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  18. The bats were anesthetized only for initial surgery, and recording of single-unit activity was made 3 to 15 hours after the injection of 30 mg of sodium pentobarbital per kilogram of body weight. If an electrode was placed at nearly the same place in the auditory cortex of the same animal a few days or a few weeks later, using no general anesthesia, the data obtained were nearly the same as those obtained from the lightly anesthetized bat. We thus pooled the data obtained from anesthetized and unanesthetized bats. In the experiments with anesthetized animals the effect of sodium pentobarbital on neural activity was apparently minimal, because we recorded 3 to 15 hours after the injection from bats that showed many different reflexes, voluntary movements, and occasional sound emissions. By unanesthetized animals we mean those that do not receive any general anesthetic for at least 48 hours prior to and during the experiments and that can eat, drink, and fly voluntarily. When unanesthetized or very lightly anesthetized bats were used for the experiments, a local anesthetic (lido-caine) was applied to their surgical wounds.
  19. The dash and slash mean, respectively, successive and simultaneous deliveries of two sounds for maximum excitation of combination-sensitive neurons. For instance,  $H_1$ -FM<sub>2</sub> means that FM<sub>2</sub> should be delivered after  $H_1$  for best facilitation, and CF<sub>1</sub>/CF<sub>2</sub> means that CF<sub>1</sub> and CF<sub>2</sub> should be delivered simultaneously. A multiple suffix such as CF<sub>2,3</sub> in CF<sub>1</sub>/CF<sub>2,3</sub> means that either CF<sub>2</sub> or CF<sub>3</sub> delivered together with CF<sub>1</sub> effects similar facilitation. The CF<sub>1</sub>/CF<sub>2</sub> facilitation neurons are those whose response (or subthreshold response) to CF is facilitated by CF<sub>1</sub>, so this category includes CF<sub>1</sub>/CF<sub>2</sub>, CF<sub>1</sub>/CF<sub>3</sub>, CF<sub>1</sub>/CF<sub>2,3</sub>, CF<sub>1</sub>/CF<sub>2,4</sub>, and CF<sub>1</sub>/CF<sub>3,4</sub>. The  $H_1$ -FM facilitation neurons are those whose response (or subthreshold response) to FM is facilitated by  $H_1$  or its components CF<sub>1</sub> and FM<sub>1</sub>, so this category includes all  $H_1$ -FM<sub>2</sub>,  $H_1$ -FM<sub>3</sub>,  $H_1$ -FM<sub>4</sub>,  $H_1$ -FM<sub>2,3</sub>,  $H_1$ -FM<sub>2,4</sub>,  $H_1$ -FM<sub>3,4</sub>, and  $H_1$ -FM<sub>2,4</sub>. The FM<sub>1</sub>-FM facilitation neurons are those whose response (or subthreshold response) to FM is facilitated by the FM<sub>1</sub> component of  $H_1$ , but not CF<sub>1</sub>, so this category includes FM<sub>1</sub>-FM<sub>2</sub>, FM<sub>1</sub>-FM<sub>3</sub>, and FM<sub>1</sub>-FM<sub>2,3</sub>. In a previous report (8), we said that all these neurons were in the FM processing area. However, the response properties of CF<sub>1</sub>/CF<sub>2</sub> facilitation neurons are clearly different from those of  $H_1$ -FM and FM<sub>1</sub>-FM facilitation neurons in time domain and are apparently located in a different cluster. Therefore we now introduce a new term, the CF/CF processing area. The FM processing area thus consists of  $H_1$ -FM and FM<sub>1</sub>-FM facilitation neurons, only.
  20. Threshold (or facilitation threshold) is defined as the smallest amplitude of the stimulus that evokes just-noticeable response (or facilitation). The criterion of just-noticeable response is 0.1 impulse per stimulus when neurons are not spontaneously active or are discharging at low rates.
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  22. The orientation and nonorientation sounds of the mustache bat are discrete, so our speculation concerning a possible role of CF/CF neurons is probably reasonable. However, an additional role may become evident when the communication sounds are more thoroughly studied in the future.
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27. K. M. Mudry and R. R. Capranica [Abstr. 8th Annu. Meet. Soc. Neurosci. **4**, 101 (1978)] found that, in the dorsal thalamus of the bullfrog *Rana catesbeiana*, responses of neurons were facilitated by simultaneous presentation of two major signal elements of its call. This is particularly interesting for us because this strengthens our

view that biologically significant complex sounds may generally be processed by neurons sensitive to combinations of information-bearing elements, even though peripheral neurons show phase-locked discharges to low-frequency acoustic waves.

28. We thank P. Wasserbach for the design and construction of the harmonic generators used in these experiments, and J. Jaeger for his assistance in our laboratory. Supported by NSF grant BMS 75-17077 and BNS78-12987 to N.S. and NINDS (PHS) training grant 1-T32-NS07057-01 to W.E.O.

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## Psychophysical Evidence for a Monocular Visual Cortex in Stereoblind Humans

**Abstract.** Human observers who lack stereopsis reliably make eye-of-origin discriminations for grating patterns under conditions that render the performance of normal observers unreliable. This lends support to the view that stereoblind individuals possess proportions of monocular and binocular cortical cells similar to those of cats and monkeys deprived of early binocular visual experience.

The visual cortex of normally raised cats and monkeys contains a high proportion of binocularly innervated cells (1). In contrast, the visual cortex of animals deprived of early binocular visual experience shows a high proportion of monocularly driven cells (2). Compared to normal animals, cats with a paucity of binocular cortical neurons perform poorly on behavioral tasks requiring binocular depth discrimination (3). Some humans, too, perform poorly on such tasks. These so-called stereoblind individuals

also display little, if any, interocular transfer of visual aftereffects (4) and show no binocular summation on visual threshold tasks (5). Stereopsis, interocular transfer, and binocular summation are believed to depend on binocularly driven cells, and their combined absence in stereoblind humans suggests that these individuals have fewer than usual binocular cells. Presumably, they also have more than the usual number of monocular cells, but neither stereopsis, interocular transfer, nor binocular summa-

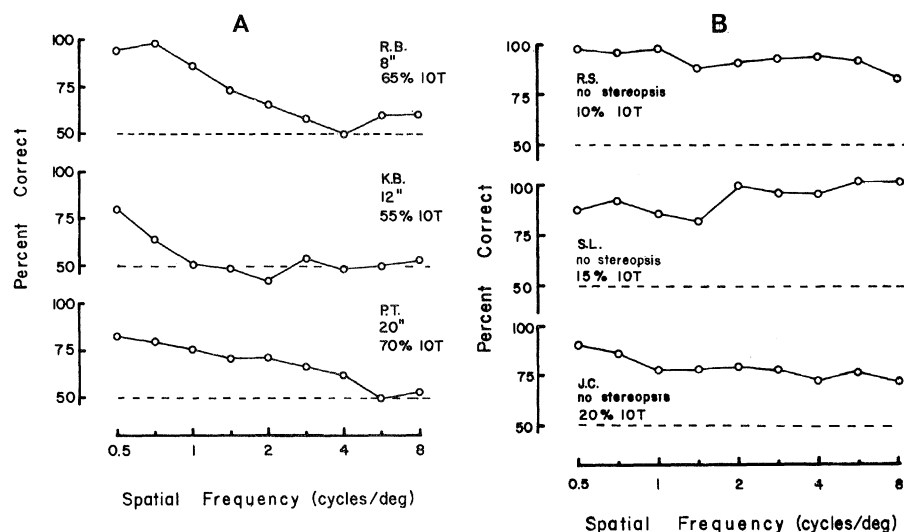


Fig. 1. Percent correct on a two-alternative, forced-choice task on which observers reported which one of the two eyes received a briefly presented, vertical grating pattern. Each point is based on at least 100 trials, and the dotted line denotes the level of performance expected purely on the basis of chance. (A) Representative results for three observers with good stereoacuity. The values under each observer's initials refer to stereoacuity in seconds of arc and the percentage of interocular transfer (IOT) on a conventional threshold-elevation aftereffect. Subject P.T. was the best performer of the seven normal subjects tested; K.B. was the worst. (B) Results from three stereoblind observers on the same task.

tion could possibly reveal this. Psychophysical evidence indicating a high proportion of monocularly driven cells in stereoblind humans would support the hypothesis that the modification of the visual system observed in visually deprived animals finds its analog in the cortex of stereoblind humans. Moreover, such evidence would strengthen the hypothesis that cortical units play a crucial role in binocular vision.

One task on which performance could be directly related to the density of monocular cortical cells is utricular discrimination, the task of identifying which one of the two eyes has received stimulation. Activity in a cell which can be driven by either eye cannot, by itself, indicate which of the two eyes was stimulated. On the other hand, activity in a monocularly driven cell does carry eye-of-origin information (6). Extrapolating from this notion suggests that if stereoblind individuals possess a high proportion of monocularly driven cortical cells, they will be able to identify which of their two eyes has been stimulated more easily than normal observers. Consistent with this idea, we find that stereoblind humans accurately make utricular discriminations under conditions that render the performance of normal observers highly unreliable.

In our experiments, observers were required to indicate which of the two eyes received a brief (350 msec), 10 percent contrast grating pattern presented just to one eye randomly selected from trial to trial. The observer viewed two matched cathode-ray tubes (CRT) in a mirror stereoscope such that each eye saw a 8° by 10° region that normally appeared unoutlined (7). By depressing a button the observer triggered a grating presentation and indicated which of the eyes actually received the pattern. Care was taken to eliminate potential cues, such as apparent contrast or phase differences, that might differentiate the two CRT displays. We tested both normal observers and those with no stereopsis (8).

Individuals with good stereopsis are able to perform with almost perfect accuracy on this task when the spatial frequency of the grating is low, but at higher spatial frequencies their performance falls to chance levels (Fig. 1A). To date seven normal observers have been tested, and the results for all are qualitatively similar. Extensive practice (700 trials with feedback) fails to improve performance at higher spatial frequencies, and paralysis of accommodation and pupillary reflex has no influence on the ac-

curacy of discrimination at low spatial frequencies (9). Stereoblind observers, unlike normal ones, are able to distinguish which eye has been stimulated regardless of the spatial frequency of the grating (Fig. 1B). Their consistently accurate performance is unimpaired by random, trial-to-trial variations in grating contrast and phase, and performance is equally good with horizontal or vertical gratings. We have been unable to discover stimulus conditions which degrade the accurate eye-of-origin judgments made by these observers (10). Further, the performance of the stereoblind observers with essentially balanced right-left acuities equaled that of the other observer. On occasion we included blocks of control trials on which a grating was presented to both eyes simultaneously; observers were uninformed of this manipulation and later reported no awareness that both eyes had been stimulated (11). If the accuracy of these stereoblind observers was the result of suppression of one eye or some other unspecified cue associated with one eye, we would expect a response bias toward that eye for these control trials. This did not occur. Responses were distributed equally between the two eyes.

These findings demonstrate that eye-of-origin information is retained in the visual system of the stereoblind individual. Stereoblindness is frequently associated with a childhood history of strabismus, a condition that, when artificially induced in kittens and monkeys, disrupts the normal binocular connections in the visual cortex, so that most neurons can be activated through only one eye or the other. We think that the consistent knack of knowing which eye has been stimulated may reflect a predominantly monocular composition of the visual cortex of stereoblind observers.

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6. Of course, given a population of cortical neurons with varying degrees of ocular dominance, information concerning eye of origin could be contained in the overall pattern of firing among these neurons. As our working model we are suggesting that this information may be more readily available to those with a high proportion of monocular neurons.
7. Details of the apparatus are given elsewhere [R. Blake, *J. Exp. Psychol.* **3**, 251 (1977)]. In brief, the displays were viewed with natural pupils from a distance of 110 cm, with the observer's head securely positioned on a dental impression board. Conventional electronic techniques [C. Enroth-Cugell and J. Robson, *J. Physiol. (London)* **187**, 517 (1966)] were used to generate on the matched CRT grating patterns of sinusoidal luminance profile. The average luminance of each CRT screen, whether contoured or not, was 7.1 cd m<sup>-2</sup>, which remained constant with changes in spatial frequency and contrast; this obviated the need for artificial pupils. Interocular matches using a flicker method ensured equal apparent contrast for the two displays. A shaped rise-fall gate could introduce and withdraw the grating gradually, in order to eliminate abrupt transients. The sharp borders of the CRT displays provided good fusion stimuli and the cover-uncover test was employed to assure accurate binocular alignment and to minimize fixation disparity.
8. The stereoscopic abilities of each participant were determined with a modified Howard-Dolman device, the modified Ortho-Rater and random-element stereograms [B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971)]. Results from all three tests were consistent. For the three stereoblind observers, additional relevant visual characteristics are as follows: R.S. displays a convergent strabismus of approximately 10°, with corrected visual acuities of 20/22 [oculus dexter (O.D.)] and 20/40 [oculus sinister (O.S.)]; J.C. is a former exotropo who was corrected surgically at 4 years and who now has corrected acuities of 20/20 (O.D.) and 20/25 (O.S.); S.L. displays a 6.33° esophoria, has no history of manifest strabismus, and has corrected visual acuities of 20/18 (O.D.) and 20/17 (O.S.). All three stereoblind observers wore their corrections during testing. To equate apparent contrast for amblyopic and nonamblyopic eyes, an interocular contrast matching procedure was used prior to testing at each spatial frequency.
9. The ability of normal observers to perform reliably at low but not high spatial frequencies would seem to reflect some rather interesting properties of the normal binocular visual system. A more extensive description of our work on utricular discrimination in normal observers will be forthcoming.
10. J. Enoch, H. Goldmann, and R. Sunga [*Invest. Ophthalmol.* **8**, 317 (1969)] demonstrated that both normal and strabismic observers can make eye-of-origin judgments reliably better than chance. Their stimuli were 1.33° circular, blurred (defocused) targets presented briefly (50 to 1000 msec) against a dark background. The blurring was used to reduce cues resulting from accommodative asymmetries between the eyes, but it also reduced high spatial frequencies in the targets. In view of our findings, this blurring may account for the lack of difference between the performances of normal and strabismic subjects in their study. Enoch *et al.* did not report stereoacuity data for their observers, so we do not know whether any of their subjects were stereoblind.
11. Under conditions of successful utricular discrimination, both stereoblind and normal observers reported that right and left eye displays were phenomenally identical except that they appeared to be in either the right eye or left eye. Observers failed to detect stimulation of both eyes and reported frustration at the difficulty of the task.
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