1% agarose gel, transferred to a nylon membrane overnight in 6× saline sodium citrate (SSC), and hybridized overnight with a radiolabeled complementary DNA probe for rat Cx32 (7). The blot was washed at a final stringency of 0.2× SSC for 30 min at 65°C and exposed to x-ray film with an intensifying screen for 5 days at −80°C. Approximately equal loading of samples in each lane was assured by comparison of the intensity of ethidium-stained ribosomal RNA bands in the gel and by rehybridization of the membrane with a complementary DNA probe for the housekeeping gene glyceraldehyde-3-phosphate dehydrogenase.

20. Blood was obtained from CMTX patients by informed consent, and genomic DNA was isolated from venous blood by standard methods (4). The connexin32 coding region was amplified with PCR with various primer sets spanning this region. The segment including bases 54 to 359 (13) was amplified with the primer set 5′-TGAGGCAGGATGAACTGGACAGGT-3′ (bases 54 to 77) and 5′-TTGCTGGTGAGCCACGTGCATGGC-3′ (bases 336 to 359), and the segment including bases 273 to 938 was amplified with the primer set 5′-ATCTCCCATGTGCGGCTGTGGTCC-3′ (bases 273 to 296) and 5′-TGGCAGGTTGCCTGGTATGT-3′ (bases 919 to 938). Twelve picomoles of each primer set was used in a reaction volume of 100 μl with 100 to 200 ng of genomic DNA as a template. PCR conditions for the first primer set were 94°C for 7 min; 94°C for 30 s, 65°C for 30 s, and 72°C for 30 s (35 cycles); and 72°C for 10 min. Conditions for the second primer set were 94°C for 5 min; 94°C for 1 min, 63°C for 1 min, and 72°C for 1 min (35 cycles); and 72°C for 10 min. Amplified products were purified with the Gene Clean protocol (BIO 101) and subsequently used as templates for sequencing at 20 to 50 ng per reaction. The primers listed above were used for sequencing; in addition, the following primers were used for bases 273 to 704 and 635 to 933, respectively: 5′-GATGATGAGGTACACCACCT-3′ (bases 685 to 704) and 5′-CGTCTTCATGCTAGCTGCCTCTGG-3′ (bases 635 to 658). The sequencing reactions were set up according to manufacturer's recommendations with the Sequenase Version 2.0 kit (U.S. Biomedicals) with minor modifications (10 pmol of primer per reaction; 50°C termination for 5 min).

21. Abbreviations for the amino acid residues are: A, Ala; C, Cys; D, Asp; E, Glu; F, Phe; G, Gly; H, His; I, Ile; K, Lys; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; R, Arg; S, Ser; T, Thr; V, Val; W, Trp; and Y, Tyr. Mutations are indicated with the single-letter code; thus, $Gly^{12} \rightarrow Ser$ is given by G12S.

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24. Adult rat sciatic nerve was fixed in 1.6% formaldehyde in Hank's buffered salts (Gibco) for 1 hour at room temperature. The tissue was then transferred to tris-buffered saline (TBS) and incubated for 2 hours at 4°C, followed by incubation in 0.5 M sucrose overnight for cryoprotection. Samples were quick-frozen in OCT (Miles Scientific, Elkhart, IN) with liquid freon, and 10- to 12-μm cryosections were collected. The sections were mounted on slides, air dried, then incubated in acetone for 5 min at room temperature. After rehydration in TBS for 5 min, the sections were blocked for 15 min in 2% fish skin gelatin (Sigma), 1% normal goat serum, and 0.25% Triton X-100 in TBS (blocking solution), then incubated with a 1/1000 dilution of Cx32 antiserum (anti-98/124) [D. A. Goodenough, D. L. Paul, L. Jesiatis, *J. Cell Biol.* **107**, 1817 (1988)] in blocking solution for 1 hour at room temperature. The sections were washed twice in 50 ml of TBS with 0.25% Triton X-100 and once with TBS, then incubated with 1/500 rhodamine-conjugated goat antibody to rabbit (Pierce) in blocking buffer. The sections were washed and mounted for immunofluorescence microscopy as described (12).

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Perceptual Organization and the Judgment of Brightness

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The perceived brightness of a gray patch depends on the surrounding context. For example, a medium-gray patch appears darker when placed on a bright background and brighter when placed on a dark background. Models to explain these effects are usually based on simple low-level mechanisms. A new set of brightness illusions cannot be explained by such models. In these illusions, the brightness percept is strongly influenced by the perceptual organization of the stimuli. Simple modifications of the stimuli that should have little effect on low-level mechanisms greatly alter the strength of the illusion. These effects may be ascribed to more complex mechanisms occurring later in the visual system.

A gray patch appears brighter when viewed against a dark background and darker when viewed against a bright background. This effect, known as "simultaneous contrast," is one of many brightness effects that are commonly attributed to simple visual processes, such as the lateral inhibition that occurs in the retina (*1*), whereby cells in one region inhibit cells in adjacent regions. Another class of models, known as retinex models, have been offered to explain the perception of surface colors in terms of the propagation of information about local luminance changes (*2*). Both kinds of model are founded on low-level processes that involve simple interactions between neighboring neurons. The outputs of such models should be unaffected by a display's higher-level perceptual properties, such as the perceived depth and form. But we have found that a change in perceptual interpretation can have a profound effect on the judgment of brightness.

Following the customary terminology (*3*), lightness refers to the apparent reflectance of a surface in a scene, whereas brightness refers to the apparent luminance of a patch in the image itself. That is, an observer in a brightness experiment is asked to judge the shade of ink on the page but not to make any inferences about the surfaces of the objects portrayed. In Fig. 1, patches a and c are obviously brighter than patch b because they are seen to have higher luminance on the page. Patch c also appears lighter than patch b, in that the three-dimensional (3D) physical surface represented by c seems to be painted a lighter shade of gray than b. On the other hand, patches a and b seem to have the same lightness, as they appear to represent surfaces painted the same shade.

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Lightness judgments can be influenced by high-level perceptual factors (*4*, *5*). Figure 1 makes the point with a simple image: The geometry leads to a 3D interpretation that causes patch b to match patch a in apparent reflectance (lightness) but not to match patch c, which has the same luminance as patch a. Lightness can also be affected by the perception of surface curvature (*6*). These various lightness phenomena cannot be explained by low-level models. Because an observer in a lightness experiment is judging properties of the objects portrayed, rather than merely estimating the brightness of the ink on the page, one might not be surprised to find that low-level mechanisms fail to explain the results.

In our experiments, we used simple stimuli displayed on a computer screen and used the more "sensory" brightness judgment

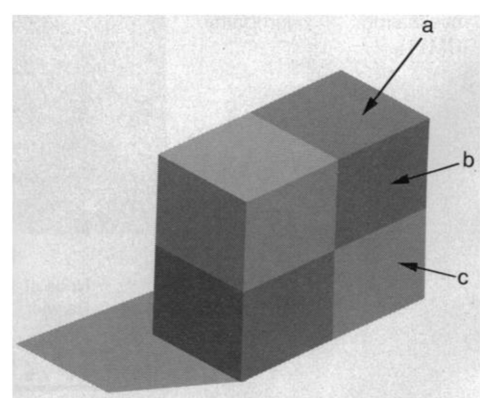

Fig. 1. Distinction between lightness and brightness. Patch c is both lighter and brighter than b. Lightness refers to apparent reflectance of a perceived surface; brightness refers to the apparent luminance of a patch in an image.

rather than the more "perceptual" lightness judgment. Thus, both the stimuli and the task favored the success of low-level models. Nonetheless, the low-level models failed.

The "wall-of-blocks" pattern (Fig. 2A) is built from the two square tiles shown above it. Diamond a_1 looks darker than diamond a_2 although it is actually the same. One might propose that this is an ordinary simultaneous contrast effect because the region surrounding a_1 is of higher mean luminance than the region surrounding a_2. A modified pattern (Fig. 2B) was used to test this proposition. This pattern is made of tiles containing the same gray shades as before but with a hexagonal shape. The gray shades and the adjacency relationships remain exactly as before. The new pattern differs only in that the straight horizontal strips of Fig. 2A are now bent into zig-zags. The illusion is significantly reduced: b_1 and b_2 appear almost the same.

To quantify the brightness illusions, we asked subjects to perform a nulling task. They adjusted the luminance of the diamonds in the middle row to cancel the illusion and attain a subjective match with the diamonds in the top and bottom rows. The pattern was presented for 0.5 s, and the subjects adjusted the luminance up or down after each trial. The brief presentation was used to prevent extended scrutiny of the patterns. The images were shown on a Macintosh II computer equipped with a calibrated Sony Trinitron monitor and an eight-bit video card. Six naïve subjects made three judgments of each pattern; they were told to judge brightness of the patches on the screen and not to judge the lightness of the 3D surfaces portrayed.

The top and bottom rows of diamonds had a luminance of 10.7 mL. For Fig. 2A, the perceived match occurred when the center row had a luminance of 7.9 mL, that is, when the rows were in a 1.35 to 1 ratio, for a 35% effect. For Fig. 2B, the match occurred at 9.7 mL, or a 1.10 to 1 ratio, for a 10% effect. If we take the ratios as a nominal measure of illusion strength, we can say that the brightness illusion in Fig. 2A was over three times as large as that in Fig. 2B.

Figure 2A is seen as a wall of cubical blocks viewed through light and dark horizontal strips, as if there were light and dark transparent filters interposed between the observer and the blocks. The luminance may be perceptually divided between the strips and the blocks (7) so that a diamond of a given luminance can be seen either as a dark diamond behind a light strip or a light diamond behind a dark strip. The perceptual inferences apparently influence the brightness judgments. In Fig. 2B, there is no impression of transparency and thus only a small residual brightness illusion, which might be attributed to low-level processes such as those underlying standard simultaneous contrast effects.

It is plausible that the configurations of

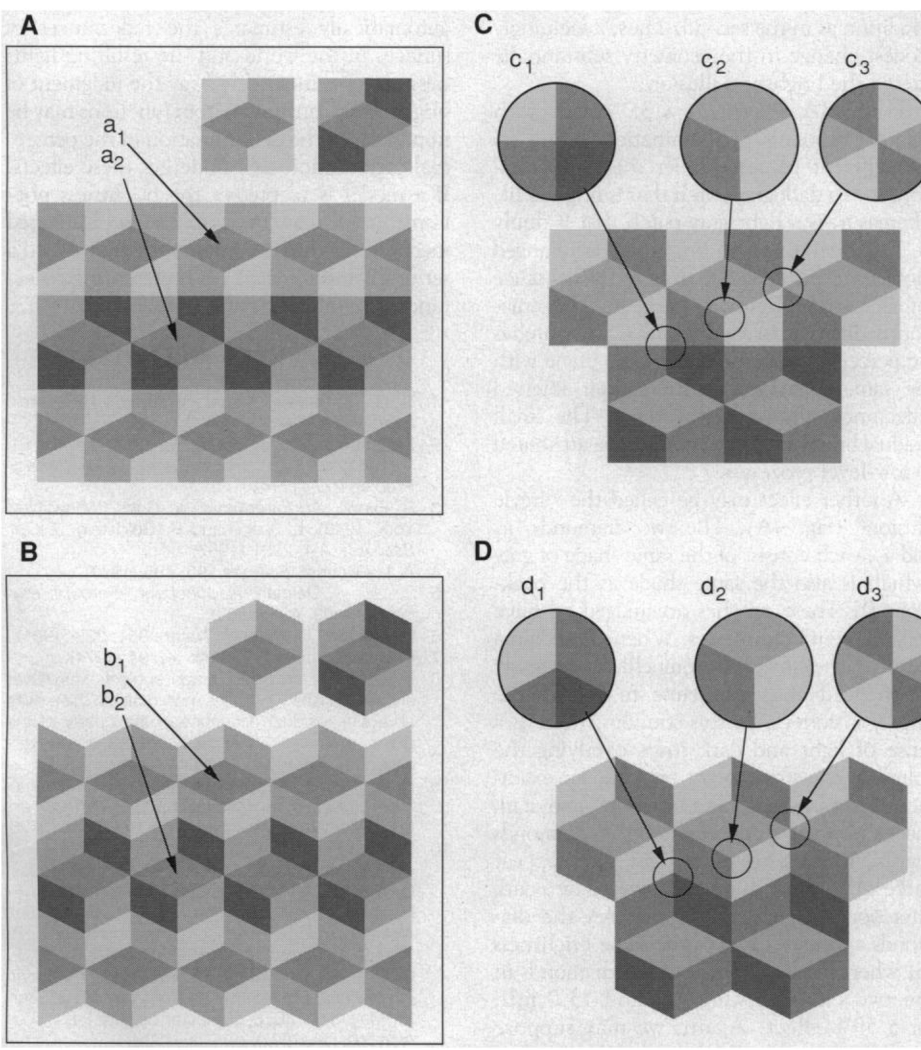

Fig. 2. Effect of perceived transparency on brightness judgments. (**A**) A pattern made by repeating two square tiles. A brightness illusion results: The diamonds a_1 and a_2 are the same shade of gray but appear quite different. (**B**) Pattern generated with hexagonal tiles with the same shades of gray as the pattern in (A), producing the same edge relationships but a reduced brightness illusion. (**C** and **D**) The junction types found in the two figures.

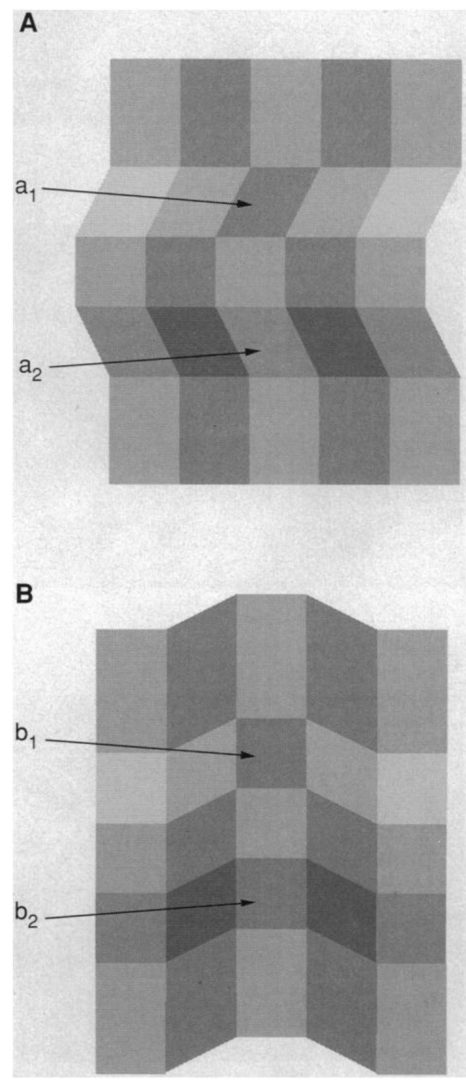

Fig. 3. Effect of perceived shading on brightness judgments. (**A**) The patches a_1 and a_2 are the same shade of gray, but a_1 appears much darker than a_2. (**B**) Pattern made of patches with the same gray shades as in (A) but with different geometry, leading to a different interpretation and reduced brightness illusion.

gray-level junctions are critical for determination of the perceptual organization and thereby the lightness and brightness percepts. When the X junctions of Fig. 2A (marked c_1 in Fig. 2C) are bent into the Ψ junctions of Fig. 2B (marked d_1 in Fig. 2D), a new set of constraints are imposed, leading to a new interpretation. Thus, one promising class of models for this reorganization would involve the propagation of constraints from gray-level junctions.

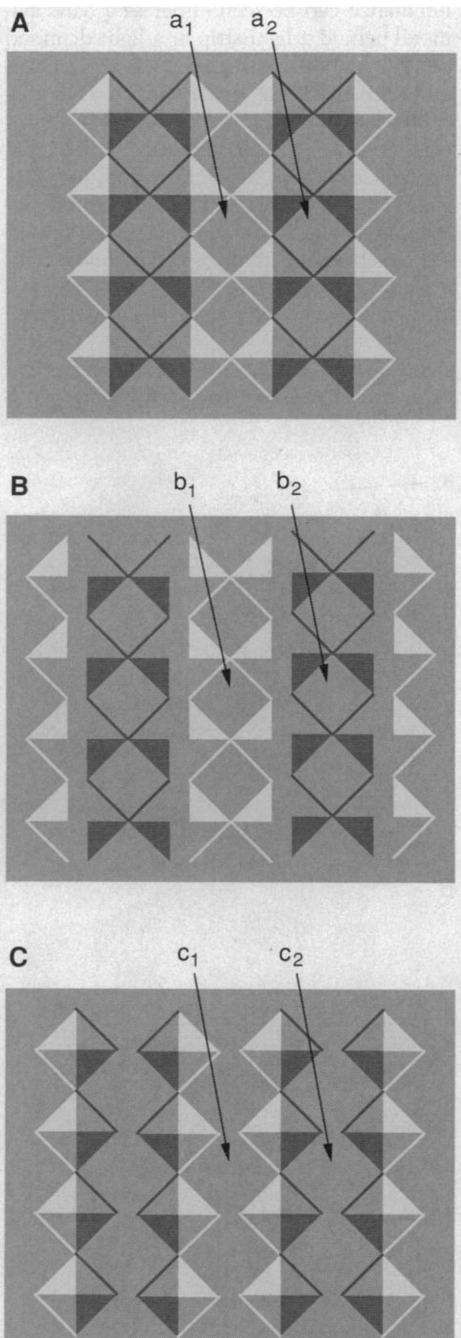

Fig. 4. Variants of the argyle illusion. **(A)** The basic pattern for generating the illusion. **(B)** The same pattern as (A) with the inducing elements spread apart so as to destroy the sense of transparency. The illusion is reduced. **(C)** The same pattern with the inducing elements spread apart so as to retain the sense of transparency. The illusion remains.

A second example is shown in the "corrugated plaid" pattern (Fig. 3). Each figure is derived from the same 5 by 5 matrix of gray levels in the same orientation. That is, the upper left patch is the same gray shade for each, and so on, in raster sequence (note the images are not rotated versions of each other). The only difference is in the shapes of the patches. The gray levels and the edge-adjacency relationships are identical in the two figures.

A strong brightness illusion is produced in Fig. 3A: Patch a_1 appears much darker than a_2 even though it is in fact the same. On the other hand, Fig. 3B displays only a weak brightness illusion: Patch b_1 appears only slightly darker than b_2. The nulling task verified this effect: When a_2 had a luminance of 8.1 mL, a_1 was judged to match when its luminance was 13.8 mL, for a 70% effect; but b_1 was judged to match b_2 when its luminance was 9.7 mL, for a 20% effect. As before, the effect was over three times as large in the first condition as in the second. Thus, a seemingly modest change in the geometry substantially altered the brightness illusion.

Figure 3A is seen as a 3D object with different amounts of illumination falling on the different planes. Under this interpretation, a_1 is a dark gray patch that is brightly lit, whereas a_2 is a light gray patch that is dimly lit. The fact that the brightness is changed suggests again that the inferred reflectance influences the brightness estimate. The situation is different in Fig. 3B. The two patches are perceived as lying in the same plane with the same illumination; thus, their inferred reflectances should be the same. The small residual brightness illusion might be attributed to low-level processes.

Another effect may be called the "argyle illusion" (Fig. 4A). The two diamonds, a_1 and a_2, each consist of the same shade of gray (which is also the same shade as the background). These patches are judged to have very different brightnesses. When viewed on a monitor, the effect is so compelling that many experienced observers refuse to believe the display is correct. In this stimulus, there is a sense of light and dark strips overlying the columns; the strips might be seen, for example, as transparent filters of light and dark shades. Subjects report that the diamonds that seem covered by a light filter appear darker, and those that seem covered by a dark filter appear brighter. For Fig. 4A the diamonds appeared to be of the same brightness (8) when the luminances of the diamonds in the two columns were 8.2 and 13.0 mL, for a 59% effect. Again, we may suppose that the inferred reflectance of the patch is altered by the process of discounting an overlying filter and that this influences the brightness judgment.

The sense of transparency is destroyed if the inducing elements are spread apart (Fig. 4B). The illusion is substantially reduced: The diamonds b_1 and b_2 were judged to match when their luminances were 9.8 and 11.3 mL, respectively, for a 15% effect. The illusion strength is reduced to less than one third of its original size.

The inducing elements can also be spread apart in such a way that the impression of transparency is retained (Fig. 4C). In this case, the regions marked c_1 and c_2 appear to have significantly different brightnesses, in spite of the fact that they are part of a continuously connected region of constant luminance. The sense of transparency tends to be reinforced by the X junctions, which are maintained in Fig. 4, A and C, but disrupted in Fig. 4B.

All of the phenomena discussed above lead to the same conclusion: Brightness judgments cannot be simply explained with low-level mechanisms. Geometrical changes that should be inconsequential for low-level mechanisms can cause dramatic changes in the brightness report. It is as if the visual system automatically estimates the reflectances of surfaces in the world and the resulting lightness percepts inevitably sway the judgment of brightness. Constraints from junctions may be important to the determination of the perceptual organization that underlies these effects. If a model is to predict the brightness phenomena, it may need to use sophisticated mechanisms that decompose the image into a set of intrinsic images (9) representing reflectance, illumination, and transparency (*10*).

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