

and Eastern Africa “are likely to outweigh the magnitude of any likely declines in the other two regions” [19]. It fails to mention that growing Southern and Eastern African populations of savanna elephants belong to a species that is as divergent from the Central and West African forest elephant populations being decimated as woolly mammoths were from Asian elephants [1,2,14]. Will the IUCN continue to turn a blind eye as an elephant species in the tropical forests of West and Central Africa follows the woolly mammoth to extinction?

**REFERENCES**

- Brandt, A.L., Ishida, Y., Georgiadis, N.J., and Roca, A.L. (2012). Forest elephant mitochondrial genomes reveal that elephantid diversification in Africa tracked climate transitions. *Mol. Ecol.* *21*, 1175–1189.
- Rohland, N., Reich, D., Mallick, S., Meyer, M., Green, R.E., Georgiadis, N.J., Roca, A.L., and Hofreiter, M. (2010). Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. *PLoS Biol.* *8*, e1000564.
- Lister, A., and Bahn, P.G. (2007). *Mammoths: Giants of the Ice Age*. Rev. Edition. (Berkeley, Calif: University of California Press).
- Barnes, I., Shapiro, B., Lister, A., Kuznetsova, T., Sher, A., Guthrie, D., and Thomas, M.G. (2007). Genetic structure and extinction of the woolly mammoth, *Mammuthus primigenius*. *Curr. Biol.* *17*, 1072–1075.
- Gilbert, M.T., Drautz, D.I., Lesk, A.M., Ho, S.Y., Qi, J., Ratan, A., Hsu, C.H., Sher, A., Dalen, L., Gotherstrom, A., et al. (2008). Intraspecific phylogenetic analysis of Siberian woolly mammoths using complete mitochondrial genomes. *Proc. Natl. Acad. Sci. USA* *105*, 8327–8332.
- Miller, W., Drautz, D.I., Ratan, A., Pusey, B., Qi, J., Lesk, A.M., Tomsho, L.P., Packard, M.D., Zhao, F., Sher, A., et al. (2008). Sequencing the nuclear genome of the extinct woolly mammoth. *Nature* *456*, 387–390.
- Palkopoulou, E., Dalen, L., Lister, A.M., Vartanyan, S., Sablin, M., Sher, A., Edmark, V.N., Brandstrom, M.D., Germonpre, M., Barnes, I., et al. (2013). Holarctic genetic structure and range dynamics in the woolly mammoth. *Proc. Biol. Sci.* *280*, 20131910.
- Debruyne, R., Chu, G., King, C.E., Bos, K., Kuch, M., Schwarz, C., Szpak, P., Grocke, D.R., Matheus, P., Zazula, G., et al. (2008). Out of America: ancient DNA evidence for a new world origin of late quaternary woolly mammoths. *Curr. Biol.* *18*, 1320–1326.
- Palkopoulou, E., Mallick, S., Skoglund, P., Enk, J., Rohland, N., Li, H., Omrak, A., Vartanyan, S., Poinar, H., Gotherstrom, A., et al. (2015). Complete genomes reveal signatures of demographic and genetic declines in the woolly mammoth. *Curr. Biol.* *25*, 1395–1400.
- Li, H., and Durbin, R. (2011). Inference of human population history from individual whole-genome sequences. *Nature* *475*, 493–496.
- Nogues-Bravo, D., Rodriguez, J., Hortal, J., Batra, P., and Araujo, M.B. (2008). Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biol.* *6*, 685–692.
- Nystrom, V., Dalen, L., Vartanyan, S., Liden, K., Ryman, N., and Angerbjorn, A. (2010). Temporal genetic change in the last remaining population of woolly mammoth. *Proc. R. Soc. B. Biol. Sci.* *277*, 2331–2337.
- Thomas, M.G. (2012). The flickering genes of the last mammoths. *Mol. Ecol.* *21*, 3379–3381.
- Roca, A.L., Ishida, Y., Brandt, A.L., Benjamin, N.R., Zhao, K., and Georgiadis, N.J. (2015). Elephant natural history: a genomic perspective. *Annu. Rev. Anim. Biosci.* *3*, 139–167.
- Roca, A.L., Georgiadis, N., and O’Brien, S.J. (2005). Cytonuclear genomic dissociation in African elephant species. *Nat. Genet.* *37*, 96–100.
- Petit, R.J., and Excoffier, L. (2009). Gene flow and species delimitation. *Trends Ecol. Evol.* *24*, 386–393.
- Hedrick, P.W. (2007). Sex: differences in mutation, recombination, selection, gene flow, and genetic drift. *Evolution* *61*, 2750–2771.
- Grubb, P., Groves, C.P., Dudley, J.P., and Shoshani, J. (2000). Living African elephants belong to two species: *Loxodonta africana* (Blumenbach, 1797) and *Loxodonta cyclotis* (Matschie, 1900). *Elephant* *2*, 1–4.
- IUCN (2015). *Loxodonta africana* (African elephant). In *The IUCN Red List of Threatened Species*, Version 2014.3. Downloaded on 29 April 2015.
- Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A., Aba’a, R., Abitsi, G., Ambahe, R.D., Amsini, F., et al. (2013). Devastating decline of forest elephants in Central Africa. *PLoS One* *8*, e59469.

## Colour Vision: Understanding #TheDress

David H. Brainard<sup>1,\*</sup> and Anya C. Hurlbert<sup>2,\*</sup>

<sup>1</sup>Department of Psychology, University of Pennsylvania, 3401 Walnut Street, Philadelphia, PA 19104, USA

<sup>2</sup>Institute of Neuroscience, Framlington Place, Newcastle University, Newcastle upon Tyne, NE2 4HH, UK

\*Correspondence: brainard@psych.upenn.edu (D.H.B.), anya.hurlbert@ncl.ac.uk (A.C.H.)

<http://dx.doi.org/10.1016/j.cub.2015.05.020>

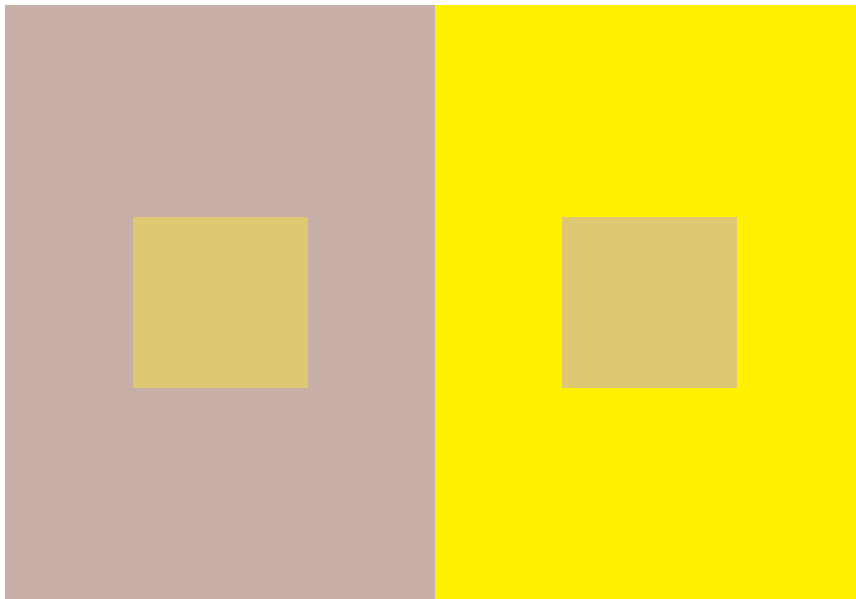
**A widely-viewed image of a dress elicits striking individual variation in colour perception. Experiments with multiple variants of the image suggest that the individual differences may arise through the action of visual mechanisms that normally stabilise object colour.**

At the end of February 2015, a photograph of a dress went viral on the internet. Around the world, people disagreed on its colour: some said it was “blue and black” while others insisted on “white and gold”. The strident dispute aroused a media frenzy. To the general

public, it seemed a revelation that perception is subjective, and that what we see need not match objective reality. To the vision science community, #thedress presented the challenge of how to explain the individual differences. Three short communications [1–3] in this issue of

*Current Biology* now confirm the variation in reported dress colours and explore ways to modulate it. The authors of these communications suggest that the individual differences in colour perception elicited by the dress may originate with the action of visual mechanisms that





Current Biology

**Figure 1. The dependence of colour on context: simultaneous chromatic contrast.**

The central square is physically the same on the two halves of the figure, but differs in colour appearance because of the surrounding context.

normally serve to stabilise the colours of objects.

Many illusions illustrate the subjective nature of perceived colour as well as the fact that colour depends on the context in which a stimulus is viewed. Yet these colour illusions tend to evoke the same response in everyone. For example, almost all agree on the change in colour of the central squares in [Figure 1](#) across the change in background. The striking feature of the dress is that different people see the same image but report such different colours. Although there are well-documented sources of individual differences in how colours are named [\[4\]](#) and matched [\[5\]](#), none obviously explains the range of percepts experienced for the dress image.

The communications [\[1–3\]](#) document and begin to characterize the variety of perceptions evoked by the dress, and provide some initial clues as to what makes this image special. As a prerequisite for further study, they bring the phenomenon into the lab and rule out the possibility that the initial excitement was generated simply by physical changes in how the image was displayed on different peoples' devices. For example, Lafer-Sousa *et al.*'s [\[2\]](#) laboratory test of 53 people, using a single calibrated monitor, replicated the

essential features of the online experiment they performed with 1401 people.

In addition, the effects are not simply a matter of language. When subjects adjust an isolated patch to match what they see in the dress, large individual variation persists [\[1,2\]](#). Moreover, matches made to the dress are generally consistent with the colour terms used to describe it. People who match the dress body to lighter, paler blues tend to name it as “white”; those who match it to darker, deeper blues tend to name it as “blue”. These observations rule out explanations based solely on differences in how people deploy colour names. (Note that here we use the terms blue, yellow, white, warm and cool as short-hand for accurate colorimetric descriptions.)

So, what causes the individual variability? The authors of all three communications [\[1–3\]](#) invoke explanations related to a central feature of human colour vision: colour constancy [\[6,7\]](#). In real life, we often use colour to identify and name properties of objects: “the red apple”, “my blue car”. Yet, the light reflected to the eye from an object depends on both the intrinsic reflectance properties of the object, which are constant, and on the illumination spectrum, which is variable over space and time. Thus, an unchanging object under changing illumination will

send a varying and hence ambiguous light signal to the eye. In most cases, the brain resolves this fundamental ambiguity and people perceive objects as having a stable colour related to their surface reflectance. Without some degree of colour constancy, it would not even make sense to speak of objects as having an intrinsic colour.

A plausible explanation for the differences in dress colour is that the dress image is a stimulus that breaks through the brain's mechanisms of colour constancy. The idea is that different brains cope differently with the colour constancy challenge, latching onto different cues to the illumination or bringing different prior assumptions to bear. People who correct — unconsciously — for a cool illumination see the dress in the image as “white” and for the same reason see the lace as “gold”. People who correct — again unconsciously — for a warm illumination see the dress as “blue” and “black” ([Figure 2](#)). The basic logic of this explanation is demonstrated by embedding the dress image into a larger context designed to make the illumination less ambiguous, as Lafer-Sousa *et al.* show [\[2\]](#) (see their [Figure S2](#)). When the cues to the illumination are enhanced in this way, people agree more and their colour judgments are consistent with the intended bias in cues to the illumination.

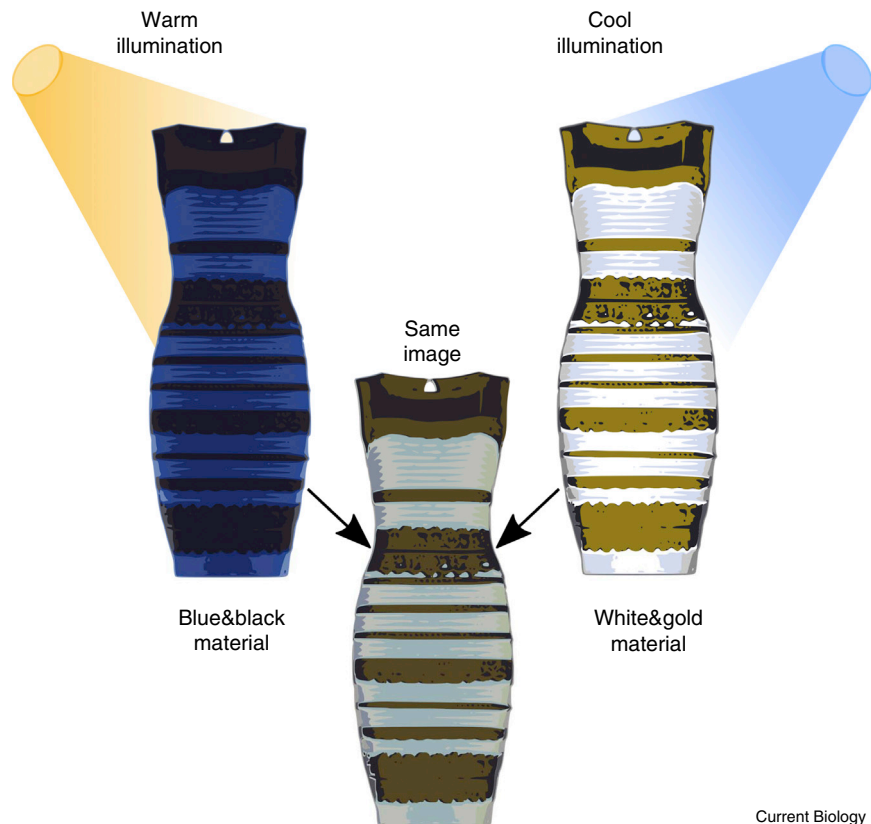
Yet, even if correct, the colour constancy explanation in itself does not tell us why this particular image — a partially-overexposed, slightly blurry photograph of a dress — should expose such individual differences in the operation of colour constancy. On this point, all three studies note that the RGB values in the dress image vary mainly along a blue–yellow axis in colour space, the same axis that describes the variation of natural daylight. The importance of this observation is evidenced by data showing that the ambiguity of the dress colour is reduced when the blue–yellow variation in RGB values is altered [\[1,3\]](#). When the values are shifted systematically away from the daylight locus, around the hue circle, so that the bluish values become pinkish and the yellowish values become greenish, the dress body is seen consistently as “pink” or “red”, and the lace trim as “green” [\[1\]](#). More surprisingly, perhaps, when the values are

inverted — so that blues become yellow, and yellows become blue — the dress body appears “yellow”. Even when the chromatic contrast of the yellow is reduced to near-grey, no one sees it as “white” [3].

If the brain’s mechanisms of constancy have internalized the blue–yellow regularity of daylight variation, there might be something especially ambiguous about images whose RGB values vary primarily in this way. For example, such images might evoke a response shaped more than usual by implicit prior expectations about illumination spectra [1,2], which in turn might vary across individuals. In support of this notion, previous studies have shown that the stimuli people see as “white” vary largely along the same blue–yellow axis [8,9]. Whether this variation in what is seen as “white” predicts variation in the perception of the dress colours, though, awaits investigation.

A slightly different tack towards constancy is taken by Winkler *et al.* [3], who demonstrate that subjects are more likely to name as “white” uniform patches displaced in a bluish direction in colour space, compared to patches of equivalent chromatic contrast but displaced in yellowish, reddish, or greenish colour directions. The authors connect this observation with perceptual demonstrations suggesting that, all else equal, people tend to interpret bluish variation in an image as due to the illumination (see Figure 1 in [3]). Other measures of colour constancy also indicate a bias in favour of bluish illuminations [10]. Left unexplained, nonetheless, is why such a bias would generate individual differences. Indeed, caution is especially warranted because the individual variation in “white” naming of simple patches did not correlate with individual variation in how the dress image was perceived [3].

Although the hypothesis that individual differences in colour constancy cause large individual differences in the perception of the dress is attractive, the present communications [1–3] by no means prove it. First, the fact that the pixel colours of the dress vary along a blue–yellow axis cannot be the entire explanation of what makes the dress special; there is no reason to think that every image whose pixels vary in this general way would elicit large individual



Current Biology

**Figure 2. The colour constancy explanation for #thedress.**

The image formed on the retina by the dress photograph might, in the actual scene, have arisen from a dress consisting of blue and black material under warm illumination (left) or of white and gold material under cool illumination (right). The colour constancy explanation for the different perceptions of the dress suggests that cues to the illumination in the dress image are unusually ambiguous, and lead to different people unconsciously correcting for different illuminations, in turn evoking different colour percepts. (Acknowledgment to co-illustrator Bradley Pearce.)

differences. Nor is it immediately clear that images that vary in this way are fundamentally more ambiguous about the illumination — confirmation of this idea awaits a careful computational analysis that accounts for not only the statistics of natural variation in illumination variation but also the variation in naturally occurring surface reflectances. We suspect that other aspects, perhaps the spatial structure of the dress image, also play an important role. For example, the warm highlights on the lace trim may be variously interpreted as due to the surface reflectance of the lace or as specular highlights related to the illumination — it is known that under some circumstances specular highlights are taken by the visual system as a cue to the illumination [7,11–12].

Also unresolved under the colour constancy explanation is which factors that vary across people cause individual

differences in colour constancy, both in general and specifically for the dress. There are, in fact, a number of well-documented individual differences in the sensory apparatus that supports colour vision (reviewed in [13,14]). These include differences in pre-retinal filtering of light (for example, by the lens and macular pigment) — which, intriguingly, mostly affect short-wavelength or “bluish” light — differences in the spectral sensitivities of the retina’s cone photoreceptors, and differences in the relative numbers of cones of different classes. This type of front-end difference affects the information extracted from an image by different individuals, and might thus lead to differences in colour constancy. Other individual differences that can be revealed with much simpler stimuli may also be important. For example, as noted above, the stimulus seen as achromatic differs from one

person to another, as do the stimuli that are perceived as pure examples of the unique hues (red, green, blue, and yellow) [15]. These differences themselves may be driven by front-end sensory differences, by differences in neural mechanisms that calibrate the colour vision system [16,17], or by an interaction between the two. Lastly, there might be individual differences in higher-order neural processes that specifically mediate colour constancy. A full understanding of the individual differences in how the dress is perceived will ultimately require data that relate, on a person-by-person basis, the perception of the dress to a full set of individual difference measurements of colour vision. The rich dataset of Lafer-Sousa *et al.* [2] suggests that age and gender do predict, to some extent, the variability in people's response to the dress. Intriguingly, the density of pre-retinal pigments is also known to vary systematically with age.

So in the end, these initial studies [1–3] of the dress raise at least as many questions as they answer. We now must ask not only why do people give different colour names to the dress, but why do they make such different matches when asked to replicate its colour? What, exactly, about the dress image is crucial for producing individual differences and how do these features of the image interact with known individual differences in colour vision? Is the colour constancy hypothesis about the dress correct, and if so does prior experience or familiarity with object surface properties (spectral reflectance and material) play any role, or does the brain embed expectations about the illumination only? The one certainty is that vision scientists have rarely deliberately devised such a powerful stimulus for studying individual differences in colour perception, much less encountered one accidentally. The generation of experiments it spawns will reveal much about how the brain works, both in making colours and in making science.

## REFERENCES

- Gegenfurtner, K.R., Bloj, M., and Toscani, M. (2015). The many colours of 'the dress'. *Curr. Biol.* 25, R543–R544.
- Lafer-Sousa, R., Hermann, K.L., and Conway, B.R. (2015). Striking individual differences in color perception uncovered by 'the dress' photograph. *Curr. Biol.* 25, R545–R546.
- Winkler, A., Spillmann, L., Werner, J.S., and Webster, M.A. (2015). Asymmetries in blue–yellow color perception and the color of 'the dress'. *Curr. Biol.* 25, R547–R548.
- Webster, M.A., and Kay, P. (2007). Individual and population differences in focal colors. In *Anthropology of Color: Interdisciplinary Multilevel Modeling*, R.E. MacLauray, G.V. Paramei, and D. Dedrick, eds. (Amsterdam/Philadelphia: John Benjamins Publishing).
- Bloj, M., Kersten, D., and Hurlbert, A.C. (1999). Perception of three-dimensional shape influences colour perception through mutual illumination. *Nature* 402, 877–879.
- Brainard, D.H., and Radonjić, A. (2014). Color constancy. In *The New Visual Neurosciences*, L.M. Chalupa, and J.S. Werner, eds. (Cambridge, MA: MIT Press), pp. 545–556.
- Hurlbert, A.C. (1998). Computational models of color constancy. In *Perceptual Constancy: Why Things Look As They Do* (Cambridge: Cambridge University Press), pp. 283–322.
- Chauhan, T., Perales, E., Xiao, K., Hird, E., Karatzas, D., and Wuerger, S. (2014). The achromatic locus: Effect of navigation direction in color space. *J. Vis.* 14, 1–11.
- Witzel, C., Valkova, H., Hansen, T., and Gegenfurtner, K.R. (2011). Object knowledge modulates colour appearance. *i-Perception* 2, 13–49.
- Pearce, B., Crichton, S., Mackiewicz, M., Finlayson, G.D., and Hurlbert, A. (2014). Chromatic illumination discrimination ability reveals that human colour constancy is optimised for blue daylight illuminations. *PLoS One* 9, e87989.
- Yang, J.N., and Maloney, L.T. (2001). Illuminant cues in surface color perception: tests of three candidate cues. *Vis. Res.* 41, 2581–2600.
- Xiao, B., Hurst, B., MacIntyre, L., and Brainard, D.H. (2012). The color constancy of three-dimensional objects. *J. Vis.* 12, 6.
- Brainard, D.H., and Stockman, A. (2010). Colorimetry. In *The Optical Society of America Handbook of Optics*, 3rd edition, *Volume III: Vision and Vision Optics*, M. Bass, C. DeCusatis, J. Enoch, V. Lakshminarayanan, G. Li, C. Macdonald, V. Mahajan, and E. van Stryland, eds. (New York: McGraw Hill), pp. 10.11–10.56.
- Hofer, H.J., and Williams, D.R. (2014). Color vision and the retinal mosaic. In *The New Visual Neurosciences*, L.M. Chalupa, and J.S. Werner, eds. (Cambridge, MA: MIT Press), pp. 469–483.
- Webster, M.A., Miyahara, E., Malkoc, G., and Raker, V.E. (2000). Variations in normal color vision. II. Unique hues. *J. Opt. Soc. Am. A* 17, 1545–1555.
- Brainard, D.H., Roorda, A., Yamauchi, Y., Calderone, J.B., Metha, A., Neitz, M., Neitz, J., Williams, D.R., and Jacobs, G.H. (2000). Functional consequences of the relative numbers of L and M cones. *J. Opt. Soc. Am. A* 17, 607–614.
- Neitz, J., Carroll, J., Yamauchi, Y., Neitz, M., and Williams, D.R. (2002). Color perception is mediated by a plastic neural mechanism that is adjustable in adults. *Neuron* 35, 783–792.

## Cell Division: A New Role for the Kinetochore in Central Spindle Assembly

Tatsuo Fukagawa

Graduate School of Frontier Biosciences, Osaka University, Suita, Osaka 565-0871, Japan

Correspondence: [tfukagawa@fbs.osaka-u.ac.jp](mailto:tfukagawa@fbs.osaka-u.ac.jp)

<http://dx.doi.org/10.1016/j.cub.2015.05.016>

The central spindle, which is formed between segregating chromosomes, is a critical structure for cell division. However, it was unclear how the central spindle is assembled at anaphase onset. A recent study reveals that a conserved kinetochore protein network plays an essential role in initiation of central spindle assembly.

The central spindle forms a specific structure between segregating chromosomes during anaphase (Figure 1). It consists of microtubule bundles, which recruit several

microtubule-binding proteins and act as a hub for signaling molecules required for the progression and completion of cytokinesis [1,2]. However, as this structure does not exist during