

to probe the function of the archaic alleles to obtain a clearer picture of mechanisms that may be involved in neurodevelopmental processes [19,20]. For example, one could test the Neandertal variants that potentially influence expression of *UBR4* and *PHLPP1* in an experimental model system and measure changes in neurogenesis and myelination. Another question is whether variation in brain globularity among humans has any association with aspects of cognition, motor performance or perception. It also remains unknown whether human brain globularity covaries with other neural phenotypes related to fiber tract connectivity patterns, network architecture of brain modules or volumetric sizes of neural structures. Finally, in the future it will be critical to explore developmental neuroimaging datasets to ascertain whether Neandertal variants have an effect on brain development and might impact the neural substrates of learning.

We are witnessing a revolution in the analytical power now available to relate ancient genomes to phenotypes, improving our understanding of human evolution. This information will help us zero in on the genomic regions underlying other human-specific traits, such as our pronounced chins and lanky skeletons, by investigating the effects of archaic variants in large samples of living people. We are just scratching the surface.

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Shape Perception: Boundary Conditions on a Grey Area

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Modulations in light intensity across a visual image could be caused by a flat object with varying pigmentation, such as wallpaper, or differential light reflection from a three-dimensional shape made of uniform material, such as curtains. A new study identifies key image cues that help the brain work out which interpretation to select.

According to Pliny [1], the Ancient Greek artist Zeuxis was able to paint grapes with such felicity that birds would peck at them. Rendering a canvas into a three-dimensional impression is central to much of classical art. Yet, how is the brain

tricked into interpreting three-dimensional structure from pigments on an objectively flat object? In seeking to understand depth perception, a range of ‘pictorial’ cues, such as texture, perspective, shading, have been studied



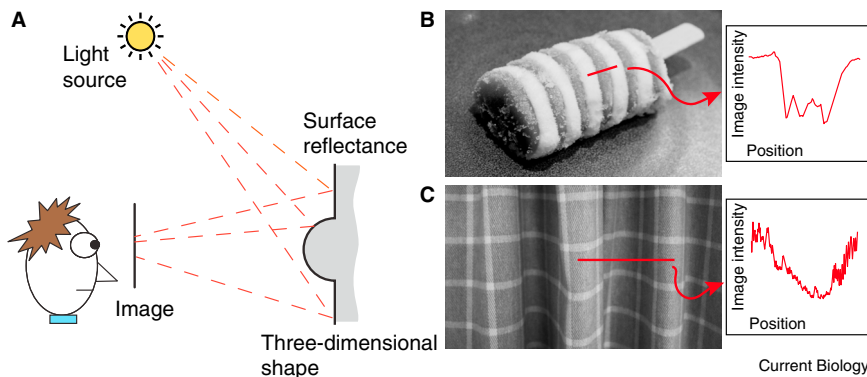


Figure 1. Cartoon of image formation and intensity variations in natural images.

(A) An illustration of the geometry of image formation to highlight the dependence on the position of the viewer, the shape of the three-dimensional object, the surface reflectance properties of the object, and the position of the light source. (B) Greyscale photograph of an ice cream whose surface consists of alternating stripes that reflect more or less light. The object itself is cylindrical and does not have significant depth variation with respect to the cylinder's surface. The red line shows the intensity profile of the image along a single line in the image: here this is not a shading pattern. (C) Greyscale photograph of hanging fabric: the depth variation of the object creates a shading pattern (illustrated for along the red line) with the troughs being darker than the peaks. Here changes in the image intensity profile are largely due to the shading cue.

[2,3]. The use of these signals depends on the visual system deciding whether variations in the viewed image are caused by changing properties of the object, as for example with a zebra's striped pelt, or the way that light naturally reflects from different portions of a three-dimensional object, for example, concavities reflect less light than convex regions. Until recently, most explanations for how the visual system interprets such inputs invoked high-level assumptions about the structure of scenes. A study reported recently in *Current Biology* by Marlow *et al.* [4], however, reveals key image signatures that determine whether patterns of shading should be interpreted either as changes in the depth profile of the surface or as variations in the surface properties of the object.

The geometry of image formation depends on the interaction between (a) the viewer, (b) a three-dimensional object with (c) specific surface reflectance properties and (d) the light source (Figure 1A): by loose mathematical analogy, the image $i = a \times b \times c \times d$. Given that the visual system only has access to the end result (the image), it is difficult to understand how the brain could perform the inverse calculation to unpick the individual components of the scene — mathematically the problem of recovering b or c from i is ill-posed. In particular, variations in light intensity in an image could be caused by changes in the

surface albedo (the bright and dark portions of an ice cream in Figure 1B) or the different amounts of light reflected from different parts of an object (compare the ridges and troughs in the folds of the fabric in Figure 1C). How does the brain, sensing intensity changes across an image, infer whether these are due to surface markings or variations in the depth profile?

Marlow *et al.* [4] have provided an important advance in demonstrating that easily measurable image signals can provide a direct cue that resolves this challenge. They started by considering the geometry of image formation and highlight potentially valuable information that is available at the contours of the object. First, they noted that the lawful way in which a smooth object occludes itself — for example, the folds of the fabric in Figure 1C hide other parts of the continuous sheet — provides information about the viewing direction. Specifically, it is useful to use the orientation of points along the contour of the object. Second, they noted that image intensity provides a cue to the direction of the illumination: for illustration, more light will be reflected towards the viewer at the top of the extruding bump in Figure 1A than will be reflected from the underside (classical shading). Their insight is to combine these two pieces of information into a single geometrical constraint that links the local orientation of the shape's contour to the intensity of the image at

those locations. Specifically, using a range of simulations they demonstrated that shading intensity along the rims of smooth self-occluding objects covaries with the orientation of the image contour: an image intensity–orientation correlation cue.

The conceptual formulation of Marlow *et al.* [4] is elegant in highlighting information that has been hidden in plain sight. Perhaps more compelling for many readers are the demonstrations that illustrate this insight. Specifically, the authors created images with smoothly varying undulations in shades of grey (their Figure 2A). They bound these undulations with sinusoidal contours at the top and bottom, and independently manipulated the spatial period of the shading undulations and the spatial period of the bounding contour. In many situations, these stimuli simply look like a stripy flat object with a wavy edge. But at the 'sweet spot' where the contours are configured such that there is an image intensity–orientation correlation, the percept changes dramatically: the object is now perceived as a twisted three-dimensional screw shape with a uniform grey surface. A simple change of the contours changes both the three-dimensional shape and the material appearance of the object.

Marlow *et al.* [4] then considered an additional cue to object shading that arises from the geometry of light reflection: concave intrusions receive less light than concave extrusions from a surface. This relationship could be used by the brain to help interpret patterns of shading: an intensity–convexity cue. They demonstrated this using undulating shades of grey where they vary the alignment between the wavy outer contours and the shading pattern (their Figure 3B). They showed that the perception of three-dimensional shape varies in line with both the intensity–convexity cue and the intensity–orientation cue. In fact, a very simple model based on these image-derived metrics can explain perceptual judgments almost perfectly: human observers rely slightly more on the intensity–orientation cue (65%) than the intensity–convexity cue (30%). Importantly, these signals are easy to measure, and provide a direct image cue to help resolve perceptual interpretation.

These findings add to the growing appreciation of the role of specific image

signatures in guiding the perception of properties that seem like complex, high-level judgements: such as translucency [5] and gloss [6,7]. The images used by Marlow *et al.* [4] were purposefully kept simple to parametrically explore the image cues they identified. Real objects pose additional challenges: surfaces vary in more than one direction, the bounding contours may not be visible (for example, the ends of the fabric are out of the frame in Figure 1C) and real surfaces typically have changes in both surface pigmentation and depth profile (for example, the plaid pattern on the fabric in Figure 1C), meaning the different types of variation should be parsed by the brain [8].

Nevertheless, Marlow *et al.* [4] have taken us a step closer to formulating the types of image signature that are characteristic of the different physical causes of images. Given the availability of this information, it seems sensible that the brain is attuned to detect it. Moreover, their stimuli provide a useful new tool with which to investigate the neural architecture that extracts shape from shading in the human brain [3]. Previous studies wrestled with the difficulties of controlling for the image differences between three-dimensional shading

versus non-three-dimensional greyscale contrasting stimuli needed for functional magnetic resonance imaging (fMRI) [9]. The stimuli developed by Marlow *et al.* [4] would provide an ideal means of comprehensively testing shape-from-shading in human fMRI studies using parametrically-controlled stimuli.

Artists have long used *chiaroscuro* — dramatic directional lighting — to enhance the sense of three-dimensional volume in paintings. The Marlow *et al.* [4] paper reveals key image signatures that combine intensity signals with local orientation and curvature to determine the impression of three-dimensional shape from shading. These simple cues appear to underlie human perceptual judgments, and may allow a relatively simple neural processing architecture that could explain the apparent innate ability of newborn chicks to interpret shading patterns as three-dimensional objects when pecking for food [10].

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Evolution: A Plant Plastid Genome that Has Forsaken Guanine and Cytosine

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The plastid genomes of the non-photosynthetic plants *Balanophora reflexa* and *B. laxiflora* are among the most GC-biased genomes observed to date. A new study shows that ~80% of the plastid-derived proteome is represented by only six amino acids, and several genes are in excess of 95% AT.

“The road of excess leads to the palace of wisdom... You never know what is enough until you know what is more than enough.”

—William Blake

As a long-time connoisseur and surveyor of unconventional organelle genomes,

I thought I had seen it all. However, the recent sequencing and characterization of two plastid DNAs (ptDNAs) from the holoparasitic plant genus *Balanophora* (Figure 1) has proved me wrong and raised the bar of what defines an extreme genome [1]. With AT compositions of 88.4% and 87.8%, the *B. reflexa* and

B. laxiflora plastomes have a smaller proportion of GC base pairs than any other ptDNA explored to date. Even more remarkable, the AT bias is most prominent in the true heart and soul of these genomes: the protein-coding genes.

It stands to reason that coding DNA should contain at least some guanine and

