A probabilistic explanation of brightness scaling

Surajit Nundy*†‡ and Dale Purves*

*Department of Neurobiology, Duke University Medical Center, Durham, NC 27710; and †Washington University School of Medicine, St. Louis, MO 63110

Contributed by Dale Purves, August 27, 2002

The perceptions of lightness or brightness elicited by a visual target are linked to its luminance by a nonlinear function that varies according to the physical characteristics of the target and the background on which it is presented. Although no generally accepted explanation of this scaling relationship exists, it has long been considered a byproduct of low- or mid-level visual processing. Here we examine the possibility that brightness scaling is actually the signature of a biological strategy for dealing with inevitably ambiguous visual stimuli, in which percepts of lightness/brightness are determined by the probabilistic relationship between luminances in the image plane and their possible real-world sources.

lightness | luminance | context

he relationship between the physical intensity of a light stimulus and its subjective perception has been debated since at least the middle of the 19th century (1–3). The central problem in ongoing attempts to rationalize this linkage has been the variability between luminance (i.e., the intensity of the light returned to the eye from object surfaces or light sources) and the sense of lightness or brightness elicited by the stimulus. Although intuition suggests that these sensations should scale in direct proportion to the intensity of the light that activates retinal receptors, the intensity of the sensation varies in a manner that is difficult to rationalize (Fig. 1). Thus, when targets are presented as luminance increments relative to a given background luminance, the scaling relationship is a power function referred to as Stevens' Law. Despite the canonical implication, the exponent of this function varies widely according to the size of the target, the duration of its presentation, the nature of the source, and other experimental variables (2, 4). Moreover, the relationship changes markedly and systematically as function of the intensity of the background luminance (6, 7). Although no consensus exists about the basis of these phenomena, many authors have interpreted them as consequences of neural processing early in the visual pathway (8–10).

Although these effects are certainly initiated by low- and midlevel neural processing, the observed peculiarities of scaling may signify an important purpose. The possibility that we examine here is that the relationship between luminance and the resulting perceptions of lightness or brightness reflects a probabilistic strategy of visual processing demanded by the inherent ambiguity of visual stimuli. In these terms, the perceived intensity of any luminant stimulus is determined by the probability distribution of the possible underlying sources, or, more precisely, by the probable contributions of reflectance (R) and illumination (I) to the luminances experienced in the past (11). The amount of light associated with any part of a scene—that is, its local luminance—is typically the product of the I of that region and the R efficiency function(s) of the relevant object surfaces (12). In consequence, an infinite set of possible combinations of I and R could have given rise to any particular value of luminance. Here we use this simple physical relationship to explore how the major features of the luminance/brightness scaling relationship could be rationalized in terms of the possible sources of a luminant stimulus.

Materials and Methods

All modeling, testing, and analysis were performed on Power Macintosh DP/500 MHz/G4 and SP/350 MHz/G3 computers (Apple Computer, Cupertino, CA) and Sony Trinitron GDM-

F500R cathode-ray tubes (Sony, Tokyo) by using the programming packages MATLAB (Mathworks, Natick, MA), PSYCHOPHYSICS TOOLBOX (13), OPENGL (www.opengl.org), and CODEWARRIOR 6.0 (Metrowerks, Austin, TX).

Subject Testing. The observers were the two authors and three naïve subjects. Each subject was adapted to the ambient light of the darkened test room before each of three blocks of trials in which the brightness scaling tasks were presented pseudorandomly. The testing monitor was viewed from 60 cm, at which distance the screen occupied 25° (V) \times 36° (H). The task for all tests was to adjust the test stimuli to make equal brightness steps between adjacent targets, taking as much time as needed in making this judgment.

For the stimuli illustrated in Fig. 3A, subjects selected the patch whose brightness they wanted to change with a mouse, and altered its luminance by pressing the up-down arrows on a keyboard; each keystroke generated a step change in the luminance of the selected patch by a fixed amount (2 cd/m²) over the luminance range presented. The step values were calculated on the basis of the generation of a look-up table of luminance (measured with a photoluminometer; Graseby Optronics, Orlando, FL) plotted against frame buffer values across the range tested. The extreme values of the targets corresponded to 1.6 cd/m² for the lowest value tested and 111 cd/m² for the highest. Once calculated, this look-up table allowed us to convert RGB values to luminance, to change the luminance by a fixed amount, and to convert the new luminance values back into RGB values. For the test stimuli with richer contextual information illustrated in Fig. 3B, subjects moved the test targets interactively, as in a video game. The target luminances were randomly arranged for each test, and had the same area when placed in the set position and the same range of values as the possible adjustments in the standard scaling paradigm. Finally, the local and global spatial average of the target surrounds was identical in both types of tests for all three levels of background luminance tested (28.9, 56.3, and 83.6 cd/m²).

Statistical Analysis. A pairwise, two-way ANOVA test was performed between data sets comparing subject performance in the presence and absence of contextual information at the same background luminance at the three different values of background luminance used. In all cases, subject performance came from different normal distributions and had P values < 0.05.

Results

Generation of Luminance Values. If I and R are assumed to be independent variables, they can be plotted as orthogonal dimensions of a space that, to a first approximation, represents human experience with the relative contributions of these factors to the luminance of a target in any given scene (Fig. 2). Thus, the dimensions of this space are relative I and relative R, defined as the I and R values of a particular target relative to the average values of I and R of the scene in which the target is presented. To facilitate the analysis of the relative contributions of these two primary determinants of luminance, we have omitted from consideration the influence of transmittance, the distance of the objects from the observer, any differences in the distribution of the spectral power

Abbreviations: I, illumination; R, reflectance.

[‡]To whom correspondence should be addressed. E-mail: nundys@neuro.duke.edu.

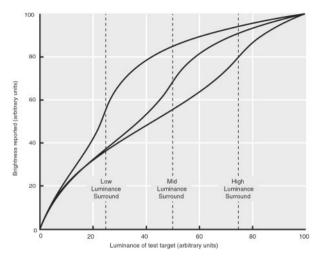


Fig. 1. The relationship between luminance and lightness or brightness (generally called "brightness scaling"), summarizing the major features that have been described in many different studies (graph shows scaling tests at three levels of background luminance, indicated by the three vertical lines). These features include the nonlinearity of the relationship; the more-or-less opposite form of the function for increments and decrements [the relationship for increments of the test target above background has been called Stevens' Law (2, 18)]; the different shape of the relationship as a function of the background luminance; and the steeper slope of the relationship when the luminance of the target is near that of the background. The functions illustrated here were generated by the Naka-Rushton equation, as modified by Whittle (6, 14); similar data have also been reported (7). The units are arbitrary, but linearly scaled.

(color), the shape of object surfaces, and a host of other factors that are less central to the determination of luminance than R and I. Their inclusion changes the dimensionality of the analysis, but not the basic argument. Each of the isoluminance lines in Fig. 2A represents all of the possible (I, R) values that could have given rise to that luminance. It should be clear that the space illustrated in Fig. 2A (and see Fig. 4A) is a didactic representation of the relative values of the I and R of a target with respect to the average values in the scene; thus, these values cannot be linearly mapped onto the physical relationship of I and R as such. The likelihood that any particular (I, R) pair along an isoluminance line is actually the source of the luminance of a target is, in this framework, a function of the probability distribution of the (I, R) values over the line, given a particular image. (This probability can be thought of as a third dimension of the space.)

Thus, the framework in Fig. 2A provides a simple way of exploring how the luminance-brightness relationship would be expected to change as a function of the possible sources of target and background luminance. If, for example, the conditions for a given brightness scaling test changed the probable contribution of either I or R to the luminance of the target, then the probability distribution of the possible (I, R) values along any isoluminance line in Fig. 2A would change accordingly. More specifically, if the change in experimental conditions increased the probability that the change in target luminance derived predominantly from changes in R, then the central tendency (i.e., the mean, median, or mode) of the probability distribution of the possible (I, R) combinations that could have given rise to a particular target luminance would shift parallel to the blue line in Fig. 2A. By the same token, if the experimental conditions increased the probability that the change in luminance derived predominantly from changes in surface I, then the central tendency of probability distributions of the (I, R) values would shift parallel to the green line. If, however, the experimental conditions provided little or no information about the generative sources of the luminance value (or if the information

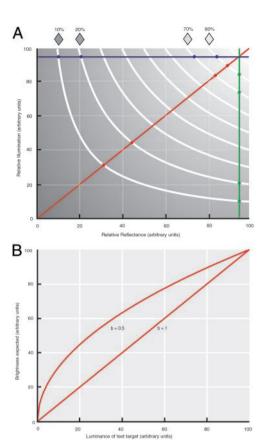


Fig. 2. A probabilistic framework for evaluating the generative sources of luminance. (*A*) Space defined by all the possible combinations of I and R that could have generated particular values of luminance. The relative Rs (*x* axis) and relative Is (*y* axis) are plotted in arbitrary, linearly scaled units relative to the average values of these parameters in a scene (see text). (*B*) The scaling relationships between luminance and brightness predicted by the probabilistic framework (*A*). If the information in the stimulus is consistent with the generative source of the target luminance being predominantly I or R, the exponent of the function should approach 1 (i.e., should be determined by distance as a function of luminance along the green or blue line in *A*); if, on the other hand, the information is consistent with a roughly equal contribution from these sources, then the exponent should approach 0.5 (i.e., should be determined by distance as a function of luminance along the red line in *A*).

indicated that the likely contributions of I and R were about equal), then the central tendency of the distribution of the possible (I, R) combinations underlying the I value would be those more centrally located along any particular isoluminance line (as indicated by the red line in Fig. 2A). Thus, the Euclidean distance between physically proportional luminances in this space varies as a function of any factors that change the probability of the generative sources of those luminances. For instance, the distance between the 10% line and the 20% isoluminance line is the same as the distance between the 70% and 80% lines when distances are measured along a line parallel to either the R or I axis (see dots along the blue and green lines in Fig. 2A). If, however, the distance between isoluminance lines is measured along a line equidistant from the axes of R and I, then the distance between the 10% and 20% isoluminance lines is greater than the distance between the 70% and 80% lines (see dots along the red line).

Accordingly, if the information in a scene were to bias the probable sources of luminance values toward either the I or the R axis, and if the sensations of lightness/brightness elicited by any two luminance values are a consequence of the distances between the probable (I, R) sources in this space (the issue that is subsequently tested here), then differences in the brightness of the targets in a

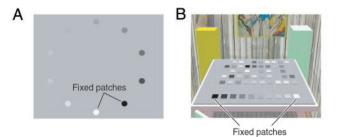
scene should vary according to the distance along a line running more nearly parallel to the axes of I or R (i.e., parallel to the blue or green lines in Fig. 2A). If, on the other hand, the information in the scene biased the central tendency of the probability distributions of the possible sources of luminance values toward (I, R) combinations in the middle of this space, then the brightness difference elicited by different luminances should be proportional to the distance along the red line in Fig. 2A.

Rationalizing the Phenomenology of Brightness Scaling. Given the phenomenology of brightness scaling illustrated in Fig. 1, the following features would have to be explained in these terms: (i) the power function observed when luminance increments above the background luminance are presented and the sensitivity of this relationship to various experimental conditions (i.e., Stevens' Law); (ii) the different scaling relationship observed when decrements of the target relative to the background are tested instead of increments; (iii) the marked shift in the overall scaling function when the intensity of the background is altered; and (iv) the increase in the slope of the scaling relationship when the luminance of the target is close to the luminance of the background (the so-called "crispening effect").

Stevens' Law and Its Sensitivity to Experimental Conditions. The framework illustrated in Fig. 2A predicts a power relationship between luminance and lightness/brightness whose exponent should vary according to the probable source of the test stimulus with respect to the relative contributions of I and R (Fig. 2B). Thus, for a series of test targets whose luminances are all above the background, the exponent of luminance/brightness scaling should approach unity if the information in the scene is made consistent with either R or I as the probable source of the differences in a series of luminances. Conversely, the exponent should approach 0.5 if the information in the scene is consistent with an approximately equal contribution of I and R to the possible (I, R) combinations underlying the stimulus (or if such information is simply lacking).

To test these predictions, subjects were presented with 10 patches on a computer screen with a minimum of information concerning the relative contribution of I and/or R to the luminances of the target stimuli (Fig. 3A). This experimental circumstance is thus similar to a standard scaling test in which increments (or decrements; see below) of target luminance are examined with respect to a given background (see Fig. 1). Two patches were fixed at the minimum and maximum gray levels tested; the gray levels of the eight intervening patches could be changed to match any of 50 linearly distributed luminance values. The participants' task was to adjust the eight patches in the intervening series such that brightness of adjacent patches increased in equal steps (see Materials and Methods). The results, as expected, follow the curves in Fig. 1 for these conditions (compare the red curve in Fig. 3C with the corresponding curve in Fig. 1); moreover, for the observed function follows Stevens' Law with an exponent of about 0.5 (compare the upper portion of the red curve in Fig. 3C and the corresponding function in Fig. 1).

We then asked whether the addition of contextual information that altered the probability distribution of the possible sources of the luminance values in such tests would also change the scaling relationship in the manner predicted by the analysis illustrated in Fig. 2. For this purpose, a scene with 50 objects having the same area as the patches in the standard type of scaling test illustrated in Fig. 3A were presented in a random array (Fig. 3B). The patches varied in identical steps over the same luminance range as the steps in the standard scaling test, and were shown on a background of the same local (2–3° of visual field) and global (average over the whole monitor) spatial luminance. Subjects interacted with this 3D scene in real time, which increased the sense of immersion in an actual scene, and thus the plausibility of patches being uniformly illuminated. The parallel task in this case was to select eight objects from



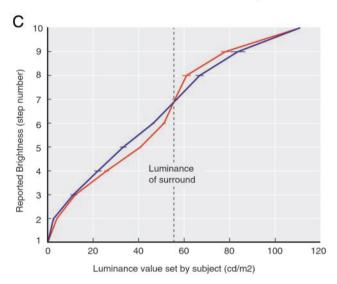


Fig. 3. Comparison luminance/brightness scaling in scenes that contain information that differently biases the probability distribution of the possible (I, R) combinations that could give rise to the luminances in the test series. (A) Scene in which the minimal information is consistent with a more-or-less equal contribution of I and R to the luminance values in the test series. (B) Scene in which the information is consistent with reflectance differences as the predominant factor giving rise to the luminance differences in the test target series. (C) The results of the same scaling task in these two conditions; the red line shows performance in response to the stimulus in A, and the blue to the stimulus in B. Error bars shown are standard errors of the mean.

the array and place them between two flanking objects fixed at the maximum and minimum grayscale values, so that the brightness increments between adjacent patches again appeared to be equal. The overall scaling relationship determined under these conditions (the blue line in Fig. 3C) is more nearly linear, the exponent of the function for the incremental portion of the curve (i.e., the part specifically pertinent to Stevens' Law) approaching unity (≈0.8 compared with about 0.5 for the corresponding portion of the red line in Fig. 3C).

These results are consistent with the conclusion that: (i) Stevens' Law reflects the relationship between the generative sources of luminance, as illustrated in Fig. 2; and (ii) the sensitivity of the exponent to experimental conditions is explained by the influence of contextual information in the scene on the probability distribution of the possible physical sources of any particular luminance (see Discussion).

The Different Scaling Relationship for Increments and Decrements.

We next examined the rationale in these terms for the scaling relationship when stimulus decrements with respect to the background luminance are tested rather than increments [a condition not examined by Stevens, but reported by others (6, 14)]. The space for decrements (comparable with the didactic space illustrated for increments in Fig. 2A) is shown in Fig. 4A; the luminance/brightness relationship that would be expected under these

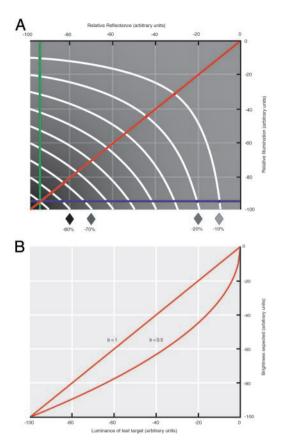


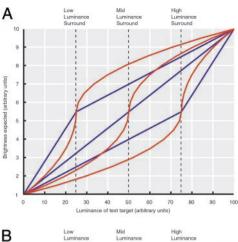
Fig. 4. A probabilistic framework for the generative sources of luminance. when the values of the test target series are less than the values of the background (generally referred to as testing "decrements" rather than "increments"). (A) The relationship of R and I in this circumstance (the decrements are necessarily indicated here by negative numbers; compare Fig. 2). (B) The scaling relationship predicted on this basis (compare Fig. 1).

circumstances, which is opposite that for increments, is shown in Fig. 4B (compare Fig. 2B).

This expectation is consistent with the observed relationship reported in tests where decrements have been measured (see also the decremental portion of the red curve in Fig. 3C). Moreover, when we examined the decremental scaling function with scene information that biased the probable generative source toward the contribution of R to the target luminances in the stimulus series, the slope of the relationship shifted in the expected direction. (The red and blue curves in the decremental portion of the tests illustrated in Fig. 3C should be compared with the predicted functions in Fig. 4B.) The only aspect of the observed relationship not predicted by the model in Figs. 2 and 4 is the scaling relationship at very low levels of I (see *Discussion*).

The Shift in Scaling as a Function of Background Intensity. The third aspect of brightness scaling that requires an explanation is the marked shift in the function induced by altering the background of the target luminances in a test series.

To examine this issue in terms of the model in Fig. 2, we first considered how the (I,R) pairs that could underlie any value of target luminance are influenced by the average values of luminance in the scene (i.e., by the background luminance). Because the average luminance of any scene varies, the relative size of the space for increments and decrements illustrated in Figs. 2A and 4A necessarily changes as the position of the origin is shifted one way or the other. (Recall that the origin in these figures is defined by the background luminance.) Thus, as illustrated in Fig. 5A, changing the background changes the expected scaling relationship in a manner



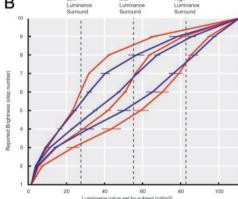


Fig. 5. Brightness scaling as a function of background luminance. (A) The predicted scaling relationships for different values of average luminance when the luminance differences in the target series are relatively unbiased with respect to generative sources (red lines), and when they are biased toward reflectance differences as the predominant factor in the differences (blue lines). The three pairs of red and blue lines correspond to the predicted relationships with different average background luminances indicated; values have been normalized to the midpoint of this space. (B) The observed effects on brightness scaling when the luminance of the background of a target is varied. The three different sets of red and blue lines show the judgments made by the subjects when the luminance of the background in the test series had a low, middle, or high value (indicated by the vertical lines). The red lines indicate subject performance in response to the context-poor scene illustrated in Fig. 3A at three different background luminances; the blue lines are the performances in response to the context-rich scene in Fig. 3B at the same three levels. Error bars shown are standard errors of the mean. The results shown in Fig. 3 with mid-level luminance background are included in B for comparison.

consistent with the known influence of background luminance (see ref. 14).

To test this explanation of the different luminance/brightness relationships elicited in the presence of different background luminances, subjects were given the tests again, but with information now biased toward reflectance differences as the predominant cause of the different luminances in the stimulus series (Fig. 3B). The result is shown by the blue lines in Fig. 5B; the scaling relationships in the absence of this biasing information are indicated by the red lines in Fig. 5B. A comparison of the curves described by the red and blue lines in Fig. 5B indicates that the scaling relationship at each different background shifts in the manner predicted by the model in Fig. 2 (compare the red and blue lines in Fig. 5A).

To quantify the difference elicited by these two conditions, we calculated a brightness contrast index by summing the absolute differences of the luminance values set by subjects for each of the eight brightness steps in the three different background luminances tested (see Fig. 5B). This sum was 490 ± 46 cd/m² when a minimum of information was presented about the target sources (red lines) compared with 317 \pm 18 cd/m² when the scene contained contextual information that made reflectance differences a more likely source of the stimuli (blue lines) (P < 0.05). We also tested subjects on a further paradigm in which they could move targets with the same shapes and choices of luminance (as in Fig. 3B), but with little or no other information about possible sources (as in Fig. 3A). The added ability to move these targets resulted in a reduction in the brightness contrast index (386 \pm 48 cd/m²; see above), presumably because this interaction increases the probability that the test patches are actually objects that differ in reflectance.

The Crispening Effect. Finally, we examined the possible basis for the fact that observers are more sensitive to changes of luminance when the values of a test target are close to the luminance of the background, compared with performance when the surrounding luminance differs from that of the target (see Fig. 1B).

Because the stimuli presented in standard tests of brightness scaling supply little or no contextual information that would bias the probability distribution of the possible sources toward either I or R as the basis for the luminance differences in the test series, the axis in the space illustrated in Figs. 2A and 4A along which the corresponding brightness differences are generated will tend to be along the red line (i.e., toward the central axis of the space). Moreover, the slope of the scaling relationship in this circumstance will be maximal for values of target luminance near the background, because the change in distance as a function of luminance along the red line near the origin is greatest in this region of the space (see Figs. 2B and 4B).

The crispening effect should thus be diminished or abolished if the information in the scene shifts the probability distribution of the possible sources of the luminances in the test series toward either the I or R axis of the space in Figs. 2A and 4A. As is apparent in Fig. 5B, the slope of luminance/brightness measurements at or near the luminance of the background is indeed diminished for all values of surround luminance when contextual information is added to the stimulus. (Compare the slopes of the red and blue curves in Fig. 5B at or near the point where they intercept the vertical lines indicating the average background luminance.)

Discussion

Psychophysical exploration of the scaling relationship between luminance and lightness/brightness has a long and interesting history. Since at least the mid-19th century, it has been appreciated that this linkage is nonlinear, sensitive to the circumstances of the test situation, and not easily explained (1, 15). More recent studies (reviewed in ref. 6) have sought to describe brightness scaling in terms of the receptive field properties of retinal neurons, in some cases by using a variation of the Naka-Rushton equation (8). Despite the apparent validity of these several descriptions for simple target-surround stimuli, the relationship between luminance and the perceptions it elicits in different circumstances remains unexplained.

Evidence for a Probabilistic Explanation of Brightness Scaling. In the light of this ongoing uncertainty, we have examined the relationship of luminance and brightness in a different way, namely in terms of the possible sources of the luminances giving rise to the stimulus. In pursuing this idea, we assumed that, to a first approximation, the luminances returned to the eve are the product of I and R. Although luminance clearly has many other determinants, limiting the argument to these two parameters provides a means of considering, in statistical terms, the provenance of the vast majority of luminant stimuli, and thus of relating perception to the possible sources of the visual stimulus.

Given the probabilistic framework illustrated in Figs. 2 and 4, the

relationship between luminance and brightness should (for both increments and decrements) be a power function with an exponent of ≈ 0.5 when the context of the target is consistent with approximately equal contributions from I and R (see red lines in Fig. 2A) and 4A). This relationship is, as already described, the result observed in standard tests of brightness scaling.

This framework further predicts that if a target is presented in a scene consistent with a predominant role of I or R in generating the luminance of the stimulus, the relationship between brightness and luminance should change accordingly (i.e., the exponent of the function should approach unity; see Figs. 2B and 4B). When we tested brightness scaling with contextual information that increased the probability of differences in R as the generative source, the exponent of the power relationship indeed increased in the expected manner (see Fig. 3C). (The reason for not conducting comparable tests with contextual cues about I is the difficulty presenting decrements on this basis, which thus limits testing the full range of effects.) Thus, the presumptive reason that classical tests of scaling define a more linear relationship when, for example, gray papers are used instead of a more abstract presentation is that the wealth of information in the former case biases the probability distribution of the possible sources of the different measured luminance values in the series toward generation by the reflectance differences of the pieces of paper. By the same token, the exponent of 0.5 observed when the luminance series is presented as changes in the intensity of a milky glass surface on a dark background is presumably the result of the more nearly equal (or simply uncertain) contribution of I and R to the luminances in the test series conveyed by these conditions.

The probabilistic framework outlined in Figs. 2 and 4 also predicts the observed changes in brightness of targets as a function of background luminance, and the increased discriminability of contrast when the luminance of a visual stimulus with minimal contextual information is close to that of its surround [the so-called crispening effect (14, 16, 17)] (see Figs. 3C and 5B). This framework therefore provides a rationale for the diminished crispening effect when targets are outlined by an annulus (14). The only feature not accounted for in this way is the anomalous scaling at very low levels of light [see Fig. 1; an effect apparent here and in some (14) but not all (7) previous studies]. A possible explanation of this feature in probabilistic terms is that the luminance of the stimulus at very low levels can only have been generated by a light source (i.e., no combination of R and I could have given rise to such a low target luminance vis-a-vis the background). If so, then the scaling relationship would be expected to become steeper again in this region, as it does

In short, the major features of brightness scaling that have been described over the years can be explained by a wholly probabilistic strategy of perceiving luminances whose biological rationale is the need to generate appropriate visually guided behavior in the face of stimuli whose meaning cannot be known directly (11).

Other Explanations of Brightness Scaling Phenomena. Early accounts of the nonlinearity of brightness scaling focused on fixed percentage changes in the intensity of a stimulus (Weber's Law; see ref. 1 for an extensive review). The integration of these fixed-percentage changes is a logarithmic function, leading to one of the standard ways of describing the luminance/brightness relationship (the Weber-Fechner Law). Stevens and others suggested that the intensity ratio of any two luminant stimuli was the value of interest, and that this ratio must therefore be equal to the ratio of the sensations they elicited [which is essentially the rationale for Stevens' Law (2, 18)]. Although the relative merits of these descriptions of the nonlinear relationship of luminance and brightness are still debated (see, for example, ref. 3), neither of these laws can explain the range of phenomenology illustrated in Fig. 1, and neither provides a biological rationale for the peculiarities of the luminance-brightness relationship.

In neurobiological terms, one suggested explanation of the relationship is a nonlinear response of input neurons in the visual pathway to some physical aspect of the stimulus [e.g., contrast ratios (8, 19)]. If, for example, input neurons responded nonlinearly to light, a readout of their activity in more central stations in the visual pathway might be expected to generate a nonlinear perceptual function (9). An extension of this idea would be to imagine that such operations are performed by the visual system on all of the luminances in the stimulus to recover surface R qualities (20–22). Many studies, however, have documented the relative independence of lightness/brightness and luminances as such. Matching studies, in particular, have shown that the same luminances can be made to look dramatically different by their context (12, 23–32). Because in many instances the activity of visual neurons is correlated with perceptual qualities rather than the physical properties of the stimulus (in the case of brightness see refs. 33 and 34), the response properties of neurons in the early stages of the visual pathway are unlikely to explain in any direct way the scaling relationship of luminance and brightness.

Other workers have tried to relate lightness/brightness to the properties of the object(s) underlying the stimulus. This approach, first taken by Helmholtz in the latter part of the 19th century [leading to his conclusion that sensations of brightness correspond to object reflectances (35)], has more recently evolved to incorporate the recovery of "intrinsic images" (i.e., images that represent the underlying physical properties of a scene) by "inverse optics" or by "anchoring" the highest luminances in a stimulus to white to properly perceive the correct range of lightness and brightness (36). The nonlinearity of scaling has also been suggested to compensate for the attenuation of light energy by the space intervening between observers and objects (37).

Although these further suggestions can again rationalize some aspects of the brightness-luminance relationship, they do not explain the range of phenomena apparent in brightness scaling tested here, including the form of the nonlinear relationship, its sensitivity to conditions [e.g., the output of the Naka-Rushton equation does not change if the nonimmediate surround of a stimulus suggests changes in R (compare Fig. 3*A*) vs. changes in both I and R (compare Fig. 3*B*)], its dependence on background luminance and the crispening effect (see Fig. 1).

- Fechner, G. T., Adler, H. E., Howes, D. H. & Boring, E. G. (1966) Elements of Psychophysics (Holt Rinehart and Winston, New York).
- 2. Stevens, S. S. (1966) J. Opt. Soc. Am. 56, 1135-1136.
- Laming, D. (1997) The Measurement of Sensation (Oxford Univ. Press, New York).
- 4. Bartleson, C. J. & Breneman, E. J. (1967) J. Opt. Soc. Am. 57, 953-957.
- 5. Warren, R. M. (1981) Behav. Brain Sci. 4, 175-223.
- Whittle, P. (1994) in *Lightness, Brightness, and Transparency*, ed. Gilchrist, A. L. (Lawrence Erlbaum, Hillsdale, NJ), pp. 35–110.
- Moroney, N. (2002) Proceedings of the 9th Congress of the International Color Association (Soc. Photo-Opt. Instrum. Eng., Bellingham, WA), Vol. 4421, pp. 571–574
- 8. Naka, K. I. & Rushton, W. A. (1966) J. Physiol. 185, 587-599.
- 9. Shapley, R. & Enroth-Cugell, C. (1984) Prog. Retinal Res. 3, 263-346.
- 10. Kingdom, F. & Moulden, B. (1991) Vision Res. 31, 851-858.
- Purves, D., Lotto, R. B., Williams, S. M., Nundy, S. & Yang, Z. Y. (2001) Philos. Trans. R. Soc. London B 356, 285–297.
- Adelson, E. H. (2000) in *The New Cognitive Neurosciences*, ed. Gazzaniga, M. S. (MIT Press, Cambridge, MA), 2nd Ed., pp. 339–351.
- 13. Brainard, D. H. (1997) Spat. Vision 10, 433-436.
- 14. Whittle, P. (1992) Vision Res. 32, 1493-1507.
- Hering, E. (1964) Outlines of a Theory of the Light Sense (Harvard Univ. Press, Cambridge, MA).
- 16. Takasaki, H. (1966) J. Opt. Soc. Am. 56, 504-509.
- 17. Semmelroth, C. C. (1970) J. Opt. Soc. Am. 60, 1685-1689.

Some Limitations of the Probabilistic Explanation Provided Here.

Despite the ability of a wholly probabilistic framework to explain brightness scaling and the changes in the relationship between luminance/brightness apparent in a variety of conditions, it is limited in several ways. First, as already noted, although luminance is determined primarily by I and R, it is also influenced by a variety of secondary factors (e.g., transmittance or the intervening medium, surface geometry, distance) that we have not taken into consideration. Second, we have used I and R to generate a conceptual framework that does not map linearly onto the physical relationship of these two parameters (target luminances are considered relative to the luminance generated by the average I and R of the scene in which they are presented). Third, the probability distributions pertinent to human experience with R and I are not known and can therefore be considered only in general terms, as we have done. Obviously, typical scenes contain a variety of information whose statistical influence will have to be combined according to the relative frequency of experience with the sources of the same or a similar stimulus. In the final analysis, determining in these terms the brightness observers see must entail an analysis of the probabilistic relation of all the elements in the image plane and the corresponding sources of those elements in natural scenes.

Conclusion

Because the light returned to the eye from any scene conflates the contributions of R and I (as well as transmittance and a host of other factors that affect these parameters), the provenance of any retinal stimulus (and therefore its significance for visually guided behavior) is inevitably ambiguous. This fact of visual perception presents a biological dilemma: successful behavior in a complex environment clearly depends on responding appropriately to the physical sources of visual stimuli, not the stimuli themselves. The ability to rationalize the major features of luminance/brightness scaling in wholly probabilistic terms suggests that the human visual system solves this problem by generating sensations of lightness and brightness according to the probability distribution of the possible sources of the luminance values in the image plane for the biological advantages this strategy provides.

- Stevens, S. S. (1975) Psychophysics: Introduction to Its Perceptual, Neural, and Social Prospects (Wiley, New York).
- 19. Wallach, H. (1948) J. Exp. Psychol. **38**, 310–324.
- 20. Land, E. H. (1986) Proc. Natl. Acad. Sci. USA 83, 3078-3080.
- 21. Land, E. H. & McCann, J. J. (1971) J. Opt. Soc. Am. 61, 1-11.
- 22. Marr, D. (1982) Vision (Freeman, New York).
- 23. Gilchrist, A. L. (1977) Science 195, 185-187.
- 24. White, M. (1979) Perception 8, 413-416.
- 25. Arend, L. E. & Spehar, B. (1993) Percept. Psychophys. 54, 457-468.
- 26. Arend, L. E. & Spehar, B. (1993) Percept. Psychophys. 54, 446-456.
- 27. Logvinenko, A. D. (1999) Perception 28, 803-816.
- 28. Todorovic, D. (1997) Perception 26, 379-394.
- 29. Adelson, E. H. (1993) Science 262, 2042–2044.
- 30. Knill, D. C. & Kersten, D. (1991) Nature 351, 228-230.
- Williams, S. M., McCoy, A. N. & Purves, D. (1998) Proc. Natl. Acad. Sci. USA 95, 13296–13300.
- Williams, S. M., McCoy, A. N. & Purves, D. (1998) Proc. Natl. Acad. Sci. USA 95, 13301–13306.
- 33. MacEvoy, S. P. & Paradiso, M. A. (2001) Proc. Natl. Acad. Sci. USA 98, 8827–8831.
- 34. Rossi, A. F. & Paradiso, M. A. (1999) J. Neurosci. 19, 6145-6156.
- von Helmholtz, H. L. F. (1909) Helmholtz's Treatise on Physiological Optics (Voss, Hamburg, Germany), transl. Southall, J. P. C. (1924) (George Banta, Menasha, WI), Vol. II, pp. 264–300.
- Gilchrist, A., Kossyfidis, C., Bonato, F., Agostini, T., Cataliotti, J., Li, X., Spehar, B., Annan, V. & Economou, E. (1999) Psychol. Rev. 106, 795–834.