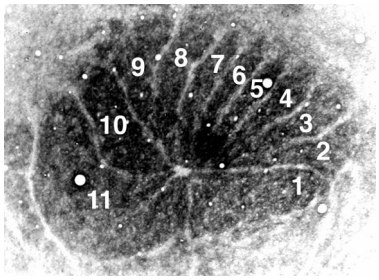
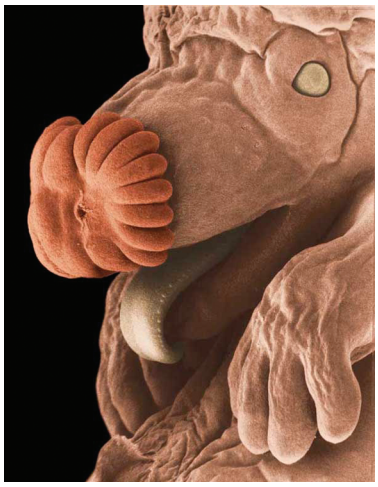
measuring the areas representing the star appendages reveals that a large proportion of somatosensory cortex is devoted to the star, and within the star representation the tactile fovea takes up a disproportionate amount of cortex for its size. The larger representation of the 11th, foveal appendage does not reflect the number of sensors or nerve fibers from this area, but instead seems to reflect the behavioral importance of the touch fovea.

How did the star evolve? The star is unparalleled in mammalian anatomy, and so it is natural to wonder how such a complicated new structure evolved. There are no fossil noses to examine, but there is a wealth of information to be found in comparative studies of living moles and studies of star-nosed mole development. Examination of mole embryos reveals a remarkable developmental sequence for the star, during which the appendages form in place on the side of the face, and later 'peel' off the face to form forward facing extensions.

This developmental sequence is unlike that of any other animal appendage, and a number of stages are arguably 'inefficient' when compared to the more straight-forward mechanism of body wall outgrowth seen for other animal appendages. But some living mole species, such as the Coast mole, *Scapanus orarius*, have a proto-star consisting of



A section of the flattened neocortex processed for metabolic enzyme cytochrome oxidase showing the area where touch information from the star projects. The 11 modules in the cortex each represent one of the 11 appendages of the contralateral side of the star. Note the greatly expanded representation of the tactile fovea (appendage 11).



A scanning electron micrograph of an embryonic star-nosed mole showing the nascent star. The appendages develop attached to the side of the face and later peel off to form the adult star. This unusual developmental sequence provides clues to the star's evolution.

backward facing, short modules of sensory organs attached to the side of their snout. This suggests that evolution 'tinkered' with such a structure in ancestral moles to arrive at the full-fledged star — leaving a trail of evidence in the unusual developmental sequence.

Where can I find out more?

Catania, K.C., and Remple, F.E. (2005). Asymptotic prey profitability drives star-nosed moles to the foraging speed limit. Nature *433*, 519–522.

Catania, K.C. (2000). Mechanosensory organs of moles, shrew-moles, and desmans: A survey of the family Talpidae with comments on the function and evolution of Eimer's organ. Brain Behav. Evol. *56*, 146–174.

Catania, K.C., Northcutt, R.G., and Kaas, J.H. (1999). The development of a biological novelty: A different way to make appendages as revealed in the snout of the star-nosed mole (*Condylura cristata*). J. Exp. Biol. *202*, 2719–2726.

Catania, K.C., and Kaas, J.H. (1997). Somatosensory fovea in the star-nosed mole: Behavioral use of the star in relation to innervation patterns and cortical representation. J. Comp. Neurol. *387*, 215–233.

Gorman, M.L., and Stone, R.D. (1990). The Natural History of Moles. Cornell University Press, Ithaca, New York, pp. 47-48.

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A way of selectively degrading colour constancy demonstrates the experience dependence of colour vision

Eli Brenner[1] and Frans W. Cornelissen[2]

A study reported recently in *Current Biology* [1] shows that monkeys reared under spectrally changing light fail to judge surface colours independently of the illumination in later life. Despite over 20 years of colour-deprivation studies, this is the first such study to show a long-lasting qualitative effect. We propose that this is due to the clever lighting scheme that was used, which did not just hinder the development of the mechanisms underlying normal colour vision, but also provided an incentive to develop a fundamentally different kind of colour vision.

The visual pathways that encode binocular depth [2,3], orientation [4,5] and motion [6] all develop abnormally if they are not stimulated by appropriate stimuli during early life. At first sight, Sugita's study [1] appears simply to indicate that this is also the case for the pathways underlying colour vision. However, rearing monkeys under far red [7,8] or very dim [9] light for the first three or four months of their life does not influence their later colour vision; neither does rearing pigeons [10] or goldfish [11] under coloured light. Modest abnormalities immediately after selective rearing were found in bees [12], cichlid fish [13] and tree shrews [14]. In guppies, colour constancy was found to be abnormal immediately after chromatic rearing, but it recovered under normal illumination [15]. So why did

Sugita's [1] monkeys have such severe deficits, even when tested nine months after being moved to a room with normal illumination?

Colour vision normally develops during the first months of life. The fact that Sugita [1] started the deprivation when the monkeys were a month old, rather than at birth, and continued it for longer than in earlier studies with monkeys [7–9], is therefore unlikely to be critical. The tasks that Sugita [1] used to evaluate the monkeys' colour vision were also not essentially different from those used in previous studies. In all previous studies, however, care was taken to ensure that the animals saw only a narrow distribution of wavelengths of light. In contrast, Sugita's [1] monkeys were exposed to several such distributions, but each narrow band was presented for just one minute at a time. But why would this completely disrupt colour constancy — as is evident from the almost complete shift with the illumination in Figure 3 of Sugita's paper [1] — without any loss in the ability to discriminate between colours (the responses were just as selective despite the shift)?

Colour vision is based on the relative stimulation of two or more kinds of photoreceptors (cones) with slightly different spectral sensitivities. Surfaces have different colours because they differ in the extent to which they reflect the light that stimulates the different kinds of cone. The perceived colour depends on the ratio between the excitation of the different kinds of cone. The perceived brightness depends on the total excitation.

This situation is complicated by the fact that the light that reaches the eye from a given surface is a product of the surface's reflectance and the spectral distribution of the light that illuminates the surface (Figure 1A–D). This complication is normally — partly [16] — dealt with by relying on the relative stimulation of each cone type by light from several surfaces (Figure 1E): doing so removes global changes in cone excitation ratios, implicitly assuming that they are

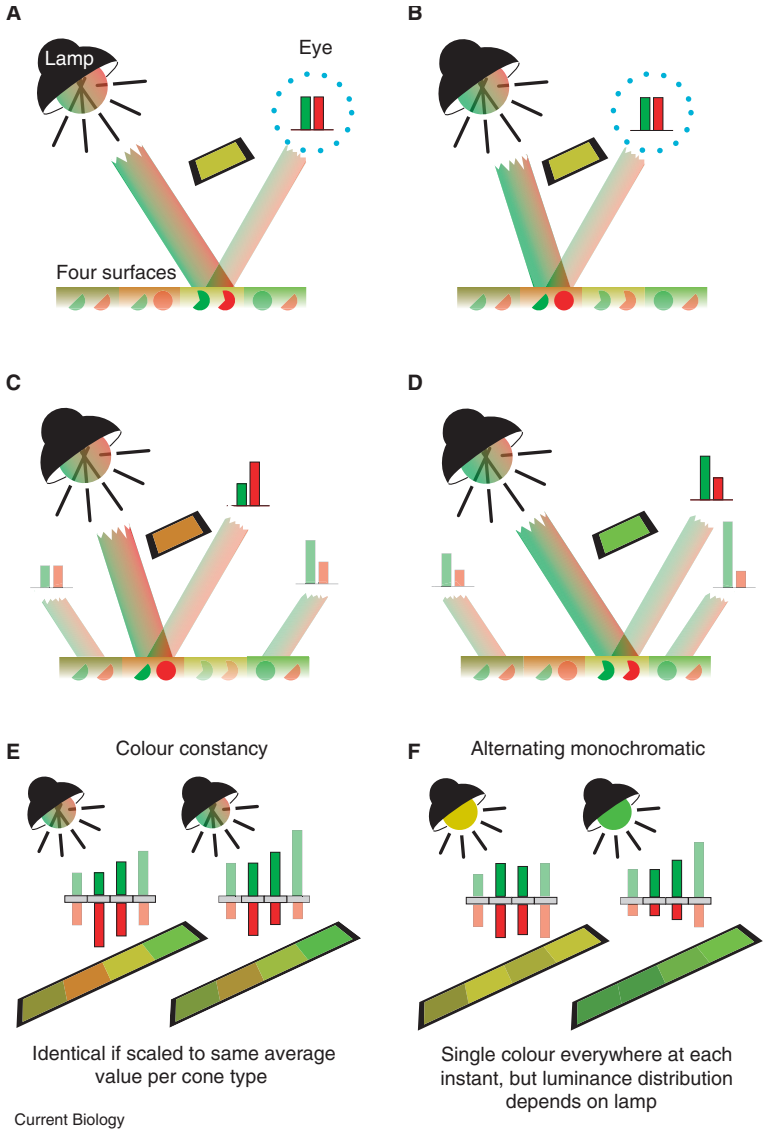

Figure 1. Judging surface colours despite changes in the illumination (colour constancy) and under alternating monochromatic illumination.

We consider a scene with four surfaces that each reflect different amounts of the light that stimulates two kinds of cones within the eye. (A) For a given surface, the stimulation of each cone type (indicated schematically by the bars) depends on the spectral content of the light that the surface reflects (indicated by the colour of the slanted square), which is a product of the spectral content of the light source (lamp) and the fractions of different wavelengths of light that the surface reflects (indicated by portions of red and green disks). (B) Exactly the same cone stimulation (compare bars within dotted circles) can be obtained with a different combination of lamp and surface reflection. (C) One can distinguish, for instance, a yellow surface under a yellow lamp (A) from a reddish surface under a greenish lamp (B) by also considering the surrounding surfaces. Under the yellow lamp, as in (A), the neighbouring reddish surface, as in (B), will reflect more red and less green light. (D) Under the greenish lamp, as in (B), the neighbouring yellow surface, as in (A), will reflect less red and more green light. (E) For each cone type, the pattern of excitation across the four surfaces under the greenish illumination (right) is approximately a scaled version of the pattern under the yellow illumination (left). Scaling all the responses within each cone type by some factor, so that the average or peak value per cone has a fixed value, would therefore lead to colour constancy. (F) Under monochromatic illumination all surfaces appear to have the same colour (the ratio of the stimulation of the different kinds of cones is constant). Only the luminance — the overall level of cone stimulation — differs between the surfaces. When switching between different colours of monochromatic light, as in Sugita's study [1], the luminance distribution changes, so that by comparing the relative luminance under the differently coloured lamps one could retrieve the colour of the surface. In that case it is a disadvantage to scale the responses as described above, because doing so makes it more difficult to judge the colour of the illumination.

irrelevant because they are caused by the illumination.

Normal colour vision is impossible under Sugita's [1] lighting regime. The ratio between the stimulation of different kinds of cones changes every minute, so it is not very informative (but early pathways will develop normally [17]). At each instant, the ratio is the same everywhere, because it only depends on the wavelength of the monochromatic illumination, so a spatial comparison of cone excitation ratios is also pointless. The luminance — the sum of cone excitations — does differ between surfaces, because it depends on the extent to which the surfaces reflect the current wavelength of light. Thus the brightness distribution changes when the colour of the light changes (see Figure 1F), raising the possibility of a temporal form of colour vision.

A surface's colour can be determined by comparing its brightness with that of other surfaces at different moments and therefore under differently coloured illumination. For instance, a red surface is one that is relatively bright when the illumination is red and relatively dark otherwise, and a white surface is one that is always relatively bright. For judging surfaces' colours in this way, the monkeys would have to remember the cone excitation ratio — the colour of the illumination — together with the relative brightness of the surface of interest.

We suggest that Sugita's [1] monkeys learnt to recognise surfaces on the basis of their reflectance in this unconventional manner during the alternating monochromatic rearing. As learning to do so requires that colour and brightness are treated in fundamentally different ways, it is not surprising that the monkeys did not readily perform a colour-matching task after having been trained on a luminance-matching task (see Figure 1 in [1]). The idea that Sugita's [1] monkeys developed a different kind of colour vision is also supported by the consistency between the monkeys' abnormal similarity judgments (Figure 2 in [1]).

Finally, as the proposed unconventional colour vision requires that the monkeys determine the colour of the monochromatic illumination at each moment, any compensation for overall changes in cone excitation ratios — which would contribute to colour constancy under normal conditions — would be disadvantageous, because it would make it more difficult to determine the colour of the illumination.

Accordingly, two of Sugita's [1] colour-deprived monkeys showed no tendency towards (conventional) colour constancy at all, while the other two showed only a very weak inclination towards colour constancy. The monkeys appeared to judge the spectral composition of the light reaching the eye from a given surface independently of the light coming from surrounding surfaces (whereas a monkey reared in red light did later consider surrounding surfaces when judging a target surface's colour [7]).

In our view, therefore, Sugita's study [1] demonstrates that selective rearing is not only capable of hindering normal visual development, but can even lead to an aspect of vision developing in a fundamentally different manner (in accordance with the statistics of the animal's experience [18]).

References

1. Sugita, Y. (2004). Experience in early infancy is indispensable for color perception. Curr. Biol. *14*, 1267–1271.
2. Wiesel, T., and Hubel, D. (1963). Single-cell responses in cortex of kittens deprived of vision in one eye. J. Neurophysiol. *26*, 1003–1017.
3. Blakemore, C. (1976). The conditions required for the maintenance of binocularity in the kitten's visual cortex. J. Physiol. *261*, 423–444.
4. Blakemore, C., and Cooper, G.F. (1970). Development of the brain depends on the visual environment. Nature *228*, 477–478.
5. Rauschecker, J.P., and Singer, W. (1981). The effects of early visual experience on the cat's visual cortex and their possible explanation by Hebb synapses. J. Physiol. *310*, 215–239.
6. Cynader, M., and Chernenko, G. (1976). Abolition of direction selectivity in the visual cortex of the cat. Science *193*, 504–505.
7. Brenner, E., Cornelissen, F., and Nuboer, W. (1990). Striking absence of long-lasting effects of early color deprivation on monkey vision. Dev. Psychobiol. *23*, 441–448.
8. Brenner, E., Schelvis, J., and Nuboer, J.F.W. (1985). Early colour deprivation in a monkey (Macaca fascicularis). Vision Res. *25*, 1337–1339.
9. Di, S., Neitz, J., and Jacobs, G.H. (1987). Early color deprivation and subsequent color vision in a dichromatic monkey. Vision Res. *27*, 2009–2013.
10. Brenner, E., Spaan, J.P., Wortel, J.F., and Nuboer, J.F.W. (1983). Early colour deprivation in the pigeon. Behav. Brain Res. *8*, 343–350.
11. Mecke, E. (1983). Absence of changes in colour discrimination ability of goldfish when reared in monochromatic light. Ann. Zool. Fennici *20*, 239–244.
12. Hertel, H. (1983). Change of synapse frequency in certain photoreceptors of the honeybee after chromatic deprivation. J. Comp. Physiol. *151*, 477–482.
13. Kroger, R.H., Knoblauch, B., and Wagner, H.J. (2003). Rearing in different photic and spectral environments changes the optomotor response to chromatic stimuli in the cichlid fish Aequidens pulcher. J. Exp. Biol. *206*, 1643–1648.
14. Petry, H.M., and Kelly, J.P. (1991). Psychophysical measurement of spectral sensitivity and color vision in red-light-reared tree shrews (Tupaia belangeri). Vision Res. *31*, 1749–1757.
15. Intskirveli, I.E., Roinishvili, M.O., and Kezeli, A.R. (2002). Experience dependent color constancy in guppies (Poecilia reticulata). Neural Plast. *9*, 205–216.
16. Brenner, E., and Cornelissen, F.W. (1991). Spatial interactions in color vision depend on distances between boundaries. Naturwissenschaften *78*, 70–73.
17. McCourt, M.E., and Jacobs, G.H. (1983). Effects of photic environment on the development of spectral response properties of optic nerve fibers in the ground squirrel. Exp. Brain Res. *49*, 443–452.
18. Beau Lotto, R. (2004). Visual development: experience puts the colour in life. Curr. Biol. *14*, R619–R621.

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