



# Visual perception and cuttlefish camouflage

Sam Reiter<sup>1</sup> and Gilles Laurent

Visual perception is inherently statistical: brains exploit repeating features of natural scenes to disambiguate images that could, in principle, have many causes. A clear case for the relevance of statistical inference in vision is animal camouflage. Although visual scenes are each composed of unique arrangements of pixels, they are usually perceived mainly as groupings of statistically defined patches (sandy/leafy/smooth etc . . . ); this fact is exploited by camouflaging animals. The unique ability of certain cephalopods to camouflage actively within many different surroundings provides a rare and direct behavioral readout for texture perception. In addition, because cephalopods and chordates each arose after a phylogenetic split that occurred some 600M years ago, the apparent convergence of texture perception across these groups suggests common principles. Studying cephalopod camouflage may thus help us resolve general problems of visual perception.

## Address

Max Planck Institute for Brain Research, Max-von-Laue-Str. 4,  
60438 Frankfurt am Main, Germany

Corresponding author: Laurent, Gilles ([gilles.laurent@brain.mpg.de](mailto:gilles.laurent@brain.mpg.de))

<sup>1</sup> Present address: Okinawa Institute of Science and Technology  
Graduate University, Okinawa, Japan.

**Current Opinion in Neurobiology** 2020, **60**:47–54

This review comes from a themed issue on **Neurobiology of behavior**

Edited by **Michael Brecht** and **Richard Mooney**

<https://doi.org/10.1016/j.conb.2019.10.010>

0959-4388/© 2019 Elsevier Ltd. All rights reserved.

## Visual textures and statistical inference

To be useful, visual systems must make the most of noisy biological measurements to solve complex problems quickly. More than being merely difficult, many of these problems are ill-posed, in that they have many possible solutions [1,2]. For example, understanding the 3d layout of a visual scene from sparse 2d images—as retinal images are—is difficult because it is usually underconstrained. In practice, however, we and other animals routinely solve such problems. This is possible because, in the vast majority of cases, we deal with natural images that contain statistical regularities (e.g. illumination typically comes from the top, objects have boundaries, low spatial frequencies dominate etc . . . ), inherited from the nature of

our physical world. Visual systems indeed exploit these regularities to encode and recognize ethologically relevant stimuli efficiently [3]. Through some combination of innate structure (itself a result of evolution and natural selection) and learning, animals can solve the many ill-posed problems of vision by correctly integrating immediate sensory input with prior (including ‘deep’ or evolutionary) knowledge [4].

Visual textures, an important subset of natural images, are rapidly and usually [5] effortlessly (i.e. without careful scrutiny) recognized by the visual system [6,7]. Textures are roughly defined as homogeneous image elements with repeating parts, characterized by randomization of position, size, shape, orientation, color and other properties [8]. More precisely, a visual texture refers to an ensemble of image elements characterized by shared statistical properties [9]. A sandy texture, for example, does not refer to a particular image of sand, but rather to an infinite collection of images that share certain ‘image statistics’. Image statistics are functions of the image ensemble, ranging from simple (e.g. mean intensity) to complex (e.g. correlations between pixel intensities, nonlinear functions of these correlations). Because it is amenable to statistical approaches, texture perception provides a window into how brains perform statistical inference in general [10].

To analyze a scene and inform a behavioral decision, visual systems appear to have evolved to extract a minimum set of summary statistics [3,11]. Texture perception is useful to segment objects, determine material properties, discern 3d shapes [12] and depth [13,14], quickly ascertain the gist of a visual scene [15,16] and inform visual search [17]. Texture is indeed so useful that convolutional neural networks (CNNs) trained explicitly for object recognition show a heavy bias in their use of texture as a discriminatory feature [18\*\*]. As coined by Adelson [19], visual scenes are typically composed of ‘stuff’ rather than ‘things’, and the perception of stuff relies heavily on texture (Figure 1a,b).

Yet, texture perception comes at a cost. By summarizing the key aspects of a natural scene in a set of image statistics, an animal’s visual system opens itself to being fooled by camouflaging predators and prey. Many animals (mammals, reptiles, birds, amphibians, fish, insects, molluscs, etc.) avoid detection by matching the visual texture of their local surroundings [20] (Figure 1c). While an animal’s camouflage ‘texture’ is often static, it can, in some cases, be modified. The most spectacular examples of this are found among coleoid cephalopods (cuttlefish,

Figure 1



Current Opinion in Neurobiology

Texture perception, synthesis, and deception **(a)** Image taken near MPI Brain Research, Frankfurt. **(b)** Selected cropped regions from the image in **(a)** converted into grayscale. Note the ease of perceptually grouping the rows, discriminating images in a column, and assigning each cropped image back to particular regions in the original. Apparently, visual systems extract statistical summaries over image regions, making many kinds of discrimination easier and others harder. **(c)** Three leaf-litter toads in Panama. Many animals have evolved camouflage abilities that exploit texture perception in their predators. The toads' camouflage fools our own visual system as well, suggesting the existence of general rules governing texture perception across animals. Photograph: National Geographic. **(d)** Synthesized textures using the PSGAN model [32\*], trained on a collection of images cropped from **(a)**. Texture-synthesis models explicitly test the set of statistics used for texture perception.

octopus and squid). Species in this subclass have evolved high-resolution skin display systems under direct neural control (unique among all animals), which they use to match the 2-D (and often, 3-D) texture of a wide range of environments at subsecond speeds [21–23].

### Describing visual textures

Which image statistics do we use to perceive textures? In 1962, Bela Julesz proposed that textures are perceived in terms of their  $N$ th-order statistics, where  $N$  is the number

of locations in an image (e.g. defined by the vertices of an  $N$ -gon) that need to be compared. Images with matching order statistics below a certain  $N$  were hypothesized to be indiscriminable [11]. In what became known as the Julesz conjecture, Julesz later hypothesized that humans are unable to discriminate textures identical up to second-order statistics ( $N = 2$ , i.e. images matching luminance levels and power spectra [9]). This conjecture was later refuted by Julesz and colleagues, by hand-crafting discriminable iso-second-order texture pairs [6,24].

Advances in computation have made it possible to investigate the relevance of a larger set of statistics in texture perception. In texture synthesis [25], statistics of interest are estimated from an image and then used to generate a new image from scratch. The perceptual differences between original and synthesized images are then assessed, typically through human psychophysics. Portilla and Simoncelli greatly extended earlier hierarchical models [26] to characterize textures statistically in terms of functions of images passed through a multi-scale filter bank, called a ‘steerable pyramid’. They could synthesize quite realistic textures using a set of ca. 700 parameters [8].

More recently, Gatys *et al.* used the correlation between activations of a set of layers (Gram matrices) of a CNN [27] pre-trained for object recognition on the Imagenet database [28] to describe textures [29]. New images of a given texture could be generated by matching Gram matrices, and the ‘style’ of an existing image could even be transferred to a new image, in a process termed ‘neural style transfer’ [30].

More recently still, a variant of Generative Adversarial Networks (GAN) [31] called periodic spatial GAN or PSGAN [32\*\*] has been shown to synthesize textures of even higher perceptual quality than with a CNN/Gramian approach. This model learns a texture manifold and can thus generate many different textures contained in single images as well as smoothly interpolate between them (Figure 1d).

In these models, perceptual quality correlates with model complexity. While a CNN-based model can generate more realistic textures than the Portilla-Simoncelli model, it does so with significantly more (>200 000 versus ~700) parameters [7]. The PSGAN model has over three million parameters. Recent developments, however, suggest the possibility of high-quality texture synthesis using relatively simple solutions. For example, a single-layer CNN with random filters can be used to generate realistic textures using Gram matrices. This depends critically on the presence of nonlinearities and on processing the images at multiple spatial scales; interestingly, it does not require training on a large set of natural images [33]. To date, however, no modeling approach seems capable yet of generating artificial textures indistinguishable from natural ones upon close inspection [7]. The set of image statistics necessary and sufficient to explain texture perception has thus not yet been fully identified.

### Evidence for texture perception in animals

How widespread is visual texture perception among animals? Human psychophysics rely on the subjective notion of ‘perceptual equivalence’ to quantify texture similarity. Different criteria are required with animals, but behavioral discrimination studies in insects and

cephalopods suggest that texture perception is not limited to mammals or even vertebrates.

Visual perception in honeybees, for example, can be readily probed in the laboratory by pairing visual stimuli of a given class with a sucrose reward and testing for the identification of novel examples drawn from the same or different classes. Using such strategies, honeybees could be trained to use the texture of visual landmarks rather than their position, to localize a food source [34], indicating texture identification. Honeybees could be trained also to discriminate between different classes of natural images (flowers of different shapes, plants, natural scenes) and generalize to new examples in an image category. Discrimination did not depend on color or mean luminance [35]. Honeybees could even be trained to discriminate sets of circular stimuli split into 4 quadrants, each filled randomly with oriented bars. The bees correctly generalized to novel stimuli that shared the pattern of orientations but differed in bar layout. Strikingly, they generalized to novel stimuli sharing a fraction of correct orientations, preferring these stimuli over ones with no correct orientations [36]. Together, these experiments strongly suggest that honeybees can perceive the global patterns of visual stimuli, and that they can extract summary statistics to inform useful behaviors.

Camouflage can be thought of as a kind of visual illusion [37], useful precisely because the predators and prey fooled by camouflage perceive textures in terms of summary statistics (Figure 1c). The fact that many animals have evolved single camouflage patterns to fool diverse prey or predators implies some degree of perceptual convergence across species. It is reasonable to assume that these common or overlapping perceptual groupings result from the fact that different visual systems exploit similar properties of natural images (even accounting for variations linked to the idiosyncrasy of each visual system—resolution, spectral tuning, etc...).

Active camouflage is particularly interesting. If an octopus chooses to adopt a camouflage pattern that fools us as well as shrimp, it must have ‘learned’ (in an evolutionary sense, by natural selection) the common structure of the statistical groupings of textures performed by our brains and by those of shrimp. Understanding how animals such as cephalopods choose different camouflage patterns in different environments thus may inform us not only about their perception of visual textures but also about texture perception in a broad sense. (Note that some aspects of crypsis behaviors may be adapted to particular features—for example wavelength and polarization sensitivity—of the visual systems of their preys or predators.)

### How do animals learn to perceive texture?

If modern deep-learning approaches do perform reasonably well in visual-texture matching tasks [29,32\*\*], they

nevertheless typically require hundreds of thousands to millions of training examples. Animals, by contrast, must extract texture statistics with very few examples. Humans become sensitive to the statistics of visual textures over early postnatal development. Simple texture discrimination can be used for object segmentation in 14-week-old infants [38]. At 2–3 months, infant brains show differential visual evoked potentials in responses to textures formed by Gabor patches at aligned versus random orientations [39]. Visual texture gradients can be used to infer depth by infants between 5 and 7 months [40]. Contrast negation, an image manipulation that disrupts texture appearance in adults [41], influences infant behavior starting between 6 and 9 months of age [42].

Children thus become sensitive to textures in relatively little time and must therefore learn from a relatively limited number of examples. This is noteworthy given that the distribution of natural images is long-tailed—many image categories are rare while a few are frequent [43]. This observation points to the necessity of an innate ‘core knowledge’ of physics [44] enabling efficient (and constrained) learning from limited data. Indeed, it is possible that these inductive biases [45] are a missing component of current machine learning techniques; integration of intrinsic structure may eventually help close the gap between computers and humans in learning from limited data [46,47,48\*\*,49].

The problems of training with limited data become particularly acute when one takes a broader look at the animal kingdom. Insects, for example, possess working vision immediately after hatching or metamorphosis. Cuttlefish can camouflage—and thus perceive textures and make appropriate adaptive camouflage choices—immediately upon hatching [50]. They have no parental training, and the cost of a mistake is immense since it can result in death. Clearly, texture perception in these animals must be largely innate, suggesting that the neural system underlying texture representation in the brain must be efficient (and low-dimensional) enough to be transmissible through genomic information. This has important implications about the neural implementation of texture perception circuits in terms of connectivity and possibly, dynamics as well [51\*\*].

### Cuttlefish as unique models for the study of texture perception

The ability of cephalopods to match their substrate has fascinated students of natural history for millenia [52]. Coleoid cephalopods are a group of molluscs whose ancestral lineage split from our own 580–610 million years ago (protostome-deuterostome divergence). Roughly 200 million years ago, these cephalopods internalized their shells, took up a predatory lifestyle, evolved by far the largest brains amongst invertebrates and developed an active camouflage ability [53]. Cephalopods therefore represent

a key example, other than among the vertebrates, of large-brain and complex-behavior evolution.

To camouflage, these animals do not match the details of their visual environment pixel by pixel.

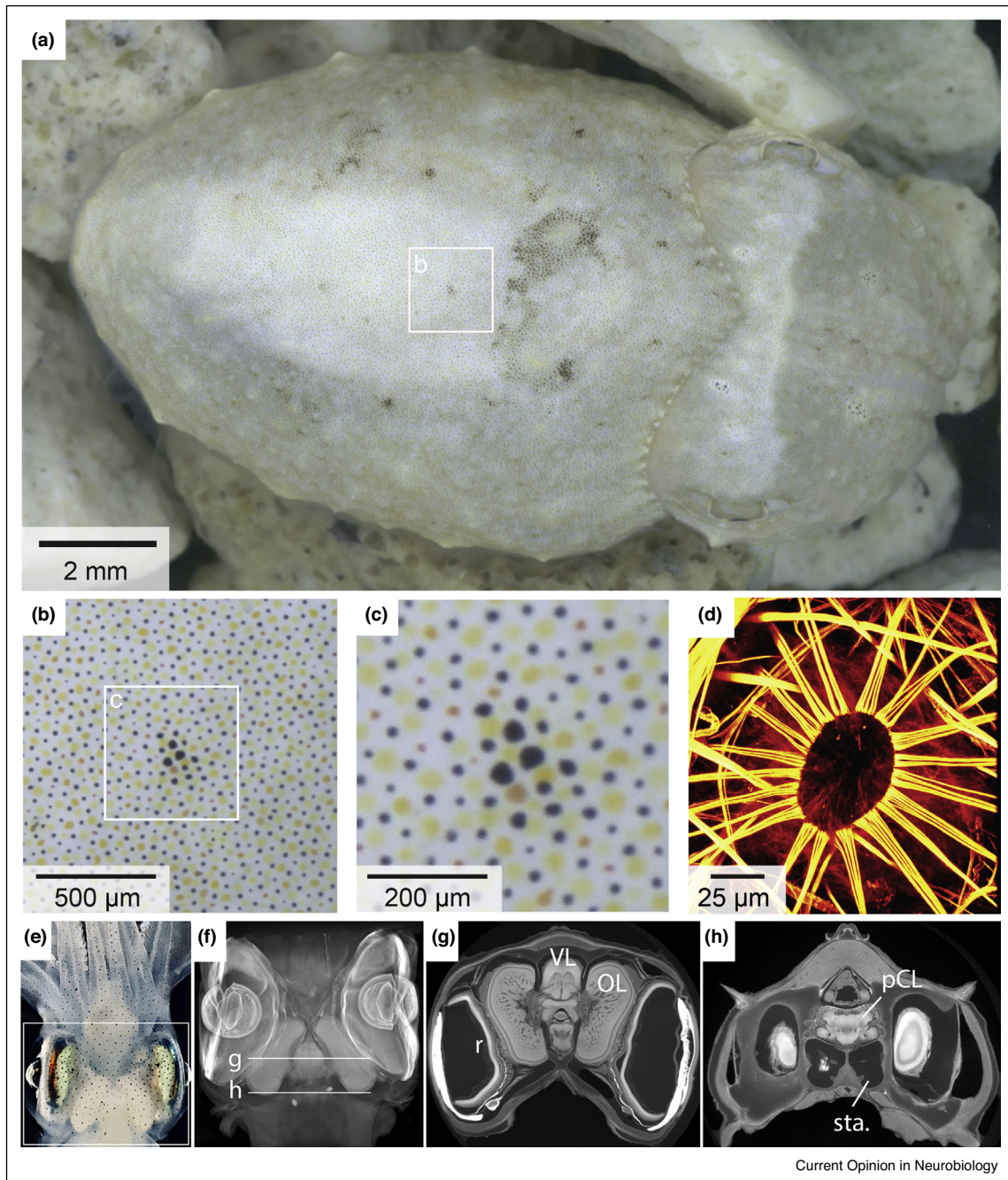
Instead, they appear to choose camouflage patterns that match the dominant visual texture surrounding them, using their sophisticated visual systems (Figure 2). The cuttlefish *Sepia officinalis*, in particular, is almost constantly camouflaged, changing pattern relatively quickly when presented with different local surroundings [21,50]. Cuttlefish-camouflage skin patterns are generated by up to millions of specialized skin cells, most notably the pigment-containing chromatophores [50]. The expansion state of these cells is controlled directly by motor neurons located in the brain’s chromatophore lobes (Figure 2), with each motor neuron controlling from just a few to ~10 chromatophores [51\*\*,54,55].

How can the remarkable size and complexity of this pigment-cell array be reconciled with the necessity of a simple, innate solution for camouflage? Part of the answer appears to be that camouflage behavior in cuttlefish may not be nearly as diverse as it seems. Studying juvenile cuttlefish (*S. officinalis*), Hanlon and Messenger identified only 54 components of camouflage. Thirty-four of these were ‘chromatic’, in which specific regions of the animal’s mantle and head showed reliable and coordinated color changes. Other components were textural, postural, or involved locomotion. These components were observed to combine in different ways to produce six types of patterns [50]. Examining hundreds of images of cuttlefish in the lab and manually labeling these 54 components, cluster analysis found 12–13 patterns [22]. Several more recent studies support the idea that there are only three main types of pattern, termed ‘uniform’, ‘mottle’, and ‘disruptive’ [56–58].

The low spatial resolution (relative to the scale of potential pattern control) of these studies, the use of static images to describe dynamic behavior, and the subjective description of patterns and components complicate these varying descriptions of cuttlefish camouflage behavior. These studies, however, all suggest that, out of the vast number of chromatophore patterns that could be produced *a priori*, only a subset is probably used. The small size of the chromatophore motor units might then be explained simply by the need to generate a few camouflage patterns of high spatial frequency (e.g. to match the texture of fine sand), rather than as a means to generate any arbitrary pattern.

Using tools from computer vision, Reiter *et al.* recently described cuttlefish camouflage at cellular resolution, recording the expansion state of tens of thousands of individual chromatophores at 60 Hz over hours [51\*\*].

Figure 2



Camouflage through a biological pixel array. **(a)** A juvenile cuttlefish matching the texture of underlying white stones. **(b),(c)** Increasingly zoomed views showing chromatophores of different colors and expansion states. **(d)** Superresolution micrograph of a chromatophore (center) and radiating muscles in a plane parallel to the skin surface (actin stain). These muscles contract in response to motor neuron action potentials, expanding the pigment-containing sacculus. Chromatophore expansion thus provides an indirect readout of motor neuron activity. See Ref. [52\*\*] for details. **(e)** Micrograph of an intact juvenile squid (*Loligo pealii*) showing the large brain (whitish lobed mass) located between the two eyes (anterior at top). Rectangular outline indicates approximate region imaged in **(f)**. **(f)** Micro-computer-aided tomography ( $\mu$ CT) stack of squid head in **(e)** after fixation and contrast-enhancement staining (16.8  $\mu$ m resolution). Viewed from top. **(g),(h)** Transverse views ( $\mu$ CT) at levels indicated in **(f)**. OL: optic lobe. pCL: posterior chromatophore lobe. r: retina. sta.: statocyst. VL: vertical lobe.

Examining chromatophore dynamics, small clusters of cells showed coordinated fluctuations suggestive of common innervation by single motor neurons. Hierarchical clustering based on the correlation of these groups revealed structure at a range of spatial scales: small groups of chromatophore-units formed larger lines, rings, spots, and other shapes, which together formed macroscopic pattern elements (eye spot, dorsal square and band) similar to ones previously described (Figure 3). Consistent with this inferred motor hierarchy, analyzing chromatophore dynamics over repeating behavioral sequences revealed stereotyped activity at the level of single chromatophores. Consequently, this behavior was actually relatively low dimensional: 85% of the variance could be explained by 9 dimensions.

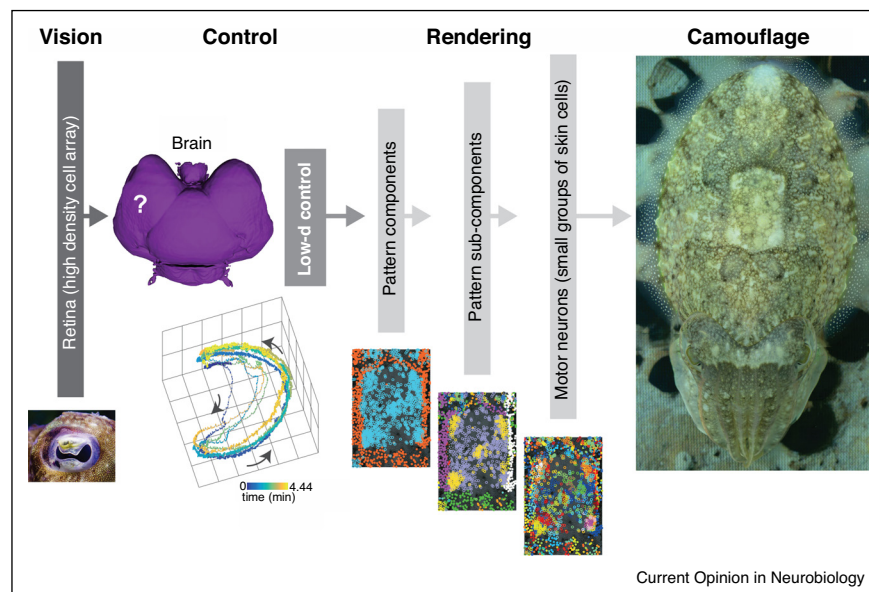
We hypothesize that future experiments will further reveal the existence of a low-dimensional system for skin patterning control, possibly implemented by recurrent circuits within higher-order centers of the cuttlefish brain. Chronically adopted camouflage patterns may take the form of fixed-point attractors within the state space of this control circuit, analogous to the dynamics observed within vertebrate brain areas involved in motor planning [59]. To link the dynamics of this putative low-dimensional system to the millions of chromatophores forming the skin patterns, we hypothesize the existence of ‘rendering’ networks,

upstream of the motoneurons. This could take the form of a feed-forward hierarchy of neural populations representing successively smaller-scale features of skin patterns as one moves towards the periphery (Figure 3). Regardless of network topology, there must exist highly constrained rules to govern the stereotyped development of neural connectivity and appropriate tuning of synaptic weights. We conceptualize those as perhaps analogous to local developmental rules governing skin pattern formation in these animals [51] and to developmental programs investigated in the mammalian motor periphery [60].

Quantitative tests of this hypothesis’ viability and its predictions about neural activity and connectomes represent interesting directions for future work. Of pressing concern are the limited size and scope of all datasets of cuttlefish camouflage to date. Addressing questions about the system’s dimensionality, dynamics, number of patterns, and ultimately how these relate to the visual environment will require filming animals at high spatial and temporal resolution in a large range of visual environments. Without such appropriate datasets, we may end up estimating the limited complexity of current experimental conditions rather than that of the animal [61].

The close study of camouflage behavior promises to reveal aspects of cuttlefish texture perception: if the

Figure 3



A hypothesized camouflage-generation strategy in cuttlefish. **Vision:** After visual information is processed by the external and internal retinae, an unknown amount of further processing takes place before informing a low-dimensional camouflage control circuit in the central brain. **Control:** Experimental observation of the activity of ~17 000 chromatophores projected onto the top 3 principal components, demonstrating repeated low-dimensional dynamics. It may be possible to infer constraints on neural dynamics through observing constraints on the dynamics of skin patterning behavior. **Rendering:** Experimental observation of a statistical hierarchy of spatially compact pattern components and subcomponents, suggesting a feed-forward hierarchy linking an underlying simple system to a complex set of skin cell types. **Camouflage:** Cuttlefish camouflage represents a uniquely expressive readout of an animal’s visual texture perception displayed as a 2d image on its skin.

animal produces different camouflage patterns reliably in two visual environments, it must be perceiving some statistical difference between them. The assumed low-dimensional control of camouflage patterns in these animals implies that many individual images should map to one of a limited number of patterns. What image statistics can thus be used to discriminate between sets of images that evoke different patterns? There is no doubt that the cuttlefish's behavior represents a lower bound on its visual discrimination abilities. Much may be perceived that does not result in a camouflage pattern change. It is reasonable to expect changes only when animals are faced with differences in the image statistics relevant for disguising themselves from their predators and their prey. This may be a particularly interesting set of statistics.

## Outlook

We have highlighted recent and older work on visual textures, the perception of which appears to be a key component of vision in many different animal groups. This is perhaps most clearly demonstrated by camouflage, which in many instances functions as an adaptation to visual texture perception in others. Cephalopods, possessing active camouflage under neural control, reveal aspects of their perception through their choice of skin pattern in different visual environments. This remarkable ability is seemingly innate, placing constraints on the complexity of the neural circuits involved. The unique biology of cephalopods allows this behavior to be described at cellular resolution, revealing aspects of its neural control. Given these advantages, our current opinion is that cephalopods hold great potential for our general understanding of visual texture perception.

## Conflict of interest statement

Nothing declared.

## Acknowledgements

We would like to thank Stephan Junek and Amber Longo for images, Marcel Lauterbach for STED imaging, Claudio Polisseni for  $\mu$ CT imaging, Dominic Evans, Theodosia Woo, and Sara Haddad for their suggestions on the manuscript, as well as Matthias Kaschube, Stephanie Palmer, Jonathan Miller, Kenji Doya, the instructors and students of the Cajal Behavior of Neural Systems course 2018, and the members of the Laurent laboratory for many useful discussions.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Kersten D: **High-level vision as statistical inference.** *The New Cognitive Neurosciences*. edn 2. Cambridge, MA: MIT Press; 1999, 353-363.
2. Poggio T, Torre V, Koch C: **Computational vision and regularization theory.** *Nature* 1985, **317**:314.
3. Simoncelli EP, Olshausen BA: **Natural image statistics and neural representation.** *Annu Rev Neurosci* 2001, **24**:1193-1216.
4. Yuille A, Kersten D: **Vision as Bayesian inference: analysis by synthesis?** *Trends Cogn Sci* 2006, **10**:301-308.
5. Joseph JS, Chun MM, Nakayama K: **Attentional requirements in a "preattentive" feature search task.** *Nature* 1997, **387**:805-807.
6. Julesz B: **Textons, the elements of texture perception, and their interactions.** *Nature* 1981, **290**:91.
7. Wallis TSA, Funke CM, Ecker AS, Gatys LA, Wichmann FA, Bethge M: **A parametric texture model based on deep convolutional features closely matches texture appearance for humans.** *J Vis* 2017, **17** 5-5.
8. Portilla J, Simoncelli EP: **A parametric texture model based on joint statistics of complex wavelet coefficients.** *Int J Comput Vis* 2000, **40**:49-70.
9. Victor JD: **Images, statistics, and textures: implications of triple correlation uniqueness for texture statistics and the Julesz conjecture: comment.** *J Optic Soc Am A* 1994, **11**:1680-1684.
10. Victor JD, Conte MM, Chubb CF: **Textures as probes of visual processing.** *Annu Rev Vis Sci* 2017, **3**:275-296.
11. Julesz B: **Visual pattern discrimination.** *IRE Trans Inf Theory* 1962, **8**:84-92.
12. Fleming RW: **Visual perception of materials and their properties.** *Vision Res* 2014, **94**:62-75.
13. Torralba A, Oliva A: **Depth estimation from image structure.** *IEEE Trans Pattern Anal Mach Intell* 2002, **24**:1226-1238.
14. Torralba A, Oliva A: **Statistics of natural image categories.** *Netw Bristol Engl* 2003, **14**:391-412.
15. Renninger LW, Malik J: **When is scene identification just texture recognition?** *Vision Res* 2004, **44**:2301-2311.
16. Oliva A, Torralba A: **Building the gist of a scene: the role of global image features in recognition.** *Prog Brain Res* 2006, **155**:23-36.
17. Rosenholtz R, Huang J, Raj A, Balas BJ, Ilie L: **A summary statistic representation in peripheral vision explains visual search.** *J Vis* 2012, **12** 14-14.
18. Geirhos R, Rubisch P, Michaelis C, Bethge M, Wichmann FA, Brendel W: **"ImageNet-trained CNNs are biased towards texture; increasing shape bias improves accuracy and robustness.** *International Conference on Learning Representations (ICLR) (May)2019* <https://openreview.net/forum?id=Bygh9j09KX>.
19. Adelson EH: **On seeing stuff: the perception of materials by humans and machines.** *Proc SPIE* 2001, **4299**:1-12.
20. Merilaita S, Scott-Samuel NE, Cuthill IC: **How camouflage works.** *Philos Trans R Soc B Biol Sci* 2017, **372** 20160341.
21. Messenger JB: **Cephalopod chromatophores: neurobiology and natural history.** *Biol Rev Camb Philos Soc* 2001, **76**:473-528.
22. Crook AC, Baddeley R, Osorio D: **Identifying the structure in cuttlefish visual signals.** *Philos Trans R Soc Lond B Biol Sci* 2002, **357**:1617-1624.
23. Hanlon RT, Messenger JB: *Cephalopod Behaviour*. Cambridge University Press; 2018.
24. Caelli T, Julesz B: **On perceptual analyzers underlying visual texture discrimination: part I.** *Biol Cybern* 1978, **28**:167-175.
25. Faugeras OD, Pratt WK: **Decorrelation methods of texture feature extraction.** *IEEE Trans Pattern Anal Mach Intell* 1980:323-332. PAMI-2.
26. Cano D, Minh TH: **Texture synthesis using hierarchical linear transforms.** *Signal Process* 1988, **15**:131-148.
27. Simonyan K, Zisserman A: **Very deep convolutional networks for large-scale image recognition.** *ArXiv14091556 Cs* 2014.
28. Russakovsky O, Deng J, Su H, Krause J, Satheesh S, Ma S, Huang Z, Karpathy A, Khosla A, Bernstein M et al.: **ImageNet large scale visual recognition challenge.** *ArXiv14090575 Cs* 2014.

29. Gatys LA, Ecker AS, Bethge M: **Texture synthesis using convolutional neural networks**. *ArXiv150507376 Cs Q-Bio* 2015.
30. Gatys LA, Ecker AS, Bethge M: **A neural algorithm of artistic style**. *ArXiv150806576 Cs Q-Bio* 2015.
31. Goodfellow IJ, Pouget-Abadie J, Mirza M, Xu B, Warde-Farley D, Ozair S, Courville A, Bengio Y: **Generative adversarial networks**. *ArXiv14062661 Cs Stat* 2014.
32. Bergmann U, Jetchev N, Vollgraf R: **Learning texture manifolds with the periodic spatial GAN**. *ArXiv1705.06566 Cs* 2017.  
The current state of the art in texture synthesis. Bergmann *et al.*'s PSGAN is able to learn a texture manifold, allowing for the generation of many individual textures as well as smooth transitions between them.
33. Ustyuzhaninov I, Brendel W, Gatys L, Bethge M: **What does it take to generate natural textures?** *International Conference on Learning Representations* 2017.
34. Dittmar L, Egelhaaf M, Stürzl W, Boeddeker N: **The behavioral relevance of landmark texture for honeybee homing**. *Front Behav Neurosci* 2011, **5**:20.
35. Zhang S, Srinivasan MV, Zhu H, Wong J: **Grouping of visual objects by honeybees**. *J Exp Biol* 2004, **207**:3289-3298.
36. Stach S, Benard J, Giurfa M: **Local-feature assembling in visual pattern recognition and generalization in honeybees**. *Nature* 2004, **429**:758.
37. Kelley LA, Kelley JL: **Animal visual illusion and confusion: the importance of a perceptual perspective**. *Behav Ecol* 2014, **25**:450-463.
38. Atkinson J, Braddick O: **Visual segmentation of oriented textures by infants**. *Behav Brain Res* 1992, **49**:123-131.
39. Norcia AM, Pei F, Bonneh Y, Hou C, Sampath V, Pettet MW: **Development of sensitivity to texture and contour information in the human infant**. *J Cogn Neurosci* 2005, **17**:569-579.
40. Yonas A, Granrud CE, Arterberry ME, Hanson BL: **Infants' distance perception from linear perspective and texture gradients**. *Infant Behav Dev* 1986, **9**:247-256.
41. Balas B: **Contrast negation and texture synthesis differentially disrupt natural texture appearance**. *Front Psychol* 2012, **3**.
42. Balas B, Woods R: **Infant preference for natural texture statistics is modulated by contrast polarity**. *Infancy Off J Int Soc Infant Stud* 2014, **19**:262-280.
43. Van Horn G, Perona P: **The devil is in the tails: fine-grained classification in the wild**. *ArXiv170901450 Cs* 2017.
44. Spelke ES, Kinzler KD: **Core knowledge**. *Dev Sci* 2007, **10**:89-96.
45. Mitchell TM: *The Need for Biases in Learning Generalizations*. *Rutgers University Department of Computer Science Report C BM-TR-5-110*. 1980.
46. Lake BM, Ullman TD, Tenenbaum JB, Gershman SJ: **Building machines that learn and think like people**. *ArXiv160400289 Cs Stat* 2016.
47. Marcus G: **Deep learning: a critical appraisal**. *ArXiv180100631 Cs Stat* 2018.
48. Zador AM: **A critique of pure learning and what artificial neural networks can learn from animal brains**. *Nat Commun* 2019, **10**:1-7.  
Zador argues for the importance of innate structure in animal's genome and neural wiring in explaining the ability of animals to learn complex behaviors from limited experience. He suggests that incorporating these insights into future AI research may help address the current gap between natural and artificial agents, especially in the few-shot learning regime.
49. Battaglia PW, Hamrick JB, Bapst V, Sanchez-Gonzalez A, Zambaldi V, Malinowski M, Tacchetti A, Raposo D, Santoro A, Faulkner R *et al.*: **Relational inductive biases, deep learning, and graph networks**. *ArXiv180601261 Cs Stat* 2018.
50. Hanlon RT, Messenger JB: **Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour**. *Philos Trans R Soc Lond B Biol Sci* 1988, **320**:437-487.
51. Reiter S, Hülsdunk P, Woo T, Lauterbach MA, Eberle JS, Akay LA, Longo A, Meier-Credo J, Kretschmer F, Langer JD *et al.*: **Elucidating the control and development of skin patterning in cuttlefish**. *Nature* 2018, **562**:361.  
Cellular-resolution imaging of cuttlefish skin patterning behavior revealed a putative hierarchy of motor control, low-dimensional dynamics, and suggested simple developmental rules governing skin pattern formation.
52. Aristotle. *History of Animal*, Books I-III, A.L. Peck (translator). 1965. Harvard University Press. ISBN-10: 0674994817. 245 pp.
53. Kröger B, Vinther J, Fuchs D: **Cephalopod origin and evolution: a congruent picture emerging from fossils, development and molecules: extant cephalopods are younger than previously realised and were under major selection to become agile, shell-less predators**. *BioEssays News Rev Mol Cell Dev Biol* 2011, **33**:602-613.
54. Ferguson GP, Martini FM, Pinsker HM: **Chromatophore motor fields in the squid, *Lolliguncula brevis***. *J Exp Biol* 1988, **134**:281-295.
55. Packard A: **Morphogenesis of chromatophore patterns in cephalopods: are morphological and physiological "units" the same?** *Malacologia* 1982, **23**:193-201.
56. Hanlon R: **Cephalopod dynamic camouflage**. *Curr Biol CB* 2007, **17**:R400-404.
57. Barbosa A, Mäthger LM, Buresch KC, Kelly J, Chubb C, Chiao C-C, Hanlon RT: **Cuttlefish camouflage: the effects of substrate contrast and size in evoking uniform, mottle or disruptive body patterns**. *Vision Res* 2008, **48**:1242-1253.
58. Chiao C-C, Chubb C, Buresch K, Siemann L, Hanlon RT: **The scaling effects of substrate texture on camouflage patterning in cuttlefish**. *Vision Res* 2009, **49**:1647-1656.
59. Inagaki HK, Fontolan L, Romani S, Svoboda K: **Discrete attractor dynamics underlies persistent activity in the frontal cortex**. *Nature* 2019, **566**:212.  
Recording intracellularly from a cortical area involved in motor planning, Inagaki *et al.* used optogenetic perturbations to demonstrate the presence of stable endpoints of neural activity predictive of future behavior.
60. Jessell TM, Sürmeli G, Kelly JS: **Motor neurons and the sense of place**. *Neuron* 2011, **72**:419-424.
61. Gao P, Trautmann E, Yu BM, Santhanam G, Ryu S, Shenoy K, Ganguli S: **A theory of multineuronal dimensionality, dynamics and measurement**. *bioRxiv* 2017 <http://dx.doi.org/10.1101/214262>.  
Gao *et al.* introduce a theory relating the complexity of a behavioral task and the smoothness of neural dynamics to the measured dimensionality of neural population activity. A prediction of this theory is that in many situations the observation of low-dimensional neural activity reflects the simplicity of the animal behavior studied, rather than an intrinsic property of a neural circuit.