

Visual neuroscience: Illuminating the dark corners

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Recent experiments suggest that our perception of lightness involves a sophisticated interpretation of illumination and shadow. This finding challenges common notions about hierarchical processing and the neural basis of perception.

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Current Biology 2000, 10:R15–R18

0960-9822/00/\$ – see front matter
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Bugaboos that lurk in the dark corners of scientific understanding have long bedeviled neuroscientists interested in visual perception. A number of recent papers on lightness perception have illuminated these corners, exposing old concerns about the neural basis of perception. The new studies suggest that seemingly simple aspects of vision involve complex processing. They also force us to face a paradox in which ‘higher level’ visual processing sometimes occurs before ‘lower level’ perception. New hypotheses about mechanisms are proposed to account for the results at the perceptual level, but it will be a challenge to relate these to the activity of neurons.

Someone unfamiliar with the neurophysiology of the visual pathways might reasonably assume that lightness perception is trivial. After all, what aspect of visual perception could be more basic than judging the lightness — apparent surface reflectance — of a small piece of paper? Yet, perhaps for reasons of efficiency, the retina appears designed to carry little explicit information about the lightness of surfaces. Within the retina, factors such as light adaptation at the scale of photoreceptors and contrast enhancement by the retinal output cells pose serious difficulties for the recovery of lightness information. Though we do not yet understand how lightness is represented, there certainly is not a ‘pixel-by-pixel’ neural representation of the lightness in the world we gaze upon.

To see how recent research challenges simple ideas about perceptual mechanisms, let’s start with two classic visual demonstrations that are usually given simple explanations. The first of these is lightness induction (Figure 1a). Two identical gray squares are surrounded by white and black, and we perceive the gray on white to be darker than the gray on black. According to a typical textbook account, lightness induction results from lateral inhibition between neurons in the retina or elsewhere in the visual system. A cell with a receptive field in the gray square surrounded by white would receive more

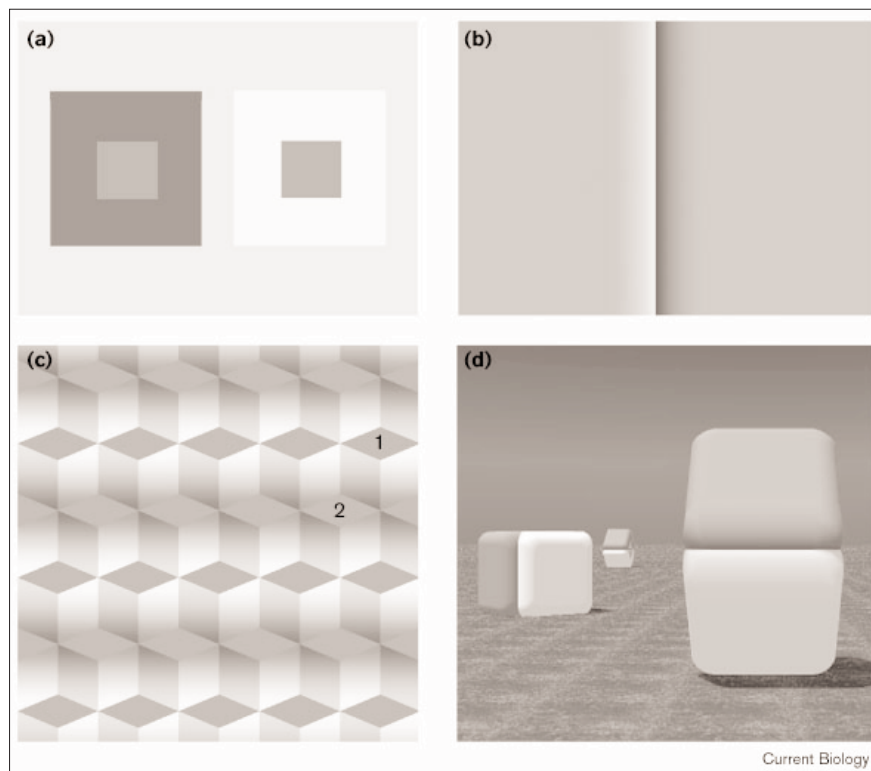
lateral inhibition than the other gray square and so have a lower firing rate. Perhaps for this reason, gray on white appears darker.

The second demonstration is the Craik-O’Brien-Cornsweet effect [1–3], illustrated in Figure 1b. Here, there is a sharp transition from black to white at the center, and luminance gradients blending to a medium gray on either side. The left side is usually perceived to be slightly lighter than the right side, even though both flanks have the same luminance (something you can demonstrate by covering the midline). Neurons early in the visual system are sensitive to luminance discontinuities and this may underlie our perception of the transition at the midline of the Craik-O’Brien-Cornsweet image. The visual system is less sensitive to gradual spatial changes in luminance. Perhaps we do not perceive the entirety of the luminance gradients to each side, so we mistakenly assume that the luminance difference at the midline extends into the flanks.

The explanations above are parsimonious, in that they employ the lowest level aspects of the visual system to account for the percepts. But from the results reported in a number of recent papers [4–10], much more appears to be involved in the simple lightness illusions. For example, lateral inhibition may not be sufficient to explain all aspects of lightness induction. In Figure 1c, the diamonds labeled 1 and 2 are identical, yet they appear quite different in lightness. The induction effect here is noticeably stronger than in the standard demonstration (Figure 1a). Indeed, the only way to convince yourself that the two diamonds have the same luminance may be to cut out two small holes in an overlaid piece of paper. Logvinenko [6] suggests that the induction is particularly strong in this case because the subtle luminance gradients are taken to be shadows rather than variations in the reflectance of the patches in the image.

A familiar situation that may be related is the appearance of a folded curtain in which you see light areas that are illuminated and dark areas in the shadows. Presumably because you are aware of the shadows, you interpret the curtain to be made of a uniform material rather than one painted with light and dark stripes. However, suppose that a portion of the curtain that is in a shadow is actually lighter than areas under direct illumination. In that case the only logical interpretation is that that portion of the curtain really is made of a lighter fabric. Similarly, in Figure 1c diamond 2 in the ‘shadow’ appears to be a lighter piece of paper than diamond 1 in the ‘illumination’. This is not the only explanation for why the induction

Figure 1



Lightness illusions and their enhancement by illumination cues. **(a)** Lightness induction. The two gray squares have the same luminance, but the square surrounded by white appears darker than the square surrounded by black. **(b)** The Craik-O'Brien-Cornsweet effect. At the midline is a sharp transition from white on the left to black on the right. Luminance gradients extend from the midline into gray flanks. The flanks have the same luminance, but the one on the left appears slightly lighter. **(c)** An enhanced version of lightness induction. The diamond labeled 1 appears darker than the diamond labeled 2 though they actually have the same luminance. **(d)** An enhanced version of the Craik-O'Brien-Cornsweet effect. The object in the foreground has an edge at its center similar to that in (b). The top half of the object is perceived to be darker than the bottom. (Panel (c) courtesy Alexander Logvinenko; panel (d) courtesy Dale Purves).

effect is stronger than in Figure 1a [5,11], but all the alternative explanations involve some 'interpretation' of the scene because 'low level' mechanisms, such as lateral inhibition, appear to be inadequate to explain the results.

A comparable challenge has been made to the standard explanation of the Craik-O'Brien-Cornsweet effect. Purves *et al.* [8] simulated a variety of two-dimensional and three-dimensional stimuli that contain lightness gradients, similar to those in the simple Craik-O'Brien-Cornsweet effect shown in Figure 1b. In Figure 1d, the large central object has the same luminance profile from top to bottom as the image in Figure 1b does from right to left. However, the lightness difference between the top and bottom is stronger in Figure 1d than that between the sides in Figure 1b. In general, luminance gradients can arise from two factors: spatial variations in the reflectance of a uniformly illuminated surface — the material itself can vary from place to place — or gradual variations in the illumination of a uniform surface. Gradients due to illumination can signify curvature of a surface or increased distance from a light source, and thus convey valuable information about the three dimensional shape of objects.

The demonstrations by Purves *et al.* [8] show that the magnitude of the Craik-O'Brien-Cornsweet effect — the difference in lightness between the two equivalent flanks

— is greater if there are three-dimensional cues, suggesting that the regions have different reflectance and are under different illumination. As in the newer explanation of lightness induction, Purves *et al.* [8] reject low level mechanisms in favor of an interpretation based on inferences about illumination. They also propose that these interpretations are wired into the brain as a result of our visual experience, an idea that holds promise for explaining surface perception in general [12].

The iconoclastic explanations of lightness induction and the Craik-O'Brien-Cornsweet effect are examples of a growing movement in research on lightness and other aspects of vision suggesting that 'low level' perception actually involves seemingly 'higher level' interpretations. This basic idea has roots dating back over 100 years. In the 19th century, von Helmholtz [13] suggested that we perceive the lightness and color of objects by first inferring the nature of the illumination. For instance, if you are dining in a room with red walls, you unconsciously compensate for the abnormally high percentage of long wavelength light in the room and your mashed potatoes appear white rather than red.

In 1866, Ernst Mach [14] discussed interactions between the perception of lightness and our interpretation of the three-dimensional structure of objects in terms quite similar

to our description of the folded curtain above. More recent studies have elaborated on this idea with striking demonstrations that lightness perception is influenced by spatial arrangement and curvature in three-dimensions [15,16]. Gilchrist *et al.* [5] have reported compelling demonstrations suggesting that, before lightness is computed, images are first segmented according to grouping principles worked out by Gestalt psychologists in the early 20th century. In a new paper reminiscent of Mach's, Bloj *et al.* [9] show that perceived color — a kind of multidimensional version of lightness — is dramatically influenced by the apparent arrangement of objects in depth. In another, Lotto and Purves [10] report that lightness is influenced by color.

So, what difference does it make whether perceived lightness does or does not depend on things such as the interpretation of illumination, grouping and curvature? The answer is that these findings bring us face-to-face with some of the thorniest issues in visual neuroscience. If the computation of lightness requires objects to be recognized, their arrangement understood and the illumination inferred, it sounds as if lightness is the last thing to be calculated. Almost surely this is not the case, but there appears to be a chicken-and-egg problem. On the one hand, some of the studies cited above suggest that the three-dimensional interpretation of a scene affects the way that lightness gradients are interpreted. On the other hand are experiments indicating that lightness gradients can play a primary role in establishing the three-dimensional shape of objects — so called 'shape-from-shading' [17,18]. Are lightness gradients used to infer depth or is depth used to interpret lightness gradients? Another example of this conundrum is the interaction between lightness and Gestalt grouping principles. Gestalt psychologists found that objects are perceptually grouped by similarity of lightness and color; but it appears that lightness perception is influenced by grouping [4,5,19,20]. Does grouping precede the lightness computation or vice versa?

If there are bidirectional interactions between different perceptual attributes, models of brain processing that involve serial hierarchies and single fixed mechanisms for the perception of certain attributes may be doomed. There is physiological evidence suggesting that induction and the Craik-O'Brien-Cornsweet effect may be reflected in the activity of neurons in primary visual cortex and area V2 [21–23]. But there is no evidence that these visual areas are involved in everything from curvature estimation to grouping to the estimation of illumination. Presumably multiple visual areas play roles in the perception of lightness, and interactions within and between brain areas are involved. For example, lateral inhibition at some point in the visual system might be the basis for lightness induction in Figure 1a, but additional information about illumination computed elsewhere may also be involved in the case depicted in Figure 1c [24].

The suggestion that multiple cortical areas underlie perception may surprise no one, but many experiments are conducted as if the system is a simple hierarchy and perception of individual attributes is based on activity in individual areas. But is it reasonable to expect that a cell's activity in any single area will correlate with perception of lightness (or anything else) in all situations? If this seems unlikely, how can we ever make a convincing case that a cell or group of cells is involved? Anything short of perfect correlation could always be taken as proof that the cell does not really underlie what we see.

Our hope for clarifying the neural basis of perception lies with approaches that complement standard single cell physiology and functional magnetic resonance imaging (fMRI). For example, by eliminating feedback between cortical areas we may be able to infer the role of interconnections [25]. By electrical microstimulation, it may be possible to slightly alter normal brain activity and influence what an animal perceives or decides [26]. In the end, the most important development may be new theories connecting brain activity to perception, either at the level of single cells or cortical areas. Research in visual neuroscience has matured to a point, long reached in other disciplines such as physics, where experiments may only achieve their greatest impact if they focus on testing theories.

In the case of lightness, early theoretical steps have been taken [5,27–32] but it will be a challenge to develop models specific enough to tackle the intricacies of perception and also make testable predictions about the response properties of neurons. A viable theory would suggest how neurons in multiple brain areas contribute to perception, despite the fact that the activity of individual neurons might not correlate with what is perceived. This is a daunting task. Fortunately, there is a wealth of physiological data and the intriguing perceptual interdependencies found in lightness will serve as valuable constraints on the models. The development of such theories will not be easy, but we need not be afraid of the bugaboos — we can make the intricacies of perceptual interactions our allies in deciphering the neural mechanisms.

Acknowledgements

I am grateful to Seth Blau, Cathy Clarke, and Barry Connors for critical comments and suggestions, and to Alexander Logvinenko and Dale Purves for providing figures.

References

1. Craik K: *The Nature of Psychology*. Cambridge, UK: Cambridge University Press; 1966.
2. O'Brien V: **Contrast by contour-enhancement**. *Am J Psychol* 1959, **72**:299-300.
3. Cornsweet TN: *Visual Perception*. New York: Academic Press; 1970.
4. Adelson EH: **Lightness perception and lightness illusions**. In *The Cognitive Neurosciences*. Edited by Gazzaniga M. Cambridge, MA: MIT Press; in press.
5. Gilchrist A, Kossyfidis C, Bonato F, Agostini T, Cataliotti J, Li X, Spehar B, Annan V, Economou E: **An anchoring theory of lightness perception**. *Psychol Rev* 1999, **106**:795-834.

6. Logvinenko AD: **Lightness induction revisited.** *Perception* 1999, **28**:803-816.
7. Williams SM, McCoy AN, Purves D: **The influence of depicted illumination on brightness.** *Proc Natl Acad Sci USA* 1998, **95**:13296-13300.
8. Purves D, Shimp A, Lotto RB: **An empirical explanation of the Cornsweet effect.** *J Neurosci* 1999, **19**:8542-8551.
9. Bloj MG, Kersten D, Hurlbert AC: **Perception of three-dimensional shape influences colour perception through mutual illumination.** *Nature*, in press.
10. Lotto RB, Purves D: **The effects of color on brightness.** *Nat Neurosci* 1999, **2**:1010-1014.
11. Adelson EH: **Perceptual organization and the judgement of brightness.** *Science* 1993, **262**:2042-2044.
12. Nakayama K, Shimojo S: **Experiencing and perceiving visual surfaces.** *Science* 1992, **257**:1357-1363.
13. von Helmholtz H: *Treatise on Physiological Optics vol. 2 (from the Third German Edition, vols 1-3).* Menasha, Wisconsin: George Banta; 1924.
14. Mach E: *The Analysis of Sensations*, New York: Dover; 1959.
15. Knill DC, Kersten D: **Apparent surface curvature affects lightness perception.** *Nature* 1991, **351**:228-230.
16. Gilchrist AL: **When does perceived lightness depend on perceived spatial arrangement?** *Percept Psych* 1981, **28**:527-538.
17. Ramachandran VS: **Perception of shape from shading.** *Nature* 1988, **331**:163-166.
18. Todd JT, Mingolla E: **Perception of surface curvature and direction of illumination from patterns of shading.** *J Exp Psychol: Hum Percept Perform* 1983, **9**:583-595.
19. Agostini T, Proffitt DR: **Perceptual organization evokes simultaneous lightness contrast.** *Perception* 1993, **22**:263-272.
20. Todorovic D: **Lightness and junctions.** *Perception* 1997, **26**:379-394.
21. Rossi AF, Rittenhouse CD, Paradiso MA: **The representation of brightness in primary visual cortex.** *Science* 1996, **273**:1391-1398.
22. Rossi AF, Paradiso MA: **Neural correlates of perceived brightness in the retina, lateral geniculate nucleus, and striate cortex.** *J Neurosci* 1999, **19**:6145-6156.
23. Hung CP, Ramsden BM, Chen LM, Roe AW: **Edge-induced brightness perception studied through the Cornsweet illusion in visual cortex.** *Invest Ophthalmol Vis Sci* 1999, **40**:S640.
24. Kingdom F: **Old wine in new bottles? Some thoughts on Logvinenko's 'Lightness induction revisited'.** *Perception* 1999, **28**:929-934.
25. Tomita H, Ohbayashi M, Nakahara K, Hasegawa I, Miyashita Y: **Top-down signal from prefrontal cortex in executive control of memory retrieval.** *Nature* 1999, **401**:699-703.
26. Salzman CD, Britten KH, Newsome WT: **Cortical microstimulation influences perceptual judgements of motion direction.** *Nature* 1990, **346**:174-177.
27. Grossberg S: **Cortical dynamics of three-dimensional form, color and brightness perception: I. Monocular theory.** *Percept Psychophys* 1987, **41**:87-116.
28. Pessoa L, Mingolla E, Neumann H: **A contrast- and luminance-driven multiscale network model of brightness perception.** *Vision Res* 1995, **35**:2201-2223.
29. Kingdom F, Moulden B: **A multi-channel approach to brightness coding.** *Vision Res* 1992, **32**:1565-1582.
30. Land EH, McCann JJ: **Lightness and retinex theory.** *J Opt Soc Am* 1971, **61**:1-11.
31. Todorovic D: **The Craik-O'Brien-Cornsweet effect: new varieties and their theoretical implications.** *Percept Psychophys* 1987, **42**:545-560.
32. Adelson EH, Pentland AP: **The perception of shading and reflectance.** In *Perception as Bayesian Inference*. Edited by Knill D, Richards W. New York: Cambridge University Press; 1996:409-423.

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