after it had been made insentient; this was done by inflating a pressure cuff around the wrist and occluding the circulation for the appropriate time. We have also observed, but not measured, similar illusions concerning motion at the knee and ankle joints, although these illusions have not been nearly as well developed as those for the elbow. Others have found that at these sites, vibration may induce misjudgments of a few degrees in estimates of the steady position of the joint (*7*).

The illusions of position can be attributed to the excitation of intramuscular receptors rather than of extramuscular receptors, since the effects were not obtained when the vibrator was applied directly over the elbow joint or to regions of skin overlying bone. Nor did such nonspecific application of vibration distort position sense, since the subjects did not then make systematic tracking errors when the vibrated arm was moved by the experimenter. Thus the widespread excitation of Pacinian corpuscles, which must undoubtedly have occurred, seems to have produced merely a sensation of vibration itself and cannot be held responsible for the illusory sensations of limb position. Of the intramuscular receptors, the muscle spindle primary endings may reasonably be held responsible, for these are far more powerfully excited by vibration than are any of the other muscle receptors (*8*). However, both the Golgi tendon organs and the spindle secondary endings do show some sensitivity to vibration, and so it is impossible to say whether or not they contributed to the development of the present illusions; all three types of proprioceptors have been believed to be denied access to consciousness.

The findings are compatible with the idea that during muscle contraction, the spindle primary discharges that are set up by the vibration are interpreted by the higher neural centers as if they were due to excitation of the spindles by stretching the muscle; the increased discharges would then indicate that the vibrated muscle was longer than it actually was and would so produce a corresponding error in the central judgment of the angle at the elbow. In addition, the illusion induced by vibration may be as much one of velocity of movement as of position per se. This may perhaps be why the reversed motion of the tracking arm continued for so long after the reflex movement was arrested (Figs. 1 and 2); the volume of driven spindle discharge may be presumed to have risen to a plateau soon after the reflex movement was impeded. Be that as it may, the present illusion appears sufficient to throw serious doubt on the current view that muscle afferent firing is without influence on perception. The perceived position of a limb may thus be attributed to the compounding of three kinds of signals: afferent from joint receptors, efferent from motor centers, and afferent from muscle spindles.

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4 October 1971; revised 8 December 1971 ■

A Neural Effect of Partial Visual Deprivation in Humans

Abstract. *Certain human subjects have considerable sensitivity differences in the visual resolution of vertical gratings as compared to horizontal gratings. Although only subjects with pronounced ocular astigmatism exhibit this effect, the differences are of neural, rather than optical, origin. It is argued that the resolution anisotropies result from early abnormal visual input caused by astigmatism. This abnormal input permanently modifies the brain.*

The influence of early visual experience on the organization of cortical neurons in the developing brain has been strikingly demonstrated in two recent studies. Hirsch and Spinelli (*1*) raised kittens so that each kitten had one eye viewing horizontal bars and the other eye viewing vertical bars. After the rearing period, they found that all cortical neurons with elongated receptive fields responded to input from only one eye. Furthermore, the receptive field orientations were coincident with the bar pattern to which the eye had been exposed. Blakemore and Cooper (*2*) limited the binocular visual environment of kittens, during the period from 2 weeks to 5 months of age, to only vertical or horizontal stripes. They found that stimuli presented in the orientation of the earlier visual exposure produced essentially normal behavioral and neurophysiological responses. However, when stimuli were presented in an orthogonal orientation, behavioral blindness was evident and no responsive neurons were encountered. These experiments show that functional neural connections can be altered, in a predictable and selective manner, by visual environment.

We propose here that an analogous modification in the organization of neurons in the human visual system can be induced by early abnormal visual input. We have found subjects who show considerable differences in their resolution sensitivities for vertical and

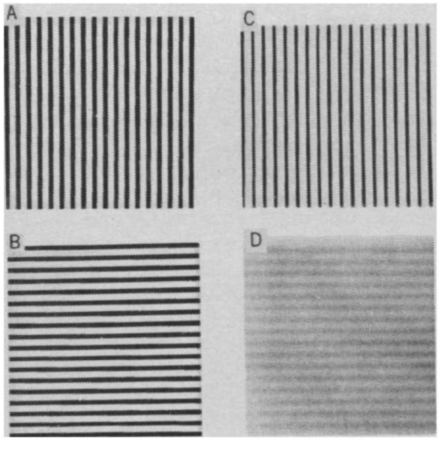

Fig. 1. The effect of astigmatic optics on image formation. In astigmatism, a point source in object space is imaged as two mutually perpendicular focal lines separated by a distance that is determined by the amount of astigmatism. (A and B) Identical square wave gratings which consist of alternate black and white bars oriented vertically and horizontally. (C and D) The gratings shown in (A) and (B) are imaged through an astigmatic lens which defocuses the vertical meridian. In (C), the bars are parallel to the direction of blur and it is evident that image quality is unaffected except for slight bar narrowing and edge blur. But in (D), the grating bars are perpendicular to the direction of blur which results in severe image degradation.

horizontal detail. The resolution anisotropies are only found in subjects with notable astigmatism, but the disparities are of a neural, rather than optical, nature; they remain when optical factors are accounted for. Our findings suggest that the neural "circuitry" required to resolve features of a given orientation can develop imperfectly as a result of uncorrected ocular astigmatism.

Astigmatism is a condition in which the eye's refractive power differs in various meridians. Outside the meridians of maximum and minimum powers, which are mutually perpendicular, no sharp images can be produced and a point focus is never possible. Figure 1 shows the effects of astigmatism on the appearance of square-wave gratings. Identical gratings, oriented vertically and horizontally (Fig. 1, A and B), are imaged through an astigmatic lens that produces blur along a vertical axis (Fig. 1, C and D). When the grating bars are parallel to the direction of blur (C), image quality is maintained. But when the grating is oriented orthogonally (D), the resulting image is substantially degraded. Figure 1 illustrates that asymmetries in visual exposure, similar to those created in space in the kitten investigations described above, can be introduced via the eye's optics.

Suppose that the retinal image of a developing visual system suffers from astigmatism that causes extensive blur along the horizontal, but not the vertical, axis. The visual cortex could adapt to the discordant input from the retina by "tuning" itself to the features clearly imaged along the vertical axis. A logical effect of the cortical adaptation would be an anisotropic development of the neural connections involved in resolution. And as a consequence, the resolution capacity for horizontally imaged details would be reduced.

In an earlier study concerned with the influence of target orientation on visual resolution, we unexpectedly encountered some subjects who showed resolution differences between vertical and horizontal gratings, in addition to the usual reduction observed with oblique targets (*3*). These subjects all had considerable astigmatic refractive error. We have pursued the initial observation with determinations of visual resolution on three groups of subjects in Berkeley, California, and Halifax and Montreal, Canada. With sinusoidal gratings generated on the face of an oscilloscope, or, with photographed square-wave gratings, we measured the maximum number of lines that could be resolved for different target orientations on subjects that had varying amounts of optically corrected astigmatism (*4*). We very carefully checked the eyeglass lens corrections to insure that they were optimal under the conditions of each test.

The results of experiments on subjects who exhibit marked vertical-horizontal resolution disparities are shown in Fig. 2. The vertical grating sensitivity is highest for the subjects shown in (**B**) and (**D**), while the opposite is true for those of (**C**) and (**E**). In each case, the retinal meridian with reduced resolution also has maximum astigmatic blur when uncorrected (*5*). For comparison, the results of subjects with negligible astigmatism are given in (**A**). Although the typical reduction in resolution for oblique orientations is evident, there are no significant differences between the horizontal and vertical. This finding agrees with a number of studies (*6*).

In spite of our precautions regarding optical corrections, it could be argued that residual optical factors influenced our results. To eliminate this possibility, we determined modulation sensitivities at fixed spatial frequencies for laser-generated interference fringes, by a technique that largely bypasses the effects of the eye's optics (*7*). The results (Fig. 2, D and E) are clearly in accord with those for gratings in object space. Therefore, we conclude that the observed meridional resolution differences must be of neural origin.

The horizontal-vertical variations in sensitivity, presented in Fig. 2, are the most pronounced we have seen. The data in (C) and (E) indicate a 2 : 1 difference in spatial frequency resolution between the vertical and the horizontal. These subjects also manifest a larger than normal reduction in resolution for oblique orientations. This finding supports the notion that image quality is the operant factor causing selective resolution reduction because,

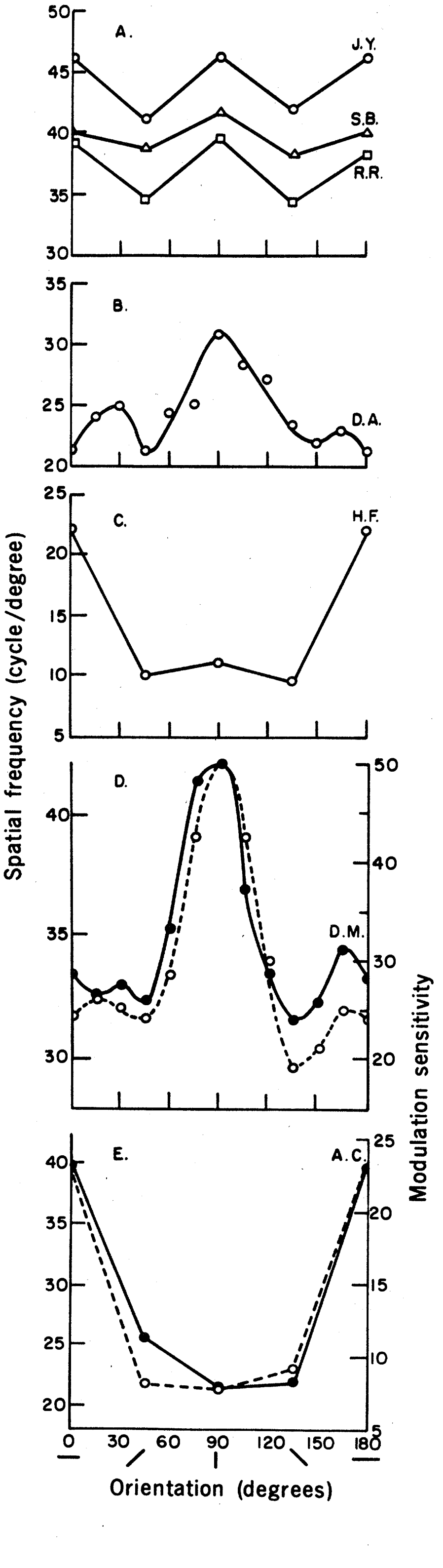

Fig. 2. Visual resolution of high-contrast sinusoidal or square-wave gratings that have different orientations. The ordinates on the left denote sensitivity in terms of the maximum number of cycles per degree of visual angle that can just be resolved. Each point represents the mean of at least five determinations. (A) Subjects with negligible refractive error show the typical resolution decrement for obliquely oriented gratings but insignificant differences between horizontal and vertical gratings. (B through E) Highly astigmatic subjects whose resolution sensitivities are markedly different for vertical and horizontal gratings. (D) and (E) also show the modulation or contrast sensitivities (ordinates on the right) for sinusoidal interference fringes, created by a laser, of fixed spatial frequencies [22 and 16 cycles per degree in (D) and (E), respectively]. The close agreement between the modulation sensitivities (dashed lines) that are independent of the eye's optics and the results for targets in object space (solid lines) is conclusive evidence that the resolution differences cannot be ascribed to optical factors.

in astigmatism, the interval between the focal lines is never in focus.

We have not found any nonastigmatic subjects who showed significant vertical-horizontal resolution differences. However, not all of our astigmatic subjects exhibited the substantial resolution imparities noted above. This is not surprising considering the nonstatic nature of the eye's effective refractive state. By virtue of accommodation or changes in observation distance, the eye can receive focused input over a considerable range of distance in visual space. In most cases of astigmatism, the meridian that is blurred by unaccommodated distant observation can be brought into focus by accommodation or by a change in viewing distance. The extent to which this will occur depends on the nature and amount of the astigmatism (*8*). These considerations suggest that, for astigmatic subjects with only the normal reduction in resolution of the oblique orientation, the frequency with which each meridian was brought into focus during development of the visual system was sufficient to prevent neural consequences.

Our supposition that ocular astigmatism can alter neuronal connections requires that the astigmatic condition was present during the "critical period" of the development of the visual system (*9*). Although we cannot be sure that this holds for our subjects, considerable clinical evidence makes the likelihood high (*10*). Even so, an alternate explanation could also account for meridional resolution differences. The differences could be explained if there were anomalous structural asymmetries in the retina or visual pathways of astigmatic eyes that developed totally independently of visual input. If this were the case, our findings would require that minimal resolution and maximal image blur occur along the same axis. While the possibility cannot be eliminated, we know of no evidence in its favor.

On the other hand, a number of investigations have shown that, if visual form is absent during development of the nervous system, the receptive fields and synaptic properties of cortical neurons and the morphology of lateral geniculate cells can be markedly altered (*9, 11*). At the cortical level, the physiological effect of monocular deprivation is considerable, but if both eyes are visually deprived the effect is minimal (*12*). This implies that consequences of deprivation depend on interactions between sets of afferents from both eyes. The experiments with a controlled visual environment, described earlier, suggest that meridional afferent interactions are also important (*13*). These studies, in conjunction with our findings, are consistent with the view that modifications in neural connections, induced by astigmatism, are responsible for meridional resolution anisotropies.

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4. Sinusoidal gratings were generated on a cathode-ray tube by standard methods except that grating orientation was varied electronically. Sawtooth and sinusoidal sweep wave forms were mixed in proportion to the sine and cosine of the angle of orientation desired. A pair of step voltage dividers provided sine-cosine amplitude proportions to the x and y axes of the oscilloscope. The spatial frequency data presented here were obtained for a grating contrast of 0.7 and screen luminance of 10 cd/m^2. The square-wave gratings had a contrast close to 1.0 and a luminance of about 50 cd/m^2.
5. The refractive errors for the subjects shown are as follows: D.A., —3.75 —3.75 × 170; D.M., +1.50 —2.75 × 180; H.F., +2.75 —4.25 × 2; and A.C., +4.50 —5.00 × 180.
6. For a review of studies on target orientation and visual resolution, see M. M. Taylor, *J. Opt. Soc. Amer.* **53**, 763 (1963).
7. The method was a modification of the technique described in (*3*). Modulation sensitivity is a measure of the ability to detect differences in contrast between alternate bars of a grating.
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9. Susceptibility to deprivation, in cats and monkeys, is evident from about 1 to 3 months of age [D. H. Hubel and T. N. Wiesel, *J. Physiol.* **206**, 419 (1970); G. K. von Noorden, J. E. Dowling, D. C. Ferguson, *Arch. Ophthalmol.* **84**, 206 (1970)]. There is considerable vulnerability to deprivation amblyopia, in humans, during the first 5 or 6 years of life [S. Duke-Elder, *Textbook of Ophthalmology* (Mosby, St. Louis, 1949), vol. 4, p. 3837]. It is important to note that none of our subjects with marked vertical-horizontal resolution differences had received spectacle corrections in early childhood.
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13. The importance of afferent interrelations has been further demonstrated. Kittens reared with vertical disparity created by prisms seemed to adjust to the imposed condition. This was seen by a shift in the distribution of disparities that maximally stimulated the binocular cortical units [R. Shlaer, *Science* **173**, 638 (1971)]. It appears that, during development, the nervous system attempts to adapt to any alteration in the normal symmetry of visual input.
14. We thank G. Haegerstrom for help with the experiments. Supported in part by NIH Biomedical Sciences Support grant FR-7006 to R.D.F. and National Research Council of Canada grant APA 7660 to D.E.M.

13 September 1971; revised 16 December 1971 ■

Sound Production in Scolytidae: Chemostimulus of Sonic Signal by the Douglas-Fir Beetle

Abstract. *Stridulation by male* Dendroctonus pseudotsugae *was recorded in response to the natural female attractant (frass) or to three synthetic components of the attractant (frontalin, 3-methyl-2-cyclohexen-1-one, and* trans-*verbenol). This stridulation was acoustically distinct from stress sound and correlated with known attraction behavior. The response of female* D. pseudotsugae *to male stridulation—negation of her attraction—was induced by playback of recorded attractant stridulation but not by that of stress sounds. Acoustic communication must be more important in scolytid behavior than it was heretofore believed to be.*

Although many bark and timber beetles (Scolytidae) stridulate, or produce sound by friction of body surfaces (*1, 2*), there are few behavioral studies of this phenomenon; research has centered on the strong chemical signals of these insects. Stridulatory organs have been recognized in only that sex that does not select the host tree (*1, 2*), and Barr proposed that the function of this sound is to announce the arrival of the stridulating sex to the host-finding, gallery-initiating sex (*1*). With two North American *Ips* species, stridulation is necessary for natural entrance into the gallery of the opposite sex (*1–3*).

In field studies with *Dendroctonus pseudotsugae,* Rudinsky (*4*) found that stridulation by the male beetle at the entrance of the gallery of an attractive female induced the female inside the bark to quickly and entirely negate her chemical attraction for flying beetles.