Table 2. Segregation frequencies in spore samples.

Gene	Controls	Outlet 11	Outlet 13
TR_5	0.631	0.567	0.552
LE_1	.656	.567*	.533*
P_1	.458	.557*	.486
AR_4	.542	.567	.500
HI_2HI_8	.321	.295	.248*
LY_2	.524	.548	.495
UR_1	.536	.552	.467
AD_2	.540	.533	.448*
	Number of spores assayed		
	504	210	210

* Indicates that the ratio differs from the corresponding control ratio at the 5 percent level of significance.

rent density was 8.3×10^{-4} amp/cm². The data presented in columns (a) and (b) of Table 1 demonstrate that separation of spores from diploid cells can be attained, the maximum separation being 99.04 percent in outlet 13. Separation is possible because the diploid cells have a distribution of electrophoretic mobilities lower than that of the spores; the weighted averages of the two distributions are 1.1×10^{-4} and 2.0×10^{-4} (cm/sec)/(volt/cm), respectively, for this experiment.

The spore colonies were examined genetically, by omission media tests, to determine if the cell populations exiting from each outlet were different from the controls. Omission tests involve replica plating to a series of synthetic media, each member of which lacks one of the different nutrients associated with the genetic blocks in strain X801. Therefore, the presence or absence of functional genes can be determined. With regard to the segregation frequencies of different genes (spores growing on a given omission medium divided by the total spores tested) outlets 10 and 12 did not differ from the controls. However, the segregation frequencies in samples from outlets 11 and 13 were significantly different from the controls for certain genes (Table 2). These results could indicate that the absence or presence of various biochemical functions can affect the electrophoretic properties of a cell. The deviations from .50, or .25 for histidine, observed in the controls may have been the result of colonies arising from aggregations of spores rather than from individual spores. Also, presence of a nonrandom sample of spores in two- and three-spore asci, or selective germination and growth of spores of particular genotypes, may have caused these deviations.

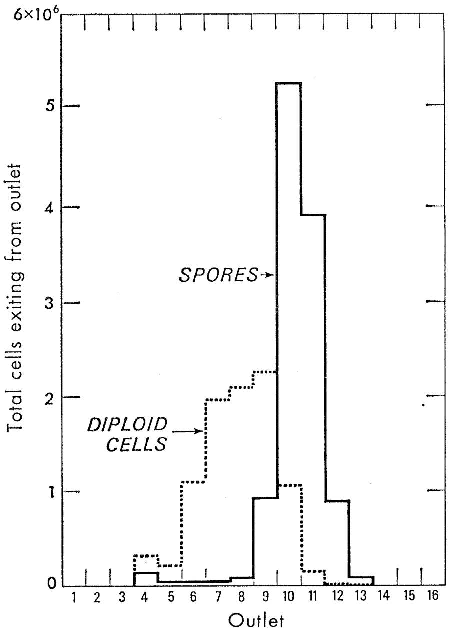

Fig. 1. Distribution of spores and diploid cells in the center column of outlets.

Although the segregation frequencies in some outlet populations differed from the controls with regard to individual genes, gene linkages were not appreciably affected. In the controls and outlet populations all unlinked gene pairs assorted randomly. The linkage of the gene pair tr_5-le_1 was observed to differ somewhat from the controls: the percent recombinants for the controls was 18.7; corresponding values of 12.8, 13.6, 11.7, and 9.6 were obtained for spores sampled from outlets 10, 11, 12, and 13 respectively. These outlet recombination frequencies are comparable to the value 13.3 reported by Mortimer and Hawthorne (*9*).

These experiments demonstrate the following: (i) spores and diploid cells have different electrophoretic mobilities which presumably reflect differences in cell wall electrical charge density; (ii) utilizing these differences in mobilities, Staflo electrophoresis enables the separation of spores from diploid cells; and (iii) the spore sample so obtained can be used to determine genetic linkages.

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References and Notes

1. J. R. S. Fincham and P. R. Day, *Fungal Genetics* (Davis, Philadelphia, ed. 2, 1965); G. Pontecorvo, *Advan. Genet.* **5**, 141 (1953); D. Newmeyer, *Genetics* **39**, 604 (1954).
2. R. K. Mortimer and D. C. Hawthorne, *Ann. Rev. Microbiol.* **20**, 151 (1966).
3. C. C. Emeis and H. Gutz, *Naturforsch.* **13**, 647 (1958).
4. H. Svensson, L. Hagdahl, K. D. Lerner, *Sci. Tools* 4, 1 (1957).
5. H. C. Mel, *Science* **132**, 1255 (1961); *Theoret. Biol.* **6**, 159, 181, 307 (1964).
6. The symbols used to define the genotype are the following: *a/α*, mating type; carbohydrate utilization: *SU*, sucrose; *MA*, maltose; *GA*, galactose; *MEL*, melibiose; nutritional requirements: *TR*, tryptophan; *LE*, leucine; *AR*, arginine; *HI*, histidine; *AD*, adenine; *UR*, uracil; *LY*, lysine; genetic petite: *P*. Upper and lower case refer, respectively, to ability and inability to ferment the particular sugar, to grow in the absence of a particular nutrient, and, for petite, to grow in the absence of a fermentable carbon source. The subscripts refer to particular loci.
7. D. O. McClary, W. L. Nulty, and G. R. Miller, *J. Bacteriol.* **78**, 362 (1959).
8. R. D. Tippetts and H. C. Mel, in *Chemical Engineering in Medicine and Biology*, D. Hershey, Ed. (Plenum, New York, 1967); R. D. Tippetts, *U.S. At. Energy Comm. Doc. UCLRL-16290* (1965).
9. R. K. Mortimer and D. C. Hawthorne, *Genetics* **53**, 165 (1966).
10. Supported by U.S. Atomic Energy Commission. We thank Dr. Theodore Regimbal for his generous assistance.

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Minimum Condition for Stereopsis and Anomalous Contour

Abstract. *Horizontal borders were deleted progressively from square and circular dot patterns containing disparate forms. Stereoscopic depth and anomalous contour occur in the absence of horizontal borders and the form in depth does not always assume the shape of the dot patterns. The stereoscopic effects depend on a laterally disparate form in the stereogram.*

The recent use of dot and letter matrix stereograms has raised again the issue of the necessary conditions for stereoscopic vision (*1–3*). When the half-images in Fig. 1a are viewed stereoscopically an inner white square appears in the dashed plane in front of two squares of dots, whereas viewing Fig. 1b produces a white surface in depth (dashed plane) with curved vertical and *straight* horizontal contours. The perceived contours are anomalous because they occur in the absence of any corresponding brightness gradient in the visual displays. Furthermore, the depth effects contradict traditional theories of stereopsis, inasmuch as all of the dots in the half-images are equidistant, thus prohibiting any contour or edge disparity (*4*).

It has been suggested that the dot patterns contain lateral form disparity which accounts for the depth effects (*3*). In the square matrices (Fig. 1a), the enclosed white forms are located differently within each half-image due to the selective omission of dots. Notice that the right inner column is absent for the left half-image whereas the left inner column is missing for the right half-image. Similarly, the circular matrices (Fig. 1b) contain form disparity even though the form in depth (dashed plane) cannot be recognized in the monocular arrays. The size and shape of the perceived interposed form are adequate to produce the observed differences in the half-images.

The present experiment tested the hypothesis that if lateral form disparity produces depth and anomalous contour, then removing the horizontal borders of dots from the square and circular patterns should not affect depth perception because the lateral disparity of the form would not be altered. Further deletion of the inner vertical borders of dots would eliminate the lateral disparity of the form and consequently stereoscopic depth and anomalous contour should be absent.

Figure 1c presents the eight experimental stereograms in which zero, four, and eight horizontal dot borders were eliminated progressively from the half-images. The bottom stereograms contain no form disparity and consist of only single columns of dots (ten borders removed). The experimental and five control stereograms (pairs of identical images, chosen at random from the experimental images) were punched out of white paper by means of a steel punch template. After punching, the white paper was placed over flat black paper and photographed. The positive prints were placed in slide mounts and displayed in an Angermeier stereoscope (5). Under the conditions of viewing, each dot in the experimental stereograms subtended a visual angle of 0.044°, and the interdot distance, measured center to center, equaled 0.088°.

In all experimental stereograms the luminance of the dots and surround were constant at 0.42 and 8.98 ft-lam (0.45 and 9.66 mlam), as measured with a Macbeth illuminometer. These values were obtained from photographs of the white and black paper mounted in the stereoscope under the same conditions as were employed in the experiment.

Five male and three female undergraduate students (mean age 21) with uncorrected normal near-visual acuity (20/17 to 20/25), lateral (3 to 6) and vertical (6 to 9) phoria, and stereopsis (90 percent Fry-Shepard), as measured by a Bausch and Lomb Orthorater (Model 71-21-31), served as observers. Although each had experience with stereoscopic phenomena, none was familiar with the purpose of the experiment.

All observers estimated depth in five training stereograms, using a magnitude estimation technique. The half-images employed in training consisted of two line-drawn squares, one within the other, in which lateral retinal disparity was increased from 0.0° to 0.220° in 0.044° steps of visual angle. The disparity was such that the inner square always appeared in front of the outer one.

Each observer was instructed to consider the base of the inner square as a ruler of ten units and to turn the ruler 90° in his mind's eye and measure the distance between the nearer and more distant objects. The base of the inner square subtended a visual angle of 1.510° for all the depth-training stereograms. Random presentation of the stereograms yielded reliable depth estimates by each observer.

The same technique was employed for estimating depth in the experimental stereograms. Each observer used the base or the diameter of the form in depth and estimated the distance between it and the dot pattern in the same fashion as he practiced previously with the line-drawn stereograms. The dot patterns employed in all experimental stereograms held constant and made equivalent the side of the inner squares and the diameter of the inner circle at 1.510° visual angle. The experimental and control stereograms were presented randomly to each observer.

The results indicate that the horizontal borders of dots are not necessary for the perception of depth and anomalous contour in either square or circular dot patterns. Figure 2 represents the

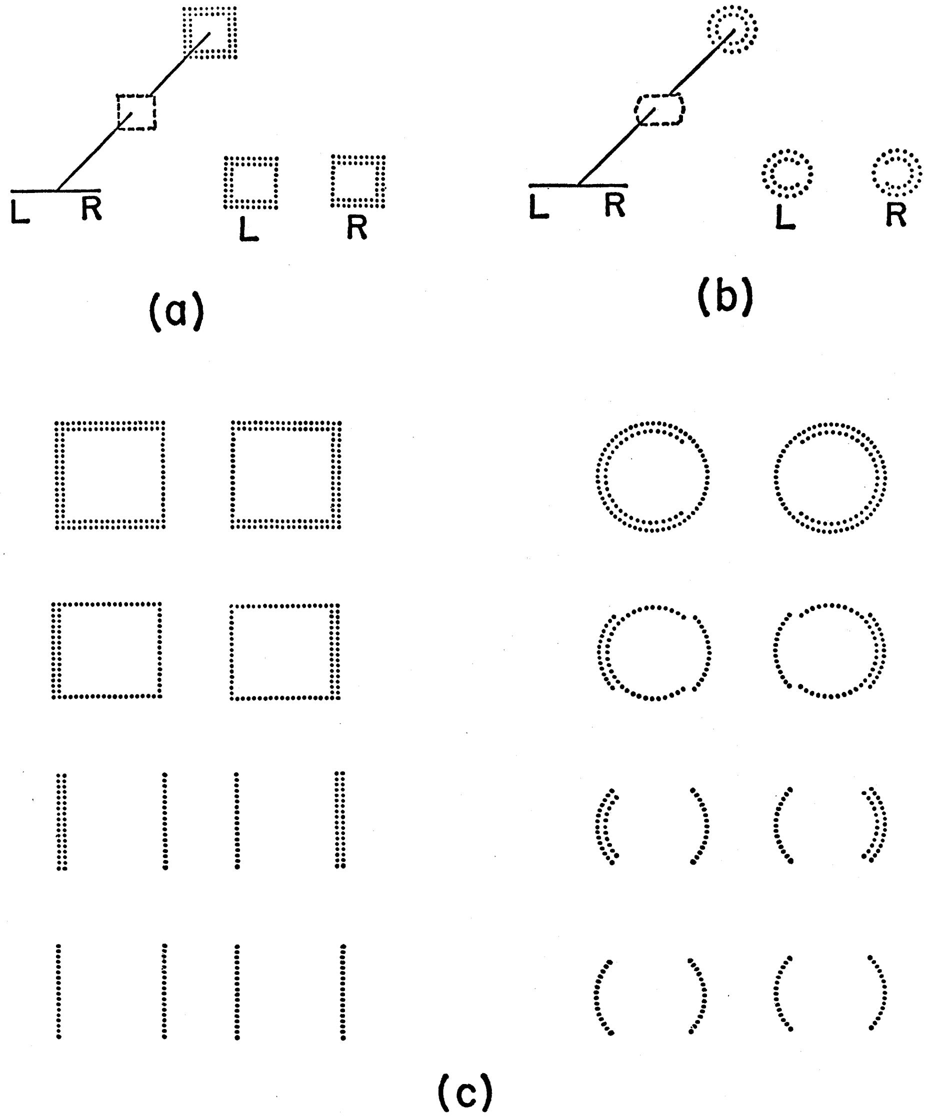

Fig. 1. Schematic representation of the perceptual results produced by viewing stereoscopically the square (a) and circular (b) half-images. (c) Experimental stereograms with 0, 4, and 8 horizontal dot borders deleted, and at bottom, stereograms that contain no form disparity and have ten dot borders deleted.

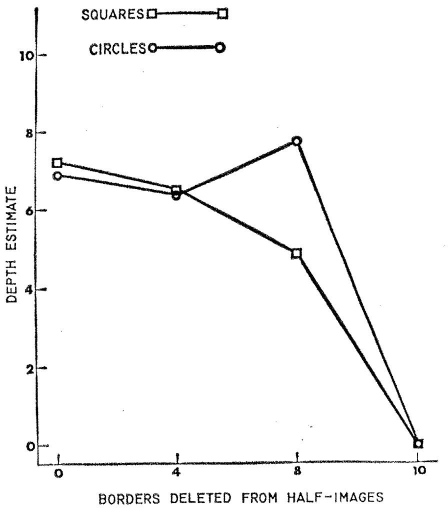

Fig. 2. The mean depth estimates based on eight observers for each experimental stereogram.

mean depth estimates for eight observers for each of the experimental stereograms. The depth estimates remained relatively stable despite the removal of the horizontal borders of dots from the square and circular patterns; however, depth was not reported when the stereograms contained no form disparity and had ten dot borders removed. Anomalous contours were reported *only* when the white planar surface appeared in depth, and none of the observers reported depth when viewing the control stereograms.

To assess the effects of dot configuration (square and circular) and the number of borders removed from each half-image upon the depth estimates, an analysis of variance was computed. The only significant factors were the subject ($F = 12.58$, 7/21 df, $P < .005$) and border deletion effects ($F = 88.09$, 3/21 df, $P < .005$). A Duncan's multiple range test revealed that only the depth estimates for the experimental half-images without any form disparity differed significantly from the other half-images with form disparity ($P < .001$). The slight enhancement of the depth effect for the circular pattern in the absence of the upper and lower quadrants of dots was not significant and was due to the fact that two observers had difficulty in reporting depth for the comparable square pattern ($t = 1.68$, 18 df, $P < .01$). The shape of the forms in depth remained the same regardless of the number of dot borders removed from the disparate half-images.

For those patterns with only vertical dot borders that produced depth, all observers reported that the vertical contours (straight and curved) were much sharper than the contours along the horizontal dimension of the planar surface in depth. The horizontal edges represent a striking example of visual contours in homogeneous space and indicate that contiguous dots in the stereoscopic field are not essential for the contour effects (*6*).

Similar stereoscopic depth and contour effects as reported above were also found with Julesz dot patterns (*1*) and Kaufman letter patterns (*2*) when all of the nondisparate background elements were deleted except for two vertical borders in each half-image.

The present results indicate that neither horizontal dot borders nor monocular recognition of disparate forms is essential for stereopsis and anomalous contour perception in dot and letter matrix targets. However, form disparity which can be produced by shifting laterally a central submatrix of dots (*1*), by superimposing a laterally shifted brightness pattern upon a matrix of nondisparate elements (*2*), or by the selective omission of elements in a visual pattern (*3*) is essential. The disparate form is detected from the combined monocular images and the location of the anomalous contours cannot be specified completely in terms of the characteristics of the change in gradient of the reflected light within the optical array.

The findings with matrix-defined disparate forms can be accommodated by traditional theories of stereopsis provided disparity is extended to include certain properties of visual arrays besides contours (*4*). The fact that with form-disparate stereograms depth is restricted to the corresponding yet spatially disparate feature of the visual display supports this conclusion. Furthermore, data on depth magnitude judgments indicate clearly that perceived depth varies directly as a function of the lateral displacement of the forms (*1, 3*).

That contour can be perceived in homogeneous space (*7*) suggests that new conceptualizations of contour processes are necessary.

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References and Notes

1. B. Julesz, *Bell System Tech. J.* **39,** 1125 (1960).
2. L. Kaufman and C. Pitblado, *Amer. J. Psychol.* **78**, 379 (1965).
3. R. B. Lawson and W. L. Gulick, *Vision Res.* **7**, 271 (1967).
4. K. N. Ogle, in *Psychology: A Study of a Science*, S. Koch, Ed. (McGraw-Hill, New York, 1959), vol. 1, p. 362.
5. Details of the Angermeier stereoscope may be obtained from the authors.
6. The stereoscopic effects are visually quite striking and the reader can see them with a hand stereoscope or simply by viewing the dot patterns cross-eyed.
7. T. Shipley, *Science* **150**, 348 (1965).
8. Supported by PHS grant NB 07301-01 to R.B.L., and by NSF grant GY146 for undergraduate research participation.

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Total Luminous Flux: A Possible Response Determinant for the Normal Monkey

Abstract. *Thirteen normal monkeys* (Macaca mulatta) *trained to discriminate between transilluminated figures of equal area and different luminance, and consequently different luminous flux, made similar numbers of errors during training on a new problem with the same luminance values but with targets equated for luminous flux. These findings together with results of "critical trials" suggest that the significant cue in the original problem was luminous flux. This behavior is strikingly similar to what has been reported for the monkey following exclusion of the geniculostriate system.*

It is well known that normal monkeys can be trained to discriminate between two figures of equal area (A) that differ in luminance (amount of light per unit area, B) and consequently also in luminous flux (total quantity of light, F) (*1*). Although it has been stated that a "brightness" or "intensity" discrimination (*2*) was established in this case (*3*), the experiment to be described suggests that this conclusion does not apply to all conditions of testing. In fact, there are several possible response determinants for this discrimination when transilluminated targets are used: (i) the absolute dimensions of one or the other stimulus, that is, the selection of one because of its own level of brightness or flux, without reference to the other figure;