

Visual Development: Experience Puts the Colour in Life Dispatch

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Recent findings show that colour processing, like most other sensory attributes, is shaped by experience. While such studies can reveal the mechanisms of development, can they also help uncover the mechanisms of perception?

Understanding the morphogenesis of the brain is a wonderful challenge for neurobiologists: investigating how nerve cells and their connections are organised into a coherent functional unit is both intrinsically interesting, and medically relevant. As more is known about the visual part of the brain than any other, it is not surprising that much work has focused on visual development. And measuring how abnormal experience affects this process has been an integral tool in demonstrating that experience can significantly alter the physiological landscape of vision (for example, see [1–4]).

From the several recent studies, one can now add colour vision to the list of perceptual modalities that are modulated by experience. For instance, it has been reported that the organisation of the primary visual cortex is different in people lacking a functional cone system — so-called ‘rod monochromats’ — who are consequently colour blind. What Baseler *et al.* [5] discovered was that the area of cortex that normally receives information only from the central part of the retina — the foveola — is activated by the rod system in rod monochromats. Because there are no rods in the foveola in either these or normal individuals, this central activation could only arise from a reorganisation of the primary visual cortex resulting from their altered visual experience.

Another piece of evidence for the plasticity of the colour processing involves the perception of unique yellow. While many different colour terms are typically used to describe colour experience that vary from culture to culture, all sensations of colour reduce to one of four perceptual categories (five if you include grey-ness): redness, yellowness, greenness and blueness [6]. So, for any individual with normal colour vision, there should be a specific wavelength that causes a ‘unique’ sensation of yellow, that is, a colour percept that contains neither redness nor greenness (the same of course should be true for perceptions of red, green and blue). Recent results have shown that the identity of this wavelength remains fairly constant from individual to individual [7]. What makes this result unexpected is the known variability in the underlying retinal architecture in humans, which one might expect would cause large variations in the physical locus of unique yellow. The reason that it does not, it seems, is because — through

experience — the visual system compensates for the genetically determined differences in colour processing [8].

Further studies also suggest a role for experience in ‘higher-level’ aspects of colour perception. As reported recently in *Current Biology*, Yoichi Sugita [9] raised monkeys in fairly extreme conditions of visual deprivation, in which each animal spent their first year of life in a room illuminated for 12 hours a day by monochromatic lights. Throughout the light cycle, the illuminant would switch randomly between four monochromatic lights every minute. As a result of this unusual experience, the monkeys’ colour perception was degraded in two ways: first, their judgments of colour similarity differed (fairly incoherently) from control animals; and second, they were unable to recognise a target surface under an illuminant they had not experienced [9]. A similar effect on perception has also been observed in fish raised under a single chromatic light [10]. Thus, colour perception, like that of motion, form, sound and touch, is modulated by experience.

Developmental studies such as these provide considerable insight into the principles that guide the formation of the visual system. What they do not tell us is how and why we (and other animals) see what we do. But then that was not their original intention. After all, whilst the formation of ocular dominance columns and the like have been the principle focus of developmental neuroscience [4], whether these structures are necessary for perception is still a matter of debate [11]. Rather, the aim of such studies is to understand how the visual system is formed, not how the formed system functions. Nonetheless, augmenting experience during development does have the potential to tell us a great deal about the principles of perception.

To understand why, consider what sensations of colour ‘represent’. Everyday experience suggests that we see an accurate representation of a world composed of differently colored objects of various sizes, orientations and locations in three-dimensional space. This common sense impression is extraordinary, given that the two-dimensional patterns of light that fall

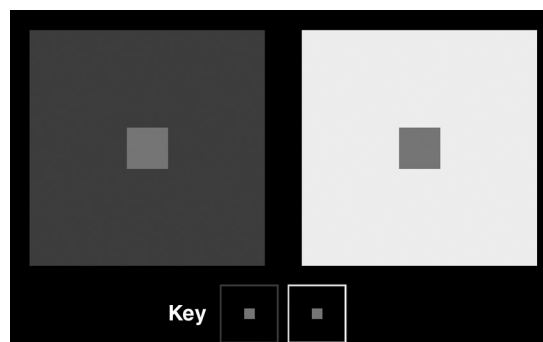


Figure 1. An illusion of simultaneous brightness contrast (see text for explanation).

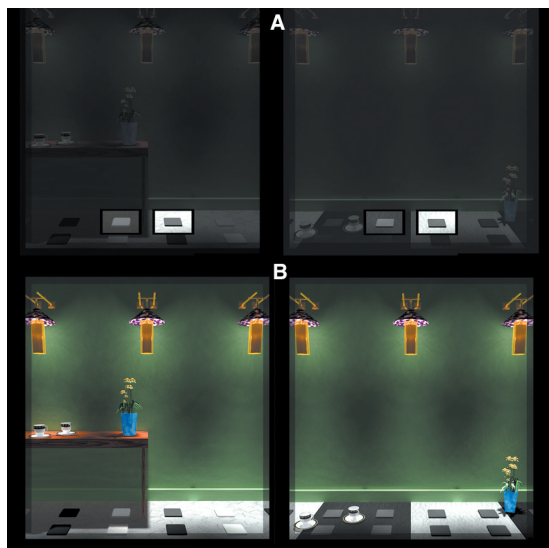


Figure 2. An illustration of the empirical basis for illusions of colour (see text for description).

on the retina completely lack these attributes. For instance, despite the wide diversity and continuity of spectral stimuli, and even though the physical dimension that describes light is linear from 400–700 nm, we experience a circular relationship of only four opponent colour categories, each defined by a unique colour sensation (see [12] and citations therein for why this may be the case). This lack of isomorphism between stimuli and perception would, however, be trivial if there were a simple one-to-one relationship between objects in the world and the stimuli they generate — all the visual brain would have to do is represent each relationship, say between a particular reflectance and its corresponding stimulus, as one color or another.

The deeper problem is that visual stimuli are in fact determined by multiple real-world factors — reflectance and illumination in the case of colour. As a result, any given stimulus could have arisen from an infinite number of different sources. Vision must overcome this ambiguity if it is to usefully guide behaviour; this is rather like trying to solve the equation $x \cdot y = z$ for x without ever knowing y . Though a seemingly impossible task, visual animals from bees to humans ‘recognize’ objects under different illuminants, a phenomenon called color constancy (for example, see [13–15]). Given the indeterminate nature of stimulus information for behaviour, the only way this can be achieved is empirically: by shaping perception and processing according to the statistics of experience [15–20].

The colours that we, and presumably other animals, see are thus accurate representations neither of the physical world — with which we have no direct access — nor of the physical qualities of light stimuli (which would be behaviourally useless given their inherent ambiguity). Rather, they represent an empirical, and thus probabilistic, correlation between a stimulus and sources that have typically generated similar stimuli in past experience.

To illustrate this important point, consider Figures 1 and 2. Figure 1 is a demonstration of the well-known

‘illusion’ called simultaneous brightness contrast. The two central squares are physically identical (as shown in the key below), but appear to differ in brightness as a consequence of their different surrounds (bright on the dark surround and dark on the light surround). Thus, as is true in so many other aspects of what the brain does, context is everything when it comes to the colours we see. Indeed, a single patch of light can be made to appear red, green, blue, yellow, black or white depending on the information that surrounds it (examples can be found at www.lottolab.org). While such contextual phenomena are often explained away as incidental consequences of the intensity differences across a stimulus, few now would hold this view, as it is straightforward to create stimuli that are not consistent with this sort of interpretation (as shown in Figure 2). Rather, the effects of context, even in the simplest of illusions, are determined by whether the added information makes the stimulus more or less consistent with one source or another.

Thus, when identical simultaneous brightness contrast stimuli (as in Figure 2A) are embedded in scenes that change their probable sources (as in Figure 2B), the relative brightness of the targets changes accordingly. In the left panel in Figure 2B, the stimuli are now consistent with two differently reflective objects, under different conditions of illumination, with the consequence that the difference in apparent brightness of the targets is dramatically increased. In the right panel of Figure 2B, however, where the context is consistent with similarly reflective surfaces (on differently reflective surrounds), the targets now appear nearly identical in brightness. Thus, the strength of the brightness ‘illusion’ in Figure 1 varies according to its probable sources according to past experience. What is true for brightness is also true for other perceptual attributes, such as colour, motion, form, and depth (again, see www.lottolab.org for examples).

Thus, the colours we see represent the empirical significance of inherently ambiguous stimuli in past experience, which creates at least two requirements for explaining vision. The first is to fully quantify an animal’s ecological history, not just in terms of the patterns of light that fall on the eye [19], but also the probabilistic relationship between stimuli and their sources [20]. As this information is currently lacking, most probabilistic models include general assumptions about the world and its relation to the observers. While some assumptions may be intuitive, they are frequently arbitrary simplifications, and/or assumptions based on post hoc agreement between the predictions of the model and psychophysical (behavioural) data. The second requirement is to compare animals from different ecological/statistical histories. Without this information, it will not be possible to directly test the adaptive, causal relationship between stimuli, processing and perception.

In principle, both aims could be met by raising animals within carefully constructed spectral environments that specifically, and quantitatively alter the animal’s experience towards ambiguous spectral stimuli — rather than simply depriving it of normal experience — and then correlating this known experience with

ensuing biases in visual circuitry and perception. In other words, by taking advantage of developmental mechanisms, which presumably evolved to adapt vision to the more subtle statistics of ontogenetic experience (arising from variations in genetic and epigenetic determinants), developmental neuroscience could be integral in explaining how and why we see what we do.

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