Fig. 2 Polar plots of preferred orientations for cortical cells are shown. Each line represents the optimal stimulus orientation for a single cell. The cat shown at the top is normal and below its name (M 23) several lines indicate that all orientations were present during rearing. The other cats have had a biased environmental upbringing caused by ocular astigmatism. As in Fig. 1, the lines above left (L) and right (R) eyes indicate the orientation which was in clear focus during rearing.

selectivity, as discussed in a detailed account of this work (Freeman and Pettigrew, unpublished).

Another finding, shown in Fig. 2, is the small number of units in the astigmatic kittens that are driven by both eyes. Only 25–35% of the cells are binocular as opposed to around 85% in the normal cat. One would expect a loss of binocularity in the case of oblique cylinders with different axes in front of each eye, but a reduction in the number of binocular cells also occurred with the bilaterally symmetrical biased kittens. The most likely explanation for the preponderance of monocular units is that the lenses were somewhat decentred during rearing. Even a slight misalignment between the pupils and geometrical centres of the lenses would lead to considerable prismatic displacement.

The astigmatic rearing conditions also affected the limits of orientation selectivity. For normal cortical cells, stimulus orientation is usually very important, but the range over which the cell responds can vary considerably. Some cells are active over an angular region of only a few degrees while others respond over very wide ranges. In the astigmatic kittens, cells whose optimal orientation fell near the meridian of clear focus were also responsive over narrow to wide angular ranges as in normal kittens. But for the less frequently encountered units whose activity was highest when stimuli were presented away from the experienced meridian, we found that the response limits became broader. At a large angular distance from the clearly focused meridian, there were no finely tuned units. The implication is that a deficiency of features of a given orientation during early visual experience results in both a reduced number and a diminished selectivity of neurones which respond to that orientation.

Our results demonstrate that a subtle bias in the visual environment of a developing kitten is sufficient to markedly alter cortical physiology. The effects are graded in that our moderately biased kittens are modified less than the group for which bias was more severe. Thus, it appears that a kitten who has no previous visual experience is extremely sensitive to an environmental nuance. Even a relatively minor variation from normal exerts an influence on cortical connectivity.

It should, however, be mentioned that the type of approach

used in this investigation may be very useful in studying the physiological correlates of ocular refractive error.

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Perception of Random Dot Interference Patterns

THE observation that circular patterns are immediately perceived if a random dot pattern (Fig. 1a) is superimposed on itself and rotated slightly (Fig. 2a) indicates that the visual system detects local autocorrelations and integrates these to form a global circular percept[1]. By varying both the local and global parameters describing the interference patterns, the functional organisation of the visual system can be probed and new perceptual effects discovered.

There is nothing special about the circular morphology of the random dot interference patterns. By performing other transformations of the random pattern about a fixed centre point before superposition new morphologies arise. For example, by uniformly expanding Fig. 1a, we obtain Fig. 1b. A starlike pattern is produced when Figs 1a and 1b are superimposed (Fig. 2b). If they are superimposed in a rotated position, spirals will result (Fig. 2c). If Fig. 1a is expanded in one direction and contracted in the orthogonal direction (Fig. 1c) a hyperbolic pattern will result after they are superimposed (Fig. 2d). In these cases, for each point, P_i (x_i, y_i), in the initial pattern, the transformations generate a new point, P_i' (x_i, y_i), given by

$$x'_i = ax_i \cos \theta - by_i \sin \theta$$
$$y'_i = ax_i \sin \theta + by_i \cos \theta \qquad (1)$$

where the x coordinate is multiplied by a, the y coordinate is multiplied by b, and the pattern is rotated through an angle of θ. Since this finite transformation can be thought of as an iteration of an infinitesimal transformation, each pair of correlated points can be thought of as lying on a single trajectory in a phase plane representation of two coupled, autonomous linear differential equations corresponding to the infinitesimal transformation. The dot patterns have the same morphologies as the trajectories of this underlying differential equation and can be predicted using the qualitative theory of differential equations[2]. The eigenvalues, $\Gamma_\pm$, of the linear transformation of equation (1)

$$\Gamma_\pm = [(a+b) \cos \theta \pm ((a-b)^2 - (a+b)^2 \sin \theta)^{\frac{1}{2}}]/2 \qquad (2)$$

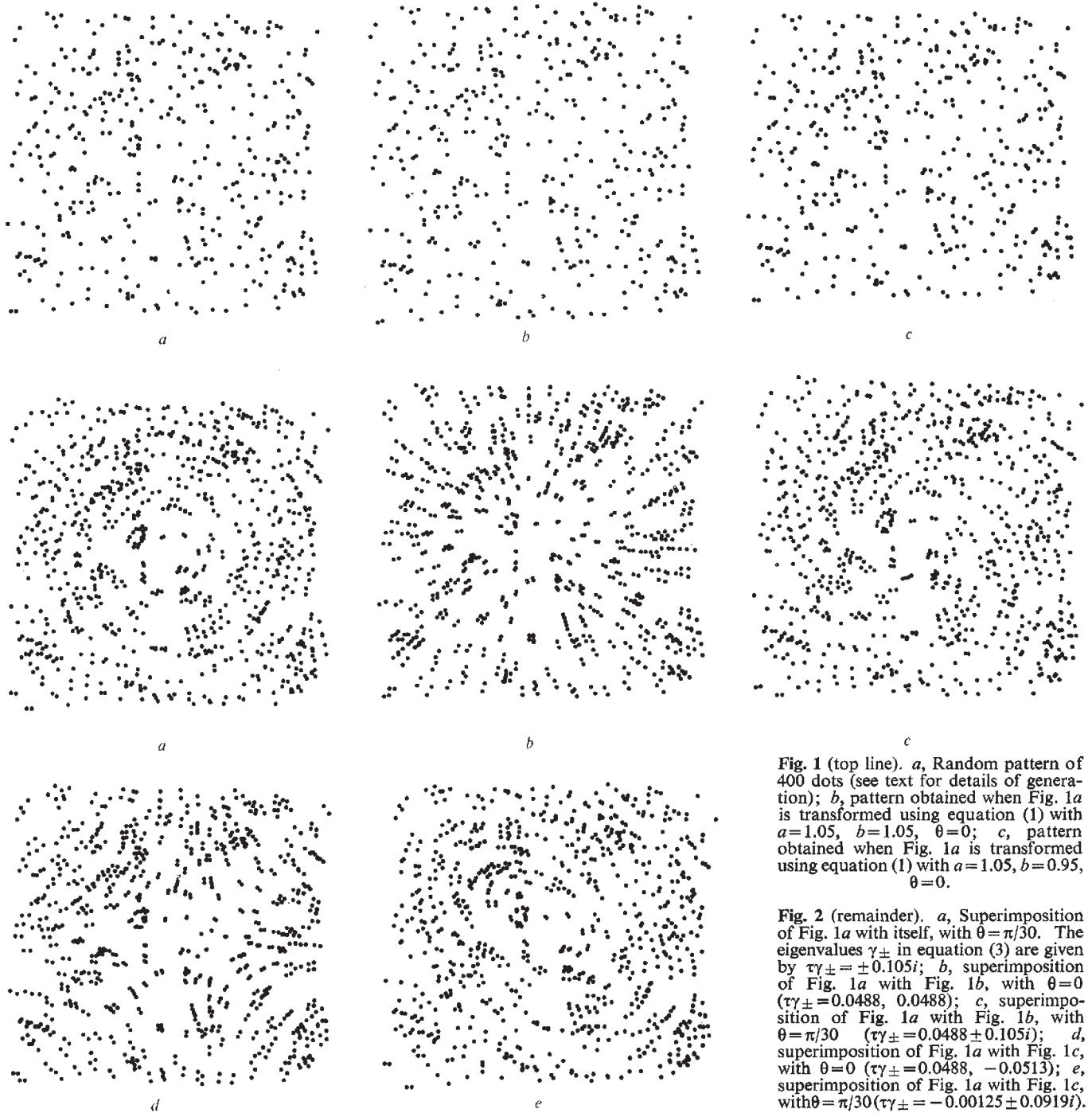are related to the eigenvalues of the underlying differential

Fig. 1 (top line). *a*, Random pattern of 400 dots (see text for details of generation); *b*, pattern obtained when Fig. 1*a* is transformed using equation (1) with $a=1.05$, $b=1.05$, $\theta=0$; *c*, pattern obtained when Fig. 1*a* is transformed using equation (1) with $a=1.05$, $b=0.95$, $\theta=0$.

Fig. 2 (remainder). *a*, Superimposition of Fig. 1*a* with itself, with $\theta=\pi/30$. The eigenvalues $\gamma_\pm$ in equation (3) are given by $\tau\gamma_\pm = \pm 0.105i$; *b*, superimposition of Fig. 1*a* with Fig. 1*b*, with $\theta=0$ ($\tau\gamma_\pm =0.0488$, 0.0488); *c*, superimposition of Fig. 1*a* with Fig. 1*b*, with $\theta=\pi/30$ ($\tau\gamma_\pm =0.0488\pm0.105i$); *d*, superimposition of Fig. 1*a* with Fig. 1*c*, with $\theta=0$ ($\tau\gamma_\pm =0.0488$, -0.0513); *e*, superimposition of Fig. 1*a* with Fig. 1*c*, with $\theta=\pi/30$ ($\tau\gamma_\pm = -0.00125\pm0.0919i$).

equation, $\gamma_\pm$, by the relation[3]

$$\gamma_\pm =(1/\tau)\ln\Gamma_+ \qquad (3)$$

where τ is a non-negative, real constant

The dot interference patterns given in Figs 2*a-d* correspond to the only possible morphologies for two coupled, autonomous, first order, linear differential equations (or non-linear equations with non-zero linear terms) in the neighbourhood of a critical point and are called, respectively, a centre ($\gamma_\pm$ are pure imaginary), a node ($\gamma_\pm$ are real with the same sign), a focus ($\gamma_\pm$ are complex conjugates), and a saddle point ($\gamma_\pm$ are real with opposite signs)[2]. If Figs 1*a* and 1*c* are superimposed and rotated the theory predicts that for $\theta>\sin^{-1} 0.05$, a focus will result, and this is observed (Fig. 2*e*). (For rotations in the range $2\sin^{-1} 0.025<\theta<\sin^{-1} 0.05$ there is a node, but as this comprises an angle of approximately $(0.025)^3$ rad or about 3 arc s it is not easily observed.) For any other differentiable transformation of the random dot pattern, the perceived patterns after superimposition of the original and its trans-

formed image correspond to the patterns generated by the trajectories of an underlying differential equation. This suggests that random dot interference patterns can be used to obtain qualitative information about the trajectories of first order differential equations of two variables. (The coordinates of each point in Fig. 1*a* were generated using a pseudorandom number generator (the RAND subroutine of FORTRAN IV implemented on an IBM 360 computer). The coordinates of the points in Figs 1*b* and 1*c* were then computed using equation (1). Figs 1*a-c* were plotted in a 6×6 inch area using a Calcomp plotter which printed an asterisk centred at each coordinate locus to ±0.01 inch. To improve presentation, Figs 1*a-c* were drafted by hand from the computer printout. Transparencies of Figs 1*a-c* were made and these were superimposed to give Figs 2*a-e*. In the drafting process errors of approximately $\pm1/16$ inch were introduced in the coordinate positions. By inspection of the interference patterns, in particular Figs 2*b* and 2*d*, these errors can be noted.)

The perception of random dot interference patterns requires integration of the correlated signals over a large portion of the visual field. This can be shown in a variety of ways. If all but a small region of the pattern (which is, however, large enough to contain several correlated pairs) is occluded, the structure of the unoccluded region can no longer be perceived. By selective attention the viewer will notice several local features which arise as a result of the random generation procedure, but which are generally overlooked when the global organisation is perceived. Calling the length of one side of Fig. 2a, L, it can be shown that for a point at a distance $3L/8$ from the centre (where the circular pattern is readily seen), the number of uncorrelated points lying closer to a given point than the correlated point is approximately four. This shows that information from several pairs of correlated points must be integrated to detect the local correlations.

Transparent negatives of the patterns in Fig. 1 were made and correlated pairs were mounted so that when the images were projected using a stereoscopic projector and viewed without polaroid glasses, the negative images of the patterns in Fig. 2 could be seen. The intensities of each dot pattern could then be varied independently by rotating polarizers in the optical path. Consider the superimposition of Fig. 1a with itself, where the two patterns are labelled P and P', with P' rotated clockwise with respect to P: as the intensity of P' decreases with respect to P the entire figure appears to rotate in an anticlockwise direction; as the intensity of P' increases with respect to P a clockwise rotation is seen. Analogous results occur from the superimposition of the other pairs of figures used to construct Fig. 2. For example, calling Figs 1a and 1b, P and P', respectively, we find that decrease of intensity of P' results in a perceived contraction of the figure, while increase of the intensity of P' leads to a perceived expansion of the figure. For each case, although there is no real motion, there is a perceived apparent motion which can be described by saying that we perceive the movement of the centre of intensity of each pair of correlated points. Partial changes of intensity lead to partial motions. Although the perceived apparent motion is similar to the familiar "phi phenomenon"[4], important differences distinguish the two effects. First, we have unsuccessfully attempted to observe partial motion as a result of incomplete intensity changes for the phi phenomenon, and have also been unable to locate any other reports in the literature of partial motion for this effect. Second, the motion effect described here requires a large region of correlated pairs of dots. If only a small portion of a pattern is presented, the effect disappears, mimicking the disappearance of perceived patterns of Fig. 2 under presentation of a small portion of the pattern. Over a wide range of intensity differences of the two subpatterns, the patterns of Fig. 2 can still be perceived. At very low intensities of one pattern with respect to the other, the patterns of Fig. 2 can, however, no longer be perceived and a random pattern is observed. The motion effect is particularly striking using the more easily generated splatter patterns presented in ref. 1.

The colours of each of the subpatterns of Fig. 2 can also be changed independently by interposing coloured filters in the optical path. The effects previously described remain unchanged, The patterns of Fig. 2 as well as the apparent motion effect can still be observed when the two subpatterns are of different colours. In addition, the resulting patterns give a striking presentation of the colour stereo effect[5-7], in which different colours appear in different depth planes as a consequence of chromatic aberration of the eye; the effect is strongest with red and blue filters and low light intensities.

The patterns of Fig. 1 were presented binocularly as random dot stereograms (Julesz patterns)[8]. Negative slides for use with the stereoscopic projector, as well as positives which can be fused directly (or by using a stereoscopic viewer), were prepared. Initial experiments were performed using a random pattern and its rotated image. Using this stimulus it is possible that torsional peripheral movement of the eyeball could bring both subpatterns into correspondence. To eliminate this possibility slides were prepared with vertical and horizontal axes passing through the centre of both the original and its rotated image. When these slides were projected and viewed without polarising stereo viewers, a circular pattern intersected by a single set of orthogonal axes is observed. Upon binocular presentation (with polarising glasses) the circular pattern disappears. The coordinate axes are fused, and with stereopsis a single set of random points are perceived lying on a tilted plane passing through the horizontal axis. No peripheral eye movements can bring the other subpatterns, presented as stereo pairs, into correspondence. Stereopsis can be readily performed with Figs 1a and 1b and also with Figs 1a and 1c. In each case, the interference patterns of Fig. 2 are destroyed and a single pattern of dots seen in depth is always perceived. In binocular presentation of random dot stereograms, cross correlations between the images in the eyes are computed with any disparities leading to depth perception. (See ref. 8, especially Figs 2.8-8, 6.5-3 and 6.5-4 and related discussions.) In binocular fusion of the patterns the small errors introduced by hand drafting are particularly noticeable and can be seen as small deviations away from the smooth surfaces defined by the disparities.

A major problem facing neurophysiologists is the determination of the physiological basis of form perception in higher animals. Major steps forward have been made in elegant demonstrations of cortical units which respond to a variety of local features in the visual field: stationary oriented stimuli[9], moving oriented stimuli[9,10], and disparities between oriented stimuli in the right and left eyes[11,12]. Although the demonstration of local feature extractors at the cortical level is suggestive, this demonstration is in itself insufficient to show the involvement of these units in perception processes requiring integration of local features to form global percepts. Further, few data are available concerning neutral units sensitive to global parameters of the visual input. The random dot interference patterns and stereograms provide uniquely simple stimuli in which local correlations must be integrated to form global percepts and in which both local and global features of the patterns can be independently varied. The use of these patterns as input stimuli in physiological experiments seems justified.

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