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## Cuttlefish Cue Visually on Area—Not Shape or Aspect Ratio—of Light Objects in the Substrate to Produce Disruptive Body Patterns for Camouflage

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Cephalopods have at least 20 body patterns for camouflage, yet these can be organized into four categories: uniform, stipple, mottle, and disruptive (1). Among them, disruptive coloration is probably the most striking because it breaks up the animal's body outline by visual deception (2). Cuttlefish produce (by direct neural control of chromatophores) an array of white skin components that produce a disruptive coloration on their bodies, and this helps them achieve camouflage as it is defined by Endler (3), "A colour or pattern is cryptic if it resembles a random sample of the visual background as perceived by the predator at the time and place at which the prey is most vulnerable to predation." The so-called "White square" on the dorsal mantle of cuttlefish represents a random sample of white background objects (Fig. 1) that are common in marine habitats, thereby distracting the attention of visual predators away from the body outline (2). How do cuttlefish "decide" to switch to disruptive coloration, and what sensory cues are involved? We developed a non-invasive assay that monitors motor output (*i.e.*, the body pattern of the cuttlefish) resulting from different visual inputs (computer-generated artificial substrates). Although many aspects of cephalopod vision are known (4), little is known about the visual features of the substrate that elicit disruptive coloration. A recent study (5) of young cuttlefish, *Sepia pharaonis*, showed that the size, contrast, and number of white squares on a black background are the main visual features that cause cuttlefish to switch from general resemblance of the substrate to disruptive coloration. In this study, we examine the shapes and aspect ratios of white objects on black backgrounds that lead cuttlefish to show disruptive coloration.

Five young cuttlefish, *Sepia pharaonis* (8–10 cm mantle length, 10 weeks old), were reared from eggs in the laboratory of the National Research Center for Cephalopods (University of Texas Medical Branch, Galveston) and were maintained in the Marine Resources Center at the Marine Biological Laboratory, Woods Hole, Massachusetts. Each animal was placed in a running seawater tank (25 cm × 40 cm × 10 cm) and was restricted by a four-wall divider (inside covered by black cloth to prevent light reflection) to an area (20 cm × 26 cm) where various computer-generated backgrounds (laminated to be waterproof) were presented as the substrate. Acclimation to the tank was gauged by the cessation of excessive swimming and hovering movements and by the chronic expression of a stable body pattern. A digital video camera was used to record the body patterning of *S. pharaonis* over a period of 30 min (*i.e.*, record 2 s for every 1-min interval;

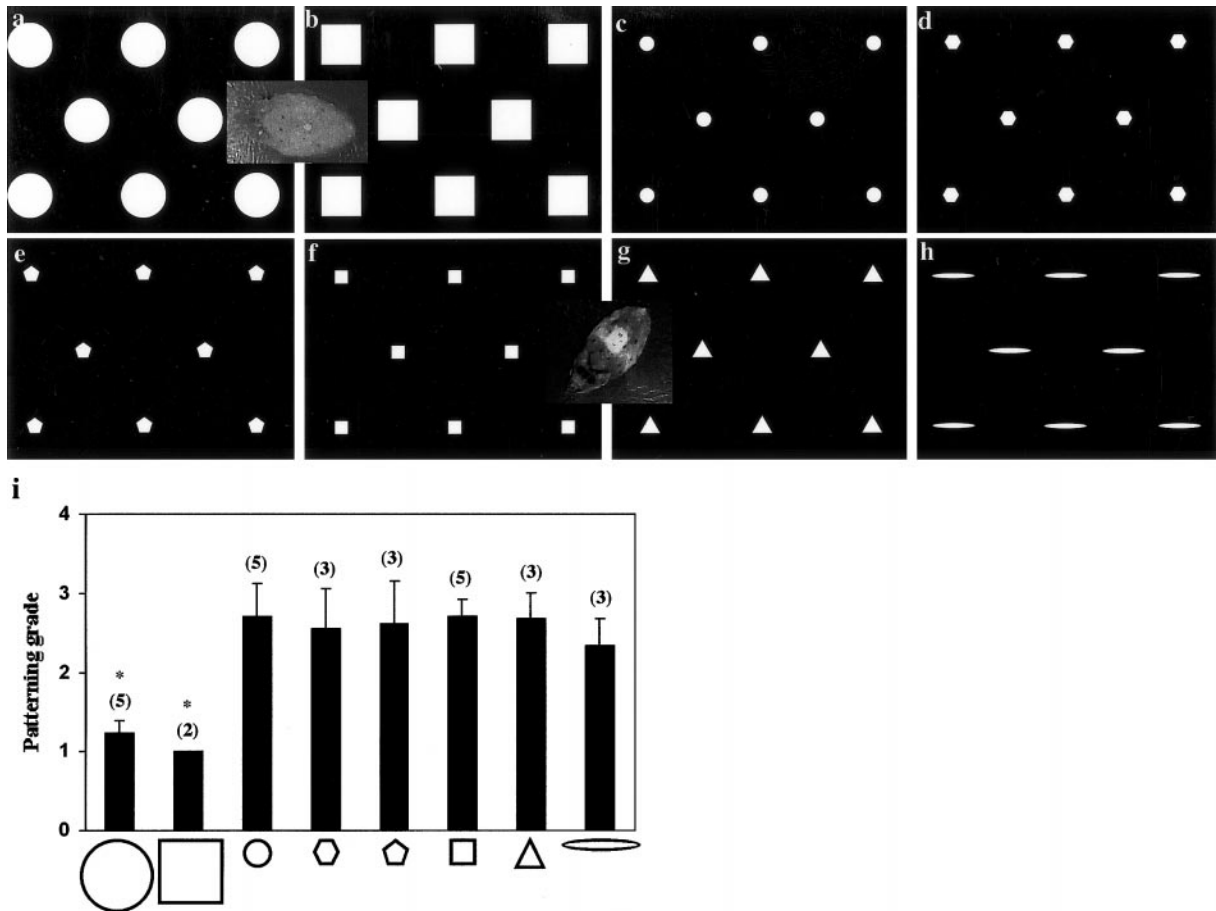
total 60 s for each cuttlefish on each substrate). Although cuttlefish cannot perfectly match backgrounds that are completely artificial, they do show various grades of disruptive patterns based on certain visual features of these substrates. Thus, it was possible to quantify the body patterns corresponding to the shapes or areas of the white objects in the black background. A simple system for grading patterns was used to assess an animal's responses to different substrates (see Ref. 5 for details). The assigned grades were: 1 = uniformly stippled pattern; 2 = indistinct pattern; 3 = disruptive pattern. Grading was conducted by playing the videotape and assigning a grade (1–3; whole integers only) every 10 s. Since all tapes were 60 s long, six grades were assigned for each animal on each substrate. The combined mean values (and overall standard deviation) of all animals were plotted in Figure 1.

Six different shapes of medium-sized white objects (same area, 1.53 cm<sup>2</sup>) were tested to determine whether they would elicit disruptive coloration (Fig. 1). Two control images were also used: large circle and large square (same area, 13.80 cm<sup>2</sup>), which are too large to elicit the White square in the cuttlefish. The generation of disruptive or uniform skin patterns in the cuttlefish did not depend on the shape and aspect ratio of white objects (Fig. 1). Although shapes with equal aspect ratio (*i.e.*, circle, hexagon, pentagon, square, and triangle—all generally similar to the shape of White square on the mantle) did not affect the display of a disruptive body pattern, we were surprised that the elongated oval shape also elicited the White square and disruptive coloration. This indicates that cuttlefish may integrate the whole area of white objects to determine the display of disruptive coloration, regardless of the shapes and aspect ratios of white objects.

Cuttlefish live in much more complex environments than these computer-generated backgrounds, and the ability to display appropriately camouflaged body patterns is critical to survival of this soft-bodied creature. We are gradually learning how cuttlefish use certain features of the visual background to decide upon the type of camouflage that will avoid detection by predators. The sophisticated skin of cephalopods provides a novel system with which to study visual perception and decision-making (6). Further studies should be aimed at exploring these processes on more natural backgrounds.

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**Figure 1.** Two large control images (a,b) on which the cuttlefish (centered) did not show its White square. For five images (c–g), cuttlefish were expected to—and did—show White square disruptive coloration. On one image (h) they were not expected to elicit White square due to its highly different aspect ratio, yet they did. (i) A summary of results from all eight images. Patterning grade 3 is disruptive. The number enclosed in parentheses indicates the number of cuttlefish tested. Results of the first two images were significantly different from the remaining six images ( $P < 0.00001$ ).

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