

- um Function, C. P. Channing, J. M. Marsh, W. A. Sadler, Eds. (Plenum, New York, 1979), p. 757.
5. Prostaglandins for injection were prepared as emulsions in 1 ml of 4 percent ethanol and 96 percent sterile aqueous vehicle (by volume); the aqueous vehicle contained (per milliliter): 10 mg of carboxymethylcellulose, 4 mg of polysorbate 80, and 0.42 mg propylparaben.
 6. F. A. Kimball, G. L. Bundy, A. Robert, J. R. Weeks, *Prostaglandins* 17, 655 (1979); G. L. Bundy *et al.*, *J. Med. Chem.* 26, 1089 (1983).
 7. Pregnancy maintenance was confirmed by continued normal secretion patterns of mCG, detection of uterine enlargement by bimanual palpation, and failure of the monkeys to show cycles of menstrual bleeding.
 8. W. W. Tullner and R. Hertz, *Endocrinology* 78,

- 1075 (1966); A. L. Goodman and G. D. Hodgen, *J. Clin. Endocrinol. Metab.* 49, 469 (1979).
 9. A. I. Csapo, M. O. Pulkkinen, B. Ruttner, J. P. Sauvage, W. G. Wiest, *Am. J. Obstet. Gynecol.* 112, 1061 (1972).
 10. Pregnancy was terminated in one of two monkeys treated with a single injection of 3.75 mg of PGF-analog plus 0.5 mg of PGE-analog and in one of two monkeys treated with a single injection of 3.75 mg of PGF-analog plus 0.25 mg of PGE-analog.
 11. Mild anorexia lasting only one day was observed in one of the monkeys given the highest doses of the PGF-analog plus PGE-analog.
 12. I thank A. D. Forbes, K. K. Forbes, and R. L. VanEyk for technical assistance.
- 12 April 1983; revised 24 June 1983.

feeding an additional (equal and opposite) signal to the x-inputs of the display scopes. The shape of the signal, in this case that of the Cornsweet profile, determined the shape of the simulated depth surface.

For the motion parallax display, the depth information was provided by the patterns of relative motion projected onto the retina during lateral movements of the observer's head. We demonstrated previously that the shape and relative depth of a three-dimensional surface can be perceived readily and unambiguously under these conditions (2). In this study, subjects monocularly viewed a single random dot array while making lateral head movements through a distance of 13 cm. The random dot array was systematically transformed during each head movement so as to produce a pattern of relative motions identical to that produced by a real three-dimensional surface. The relative motion between the rows of dots was produced by feeding an additional x-signal to the display oscilloscope and modulating the amplitude according to the lateral position of the observer's head. The shape of the signal again determined the shape of the simulated depth surface. In both displays the angular extent of the central, changing region of the depth surface was 10 degrees of visual angle. The depth change at the discontinuity corresponded to a disparity of 8 arc minutes.

The size of the illusion in both cases was measured with a nulling technique. The subject's task was to introduce a physical disparity between the outer flanks of the depth profile until any perceptual difference was canceled out and the flanks appeared to be equidistant. The curvature of the slowly changing

Anisotropies in the Perception of Three-Dimensional Surfaces

Abstract. *The appearance of certain three-dimensional surfaces was found to depend on the orientation of the depth contours forming the surface. This was true both when the depth was specified by motion parallax and when it was specified by binocular disparities. Slowly changing depth surfaces that generated a pattern of relative motions or disparities characterized by a one-dimensional expansion-compression were perceived differently from those that produced a shear transformation.*

The small differences between the two retinal images (binocular disparities) and the relative motion in each image when the observer moves (motion parallax) have both been shown to accurately specify the structure of three-dimensional surfaces (1, 2). We report here that the perception of depth surfaces can be orientationally anisotropic, that is, the appearance of a surface can vary with the retinal orientation of the surface contours (3). Anisotropic effects were initially observed for surfaces in which the three-dimensional structure was specified stereoscopically, but we have since found similar effects for surfaces in which the structure was specified by motion parallax.

The most striking demonstration of these effects was found with the depth surfaces depicted in Fig. 1, a and b. The profile of the surface (Fig. 1c) consists of a sharp step or discontinuity in depth, flanked on either side by more gradual depth changes to areas that are equidistant from the observer. When this profile defines luminance (rather than depth) changes across a surface, observers typically report that the left-hand side appears lighter than the right. This effect is known as the Craik-O'Brien-Cornsweet illusion (4). In the luminance domain, the effect is usually attributed to the visual system's poor sensitivity to slow or low spatial frequency changes (which characterize the sloping areas of the profile) compared with its sensitivity to the sharp discontinuity at the center (5). We investigated the analogous effect in the depth domain. When the surface depicted in Fig. 1a was presented stereoscopically,

the right flank of the surface appeared to be nearer the observer than the left (6). However, when the surface depicted in Fig. 1b was presented there was no illusion and the outer flanks appeared to be equidistant. Moreover, when the same depth surfaces of Fig. 1 were specified by parallax motions, rather than by binocular disparities, a similar anisotropy was observed.

Random dot techniques were used to study these anisotropies in both the stereoscopic and motion parallax domains. For stereopsis, two identical 256 by 256 pixel arrays were displayed on a pair of large-screen oscilloscopes (20 by 20 degrees of visual angle) and viewed independently by the two eyes at a distance of 57 cm. Disparities were introduced by

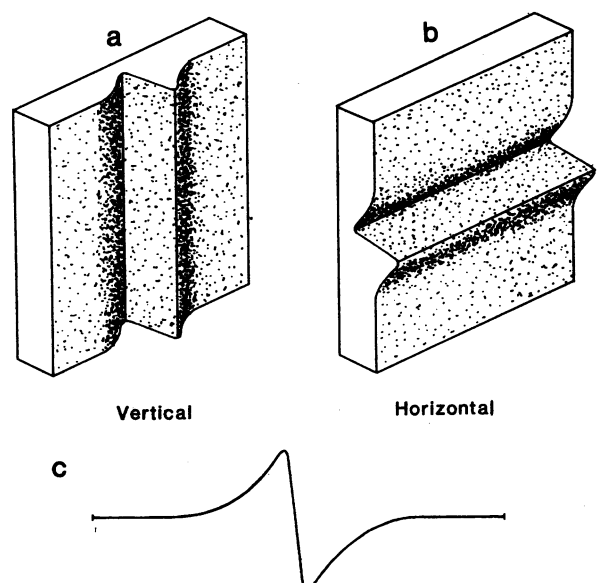


Fig. 1. (a and b) Perspective drawings of the depth surfaces used in the experiments. (c) Approximate shape of the Cornsweet profile, as constructed by adding a positive-going half-cycle sine wave and a negative-going half-cycle sine wave of one-eighth the spatial extent.

regions of the Cornsweet profile remained constant during these adjustments, so that only the relative disparity of the outer flanks and the size of the discontinuity at the center of the profile were altered. The extent of the illusion was measured when the Cornsweet depth surface was oriented vertically (as in Fig. 1a) and when it was oriented horizontally (as in Fig. 1b). The rate of change of depth over space was identical in these two conditions.

The results are shown in Fig. 2a. If the orientation of the depth discontinuity was vertical the illusory depth effect was large and very noticeable, both when depth was specified by binocular disparities (left pair of histograms) and when it was specified by motion parallax (center pair of histograms). Typically, the outer flanks had to have a stereoscopic or parallax disparity of up to 3 arc minutes (40 percent of the size of the depth discontinuity) before they appeared to be equidistant. However, if the depth discontinuity was oriented horizontally there was little or no Cornsweet effect and the outer flanks of the depth surface were perceived to be equidistant when there was little or no disparity between them.

Two features of the results are significant. First, the size of the Cornsweet depth illusion is very similar for surfaces

specified by both binocular disparity and motion parallax. This finding is consistent with previous results showing extensive similarities between the characteristics of the two depth-processing systems (7). Second, the results reveal a marked anisotropy in the perception of the Cornsweet surface as a function of the orientation of the depth contour. What is the cause of this anisotropy? In the stereoscopic system there is an obvious inbuilt disparity, in that depth-related disparities are principally horizontal, but for the parallax system there is no such anisotropy since parallax motions can be generated along any axis. In our parallax experiments, however, the parallax motions were always horizontal and coupled to horizontal head movements. Hence a similar stimulus anisotropy existed in both the stereo and parallax displays. Changes in disparity or parallax motion across the surface were always parallel to the direction of the actual disparities or parallax motions for the vertically oriented contour (Fig. 2b), but were orthogonal for the horizontally oriented contour (Fig. 2c). Expressed another way, the spatial pattern of relative motion or disparity generated by the vertically oriented contour was equivalent to a one-dimensional expansion-compression (Fig. 2b), while the pattern created by the horizontally oriented con-

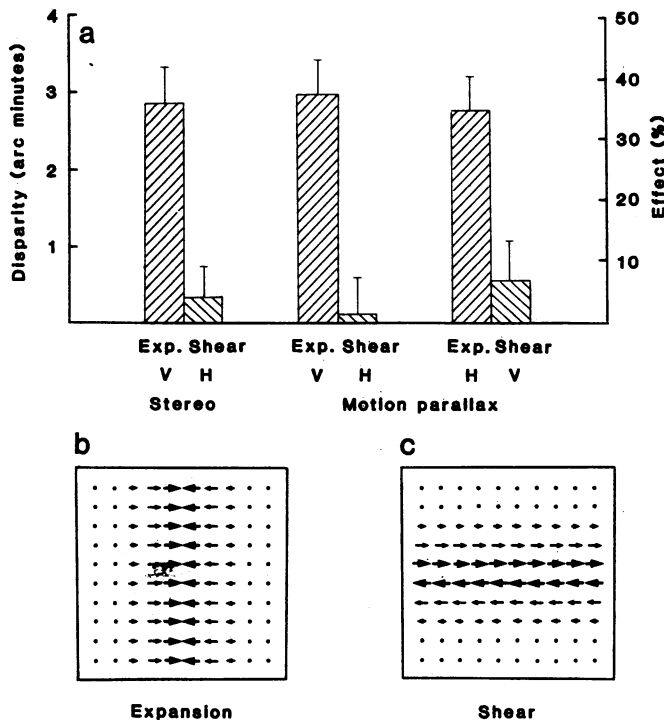
tour was that of a shear transformation (Fig. 2c) (8).

It is possible, therefore, that the anisotropies found experimentally were not due to the retinal orientation of the contour per se, but rather to the different transformations that were generated in the two cases. In the stereo domain these two possibilities are necessarily confounded, but for motion parallax it is possible to dissociate the orientation of the contour from the transformation by using vertical parallax motions coupled to vertical movements of the head. If the anisotropy is truly dependent on the orientation of the depth contour, then, for vertical motions, we would predict that the Cornsweet illusion be present for a vertically oriented profile and absent when it is oriented horizontally (as found for horizontal motions). On the other hand, if the anisotropy is the result of the different types of transformation, we would predict that the illusion be present for the horizontally oriented profile and absent for the vertically oriented profile (in the opposite direction to the previous findings).

Our results are consistent with the second prediction (right-hand pair of histograms in Fig. 2a). A large Cornsweet depth illusion was found with the horizontally oriented contour, which now produced a one-dimensional expansion with each vertical movement of the observer's head. In contrast, little or no illusion was found with the vertically oriented contour, which generated a shear transformation.

In summary, these results suggest that there is substantial asymmetry in the visual system's ability to pick up shear versus expansion transformations, both in the dynamic task of extracting parallax information and in the static comparison of disparate retinal images. Subsequent work has revealed that the anisotropy is most marked for depth surfaces with slow or low spatial frequency depth changes. Moreover, the anisotropies are not limited to surfaces with a Cornsweet profile. In a suprathreshold matching task there was a marked difference in the amount of apparent depth in low spatial frequency sinusoidal corrugations as a function of the type of transformation produced. The perceived depth was substantially less when the depth corrugations were vertical and produced expansion transformations of relative motion or disparity. Hence the anisotropy of the Cornsweet depth illusion described earlier might reflect the visual system's poor sensitivity to the slowly changing regions of the surface in the case of the expansion transformation. In addition, we

Fig. 2. (a) Size of the illusory depth effect as a function of the type of transformation generated by the surface (expansion-contraction or shear), and orientation of the Cornsweet edge [vertical (V) or horizontal (H)]. Results for stereoscopic surfaces are shown on the left and for parallax surfaces in the center (horizontal movements) and on the right (vertical movements). (b and c) Two different patterns of relative motion that would be produced on the retina of a subject viewing the surfaces depicted in Fig. 1, a and b, and moving the head laterally from left to right. The size and direction of the arrows indicate the magnitude and direction of parallax motions in each surface and the disparity differences between stereoscopic views of each surface.



have found that thresholds for perceiving very low spatial frequency depth corrugations (< 0.1 cycle/degree) are substantially higher when the depth contours generate expansion transformations than when they generate shear transformations. This was true for both stereoscopic and parallax depth corrugations.

Taken together, these results suggest that the falloff in low spatial frequency sensitivity is greater when the surfaces generate expansion-compression rather than shear transformations. Alternatively, the overall shape of the sensitivity functions may be similar, but the curves may be displaced relatively along the spatial frequency axis. The latter hypothesis would predict that the sensitivity for high spatial frequency depth corrugations should be greater for surfaces that produce expansion transformations. Such an anisotropy was recently reported for the simpler task of detecting patterns of relative motion (9). Our own studies of sensitivity to depth corrugations show a slight tendency in this direction, together with a small shift in the region of peak sensitivity toward a higher spatial frequency for surfaces that generate an expansion transformation. This would be expected if the spatial extent of local processing is less in a direction parallel to the direction of disparity or parallax motion.

BRIAN J. ROGERS

MAUREEN E. GRAHAM

Psychological Laboratory,
University of St. Andrews,
Fife, Scotland KY16 9JU

References and Notes

1. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971).
2. B. J. Rogers and M. E. Graham, *Perception* 8, 125 (1979).
3. The best known visual anisotropy is probably the so-called oblique effect, in which sensitivity for detecting lines or grating patterns is somewhat poorer when the lines are oriented obliquely [I. P. Howard, *Human Visual Orientation* (Wiley, Chichester, 1982)].
4. K. J. W. Craik, *The Nature of Psychology* (Cambridge Univ. Press, Cambridge, 1966); V. O'Brien, *J. Opt. Soc. Am.* 48, 112 (1958); T. Cornsweet, *Visual Perception* (Academic Press, New York, 1970).
5. F. Ratliff, *Sci. Am.* 226, 6 (June 1972); S. M. Anstis, *Handbook of Psychobiology*, C. Blake-More and M. Gazzaniga, Eds. (Academic Press, New York, 1975).
6. S. M. Anstis, I. P. Howard, B. J. Rogers, *Vis. Res.* 18, 213 (1978).
7. B. J. Rogers and M. E. Graham, *ibid.* 22, 261 (1982); M. E. Graham and B. J. Rogers, *Perception* 11, 247 (1982).
8. H. C. Longuet-Higgins and K. Prazdny, *Proc. R. Soc. London Ser. B* 208, 385 (1980).
9. K. Nakayama, G. Silverman, J. Mulligan, D. I. A. MacLeod, paper presented at the Annual Meeting of the European Conference on Visual Perception, Leuven, Belgium (1982).
10. Supported by grants from the Science and Engineering Research Council (GR/C/09579) and the Royal Society (PG/Inv.WMN/JMW). A partial report of these findings was presented at the Annual Meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Fla., (1982).

1 February 1983; revised 23 May 1983

Territorial Bell Miners and Other Birds Affecting Populations of Insect Prey

Abstract. *Bell miners (Manorina melanophrys) feed primarily on the lerps and nymphs of psyllids, and they defend communal territories against other bird species. As bell miners were removed experimentally from a psyllid-infested patch of eucalypt forest, birds of 11 other species moved in to feed on psyllids and within 4 months they eradicated the infestation. This shows the ability of other birds to control these insects in the absence of bell miners and the value of interspecific territoriality to bell miners.*

Bell miners (*Manorina melanophrys*) are aggressive honeyeaters (Meliphagidae) from southeastern Australia. They defend communal territories in the eucalypt forest canopy against other birds (1), including much bigger species. Up to 90 percent of the bell miners' diet consists of nymphs, sweet secretions, and lerps (protective carbohydrate covers) of psyllids (Homoptera: Psyllidae) (2-4), but wherever bell miners occur trees appear unhealthy, and foliage remains infested with these insects. Trees recover only if bell miners depart, and it was assumed that both events follow an initial decline in psyllids. However, when a landowner removed bell miners he observed that other birds invaded and controlled the psyllids, and the trees then recovered (5).

We repeated the experiment by removing all 34 bell miners from a small colony in Olinda State Forest between 22 July and 5 August 1981. The site of about 3 ha is at an altitude of 250 m, at 37° 50'S, 145° 22'E (near Melbourne), with annual rainfall of 1200 mm. Trees were mainly *Eucalyptus obliqua* and *E. cypellocarpa*, reaching heights of 30 m and showing severe defoliation and dieback due to endemic psyllids (*Glycaspis* spp). The birds were caught in barely visible stationary mist-nets; they were banded and released in psyllid-infested forest 45 km southeast, where there was already a larger colony of bell miners. They did not return to Olinda.

Bird populations were measured at intervals before and after removal by standard 20-minute searches in which all birds observed on the 3 ha were counted. Psyllid populations were estimated mainly by counting lerps on fallen leaves and litter that were collected monthly from 24 trays (0.2 m²) under selected trees. Similar measurements of birds and psyllids were made in comparable study sites in adjacent healthy forest and in a psyllid-infested forest nearby.

The experimental site was not reinvaded by bell miners (Fig. 1), although another colony remained only 300 m away. Instead, small flocks of nomadic insectivorous birds invaded and began eating

psyllids at a greater rate than had been achieved by the bell miners. A few bark-gleaning species also appeared. Numbers of birds remained high in August and September and suddenly declined in October. A smaller temporary influx occurred in early November, possibly corresponding with another generation of psyllids, but thereafter numbers were low and similar to those on the healthy control nearby. Numbers of birds on the two control areas showed much smaller seasonal changes.

Numbers of psyllids at the experimental site dropped rapidly when bell miners were removed and remained close to zero thereafter (Fig. 1). Few psyllids occurred on the healthy control at any time. Numbers in the psyllid-infested control fluctuated, but the dramatic disappearance on the experimental site was not paralleled there or at any of several other sites monitored. Subsequent improvement in tree health was revealed by a 15 percent increase in epicormic foliage observed on the experimental site 6 months after bell miners were removed, compared with a 4 percent increase on the healthy control and no net change on the psyllid-infested control.

Before removal bell miners constituted 64 percent of birds observed on standard searches; most others were understory species. The bell miners spent about 36 percent of the daylight hours foraging, and each consumed psyllids or lerps at an overall mean rate of 12 per minute (30 observations, each of about 1 minute). The mean weight of a bell miner was 30 g. After removal of bell miners, the most common psyllid-eating birds were striated thornbills, *Acanthiza lineata* (mean weight, 7 g; 24 percent of birds observed on standard searches), then white-naped honeyeaters, *Melithreptus lunatus* (14 g; 16 percent), crimson rosellas, *Platycercus elegans* (131 g; 6 percent), eastern rosellas, *P. eximius* (111 g; 3 percent), and spotted pardalotes, *Pardalotus punctatus* (9 g; 3 percent). The small birds fed almost continuously in daylight, each consuming psyllids at mean rates of about 25 per minute. Rosellas are mainly frugivorous but here