PHYSIOLOGICAL MECHANISMS OF COLOR CONSTANCY

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Color constancy is the term given to the ability to recognize the color of objects correctly under different conditions of illumination. For this purpose the visual system must determine the character of the illumination, introduce a correction for it into the spectal composition of the light received from the object, and hence recreate the true color of its surface. Behavioral experiments on fish showed that they possess constant color vision of objects. Electrophysiological experiments on ganglion cells of the color type showed that the simplest mechanisms of correction for illumination are found at the retinal level. An investigation of model algorithms providing for color constancy showed that the presence of color vision makes it much easier to recognize the three-dimensional form of objects. This fact compels a reexamination of established views regarding the place and role of color vision in functions of the animal visual system as a whole.

INTRODUCTION

The main function of the visual system is to recognize surrounding objects. The difficulty in this task is that the retinal images even of unchanging objects vary constantly depending on their distance away, rotation, the conditions of illumination, and so on. To ensure constancy of perception of external objects it must therefore be possible to extract from the retinal image information on certain invariant properties of the objects themselves. One such invariant property of objects is the reflecting power (color) of their surface. Light reflected from the surface depends not only on its color, but also on the character of illumination. Correct recognition of color under changing conditions of illumination is called color constancy. Hence, determination of the color of an object is possible only provided that characteristics of both the reflected and the incident light are known. For this purpose objective parameters of illumination in the field of vision must exist. In the simplest cases these would be areas reflecting nearly all the incident light, i.e., white surfaces [5]. Recognition of color is thus reduced to the determination of the conditions of illumination and the introduction of an appropriate "correction for illuminations" [8].

We now know that an external manifestation of the operation of constancy mechanisms is invariance of the response to a colored surface under constant conditions of illumination, and that the condition for
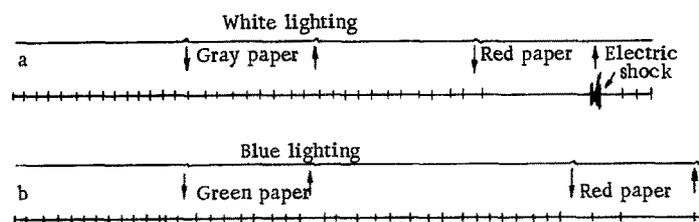

Fig. 1. Conditioned-reflex changes in heart rate of fish to presentation of positive and differential stimuli: a) during training, b) control experiments with change in conditions of illumination.
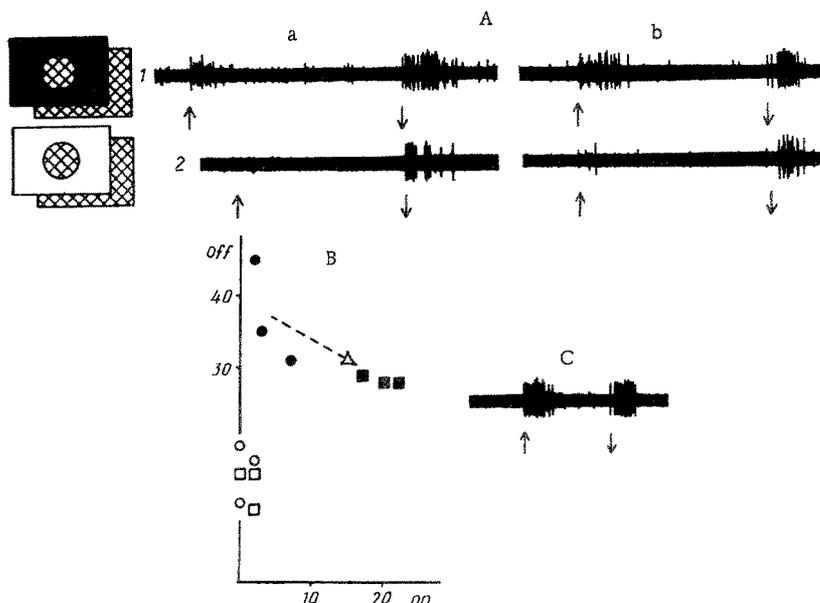
Fig. 2. Response of ganglion cell of the carp retina to presentation of green paper in white and red illumination. A) Response of cell to introduction of green paper into receptive field (arrows below) in white (a) and red (b) light, and in the black (1) and white (2) periphery; B) response of cell (for comparison) to presentation of pink paper in white periphery with white illumination; C) total number of spikes in response to bringing stimulus into (abscissa) and removing it from (ordinate) visual field with white (circles) and red (squares) illumination. Black symbols denote black periphery, white symbols — white. Three experimental points correspond to each type of experiment. Arrow indicates shift of cell response (to presentation of stimulus in black periphery) evoked by "reddening" of illumination.

their normal operation is the presence of objective parameters of illumination. Fishes are convenient objects with which to study the physiological mechanisms of color constancy, for their well-developed color vision has already been thoroughly studied [9].

EXPERIMENTAL METHOD

Behavioral Experiments

Experiments were carried out on carp Cyprinus carpio L. Permanent electrodes to record the ECG were implanted into the fish which were fixed during the experiment in a frame in an aquarium. With constant illumination a conditioned autonomic defensive reflex to electrical stimulation was formed in the fish: the heart rate decreased in response to presentation of positive stimuli (pieces of red paper measuring 2×3 cm) with differentiation to gray and green paper. The stimuli were presented consecutively against a white background (a sheet of white paper measuring 8×10 cm) 15 cm away from the aquarium. The fish could not see the source of illumination. The character of illumination was varied with the aid of color filters.

The results of these experiments showed [1] that the reflex to red stimuli and differentiation to green and gray stimuli produced in the fish during constant illumination also persisted after a change in the illumination (for example, toward blue-green), although the light reflected from the pieces of red paper became (colorimetrically speaking) even greener than the light reflected from the green stimuli under the conditions of illumination used during training (Fig. 1).

Since the only parameter of illumination was light reflected from the white background, a change in the color of the background would be bound to alter the assessment of the illumination and would lead to incorrect responses (the phenomenon of "pseudoconstancy" [6]). In fact, replacement of the white background
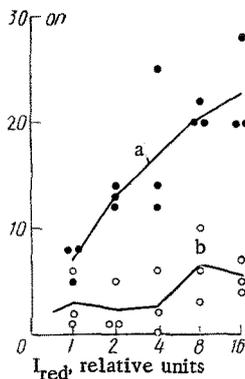
Fig. 3. Cell response to movement of piece of green paper into visual field: a) variation against black periphery, b) relative stability against white periphery during variation in character of illumination within wide limits. Number of spikes in on response to stimulus (on) plotted against intensity of additional red illumination(I_{red}).

by blue, corresponding to an apparent "blueing" of the illumination, led to a sharp increase in the responses to the differential (green and gray) stimuli. Against a crimson background, on the other hand, the response to the positive stimuli was reduced.

Constancy of the reflexes to the colored pieces of paper with a change in the conditions of illumination and the predictable incorrect responses when the information on the conditions of illumination was distorted thus indicate that the carp possesses color constancy and that the light reflected from a white surface can be used by the carp's visual system as an objective criterion of illumination.

Investigation of the Cellular Mechanisms of Color Constancy

Attempts to simulate color constancy have shown [6] that in the simplest situations a correction for illumination must be introduced separately for each color channel. In the visual system operations of this sort are evidently carried out somewhere at the periphery, for example, at the retinal level, where separate color channels still exist.

Spike responses of color-opponent ganglion cells of the carp Cyprinus carpio L. and the crucian carp Carassius carassius, recorded extracellularly from endings of their axons in the tectum opticum, were investigated by the usual method [3, 4]. The receptive field of these cells (the area of the field of vision of the fish within which a given cell responds to moving stimuli) measures $5 \pm 1°$.

The stimuli (pieces of colored paper measuring more than 10° moved on an endless black band at a speed of 20 deg/sec under a disk containing a round (diameter 10°) hole concentric with respect to the receptive field of the cell. The disk could be white (objective criterion of illumination at the periphery of the field of vision of the cell present), black (criterion of illumination absent), or colored. The field of vision was uniformly illuminated by two sources (diascopes). The intensity and spectral composition of illumination were varied with the aid of filters.

Preliminary experiments showed that the cell response depended both on the intensity (number of spikes in responses to bringing the stimulus into and taking it out of the receptive field increased with an increase in intensity) and on the relative spectral composition of the light reflected from the stimulus. The response to bringing the stimulus into the receptive field showed closer correlation with the latter. In the series blue—green—yellow—red it increased from almost zero to a powerful discharge.

In the main experiment one of the pieces of colored paper was presented separately in the black and white periphery under different conditions of illumination. The presence of an objective criterion of illumination (the white periphery) in the field of vision was found to make the cell virtually insensitive to changes in the character of illumination (Fig. 2). For instance, increasing the fraction of red light in the spectrum of illumination resulted in the light reflected from the stimulus (blue or green paper) containing a high proportion of red light, and could be judged from the large response to bringing the same stimulus into the black periphery. Under the same conditions of illumination, but in the white periphery, the response to the same piece of paper was virtually indistinguishable from the response to it in white light (Fig. 2A) and it depended only on the color of the paper.

The results of an experiment in which the intensity of the additional red illumination was varied within wide limits (by 16 times) are given in Fig. 3. The cell response to bringing the piece of green paper into the black periphery increased fourfold, whereas in the white periphery it remained practically unchanged. Similar results were obtained in response to a change in one color of illumination toward blue, and with the use of pieces of yellow or crimson paper as stimuli.

A phenomenon of "pseudoconstancy" (arising as a result of actuation of the mechanism introducing a "correction for illumination" under conditions when the periphery gave incorrect information about the

illumination) could also be observed in the experiments on these cells. Changing the white periphery for green led to the appearance of a clear response to gray-blue paper (this was characteristic of the response to pink). Conversely, against a red periphery a piece of yellow paper "turned blue" — the response to its presentation disappeared.

At the retinal level in the visual system of fish very simple mechanisms for determining the color of objects from the radiation emitted from them thus exist.

Mechanisms of Recognizing the Color of Solid Objects

Recognition of the color of solid objects is made more difficult (than that of the flat objects so far examined) by the fact that knowledge of only the character of the illumination is not sufficient: the visual system must be able to extract certain information about the shape and position of the objects in the visual field, for radiation $F(\lambda)$ reflected by the surface is determined by the color of this surface $\Phi(\lambda)$, the spectrum of the source $S(\lambda)$, and also by the orientation (α) of this surface relative to the source (in the case of illumination by a distant point source):

$$F(\lambda) = S(\lambda) \cdot \Phi(\lambda) \cdot \cos \alpha. \tag{1}$$

In this case, to recognize the color $\Phi(\lambda)$ not only must a "correction be introduced" for the spectrum of the source $S(\lambda)$, but $\cos \alpha$ must also be "eliminated."

In dicromatic color vision, instead of all the functions of wavelength λ in this equation, it is sufficient to consider only pairs of values characterizing the corresponding parameters separately in the red (R) and green (G) regions of the spectrum:

$$F^R = S^R \cdot \Phi^R \cdot \cos \alpha. \tag{2}$$

$$F^G = S^G \cdot \Phi^G \cdot \cos \alpha. \tag{3}$$

Solid objects, illuminated by a point source, throw shadows. Analysis of the shadowed areas of the field of vision is made much simpler if it is assumed that objects in the shadow are illuminated by diffuse light from another source (for example, by scattered light from the sky). In that case a ready-made algorithm for recognizing the color of solid objects illuminated by diffuse light can be used [2]. The presence of uniformly colored areas of surface in the field of vision, crossed by boundaries between light and shade, enables the information regarding the color of these surfaces "in the shade" to be used later to determine the character of illumination on the other side of this boundary — in the light."

Since it is impossible here to dwell in more detail on the method of solving the problem of color constancy for solid objects illuminated by a point source, we shall describe only a basic idea, by the use of which the contribution of surface orientation ("elimination" of $\cos \alpha$) in the reflected radiation can be taken into account. Since the surface orientation at the same point is always the same for radiations in different parts of the spectrum, the ratio between excitations of two different photosensitive receivers will be independent of that orientation. In other words, in order to "eliminate" $\cos \alpha$ it is simply necessary to divide one of the equations (2) and (3) by the other.

The model of a flat "retinal" image of a certain three-dimensional situation, illuminated by two (point and diffuse) sources, can thus reproduce the spectra of radiations from these sources, the true color of surfaces falling in the field of vision, and the orientation of those surfaces at each point relative to the source.

The proposed model for the recognition of color and orientation of the surface of solid objects was constructed for the simplest case of color vision with two photosensitive receivers present. Three or more receivers improve its function. Conversely, reducing the number of receivers to one (the change to achromatic vision) immediately makes it impossible to separate the contribution of the source, of orientation of the surface, and of its color.

Since the distribution of $\cos \alpha$ at all points of the surface of an object arising as a by-product of the working of the model is in fact information about the shape of the object, color vision thus facilitates the determination of the shape of a solid object. A similar conclusion can be drawn on the basis of general arguments: the recognition of shape can be substantially simplified if the visual system uses information about the same solid shape obtained by two (or more) independent color channels.

We thus reach the rather unexpected conclusion that color vision in most animals is designed not only to recognize the color of surrounding objects, but also (and perhaps mainly) to recognize their solid shape.* From this point of view it is easy to understand why the principal classes of vertebrates (actively using vision in their behavior) — bony fishes, amphibians, reptiles, and birds, possess color vision [7], and that only in the class of mammals (possessing a brain that is so highly developed that it can recognize the solid shape of objects even without color vision) whole orders (for example carnivores and ungulates) of animals are found that evidently do not possess color vision or do not use it in their behavior.

The following main conclusions regarding color constancy can be drawn.

1. Under natural conditions the visual system, starting from the retinal level, can encode the color of objects in the field of vision and not the radiation falling on the retina. This fact largely invalidates research in which the coding of information on color in the visual system has been investigated in the inadequate terms of distribution and spectra of radiation on the retina (and not of the color of surrounding objects).

2. The recognition of the color of surrounding objects is inseparably connected with recognition of the solid shape of those objects.

3. The opposite conclusion is evidently valid also: the mechanisms of recognition of shape, at least in some animals, include color vision as an important element. This means that the study of the physiological mechanisms of recognition of shape by animals possessing color vision may be beset by fundamental difficulties.

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*In the writers' opinion, the role of binocular vision in this case is greatly exaggerated.