reflect a unique predisposition for individual LRR-containing proteins to promiscuity in their functional interactions with other proteins, spelling trouble for functional genomics studies in the future.

References

- Yamamoto, R., Fujioka, S., Demura, T., Takatsuto, S., Yoshida, S., and Fukuda, H. (2001). Brassinosteroid levels increase drastically prior to morphogenesis of tracheary elements. Plant Physiol. 125, 556–563.
- Lam, E. (2004). Controlled cell death, plant survival and development. Nat. Rev. Mol. Cell Biol. 5, 305–315.
- He, K., Gou, X., Yuan, T., Lin, H., Asami, T., Yoshida, S., Russell, S.D., and Li, J. (2007). BAK1 and BKK1, two *Arabidopsis* LRR receptor-like kinases, regulate BR-mediated growth and BR-independent cell death pathways. Curr. Biol. *17*, 1109–1115.
- Kemmerling, B., Schwedt, A., Rodriguez, P., Mazzotta, S., Frank, M., Abu Qamar, S., Mengiste, T., Betsuyaku, S., Parker, J.E., Mussig, C., *et al.* (2007). A brassinolide-independent role for the BRI1 Associated receptor Kinase 1 (BAK1) in plant cell death control. Curr. Biol. *17*, 1116–1122.
- Shiu, S.H., and Bleecker, A.B. (2003). Expansion of the receptor-like kinase/ Pelle gene family and receptor-like proteins in Arabidopsis. Plant Physiol. *132*, 530–543.
- Belkhadir, Y., and Chory, J. (2006). Brassinosteroid signaling: a paradigm for steroid hormone signaling from the cell surface. Science 314, 1410–1411.

- Wang, X., Li, X., Meisenhelder, J., Hunter, T., Yoshida, S., Asami, T., and Chory, J. (2005). Autoregulation and homodimerization are involved in the activation of the plant steroid receptor BRI1. Dev. Cell 8, 855–865.
- Wang, X., Goshe, M.B., Soderblom, E.J., Phinney, B.S., Kuchar, J.A., Li, J., Asami, T., Yoshida, S., Huber, S.C., and Clouse, S.D. (2005). Identification and functional analysis of in vivo phosphorylation sites of the Arabidopsis BRASSINOSTEROID-INSENSITIVE1 receptor kinase. Plant Cell *17*, 1685–1703.
- Li, J., Wen, J., Lease, K.A., Doke, J.T., Tax, F.E., and Walker, J.C. (2002). BAK1, an *Arabidopsis* LRR receptor-like protein kinase, interacts with BRI1 and modulates brassinosteroid signaling. Cell *110*, 213–222.
- Nam, K.H., and Li, J. (2002). BRI1/BAK1, a receptor kinase pair mediating brassinosteroid signaling. Cell 110, 203–212.
- Hecht, V., Vielle-Calzada, J.P., Hartog, M.V., Schmidt, E.D., Boutilier, K., Grossniklaus, U., and de Vries, S.C. (2001). The Arabidopsis SOMATIC EMBRYOGENESIS RECEPTOR KINASE 1 gene is expressed in developing ovules and embryos and enhances embryogenic competence in culture. Plant Physiol. 127, 803–816.
- Godiard, L., Sauviac, L., Torii, K.U., Grenon, O., Mangin, B., Grimsley, N.H., and Marco, Y. (2003). ERECTA, an LRR receptor-like kinase protein controlling development pleiotropically affects resistance to bacterial wilt. Plant J. 36, 353–365.
- Llorente, F., Alonso-Blanco, C., Sanchez-Rodriguez, C., Jorda, L., and Molina, A. (2005). ERECTA receptor-like kinase and heterotrimeric G protein from *Arabidopsis* are required for resistance to the

necrotrophic fungus Plectosphaerella cucumerina. Plant J. *43*, 165–180.

- Dievart, A., Dalal, M., Tax, F.E., Lacey, A.D., Huttly, A., Li, J., and Clark, S.E. (2003). *CLAVATA1* dominantnegative alleles reveal functional overlap between multiple receptor kinases that regulate meristem and organ development. Plant Cell 15, 1198–1211.
- Shpak, E.D., McAbee, J.M., Pillitteri, L.J., and Torii, K.U. (2005). Stomatal patterning and differentiation by synergistic interactions of receptor kinases. Science 309, 290–293.
- Russinova, E., Borst, J.W., Kwaaitaal, M., Cano-Delgado, A., Yin, Y., Chory, J., and de Vries, S.C. (2004). Heterodimerization and endocytosis of *Arabidopsis* brassinosteroid receptors BRI1 and AtSERK3 (BAK1). Plant Cell 16, 3216–3229.
- Kedzierski, L., Montgomery, J., Curtis, J., and Handman, E. (2004). Leucine-rich repeats in host-pathogen interactions. Arch. Immunol. Ther. Exp. (Warsz) 52, 104–112.
- Gordon, S. (2002). Pattern recognition receptors: doubling up for the innate immune response. Cell 111, 927–930.
- Kinoshita, T., Cano-Delgado, A., Seto, H., Hiranuma, S., Fujioka, S., Yoshida, S., and Chory, J. (2005). Binding of brassinosteroids to the extracellular domain of plant receptor kinase BRI1. Nature 433, 167–171.

Institute for Molecular Plant Sciences, Rutherford Building, Kings Buildings, University of Edinburgh, Edinburgh EH9 3JR, UK.

E-mail: gwyneth.ingram@ed.ac.uk

DOI: 10.1016/j.cub.2007.05.062

Color Vision: Color Categories Vary with Language after All

An intriguing new study with Russian and English participants has provided compelling support for the view that 'categorical perception' of color categories is verbally mediated and varies with culture and language.

Debi Roberson and J. Richard Hanley

Humans can perceptually discriminate several million shades of color, but generally we classify them into a small number of 'basic' categories. Basic color categories are those that are used by all observers, described with mono-lexemic terms and not subsumed within the range of any other color word [1]. Languages vary considerably in the number of basic categories that they use; different cultures use anything between 2 and 22 terms to describe the full range of perceptible colors [2]. Yet, until recently, it was widely accepted that the underlying cognitive categorization of color is universal [3,4] and impervious to these variations in linguistic description. According to this view, there is a fundamental, possibly innate, set of universally perceived category divisions - red, blue, green, yellow, pink, purple, orange, brown, black and white - and all the world's languages are at some point along an evolutionary trajectory towards a fully formed system in which all these categories will eventually be labeled.

This account stemmed, in part, from an influential cross-cultural investigation of a traditional culture [3,5]. Recent reports [6-9] from studies of other remote cultures, however, have consistently failed to find evidence of a universal set of cognitive color categories. For example, Himba speakers fail to show categorical perception at boundaries that they do not distinguish linguistically, such as that between green and blue. Categorical perception is a phenomenon that has been reported not only for color, but for other perceptual continua, such as phonemes, musical tones and facial expressions, in which a smooth perceptual continua comes to be perceived as a discontinuous set of discrete categories with a sharp increase in discriminability around the category boundary [10]. These findings suggest that the cognitive organization of color categories reflects linguistic organization and

varies considerably between cultures.

A new study of Russian and English color matching [11] has shown that Russian speakers show categorical perception at a boundary between two different types of blue that is unique to the Russian language. We already knew that siniy (dark blue) and goluboy (light blue) are distinct 'basic' color terms for speakers of Russian [12,13]. In the new study [11], when asked to select which of two colors matched a siniy target, participants were faster if the distractor was goluboy than if it was a different shade of siniy. These results were observed even though the physical difference between targets and distractors was equated and the target remained on the screen throughout so that participants did not have to hold it in memory. Such a discrimination advantage for cross-category over withincategory discrimination is the hallmark of categorical perception. English speakers, who would call all the stimuli 'blue'. did not show the same cross-category advantage. When Russian participants had to perform a secondary task that was designed to interfere with verbal coding, the category advantage disappeared, suggesting that it arose because participants accessed their verbal labels for colors whilst performing the matching task.

Previous cross-cultural studies found differences in categorical perception as a function of differences in linguistic categorization, but this new work [11] addresses several criticisms of those earlier studies. It has been argued that the poor color memory displayed by participants, such as the Himba, who are speakers of languages from remote communities reflects a lack of education and lack of experience with man-made colors, rather than simply a lack of an extensive color vocabulary [14]. The use of Russian participants [11] answers this criticism. It cannot reasonably be argued that Russian speakers perform differently from English speakers simply because they lack education or technological expertise.

The new study [11] also addresses a second criticism of previous field studies, which is that they employed memory tests to investigate the underlying cognitive organization of color. Such tasks may encourage the use of verbal labeling as a short-term memory code and thus over-estimate differences in categorization across cultures [14]. Russian participants instead demonstrated categorical effects on a perceptual matchingto-sample task that makes little or no demands on memory.

Recent studies with English speakers [15,16] have also employed perceptual tasks without any obvious memory component such as visual-search. The visual-search procedure requires participants to fixate on a cross in the centre of the computer screen. They are then asked to report the location of an 'oddball' colored target appearing amongst an array of identically colored distractors. The results showed that English speakers were faster to locate a target from a different category to distractors (for example, a green target amidst blue distractors). than from the same category (for example, a blue target amidst blue distractors), even though the degree of physical difference of targets from distractors was equated [15].

But this effect was only observed when the target appeared in right visual field; participants were no faster for cross-category targets than within-category targets in the left visual field. Because information presented to the right visual field has preferential access to lexical representations in the left hemisphere, whereas access to these representations from the left visual field would require transfer of information across the corpus callosum, this finding was interpreted as providing strong evidence for a linguistic influence on the cognitive representation of color.

A second study [16], using another visual search task, replicated the basic finding of stronger categorical perception effects in the right visual field, suggesting that categorical perception of color arises through labeling, but both these studies used English speakers and investigated the boundary between green and blue, two categories that have been proposed to be part of a cognitively universal set.

This new study's [11] importance lies in its demonstration of categorical perception at the boundary between two categories, siniy and goluboy, that do not exist for English speakers and have never been proposed to be part of a universal set of categories. Russian is not the only language that has more basic color terms than English [2,6], and our unpublished study of Korean color categories with a visual search task supports the findings of Winawer et al. [11] for a boundary that exists for Korean speakers, but which is not marked in English. Using a visual search task similar to that used by Winawer et al. [11], we also found categorical perception at the category boundary by Korean, but not by English speakers, and we also found that the effect appeared to originate from processing in the left hemisphere. Together, these results suggest that perceptual categorization of color varies between cultures with different linguistic terminology.

These results are incompatible with the view that there is a restricted set of universally perceived category divisions - red, blue, green, yellow, pink, purple, orange, brown, black and white - representing basic colors. or that all the world's languages are developing towards a fully formed system in which all these categories will eventually be labeled. Russian, at least, has already surpassed that restricted set, and their additional categories display all the same advantages of categorical perception that English speakers display for their basic set of 11 color categories, and Himba and Berinmo show for their 5.

The methodologies employed by recent color studies, such as the one carried out with Russian speakers [11], have avoided many of the potential pitfalls of earlier investigations. The participants were drawn from populations with

equal degrees of technological sophistication, and similar educational levels. Nevertheless, the findings mirror those with traditional cultures [7-9] and confirm that superior discrimination of stimuli that cross a category boundary - such as that found for English speakers at the boundary between blue and green — is not sufficient evidence for a set of universal color categories, hard-wired in the human visual system. These studies provide a clear demonstration that categorical perception of colors is constrained by culture and language.

References

- Kay, P., Berlin, B., and Merrifield, W. (1991). Biocultural implications of systems of color naming. J. Ling. Anthropol. 1, 12–25.
- Berlin, B., and Kay, P. (1969). Basic Color Terms: Their Universality and Evolution (Berkeley California: University of California Press).
- 3. Heider, E.R., and Olivier, D.C. (1972). The structure of the color space in naming and

memory for two languages. Cogn. Psychol. 3, 337–354.

- Kay, P., and McDaniel, C.K. (1978). The linguistic significance of the meanings of basic colour terms. Language 54, 610–646.
- Heider, E.R. (1972). Universals in color naming and memory. J. Exp. Psychol. 93, 10–20.
- Jameson, K.A., and Alvarado, N. (2003). Differences in color naming and color salience in Vietnamese and English. Color Res. Appl. 28, 113–138.
- Davidoff, J., Davies, I., and Roberson, D. (1999). Colour categories in a stone-age tribe. Nature 398, 203–204.
- Roberson, D., Davidoff, J., Davies, I., and Shapiro, L. (2005). Colour categories in Himba: Evidence for the cultural relativity hypothesis. Cogn. Psychol. 50, 378–411.
- Roberson, D., Davidoff, J., Davies, I.R.L., and Shapiro, L.R. (2004). The development of color categories in two languages: a longitudinal study. J. Exp. Psychol. General *133*, 554–571.
- Harnad, S. (1987). Psychophysical and cognitive aspects of categorical perception: A critical overview. In Categorical Perception: The Groundwork of Cognition, S. Harnad, ed. (Cambridge: Cambridge University Press).
- Winawer, J., Witthoft, N., Frank, M.C., Wu, L., and Boroditsky, L. (2007). Russian blues reveal effects of language on color discrimination. Proc. Natl. Acad. Sci. USA 104, 7780–7785.

- Paramei, G.V. (2005). Singing the Russian blues: An argument for culturally basic color terms. Cross-Cultural Res. 39, 10–38.
- Corbett, G.G., and Davies, I.R.L. (1997). Establishing basic color terms: Measures and techniques. In Color Categories in Thought and Language, C.L. Hardin and L. Maffi, eds. (Cambridge: Cambridge University Press).
- Munnich, E., and Landau, B. (2003). The effects of spatial language on spatial representation: Setting some boundaries. In Language in Mind: Advances in the Study of Language and Thought, D. Gentner and S. Goldin-Meadow, eds. (Cambridge, Massachusetts: MIT Press).
- Gilbert, A.L., Regier, T., Kay, P., and Ivry, R.B. (2006). Whorf is supported in the right visual field but not the left. Proc. Natl. Acad. Sci. USA 103, 489–494.
- Drivonikou, G.V., Kay, P., Regier, T., Ivry, R.B., Gilbert, A.L., Franklin, A., and Davies, I.R.L. (2007). Further evidence that Whorfian effects are stronger in the right visual field than in the left. Proc. Natl. Acad. Sci. USA 104, 1097–1102.

Department of Psychology, University of Essex, Wivenhoe Park, Colchester, Essex CO4 3SQ, UK. E-mail: robedd@essex.ac.uk

DOI: 10.1016/j.cub.2007.05.057

Retinal Circuits: Tracing New Connections

The retina detects light so that our body clock runs in time with the rising and setting of the sun. A recently identified class of photoreceptive neuron in the retina underlies this function and a new study has used viruses to unravel its connections.

Benjamin Odermatt and Leon Lagnado

The function of the eve that we are most aware of is vision. To see the world around us, an image is formed on the retina, and this is sampled 'pixel-by-pixel' by a planar array of photoreceptors [1,2]. But the retina carries out a second key function - telling our body clock the time so that our physiology and behaviour is adjusted in synchrony with the daily rhythm of light and dark [3]. Many types of cell have intrinsic rhythms, but the body as a whole is synchronized by a master clock in the hypothalamus of the brain, where a group of a few thousand neurons form the suprachiasmatic nucleus (SCN). The SCN controls functions as diverse as hormone

release, body temperature and appetite. We know that information about the amount of light in the environment reaches the SCN from the retina, because these two parts of the brain are directly connected and removing the eyes completely blocks entrainment of the body clock to the light–dark cycle [4,5].

Detecting dawn and dusk does not require formation of an image — it is the average brightness of the environment that is the important quantity. But which type of photoreceptor conveys this information? Rods and cones are the photoreceptors that underly vision, and are beautifully designed to convert light into an electrical signal [6]. The visual pigment that absorbs light is based on the opsin protein; the change in conformation of this protein when a photon is absorbed triggers an enzymatic cascade that generates an electrical signal for transmission to postsynaptic bipolar cells and horizontal cells. The visual signal is transformed as it passes through the retina, and the results are relayed to the brain by ganglion cells sending axons through the optic nerve [2]. A small number of these ganglion cells send signals to neurons in the SCN, and it was generally assumed that these transmit information about light and dark sensed by rods and cones. This idea has been spectacularly revised by experiments using a mouse completely lacking functional rods and cones; the mouse was still perfectly capable of adjusting its body clock to changes in the lightdark cycle, although this ability was lost when the eyes were removed [7,8]. The obvious conclusion was that the retina contains some other type of light-sensitive neuron that controls circadian entrainment.

This mysterious new photoreceptor has now been identified as a special class of intrinsically photosensitive retinal ganglion cell (ipRGC), which