Cephalopods' Polyphenism

Wai-Yin Vivien Li and Emmanouil Protonotarios

Centre for Mathematics and Physics in Life Sciences and Experimental Biology

Introduction

One of the most impressive features of cephalopods (octopus, cuttlefish and squid) is their ability to exhibit enormous phenotypic plasticity. This functions as a defense system against predators, as an advantage for prey hunting and as a possible means of interspecies communication. Cephalopods' skin can change constantly in both colour and texture in a very sophisticated way. [1]

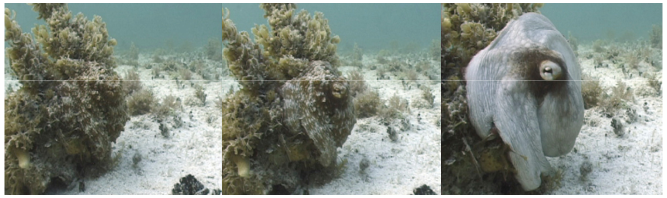
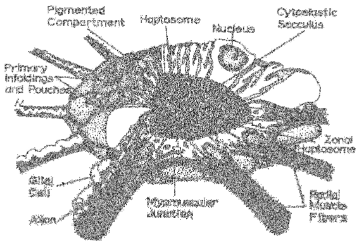


Figure 1. Octopus vulgaris changing from camouflaged to conspicuous reacting to a diver. (adapted from [2])

Chromatophores as elements in Packard's hierarchy

Chromatophores produce the yellow, orange, red and brown colours on the cephalopod skin. They are neuromuscular organs rather than cells controlled hormonally like in other animals. The size, density and distinct colours of the chromatophores vary in different species and in different regions of the body. The proportion of the differently coloured expanded chromatophores and the spread of the pigment granules determines the colour pattern of the cephalopod. This colour pattern also depends on the quality and orientation of the light striking on them. [3]

Figure 2. Ultrastructure of a retracted cephalopod chromatophore organ. The pigment-containing cell has a highly elastic membrane and is located in the center of the chromatophore. 6-20 striated radial muscle cells attached to it produce graded contractions, resulting in many intermediate expansion states. [3][4] (adapted from [3])



Chromatophores are innervated directly from the brain and this neural control enables an almost instantaneous change in the appearance. A single chromatophore can receive multiple innervations, therefore it can participate in different patterns. [3]

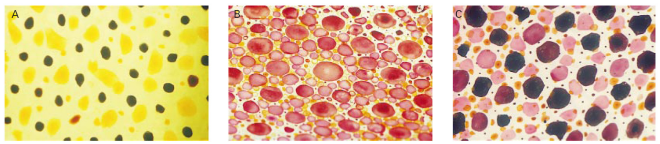


Figure 3. Differently coloured chromatophores of three cephalopods: (A) Cuttlefish *Sepia officinalis*, (B) *Loligo plei* and (C) *Sepioteuthis sepioidea*. Chromatophore pigments reflect the longer wavelengths of the visible spectrum. (adapted from [3])

Reflecting cells and muscles

Iridophores: Thin chitin platelets on multi-layer stacks alternating with cytoplasm layers. Although colourless, they function as quarter wavelength reflectors producing spectral colours by constructive interference. [3][5]

Leucophores: Elongated, flattened cells, each covered with almost a thousand small stalked knobs (*leucosomes*). They reflect or scatter the light to produce chalky whites when white light falls upon them. The leucophores aid the cephalopods to match the brightness and also the hue of the background, since the reflective light has similar spectrum to the incident light. [3]

Skin muscles: Muscles underneath cuttlefish and many octopods skin can form papillae (bumps or spikes than can be more than 10mm in height). Visual cues of rough textures, such as coralline algae, can trigger the generation of these papillae that can maximize the efficiency of their camouflage. [3][6]

Body muscles: Arms, head and mantle muscles contribute to the camouflage posture and enable the cephalopod to display the appropriate regions of the body. [3] The swimming motion or the posture can also mimic, in some cases, other organisms (*mimic octopus*) [2].

The three major camouflage categories

Uniform, *mottle* and *disruptive* are the three categorical patternings that enable cuttlefish to camouflage efficiently within milliseconds without processing of all the visual information.

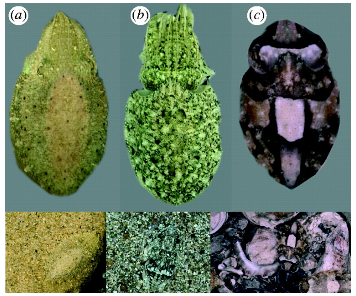


Figure 4. Three major categories in Cuttlefish camouflage:

a) Uniform, with few or no chromatic components expressed.

b) Mottle, with small-to-moderate light and dark patches expressed regularly and repeatedly.

c) Disruptive, with large light and dark patches expressed in different shapes, orientation and scales. White square components are often observed on the mantle, and the marginal pattern usually touches the outline.

These patternings are varied and mixed with great flexibility, however they are constrained by the fixed chromatic components on the skin. (adapted from [7])

Uniform and mottle patterns exhibit three major forms of background matching so as to evade detection from predators' far viewing or peripheral vision:

1. *Specific matching* to the immediate background such as physical textures, overall colour, contrast and intensity.
2. *General resemblance* of certain patterns of their immediate background.
3. *Deceptive resemblance* of objects that lie beyond their immediate background. A cuttlefish may sit on a sand substrate, and resemble distant but distinctive objects as rocks, algae or corals. [7]

Disruptive patterning performs differential blending. Cephalopods blend into their immediate background but also try to stand out from their surroundings. By constructive shading, coloured patches could look elevated or depressed, confusing the figure/background interaction. [7]

Cuttlefish camouflage 2-stage visual process

1. Sensing for multiple low-level cues, including the presence of edges, sizes and depth of background objects, and contrast within the background.
2. Identification of the 3-D environment adopting the appropriate body pattern. [8]

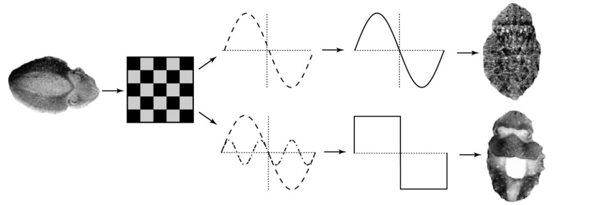


Figure 5. A simple model of cuttlefish edge detection. Zylinkski et al [8] proposed a single modulation transfer function (MTF), which sets the visual thresholds of cuttlefish in classifying textures and detecting edges. Discrimination of a visual pattern from a uniform surface requires a single spatial frequency component (above). This results in a visual interpretation of a non-edgy background, thus resulting in a mottle pattern. The detection of edges requires 2 spatial frequency components (below), the fundamental wave and the third harmonic. This on the other hand leads to the perception of an edgy object, resulting in a disruptive pattern. Also, Mottle pattern is expressed when checks are of sizes 1 to 3mm, and when checks are larger (up to 10mm), disruptive patterns are shown. (adapted from [8])

Interesting recent discoveries

The skin of the cuttlefish has been shown to exhibit distributive light sensing. This suggests a possible mechanism that matches the overall skin brightness contrast to the immediate background. Cuttlefish are colour blind, however they can achieve high-fidelity colour match for camouflage, even at spectrally rich environment such as coral reefs and kelp forests. [9]

Iridophores produce linearly polarized patterns of light which their rhabdomeric visual system is able to detect, suggesting their function as a communication channel. [1][10]

Conclusion

Cephalopods evolved to exhibit a truly remarkable body patterning behaviour. The underlying mechanisms of their highly effective camouflage as well as the role of their skin in visual communication remain to be elucidated by further research. [3]

References

1. Mäthger LM, Hanlon RT. Anatomical basis for camouflaged polarized light communication in squid. *Biol Lett*. 2006;2(4):494-496.
2. Hanlon R. Cephalopod dynamic camouflage. *Current Biology*. 2007;17(11):R400-R404.
3. Messenger JB. Cephalopod chromatophores: neurobiology and natural history. *Biological Reviews*. 2001;76(4):473-528.
4. Tublitz NJ, Gaston MR, Loi PK. Neural regulation of a complex behavior: body patterning in cephalopod molluscs. *Integrative and Comparative Biology*. 2006;46(6):880 -889.
5. Cooper KM, Hanlon RT, Budelmann BU. Physiological color change in squid iridophores. *Cell Tissue Res.* 1990;259(1):15-24.
6. Allen JJ, Mäthger LM, Barbosa A, Hanlon RT. Cuttlefish use visual cues to control three-dimensional skin papillae for camouflage. *J Comp Physiol A*. 2009;195(6):547-555.
7. Hanlon RT, Chiao C-C, Mäthger LM, et al. Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2009;364(1516):429 -437.
8. Zylinski S, Osorio D, Shohet AJ. Edge detection and texture classification by cuttlefish. *Journal of Vision*. 2009;9(13):13-13.
9. Chiao C-C, Wickiser JK, Allen JJ, Genter B, T. Hanlon R. Hyperspectral imaging of cuttlefish camouflage indicates good color match in the eyes of fish predators. *Proceedings of the National Academy of Sciences*. 2011. Available at: http://www.pnas.org/content/early/2011/05/10/1019090108.abstract. Accessed May 26, 2011.
10. Mäthger LM, Shashar N, Hanlon RT. Do cephalopods communicate using polarized light reflections from their skin? *Journal of Experimental Biology*. 2009;212(14):2133 -2140.
11. Barbato M, Bernard M, Borrelli L, Fiorito G. Body patterns in cephalopods: "Polyphenism" as a way of information exchange. Pattern Recognition Letters. 2007;28(14):1854-1864.

EPSRC Pioneering research and skills

British Heart Foundation

IKY