Why are angles misperceived?

Surajit Nundy, Beau Lotto, David Coppola, Amita Shimpi, and Dale Purves*

Box 3209, Duke University Medical Center, Duke University, Durham, NC 27710

Contributed by Dale Purves, February 22, 2000

Although it has long been apparent that observers tend to overestimate the magnitude of acute angles and underestimate obtuse ones, there is no consensus about why such distortions are seen. Geometrical modeling combined with psychophysical testing of human subjects indicates that these misperceptions are the result of an empirical strategy that resolves the inherent ambiguity of angular stimuli by generating percepts of the past significance of the stimulus rather than the geometry of its retinal projection.

The fact that the subtense of any acute angle is seen as being somewhat larger than the measured angle of the stimulus, whereas the subtense of any obtuse angle is seen as being somewhat smaller, was first reported by Wundt (1) and subsequently by both Hering (2) and Helmholtz (3), all of whom surmised that these distortions might underlie some of the classical geometrical illusions (4). These 19th century investigations were, however, descriptive rather than experimental, and the interpretations, speculative. Despite numerous modern studies (5–15), the phenomenon of angle misperception has never been explained.

Here we provide evidence that the systematic misperception of angle subtense is the consequence of a radically empirical strategy of perception in which the angle seen is determined by the relative frequency of the possible sources of angle projections that observers have experienced. The biological rationale for this strategy is a solution to the problem posed by the inevitable ambiguity of angular stimuli. The inability of an angle projected onto a plane to specify uniquely the source is illustrated in Fig. 1. Indeed, because space is divisible without limit, the number of possible real-world sources underlying a given retinal projection is infinite.

Because the well being of an observer depends on appropriate interactions with the sources of visual stimuli, the ambiguity of retinal images has long been regarded as a central problem in vision (16). Recent studies of simultaneous brightness contrast (17, 18), Mach bands (19, 20), filling-in (21), and the perception of color (22) have all suggested that this dilemma is solved by an empirical strategy in which retinal activation triggers associations (percepts) determined by the relative frequencies of the possible sources of the stimulus in past experience. A limitation in validating this concept of vision has been the practical difficulty of quantifying the frequency distribution of the real-world sources underlying the various categories of visual experience. (This problem has also been an obstacle to psychologists who have sought to model perception in terms of Bayes' decision theorem; see ref. 23 for a recent review.) Examining the perception of oriented lines circumvents this obstacle in that the frequency distribution of the possible sources of a given retinal projection—for example, the subtense of the typical source of a given angle projected on the retina—can be computed by geometrical principles, thus providing a more concrete basis for predicting perceptual performance.

Experimental Methods

Tests of angle perception were presented on a high-resolution monitor (Sony, GDM 400; 1,200 × 1,600 pixels) in an otherwise darkened room. The stimuli, which appeared on a white circular background 15 cm in diameter, and the responses to them were controlled by a Dell XPS R PC (400 MHz) by using software written expressly for these experiments. A paraffin paper diffuser covered the screen face to obscure the pixilation of the lines. The luminance of the white background was 83 cd/m^2 and the test stimuli, 0.8 cd/m^2.

To eliminate objects in the room from view, subjects observed the stimuli binocularly from a distance of 140 cm through a black matte cone that allowed only the white circle to be seen; the subject's head was supported in a fixed position by a chin rest adjusted so that the eyes were level with the display. The inducing angle and test line (see Fig. 4) were 0.2° (4 pixels) wide and 1.2° long, and the test line was never closer than 0.8° from the nearest part of the inducing angle. Subjects used the computer keyboard to adjust the orientation of the test line either clockwise or counterclockwise until it appeared exactly collinear with, perpendicular to, or parallel to the test arm, depending on the task in each test. After each trial, the screen went blank for 1 sec to indicate the end of one trial and the onset of the next; otherwise tests were self paced and untimed. A maximum-likelihood adaptive ("staircase") procedure was used to determine the point of perceptual equality in each test. The test line could be rotated as much as 11° clockwise or counterclockwise with respect to the relevant arm of the inducing angle. The adjustments were initially 2°, progressing to 1°, and finally 0.5°, as the test arm was brought to within ±5° of the orientation of the comparison arm of the inducing angle. Large random discrepancies (±11°) between the test line and the comparison line were presented initially to give subjects a clear sense of "homing in" on the orientation of the test line that they perceived as the best match. The procedure ended after 15 trials, the point of perceptual equality being taken as the mean and standard deviation of the last five trials. Angles subtending 0° to 180° in 15° increments were presented in random order at one of eight orientations in the frontal plane (0°, 22.5°, 45°, 67.5°, 90°, 112.5°, 135°, and 157.5°). The 120 different angle/position combinations presented in each of the three different types of tests (collinear, right angle, and parallel setting; see text) were divided into eight test sessions, each of which took approximately 30 min to complete. The authors took the complete series of tests on two separate occasions, the total testing time being about 8 h. All subjects had normal (corrected) visual acuity.

Results

Frequency Distributions of the Sources of Angles Projected on the Retina. If the visual system resolves the dilemma of ambiguity by perceiving the empirical significance of stimuli rather than their qualities as such, then in the absence of ancillary cues the perception of any angle should be predicted by the relative frequencies of the subtenses of the sources previously experienced. Assuming, for the sake of simplicity, that all possible real-world angles are equally likely to be seen by an observer in all their possible orientations, this prediction can be tested

*To whom reprint requests should be addressed. E-mail: purves@neuro.duke.edu.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

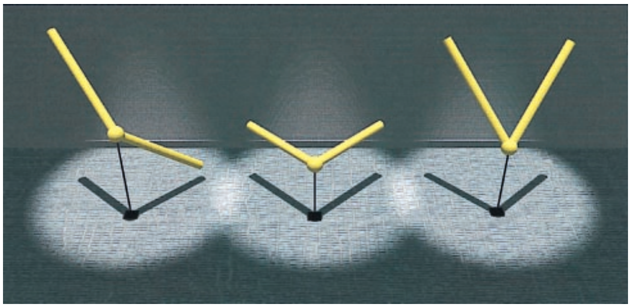

Fig. 1. Diagram illustrating the inevitable ambiguity of angle projections. Three different angular objects having real-world subtenses of 120°, 90°, and 60°, respectively, can project identically onto a plane (or the retina) as illustrated by the shadows on the ground plane.

geometrically. The observer should see an angle determined by the frequency distribution of all of the possible angular objects in three-dimensional space that could have given rise to the retinal projection in question, rather than the measured subtense of the projected angle.

The relative frequency of occurrence of all of the possible three-dimensional sources of a projected angle can be assessed by analyzing all of the ways that a given angular object can project onto a plane (Fig. 2). Obviously, a line or any other object can exist in an infinite variety of orientations with respect to the observer. The simplifying assumption in the model used here is that angular objects occupy these positions with equal probability [in fact, there is a slight bias even in natural scenes toward contours in the cardinal axes and therefore toward right angles (24); incorporating this bias into the model, however, makes little difference]. The distribution obtained in this way can be used in turn to generate the frequency distribution of the subtenses of the objects that could have given rise to any given angular projection. Fig. 3, for instance, shows the distribution of the subtenses of all of the angular objects that could have generated a representative acute angle, an obtuse angle, and a right-angle retinal projection. The most frequently occurring subtenses for any given projection are those near the actual magnitude of the subtense of the projection, generated by orientations in or near the frontal–parallel plane. The least frequent subtenses in the distribution are those furthest from the value of the projected angle, generated by orientations furthest away from the frontal plane.

The frequency distribution of the possible sources of an angle projected onto a plane, however, is not balanced around the subtense of the projected angle (or orientation in the frontal plane). For example, the distribution of the subtenses of the possible sources of the 30° projection in Fig. 3 is skewed toward values that are greater than the projected angle, whereas the distribution of the source subtenses of the 150° projection are skewed toward values that are smaller than the projection. Moreover, these differences between the projected angle and overall descriptors of the source distributions such as the median or mean vary systematically as a function of the projected angle (see Fig. 6 below). Thus the average source of an acute angle projection has a value that is, in varying amount, always greater than the subtense of the projection, whereas the average source of an obtuse angle projection has a value that is, in varying amount, always less than the subtense of the projection. In contrast, the average subtense of the sources of projected angles of 0°, 90°, and 180° is the subtense of the projection itself (see Fig. 3).

The significance of these geometrical facts is that observers will have always experienced systematic differences between the angles projected on the retina and the attributes of their sources. With respect to subtense, acute angle projections will, on average, have been generated by objects that have a larger subtense than the

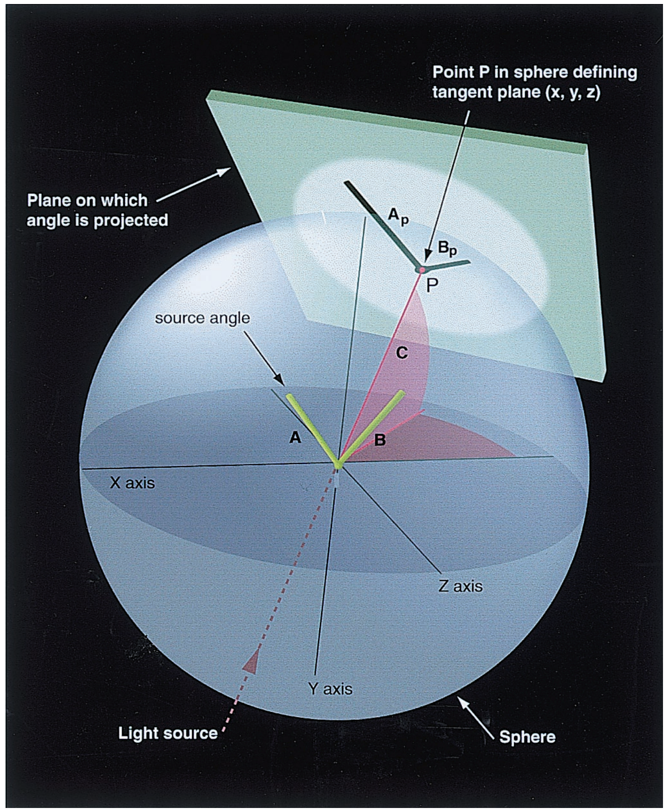

Fig. 2. A geometrical model of projected angles and their sources. The angular object whose projection was to be evaluated was placed arbitrarily in the *XY* plane with its vertex at the center of a sphere and its arms specified by the two vectors, **A** and **B**. The set of points within the sphere was generated first by calculating random values for *x*, *y*, and *z* between −1 and +1, keeping only those points satisfying $x^2 + y^2 + z^2 \leq 1$ (where *x*, *y*, and *z* are the coordinates along the three conventional Cartesian axes *X*, *Y*, and *Z* of any point *P*). The projection ($\mathbf{A}_P$,$\mathbf{B}_P$) of each of the arms of the angular object (**A**,**B**) onto a plane perpendicular to the vector joining *P* and the center of the sphere (**C**) was then determined by vector calculus based on the following relationships:

$$\mathbf{A}_P = \mathbf{A} + t_\mathbf{A}\mathbf{C}, \text{ and } \mathbf{B}_P = \mathbf{B} + t_\mathbf{B}\mathbf{C}$$

Further, $\mathbf{A}_P \cdot (t_\mathbf{A}\mathbf{C}) = 0$, and $\mathbf{B} \cdot (t_\mathbf{B}\mathbf{C}) = 0$, where $t_\mathbf{A}$ and $t_\mathbf{B}$ are scalars.

After solving for $t_\mathbf{A}$ and $t_\mathbf{B}$ and subsequently for $\mathbf{A}_P$ and $\mathbf{B}_P$, the angle of the projection onto the plane is given as:

Projected angle $= \cos^{-1}[(\mathbf{A}_P \cdot \mathbf{B}_P)/(|\mathbf{A}_P| \;\; |\mathbf{B}_P|)]$

By using this method, the projections of all angles subtending 0–180° were determined in 1° increments, rounded to the nearest 1°, and stored in a data file. The file was then searched for all of the source subtenses and orientations that could give rise to a particular projection, in this way establishing a probability distribution for the sources of any angle projected onto a plane (see Fig. 3). Because the human fovea extends across only a small fraction of the retinal surface, any central retinal projection can be modeled in this way, at least to a first approximation.

subtense of the retinal stimulus, obtuse angle projections will have been generated by objects that on average have a smaller subtense than the retinal stimulus, and right-angle projections will have been generated by objects that on average subtend 90°. If angle perception is indeed determined by the empirical significance of the proximal stimulus (that is, by what the attributes of the proximal stimulus have typically "turned out to be" as observers have interacted with real-world objects), then the perceived subtense of any given angle should be determined by the frequency distribution of the possible sources of its retinal projection.

Perception of Angle Magnitude. To determine how angles projected onto the retina are in fact perceived by normal observers,

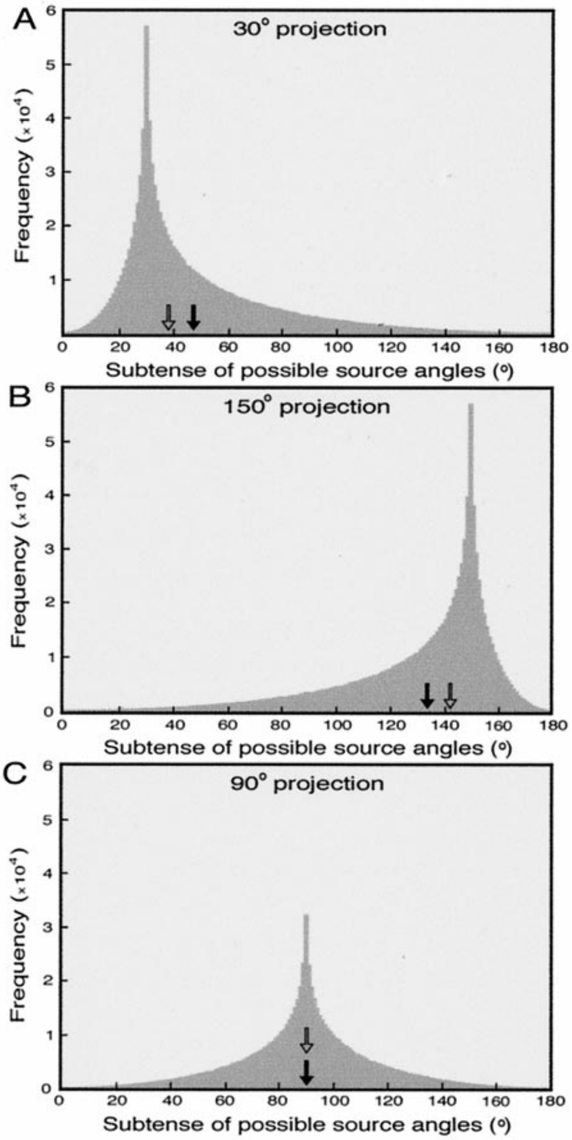

Fig. 3. Frequency distribution of the possible source subtenses of representative angles projected onto a plane (subtenses are shown from 0–180° in 1° increments). (*A*) The frequency distribution of the possible source subtenses of a representative acute angle (30°) projection. The solid arrow indicates the mean and the open arrow, the median. (*B*) The frequency distribution of the possible source subtenses of a representative obtuse angle (150°) projection. (*C*) The frequency distribution of the possible source subtenses of a right-angle projection. Because *all* angles can project specifically as 0° or 180°, the mean or median subtense of the sources that give rise to a 0° projection is more than the projection itself, and the mean or median subtense of the sources that give rise to a 180° projection is less than the projection itself. These artifacts arise from having made discrete, for practical reasons, the continuous function of angle size. When the source distributions of 0° and 180° projections are plotted in 360° circular space, they are single-peaked symmetrical distributions whose means and medians are in fact 0° and 180°.

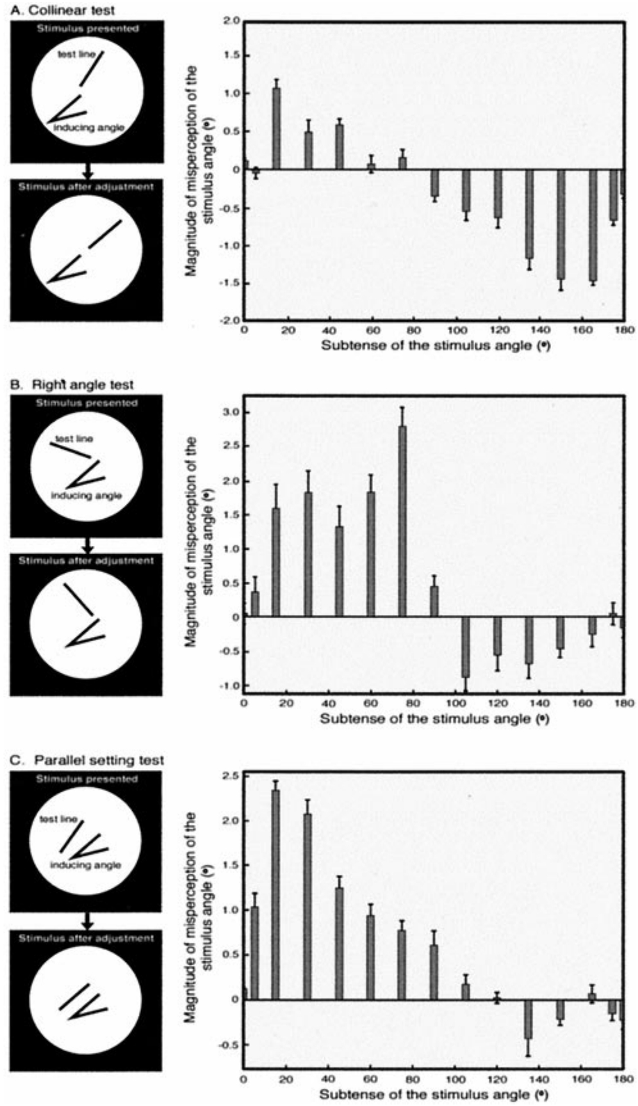

Fig. 4. Perceptual performance of the five subjects studied in detail. (*A*) In this vernier alignment test, subjects rotated the test line until it appeared colinear with the relevant arm of the inducing angle (see diagram). The subtense of the stimulus angle is plotted along the abscissa and the magnitude of the misperception, on the ordinate (mean and standard errors are shown). (*B*) Perceptual performance on the setting to a right-angle test, presented as in *A*. As indicated in the diagram, subjects rotated the test line until it appeared to make a right angle with the adjacent arm of the inducing angle. (*C*) Perceptual performance on the parallel setting test, presented as in *A* and *B*. In this case, subjects rotated the test line until it appeared parallel to the relevant arm of the adjacent angle. In all three of these tests, subjects overestimated the magnitude of acute angle stimuli and underestimated obtuse angles in systematically varying amounts.

we used three different tests in which the authors and a group of naïve subjects were asked to adjust the orientation of a line in relation to an angle that varied in subtense. The reason for using several different tests was to minimize any confounding variables that might influence perception.

Collinear Test of Angle Perception. In the first of these evaluations of angle perception, subjects were asked to rotate a test line until it appeared collinear with the indicated arm of the inducing angle (Fig. 4*A*; diagram). The rationale for this vernier alignment task is that any discrepancy between the projection of the stimulus and its perception should cause the test line to appear collinear with the indicated arm of the inducing angle when it is not. If the subtense of the inducing angle is seen as being greater than it really is, then the test line should appear collinear when it is actually rotated around its proximal end away from the bisector of the angle. Conversely, if the inducing angle is underestimated, the test line should appear collinear when rotated toward the bisector.

The performance of the five subjects studied in detail (the

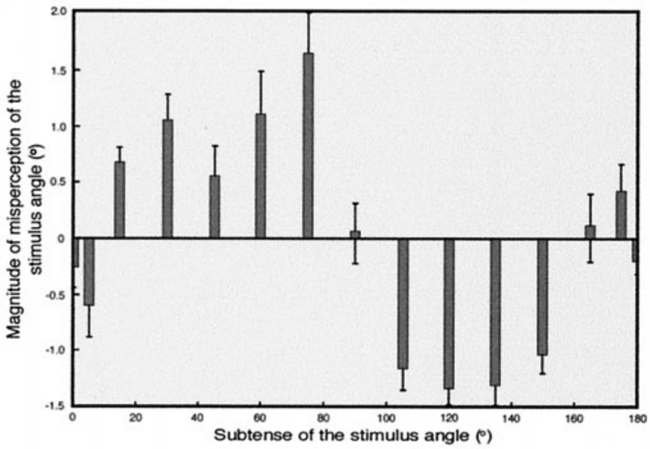

Fig. 5. The perceptual performance of six naïve subjects given more limited versions of the three tests taken by the five subjects studied in detail. The results of all three tests were similar and are shown here as the mean of these performances (the presentation is the same as in Fig. 4).

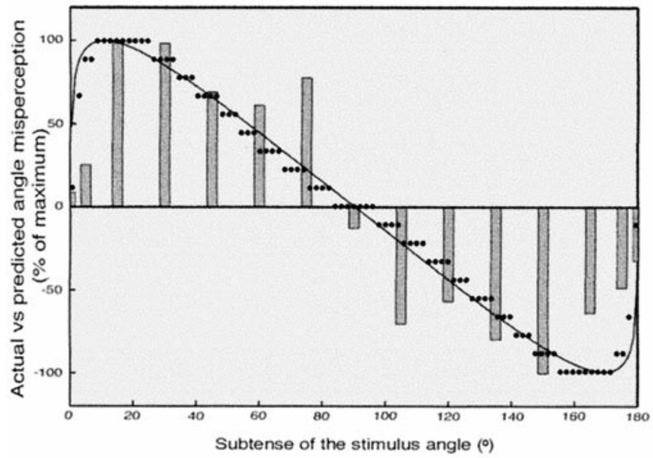

Fig. 6. Comparison of the perceptions of angular stimuli observed by the five subjects studied in detail and the misperceptions predicted by the frequency distributions of the possible sources of the angular stimuli (calculated in the same way as the mean and median values for the examples shown in Fig. 3). Vertical bars show the mean perceptual performance data from the three tests of angle perception shown in Fig. 4, normalized here for comparison with the functions predicted by the geometrical analysis in Fig. 3. The solid line indicates the misperceptions predicted by the means of the frequency distributions of the possible sources for each angle; the dots indicate the misperceptions predicted by the medians of the source frequency distributions. The maximum misperception of acute and obtuse angle stimuli predicted by the frequency distributions of experience with the subtenses of the sources of projected angles is ≈10° and 4.5° per angle arm for mean and median, respectively, compared with observed values of about 1–3°. The inevitable presence of some information about the actual orientation of the stimulus in frontal plane (subjects were obviously aware they were viewing a computer screen) may explain why the magnitude of the perceptual distortions seen by observers is a few degrees less than that predicted on the basis of the frequency distributions of the possible sources (i.e., angular objects in the frontal plane have always been experienced to have the same real-world subtense as their retinal projections).

authors) is shown in the graph in Fig. 4*A*. On average, acute angles were overestimated and obtuse angles, underestimated in amounts that varied systematically as a function of the stimulus angle subtense. In contrast, right angles (and angles approaching a straight line) were seen as being very close to the measured subtense of the stimulus.

Setting to a Right-Angle Test. In a second test of angle perception, subjects were asked to adjust the orientation of a test line to make a right angle with the indicated arm of the inducing angle (Fig. 4*B*; diagram). The rationale of this task is that, to the extent that the perception of the inducing angle is distorted, the test line should be set to an angle either more or less than 90° for underestimated or overestimated angles, respectively. On average, observers again systematically overestimated acute angles and underestimated obtuse angles, whereas right angles (and straight lines) were seen as being very close to their measured subtenses (Fig. 4*B*).

Parallel-Lines Test of Angle Perception. In a third test, subjects were asked to rotate a test line so that it was parallel to the adjacent arm of the inducing angle (Fig. 4*C*; diagram) (see ref. 10). The rationale for this test is that if the subtense of the inducing angle is distorted in perception, then an adjacent test line should appear parallel when it is not. If the inducing angle is overestimated, the test line should be seen as parallel when it is actually rotated away from the nearby arm of the angle; if underestimated, the test line should appear parallel when rotated toward the adjacent angle arm. Once again, observers systematically overestimated acute angles and underestimated obtuse ones, but not right angles or straight lines (Fig. 4*C*).

There have been many previous studies of angle perception, but only one (10) was carried out in a manner that allows comparison with the analysis here. The only significant difference between these results for the parallel-lines test and those previously reported is our failure to confirm an error in setting two straight lines parallel (in the present study, this error was, on average, only 0.05°).

Perceptual Tests of Naïve Subjects. These tests taken by the 5 authors typically took more than 8 h to complete. Because testing naïve subjects in this same way would have been impractical, a more limited test taking about 3 h was given to rule out the possibility that knowledge of the issues involved might bias performance. The same series of angles was presented, but with the test arm of the inducing angle always oriented at 45°, a choice based on the observation that the more complete testing reported above showed a slightly more robust effect at oblique orientations of the test arm, as others have also noted (7, 10, 15). This more limited testing of six subjects unfamiliar with the aims or background of the study gave similar results (Fig. 5).

In summary, three different tests of angle perception given to both trained and naive subjects (11 in total) agree in showing that the perception of angles differs slightly but systematically from the measured subtense of the stimulus. Thus, (*i*) acute angles are overestimated, the maximum effect occurring for projected angles of intermediate acuteness; (*ii*) obtuse angle are underestimated, the maximum effect occurring for angles of intermediate obtuseness; and (*iii*) angles of 0°, 90°, and 180° are minimally changed in perception, with observers seeing very nearly the angle that is projected on the retina. Because similar results were obtained with all three of the tests used, it is unlikely that the perception of the stimulus angle subtense is much affected by the structure of the test itself.

Comparison of Predicted and Observed Results. A comparison of these psychophysical observations with the misperceptions for each angle predicted by the frequency distributions of the sources of angle projections is shown in Fig. 6. The systematic differences between the angles presented to subjects and the ensuing perceptions follow closely the function predicted by the assumption that angular percepts are determined by past experience with the typical sources of angle projections.

Discussion

Heretofore, the most complete study of angle perception was carried out by Carpenter and Blakemore (10), who tested a full range of angles by using a parallel setting test (much like the third test we used here). Their results on two subjects (themselves) were similar to those shown in Fig. 4*C* (see also refs. 24 and 25). Other relevant studies (e.g., refs. 6–8, 13–15) examined a more limited range of angles and line orientations, usually in relation to the "tilt illusion" (which refers to the effect of the orientation of one line on the apparent orientation of a nearby line in the absence of an explicit angle). The results reported in these investigations are all consistent with the assertion first made by Wundt (1) that acute angles, whether explicit or implied, are overestimated and obtuse angles, underestimated.

In seeking to explain these anomalous perceptions of oriented lines, most modern investigators have proposed theories based on the receptive field properties of orientation-selective neurons in V1 of subhuman primates, lateral inhibitory interactions typically playing a central part in these accounts (5, 7, 10, 15, 26–28). In this interpretation, the closer the arms of a stimulus angle, the more likely the stimulus is to activate neighboring orientation domains in the visual cortex (or in subcortical stations) that generate mutually inhibitory interactions. In this way, the region of maximum cortical excitation is imagined to be shifted with respect to the normal retinotopic distribution of activity, with the result that the positions of the lines appear different from the actual (projected) angle of the stimulus (see ref. 29 for a more complete discussion).

Although we cannot rule out the possibility that cortical interactions of this sort play some part in the distorted perception of angles, the results we report here support a more general explanation that accords with the way a number of other puzzling perceptions have recently been rationalized (17–22). Visual percepts—whether of luminance, spectral returns, or, in the present case, oriented lines—can be understood as the consequence of an entirely empirical strategy in which the percept experienced is an association determined by the relative frequency of occurrence of the possible sources of an ambiguous retinal stimulus, this information being gleaned from the success or failure of the behavioral responses that have been made to the same or similar stimuli in the past. Therefore, an alternative explanation of the discrepancy between the angles projected onto the retina and their perception is that the angle seen is an association molded by the empirical significance of the retinal projection. The similarity of the behavioral results predicted on this basis and those observed (Fig. 6) supports this interpretation.

In fact, many investigators, from 19th century treatments to the present, have considered the possibility that past experience with angles plays some part in their perception. Gregory, for example, has argued that the Mueller–Lyer illusion is the result of familiarity with "inside" and "outside" corners and the different distances from the observer suggested by the simultaneous presentation of these two components of the stimulus (29, 30). In a similar vein, Gillam (31) has suggested that several other geometrical illusions involving angles are based on familiarity with the way the scale and size of objects are affected by perspective. In general, such explanations suppose that "top-down" cognitive information modulates "bottom-up" sensory processing, causing perceptual distortions when the stimulus is seen without its usual context.

The empirical explanation proposed here to explain the discrepancy between angles projected onto the retina and their perception is far more radical. Because light emanating from three-dimensional objects is projected onto a two-dimensional receptor sheet, the significance of the retinal image of any real-world line or angle is inherently ambiguous (see Fig. 1). In consequence, the potential significance of any projected angle for the generation of subsequent behavior cannot be determined by an analysis of the stimulus as such. On the contrary, the visual system must inevitably determine the relationship between the stimulus and its provenance statistically, i.e., by virtue of the relative frequencies of the underlying sources of the retinal projections that the observer (or the observer's predecessors) has experienced during interactions with similar scenes in the past. It is this probabilistic information about geometrical projection that we take to be the basis for the discrepancy between the subtense of angular stimuli and the angle perceived.

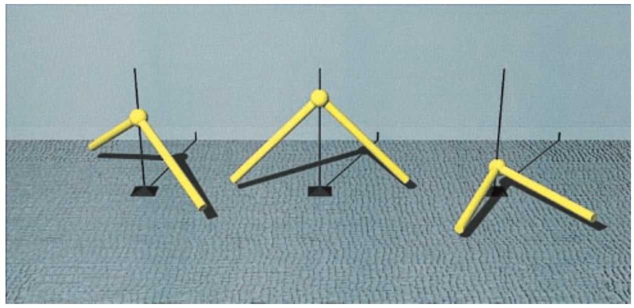

Fig. 7. A wide range of empirical factors influences the perception of angles. In this scene, the subtenses of the three angular objects are identical, each measuring 92.5° on the printed page. As a result of this variety of depicted cues about the attributes of the possible real-world sources (see text), the subtenses of the three identical angles look quite different.

Of course, empirical information in addition to experience with the underlying subtenses of retinal projections (the issue we have focused on here) can influence the perception of an angle by changing the relative probabilities of the possible sources of the retinal stimulus, but always, we would argue, according to the same fundamentally statistical strategy. These additional influences include the typical orientation of the sources giving rise to a particular projection, the typical length of the arms of the projected angle, and no doubt a host of other factors. Although we have not tested these additional influences on the perception of angle subtense, the illustration in Fig. 7 makes plain that the angle seen can be affected greatly by the inclusion of additional information in the scene that alters the relative probabilities of the possible sources of the stimulus.

Because, in contrast to Fig. 7, the stimuli we used in psychophysical testing provided little or no information about orientation (and because the length of the angle arms was kept constant; see Fig. 4), we could ask whether the systematic variation of the perceived angle agreed with the predictions based on the frequency distributions of the possible source subtenses determined by projective geometry. Despite the fact that our test paradigm could not completely eliminate cues indicating that the stimulus was actually oriented in the frontal plane (information that would tend to minimize any misperception of subtense) and that the real-world distribution of oriented lines and angles is not entirely uniform (32), as our model assumes, the perception of angular subtense is predicted remarkably well by the relative probabilities of possible sources (see Fig. 6).

Concluding Remarks

Although the distortions that occur when viewing acute or obtuse angles may seem trivial in the context of behavior, the visual strategy they signify is of great importance. A growing body of evidence indicates that visual perceptions invariably represent the empirical significance of the proximal stimulus, determined by the accumulated instruction of past experience (17–22). Narrowly put, the advantage of this strategy is that similar or even identical proximal stimuli will appear different if their sources are likely to be different, as a result of past experience. More generally, this strategy of vision ensures that the observer's perceptions will always accord with the probabilities conveyed by the information in the scene, thus providing the most successful guide to action in the face of the inevitably uncertain meaning of retinal activity.

We are grateful to Dan Cerruti for his assistance in programming the tests used here and for helpful advice with the testing procedures. We also thank Feraz Rahman for his help with some geometrical issues and Mark Changizi, Zhiyong Yang, Jim Voyvodic, and Don Katz for useful criticism. This work was supported by National Institutes of Health grant no. NS29187.

1. Wundt, W. (1897) *Beitrage zue Theorie der Sinnewahrnelmung* (Engelmann, Leipzig); trans. Judd, C. H. (1902) *Outlines of Psychology* (German), p. 137.
2. Hering, E. (1964) *Outlines of a Theory of the Light Sense* (Harvard Univ. Press, Cambridge, MA).
3. von Helmholtz, H. (1909) *Handbuch der Physiologischen Optik* (Voss, Hamburg); trans. Southhall, J. P. C. (1924) *Helmholtz's treatise on Physiological Optics* (The Optical Society of America) (German).
4. Luckiesh, M. (1922) *Visual Illusions. Their Causes, Characteristics and Applications* (Van Nostrand, New York).
5. Andrews, D. P. (1967) *Vision Res*. **7,** 975–997.
6. Bouma, H. & Andreiessen, J. (1968) *Vision Res*. **8,** 493–507.
7. Bouma, H. & Andriessen, J. (1970) *Vision Res*. **10,** 333–349.
8. Fisher, G. H. (1969) *Q. J. Exp. Psychol*. **21,** 356–366.
9. MacLean, I. E. & Stacey, B. (1971) *Percept. Psychophys*. **9,** 499–504.
10. Carpenter, R. H. S. & Blakemore, C. (1973) *Exp. Brain Res*. **18,** 287–303.
11. Hotopf, W. H. & Robertson, S. H. (1975) *Percept. Psychophys.* **18,** 453–459.
12. Heywood, S. & Chessel, K. (1977) *Perception* **6,** 571–582.
13. Wenderoth, P., Parkinson, A. & White, D. (1979) *Perception* **9,** 47–57.
14. Predebon, J. (1994) *Percept. Mot. Skills* **78,** 259–264.
15. Greene, E. (1994) *Percept. Mot. Skills* **78,** 655–674.
16. Berkeley, G. (1704) *A New Theory of Vision* (Everyman's Library, Denton, London).
17. Williams, S. M., McCoy, A. N. & Purves, D. (1998) *Proc. Natl. Acad. Sci. USA* **95,** 13296–13300.
18. William, S. M., McCoy, A. N. & Purves, D. (1998) *Proc. Natl. Acad. Sci. USA* **95,** 13301–13306.
19. Lotto, R. B. Williams, S. M. & Purves, D. (1999) *Proc. Natl. Acad. Sci. USA* **96,** 5239–5244.
20. Lotto, R. B., Williams, S. M. & Purves, D. (1999) *Proc. Natl. Acad. Sci. USA* **96,** 5245–5250.
21. Purves, D., Shimpi, A. & Lotto, R. B. (1999) *J. Neurosci.* **19,** 8542–8551.
22. Lotto, R. B. & Purves, D. (1999) *Nat. Neurosci.* **2,** 1010–1014.
23. Knill, D. C. & Richards, W. (1996) *Perception as Bayesian Inference* (Cambridge Univ. Press, Cambridge, U.K.).
24. Wallace, G. K. (1969) *Percept. Psychophys*. **5,** 261–264.
25. Nelson, J. & Frost, B. (1978) *Brain Res.* **139,** 359–365.
26. Day, R. H. (1962) *Nature (London)* **207,** 891–893.
27. Blakemore, C., Carpenter, R. H. S. & Georgeson, M. A. (1970) *Nature (London)* **228,** 37–39.
28. Howard, R. B. (1971) *Psychonom. Monogr. Suppl*. **4,** 57–72.
29. Gregory, R. L. (1963) *Nature (London)* **199,** 678–680.
30. Gregory, R. L (1998) *Eye and Brain: The Psychology of Seeing* (Oxford Univ. Press, Oxford, U.K.), 5th Ed.
31. Gillam, B. (1998) in *Perception and Cognition at Century's End,* ed. Hochberg, J. (Academic, San Diego), pp. 95–136.
32. Coppola, D. M., Purves, H., McCoy, A. & Purves, D. (1998) *Proc. Natl. Acad. Sci*. *USA* **95,** 4002–4006.