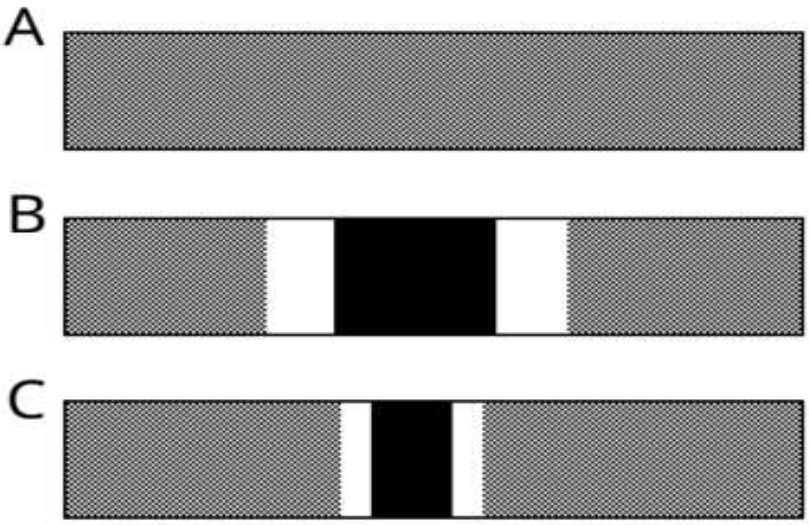

Figure 1.

Examples of the stimuli used in the trials showing the arrangement of checkerboard pattern and white and black stripes in the (A) control stimulus, (B) 70° stimulus, (C) 38° stimulus (not to scale). During trials, one stimulus would be wrapped around the inside wall of the arena with the pattern facing in.

Figure 2.

Image of the testing arena almost completely set up. The stimulus shown in this image is the 70° stimulus. Lines around the edge mark off 15° increments to estimate final positions of urchins during the trials in case of unforeseen difficulties with the video recordings. White tape marks the four directions the dark stripe would be placed when the stimuli are rotated every five trials. During trials, a cellphone would be placed in the center of the plastic board to record.

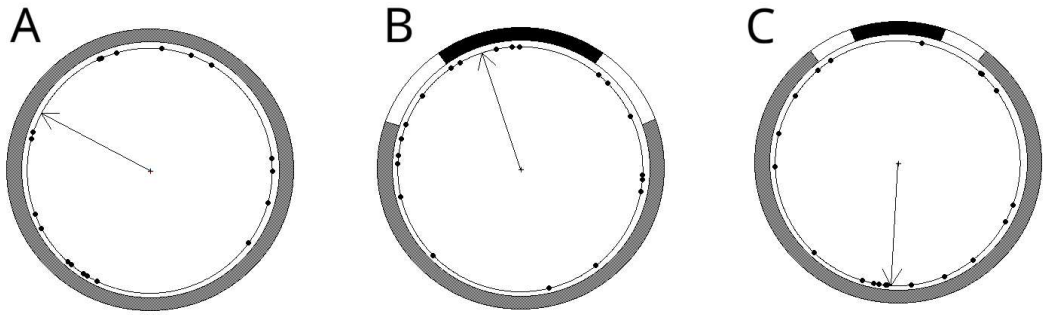

Figure 3.

Results of the three sets of trials. A shows the control stimulus trials, B shows the 70° stimulus trials, and C shows the 38° stimulus trials. Each dot is the final position of one urchin at the edge of the testing arena. The arrows show the mean orientations of all urchins in each set of trials. The ring around the outside of each plot shows the position of the stimulus relative to the urchins.