Abstract

Polymorphism in the peripheral sensory system (e.g., congenital individual differences in photopigment configuration) is important in diverse research fields, ranging from evolutionary biology to engineering, because of its potential relationship to the cognitive and behavioral variability among individuals. However, there is a gap between the current understanding of sensory polymorphism and the behavioral variability that is an outcome of potentially complex cognitive processes in natural environments. Linking peripheral sensor properties to behavior requires computational models of nervous processes transforming sensory representation into action, which are constrained by quantitative data based on physiological and behavioral studies. Recently, studies based on machine vision approaches are shedding light on the quantitative relationships between sensory polymorphism and the resulting behavioral variability. To gain a convergent understanding of the functional impact of sensory polymorphism in realistic environments, a close coordination among physiological, behavioral, and computational approaches is required. At the same time, such an interdisciplinary approach yields broad insights into the universal mechanisms in our cognitive processes and effective strategies to compensate for individual differences in daily life.
**Background: what is it like to see with different color vision?**

Color perception can be markedly different among individuals partially due to differences in the expression of color-sensitive photopigments, because of genetic polymorphisms [1], [2]. The majority of humans are trichromatic: i.e., light spectra are encoded by the population activity of long-wavelength (L)-sensitive, middle-wavelength (M)-sensitive, and short-wavelength (S)-sensitive cones. Observers lacking one class of photopigments (dichromatic observers) are insensitive to the difference between a certain pair of colors (e.g., red and green), which are sometimes called “confusing colors.

The polymorphism in color vision is an intriguing problem for science and our daily lives. Indeed, seeing color is directly related to the basic skills required for selecting fruits in supermarkets, for recognizing traffic signals, and much else. Although gene therapies under development may enable us to manipulate color vision in the near future [3], there are currently few clinical methods to “cure” the dichromatic observers to have sensitivity to the difference between confusing colors. An alternative strategy to compensate for dichromatic vision from an engineering viewpoint is to design visual materials with sufficient information to be perceived by dichromatic observers [4]–[7]. In practice, however, the compensatory design is not necessarily straightforward because it requires prediction of the mechanism of perceiving images in dichromatic observers. Such a prediction is particularly difficult for complex visual scenes, where the overall percept of scene is organized not only by color but also by several different features including luminance contrast, shape, textures and motion. Therefore, estimating the behavioral impact of polymorphic color vision is not only an issue with cones at retinal level, but also requires understanding of the central nervous system and the of the structure of the external visual environment.

Originating from ophthalmology and visual science, the investigation of polymorphic color vision has expanded to diverse research fields during the last century. Evolutionary ecologists have discussed the advantage of trichromacy in the natural environment. However, the comparison between subjective percepts in individuals having different sensory conditions also involves metaphysical issues (including questions such as “what qualia is experienced by two persons with different color-visions?”), which have interested philosophers for long times [8]. Nevertheless, certain computational techniques allow us to directly compare the visual percepts among different sensory conditions. Here I briefly review the recent progress in research linking sensory polymorphism to perception and behavior in complex visual environment. The aim of this paper is to enhance the interdisciplinary collaboration among investigators using physiological, behavioral, and computational approaches by associating the progresses in multiple research fields and by discussing how to obtain a convergent understanding.

**Ecology of polymorphic color vision**

Many primates, including human, have trichromatic color vision, which enables them to discriminate a much wider range of hues compared to dichromatic mammals including their ancestors. This characteristic visual ability in primates has been raising a long-lasting question concerning the evolution of enhanced color vision in the human lineage [9]–[11]. The primate trichromacy, which is sensitive to the spectral difference in long-to-middle (L/M) wavelengths, is widely considered to be a consequence of evolutionary adaptation, in particular for finding reddish ripe fruits in greenish foliage [10], [12]–[19]. At the same time, researchers have been puzzled by the profound inter- and intra-specific variability in primate color vision [13].

Most of the conspecific diversity in color vision is caused by a duplication and divergence of the X-chromosome opsin genes. In particular, the expression of opsin genes encoding L/M opsin is highly variable not only between but also within species. Natural selection models [12], [14], [19] predict overall superiority of trichromats over dichromats. However, surprisingly, trichromatic individuals have not been found to have higher fitness over dichromatic group members in wild populations [20]. Behavioral studies indicate a highly task-dependent nature of the superiority of trichromacy. Although captive studies have revealed the advantages of trichromacy in specific perceptual tasks [18], [21], [22], ethology in the wild environment has even demonstrated cases in which dichromats are superior
to trichromats at detecting foods, such as camouflaged insects [23], [24]. Therefore, the ecological impacts of each phenotype under natural conditions remain to be clarified.

**Computational impact of polymorphism in natural environments**

Recently, Melin et al. [25] introduced a machine learning approach to model the visual ability of new world monkeys (Cebus capucinus) expressing dichromatic and trichromatic phenotypes to detect foods in the natural environment. By training an artificial classifier (support vector machine) based on cone responses predicted from the spectral reflectance of objects in a wild tropical forest (Figure 1a), they estimated how effectively the colors of dietary fruits are discriminated from those of leaves. The classifier modeled with the trichromatic phenotypes was found to correctly discriminate ~75% of the total fruits from background leaves. In contrast, models of dichromatic phenotypes discriminated only <30% of the total dietary fruits. In particular, fruit species having greenish or brownish hues were not detectable by dichromat models. In addition, a significant superiority of trichromacy was found for fruit species with small patch sizes. These results are concordant with the hypothesis that long-distance detection of fruit patches, which provide a high finder’s reward, can exert a selective pressure on trichromacy in primates. However, the reason for maintained polymorphic color vision despite the apparent advantage of trichromacy are unclear.

Although the contrast in cone responses constrains the visual information at the retinal level, it is not the only factor that modulates cognition and behavior. The perception of a visual scene is highly dependent on the spatial structure of visual information. Hence, to account for the perceptual relevance of color vision polymorphism in complex scenes, we need to consider not only the local cone contrast but also its relationship to the surrounding context. The next section reviews the recent progress in analyzing the impact of color vision polymorphism under structured visual contents, and explains how a computational model of bottom-up visual attention explains the resulting perceptual divergence.

**Computational substitution of color vision**

In early attempts to capture the polymorphic experiences in complex visual scenes, several graphics techniques were proposed to mimic the experiences of dichromats on a trichromatic display [26], [27]. This was achieved by substituting each set of indistinguishable colors [28]–[30] with a single representative color chosen to reduce visual discrimination by trichromat observers (Figure 1b). The procedure converts the original three-dimensional color space to a two-dimensional space that simulates the color gamut in dichromatic vision. It allows trichromat observers to guess what type of color information would not be accessible for dichromats in complex visual scenes, by comparing the simulated and the original images. This substitution approach resulted in a variety of applications[4]–[6], [31]. A related method is used in behavioral ecology [32].

Although the substitution approach is appealing in that it provides precise chromatic metamers for dichromats, it has some weaknesses. In particular, interpreting the simulated colors on the trichromatic display can be problematic because the selection of representative colors is not uniquely determined but contains ambiguity that depends on the algorithm used. For example, red, orange, yellow or green can be used to simulate the appearance of those colors in red–green dichromat vision. For the same reason, the chromatic contrast for trichromats viewing those simulated images contains ambiguity depending on the algorithms. In addition, analysis of the images often relies on subjective impression of the observers in the substitution approach (because the quantitative analysis may suffer from the ambiguity of substitution).

**Perceptual salience as a common metric of the behaviorally relevant visual information**

As a solution to this problem, Tajima and Komine [33] recently proposed a machine vision approach. They introduced visual salience as a common metric with which perceptual differences due to
polymorphic color vision are quantified (Figure 1c). The salience is a concept introduced to explain visual attention and developed in the field of computational vision [34]–[40]. Computational models of salience have been reported to predict bottom-up visual attention in trichromatic human observers, including saccadic eye movements [36], [41]–[43]. However, there have been few studies examining salience models in observers lacking trichromatic color vision. Tajima and Komine [33] introduced a hypothetical salience model for non-trichromatic observers, and confirmed a positive correlation between differential salience and the divergence of psychophysical conspicuity judgments among observers with distinct color-vision types. Notably, this approach directly computes salience distributions in an image for different color-vision types, bypassing the simulation of dichromatic vision on a trichromatic display. Moreover, the divergence among color-vision types was ameliorated by manipulating the visual stimuli to reduce the salience difference among observers. It established the causal relationship between modeled salience in various color-vision types and actual perceptual judgments. It is also shown that, in their stimulus set, the inter-individual difference was not significantly correlated to the predictions by other simpler models based on LMS or RGB color contrast, thus the contribution of visual salience (which features multi-scale center-surrounding antagonism and subsequent activity normalization) seems crucial [33].

In contrast to the cone-response based characterization [25], the salience-based model predicted the case in which dichromats are likely to direct attention to where it is not salient for trichromats, consistent with the natural animal behavior [21], [23], [24], [44]. The superiority of dichromats in specific tasks is observed also in human psychophysical experiments [45]–[48]. These findings indicate the potential of salience-based approach to quantitatively bridge the color vision polymorphism and the behavioral divergence in humans and animals, as well as to provide effective applications in visual content design. In particular, “attentional metamerism” [33] based on modeled visual salience is a promising framework to discuss the universality of visual information, when no common chromatic metamer exists because of the polymorphism of peripheral sensory organs. However, the salience-based approach does not perfectly explain the all cognitive aspects. One major caveat of the salience-based method is that it does not take into account the effects of higher-level cognition, such as memory-guided object recognition, which is an important extension of this machine vision approach.

**General strategies to bridge sensory polymorphism to behavior**

The study of color vision and visual salience or foraging behavior in primates provide a good model of a strategy to link sensory polymorphism to resulting behavior. How this framework can be extended to general visual tasks, such as object recognition or material perception? Moreover, individual variability in the sensory system is observed in modalities other than color vision; this includes as low visual acuity because of cataracts or macular degeneration, and age-related degradation of auditory spectral sensitivity (the notion of salience is recently extended to auditory domain [49]). Beyond color vision, what is the general methodology to study the cognitive and behavioral impact of polymorphism in the sensory system? Here I separate it into three steps.

**Step 1: modeling.** The first step is to build quantitative models of perception for different sensory conditions. This step requires computational approaches as well as intensive physiological insights about the studied modality, including variability among individuals. In addition, we require the measurement of natural statistics if behavior in natural environment is of particular interest. (For example, to study color-vision polymorphism on object recognition, researchers can build models to predict the accuracy of object classification based on a concrete algorithm [50]–[53]. Combining those models with the quantitative data in color representation in the early nervous system, they can quantify the influence of color-vision polymorphism on object recognition.)

**Step 2: correlation.** The second step is to correlate model predictions and actual behavior. This may requires a new paradigm for behavioral experiments. (For example, when we have different stimuli of visual object, the color vision can impact differently across individual stimuli.)
Researchers can quantify the plausibility of assumed model by asking whether the model correctly predicts the variability across stimuli.

**Step 3: manipulation.** The third step is to manipulate behavior based on model prediction to examine the causal relationship between the hypothesized model and perceptual or behavioral mechanisms. This step may include iterative interactions between behavioral measurement and computational optimization of stimuli. (In the case of object recognition, researchers can manipulate the visual stimulus of object so as to mitigate or exaggerate the influence of color-vision on the object classification performance. By examining whether this expected effects of manipulation is observed in human behavior, they can test the causality of modeled mechanisms.)

Accomplishing all three steps would sometimes require new collaborations among researchers from a broad range of different disciplines.

**Implications and future directions**

For a convergent understanding about the relationship between sensory polymorphism and behavior, it is required to integrate quantitative models of different stages of the cognitive process (Figure 2). This integrative approach is expected to yield insights in a divergent research fields, ranging from basic findings in sensory processing and behavioral ecology, to clinical and engineering applications. The following are examples of potential impacts and remaining issues to be solved.

1) **Systems neuroscience**
   Studying sensory processing under the influence of polymorphism leads to an understanding of the universal mechanism of visual recognition. Visual salience is a critical determinant of bottom-up attention, the first bottleneck through which humans recognize the visual world. However, the precise mechanisms of visual recognition are not well understood the observers with non-common trichromatic color vision. Further quantification is required at the level of photoreceptors [54], [55] as well as at high-level cognition such as the categorization of colors [56].

2) **Machine vision**
   Polymorphism provides a clue to understand the functional impact of specific sensory machinery. For example, the role of color in pattern recognition has been of great interest in the context of machine vision [57], [58]. Study of polymorphic color vision in humans and animals should hint at the relevance of color information in natural behavior. However, most of the current models of visual polymorphism do not account for the effects of high-order statistics [50]–[53] or semantic context on perception. Because the extraction of visual information is guided not only by low-level saliency (bottom-up attentional processes) but also by top-down knowledge of the external world, more advanced techniques from machine vision are required to model such high-level visual recognition mechanisms.

3) **Ethology**
   Dichromats can be superior to normal trichromatic observers. A series of studies suggests that dichromats are better at finding camouflaged objects against a multicolored background [45]–[48], a perceptual ability that is critical for foraging, hunting, and avoiding predators in the wild environment [23], [24]. Quantitative models that fit such dichromacy as advantageous are yet to be developed. To account for realistic wild behavior, the models should involve viewing distance [59], multisensory integration [60], and social interaction among individuals [61].

4) **Clinical study and engineering**
   The models linking sensory polymorphism and behavior can be utilized for accessible design of visual content to avoid unintended asymmetry in the information received by observers. The methodology to quantify the perceptual divergence is expected to enhance the effectiveness in creating information graphics [62] and prosthetic tools.
Conclusion

Polymorphism in the sensory system has been studied in diverse research fields. However, bridging sensory polymorphism and behavior requires convergent understanding based on a broad collaboration among researchers adopting physiological, behavioral, and computational approaches. Recent studies in color vision provide good models of such interdisciplinary approaches. Revealing the relationship between sensory polymorphism and behavioral variability would yield rich insights into the sensory system and behavioral ecology, as well as technological applications to compensate for individual differences in our daily lives.

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Different approaches for quantifying the functional impact of color-vision polymorphism. (a) Color patch distribution in the cone response spaces. In the trichromat space (top), the fruits (magenta circles) are better dissociated from the leaves (green squares) than in the dichromat color space. Modified from Melin et al. (2012) [25]. (b) An example of the cone-model-based color substitution. The visual experience in dichromat (bottom) is mimicked by substituting the confusing colors in the original image (top) with a single color [26], [27]. (c) Salience maps based on the cone response models for the trichromat and dichromat observers [33]. The brightness corresponds to the visual salience value.
Figure 2

Overview of the integrative approach. (Top) An overall model linking the polymorphism in retinal cone pigments and the behavior. (Bottom) Quantification and modeling methodologies at different stages of the model.