sults (*9*), have been substantiated. For example, display of masculine sexual behavior in rats has been shown to depend on the neurons of the POA (*10*) and on an intact medial forebrain bundle (*11*). The occurrence of female mating behavior, however, seems to depend on the mAHA or the VM, or both (*12*, and may actually be inhibited by the mPOA (*13*). Such results correlate well with our demonstrations of mPOA axons in the medial forebrain bundle, and both axons and terminations from the mAHA in the ventromedial region. The axonal projections demonstrated thus provide a possible anatomical substrate for separate neural systems mediating male and female sex behavior.

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Deficits in Binocular Depth Perception in Cats After Alternating Monocular Deprivation

Abstract. *Allowing very young kittens to see with only one eye at a time greatly reduces the proportion of binocular cortical cells. Compared to normal cats these specially reared animals suffer deficits in binocular depth perception while retaining normal acuity in the two eyes. Evidently, binocular cells play a crucial role in stereopsis.*

Almost all neurons in the visual cortex of a normal cat can be activated through both eyes (*1*). Many of these binocular cells have receptive fields on disparate areas of the two retinas, so that for optimal response stimuli must be positioned differently for each eye. The particular disparity which elicits the strongest response varies among cells, especially in the horizonal plane (*2*). It is generally believed that these disparity-sensitive neurons provide the neural basis for stereopsis, the uniquely binocular sense of depth perception (*3*). In support of this idea we have demonstrated that cats which lack binocular cells display marked deficits in binocular depth perception despite normal visual acuity in both eyes.

In order to disrupt the normal degree of binocular interaction among cortical neurons without affecting other receptive field properties, we subjected kittens to alternating monocular deprivation (*4*). This involves covering one of the eyes with an opaque contact lens for 1 day, then the other eye for the next day, and so on. Alternating occlusion was started when the kittens' eyes first opened and was continued until the animals were 6 months old, well beyond the end of the critical period during which visual deprivation affects the response properties of cortical neurons (*5*).

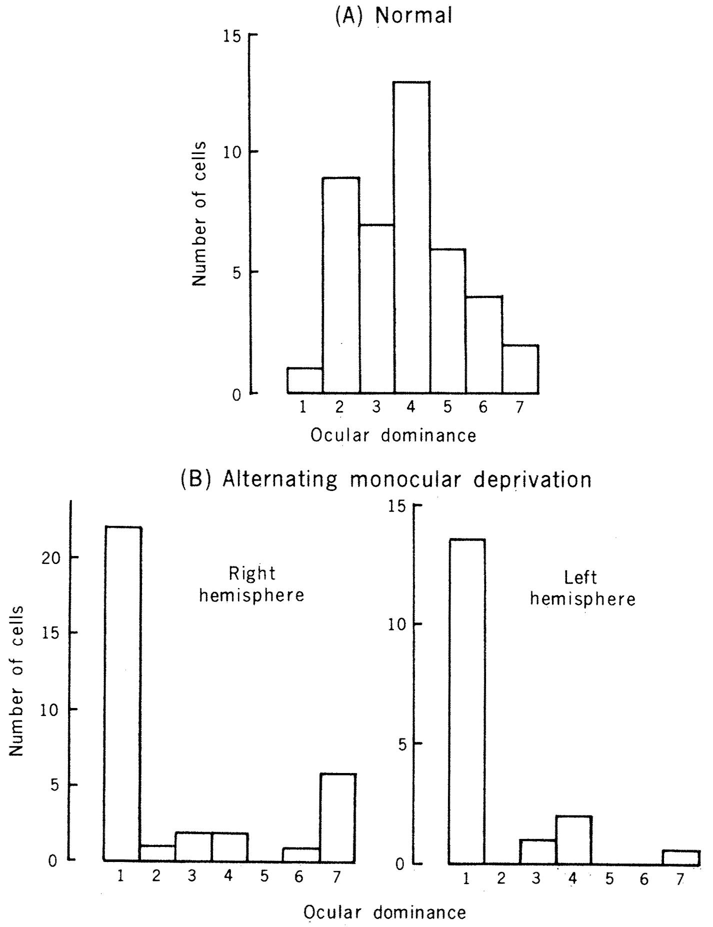
Previous electrophysiological work had shown that immediately after alternating monocular deprivation the proportion of cortical cells that can be activated through either eye is reduced significantly (*4*). In our experiments, behavioral testing was performed 1.5 to 2 years after termination of special rearing; thus each cat was allowed simultaneous use of both eyes for an extended time. To determine if this subsequent period of binocular vision altered the abnormal ocular dominance pattern seen immediately after rearing (*4*), we examined the response properties of single neurons in the visual cortex of one alternately occluded cat allowed 17 months of normal binocular experience prior to recording. We also studied a control animal that was reared normally. Prior to recording, the cats were paralyzed (Flaxedil) and anesthetized lightly (thiopental sodium); residual eye movements were reduced further by suturing the eyes to support frames. Contact lenses were used to focus the eyes on a tangent screen onto which a variety of visual stimuli could be rear-projected. Varnished tungsten microelectrodes were used to isolate individual units in visual cortex, the majority from area 17. The receptive field size, stimulus specificity, and ocular dominance of each cell was studied carefully.

In many respects neurons in the normal cat and the alternately occluded cat were indistinguishable. Most cells responded vigorously to a moving slit oriented properly and did not respond at all to a line orthogonal to this preferred orientation; receptive field size was related systematically to retinal eccentricity; and no unresponsive units were encountered. There was, however, a notable difference between the two animals in the pattern of ocular dominance. Specifically (Fig. 1A), the majority of cells studied in the normal cat were binocular and were placed into eye-dominance categories 2 to 6, while most cells in the alternately occluded cat were monocular exclusively, and thus were assigned either to category 1 or to category 7 (Fig. 1B). It is unlikely that the conspicuous absence of binocular units in the deprived cat resulted from degeneration, for each electrode penetration was rich in activity, with no regions of silent cortex. There was an obvious asymmetry in ocular dominance favoring the contralateral eye in both hemispheres of the alternately occluded cat, which may reflect an exaggeration of the bias toward contralateral input characteristic of cortical cells in normal cats [(*1*); Fig. 1A]. Still, the net effect of this asymmetry was an approximate balance between the number of cells driven through the right eye and the left eye. We conclude from the paucity of binocular cells in this animal that the physiological change resulting from our rearing technique is permanent.

Behavioral tests were administered to two normal cats and to two alternately occluded cats, which had been reared together with the animal described in Fig. 1B. In these experiments we employed a conditioned suppression technique, whereby an animal trained to emit a repetitive response will cease responding temporarily in the presence of a conditioned stimulus which warns of a forthcoming electric shock. This change in the animal's response rate following the onset of the warning stimulus provides a sensitive indication that the stimulus has been detected (*6*). Using procedures detailed elsewhere (*7*) we first determined the ability of both groups of cats to resolve high-contrast, vertical grating patterns. The animals were allowed to use one eye only; the other eye was occluded with an opaque contact lens. The grating acuities obtained for the cats subjected to alternating monocular deprivation were comparable to the values (4 to 6 cycles per degree of visual angle) obtained for the normal animals. Alternating occlusion thus produced no deficits in visual acuity for either eye, an altogether reasonable finding in view of the physiological results described above.

The next set of behavioral experiments involved measuring monocular and binocular depth detection. During these tests the cat placed its head through a porthole situated at one end of a restraining box and licked a tube through which was delivered a small amount of pureed beef liver on the average of once every 15 licks. The lick-tube was positioned behind a small Plexiglas septum, and the animal had to maintain its head upright to reach the tube. While licking, the cat faced a tunnel in which it could view three vertical rods arrayed in a frontal plane 50 cm from its eyes. At this distance each rod subtended 15′ of arc in width, and the seperation between rods subtended 50′ of arc. The rods were seen as black against a white diffusing screen (30° by 30°) which was transilluminated by an incandescent source; the screen luminance of 100 foot-lamberts (107.6 mlam) provided the only illumination within the experimental chamber.

During initial training the cat viewed the display binocularly. On each trial the center rod was moved 11 cm toward the cat by a motor-driven rank-and-pinion device located underneath the viewing tunnel. This change in real depth produced an angular disparity of 80′ of arc between the center and the flanking rods. Twenty seconds later a brief, unavoidable electric shock was



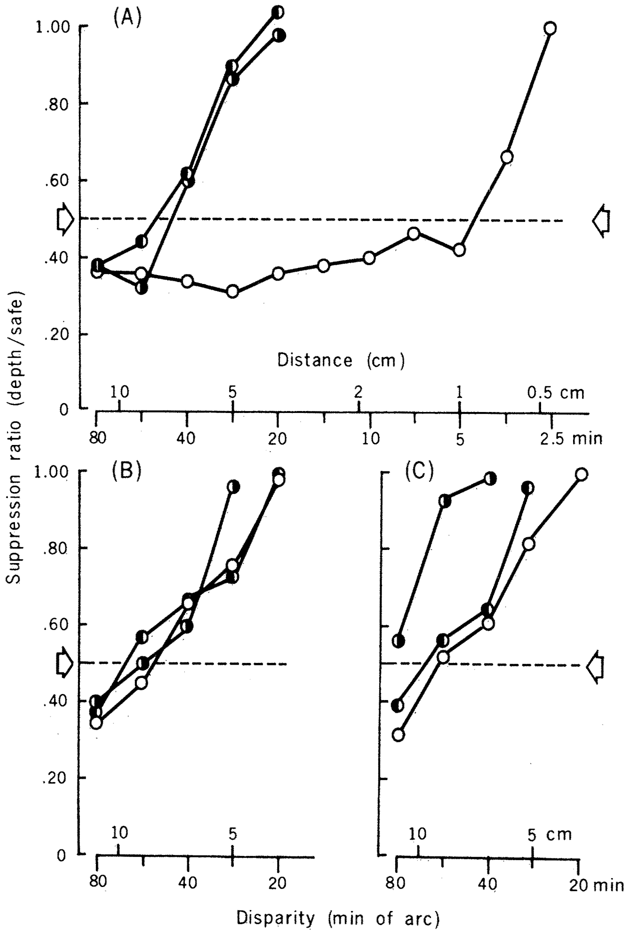


Fig. 1 (left). Histograms showing the distribution of cortical cells according to the ocular dominance scheme of Hubel and Wiesel (*1*). Cells in group 1 and 7 are exclusively monocular, driven only through the contralateral eye or the ipsilateral eye, respectively; group 2 and 6 cells are strongly dominated by the contralateral and ipsilateral eyes, respectively; group 3 and 5 cells are slightly dominated by the contralateral and ipsilateral eyes, respectively; cells in group 4 are equally influenced by the two eyes. (A) Forty-one cells from the left hemisphere of a normal cat. (B) Fifty-one neurons from the left and right hemispheres of a cat reared with alternating monocular deprivation for the first 6 months of life, followed by 17 months of normal binocular vision. Fig. 2 (right). Suppression ratio plotted against change in depth scaled in terms of real distance (cm) and retinal disparity (minutes of arc). The disparity values are based on an interpupillary distance of 40 mm and are applicable only for binocular viewing. Each point indicates the mean suppression ratio for all trials at that particular depth value. Open symbols (○) plot binocular performance; half-filled symbols plot the left-eye (◑) and right-eye (◐) performance. Dashed lines and arrows demarcate the 50 percent level of suppression. (A) A representative normal cat. (B and C) Cats reared with alternating monocular occlusion.

delivered to the cat's paws through the grid floor of the restraining box, and simultaneously the center rod was returned to its initial position. On each trial individual licks were counted and used to compute the ratio D/S, where D represents the number of licks during the 20-second depth presentation and S represents the number of licks during the 20-second interval immediately preceding the depth presentation. Intervals between successive trials varied, and daily sessions consisted of 20 to 25 trials.

Once the cat suppressed reliably on every trial, binocular depth thresholds were determined by varying randomly on each trial the distance the center rod was moved. The excursion of the rod was kept between 11 cm and the lowest value which failed consistently to produce suppression. During these trials we continued to pair rod movement and shock regardless of the depth value involved, in order to ensure that the cat associated shock with *any* change in depth, not just the 11-cm training value (*8*). Testing was continued until at least eight trials for each distance were completed. After binocular testing the procedure was repeated for each of the two eyes separately; the nontested eye was again occluded with an opaque lens.

The graphs in Fig. 2 present the results for a normal cat (Fig. 2A) and for two alternately occluded animals (Fig. 2, B and C). The abscissa is scaled in decreasing values of depth expressed in both real distance and equivalent minutes of disparity. Each point represents the average suppression ratio at various depth values; dashed lines and arrows mark 50 percent suppression, which is the conventional definition of threshold with this technique. Most significantly, notice that a normal cat allowed to use both eyes together (open symbols) can detect a disparity of less than 4 minutes; in terms of distance this is one-tenth the magnitude of the smallest depth detectable when the animal is forced to use either eye alone (half-filled symbols). Of course, the display used in this experiment offers other cues to depth (for example, changes in visual angle) besides retinal disparity (*9*). However, all cues *except* disparity would be available whether the cat views the display with both eyes or with only one eye. Thus the decided superiority of binocular over monocular performance strongly indicates that the normal cat was utilizing stereopsis in the binocular situation. In contrast, the alternately occluded cats performed no better using both eyes together than they did using either eye alone. In fact, the thresholds obtained for alternately occluded cats allowed to use either one eye or both eyes were quite similar to the monocular thresholds for the normal cats. This deficit in binocular depth perception indicates that the alternately occluded cats fail to utilize retinal disparity information and instead rely exclusively on monocular depth cues. Moreover, this deficit probably is permanent, for after the early rearing period, but prior to testing, both these cats received nearly 2 years of normal binocular experience during which disparity information was always available.

Since the only evident physiological consequence of alternating occlusion is a permanent diminution in the proportion of cortical cells responsive to stimulation of either eye, it is reasonable to conclude that these binocular neurons are crucially involved in stereoscopic depth perception. Indirect evidence suggests that stereoblindness in humans may result from similar physiological deficits (*10*).

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8. In this previous work (*7*) using conditioned suppression as a psychophysical technique, we have observed that cats, once trained to suppress upon presentation of a conditioned stimulus, also suppress to other suprathreshold stimuli as well; the animal seems to be sensitized to any perturbation in the visual display. For this reason the technique is ideally suited for measuring stimulus detectability; on the other hand, to study discriminative behavior with the use of conditioned suppression, whereby presentation of one class of stimuli is paired with shock but another class is not, requires more prolonged training [H. S. Hoffman, in *Animal Discrimination Learning*, R. M. Gilbert and N. S. Sutherland, Eds. (Academic Press, New York, 1969)].
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Stratigraphic Correlation

The methodology proposed by Southam *et al.* (*1*) represents a potentially important step forward in the analysis of stratigraphic correlation, albeit a somewhat tentative one. They list quite properly the three conditions of the Bernoulli experiment requisite to the use of the binomial distribution for the analysis. It is important to consider these conditions a bit more closely, as in fact any of the three may be violated in important cases. Departures from the Bernoulli conditions are the statistical equivalents of the facies problem that has plagued stratigraphy from its outset. Because the facies problem is disguised in the statistical treatment, it may pass unnoticed by some readers. Its presence does not invalidate the methodology, but does necessitate some special caution. The proposed methodology does not provide a route around the facies problem, but what is more useful, a way through it.

Taking the Bernoulli conditions out of order, condition (ii) requires that the outcome of each observation be one of two mutually exclusive and exhaustive possibilities—in the present context, that there be no possibility of ties. Ties are, in fact, quite common, particularly at unconformities (it is for precisely this reason that unconformities were very early given great emphasis in stratigraphy). The presence of ties creates no great difficulties and may be dealt with in either of two ways: by resorting to the trinomial distribution, or by neglecting ties and resorting to the conditional binomial distribution. The latter approach is implicit in the authors' presentation.

Condition (iii), that "the probability p_{ij}