have also played a role in the evolution of host genomic regulatory complexity. At each end of the ERV genome are long terminal repeats (LTRs), which contain regulatory sequences that can alter the expression, splicing, and polyadenylation of those host genes located near the ERV insertion site. LTRs regulate the cell type that the virus replicates in by controlling its expression, and so can be co-opted by their hosts as alternative promoters, resulting in tissue-specific expression of host genes. Often, solitary LTRs have been generated by homologous recombination between the two LTRs present in a single ERV, resulting in loss of the internal sequence. Consequently, host genomes are peppered with solo LTRs of potential regulatory significance. Intriguingly, the LTRs of an ERV in primates (HERV-H) can bind pluripotency transcription factors that lead to the expression of the retrovirus, which in turn regulates stem cell identity. Taken together, the evidence suggests that sequences sequestered from ERVs have had a considerable influence on the evolution of their vertebrate hosts. So, not only is evolution a tinkerer, but it is also a conscientious recycler.

Where can I find out more?

Aswad, A., and Katzourakis, A. (2012). Paleovirology and virally derived immunity. Trends Ecol. Evol. *27*, 627–636.

Grow, E.J., Flynn, R.A., Chavez, S.L., Bayless, N.L., Wossidlo, M., Wesche, D.J., Martin, L., Ware, C.B., Blish, C.A., Chang, H.Y., *et al.* (2015). Intrinsic retroviral reactivation in human preimplantation embryos and pluripotent cells. Nature *522,* 221–225.

Hayward, A., Cornwallis, C.K., and Jern, P. (2015). Pan-vertebrate comparative genomics unmasks retrovirus macroevolution. Proc. Natl. Acad. Sci. USA *112*, 464–469.

Hayward, A., Grabherr, M., and Jern, P. (2013). Broad scale phylogenomics provides insights into retrovirus-host evolution. Proc. Natl. Acad. Sci. USA *10*, 20146–20151.

Katzourakis, A., Gifford, R.J., Tristem, M., Gilbert, M.T.P., and Pybus, O.G. (2009). Macroevolution of complex retroviruses. Science *325*, 1512.

Katzourakis, A., Magiorkinis, G., Lim, A.G., Gupta, S., Belshaw, R., and Gifford, R. (2014). Larger mammalian body size leads to lower retroviral activity. PLoS Pathog. *10*, e1004214.

Lavialle, C., Cornelis, G., Dupressoir, A., Esnaut, C., Heidmann, O., Vernochet, C., and Heidmann, T. (2013). Paleovirology of 'syncytins', retroviral env genes exapted for a role in placentation. Phil. Trans. R. Soc. B. *368*, 20120507.

[1]Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden. [2]Department of Zoology, University of Oxford, The Tinbergen Building, South Parks Road, Oxford OX1 3PS, UK.
*E-mail: alexander.hayward@zoologi.su.se (A.H), aris.katzourakis@zoo.ox.ac.uk (A.K)

Correspondence

Human colour perception changes between seasons

Lauren E. Welbourne[1,*] Antony B. Morland[1,2], and Alex R. Wade[1]

Humans identify four 'unique hues' — blue, green, yellow and red — that do not appear to contain mixtures of other colours. Unique yellow (UY) is particularly interesting because it is stable across large populations: participants reliably set a monochromatic light to a stereotypical wavelength. Individual variability in the ratio of L- and M-cones in the retina, and effects of ageing, both impact unique *green* (UG) settings [1,2], but cannot predict the relatively small inter-individual differences in UY [2,3]. The stability of UY may arise because it is set by the environment rather than retinal physiology. Support for this idea comes from studies of long-term, artificial chromatic adaptation [4,5], but there is no evidence for this process in natural settings. Here, we measured 67 participants in York (UK) in both the winter and summer, and found a significant seasonal change in UY settings. In comparison, Rayleigh colour matches that would not be expected to exhibit environmentally driven changes were found to be constant. The seasonal shift in UY settings is consistent with a model that reweights L- and M-cone inputs into a perceptual opponent colour channel after a small, seasonally-driven change in mean L:M cone activity.

Sixty-seven participants (45 female) were tested in winter and summer (see Supplemental Information). Participants made Rayleigh matches and central and peripheral settings of UG and UY using a Wright colorimeter [6]. All measurements were made in a dark room while participants rested on a chin support. The colorimeter was recalibrated for each season with a fibre-optic photospectrometer ('Jaz', Ocean Optics, FL) operating at 2 nm resolution with a 30° integrating lens. For the Rayleigh matches, participants adjusted the radiance of red (666 nm) and green (555 nm) primaries to match a yellow reference light (585 nm), in a 1.33° x 1.33° bipartite field. Seven Rayleigh matches were averaged and converted to log(R/G) using the relative radiance of the red (R) and green (G) primaries.

For the UG and UY settings, participants adjusted a 0.67° x 1.33° monochromatic field until it was perceived as the specified unique hue, with UG appearing neither yellowish nor bluish, and UY appearing neither reddish nor greenish. Peripheral settings were obtained by fixating on a small, dim LED placed at 6.5° to the right of the stimulus, to remove any effects of macular pigment [7]. In addition, a 4 Hz square-wave flicker was applied to reduce Troxler's fading in the periphery. Participants carried out six repeats of each adjustment from randomised starting values. The first trial from each set of six was removed prior to averaging, as it was found to differ significantly from the five remaining stable trials (see Supplemental Information).

A claim, by Richter (as described in [8]), that Rayleigh matches change with season was subsequently explained by the effects of lab temperature on optical devices [8]. We therefore measured our laboratory's temperature in both seasons and found that it was comparable (winter, 24.08 ± 1.70 (°C); summer, 24.07 ± 1.63). No correlation was found between any of our behavioural measures and lab temperature.

The mean differences between seasons for both eccentricities of UY and UG, and for the Rayleigh matches, are plotted in Figure 1, with 95% CI error bars (see also Table S1 in the Supplemental Information).

A univariate repeated measures ANOVA with the dependent variable of wavelength and factors of season, eccentricity and unique hue type showed a significant interaction for unique hue type with both season ($F(1,66) = 5.20$, $p = 0.026$) and eccentricity ($F(1,66) = 22.98$, $p < 0.001$). Separate ANOVAs for UY and UG identified a significant main effect of season on UY wavelength settings ($F(1,66) = 19.28$, $p < 0.001$), but not on UG wavelength settings ($F(1,66) = 0.36$, $p = 0.551$).

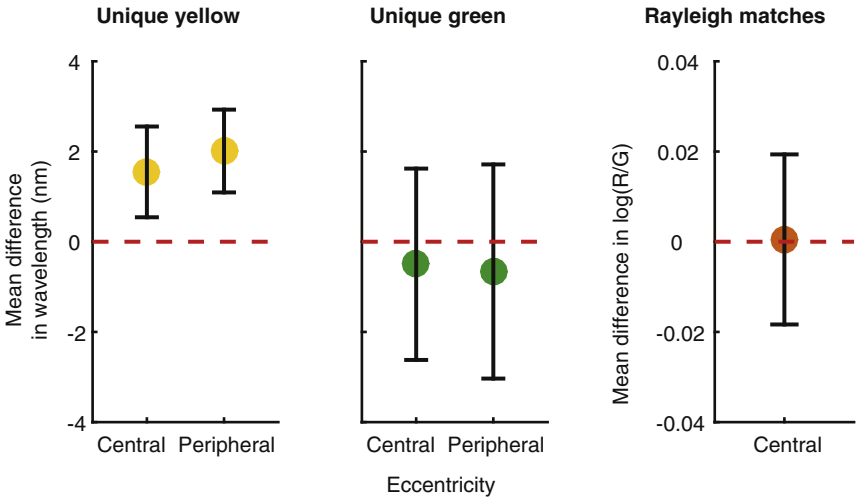

Figure 1. Mean differences between seasons for UY, UG and Rayleigh matches.
Mean differences between winter and summer (winter–summer) for the two eccentricities (central and peripheral) measured for UY (central = 1.55 nm, peripheral = 2.01 nm) and UG (central = –0.50 nm, peripheral = –0.66 nm), and for central Rayleigh matches (0.0005 log(R/G)). Error bars are ±95% confidence intervals, and the zero crossing (where the mean difference is zero) is highlighted with the dashed red line.

A significant main effect of eccentricity was also found for both UY ($F(1,66) = 9.49$, $p = 0.003$) and UG ($F(1,66) = 11.64$, $p = 0.001$).

Post hoc paired *t*-tests with Bonferroni correction showed that UY wavelength settings decreased significantly between winter and summer (central: $t(66) = 3.07$, $p = 0.012$; peripheral: $t(66) = 4.37$, $p < 0.001$). No significant changes in UG or Rayleigh matches were observed (see Supplemental Information).

UY is often modelled as the 'null point' of an opponent red/green channel. The position of the UY wavelength depends on the weighting assigned to the L and M-cone inputs to this opponent stage [4]. Altering the cone weightings therefore changes UY. We hypothesised that an increase in the ratio of M- to L-cone activations might occur in summer due to an increase in medium wavelength rich ('green') light reflected from vegetation [9]. This, in turn, may lead to a seasonal *decrease* in the relative sensitivity of M- to L-cone outputs in summer as the pathway alters its sensitivity to adapt to this increase in green light.

We modelled the shift of foveal UY wavelength settings (assuming 2° cone fundamentals [10]) by changing the weighting of the M-cone input to a putative L–M opponent stage in a manner consistent with the hypothesis above. Our model predicts a shift in UY of the same sign as the one observed in our data (Figure S1 in the Supplemental Information). To produce the observed shift, our model required a decrease in the relative M-cone weighting of ~3.2%. It remains to be seen whether this is consistent with the seasonal changes in natural scene statistics experienced by our participant population. The same normalisation model predicts ~0.14 nm shift of UG settings (see Supplemental Information). If such a change in UG were present in our participants, it would lie within the noise of our current measurements.

Neitz *et al.* [4] have shown that UY wavelength settings shift to shorter wavelengths during adaptation to an artificially induced green environment, matching the direction of shift observed here, and they propose a renormalisation model similar to the one we employ. The average UY shifts we observed were at the lower end of the range reported by Neitz *et al*. [4] (~1.3–4.6 nm), which was expected due to the larger, artificial colour bias used in their study.

In summary, we found that UY settings shifted to shorter wavelengths in summer compared to winter. The absence of a change in Rayleigh matches suggests that our result was not caused by calibration errors or instrumental bias. The shifts in UY may, however, be explained by long-term normalisation of cone outputs due to seasonal variation in the environment.

SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental procedures, results, one figure and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.06.030.

ACKNOWLEDGEMENTS

This work was partly supported by ERC grant number FP7 CIG 303797 awarded to A.R.W.

REFERENCES

1. Schmidt, B.P., Neitz, M., and Neitz, J. (2014). Neurobiological hypothesis of color appearance and hue perception. J. Opt. Soc. Am. A. Opt. Image Sci. Vis. *31*, 195–207.
2. Schefrin, B.E., and Werner, J.S. (1990). Loci of spectral unique hues throughout the life span. J. Opt. Soc. Am. A. *7*, 305–311.
3. 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.
4. 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.
5. Belmore, S.C., and Shevell, S.K. (2011). Very-long-term and short-term chromatic adaptation: are their influences cumulative? Vision Res. *51*, 362–366.
6. Wright, W.D. (1928). A trichromatic colorimeter with spectral primaries. Trans. Opt. Soc. *29*, 225–242.
7. Welbourne, L.E., Thompson, P.G., Wade, A.R., and Morland, A.B. (2013). The distribution of unique green wavelengths and its relationship to macular pigment density. J. Vis. *13*, 1–10.
8. Jordan, G., and Mollon, J.D. (1993). The Nagel anomaloscope and seasonal variation of colour vision. Nature *363*, 546–549.
9. Webster, M., Mizokami, Y., and Webster, S.M. (2007). Seasonal variations in the color statistics of natural images. Network *18*, 213–233.
10. Stockman, A., and Sharpe, L.T. (2000). The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. Vision Res. *40*, 1711–1737.

[1]Department of Psychology, University of York, York, YO10 5DD, UK. [2]Centre for Neuroscience, Hull-York Medical School, York, YO10 5DD, UK.
*E-mail: lew507@york.ac.uk