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Orientation to Objects in the Sea Urchin *Strongylocentrotus purpuratus* Depends on Apparent and Not Actual Object Size

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Sea urchins are known to move toward large visual targets, indicating that they have limited visual acuity. There is a minimum target size that elicits this response. However, it is not known whether the actual or apparent size of the target is the determining factor in whether urchins will respond. The present study builds on the results of previous work by independently altering actual and apparent target sizes. Thirty-five specimens of Strongylocentrotus purpuratus *(Stimpson, 1857) were presented with circular targets of 6-cm and 11-cm diameter, placed at distances such that their diameters circumscribed arcs of 7.5° or 12°. Urchins oriented significantly only toward targets with an apparent diameter of 12° (*$P = 0.005$ *and* $P = 0.02$*), regardless of actual target diameter. Thus, it was concluded that these urchins respond on the basis of the apparent size and not the actual size of targets.*

Echinoderms respond to shadows and changes in illumination (1–7), and sea urchins of at least three species visually detect objects (8, 9). When presented with a black target against a white background, these urchins will usually move directly toward the target. This response to large distant objects indicates that urchins possess rudimentary spatial vision. These targets do not have any meaningful effect on the overall level of illumination, and any such differences are almost certainly undetectable (8). Perception of these targets could not be accomplished through simple photoreception, and it requires at least some visual acuity.

Urchins do not move toward targets below a critical size, but there is more than one way to define the size of an object. The absolute size remains constant, but the apparent size depends on the viewer's distance. Thus, a small nearby object could appear the same size as a large distant object. Echinoderms likely use vision to find shelter (8, 9), so it would be maladaptive to move toward nearby objects that are too small for this purpose, or to expend energy moving toward large distant objects. Consequently, it would be advantageous for urchins to detect the distance and actual size of objects, allowing them to effectively locate suitable shelters. However, such perception would require a more advanced visual system than that required for a response based on apparent size.

Although urchins lack the two eyes necessary for binocular vision, perception of distance could still be accomplished through motion parallax. With lateral movement of the observer, there is a greater apparent change in position for objects that are close than for objects that are far away. An urchin could move sideways relative to objects and use the apparent position changes of distant objects to gauge absolute size. As a viewer moves toward them, closer objects also appear to get larger faster than do more distant objects. Thus, as an urchin moves toward an object, the rate at which the object appears to grow (known as "looming") could provide information on its distance and absolute size. It is not known if urchins can discern absolute size in either of these ways. They do move slowly, but they may nevertheless still collect the visual information needed.

The aim of the present study was to determine whether sea urchins respond differently to objects of the same apparent size but different actual sizes. Previous studies have dealt only with the apparent size of targets. If urchins can determine the absolute size of objects, then it is this size measurement that will predict whether there is a response. However, if urchins do not posses this ability, then it will be the apparent (*i.e.,* angular) size that is important.

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Table 1

Absolute and target-relative orientation of the urchins (n = 35)

	6 cm/7.5° target	6 cm/12° target	11 cm/7.5° target	11 cm/12° target
Unimodal orientation (absolute)				
Mean angle	155°	198°	20°	70°
95% confidence	—	—	—	—
Length of mean vector	0.16	0.21	0.18	0.18
P value for Rayleigh Test	0.43	0.20	0.34	0.34
Unimodal orientation (relative to target)				
Mean angle	97°	316°	24°	40°
95% confidence	—	±34°	—	±39°
Length of mean vector	0.08	0.38	0.16	0.33
P value for Rayleigh Test	0.81	0.005	0.42	0.02
Axial orientation (relative to target)				
Mean axis	22°–202°	165°–345°	81°–261°	24°–204°
95% confidence	—	±26°	—	±19°
Length of mean vector	0.13	0.26	0.11	0.35
P value for Rayleigh Test	0.57	0.10	0.64	0.01

Circular statistics were performed using Oriana ver. 3.21 (Kovach Computing Services, Anglesey, Wales). Confidence intervals are absent when they cannot be accurately calculated due to uniform distribution. Unimodal orientation refers to a distribution with a single mean direction, based on the prediction that urchins move directly toward targets. Axial orientation refers to a distribution with two opposite mean directions, based on prior published observations (Yerramilli and Johnsen, 2010) that urchins sometimes also move directly away from targets.

Urchins were collected from the area surrounding the Bamfield Marine Sciences Centre (48°50′N, 125°09′W) in Barkley Sound, British Columbia, and were held in sea tables with a constant flow of unfiltered natural seawater (salinity 29 ppt, temperature 10 °C). All urchins were tested within 2 weeks of collection.

The experimental arena (modeled after that described by Blevins and Johnsen (8)) was a circular white tank with a height of 1 m and a diameter of 1.7 m. Full-spectrum fluorescent lights (Spectralite F40T12, color temperature: 5900K, color rendering index: 90) were mounted 175 cm above the floor of the arena.

Two black circular targets with diameters of 6 cm and 11 cm were used. The 6-cm target was placed either 46 cm from the center of the arena to create an apparent size of 7.5°, or at 29 cm to create an apparent size of 12°. The 11-cm target was placed either 84 cm from the center to create an apparent size of 7.5°, or at 53 cm to create an apparent size of 12°. Apparent size was measured as the arc described by the diameter of the object when viewed at the stated distance.

Each urchin was tested using these four treatments in pseudorandom order. The bearing of the target in the arena was also randomly selected for each treatment, measured to a precision of 5°. A mechanical claw was used to place the urchin in the center of the arena, and then the animal was allowed to move until the center of its body was 16 cm from the center, after which its bearing was measured. Between trials, the arena floor was scrubbed to remove chemical cues that could affect subsequent trials. Four urchins out of 39 were removed from the analysis for failing to move from the center of the arena after 10 min or making repeated and dramatic direction changes. Each urchin was tested only once in each treatment.

There was no significant orientation toward any absolute direction within the arena for any of the target sizes (Table 1), or when all trials were pooled ($P = 0.56$; Fig. 1). However, in

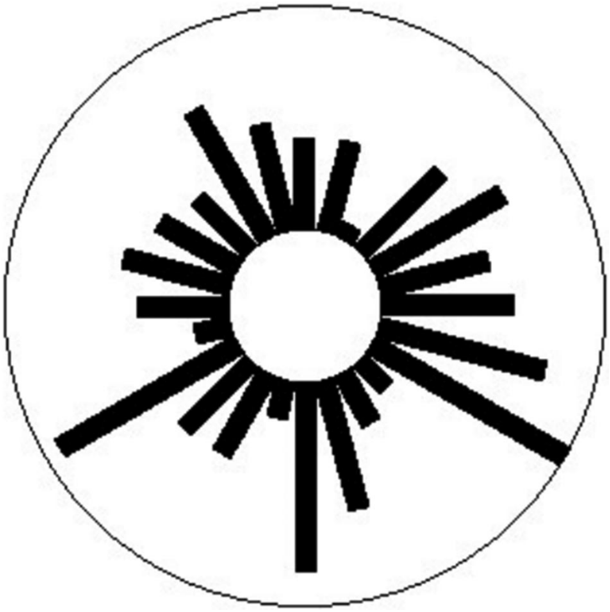

Figure 1. The orientation of urchins without correcting for the location of the targets ($n = 140$). The length of the bars indicates the number of urchins that moved in that direction, with a bar reaching the edge of the circle indicating 12 urchins.

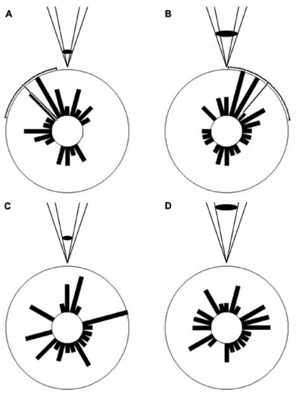

Figure 2. The orientation of urchins corrected for the target location ($n = 35$ for each). The length of the bars indicates the number of urchins that moved in that direction, with a bar reaching the edge of the circle indicating 5 urchins. The solid black lines indicate a significant mean orientation and corresponding 95% confidence intervals. (A) 6-cm /12° target; (B) 11-cm /12° target; (C) 6-cm /7.5° target; (D) 11-cm / 7.5° target.

both 12° treatments, the urchins were significantly oriented toward the target (Fig. 2A, B; Table 1). Urchin movement did not differ significantly from random in either of the 7.5° treatments (Fig. 2C, D; Table 1). These results indicate that urchin orientation depends on the apparent and not the actual size of the target.

It is possible that the design of the experimental arena made it difficult for the urchins to detect absolute size and distance. If they use motion parallax, then the uniform nature of the arena walls may have lacked useful visual cues. While they may have perceived the rate of target position change, there were no other features in the environment with which to compare this rate. However, the uniform walls would not have affected distance perception based on looming rate.

In both 12° treatments, an unusually large number of urchins also moved directly away from the target, which resulted in significant axial orientation in relation to the position of the 11-cm target (Fig. 2B). Yerramilli and Johnsen (9) also found a similar axial orientation for *S. purpuratus*.

The apparent size that elicited a response is consistent with the results of Yerramilli and Johnsen (9). As predicted, urchins moved toward (and sometimes directly away from) targets that were 12° in diameter, but not those that were 7.5° in diameter. Such results verify both the presence of spatial vision in these animals and their spatial resolution. The experimental set-up was independent of that used by Blevins and Johnsen (8) and Yerramilli and Johnsen (9), and the experiments were not performed or supervised by anyone connected with the first two papers (the senior author participated only in the analysis of the results and writing of the text). Such independence indicates that the results are not caused by experimental artifacts and represent the actual visual response of *S. purpuratus*.

The lack of ability to detect the absolute sizes and distances of objects could limit the ability of urchins to navigate using visual information. However, there may be little need for more complex visual perception. Individuals of *S. purpuratus* avoid leaving shelters once they have found them (10, 11), therefore they may only rarely need to use vision to locate shelters. Furthermore, the attenuation of light at depth, combined with uneven substrate and an abundance of kelp, could substantially reduce the distance over which vision is possible. If urchins are only able to see nearby objects, there is less advantage in determining object distance, and apparent size could act as a reasonable estimate of actual size.

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