



Osorio, D., & Cuthill, I. (2015). Camouflage and perceptual organization in the animal kingdom. In J. Wagemans (Ed.), *The Oxford Handbook of Perceptual Organization* (pp. 843-862). (Oxford Library of Psychology). Oxford University Press.
<https://doi.org/10.1093/oxfordhb/9780199686858.013.044>

Peer reviewed version

Link to published version (if available):
[10.1093/oxfordhb/9780199686858.013.044](https://doi.org/10.1093/oxfordhb/9780199686858.013.044)

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Camouflage and perceptual organization in the animal kingdom

Daniel Osorio¹ & Innes C. Cuthill²

To appear in:

Oxford Handbook of Perceptual Organization

Oxford University Press

Edited by Johan Wagemans

1. School of Life Sciences, University of Sussex. Brighton. BN1 9QG. United Kingdom.
2. School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, United Kingdom

Abstract

Camouflage allows the bearer to 'hide in plain sight' by means of colour patterns that interfere with detection. Basic principles of camouflage that were proposed over a century ago by artists and natural historians have informed recent studies that seek to tease apart the different mechanisms by which camouflage exploits perception. The probability of detection is lowered by matching background colours and textures or using sharply contrasting colours to disrupt the body's outline or salient features such as eyes. The effectiveness of much animal camouflage against humans, even though the patterns evolved to fool different viewers, suggests that diverse visual systems share similar principles of perceptual organization. As such, animal camouflage might reveal universal principles that apply regardless of retinal organisation and neural architecture. We review the recent literature on animal camouflage in this light, from experimental studies of texture perception by fish and cephalopod molluscs, to the visual effects used to defeat figure ground segregation of 2-D and 3-D objects in birds and mammals.

KEYWORDS: Camouflage, visual texture, cryptic coloration, disruptive coloration, countershading, cephalopod, bird.

There is hardly a law of vision that is not found again serving camouflage.

Metzger (1936, transl. Spillman 2009)

1. Introduction

Animal camouflage is subtle and beautiful to the human eye, but it has evolved to deceive non-human adversaries. Camouflage works by defeating figure-ground segregation, whereas patterns that disguise the animal as a commonplace object or lead to misclassification are known as masquerade and mimicry (Endler 1981; Ruxton *et al.* 2004b; but see also Stevens & Merilaita 2009 for discussion these terms). Mimicry patterns, which are often conspicuous,

work by similarity to a different animal, typically one that is avoided by the predator, whereas in masquerade the animal resembles a commonplace but valueless object, such as a bird-dropping or plant thorn. Early Gestalt psychologists used examples from animal camouflage to illustrate their principles of perception (Metzger 1936), which were, in turn, used to explain deceptive coloration (Keen 1932). What was not appreciated, or underestimated, in early studies of animal camouflage were then differences in vision between humans and other animals, even though it is these 'other animals' that have been the selective force in evolution (Endler 1978; Cuthill et al. 1993; Bennett et al. 1994). Conversely, there has been a view that certain aspects of vision, such as object completion, may require mechanisms specific to the neocortex, or even cognitive processes, and so are not expected animals without a cortex (Nieder 2002; Shapley et al. 2004; Zylinski et al. 2012; van Lier & Gerbino 2013). The fact that camouflage is effective against humans suggests that common principles of perceptual organization apply across diverse visual environments, eye designs and types of brain. In any case camouflage offers an approach to the vision of non-human animals that is both more naturalistic and very different from standard methods, such as tests of associative learning.

Historically, biological camouflage was studied from about 1860 to 1940 as evidence for the theory of natural selection and for military applications. Notable contributors included the American artist Thayer (1896, 1909), who was fascinated by countershading and disruptive coloration, and the English zoologist Cott whose beautifully illustrated book *Adaptive coloration in animals* (1940) set out principles of camouflage such as 'maximum disruptive contrast' and 'differential blending' (Figure 2A). Cott's view that these principles are attributable to the 'optical properties' of the image, rather than being physiological or psychological phenomena, ignored the possible influence of differences in perception between animals. This is illustrated by the diversity of animal colour vision. A trichromatic bee (with ultraviolet, blue and green photoreceptors), a tetrachromatic bird (with UV, blue, green and red photoreceptors), and a trichromatic human will process identical spectral radiance in different ways, but all these animals face common challenges, such as figure-ground segmentation and colour constancy. Furthermore, for camouflage that has evolved as concealment against multiple visual systems (e.g. a praying mantis in foliage, concealed both to its insect prey and reptilian and avian predators), the common denominators will prevail over viewer-specific solutions. As the ultimate common denominator is the physical world one might, for example, expect the colours of many camouflaged animals to be based on pigments that have similar reflectances to natural backgrounds across a broad spectral range, even though in principle a metamer might be effective against any one visual system (Wente & Phillips 2005; Chiao et al. 2011).

In contrast to Cott, Metzger's account of camouflage in *The laws of seeing* (2009), was explicitly cognitive, not optical, drawing attention to the Gestalt psychological principles of 'belonging', 'common fate' and 'good continuation'. Metzger also devotes a chapter to the obliteration of 3-D form, by countershading. More recently Julesz's (1971, 1981) influential work in vision was motivated by the idea that image segregation by texture, depth and motion evolved to break camouflage. His lecture at the 1998 European Conference on Visual Perception was entitled '*In the last minutes of the evolution of life, stereoscopic depth perception captured the input layer to the visual cortex to break camouflage*' (Frisby 2004). Julesz's ideas remain relevant to

understanding texture matching, and also raise the question of whether any camouflage can defeat the stereo-depth and motion sensitive mechanisms that allow figure-ground segregation in 'random-dot' images.

Recently research on camouflage has been stimulated by the realisation that direct evidence for how particular types of camouflage exploit perceptual mechanisms was sparser than textbooks might suggest. Also, such evidence as did exist had been evaluated via human perception of colour and pattern, not the evolutionarily relevant viewer. For example, the bright warning colours of toxic insects such as ladybirds has evolved under the selective pressure exerted by, among others, bird eyes and brains, and avian colour vision is tetrachromatic and extends into the ultraviolet (Cuthill 2006). This has led to experimental tests, within the natural environment, of basic camouflage principles such as disruptive coloration and countershading, informed by physiologically based models of non-human low-level vision (Cuthill *et al.* 2005; Stevens & Cuthill 2006). Biologists also recognise that animal coloration patterns often serve multiple functions, including sexual and warning signals, non-visual purposes such as thermoregulation and mechanical strengthening. Not only can animal colours only be understood in the light of trade-offs between these functions (Ruxton *et al.* 2004b), but it is often difficult to be sure which function is relevant (Stuart-Fox & Moussali 2009).

Other recent studies, which we describe here, have investigated animals that can change their appearance, such as chameleons (Stuart-Fox & Moussali 2009), flatfish and especially cuttlefish (Figure 1). Cuttlefish, like other cephalopod molluscs control their appearance with extraordinary facility, which allows them to produce a vast range of camouflage patterns under visual control. These patterns illustrate interesting and subtle features of camouflage design, including disruptive and depth effects. However, the special feature of actively controlled camouflage is that one can ask what visual features and image parameters the animals use to select coloration patterns. This gives us remarkable insights into perceptual organization in these advanced invertebrates.

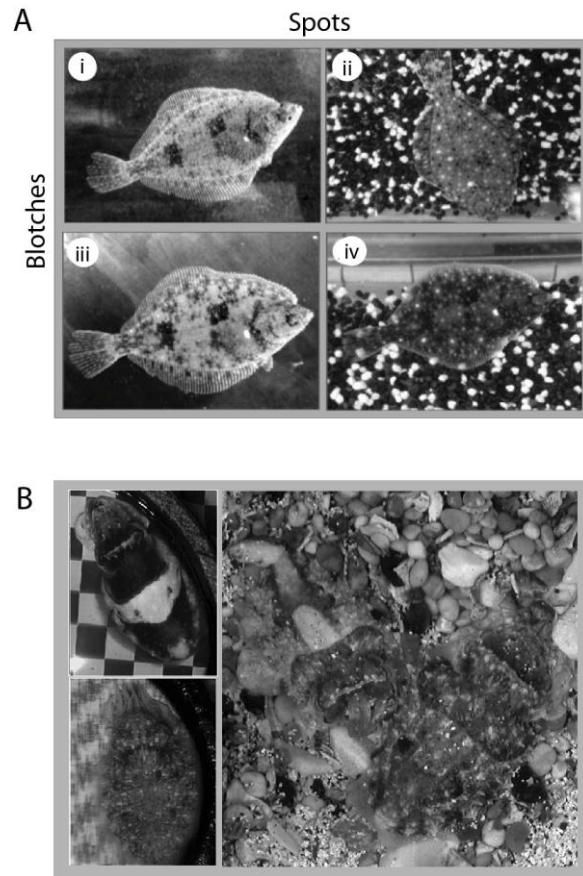


Figure 1: Images of A. a flatfish, the plaice (*Pleuronectes platessa*) and B. a cuttlefish (*Sepia officinalis*) that vary their appearance to match the background. The plaice varies the level of expression of two patterns, which we call blotches and spots. These can be expressed at low-levels (i), separately (ii, iii) or mixed (iv) (Adapted from Kelman *et al.* 2006). The cuttlefish displays a great range of patterns. Here the upper left panel illustrates an animal expressing a Disruptive type of pattern on a checkerboard background, and the lower left a Mottle on the background with the same power spectrum but randomized phase. The right-hand panel shows two animals on a more natural background expressing patterns with both disruptive and mottle elements.

2. Principles of camouflage

A naive view is that camouflage ‘matches the background’, but the simplicity of the concept has proved deceptive and led to controversies about definitions up to the present day (for instance Stevens & Merilaita’s 2009 arguments about cryptic camouflage). An exact physical match, such that pattern on the animal and the substrate against which it is viewed are perceptually identical, is possible only with a uniform background; if only because differences in pattern phase at the boundary between object and background, or 3D cues from shadowing on its surface, are almost inevitable. A fascinating example of near-perfect background matching, in this very literal sense, is produced by the scales of many fish that work as vertical mirrors. Ideally such mirrors reflect the ‘space-light’ of open water so that a viewer sees the same light as it would with uninterrupted line of sight, making the fish invisible (Denton 1970; Jordan *et al.* 2012). Accepting that invisibility through exact replication of the occluded background is rarely achievable, in the biological literature ‘background matching’ (largely replacing earlier terms such as ‘general protective resemblance’) is taken to mean matching the visual texture of the background. That texture may be a continuous patterned surface such as tree bark, or it may include discrete 3-D objects, such as pebbles or leaves, that could in principle be segregated separately. Exactly how best to match the background is a topic we return to in 3.3.

Logically distinct from crypsis is ‘masquerade’, where an animal mimics a specific background object that is inedible or irrelevant (leaf-mimicking butterflies and bird’s-dropping-mimicking insect pupae are classic examples; Skelhorn *et al.* 2010a,b). Although a stick insect benefits from both matching its generally stick-textured background as well as looking like a stick, the distinction can be made when such an animal is seen against a non-matching background. Masquerading as a stick can be successful even when completely visible, whereas matching a sample of the background texture ceases to be an effective defence when the animal is readily segmented from the background. Masquerade depends on the mechanisms of object *recognition* and relative abundance of model and mimic (frequency dependent selection), rather than perceptual organization so we say no more about it here, but refer the reader to a recent review (Skelhorn *et al.* 2010a).

Historically (Cott 1940) two main camouflage strategies have been recognised: cryptic and disruptive camouflage. Cryptic camouflage relies on the body pattern in some sense matching its background. At present there is no simple way to predict whether two visual textures will match, yet the quality of camouflage patterns is striking, especially considering the complexity of generating naturalistic visual textures in computer graphics (Portilla & Simoncelli 2000; Peyré 2009; Allen *et al.* 2011; Rosenholtz 2013). The lack of a simple theory for the classification of visual textures, as envisaged by Julesz (1981, 1984; Kiltie *et al.* 1995), has limited progress in understanding of camouflage, which leaves this area open. However, the adaptive camouflage of flatfish and cuttlefish offer an experimental approach to the question of what range of patterns is needed for one type of natural backgrounds - namely seafloor habitats -, and to test what local image parameters and features are used by these marine animals to classify the substrates that they encounter.

Disruptive camouflage, 'classically' involves well-defined (e.g. high contrast) visual features that create false edges and hence interfere with figure-ground segregation (Figures 1-3; Cott 1940; Osorio & Srinivasan 1991; Cuthill et al. 2005). However the idea can be generalised to any mechanism that interferes with perceptual grouping of the object's features. Hence disruptive camouflage gives a more direct route to understanding principles of perceptual organization. It has had more attention than cryptic camouflage, which works by matching the background matching, perhaps because, in some sense, it appears to be more sophisticated, involving active deception resembling optical illusions. A major impetus for recent research has been the realisation that the effectiveness of disruptive camouflage had been accepted for over a century without direct test (Merilaita 1998; Cuthill *et al.* 2005). It may be that the widespread use of (allegedly) disruptive patterning in military camouflage, where historically the early inspiration was often from nature (Behrens 2002, 2011), reinforced its acceptance as 'proven' in biology. Given that crypsis depends upon matching the background, whereas disruptive effects depend upon creating false edges or surfaces, it is an interesting question how crypsis and disruptive coloration work in tandem: a topic we return to later.

We now outline experimental studies of camouflage relevant to four main aspects of perceptual organization: first, cryptic coloration and background matching; second, the problem of obscuring edges; third the problem of obscuring 3-D form; and fourth the concealment of motion.

3. Cryptic coloration and background matching

Julesz (1981, 1984) proposed that just as trichromatic colour vision encodes visible spectra via three channels, which are defined by the cone photoreceptor spectral sensitivities, so there should be a small number of local texture channels (Landy & Graham 2004; Rosenholtz 2013). One could hope to replicate any texture with a small number of textons in the same way that one can reproduce colours with three primaries. Julesz found that textures were in some cases readily discriminated when they had the same mean intensity and second-order (i.e. spatial frequency power spectrum) and even higher-order statistics. This led to the hypothesis that there are channels would represent local features, such as the size and aspect ratio of 'blobs', the termination of lines and the presence of line intersections. This theory has been influential, especially in work on preattentive visual discrimination, but the limited set of textons has yet to be identified. In recent decades much effort has gone into understanding the coding of natural images, but to our knowledge a small basis-set of spatial mechanisms analogous to cone fundamentals has not been identified. Indeed the principle of sparse coding argues for a large set of low-level mechanisms (Simoncelli & Olshausen 2001). Similarly, systems for generating naturalistic visual textures in computer graphics involve many free parameters (Portilla & Simoncelli 2000; Peyré 2009), but even so graphics do not convincingly resemble match natural surfaces. It is therefore intriguing that cryptic camouflage often matches the background so well (Figure 1).

Hanlon (2007) has proposed that three main types of camouflage pattern – which he calls Uniform, Mottle and Disruptive – are widespread in both aquatic and terrestrial animals. This

classification often seems to work, but the number of distinguishable backgrounds and camouflage patterns is much greater than three. However, it is possible that a small basis-set of patterns can generate cryptic camouflage for a wide range of backgrounds (Julesz 1984). Coloration patterns are typically under genetic control and, at least in the wings of butterflies and moths, a small number of developmental mechanisms underlie much diversity (Beldade & Brakefield 2002). An animal lineage with a suitable 'basis-set' of genetically defined patterns would perhaps be able to evolve camouflage for a range of natural backgrounds. Certainly the coat pattern variation in all living cat species does not seem to be heavily constrained by taxonomic similarity (Allen *et al.* 2011). Instead the colour variation, which could plausibly be generated by slight changes in the reaction-diffusion equations underlying pattern development, has readily switched between spots, stripes and uniform fur in relation to habitat type.

3.1. Physiologically controlled coloration

Flatfish and cuttlefish provide direct evidence for the range of spatial patterns needed for camouflage. These bottom-living marine animals use a limited set of patterns or local features, whose contrast is varied under rapid physiological control (Figure 1). Both groups alter their appearance under visual control to produce superb camouflage, over a few minutes for flatfish or less than a second for the cuttlefish. In terms of ecology, the ability to change colour rapidly has major benefits for the range of habitats in which you can be concealed is increased, and changing colour rapidly can itself be employed as a distraction tactic, or to prevent the adversary developing a search image (Hanlon *et al.* 1999; Bond & Kamil 2006). In terms of how camouflage patterns actually work, it actually matters little whether the colours are produced by chromophores under neural control (as in cephalopods), fixed pigments in skin, hair, feathers or a shell, or from an artist's palette. What colour-changing animals do give us, is a powerful experimental system for asking the animal itself what matters for concealment.

3.1.1 Flatfish patterns

Three studies have looked at how flatfish vary their visual appearance (Fig 1A). We encourage the reader to view images of these animals via the internet. Saidel (1988) found that two North American species, the southern flounder (*Paralichthys lethostigma*) and the winter flounder (*Pseudopleuronectes americanus*), control the level of expression of a single pattern in response to varying backgrounds. Both species control the contrast in a pattern of dark and light, somewhat blurred, spots roughly 10mm across. In *Paralichthys* both the mean reflectance and the contrast of the background influence the coloration, and the maximum contrast across the body ranged from 14% to 70% (Saidel 1988). Another North Atlantic species, the plaice (*Pleuronectes platessa*; Figure 1A; Kelman *et al.* 2006), has an advantage over the summer and winter flounders in that it can add two patterns to a fairly uniform 'ground' pattern. One of these patterns comprises predominantly about 30 small (< 5mm diameter) dark and light spots in roughly equal numbers, the other is blurred dark blotches, which form a low-frequency grating-like pattern. The fish mixes these two patterns freely, changing appearance over the course of a few minutes according to the visual background.

The most elaborate adaptive coloration described in a fish is for the eyed flounder *Bothus ocellatus*. When Ramachandran and co-workers (1996) analysed Fourier-transformed images

of the fish they found that three principal components accounted for the range of patterns that the animals could display in their aquaria. The authors describe the components as composed of 'low vs. high' spatial frequency channel, a medium spatial frequency channel and a narrow-band channel at eight cycles per fish. It is not easy to directly relate these principal components, defined in terms of spatial frequency, to body patterns, but the 8-cycle per fish channel probably corresponds to a regular pattern of dark blotches much like those on the plaice (Figure 1A; Ramachandran *et al.* Fig 1c). Another pattern corresponds to the roughly 100 light annular (or 'ocellar') features and a smaller number (c. 30) of dark annuli that give this fish its name. In addition the fish can display a finer grained gravel-like texture. Apart from the evidence for three principal components the fish can apparently display isolated features, such as a single dark spot.

Ramachandran and co-workers (1996) pointed out that the eyed flounder lives in shallow tropical water, which is relatively clear. They suggested that this could explain why it has a more elaborate coloration system than the summer and winter flounders, which have only one degree of freedom in their pattern: changing contrast. It is tempting to suggest – though without direct evidence – that flatfish use one, two or three basic patterns according to the visual environment in which they live. Fish that live in clearer water of more varied habitats would benefit from a greater range of patterns. Shohet and co-workers (2007) make a similar proposal for different cuttlefish species.

3.1.2. Cuttlefish

Although flatfish often have good camouflage, their adaptive coloration is much simpler than that of cephalopod molluscs, especially octopuses and cuttlefishes (Figure 1B). These animals change their skin coloration under visual control in a fraction of a second, and can even produce moving patterns of dark bands. Observation of the cuttlefishes' coloration patterns, produced in response to varying backgrounds, allows unique insights into the vision of these extraordinary molluscs - and of their adversaries, especially teleost fish (Langridge *et al.* 2007).

European cuttlefish (*Sepia officinalis*) body patterns are produced by the controlled expression of about 40 visual features known as behavioural components, and they can also control the physical texture of their skin (Hanlon & Messenger 1988). The level of expression of each component can be varied in a continuous manner (Kelman *et al.* 2008). Our unpublished principal components analysis of the coloration patterns displayed on a large range of natural backgrounds indicates that there are at least six degrees of freedom in the range of cryptic patterns produced by cuttlefish (see also Crook *et al.* 2002). This is suggestive of great flexibility and independent control of the separate patterns components, which must be matched by a corresponding visual ability. At present, however, the way in which the expression of these patterns is coordinated, and the full range of camouflage patterns produced in natural conditions, remains poorly studied.

Hanlon and Messenger (1988) suggested that five main body patterns are used for camouflage. These were called: Uniform Light, Stipple, Light Mottle, Dark Mottle and Disruptive. The reader should note that the terms for body patterns are capitalised to distinguish them from camouflage mechanisms. In particular it is not certain that the Disruptive pattern works as

disruptive rather than cryptic camouflage (Ruxton *et al.* 2004; Zylinski & Osorio 2011). As we have mentioned, Hanlon (2007) has identified three basic types of pattern in cephalopods and other animals: Uniform, Mottle and Disruptive. In experimental aquaria, most cuttlefish patterns can indeed be classified by a combination of mottle and disruptive elements, which is comparable to the two degrees of freedom seen in the plaice (Figure 1). The ‘disruptive’ pattern-components, defined by expert human observers, include about ten comparatively large well-defined light and dark features, including a white square on the centre of the animal and a dark head bar (Fig 1B; Hanlon and Messenger 1988; Chiao *et al.* 2005). The mottle pattern comprises less crisply defined features, and is comparable to the blotches used by flatfish (Hanlon and Messenger 1988).

3.1.3. Selection of coloration patterns by cuttlefish

The cuttlefish’s capacity to alter its appearance according to the visual background allows us to investigate the animal’s spatial vision. Most obviously one can test the effects of varying a specific image parameter in the background. Studies have used both printed patterns, such as checkerboards (Fig 1B; Chiao & Hanlon 2001; Zylinski *et al.* 2009a), and more natural substrates, such as sand, gravel and stones (Marshall & Messenger 1996; Shohet *et al.* 2007; Barbosa *et al.* 2008). Patterns have been designed to test the animals’ sensitivity to low-level visual parameters, including colour, spatial frequency, contrast, orientation and spatial phase (Marshall & Messenger 1996, Zylinski & Osorio 2011), or local features such as edges, objects and depth cues (e.g. Chiao *et al.* 2007; Zylinski *et al.* 2009a,b). This work is reviewed elsewhere (Kelman *et al.* 2008; Hanlon *et al.* 2011; Zylinski & Osorio 2011), but the main conclusions are as follows. Regarding low-level image parameters, cuttlefish are sensitive to mean reflectance, contrast, spatial frequency and spatial phase (Kelman *et al.* 2008). They are sensitive to orientation, but this affects the body and arm orientation rather than the pattern displayed (Shohet *et al.* 2006; Barbosa *et al.* 2011). Cuttlefish are sensitive both to the presence of local edges (Zylinski & Osorio 2009a,b), and whether the spatial organization of local edge fragments is consistent with the presence of objects (Zylinski *et al.* 2012). Cuttlefish are sensitive to visual depth, and pictorial cues consistent with visual depth (Kelman *et al.* 2008). Often the contrast of the coloration patterns is varied to approximately match the contrast in the background (Kelman *et al.* 2008; Zylinski *et al.* 2009a). Despite their mastery of camouflage cuttlefish are colour-blind, having only one visual pigment (Marshall & Messenger 1996; Mäthger *et al.* 2006), but this deficiency seems to have little detriment for camouflage (Chiao *et al.* 2011), presumably because reflectance spectra of their natural backgrounds have a simple and predictable form (the monotonic slopes of yellows-through-browns), where reflectance increases linearly with wavelength and, as such, the colour is well predicted by luminance.

Many of the cuttlefish’s responses can be interpreted on the basis that the animals express the Disruptive pattern on a background composed of discrete objects, whose size approximates that of the ‘white square’ pattern component, and the Mottle on a textured surface (Fig 1B). It is striking how many image parameters, local features and higher level information are used to make this seemingly simple decision. This leads to a system that is reminiscent of the fact that humans use multiple mechanisms for figure-ground segregation (Kelman *et al.* 2008; Zylinski & Osorio 2011; Zylinski *et al.* 2012; see also Peterson, 2013).

3.2. Symmetry

Almost all mobile animals have a clear plane of symmetry, usually bilateral, and symmetry of both the outline and surface patterning are known Gestalt cues for perceptual organization (van der Helm 2013) – flatfish are an obvious exception. The absence of simple planes of symmetry in most natural backgrounds is therefore a potential problem for cryptic animals. Indeed, Cuthill and co-workers (2006a,b) showed that birds found symmetrically coloured camouflaged prey more rapidly than asymmetric patterned prey, although not all symmetrical patterns are necessarily equally easy to detect (Merilaita and Lind 2006). This makes it rather perplexing that more animals have not evolved asymmetric patterning although, in insects at least, there may be genetical or developmental constraints that make it hard for surface pattern and underlying body plan to be decoupled. Selection experiments for changed wing shape in butterflies produce tightly correlated changes in colour pattern (Monteiro *et al.* 1997). Thus the genetical control of morphological symmetry, which is probably constrained by locomotor requirements, seems tightly linked to surface patterning (see discussion in Cuthill *et al.* 2006b). Regularity could be expected to be another feature that predators use to break camouflage, and blue tits find prey with spatially regular patterns more rapidly (Dimitrova & Merilaita 2012).

3.3. The problem of multiple backgrounds

In trying to understand the complex colour patterns of animals that cannot change their appearance, Thayer (1909) painted background scenes as viewed through animal-shaped stencils: a duck-shaped segment of lakeside, a fish-shaped portion of sea-grass. Interpreting animal camouflage as sampling the background was a major conceptual advance, but the question arises: what sort of background sample is optimal? Endler (1978, 1984, 1991) proposed that crypsis should be defined as coloration that represents a random sample of the background at the place and time where predation risk is highest. Others have argued that a random sample is not necessarily optimal (Merilaita *et al.* 1999, 2001; Ruxton *et al.* 2004) supported by experiments showing that not all random samples are equally concealed (Merilaita *et al.* 1999). If the background is heterogeneous and a single sample must be chosen (i.e. no colour change by an individual), what is the best sample? Natural selection will favour the pattern with the minimum average detectability across all backgrounds it may be viewed against. The sample that is the minimum average difference from all possible backgrounds against which it might be viewed is the most likely sample (in the sense of statistical likelihood), not any random sample (Cuthill & Troscianko 2009). Defining such a maximum likelihood sample is straightforward for a single perceptual dimension, but not for multiple dimensions and not when low-level attributes such as colours, lines and textures have been integrated into features. However, if we accept such a 'most likely' pattern can be defined, three evolutionary outcomes can be imagined: selection for a single, 'typical', specialist colour pattern; negative frequency dependent selection (i.e. the predation intensity on any one pattern – phenotype -- varies with the relative abundance of that phenotype, such that rare phenotypes have an advantage and common phenotypes are at a disadvantage) for multiple patterns matching different, common, backgrounds; or selection for a single, 'compromise', pattern that combines possible backgrounds as a weighted average. The best strategy will depend on how relative discriminability varies across the multiple backgrounds (Merilaita *et al.* 1999; Houston

et al. 2007). Loosely speaking, similar backgrounds favour a compromise ‘average’ coloration, while the possibility of being seen against rather different substrates favours a single specialist pattern, or divergent selection for multiple specialist patterns. In an ingenious experiment where captive blue jays searched for computer generated prey, whose coloration was controlled by a genetic algorithm and so could evolve in response to the birds’ predation success, Bond and Kamil (2006) showed that a fine-grained homogeneous background selected for a single prey colour whereas coarse-grained heterogeneous backgrounds selected for polymorphism (multiple types). However, without a metric for perceived contrast between different textures, the evaluation of what backgrounds can be considered ‘similar’ or ‘different’ has to be evaluated empirically on a case-by-case basis. This is an important area for future research and relates directly to the need for a mechanism-rooted theory of texture perception.

The similarity to the background is not the only factor affecting detectability of a target; the complexity of the background also affects visual search; that is locating the target depends on not only target-distractor similarity but also the amount of variation between background features that are similar to the target (Duncan & Humphreys 1989). As a result, a camouflaged animal may be better concealed in more complex habitats independent of its match to the background (Merilaita *et al.* 2001; Merilaita 2003; Dimitrova & Merilaita 2010). In line with this, there is recent evidence for animals choosing backgrounds that are not merely a good match to their own patterns, but are more visually complex (Kjernsmo & Merilaita 2012).

4. Obscuring edges

The previous section has dealt with how visual textures in camouflage patterns match the background but, even when there is a close match, visual discontinuities at edges can reveal the outline of an object or salient features within the object. The latter can include phase differences at the conjunction of body parts (e.g. limbs against body) or features, such as eyes or their components, with a contour unlike those in the background. One strategy to obscure edges, which is used by flatfish and cuttlefish, is to have partially transparent marginal fins that also continue the body pattern, and hence merge the body into the background (Figure 1), partial burying has a similar effect.

Much better known are disruptive patterns, where colour is used to disguise or distract attention from the true outline of the animal or salient body parts, and hence to defeat figure-ground segregation. Thayer (1909) was the first to outline what Cott (1940) said were “certainly the most important set of principles relating to concealment”. Both Thayer and Cott were artists, having an intuitive understanding of the use of shading to create false perceptions of shape, form and movement, and both were active in campaigning for the adoption of camouflage by the military in, respectively, the First and Second World Wars (Behrens 2002, 2012). Cott greatly refined Thayer’s original ideas, and he produced a battery of illustrations from across the animal kingdom to explain how disruption could work and plausibly illustrate their action in nature (Figure 2A). However, as recent researchers have realised, the term ‘disruptive coloration’ actually comprises several mechanisms, and some of those discussed by

Thayer and Cott as disruptive are better classified differently (Stevens & Merilaita 2009). We discuss these in turn.

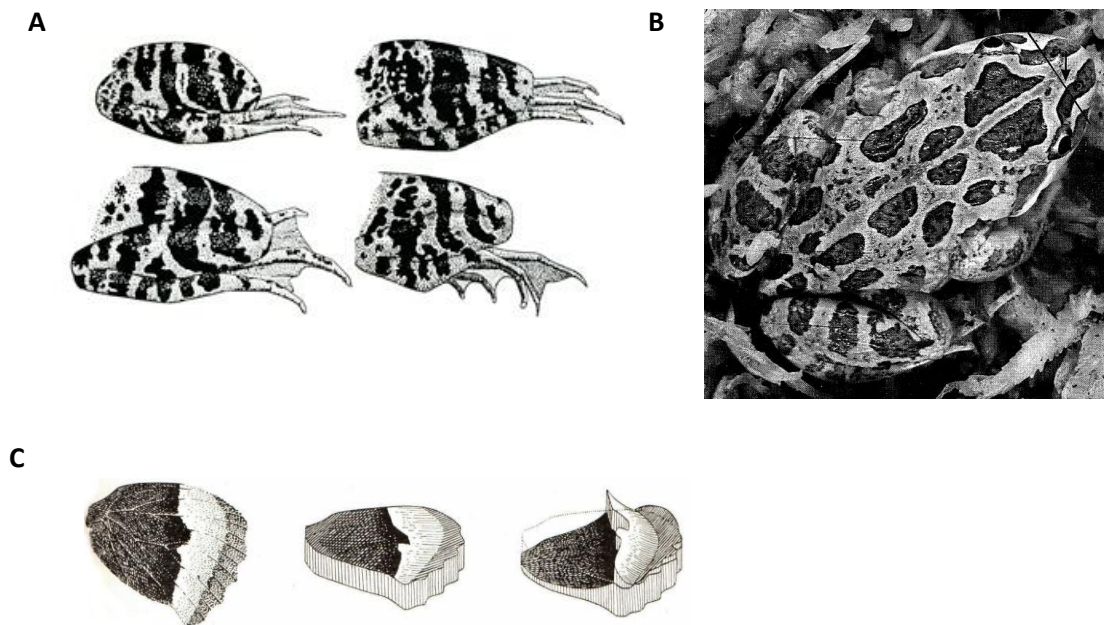


Figure 2 : A: Drawings adapted from the artwork by Hugh Cott illustrating, coincident colours that create false contours on the leg and body of the frog *Rana temporaria*, modified from Cott (1940; Figure 21). B. The frog *Lymnodynastes tasmaniensis* showing enhanced edges to the camouflage pattern (from Osorio and Srinivasan 1991). C. Cott's (1940; Fig. 17) interpretation of the enhanced border on the wing of a butterfly as being consistent with a surface discontinuity. It is an interesting question how often such intensity profiles to occur in nature.

For Thayer (1909) the central thesis was a paradox: that apparently conspicuous colours could be concealing. This included patterns we now regard as classic disruptive coloration (he used the term 'ruptive'), namely the use of adjacent high contrast colours to break up shape and form, but he also extended the principle to patterns that do not conceal but instead deceive in other ways. For example, the idea that high contrast patterns could interfere with motion perception and otherwise confuse attackers is discussed later in the section on Motion Perception.

'True' disruptive coloration, for concealment *per se*, works against object detection by perceptual grouping, but, as Merilaita (1998) clarified, it employs mechanisms above and beyond background matching. Indeed, in Cott's (1940) original formulation, it is essential that some colour patches do not resemble colour patches found in the background; in our own treatment of disruptive coloration we relax this constraint. For Cott, two components were vital and, although he did not make the connection, they relate directly to principles of perception. First, some colour patches must match the background; second, some colour patches must be strongly contrasting from the first patch type(s) and - in Cott's and Thayer's

views -, also from the background. Cott called this “differential blending”, and we can see this as working against perceptual grouping of the target by colour similarity. The background matching of some patches creates a weak boundary between the animal and its surround at these junctions. The high and sharp contrast between other patches on the animal and these background-matching regions creates strong false edges internal to the animal’s boundary. The effect is that, for the viewer, some colour patches on the animal are statistically more likely to belong to the background than they are to each other (Cuthill and Troscianko 2009). Similar ideas have been

In order to disrupt the outline of the animal, the prediction is that the contrasting colour patches should intersect the edge of the animal more often than expected if the animal’s pattern was simply a random sample of the background texture. That is, if the animal’s true outline is interrupted by high contrast, ‘strong’ pseudo-edges that are perpendicular to the animal’s boundary, then the viewer gets powerful conflicting evidence for edges that are not consistent with the continuous outline of a prey item. Merilaita (1998) showed this to be true of the dark and light colour patches on a marine isopod crustacean. More recently the efficacy of disruptive patterning against birds has been demonstrated by using simulated wing patterns on artificial moth-like baited targets pinned to trees (Cuthill *et al.* 2005). This study showed that colour blocks that intersected the edge of the ‘wing’ reduced the rate of attacks on the models compared to otherwise similar controls with only internal patterning, or uniformly coloured. A computer-based experiment using the same sort of targets on pictures of tree bark replicated the results with humans (Fraser *et al.* 2007), suggesting that the perceptual mechanisms being fooled are in common across birds and humans. Most plausible would be continuity of strong edges, suggesting a bounding contour. Consistent with this, it is striking that edges in camouflage patterns are often ‘enhanced’ with a light margin to pale regions and a dark margin to dark regions (Figure 2B), a fact remarked upon by Cott (1940). One possible interpretation (Osorio & Srinivasan 1991) is that such features strongly excite edge detectors without unduly compromising cryptic camouflage. With this in mind, Stevens & Cuthill (2006) analysed *in situ* photographs of the experimental targets used in the bird predation experiments of Cuthill *et al.* (2005), appropriately calibrated for avian colour vision. Using a straight-line detector from machine vision, the Hough transform, allied to a physiologically plausible edge detector, the Marr-Hildreth Laplacian-of-Gaussian, Stevens & Cuthill (2006) showed that edge-intersecting disruptive colouration defeated target detection, compared to non-disruptive controls, in a pattern similar to the observed bird predation (Figure 3).

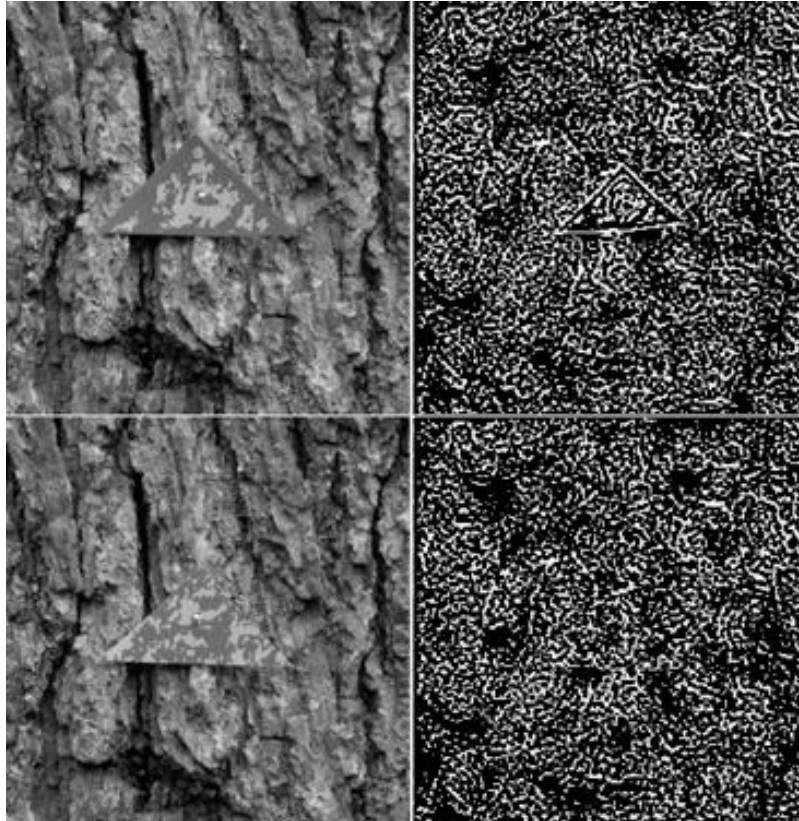


Figure 3: Artificial targets, baited with mealworms, survived better under bird predation if the contrasting colour patches intersected the ‘wing’ edges (bottom left) than targets bearing otherwise similar oak-bark-like textures that did not intersect the edges (top left). High contrast edge-disrupting patterns and differential blending with the background reduce the signal from the target’s outline (right-hand panels: edge images from applying a Laplacian-of-Gaussian filter to similar targets). Figure from Stevens & Cuthill (2006).

A camouflaged animal’s outline is not the only potentially revealing feature; mismatches in the phases of patterns on adjacent body parts, or the distinctive colour and shape of an eye are also salient features for a predator. Cott (1940) illustrated species, from birds to fish that have eye stripes that match the colour of the pupil or iris, effectively forming a background with which the eye blends. He also noted species with stripes bisecting the eye, using disruption to break up the circular shape. Similarly, he illustrated frogs whose complex body patterns matched seamlessly on different parts of the folded leg when sitting hunched up (Figure 2A). He called this coincident disruptive coloration, the adjacency of strong contrasts creating false bounding contours spanning different body parts. Recently the effectiveness of coincident disruptive coloration in concealing separate body regions has been experimentally verified in the field, using artificial targets under bird predation (Cuthill & Székely 2009).

The resurgence in interest in Cott’s theories has focused mainly on concealment of the body’s edge through peripherally placed disruptive colour patches. As we have discussed, the effects

can be explained as exploiting low-level visual processes, namely edge detection and contour integration. However, Cott's and subsequent accounts make frequent reference to disruptive coloration distracting attention from the body's edge, through internally placed coherent 'false shapes' that contrast strongly with the surrounding body coloration. Cott called this 'surface disruption' and Stevens and others (2009) showed that this can be as or more effective than edge disruption against avian predators. It is not clear whether the mechanism is actually diversion of attention, or a lower-level process such as simultaneous contrast masking nearby (true) edges. Indeed, Cott's suggestion that small, highly conspicuous 'distraction marks' could decrease predation by distracting attention has rather equivocal support. One might imagine that if the marks are both conspicuous and uniquely borne by prey, predators would learn to use these cues to detect prey. This is what has been found in field experiments on birds searching for artificial prey (Stevens *et al.* 2008). However, in laboratory experiments on birds where trials were intermixed and there was a correspondingly reduced potential to learn that a mark was a perfect predictor of prey presence, distraction marks reduced detection (Dimitrova *et al.* 2009).

There a number of open questions about disruptive camouflage. Disruptive coloration is sometimes discussed as if were a strict alternative to background matching. It is certainly true that seemingly disruptive camouflage patterns have a high visual contrast, and Cott (1940) argued for a principle of 'maximum disruptive contrast' where, subject to some patches matching the background ('differential blending'), the remaining colour patches should be maximally contrasting from these, and unlike background colours. However in principle there is no reason why features that distract from the natural outline of an animal should not present the same level of contrast as background objects, as is probably the case for the cuttlefish Disruptive pattern (Mäthger *et al.* 2006; Kelman *et al.* 2008; Zylinski *et al.* 2009a); indeed all military camouflage patterns described as 'disruptive' consist of colours found in natural backgrounds. Stevens and co-workers (2006), again using artificial moth-like prey in the field, found that bird predation was lowest for disruptive patterns where the contrast between adjacent patches was high, but all colours were within the background range. Disruptive patterns where some elements had yet higher contrast, but were rare in the background, had increased predation, although they still fared better than similarly coloured targets without outline-disrupting elements. Similarly, for humans searching for similar targets on computer screens if some prey patch colours are not found in the background, detectability increases regardless of high internal contrast (Fraser *et al.* 2007). The conclusion is that high contrast between adjacent patches is beneficial for the creation of false bounding contours but, contrary to Cott's suggestion, that contrast is constrained by the need to match common background colours.

5. Obscuring 3-D form

Both cryptic and disruptive camouflage is often studied from the point of view of 2-D image segregation. However it is perfectly plausible that animals may benefit from cryptic patterns that match the light and shade of naturally illuminated scenes, especially when the animal is larger than the objects that make up the background. The intensity difference between objects

in shadow compared to directly illuminated surfaces can be very much larger than between reflective surfaces under uniform illumination, but to our knowledge no one has attempted to establish how the dynamic range of camouflage patterns matches the intensity range of surfaces such as leaves or stones.

Although there are few if any direct studies, it seems plausible that some camouflage patterns produce a disruptive effect whereby a continuous body surface is seen as lying in different depth planes. For example matte black spots or patches can appear as holes in a surface, and white features as glossy highlights. Figure 2C illustrates Cott's (1940) interpretation of the enhanced borders as a 3-D effect. A charming example of a false 3-D effect is produced by cuttlefish, which shadow the white square on their mantle to create the effect of a pebble (Langridge 2006).

5.1. Countershading

Countershading, like disruptive coloration, is a principle of camouflage that was 'discovered' in the late nineteenth century (Poulton 1890; Thayer 1896), found military application in the early twentieth, and has recently been a subject of direct experimental study. Many animals have a dark upper surface and a pale lower surface separated by an intensity gradient. This type of pattern counters the effect of natural illumination gradients, on the 3-dimensional body, which may benefit camouflage. Thus when cuttlefish rotate from the usual orientation they move their dark and light regions so they remain on the top and bottom body surfaces, respectively (Ferguson *et al.* 1994). Historically, the taxonomic ubiquity of such dorso-ventral gradients in coloration was seen as evidence of the adaptive benefits of concealment of 3D form. However, there are many adaptive reasons to have such a gradient, some of which see the colour only as an incidental by-product of the pigment gradient: for example, protection from UV light, or resistance to abrasion – because melanin toughens biological tissues (Kiltie 1988; Ruxton *et al.* 2004a; Rowland 2009). In fact, recent experimental studies on model 'caterpillars' coloured uniformly, or with countershading or reverse countershading patterns, have demonstrated that countershading helps concealment from birds (Rowland *et al.* 2007, 2008). However the principle by which countershading patterns achieve camouflage is less obvious. In pelagic fish it is likely that countershading allows the animals to match the space light in the open water beyond the animal (an effect also achieved by mirror-like scales), so the fish becomes invisible. In other habitats countershading may either facilitate matching of the background, where the background differs according to viewing direction (e.g. for pelagic fish, the light surface when seen from below favours a light belly, the dark depths when see from above favour a dark back), or conceal the 3-D form of the body through diminished self-shading. Recently Allen and co-workers (2012) compared the predicted pattern of fur shading to counteract dorso-ventral gradients created by illumination in different light environments against the distribution of coat colours across 114 species of ruminants (grazing mammals such as deer, sheep and cattle). There is a correspondence between the observed pattern and that predicted, after controlling for possibly confounding effects of similarity due to taxonomic closeness; this lends support to the self-shadow concealment hypothesis.

6. Concealing motion

The term ‘motion camouflage’ can be discussed in two contexts: crypsis when the background itself moves, and concealment while the animal itself is in motion. To take the first, many backgrounds have moving elements – leaves in the wind, seaweed in the tide – and an otherwise background matching, but static, animal may be revealed by its failure to match the motion statistics of the background. The swaying, stop-start motion of a chameleon or praying mantis seems to mimic the rocking of leaves and twigs in the breeze, and the lack of consistent linear motion towards the prey may itself reduce salience. Analysis of the movements of an Australian lizard, the jacky dragon *Amphibolurus muricatus*, shows that when it signals to other members of its species, its motion statistics move well outside the background distribution, but when not signalling its own distribution falls within that of the background (Peters & Evans 2003; Peters *et al.* 2007). Cuttlefish reduce the contrast in their body patterns during motion (Zylinski *et al.* 2009c), perhaps because the high contrast edges seen in disruptive patterning are more easily detected in motion.

The second issue is whether a moving animal can remain concealed. Many facts point to the conclusion that motion breaks camouflage. Correlated motion is a strong cue to grouping, so that an otherwise highly camouflaged object is readily segregated from the background because its pattern elements share a common fate absent in otherwise identical background elements. Experiments on the detection of targets on complex backgrounds indicate that, for single targets, neither background matching nor disruptive camouflage offer any benefits (Hall *et al.* 2013). This would explain why big cats stalking prey, and soldiers moving across open ground, move in a combination of stealthy motion interspersed with frequent pauses.

If the need for motion precludes concealment, other means of defence must be used (e.g. capacity for flight, defensive spines or toxins), some of which involve the use of colour. Warning colours associated with unpalatability, or mimicry of such patterns, fall outside the remit of this chapter (instead see e.g. Ruxton *et al.* 2004b), but coloration designed to confuse or deceive has historically, although erroneously, been bracketed within disruptive coloration and so we discuss it briefly here. For example, the idea that high contrast patterns could interfere with judgement of velocity and otherwise confuse attackers, which goes back to Thayer (1909), was a tactic that became known as ‘dazzle’ coloration when deployed on ships during both World Wars (see Williams 2001; Behrens 2002). Part of the alleged success was attributed to interference with the optical range-finding used on U-Boats, but the difficulty of judging speed and trajectory has also been cited (Williams 2001; Behrens 2002). The mechanism(s) by which such patterns have their effects is less clear, because perception of speed is affected by many factors, notably size, contrast and texture orientation (see Scott-Samuel *et al.* 2011). Dazzle patterning may work through any or all of such factors. Recent research shows that the perceptual distortions created by high contrast stripes can be quite significant for speed (Scott-Samuel *et al.* 2011) and can affect capture success (Stevens *et al.* 2008). This can be added to the (long) list of proposed evolutionary explanations for zebra stripes (see e.g. Cloudsley-Thomson 1999; Caro 2011). Thayer (1909) argued that the stripes matched the vertical patterning created by savannah grasses, so function through background matching, but Godfrey and co-workers (1987), through Fourier analysis, showed that zebra

stripes were, unlike tiger stripes, a poor match to the background. Alternatively, given that zebra live in herds, the stripes could serve both a background matching and disruptive function, if the background is considered to be other zebras. Ironically, given their frequent occurrence in discussions on camouflage, the only function for zebra stripes that has been experimentally tested is their effectiveness in repelling biting flies (Waage 1981; Egri *et al.* 2012).

7. Conclusions

The scientific study of animal camouflage and the development of Gestalt psychology drew heavily from each other in the first half of the 20th century. Nature provides compelling examples of the sort of problems a visual system has to solve in separating figure from ground and in identifying relevant objects for attention. To explain the form of animal camouflage, it remains essential to understand not only the photoreceptors of the animal from which the target seeks concealment (photoreceptors which may be very different in number and tuning from our own), but the cognitive processes behind perception. It is clear that features such as disruptive coloration and edge enhancement, coincidence of colour patches across adjacent body parts, and gradients in shading that counter illumination gradients, to name but a few, are adaptations against the Gestalt principles used in object segregation. In turn, we believe that animal camouflage offers an excellent model system in which to test the generality of these principles beyond *Homo sapiens*.

8. References

- Allen, W. L., Cuthill, I. C., Scott-Samuel, N. E. & Baddeley, R. (2011). Why the leopard got its spots: relating pattern development to ecology in Felids. *Proc. R. Soc. B* 278, 1373-1380.
- Allen, W. A., Baddeley, R., Cuthill, I. C. & Scott-Samuel, N. E. (2012). A quantitative test of the predicted relationship between countershading and lighting environment. *Amer. Natur.* 180, 762-776.
- Barbosa, A., Allen, J. J., Mähger, L. M. & Hanlon, R. T. (2011). Cuttlefish use visual cues to determine arm postures for camouflage. *Proc. R. Soc. B* 279, 84-90.
- Barbosa A., Mähger L. M, Buresch K. C., Kelly J., Chubb C., Chiao C.-C. & Hanlon R. T. (2008). Cuttlefish camouflage: the effects of substrate contrast and size in evoking uniform, mottle or disruptive body patterns. *Vision Res.* 48, 1242-1253.
- Beldade, P. & Brakefield, P.M. (2002). The genetics and evo-devo of butterfly wing patterns. *Nature Reviews Genetics* 3, 442-452.
- Bennett, A. T. D., Cuthill, I. C. & Norris, K. (1994). Sexual selection and the mismeasure of color. *Am. Nat.* 144, 848-860.
- Behrens, R. R. (2002). False colors: art, design and modern camouflage. Dysart, Iowa: Bobolink Books.
- Behrens, R. R. (2011). Nature's artistry: Abbott H. Thayer's assertions about camouflage in art, war and nature. In Stevens, M. & Merilaita, S. (Eds). *Animal camouflage: mechanisms and function*. Cambridge: Cambridge University Press. pp. 87-100.
- Bond, A. B. & Kamil, A. C. (2006). Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proc. Nat Acad. Sci. USA.* 103, 3214-3219.
- Caro, T. (2011). The functions of black-and-white colouration in mammals. In Stevens, M. & Merilaita, S. (Eds). *Animal Camouflage. Mechanisms and Function*. Cambridge: Cambridge Univ Press. pp. 298-329.
- Chiao C.-C., Chubb C. & Hanlon R. T. (2007). Interactive effects of size, contrast, intensity and configuration of background objects in evoking disruptive camouflage in cuttlefish. *Vision Res.* 47, 2223-2235.
- Chiao, C-C., & Hanlon, R.T. (2001). Cuttlefish camouflage: visual perception of size, contrast and number of white squares on artificial substrata initiates disruptive coloration. *J. Exp. Biol.* 204: 2119-2125.
- Chiao, C-C., Kelman, E.J. & Hanlon, R.T. (2005). Disruptive body patterning of cuttlefish (*Sepia officinalis*) requires visual information regarding edges and contrast of objects in natural substrate backgrounds. *Biological Bulletin.* 208, 7-11.
- Chiao, C-C, Wickiser, J.K., Allen, J.J., Genter, B. & Hanlon, R.T. (2011). Hyperspectral imaging of cuttlefish camouflage indicates good color match in the eyes of fish predators. *Proc. Nat. Acad. Sci. USA*, 108, 9148-9153.
- Cloudsley-Thompson, J. L. (1999). Multiple factors in the evolution of animal coloration. *Naturwiss.* 86, 123-132.
- Cott, H. B. (1940) *Adaptive Coloration in Animals*, London: Methuen & Co.
- Crook, A.C. Baddeley, R.J. & Osorio, D. (2002) Identifying the structure in cuttlefish visual signals. *Phil Trans R Soc Lond B* 357 1617-1624.
- Cuthill, I. C. & Bennett, A. T. D. (1993). Mimicry and the eye of the beholder. *Proc. R. Soc. B* 253, 203-204.

- Cuthill, I. C. (2006). Color perception. In Hill, G.E. & McGraw, K.J. (Eds.) *Bird coloration. Volume 1. Mechanisms and measurement*. Cambridge MA: Harvard University Press. pp. 3-40.
- Cuthill, I. C., Hiby, E. & Lloyd, E. (2006a). The predation costs of symmetrical cryptic coloration. *Proc. R. Soc. B* 273, 1267 - 1271.
- Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, C. A. & Troscianko, T.S. (2005). Disruptive coloration and background pattern matching. *Nature* 434, 72-74.
- Cuthill, I. C., Stevens, M., Windsor, A. M. M. & Walker, H. J. (2006b). The effects of pattern symmetry on detection of disruptive and background matching coloration. *Behav. Ecol.* 17, 828-832.
- Cuthill I. C. & Székely A. (2009). Coincident disruptive coloration. *Phil. Trans. R. Soc. B* 364, 489 – 496.
- Cuthill, I. C. & Troscianko, T. S. (2009). Animal camouflage: biology meets psychology, computer science and art. *Int. J. Des. Nat. Ecodyn.* 4(3), 183-202.
- Denton, E. J. (1970). On the organization of reflecting surfaces in some marine animals. *Phil. Trans. R. Soc. B* 258, 285-313.
- Dimitrova, M. & Merilaita, S. (2010). Prey concealment: visual background complexity and prey contrast distribution. *Behav. Ecol.* 21:176-181.
- Dimitrova, M. & Merilaita, S. (2012). Prey pattern regularity and background complexity affect detectability of background-matching prey. *Behav. Ecol.* 23, 384-390.
- Dimitrova, M., Stobbe, N., Schaefer, H. M. & Merilaita, S. (2009). Concealed by conspicuousness: distractive prey markings and backgrounds. *Proc. R. Soc. B* 276, 1905-1910.
- Duncan, J. & Humphreys, G.W. (1989). Visual search and stimulus similarity. *Psych. Rev.* 96, 433-458.
- Egri, A., Blahó, M., Kriska, G., Farkas, R., Gyurkovszky, M., Åkesson, S. & Horváth G. (2012) Polarotactic tabanids find striped patterns with brightness and/or polarization modulation least attractive: an advantage of zebra stripes. *J. Exp. Biol.* 215, 736-745.
- Endler, J. A. (1978). A predator's view of animal color patterns. *Evol. Biol.* 11, 319-364.
- Endler, J. A. (1981). An overview of the relationships between mimicry and crypsis. *Biol. J. Linn. Soc.* 16, 25-31.
- Endler, J. A. (1984). Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* 22, 187-231.
- Endler, J. A. (1991) Interactions between predators and prey. In *Behavioural Ecology: an Evolutionary Approach*, 3rd Edition (ed. J. R. Krebs & N. B. Davis), pp. 169-196. Oxford: Blackwell.
- Ferguson, G., Messenger, J. & Budelmann, B. (1994). Gravity and light influence the countershading reflexes of the cuttlefish *Sepia officinalis*. *J. Exp. Biol.* 191, 247-256.
- Fraser, S., Callahan, A., Klassen, D. & Sherratt, T. N. (2007). Empirical tests of the role of disruptive coloration in reducing detectability. *Proc. Roy. Soc. B* 274, 1325-1331.
- Frisby, J. (2004). Bela Julesz 1928 - 2003: a personal tribute. *Perception*, 33, 633-637.
- Godfrey, D., Lythgoe, J. N. & Rumball, D. A. (1987). Zebra stripes and tiger stripes: the spatial frequency distribution of the pattern compared to that of the background is significant in display and crypsis. *Biol. J. Linn. Soc.* 32, 427-433.
- Hall, J.R., Cuthill, I.C., Baddeley, R., Shohet, A.J. & Scott-Samuel, N.E. (2013) Camouflage, detection and identification of moving targets. *Proc. R. Soc. B* 280(1758): 20130064.
- Hanlon, R.T. (2007). Cephalopod dynamic camouflage. *Curr. Biol.* 17, 400-404.

- Hanlon, R.T., Forsythe, J.W. & Joneschild, D.E. (1999). Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biol. J. Linn. Soc.* 66, 1–22.
- Hanlon, R. T. & Messenger, J. B. (1988). Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. *Phil. Trans. R. Soc. B* 320, 437-487.
- Hanlon, R. T., Chiao, C-C., Mäthger, L. M., Buresch, K. C., Barbosa, A., Allen, J. J., Siemann, L., & Chubb, C. (2011). Rapid adaptive camouflage in cephalopods. In: Stevens, M. and Merilaita, S. (Eds.) *Animal camouflage: mechanisms and functions*. Cambridge: Cambridge University Press. pp. 145-163.
- Houston, A. I., Stevens, M. & Cuthill, I. C. (2007). Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behav. Ecol.* 18, 769-775.
- Jordan, T. M.; Partridge, J. C.; Roberts, N. W. (2012). Non-polarizing broadband multilayer reflectors in fish. *Nature Photonics* 6: 759-763.
- Julesz, B. (1971). *Foundations of Cyclopean Perception*. Chicago: The University of Chicago Press.
- Julesz, B. (1981). Textons, the elements of texture perception, and their interactions. *Nature* 290, 91-97.
- Julesz, B. (1984). A brief outline of the texton theory of human vision. *Trends Neurosci.* 7, 41-45.
- Keen, A. M. (1932). Protective coloration in the light of Gestalt theory. *J. Gen. Psychol.* 6, 200-203.
- Kelman E. J., Osorio D. & Baddeley, R. J. (2008). A review of cuttlefish camouflage and object recognition and evidence for depth perception. *J. Exp. Biol.* 211, 1757 – 1763.
- Kelman, E. J., Tiptus, P. & Osorio, D. (2006). Juvenile plaice (*Pleuronectes platessa*) produce camouflage by flexibly combining two separate patterns. *J. Exp. Biol.* 209, 3288-3292.
- Kiltie, R. A. (1988). Countershading: universally deceptive or deceptively universal? *Trends Ecol. Evol.* 3, 21–23.
- Kiltie, R. A., Fan, J. & Laine, A. F. (1995). A wavelet-based metric for visual texture discrimination with applications in evolutionary ecology. *Math. Biosci.* 126, 21-39.
- Kjernsmo, K. & Merilaita, S. (2012) Background choice as an anti-predator strategy: the roles of background matching and visual complexity in the habitat choice of the least killifish. *Proc. R. Soc. B*, 279, 4192-4198.
- Landy, M. S. & Graham, N. (2004). Visual perception of texture. In Chalupa, L. M. & Werner, J. S. (Eds.) *The visual neurosciences*. Cambridge, MA: MIT Press. pp. 1106-1118
- Langridge, K. V. (2006). Symmetrical crypsis and asymmetrical signalling in the cuttlefish *Sepia officinalis*. *Proc. R. Soc. B* 273, 959-967.
- Langridge, K. V, Broom, M. and Osorio, D. (2007). Selective signalling by cuttlefish to predators. *Current Biology*, 17 R1044-R1045
- Marshall, N. J. & Messenger, J. B. (1996) Colour-blind camouflage. *Nature* 382, 408-409.
- Mäthger, L., Barbosa, A., Miner, S. & Hanlon, R. T. (2006) Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. *Vis. Res.* 46, 1746-1753.
- Merilaita, S. (1998). Crypsis through disruptive coloration in an isopod. *Proc. Roy. Soc. B* 265, 1059-1064.

- Merilaita, S. (2003). Visual background complexity facilitates the evolution of camouflage. *Evolution* 57, 1248-1254.
- Merilaita, S. & Lind, J. (2006). Great tits (*Parus major*) searching for artificial prey: implications for cryptic coloration and symmetry. *Behav. Ecol.* 17, 84-87.
- Merilaita, S., Lyytinen, A. & Mappes, J. (2001). Selection for cryptic coloration in a visually heterogeneous habitat. *Proc R. Soc Lond B* 268, 1925-1929.
- Merilaita, S., Tuomi, J. & Jormalainen, V. (1999). Optimization of cryptic coloration in heterogeneous habitats. *Biol. J. Linn. Soc.* 67, 151-161.
- Monteiro, A., Brakefield, P. M. & French, V. (1997). The relationship between eyespot shape and wing shape in the butterfly *Bicyclus anynana*: a genetic and morphometrical approach. *J. Evol. Biol.* 10, 787-802.
- Metzger, W. (2009). *Laws of seeing* translated by L Spillman & S Lehar. Cambridge: MIT Press. (Originally published as: Metzger, W. 1936. *Gesetze des Sehens*. Kramer, Frankfurt.)
- Nieder A. (2002). Seeing more than meets the eye: processing of illusory contours in animals. *J. Comp. Physiol. A* 188, 249–260.
- Peters, R. A. & Evans, C. S. (2003). Design of the Jacky dragon visual display: signal and noise characteristics in a complex visual environment. *J. Comp. Physiol. A* 189, 447-459.
- Peters, R. A., Hemmi, J. M. & Zeil, J. (2007) Signalling against the wind: modifying motion signal structure in response to increased noise. *Curr. Biol.* 17, 1231-1234.
- Peterson, M. A. (2013). Low-level and high-level contributions to figure-ground organization. In J. Wagemans (Ed.), *Oxford Handbook of Perceptual Organization* (in press). Oxford, U.K.: Oxford University Press.
- Peyré, G. (2009) Sparse modeling of textures. *J. Mathematical Imaging and Vision.* 34, 17-31
- Portilla, J. & Simoncelli, E.P. (2000) A parametric texture model based on joint statistics of complex wavelet coefficients. *Int. J. Computer Vision*, 40, 49-70
- Poulton, E. B. (1890) *The colours of animals: their meaning and use. Especially considered in the case of insects.* 2nd edn.. The International Scientific Series. London: Kegan Paul, Trench Trübner & Co. Ltd.
- Ramachandran, V. S., Tyler, C. W., Gregory, R. L., Rogers-Ramachandran, D., Duensing, S., Pillsbury, C. & Ramachandran, C. (1996). Rapid adaptive camouflage in tropical flounders. *Nature* 379, 815-818.
- Rosenholtz, R. (2013). Texture perception. In J. Wagemans (Ed.), *Oxford Handbook of Perceptual Organization* (in press). Oxford, U.K.: Oxford University Press
- Rowland, H. M. (2009). From Abbott Thayer to the present day: what have we learned about the function of countershading? *Phil. Trans. R. Soc B* 364, 519-527.
- Rowland, H. M., Cuthill, I. C., Harvey, I. F., Speed, M. P. & Ruxton, G. D. (2008). Can't tell the caterpillars from the trees: countershading enhances survival in a woodland. *Proc. R. Soc. B* 275, 2539–2545.
- Rowland, H. M., Speed, M. P., Ruxton, G. D., Edmunds, M., Stevens, M. & Harvey, I. F. (2007). Countershading enhances cryptic protection: an experiment with wild birds and artificial prey. *Anim. Behav.* 74, 1249–1258.
- Ruxton, G. D., Speed, M. P. & Kelly, D. (2004a). What, if anything, is the adaptive function of countershading? *Anim. Behav.* 68, 445–451.
- Ruxton, G., Speed, M. & Sherratt, T. (2004b). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford: Oxford University Press.

Saidel, W. M. (1988). How to be unseen: an essay in obscurity. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. Fay, A. N. Popper and W. Tavalga), pp.487-513. New York: Springer.

Scott-Samuel, N. E., Baddeley, R., Palmer, C. E. & Cuthill, I. C. (2011). Dazzle camouflage affects speed perception. *PLoS One* 6(6), e20233.

Shapley, R.M., Rubin, N. and Ringach, D. (2004). Visual segmentation and illusory contours. In: Chalupa, L.M. and Werner, J.S. (Eds.), *The Visual Neurosciences*, MIT Press. pp. 1119-1128.

Shohet A.J, Baddeley R.J, Anderson J.C, Kelman E.J, & Osorio, D. (2006). Cuttlefish response to visual orientation of substrates, water flow and a model of motion camouflage. *J. Exp. Biol.* **209**, 4717–4723.

Shohet, A., Baddeley, R., Anderson J. & Osorio, D. (2007). Cuttlefish camouflage: a quantitative study of patterning. *Biol. J. Linn. Soc.* 92 335–345.

Simoncelli, E. P. & Olshausen, B. A. (2001). Natural image statistics and neural representation. *Ann. Rev. Neurosci.* 24, 1193-1216.

Skelhorn, J., Rowland, H. M. & Ruxton, G. D. (2010a). The evolution and ecology of masquerade. *Bio. J. Linn. Soc.*99: 1-8.

Skelhorn, J., Rowland, H. M., Speed, M. P. & Ruxton, G. D. (2010b) Masquerade: Camouflage Without Crypsis. *Science* 327: 51.

Stevens, M. & Cuthill, I. C. (2006). Disruptive coloration, crypsis and edge detection in early visual processing. *Proc. R. Soc. B* 273: 2141-2147

Stevens, M., Cuthill, I. C., Windsor, A. M. M. & Walker, H. J. (2006). Disruptive contrast in animal camouflage. *Proc. R. Soc. B* 273, 2433-2438.

Stevens, M., Graham, J., Winney, I. S. & Cantor, A. (2008). Testing Thayer's hypothesis: can camouflage work by distraction? *Biol. Lett.* 4, 648-50.

Stevens, M. & Merilaita, S. (2009). Animal camouflage: current issues and new perspectives. *Phil. Trans. R. Soc. B* 364: 423-427.

Stevens, M., Winney, I. S., Cantor, A. & Graham, J. (2009). Object outline and surface disruption in animal camouflage. *Proc. R. Soc. B* 276, 781-786.

Stevens, M., Yule, D. H. & Ruxton, G. D. (2008) Dazzle coloration and prey movement. *Proc. R. Soc. B* 275: 2639–2643.

Stuart-Fox D. & Moussalli, A. (2009) Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Phil. Trans. R. Soc. B* 364, 463-470.

Thayer, A. H. (1896) The law which underlies protective coloration. *The Auk* 13, 477-482.

Thayer, G. H. (1909). *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries*. New York: The Macmillan Co.

van der Helm, P. (2013) Symmetry perception. In J. Wagemans (Ed.), *Oxford Handbook of Perceptual Organization* (in press). Oxford, U.K.: Oxford University Press.

van Lier, R. & Gerbino, W. (2013). Perceptual completions. In J. Wagemans (Ed.), *Oxford Handbook of Perceptual Organization* (in press). Oxford, U.K.: Oxford University Press.

Waage, J. (1981). How the zebra got its stripes - biting flies as selective agents in the evolution of zebra coloration. *J. Ent. Soc. S. Afr.* 44, 351-358.

Wente, W.H. & Phillips, J.B. (2005). Microhabitat selection by the Pacific treefrog, *Hyla regilla*. *Animal Behaviour* 70, 279–287

Williams, D. (2001). *Naval Camouflage 1914-1945*. Barnsley, UK: Pen and Sword Books.

- Zylinski, S. & Darmaillacq, A. S. & Shashar, N. (2012) Visual interpolation for contour completion by the European cuttlefish (*Sepia officinalis*) and its use in dynamic camouflage. *Proc. R. Soc. B* 279, 2386-2390.
- Zylinski, S. & Osorio, D. (2011). What can camouflage tell us about non-human visual perception? A case study of multiple cue use in the cuttlefish. Pp. 164-185 in Stevens, M. & Merilaita, S. (eds.) *Animal Camouflage: Mechanisms and Function*. Cambridge: Cambridge University Press.
- Zylinski, S., Osorio, D. & Shohet, A.J. (2009a). Edge detection and texture classification by cuttlefish. *J. Vision* 9, 1-10.
- Zylinski, S., Osorio, D. & Shohet, A. J. (2009b). Perception of edges and visual texture in the camouflage of the common cuttlefish, *Sepia officinalis*. *Phil. Trans. R. Soc. B* 364, 439-448.
- Zylinski, S., Osorio, D. & Shohet, A. J. (2009c). Cuttlefish Camouflage: context-dependent body pattern use during motion *Proc. R. Soc. B* 276, 3963-3969.

FIGURES