# Cephalopod dynamic camouflage

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Everyone knows what camouflage is and how it works. And many people (some scientists included) think chameleons are the masters of color change. Wrong on both counts. In this primer, I provide an overview of recent work on the mechanisms and principles of rapid adaptive camouflage of cephalopods — octopus, cuttlefish and squids. These strange but capable marine invertebrates can camouflage themselves against almost any background, a feat well appreciated by Aristotle, and one never mastered by any land animal. Yet their ability to quickly alter their body patterns on different visual backgrounds poses a vexing challenge: how to pick the correct pattern amongst their repertoire. The cephalopod ability to change appropriately requires a visual system that can rapidly assess complex visual scenes and produce the motor output — the neurally controlled body patterns — that achieves camouflage. The body patterns themselves must be well designed and

sophisticated enough to defeat the visual prowess of diverse predators — teleost fishes, diving birds and marine mammals. Curiously, the quantification and experimental testing of camouflage principles have scarcely been addressed by biologists. By studying the cephalopods, we may have stumbled onto some general principles of animal coloration.

Most animals with a fixed or slowly changing body pattern must move to the correct visual background, at the right time and lighting conditions, to implement camouflage. Cephalopods have evolved a different life history tactic: with their keen vision and sophisticated skin — with direct neural control for rapid change and fine-tuned optical diversity — they move where they wish and can adapt their body pattern for appropriate camouflage against a staggering array of visual backgrounds: colorful coral reefs, temperate rock reefs, kelp forests, sand or mud plains, seagrass beds, and others. How they choose the appropriate pattern can tell us something about both cephalopod and predator vision, and will lend understanding to which visual cues are likely to play key roles in accomplishing camouflage.

Figure 1 illustrates three features of cephalopod camouflage. First, the degree of background matching can be superb. This *Octopus vulgaris* in the Cayman Islands

is mottled to match the overall pattern, intensity, color and three-dimensional physical texture of the algae on this rock. Background matching does not always require an exact match as in Figure 1; in fact, this octopus more often achieved a general background resemblance while I filmed it over 90 minutes as it foraged slowly throughout this backreef area. Second, the speed of change is rapid, as shown in the time lapse of 270 milliseconds between images one and two. The total body pattern change as the octopus switched from camouflaged to fully conspicuous took place in 2.02 seconds.

Rapidity of visual change is accomplished by direct neural control of chromatophore organs, which are cytoelastic sacs of pigment with radial muscles attached around the periphery. Each muscle is innervated by motoneurons that originate in the lower motor centers of the brain, and they travel without any synapse to each chromatophore organ. Third, camouflage benefits from both optical and physical three-dimensional effects, the latter being due chiefly to the changeable skin papillae. Note in Figure 2 how the three-dimensionality of the skin is also under fine motor control. Curiously, although papillae expression is regulated by visual input, neither this nor the biomechanics of how the papillae operate as a muscular hydrostat in the skin has been studied in any detail.



Second:frame 0:00            0:08 (270 msec)            2:02 (2,070 msec)

Current Biology

Figure 1. *Octopus vulgaris* reacting to a diver (predator).

The initial change from camouflaged to conspicuous takes only milliseconds due to direct neural control of the skin. Full expression of the threat display (right) is two seconds. Video frame rate is 30 frames per second. Video clip available at http://www.mbl.edu/mrc/hanlon/video.html.

How many camouflage patterns are there, and how many visual tricks have evolved to deceive visual predators? By studying over 20 cephalopod species in the field and laboratory over several decades, my colleagues and I have been able to categorize the patterns into three broad classes. Of course, there is variation within each broad pattern class, but it begs the question of how many camouflage patterns exist among all animals, not just the changeable cephalopods. Recently, we have accumulated approximately 5,000 images of animals of many taxa — large and small, wet and dry — but with emphasis on insects, fish, reptiles, amphibians, birds and primates. With some artistic license, it is possible to sort these images into the three basic pattern classes: uniform, mottle and disruptive (note, common striped patterns are grouped under disruptive). This initial analysis, albeit preliminary, compels us to contemplate whether nature's parsimony is at work here. While evolution has produced body colorations and patterns of bewildering diversity, we may be observing a trend in which certain effective pattern types are conserved across phyla and ecological habitat. I posit that all camouflage patterns among animal taxa may fit into these few basic pattern categories. This hypothesis is at least partly testable based upon two key issues: the definitions of each pattern type, and the visual mechanisms that each pattern type uses to trick predator vision.

Uniform body patterns are those characterized by minimal variation in contrast (Figure 3). Mottle patterns are characterized by small-scale light and dark patches, and some repetition of parts of the pattern. Both of these pattern types work by the principle of general resemblance to the background (sometimes referred to as background matching, although the match can be of varying quality). Disruptive patterns are characterized by



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Figure 2. Skin papillae are evoked by visual input and can appear long and spiky, short and rounded, or not at all.
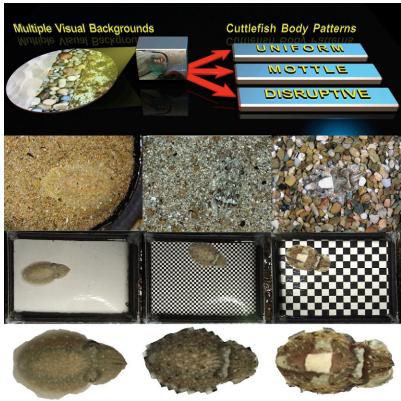Images extracted from Figure 1.

light and dark patches of varying shapes, scales and orientations, and some patches are usually of high contrast. Disruptive patterns incorporate several visual tricks: one is to disrupt the recognizable shape of the animal, helping to obscure the outline or true edge of the animal, partly by providing false outlines and edges throughout the pattern; another is to produce large light conspicuous objects that selectively attract attention away from the true outline of the animal. Disruptive patterns can also achieve some level of general resemblance to the background; that is, they often contain small regions with mottle or even uniformity. There are many fine points of distinction between the visual mechanisms of general background resemblance and disruptive coloration, and full understanding of these and related aspects of camouflage are receiving some long-overdue attention among sensory and behavioral ecologists.

Testing the basis of this three-pattern thesis is possible with the rapid, visually guided camouflaging capability of cephalopods. European cuttlefish, *Sepia officinalis*, are particularly suited for this task because they are well adapted to laboratory environments and they are, like many shallow-water benthic cephalopods, behaviorally driven to camouflage themselves on almost any background. The selective pressure for this

behavior is that soft-bodied cephalopods are preyed upon by nearly all of the major carnivores in the ocean (it is not merely coincidence that squid is the preferred bait of many saltwater fishermen). Thus, camouflage is the primary defense of these unusual mollusks, and they deploy some form of camouflage most of the time when they are out foraging or seeking mates.

How does a cephalopod view a background and so rapidly produce a camouflaged pattern? Whatever visual processing underlies the selection of the camouflage pattern, it must be very efficient. This suggests that cephalopods are using select visual cues in complex backgrounds to evoke uniform, mottle or disruptive. By taking a psychophysics approach and providing quantified, rather simple backgrounds in the laboratory, we can probe the visual capabilities of cuttlefish and see whether we can evoke uniform, mottle or disruptive body patterns with specific background cues. This basic experimental approach is explained in Figure 3 and its caption. Details of the visual background are controlled because we create them in software programs such as Adobe Illustrator© and Matlab©, and we have developed a quantitative, objective method to grade the resultant body pattern of the cuttlefish. Hundreds of experimental trials over the past five years have enabled us to begin to understand this system.

Figure 3. A visual sensorimotor assay for probing cuttlefish perception and subsequent dynamic camouflage.

Row 1: visual backgrounds with different size, contrast, edge characteristics and arrangement are perceived by the cuttlefish, which quickly translates the information into a complex, highly coordinated body pattern type of uniform, mottle or disruptive (left to right in each row of photographs). Row 2: examples of how small sand particles elicit a uniform pattern in *Sepia officinalis*; slightly larger gravel particles of varying higher contrast elicit a mottle pattern; and large light and dark particles elicit a disruptive pattern. Row 3: simple visual stimuli — such as uniformity or small to large high-contrast checkerboards — can elicit uniform, mottle or disruptive camouflage patterns in cuttlefish. The chief difference in the latter two backgrounds is the scale of the checker. Both the visual background and the body pattern can be quantified so that correlations can be made between visual input and motor output. Row 4: enlarged images of the uniform, mottle and disruptive body patterns. Note especially the diverse shapes, orientations and contrasts in disruptive.

Most of our experiments have been on disruptive coloration. The primary visual cue that evokes disruptive is a light, often white, area in the background that is approximately the size of the cuttlefishes' White square skin component in the middle of its mantle. The edge characteristics of the white area, such as the white checkers or white stones, have to be well delineated, and contrast with the adjacent dark components has to be high. The presence of even a few white areas (or objects) on an overall dark background is enough to evoke disruptive coloration. This makes ecological sense, since on a natural background, the animal's White square becomes a random sample of other white objects scattered in the visual background — one of the visual mechanisms of disruptive coloration. We found, somewhat surprisingly, that cuttlefish seem to be using this rather simple visual sampling rule — that is, light areas the approximate size of their own White square — throughout their short life span, during which time the size of their skin component White square increases by a factor of 28.

How does the cuttlefish correlate object size in the visual background with their own skin component when they cannot even see their own skin White square? Additional questions arise: do cuttlefish pay more attention to visual features on the substrate than those in the vertical field of view? Do they respond differently to two-dimensional computer printouts than to real three-dimensional objects in the background? Current experiments are focused on the interactive effects of size, contrast, intensity and configuration of background objects. We are also testing the visual cues that evoke mottle and uniform body patterns. These and many other questions remain to be addressed with this visual sensorimotor assay.

Color blindness is another curious feature of cephalopods. Their color matches to natural visual backgrounds appear to be excellent; this is not surprising as many of their predators have two, three or even four visual pigments (humans have three: red, green, blue). There has been a growing body of evidence that cephalopods are color blind, and recently we used the large checkerboard assay (explained above and in Figure 3) to test if cuttlefish would show disruptive patterning on checks that were not black and white, but rather — to our vision — highly contrasting yellow and blue shades. These shades were chosen to have the same intensity as the cuttlefish's sole known visual pigment at wavelength 492 nm (green). The presence of a second visual pigment would be necessary for the cuttlefish to tell these colors apart. In a second experiment, we presented them with 16 checkerboards in which half the checks were consistently green (close to 492 nm) and the complementary checks ranged from white through various shades of gray to black. One of these gray shades was expected to have the same intensity as the green shade, so that the two shades could only be distinguished based upon wavelength. The animals failed both tests: they perceived

Figure 4. The 'mimic octopus' *Thaumoctopus mimicus* on a sand plain (left) in Indonesia.
In the middle photo, the octopus takes on the shape and swimming motion of a flounder, including the fish-like undulations of body and fins and similar swimming speeds. The most common flounder in this area was *Bothus mancus* (right). (Photo credits: Denise Tackett for octopuses and Dave Downs for flounder.)

the yellow/blue checkerboard as a uniform background; nor could they distinguish the gray checks from the green checks when intensities matched. In each experiment, the cuttlefish responded with a uniform body pattern. This and other tests provide convincing behavioral evidence that cuttlefish do indeed have only one visual pigment, but we continue to search for mechanisms that help them achieve color-blind camouflage.

Dynamic night camouflage, hitherto unknown in the animal kingdom, has recently been demonstrated in cuttlefish in southern Australia. Each cuttlefish showed a specific uniform, mottle or disruptive pattern depending on the microhabitat it settled upon soon after sunset. The implications of this study are that cuttlefish vision at night is excellent — so that they can evaluate the background for proper pattern choice — but also that predator nocturnal vision is keen and predation at night is a strong selective force. Otherwise the cuttlefish would be found in no camouflaged patterns or a single camouflaged pattern regardless of background features.

Dynamic mimicry has recently been discovered as a complement to dynamic camouflage in cephalopods. The first-line defense of cephalopods is camouflage in the form of remaining motionless and showing appropriate uniform, mottle and disruptive patterns. In general, motion gives away camouflage (note, some octopus species can

maintain a camouflaged pattern and posture while moving very slowly). However, *Thaumoctopus mimicus* in Indonesia (Figure 4) and *Octopus defilippi* in the Caribbean mimic flounders when moving swiftly across exposed, featureless sand plains. Each time they stop, they instantly go camouflaged. Thus, flounder mimicry appears to be a guise to 'look unlike an octopus, but rather like a very common fish' when swift movement would give away its camouflage. Put another way, the octopus is camouflaging itself as a flounder. We do not yet understand the type of mimicry involved (for example, Batesian or Mullerian), the evolution of this form of camouflage, or the visual stimulation that may evoke it.

Other features of the cephalopod dynamic camouflage system have yet to be studied in detail. The skin, for example, is a marvelous example of rapid, highly coordinated optical malleability: pigmentary and structural coloration are combined in many ways to achieve vastly different appearances, both from close-up and distant viewing. The directional structural reflectors known as iridophores (which in most animals are passive reflectors) are not only under active control by cephalopods, but they produce polarized signals that pass unaffected through the overlying pigmented chromatophores. This raises the possibility that a dynamically camouflaged cephalopod could be simultaneously sending a 'hidden' signal to a conspecific, because cephalopods can

perceive polarized light while most of their predators cannot, while remaining well camouflaged using pigmented chromatophores. Future studies on fish vision would help us understand not only the anatomical organization of cephalopod pigments and structural reflectors, but the details of the whole-animal patterns that have evolved in response to the wide array of predator visual systems.

Field studies of cephalopods are needed to gather quantitative empirical evidence of background matching and disruptive coloration to natural backgrounds, and to relate this information to visual capabilities of local predators. Such underwater studies, taking advantage of new small spectrometers and miniature computers that can be adapted to custom-made waterproof housings, have just begun. Eventually, these approaches may enable us to precisely test color matching and determine correlations between microhabitat and the many features of the body patterns that achieve such effective dynamic camouflage in cephalopods.

Visual predator-prey interactions abound on planet Earth — terrestrial and aquatic, large and small — and it is hard to think of a behavioral trick that is more widespread and important to survival than camouflage. The finding that cephalopods — the most changeable in appearance among animal taxa — appear to have only three basic pattern

classes for camouflage is surprising, and quite provocative since initial investigation indicates that all animal coloration patterns tend to show a similar organization. This is a counter-intuitive notion, and may be oversimplified. Yet the idea suggests a powerful solution to a complex problem, and stimulates new ways to view the natural world, not only from our human-vision viewpoint, but in the way we investigate animal visual systems. Could it be that the vast diversity of visual systems (of active carnivores, at least) can be fooled by a handful of tricks, such as three camouflage pattern templates that implement either general background resemblance or disruptive camouflage?

The subtle ways in which edges, shadows, outlines, patterns, colors, contrast and papillae are used by animals for camouflage or communication also seem to have much in common with art, photography, landscape architecture and related fields, because light and dimensionality are being manipulated in similar fashion. When watching the video from Figure 1, the aphorism "truth is stranger than fiction" comes to mind, especially when compared to the 'invisibility cloaks' that have recently received so much attention in the popular media. The speed and fluidity with which cephalopods simultaneously maintain predator awareness, search for prey, and coordinate a camouflage body pattern with each microhabitat offers insight into how a complex biological organism works as an intact system. There are great challenges yet to confront in understanding the sensory and behavioral interactions between visual predators and prey, and it is humbling yet intriguing to think that such an ancient lineage as the mollusks has evolved such a sophisticated system with which to test camouflage.

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# Temporal freezing of visual features

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Our perception at any moment has been thought to reflect neural activities at that moment. Recent psychophysical studies, however, have revealed severe dissociations between the perceptual and physical timing of visual events, as for example in the 'flash-lag' effect [1–3] and illusory asynchrony [4,5]. Here, I introduce a novel illusion in which time (transition) appears to stand still. When a subjective surface formed by a 'Kanizsa' figure is abruptly presented on a background of dynamically changing color and texture, the color and texture appear to be stable within the surface for approximately 200 milliseconds. The illusion is consistent with the notion that the visual system fills-in color and texture information over a wide temporal interval unless a salient signal of the change is given.

We showed nine human subjects a display in which four circular patterns were located in a uniform field whose color changed gradually from green to red at a clearly visible speed (Figure 1A). During the movie, a Kanizsa-type subjective square (or disc) was presented for periods in the 80–600 milliseconds range. The subjects viewed the display while gazing at a peripheral dot, and matched the initial and final colors of the figure during its presentation. The matched colors differed only slightly when the figure was presented for less than about 200 milliseconds (circles in Figure 1C). Thus, the color within the figure appears to stop changing and remain nearly the same while the outside continues to change. The display also induces an extremely vivid perception of the subjective figure, which appears to be a clearly different color from the background (Figure 1A; the perceived color of the figure lagged ~90 milliseconds behind the background [2]; see also the