Perceived Lightness Depends on Perceived Spatial Arrangement

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of the light chain by a phosphatase. Cyclic GMP might also in some manner modulate the binding of cations, perhaps calcium, in the components of myosin, since evidence in other tissues suggests a close interrelation between calcium uptake and changes in cyclic GMP concentrations (*5, 6*). Cyclic GMP might also be involved in the regulation of the structural integrity of myosin in some other manner.

These findings might have wider applicability in the study of cellular motion. Actin and myosin, in addition to their role in muscle contraction, are also found in association with plasma membrane and other intracellular organelles which may regulate intracellular rearrangement (*12*). Furthermore, cyclic nucleotides have been postulated to play a role in the modulation of cell surface and cytoskeletal movement (*13*). Thus, cyclic nucleotide immunocytochemistry should be helpful in establishing in further detail the role of the cyclic nucleotides in these contractile processes.

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Perceived Lightness Depends on Perceived Spatial Arrangement

Abstract. *The perceived shade of gray depends primarily on the luminance relationship between surfaces perceived to lie in the same plane and not between surfaces that are merely adjacent in the retinal image. This result implies that depth perception must precede lightness perception and that lateral inhibition cannot explain lightness constancy.*

A change in the perceived spatial position of a surface can change its perceived color from black to white or from white to black. This finding challenges the widespread view that denies any substantial role of depth perception in the perception of surface lightness (the shade of gray between white and black).

Since 1948, when Hans Wallach published his classic experiments in lightness constancy (*1*), a consensus in this field has held that perceived lightness is a function of luminance ratios between adjacent parts of the retinal image, regardless of where those parts are perceived to lie in three-dimensional space. Moreover, because of Wallach's emphasis on retinal adjacency, many researchers (*2*) have concluded that lateral inhibitory connections among retinal cells provide the neural mechanism underlying the ratio principle.

A number of investigators (*3–7*) have sought to show that retinal ratios do not tell the whole story. Essentially the approach has been to change the apparent spatial position of a target surface so that it either appears to lie in the same plane as that of its surrounding surface or in a different plane in order to determine whether the apparent spatial separation between the surfaces reduces their interaction and thus produces a different perceived color in the target even though the two-dimensional retinal pattern remains unchanged. Two studies (*3, 4*) reported changes as great as one and a quarter steps on the Munsell scale (*8*), or 17 percent of the difference between black and white. Most (*5–7*) have reported little or no change.

With a few exceptions (*9*), it is now generally agreed (*10*) that perceived lightness is essentially determined by the relative intensities of adjacent parts of the retinal array. The experiments that I report here grew out of a seeming inconsistency between the retinal ratio theory and everyday experience. Rarely are black, white, and gray surfaces grossly misperceived. Yet the retinal ratio theory would predict consistently accurate lightness perception only when the difference in luminance at the retina is produced by a difference in the reflectance of the external surfaces. When the difference occurs because external surfaces that receive unequal amounts of illumination are imaged on adjacent parts of the retina, sizable lightness illusions should be expected. This difficulty is mitigated by the fact that the boundary between different levels of illumination is frequently gradual. However, illumination boundaries are by no means always gradual. For example, the retinal image can con-

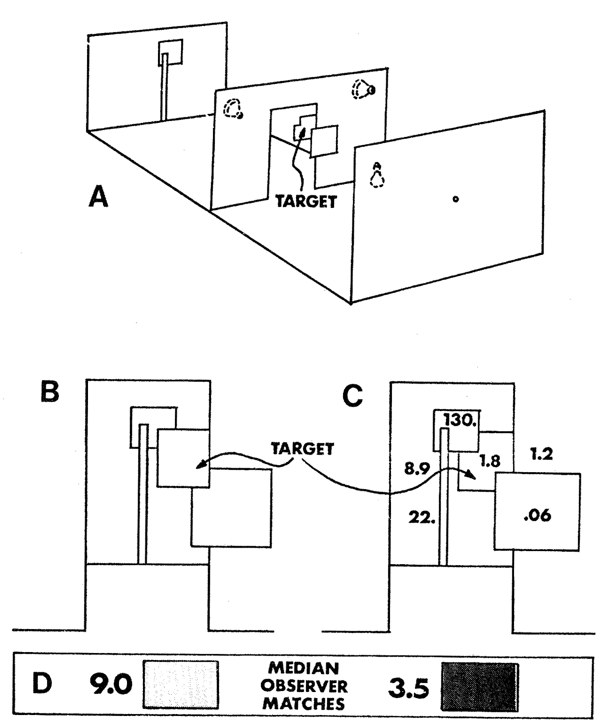
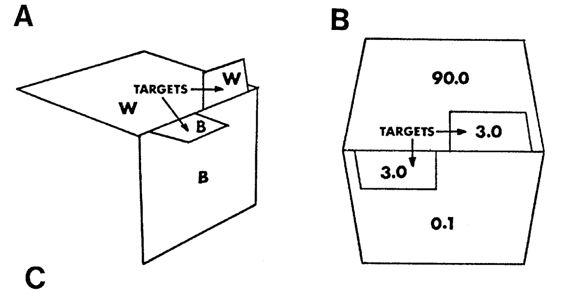


Fig. 1. (A) Perspective view of the apparatus showing hidden light bulbs. The displays (as seen through the pinhole) in which the target appeared to be located either (B) in the near plane or (C) in the far plane. (D) The average match from a Munsell chart for the two displays. Luminances (C) are in foot-lamberts.



C

TARGET	MEDIAN OBSERVER MATCH	
	MONOCULAR	BINOCULAR
UPPER TAB	3.75	8.0
LOWER TAB	7.75	3.0

Fig. 2. (A) Perspective view of the stimulus display showing color (*B*, black; *W*, white) of each part. (B) Monocular retinal pattern showing luminances in foot-lamberts. (C) Average Munsell matches for monocular and binocular viewing conditions.

tain adjacent, sharp-edged patches of radically different luminances when two walls of equal color but unequal illumination meet at a corner, or when a near surface partially occludes an unequally illuminated far surface. Yet no one has suggested that lightness constancy is poorer near such corners.

Perceived lightness might be determined primarily by ratios within perceived planes rather than by all retinal ratios regardless of perceived depth. This "coplanar ratio hypothesis" is illustrated by the following experiment, in which a depth illusion is created in order to determine whether perceived lightness is affected. Observers looked through a pinhole in a screen (Fig. 1) through which they saw a dimly illuminated near wall. Through an opening in this wall, a brightly illuminated far wall could be seen. A piece of white paper (the target surface) and a piece of black paper were attached to the near wall so that they extended into the opening. Another piece of white paper (the same white as the target) was attached to the far wall and was partly overlapped by a gray strip, the purpose of which was simply to prevent the white piece from appearing to float in midair. Interposition cues were used to create two variations of the display. The unaltered square target (Fig. 1B) appeared to lie in the plane of the near wall. The target could also be made to appear on the distant wall by means of two notches, cut out of the corners of the target so as to coincide with edges of both the near black and the far white paper (Fig. 1C). A separate group of eight observers viewed each array and indicated the apparent lightness of the target by selecting a matching sample from a 16-step Munsell scale on which black was 2 and white was 9.5.

Changing the perceived location of the target in this way caused its perceived color to vary from white (near condition) to almost black (far condition) (Fig. 1C). Note that this difference was obtained without any significant change in the retinal pattern (*11*) nor any change in retinal intensities.

Theories that emphasize retinal interactions would have predicted no differences in the study just described. On the other hand, the results follow from the coplanar ratio hypothesis. That is, the perceived lightness of the target is governed by the luminance relationships between the target and whatever regions are seen as coplanar. The luminance relationship between the target and noncoplanar regions (despite retinal adjacency) is substantially irrelevant to the lightness of the target.

It is possible to construct a critical test in which the coplanar ratio hypothesis would make opposite predictions to those of a retinal theory. In the stimulus display shown in Fig. 2, the horizontal plane contained a large white square with a black trapezoidal tab that extended outward toward the observer. The vertical plane contained a large black square and a small white tab that extended upward. The tabs were trapezoidal in order to permit a spatial position illusion (*4, 5*). Seen with one eye through a carefully positioned hole, each tab appeared to be a square lying in the same plane as the larger square that surrounded it on three sides. Seen with both eyes the tabs were seen to be trapezoids lying in their actual planes. A light bulb, unseen by the observer, was located above the display so that the horizontal surfaces received 30 times as much illumination as the vertical surfaces. Therefore the tabs were equal in luminance.

A retinal ratio theory would predict that, as the upper tab is surrounded on three sides by a very intense region, it should appear darker than the lower tab, which is mostly surrounded by a very dark region.

The results were the opposite of this prediction (Fig. 2C). When viewed binocularly and the actual spatial layout was correctly perceived, the upper tab was seen as near white, the lower tab as black. When viewed monocularly so that each tab appeared to lie in the plane of its principal background, the perceived colors reversed, the upper appearing black, the lower, white.

The central conclusion of this research is that perceived surface lightness depends on ratios between regions perceived to lie next to one another in the same plane. Kardos (*12*) proposed the similar idea that relative luminance within coplanar spatial regions determines perceived lightness, because illumination tends to be uniform within planes but separate planes tend to be unequally illuminated. This view, however, reflected the general opinion of that period that the perception of lightness depends on the prior registration of the level of illumination.

Koffka (*13*) argued that perceived lightness depends on gradients of light intensity (at the retina) but added the important qualification that some gradients are more effective than others with regard to lightness. Gradients of intensity between coplanar surfaces, he said, are more effective than those between noncoplanar regions.

Gogel and Mershon (*6*) interpreted their results in terms of simultaneous lightness contrast governed by the adjacency principle. Their view is that the degree of simultaneous lightness contrast is inversely related to the separation of the target and "induction" surfaces, both in depth (as they showed) and laterally [as others have shown (*14*)]. Thus the present results would have been predicted, at least qualitatively, by their adjacency principle (*15*).

We can now understand why previous studies (*4–7*) have shown such a small effect of depth on perceived lightness. If lightness is a frame of reference phenomenon, as the coplanar ratio principle implies, then it is not sufficient to merely remove the target surface from the plane of its retinally neighboring surface. The array must be such that the target will be seen as a member of one coplanar ratio when it appears in one spatial position, but a member of quite a different ratio when seen in the alternative plane (*16*).

These experiments show that the perceived lightness of a surface can vary from white to black depending merely on its perceived spatial position, without any significant change in the retinal array. This result implies that lateral inhibition at the retina has little to do with everyday perception of lightness. Certainly the available theories that reduce lightness perception to lateral inhibition are in error.

Another important implication also follows. If the perceived lightnesses of surfaces depend on their perceived location in space, depth processing must occur first and be followed by the determination of surface lightness. That is, processing is initiated by a pattern of intensity differences on the retina; then the nervous system uses various depth cues to construct a spatial model to fit the retinal pattern. As this spatial model is completed, lightnesses are assigned to the various surfaces in accord with the coplanar ratio principle.

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15. Two features of the adjacency principle suggest ways in which it could be tested against the coplanar ratio principle. (i) According to the adjacency principle, the perceived lightness of a target should move continuously through the gray scale as its apparent position between two inducing fields is varied continuously. The coplanar ratio principle would predict a sharp break in perceived lightness at whatever point in space the target changes its plane of reference. (ii) Gogel and Mershon use adjacency to describe the workings of contrast. The coplanar ratio principle need imply no contrast process. Indeed, a subsequent article will provide further evidence that lightness perception does not involve contrast in any important way (A. L. Gilchrist, in preparation).
16. Mershon (*3*) did provide separate inducing fields for two of the depth planes in which the target appeared. Presumably his results involved less change in lightness than those reported here, because even when his target and inducing fields were coplanar, they were still somewhat separated retinally. In addition, both of his inducing fields had luminances greater than that of the target whereas, in the present studies, the luminance relationship of the target and the surrounding coplanar surfaces reversed for the two different conditions of each experiment.
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Ionochromic Behavior of Gecko Visual Pigments

Abstract. *Digitonin extracts of the retina of* Gekko gekko *prepared to minimize the presence of chloride ions show the photopigment to be at about 490 nanometers rather than at 521 nanometers, the position found for the same pigment in situ. The addition of chloride to the extract causes a bathochromic shift in spectral absorbance, the magnitude of the shift being related to the concentration of chloride, within limits. The effect is a specific one, and of all the anions tested only bromide causes a similar bathochromic shift. The nature of the cation is not involved since the same action is produced by the chlorides of sodium, lithium, potassium, rubidium, cesium, calcium, magnesium, beryllium, lanthanum, and choline.*

Proteins that respond selectively or specifically to inorganic ions are of special interest to biological scientists, especially if these proteins are derived from excitable membrane systems. At this time I wish to report the behavior of a visual pigment whose color is altered reversibly by certain specific inorganic anions. This pigment, a retinal-based chromoprotein from the retina of *Gekko gekko*, has a spectral absorbance maximum of 521 nm within the outer segments (*1*). In aqueous digitonin solution the spectral maximum varies according to particular physical and chemical conditions of the extract. One of these conditions is the inorganic ion composition.

The main effect is a chloride response (Fig. 1) that can be elicited in the following manner. The photopigment is extracted out of the visual cells with 1 or 2 percent digitonin made up either in tris-maleate buffer (pH 7.2) or in borate buffer (pH 8.8). Prior to extraction the isolated retinas are washed once with distilled water and placed in 4 percent potassium alum for 3 to 6 hours at 5°C. The alum-hardened retinas are washed twice with double-distilled water and once with the buffer, and then extracted with 0.1 to 0.2 ml of digitonin per retina. During these operations the temperature is kept close to 5°C. Extracts prepared in this manner never have absorbance maxima (λ_{max}) close to 521 nm, but instead the spectra are located at shorter wavelengths. For the extract represented in curve 1 (Fig. 1) the λ_{max} is at 487 nm, typical for this procedure. The spectral absorbance is not stabilized at this location, for on adding a drop of the same buffer containing NaCl (*2*) the spectrum shifts rapidly toward 521 nm (curve 2, Fig. 1). This shift is quantitatively related to the NaCl concentration, a definite shift appearing with about $4 \times 10^{-5}M$ NaCl and increasing in magnitude up to about $2 \times 10^{-2}M$ (Fig. 2). It seems likely, therefore, that the photopigment extracted in the manner described exists in a deficient state in which its spectral absorbance lies some 25 to 30 nm toward lower wavelengths from the normal 521-state. Addition of NaCl repairs the deficiency but the λ_{max} never shifts beyond 521 nm. While in the hypsochromic, deficient state the pigment is still photosensitive and the shape of the absorbance curve is that of a Dartnall nomogram type. The chloride shift is completed within the time required to add the NaCl and to remeasure the spectral maximum, and is reversed as quickly by diluting the extract with chloride-free buffer. This reversibility is best demonstrated by adding NaCl to a concentration that causes a shift of only 5 to 10 nm and then diluting. In this way the operation is kept within the steep, functional portion of the curve in the inset (Fig. 2).

The chloride effect appears to be independent of the nature of the cation coupled with the chloride, and I have obtained the same shift in the presence of sodium, potassium, lithium, rubidium, cesium, calcium, magnesium, beryllium, cadmium, and lanthanum. Even the organic chloride, choline chloride, produced the same bathochromic shift. Of the anions tested (bromide, phosphate, borate, thiocyanate, nitrate, sulfate, fluoride, and iodide) only bromide elicited the same response as chloride. The effect is anion-specific and the behavior toward the halides suggests some role for ion size. The small fluoride ion is inert as is the large iodide ion, while the intermediate chloride and bromide ions are the active ones (Figs. 1 and 3).