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9. All behavioral testing was done in three identical Lehigh Valley operant chambers and cubicles (No. 1417). All rats were trained to lever press and then given daily 20-minute CRF sessions until 500 responses were accumulated. Continuous reinforcement training was given before the extended experimental diet period because we have found it more difficult to train older rats to bar press.
10. D. W. Walker and G. Freund, *Physiol. Behav.* **7**, 773 (1971). The liquid diets were fortified with vitamin diet fortification mixture (0.3 g per 100 ml of diet) and salt mixture XIV (0.5 g per 100 ml of diet) (Nutritional Biochemicals).
11. The mean body weights of the three groups on the first day of the experimental diet period were 416 g (342 to 444 g) for the alcohol group, 400 g (353 to 451 g) for the sucrose group, and 405 g (349 to 439 g) for the lab chow group. At the end of the 5-month experimental diet period the mean body weights were 483 g (439 to 523 g) for the alcohol group, 461 g (423 to 537 g) for the sucrose group, and 463 g (430 to 505 g) for the lab chow group. No clinical signs of malnutrition were observed. The mean daily alcohol consumption of the alcohol-consuming rats was 10.25 g/kg per rat (range, 9.65 to 11.64). In a previous experiment (*10*) we noted that rats consuming identical liquid diets ingested from 3 to 34 times the minimum daily requirements of vitamins and minerals.
12. Supported by the Veterans Administration and by grants AA-00200 and AA-00218 from the National Institute of Mental Health. We thank Larry Ezell, Dorothy Robinson, and Cornelia Williams for technical assistance. Send reprint requests to D.W.W.

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Visual Experience without Lines: Effect on Developing Cortical Neurons

Abstract. *Kittens were reared in a planetarium-like visual environment that lacked straight line contours. Cortical neurons were subsequently highly sensitive to spots of light but not to straight lines, in marked contrast to those from a normal cat. If linear contour processing is an innate function it appears to be subject to substantial modification by early visual experience.*

At successive stages of the visual system, information is abstracted from different environmental features. Neurons in the mammalian visual cortex are sensitive almost exclusively to linear contours (*1*).

But is the sensitivity of the cortex to straight lines an immutable consequence of evolution? The rationale of this question stems from the recent series of experiments concerned with the influence of early visual experience on the subsequnt organization of the visual system. These studies have shown that during early development, the connections of visual neurons are remarkably plastic. Cells not only become sensitive to the orientation of the contours that were predominant in the early visual environment (*2*), they do so within exceedingly brief periods of exposure (*3*).

One would expect that there must be a limit to the degree of environmental shaping of neuronal circuitry. We sought to probe the limit by producing a severe alteration in the normal environment of growing animals. We reared kittens so that they never saw lines or linear shapes. Their only visual experience was from a pseudorandom array of point sources of light, which appeared like bright stars in a dark sky. For controls, we used a normally reared cat and one raised in total darkness. Subsequent physiological study of the kittens reared so that they never saw lines (random dot kittens) showed that their visual cortical neurons were remarkably atypical in that they were selectively responsive to small, moving spots of light, much smaller than the receptive field sizes. Of the few cells that seemed sensitive to edges, only two could be said to approach the normal variety that are most responsive and selective to elongated stimuli. We conclude that if linear contour processing is an innate property of the visual cortex, it is one which can be readily modified.

For the initial experiment, we chose a kitten with an all black coat to reduce the chance of self-observation during the exposure periods. He was kept in a totally dark room until he was 28 days old (*4*). During the next 13 days, he spent 3 hours daily in a large (90 cm diameter), opaque polyethylene sphere. There were 1 mm diameter holes in the upper hemisphere, spaced so that no two would fall within the typical receptive field of a single cortical neuron (*5*). The arrangement of holes was pseudorandom in order to minimize the chance that linear contours would be synthesized from several points. A bank of lights surrounded the sphere, and the utmost precautions were taken to eliminate stray light and to insure that the kitten saw only the point sources of light (*6*). We attempted to gain the kitten's attention by moving the bank of lights around the sphere and by making noises, and he seemed to be active for most of the time. At the end of the 39-hour exposure period, he was returned to the dark room for a week prior to the neurophysiological observations.

The electrophysiological techniques were standard (*7*). Action potentials were recorded extracellularly in area 17 with tungsten-in-glass microelectrodes (*8*). All firing units were tested with a wide variety of stimuli (*9*). These stimuli were also presented continually as we advanced the electrode so that we would not miss neurons that were "edge-detectors" and which lacked spontaneous activity. The stimuli were positioned in the object plane of an overhead projector with a frame attached to an X-Y recorder. All directions of movement could be produced manually or by computer controlled commands to the X-Y recorder. After initial plotting of the receptive field, we used the computer to obtain quantitative estimates of stimulus preference.

The results from the first random dot kitten were most striking. Over a 72-hour period, we made a detailed study of 69 single units from three electrode tracks. On the basis of waveform or binocularity or both (*10*) all of the units were identified to be cortical cells except for three incoming fibers from the lateral geniculate nucleus (*11*). Of the cortical cells studied, 19 were insufficiently responsive for receptive field plotting and 47 had clearly defined fields. Twenty-seven of the latter group gave vigorous and dependable responses to a completely atypical range of stimuli which led us to call them "spot detectors." These cells had the following characteristics. (i) Their optimal response was to moving, circumscribed, bright targets always less than 0.5° and often less than 0.2° in diameter (*11*). (ii) There were vigorous ON or

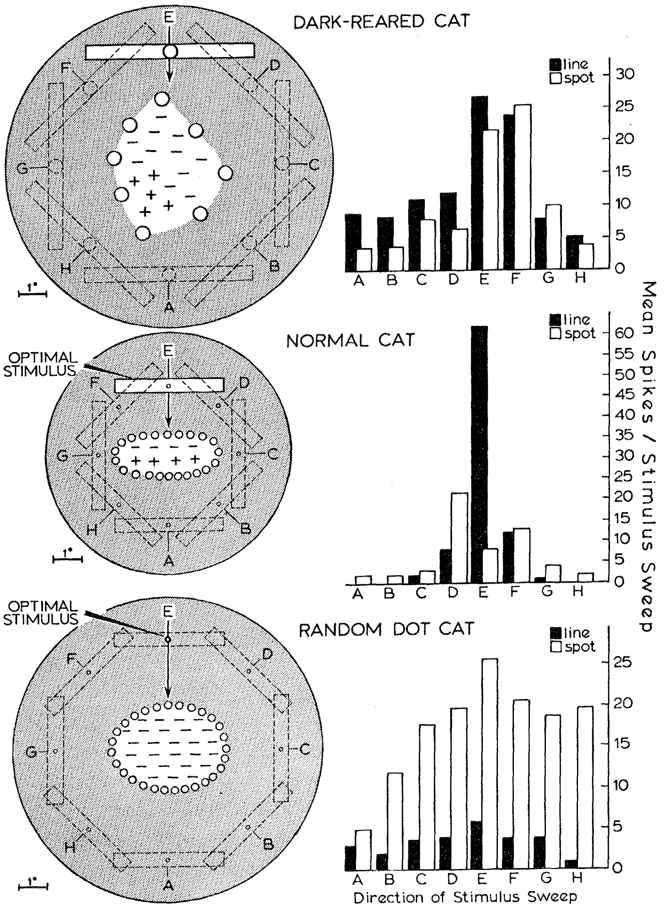

Fig. 1. Comparison of typical neurons from the striate cortex of cats raised under three conditions: (i) total absence of visual stimulation, (ii) normal visual experience, (iii) visual experience confined to randomly arranged light spots. All neurons had receptive fields that could be plotted with small (0.1° to 0.5°) flashing spots of light. Plus signs indicate responses only at ON, minus signs indicate responses at OFF and an open circle designates no response. The neuron from the cat raised in the dark gave variable responses from trial to trial but averaged responses were biased for downward moving stimuli. This bias was independent of the configuration of the stimulus used, and small spots were as effective as lines matched to the field size. The normal cell responded to moving stimuli in a manner that could be predicted from its receptive field: elongation of the stimulus resulted in a summation of the response so that the optimal stimulus had dimensions (0.5° by 4°) that corresponded to the receptive field dimensions. In contrast to all cells in the normal cortex, the dot-detecting neuron does not show spatial summation along any receptive field dimension and the optimal stimulus is 0.1° in diameter, much smaller than the receptive field (4° across): a line (4° by 0.5°) carefully matched to field size gave a poor response. The histograms are obtained from computer-presented stimuli, and they give the mean number of spikes for a narrow bar (0.5° by 4°) and a light spot (0.1°) for five stimulus sweeps in each of the eight directions indicated. Sweep amplitudes and velocities are, respectively: 8°, 2° per second (dark-raised cat); 5°, 1° per second (normal cat neuron); and 8°, 2° per second (random dot cat neuron).

OFF responses to stimuli in an irregularly shaped receptive field of much larger dimensions than the optimal stimulus (average field size was 2.8° wide and 3.5° high). (iii) There was an absence of spatial summation within the plotted receptive field (*12*). (iv) The majority of cells were activated from both eyes (*13*). The third feature was the least expected. Although many of the receptive fields in the visual cortex were elongated, usually in the vertical direction, the irregularity of the receptive field shape bore no relation to the optimal stimulus. Enlarging or lengthening the stimulus to match the field shape always led to a diminished response, in marked contradistinction to the behavior of cells in the normal cortex (Fig. 1). The neuron from the cat raised in the dark showed no obvious preference for either spots or lines. On the other hand the cells of both the normal and the random dot cats were selective for stimulus configuration. Among the stimuli used, a linear contour was optimal for the cell of the normal cat and a small spot of light was optimal for the random dot cat. In the latter case, the findings conform to what is predicted if cortical physiology is correlated with early visual environment.

Of the remaining 20 responsive cortical cells, 12 responded best to moving circular patches of light. This response was nonselective for size, although 8 were selective for the direction of stimulus motion.

Of the 8 cells that did not respond preferentially to light spots, two were unquestionably edge detectors. They had elongated fields, and were most responsive and selective to elongated stimuli. The remaining 6 appeared to favor an edge stimulus, but responses were highly variable or sluggish or both. Furthermore, a circular patch stimulus was usually as effective as a line. None of these 8 cells had receptive fields that could be mapped with flashing stimuli.

We have confirmed these findings for a second random dot kitten. We could find no edge detectors among the 40 neurons studied in this animal's cortex. Twelve of these neurons were spot detectors (*12*) and the remainder were nonselective for stimulus configuration.

The present results are sufficiently detailed and striking to raise again the question of nature and nurture in regard to neuronal connections. The report that certain neurons in the cortex of visually inexperienced kittens have the same properties as neurons in the adult (*14*) has been recently questioned (*15*). Our findings that only two cells of the random dot kittens had the specific properties of normal adult neurons suggest that the usual high degree of specialization in cortical cells is largely derived from visual experience. Or, if the specificity is determined via innate connections, it can easily be altered to match the requirements of the early visual input.

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4. At this age, kittens are extremely sensitive to the nature of their visual input [see (*14*)].

5. The minimum and maximum possible viewing distances to each hole were used to compute spacing so that no two holes were closer together than 3°, a typical central field size [J. D. Pettigrew, T. Nikara, P. O. Bishop, *Exp. Brain Res.* **6**, 373 (1968)].
6. We verified the adequacy of the precautions prior to the investigation. A 35-mm camera with a wide angle lens, loaded with Tri-X film, was transported with its shutter locked open from the dark room to the sphere in the same lighttight bag to be used for the kitten. The camera was left in the sphere for a period of 30 minutes. With the film developed to its maximum sensitivity, we found no evidence of stray light or of shadows cast from the point sources to the blackened lower hemisphere.
7. Preliminary surgery was carried out under fluothane. After intravenous and tracheal cannulation, positioning in the head holder and craniotomy, ventilation was controlled with a mixture of oxygen, carbon dioxide, and nitrous oxide. Standard controls for corneal maintenance, eye position, stimulus presentation, and recording were used. [H. B. Barlow, C. Blakemore, J. D. Pettigrew, *J. Physiol. Lond.* **193**, 327 (1967).]
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9. The stimuli were bright spots which varied in size between 0.05° and 10°, extended black or white (or both) edges of all orientations, and bright line stimuli of all orientations which could be varied upward in size from 0.1° by 0.5°.
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11. Since incoming fibers from the lateral geniculate nucleus in a normal cat have concentrically organized receptive fields, it might be thought that they would be confused with the spot detector cortical cells. But apart from waveform criteria, the spot detector cells could always be distinguished by their irregular field shape, absence of spatial summation and binocularity. The lateral geniculate nucleus fibers studied in this preparation were in marked contrast to those of a normal cat because of their tiny, hard-to-locate, regularly shaped receptive fields. The fields were only 0.2° in diameter, which is unusually small considering the 8° eccentricity at which they were recorded. In addition, they were monocular and exhibited an exact correspondence between field size and optimal stimulus size.
12. Area threshold estimations were carried out in one case for a unit with a field size of 1.7° by 2.7°. Over a narrow range of spot sizes (0.05° to 0.3°) we could maintain a constant response by increasing the spot size while decreasing intensity or by decreasing the spot size while increasing the intensity. A 0.5° spot, however dim or bright, gave no response, suggesting that the large field was made up of small subunits less than 0.5° in size.
13. The ocular dominance histogram was slightly atypical, with a bias toward cells dominated by the ipsilateral eye.
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16. We thank B. Rogers and C. Olson for help with the investigation. Supported by PHS grants from the National Eye Institute to R.D.F. (EY01175) and H. B. Barlow (EY-00276).

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Oceanic Growth Models

Chase and Perry (*1*) have presented a model involving isotopic interactions between crustal and mantle rocks and oceanic waters that allows the calculation of δ_O, the $\delta^{18}O$ value (*2*) of the oceans, during the past 3.3×10^9 years. Using this model, they obtained a limit of about 10 percent for the amount of oceanic growth that would be compatible with the increase of 15 per mil in δ_O suggested by the $\delta^{18}O$ values of chert samples formed within this time period. Although the model itself is reasonable, some errors made by Chase and Perry in its evaluation nullify the conclusions they have drawn (*1, 3*).

The model assumes that just four processes control both the mass of the oceans (measured in terms of the moles of $^{16}O_2$ making up the water) and the value of δ_O. These are (i) outgassing of water from the mantle into the oceans, affecting both the mass and δ_O; (ii) subduction of water trapped in the oceanic crust, affecting the mass but not δ_O; (iii) formation of sediments, in isotopic equilibrium with ocean water, from igneous rocks; and (iv) formation of metamorphic rocks, having a constant fractionation with respect to ocean water, from both igneous rocks and sediments. These last two processes affect δ_O but not the mass of the oceans; they can be regarded as consisting of the 1 : 1 transformation (in terms of $^{16}O_2$ contents) of igneous rocks to either sediments or metamorphic rocks. The rate of change of δ_O with time t (in years) derived by Chase and Perry from these four processes can be written as

$$\frac{d\delta_O}{dt} = \frac{m_{UO}\delta_{UO} + q_{IS}\delta_{ISO} + q_{IM}\delta_{IMO} - (m_{UO} + q_{IS} + q_{IM})\delta_O}{M_O(0) + \int_0^t m_{UO}dt + \int_0^t p_{OU}dt} \tag{1}$$

where m_{UO}, q_{OU}, q_{IS}, and q_{IM} are the rates of processes (i) to (iv), respectively, in units of moles of $^{16}O_2$ transferred per year; δ_{UO} is the $\delta^{18}O$ value of the water outgassed from the mantle; $\delta_{ISO} = \delta_I - \delta_S + \delta_O$, where δ_I is the $\delta^{18}O$ value of igneous rocks and δ_S is the $\delta^{18}O$ value of sediments forming in equilibrium with the ocean at any given time; $\delta_{IMO} = \delta_I - \delta_M + \delta_O$, where δ_M is the $\delta^{18}O$ value of the metamorphic rocks being formed in equilibrium with the ocean at any given time; and $M_O(0)$ is the mass of the oceans (in moles of $^{16}O_2$) at the time $t = 0$. As defined in the model, δ_{UO}, δ_{ISO}, and δ_{IMO} are constants, p_{OU} is negative, and the denominator of Eq. 1 is always positive. Equation 1 is general, in the sense that all rates may be varied with time.

Two properties of the model are particularly relevant to a discussion of the conclusions of Chase and Perry. First, it can be seen from Eq. 1 that the value of δ_O should be subject to certain limits, independent of the various rates of transfer, determined only by the values of δ_{UO}, δ_{IMO}, and δ_{ISO}. When δ_O equals the largest of these three values, $d\delta_O/dt$ must be either zero or negative, and δ_O cannot become any larger. When δ_O equals the smallest of these values, $d\delta_O/dt$ must be either zero or positive, so that δ_O cannot become any smaller. Thus, if δ_O has a value at $t = 0$ lying within the limits set by δ_{UO}, δ_{IMO}, and δ_{ISO}, it must remain within these limits for all values of t greater than zero. Should δ_O have a value at $t = 0$ which lies outside these limits, the model will cause it to move within the limits and then remain there. The actual limits turn out to be determined by the values of δ_{UO}, approximately +7 per mil as chosen by Chase and Perry, and δ_{ISO}, which has an extreme value of about −30 per mil for the formation of pure chert sediments (*4*).

The second significant property of the model is seen when Eq. 1 is integrated. For the simplest situation, where all four processes have constant rates, there are two solutions: one for an ocean of constant mass ($m_{UO} + p_{OU} = 0$) and one for an ocean of changing mass ($m_{UO} + p_{OU} \neq 0$). For the second case, δ_O as a function of time is given by

$$\delta_O = \frac{A}{B} - \frac{A - B\delta_O(0)}{B} \times \left[\frac{M_O(0)}{M_O(0) + (m_{UO} + p_{OU})t}\right]^{B/(m_{UO} + p_{OU})} \tag{2}$$

where $A = m_{UO}\delta_{UO} + q_{IS}\delta_{ISO} + q_{IM}\delta_{IMO}$, $B = m_{UO} + q_{IS} + q_{IM}$, and $\delta_O(0)$ is the value of δ_O at $t = 0$. Inspection of Eq. 2 shows that, as t increases, δ_O changes monotonically from the value $\delta_O(0)$ to a final value of A/B. These initial and final values are independent of the rate of variation of the mass of the ocean (independent of $m_{UO} + p_{OU}$); only the path taken by δ_O between these initial and final values varies somewhat with the value of $m_{UO} + p_{UO}$, and δ_O for any particular t is as sensitive to the values of A and B as it is to the value