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Holes in the camouflage

In their recent *Journal of Experimental Biology* paper on mottle camouflage patterns of cuttlefish and the visual background stimuli that evoke them, Chiao et al. state that ‘the mottle body pattern works by the principle of background matching’ (p. 188) (Chiao et al., 2010). ‘Mottle’ and ‘disruptive’ patterns doubtless contribute to camouflage in the animal kingdom – see Hugh B. Cott’s classic *Adaptive Colouration in Animals* [referenced in Chiao et al. (Chiao et al., 2010)] – and the main contribution of Chiao et al.’s recent paper is to have classified the patterns worn by young cuttlefish during experiments with artificial backgrounds [figures 4–7 in Chiao et al. (Chiao et al., 2010)] according to granularity characteristics.

However, the fact is that none of the small cuttlefishes in the 19 photographs of experiments designed to test their statement is ‘matching’ the background. All stand out because average reflectance (albedo) of the body surface is different from average background reflectance; the one instance where the cuttlefish comes close to tone matching on a background critically darker than the others [figure 6A and supplementary figure S3 in Chiao et al. (Chiao et al., 2010)] is explained in terms of a ‘key’ switch from ‘mottle’ to ‘disruptive’. The terms ‘tone matching’ and ‘brightness contrast’ – universal phenomena – appear nowhere in the paper.

The cephalopod chromatophore system effecting camouflage has been widely explored in the past. Its structure is modular. Generation of brightness contrast ‘mottles’ of given granularity involving lateral inhibition is one kind of brain function with known location [for an account of the results of brain lesion experiments, see Packard (Packard, 1995a) and figure 10 in Packard (Packard, 1995b)]; neuromuscular gain controls for neutral density screens that modulate tone matching is another. The octopus in the middle and lower photographs of figure 3 in Packard (Packard, 1988) illustrates this functional separation so instructively that I (we) have reproduced them several times in the last 40 years. Text alongside the three photographs summarizes the matching principles.

Movie 1 in supplementary material (sub-adult *Sepia officinalis* from the Bay of Naples filmed against a plain unchanging background) comprises the same separation of functions in a cuttlefish under experimental conditions (exposure to CO₂-bubbled seawater). The ‘mottle’ ‘template’ of Chiao et al. (Chiao et al., 2010) remains the same until near the end of the 20 s movie – i.e. spatial frequency (granularity) settings (but not energy levels) are unaltered. The screening function changes rapidly and over the extremes of its range – incidentally also turning the animal from ‘mottle’ to ‘uniform’.

Although not stated by Chiao et al. (Chiao et al., 2010), the set of chromatophores producing these dramatic changes from light to dark and back, and responsible for tone matching in the normal animal, is the same as (or currently indistinguishable from) the ‘small splotches of expanded dark chromatophores’ [said to be ‘roughly equal’ in ‘number and size’ to the light ‘splotches’ (p. 189)] in the static detail of the cuttlefish skin [figure 2A in Chiao et al. (Chiao et al., 2010)]. They are functionally the same as those creating the ‘chronic general mottle’ (or ‘trellis’) of the octopus. They contribute (1) to brightness contrast in the high-frequency band of the ‘mottle’ or ‘stipple’ and (2) to overall grey level in the lowest frequency band (body-wide dimension) through spatial recruitment of screening chromatophores (compare middle image with top and bottom images in Fig. 1), and not as described on p.188 of Chiao et al. (Chiao et al., 2010).

Full descriptions may be found in my previous papers [pp. 94–95 of Packard (Packard, 1988); pp.114–119 of Packard (Packard, 1995b)]. [The general mechanism illustrated in Fig. 1 was explained previously as ‘variations in the state of contraction of chromatophores’ that produce ‘changes in the proportion of light and dark on the network of

patches and grooves from one moment to the next’ (Packard and Sanders, 1971). NB The citations to my other work (Packard, 1982; Packard, 1995a) by Chiao et al. (Chiao et al., 2010) are without relevance.]

So why did Chiao et al. apparently miss the failure of the system to match the albedo in experiments with artificial backgrounds [figures 4–7 in Chiao et al. (Chiao et al., 2010)], and why did it fail?

The Chiao et al. paper makes a false distinction between ‘morphological’ and ‘functional’ approaches (p. 187). What is termed ‘morphological analysis’ is in fact pictorial analysis. We are thus two steps removed from the natural; experimenters’ attention is directed elsewhere. Visuo-motor relationships may well be operating outside the normal dynamic range; why were 1000 lx light levels chosen for the photographs and not altered during experiments? 1.07 and 1.03 klx (p. 190), unlikely even in the shallows of its natural habitat, may be enough to blind the tone-matching function of European *Sepia officinalis*. Choosing a procedure in which ‘each animal image was cut out from its context’ (p. 192) and reporting total energy spectra for ‘background’ pixels and relative energy spectra for ‘animals’ [see figures 4–7 in Chiao et al. (Chiao et al., 2010)] may help to account for not noticing the lack of matching.

In conclusion, the experiments reported by Chiao et al. are too static. They do not reflect the dynamic nature of cephalopod camouflage nor its literature. Moreover, there are dozens of simple interventions for testing whether or not screens and mottles are functionally different – e.g. altered illumination, electronic flash, anaesthetics (such as CO₂ or alcohol). Information is easy enough to come by, with better

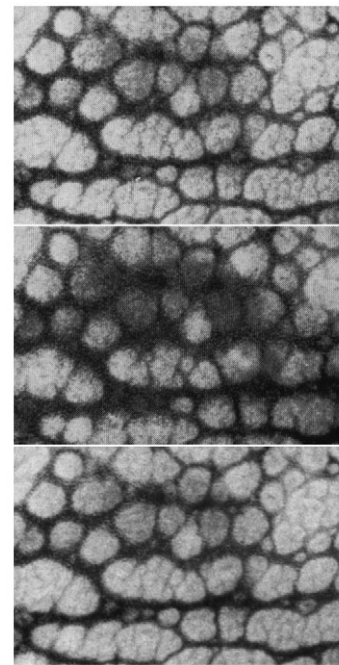


Fig. 1. Fine grain ‘mottle’ of an adult *Octopus vulgaris* illustrating the effect that increased gain amongst dark screening chromatophores (middle photograph) has upon average reflectance without alteration in grain (granularity). Top and bottom images are different prints of the same original. Image width 15 mm; individual chromatophores not resolvable. Reproduced with permission from figure 28, plate XIX of Packard and Sanders (Packard and Sanders, 1971).

communication between experimental subject and participant observer – what I call ‘letting the animal tell its own story’ – and also between one side of the Atlantic and the shores of the Mediterranean. [NB Previous written and illustrated accounts of cephalopod body patterns over the last century have been exhaustively catalogued (Borrelli et al. 2006).]

Supplementary material available online at
<http://jeb.biologists.org/cgi/content/full/213/17/3074/DC1>

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Response to ‘Holes in the camouflage’

In his Correspondence article, Dr Packard questions our approach to studying cuttlefish camouflage body patterning (Chiao et al., 2010). While we respect Packard's invaluable contribution to the study of cephalopod chromatophores and freely acknowledge that he has inspired us to continue to investigate them, it seems to us that his criticism of our paper misses the point. His major concern was that cuttlefish did not match the brightness of the artificial substrates in most of our experiments, but our experiments were specifically concerned with pattern and contrast, not brightness. The reason for using these carefully designed substrates was not to test all aspects of ‘background matching’ but rather to apply psychophysical methods to examine systematically the visual features of the background that elicit the pattern design in Mottle camouflage, a particular type of body pattern whose function falls within the scope of general resemblance to the background [or what Stevens and Merilaita term ‘background matching’ (Stevens and Merilaita, 2009)].

Earlier experiments using checkerboards to study the dynamics of body patterns in flounders and cuttlefish have demonstrated the clear advantages of using artificial backgrounds to investigate the visual sampling rules used by camouflaging animals (Chiao and Hanlon, 2001; Ramachandran et al., 1996) and this was the starting point for our investigation. In the artificial substrate experiments in our paper, quantification of substrate and body patterning was carried out to categorize the effect of specific visual cues on pattern expression (which is only one aspect of the overall ‘body pattern’ that is defined as the overall appearance of the animal, to include pattern, color, brightness, contrast and skin texture).

It is crucial to realize that the artificial substrates used in our experiments lie outside the luminance space of substrates that cuttlefish have evolved to match; i.e. none of the substrates that cuttlefish encounter in their natural habitats are simultaneously as high in average reflectance and in contrast as the substrates on which they were tested in this study. There is thus no reason to suppose that the animals will match both the textural properties and the brightness of these checkerboard substrates. To achieve even a rough brightness match to these artificial substrates, our animals would have had to deploy very light uniform patterns that would have failed to match any of the textural properties of the substrates. Instead, as we have documented, they showed a very strong tendency to match the granular structures rather than the brightness of the substrates. That they preferred to make these pattern matches at the expense of brightness matches testifies to the potency of pattern in controlling their responses.

We made reference to this issue in our explanation of supplementary material figure S1 (Chiao et al., 2010), where we compared the

granularity of each artificial substrate with the granularity of the animal's body pattern. We stated on p. 197 that, ‘It is apparent that the overall shape of the granularity spectrum of the backgrounds is similar to that of the animals. However, close examination of these curves reveals that the magnitude and the peak of the backgrounds do not exactly match that of the animals, even in the case of natural substrates.’ Thus we did not ‘apparently miss’ that the animals are not exactly matching the background as Packard asserts. Moreover, we have published numerous images from the laboratory and the field showing the brightness match of various cephalopods to many backgrounds (e.g. Hanlon and Messenger, 1988; Hanlon and Messenger, 1996; Hanlon et al., 2009).

Additionally, our granularity statistic method was not designed to capture the overall reflectance of body patterns, because the mean intensity is subtracted out before analyzing the image of the animal in different spatial frequency bands. This method addresses a different problem: it provides a measure of the size and contrast of the light and dark patches in the skin [see Barbosa et al. (Barbosa et al., 2008) where the method was introduced] (see also Spottiswoode and Stevens, 2010). Although this particular quantitative approach to define statistically the main pattern types deployed by cuttlefish ignores the ‘tone matching’ between animals and backgrounds in this paper, our previous research has emphasized that mean substrate intensity (among other factors) plays an important role in modulating cuttlefish body patterns (Chiao et al., 2007).

Packard's concern with the distinction between morphological and functional approaches is understandable, although he may have misunderstood our efforts entirely. We recognized his neurophysiological work in determining the skin patch organization of chromatophores as the ‘physiological units’ (Packard, 1982), and his explanation of the production of Mottle body patterns by lateral inhibition and neuromuscular gain controls (Packard, 1995). However, the important facet of our analysis of the Mottle body pattern for this paper lies in the animal's ability to control both small- and large-scale Mottle skin components to resemble the size scale and contrast of light and dark objects in the immediate visual background. Although Packard's observations, such as exposing cuttlefish to CO₂-bubbled seawater in his supplementary Movie 1, could distinguish whether ‘screens and mottles’ are functionally different, we consider cuttlefish to be camouflaged only if the animals show stable body patterns while stationary on both natural and artificial substrates. We believe these criteria enable us to reveal key background visual features that cuttlefish detect and respond to for camouflage, and not to secondary

defenses such as deimatic or protean behaviors that were evoked in his Movie.

While it is true that our use of 1000 lx illumination may exceed the amount of light that cuttlefish would encounter in most natural habitats, our recent research indicates that their camouflage body patterns on the various artificial substrates remain the same as reported here when subjected to lower light levels, all the way to starlight, 0.003 lx (J. J. Allen, L. M. Mäthger, K. C. Buresch, T. Fetchko, M. Gardner and R. T. Hanlon, submitted). As for Packard's conclusion that our experiments 'are too static', we contend that effective camouflage patterns are indeed static when the animals are settled on a background with unchanging light fields. We are keenly aware of the dynamic nature of cephalopod adaptive coloration (Hanlon, 2007) and have been building a library of high-definition video of cuttlefish and octopus as they forage in highly diverse natural habitats worldwide. Such footage – representing hundreds of hours of observations under natural lighting fluctuations – has guided our laboratory experimentation from the outset. In this respect, our approach to studying cephalopod adaptive camouflage complements that of Packard.

In conclusion, our goal in this paper and other recent publications has been to study experimentally the visual cues that might elicit certain patterns in cuttlefish. When doing experiments there is inevitably a tradeoff between reducing the number of variables and obtaining a biologically meaningful result. It is a pity that Packard does not seem to recognize this dilemma in his critique of our work.

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