## References

1. Grosberg, R.K. (1988). The evolution of allorecognition specificity in colonial invertebrates. Quart. Rev. Biol. 63, 377-412.
2. Hildemann, W.H. (1979). Immunocompetence and allogeneic polymorphism among invertebrates. Transplantation 27, 1-3.
3. Burnet, F.M. (1971). 'Self-recognition' in colonial marine forms and flowering plants in relation to the evolution of immunity. Nature 232, 230-235.
4. Khalturin, K., and Bosch, T.C. (2007). Self/ nonself discrimination at the basis of chordate evolution: limits on molecular conservation. Curr. Opin. Immunol. 19, 4-9.
5. Boehm, T. (2006). Quality control in self/nonself discrimination. Cell 125, 845-858.
6. Nicotra, M.L., Powell, A.E., Rosengarten, R.D., Moreno, M., Grimwood, J., Lakkis, F.G., Dellaporta, S.L., and Buss, L.W. (2009). A hypervariable invertebrate allodterminant. Curr. Biol. 19, 583-589.
7. Mokady, O., and Buss, L.W. (1996). Transmission genetics of allorecognition in Hydractinia symbiolongicarpus (Cnidaria:Hydrozoa). Genetics 143, 823-827.
8. Powell, A.E., Nicotra, M.L., Moreno, M.A., Lakkis, F.G., Dellaporta, S.L., and Buss, L.W. (2007). Differential effect of allorecognition loci on phenotype in Hydractinia symbiolongicarpus (Cnidaria: Hydrozoa). Genetics 177, 2101-2107.
9. Cadavid, L.F., Powell, A.E., Nicotra, M.L., Moreno, M., and Buss, L.W. (2004). An invertebrate histocompatibility complex. Genetics 167, 357-365.
10. Borghans, J.A., Beltman, J.B., and De Boer, R.J. (2004). MHC polymorphism under host-pathogen coevolution. Immunogenetics 55, 732-739.
11. Trowsdale, J. (2001). Genetic and functional relationships between MHC and NK receptor genes. Immunity 15, 363-374.
12. Buss, L.W. (1982). Somatic cell parasitism and the evolution of somatic tissue compatibility. Proc. Natl. Acad. Sci. USA 79, 5337-5341.
13. Scofield, V.L., Schlumpberger, J.M., West, L.A., and Weissman, I.L. (1982). Protochordate allorecognition is controlled by a MHC-like gene system. Nature 295, 499-502.
14. Grosberg, R.K., Levitan, D.R., and Cameron, B.B. (1996). Evolutionary genetics of allorecognition in the colonial hydroid Hydractinia symbiolongicarpus. Evolution 50, 2221-2240.
15. Kuznetsov, S.G., and Bosch, T.C. (2003). Self/ nonself recognition in Cnidaria: contact to allogeneic tissue does not result in elimination of nonself cells in Hydra vulgaris. Zoology (Jena) 106, 109-116.
16. Bigger, C.H. (1988). Historecognition and immunocompetence in selected marine invertebrates. In Invertebrate Historecognition,
R.K. Grosberg, D. Hedgecock, and K. Nelson, eds. (New York: Plenum Press), pp. 55-65.
17. Rinkevich, B. (2004). Allorecognition and xenorecognition in reef corals: a decade of interactions. Hydrobiologia 530/531, 443-450.
18. De Tomaso, A.W., Nyholm, S.V., Palmeri, K.J., Ishizuka, K.J., Ludington, W.B., Mitchel, K., and Weissman, I.L. (2005). Isolation and characterization of a protochordate histocompatibility locus. Nature 438, 454-459.
19. Litman, G.W., Cannon, J.P., and Dishaw, L.J. (2005). Reconstructing immune phylogeny: new perspectives. Nat. Rev. Immunol. 5, 866-879.
20. Bosch, T.C., Augustin, R., Anton-Erxleben, F., Fraune, S., Hemmrich, G., Zill, H., Rosenstiel, P., Jacobs, G., Schreiber, S., Leippe, M., et al. (2009). Uncovering the evolutionary history of innate immunity: the simple metazoan Hydra uses epithelial cells for host defence. Dev. Comp. Immunol. 33, 559-569.

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# Color Vision: Appearance Is a ManyLayered Thing 

The color of a surface changes when it is surrounded by other colors. A new illusion shows these changes are much stronger when seen through other colors as transparency, suggesting the brain parses the causes of color into separate layers.

## Michael A. Webster

Compared to some feats of our vision - like recognizing the same object from different angles or spotting an old face in a new crowd - the ability to judge the color or brightness of a spot may seem like a simple feat. Yet the ease with which we recognize colors is deceptive. A new color illusion reported recently in Current Biology [1] adds another dramatic illustration that how we experience colors depends on many sophisticated steps designed to reveal the causal structure of the world.

Information about color is carried by the wavelengths emanating from illuminants and reflected from objects. But if there is a mantra for color scientists it is that color is not a property of the light. The same light can look completely different in hue or brightness depending on the context in which it is viewed. A major focus of color science is to understand these contextual cues - how they are processed in the
visual system and what they imply about the physical information that color percepts represent [2,3].
One ongoing problem has been to understand how the visual system can perceive the reflectance of the object separately from the spectrum of the illuminant [4]. These two factors are confounded in the wavelengths reaching the eye from each point in the scene, and they can only be decomposed by considering different points or the scene geometry. It has long been known that we can bias the color and brightness of a spot by changing the surrounding area, though for uniform surrounds the effects are often subtle. But when even subtle changes are instead made to the layout of the scene, then the perceived color and brightness shifts can be striking [5-10]. The bases for these contextual effects are not always certain, and may include visual computations ranging from 'low-level' filtering to 'high-level' inferences about the three-dimensional
geometry and lighting. Moreover, the effects of context are not unique to color, and strongly influence many perceptual judgments [11].

In the new study by Wollschlaeger and Anderson [1], color appearance is manipulated by adding cues that cause the target to be perceived through a partially transparent filter (Figure 1). This generalizes recent work by Anderson and Winawer $[12,13]$ with grayscale images, and suggests that common principles are involved for both lightness and color. The perception of transparency has been widely studied and is not as rare in viewing as one might think, for it is closely related to seeing through cast shadows, and may blend seamlessly with occlusion [13], where a surface completely screens the objects behind it. Even in occlusion there is evidence that the visual system works from a representation of the hidden surfaces [14,15]. Thus it is plausible that in transparency we decompose the color and lightness at a single point into separate 'layers' that can represent different surfaces and illuminants.

These layered percepts are accentuated in the new work by a clever twist - the opacity of the transparent layer is not uniform, but instead varies continuously across the image. According to the authors [1], this leads to strong induction effects
because the target's color is attributed to the area that differs most from the surround, where the inferred transparency is weakest. The resulting hue shifts are much larger than conventional induction effects, surpassing even the theoretical optimum of many models where the shift corresponds to completely neutralizing the surround color. It would be wrong, however, to think that perception is more or less veridical in either case; rather, the work shows that, as different cues are added, the visual system can draw on these to reinterpret the scene.

At a theoretical level, these transparency effects are important because they more firmly reveal cases where the visual system appears to form separate representations of lights and surfaces and the media through which we view them. An alternative to this interpretation has been framework models, where surface reflectance is instead estimated within local regions of common lighting or shadow [5,16]. This can also account for many lightness illusions, but differs from layering because the illumination is not explicitly modeled and lightnesses are anchored by the brightest local element. In the layered account this anchoring is instead assumed to depend on the image region that is least occluded and thus in 'plain view'. Wollschlaeger and Anderson [1] demonstrate the importance of layering for their effects by showing that the degree of induction depends on whether the color relationships support the perception of transparency, while leaving factors like the spatial structure and colors intact. As the authors note, however, this does not preclude a role of other processes, nor is it likely to quell the intense interest and debate about the primary mechanisms of lightness and color perception.
The idea that we can explicitly encode different causal components of the color at each point in the scene is also suggested by how we experience these colors. Studies of color constancy have emphasized that there can be multiple simultaneous modes of appearance [4,17]. For example, for the same stimulus an observer can make very different judgments about whether two surfaces have the same hue or whether they were cut from the same piece of cloth, and thus the degree of constancy and contextual effects depends importantly on what you are


Figure 1. A variant of the new color induction effects [1].
Identical squares appear different in color when placed in surrounds with different mean colors. The study shows that these effects are much stronger when the squares appear to be viewed through a transparent colored medium (top) than when the same average colors are shown in the conventional induction stimulus as uniform fields (bottom).
asking the observer to do. These varying interpretations of the same stimulus seem to parallel the notion that we can draw on separate representations of the sources of color, and raise the question of how modes of appearance might map on to layering or to other potential mechanisms influencing appearance.

Even if we solve how the visual system disentangles the causes of color, we are still left with the separate problem of why a surface appears a particular color. A flat or unbiased spectrum (in a spectrally flat surround) looks gray, and this 'colorless' percept makes sense as a model of the stimulus. Yet how we are able to perceive gray (let alone different hues) is not trivial, for there are many additional layers of filtering within the
observer. These include the screening pigments in the lens and macular region of the retina, which both tend to block shorter wavelengths from reaching the receptors. To correctly represent the object's color, the visual system must again take into account these filtering effects - otherwise color appearance would change markedly as we age or even when we shifted our gaze $[18,19]$. The neural computations that correct for the observer may share many of the processes that correct for the scene. In the former case, however, we are not left with a separate layer of experience corresponding to our own eyes. Just as we fill in the picture at our blind spot to represent the scene [20], there is similarly little to be gained by sensing the limits of our spectral sensitivity, and
the colors we see are instead our best guess in spite of these limits about the world outside us.

## References

1. Wollschlaeger, D., and Anderson, B.L. (2009). The role of layered scene representations in color appearance. Curr. Biol. 19, 430-435.
2. Kingdom, F.A.A. (2008). Perceiving light versus material. Vision Res. 48, 2090-2105.
3. Shevell, S.K., and Kingdom, F.A.A. (2008). Color in complex scenes. Annu. Rev. Psychol. 59, 143-166.
4. Smithson, H.E. (2005). Sensory, computational and cognitive components of human colour constancy. Phil. Trans. R. Soc. B 360, 1329-1346.
5. Adelson, E.H. (1999). Lightness perception and lightness illusions. In The New Cognitive Neurosciences, M. Gazzaniga, ed. (Cambridge, MA: MIT Press), pp. 339-351.
6. Bloj, M., Kersten, D., and Hurlbert, A. (1999). Perception of three-dimensional shape influences colour perception through mutual illumination. Nature 402, 877-879.
7. Gilchrist, A.L. (1977). Perceived lightness depends on perceived spatial arrangement Science 195, 185-187.
8. Knill, D.C., and Kersten, D. (1991). Apparent surface curvature affects lightness perception. Nature 351, 228-230.
9. Monnier, P., and Shevell, S.K. (2003). Large shifts in color appearance from patterned chromatic backgrounds. Nat. Neurosci. 6, 801-802.
10. Pinna, B., Brelstaff, G., and Spillmann, L. (2001). Surface color from boundaries: a new 'watercolor' illusion. Vision Res. 41, 2669-2776.
11. Schwartz, O., Hsu, A., and Dayan, P. (2007). Space and time in visual context. Nat. Rev. Neurosci. 8, 522-535
12. Anderson, B.L., and Winawer, J. (2005). Image segmentation and lightness perception. Nature 434, 79-83.
13. Anderson, B.L., and Winawer, J. (2008). Layered image representations and the computation of surface lightness. J. Vision 8 , 1-22.
14. Gold, J.M., Murray, R.F., Bennett, P.J., and Sekuler, A.B. (2000). Deriving behavioral receptive fields for visually completed contours. Curr. Biol. 10, 663-666.
15. He, Z.J., and Nakayama, K. (1992). Surfaces versus features in visual search. Nature 359, 231-233.
16. Gilchrist, A.L., Kossyfidis, C., Bonato, F., Agostini, T., Cataliotti, J., Li, X., Spehar, B., Annan, V., and Economou, E. (1999). An anchoring theory of lightness perception. Psychol. Rev. 106, 795-834.
17. Reeves, A.J., Amano, K., and Foster, D.H. (2008). Color constancy: phenomenal or projective? Percept. Psychophys. 70, 219-228.
18. Webster, M.A., and Leonard, D. (2008). Adaptation and perceptual norms in color vision. J. Opt. Soc. Am. A 25, 2721-2733.
19. Werner, J.S., and Schefrin, B.E. (1993). Loci of achromatic points throughout the life span. J. Opt. Soc. Am. A 10, 1509-1516.
20. Ramachandran, V. (1992). Filling in the blind spot. Nature 356, 115.

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# Meiotic Spindle Self-Organization: One Plus One Equals Only One 

Like other cellular organelles, the bipolar spindle is a structure of well-defined size and shape. Now, spindle fusion experiments using micro-manipulation have allowed current models for spindle morphogenesis and size control to be tested.

## Radhika Subramanian and Tarun Kapoor*

The assembly of a microtubule-based bipolar spindle is required for accurate partitioning of chromosomes to daughter cells [1]. The size and shape of this structure shows little variability within a particular cell type [2]. Although the bipolar spindle is maintained for many minutes during cell division, the microtubules that provide the mechanical framework turn over on much faster timescales $[3,4]$. How spindle size and shape is maintained while its constituents undergo rapid dynamics is not yet fully understood and remains an area of intense research.
In general, there appear to be at least two classes of mechanisms that account for size control of cellular organelles: competing assembly and disassembly processes with at least one of these being length dependent or, alternatively, length control by molecular rulers which sense and restrict organelle size [5]. In fact, the mechanisms proposed for size control
of the meiotic spindle at metaphase also fall into these two categories (Figure 1).
In the first model, spindle size is set by microtubule length and overlap control. Microtubules are dynamic polymers whose length is set by competing polymerization and depolymerization reactions at their ends. Filament length control can be achieved if the kinetics of either of these processes is modulated in a length-dependent manner. This modulation could be mediated by motor and non-motor proteins, and at least for one family of microtubuledepolymerizing kinesins, kinesin-8, microtubule length-dependent activity has been demonstrated in vitro [6]. Similarly, end-to-end distance between cross-linked microtubules can be increased by antiparallel sliding by motor proteins such as kinesin-5. Resistance to this sliding by other proteins, with either one of the opposing forces being proportional to the extent of microtubule overlap, may also help set spindle size. In the second class of models, signaling gradients
emanating from the chromosomes can act as a molecular ruler to determine the size and shape of the spindle by controlling microtubule dynamics spatially. In particular, the observed concentration gradient of Ran-GTP could result in preferential microtubule stabilization near chromosomes to maintain spindle size [7,8]. Another possible molecular ruler could be the spindle matrix. The spindle matrix is proposed to be a structure with slower dynamics than microtubules and can act as a scaffold for spindle assembly and maintenance [9,10]. In this model, spindle size and shape is determined by the matrix.

In a recent issue of Current Biology, Gatlin et al. [11] examined spindle self-organization. In an interesting set of experiments, the authors used micro-manipulation to perturb a spindle at metaphase by moving a second spindle, in specific orientations, into close proximity. They observe that on the timescale of several minutes, fusion of the two spindles results in one spindle that is almost the same size as either of the unperturbed spindles. Furthermore, fusion was not dependent on the initial orientations of the two spindles. When spindles were held in parallel orientations, they fused by sliding and then joining at the poles, resulting in a bipolar spindle.
Remarkably, even a spindle initially oriented perpendicular to a second spindle rotated to achieve a parallel orientation and then fused to form

