the width of the Taurus-A line; thus the only predicted shift that could be observed was the Fürth effect. The Taurus-A 21-cm absorption line was observed during June and July 1967 with a multichannel 21-cm receiver. The method used for determining the shift in frequency was the same as the one used for current experimental measurement of the astronomical unit (*8*). All known Doppler shifts, such as those due to Earth's orbital revolution, rotation, motions in the Earth-Moon orbit, and other minor effects, were computed and subtracted from the frequency measured by observation so as to give the residuals. Observations made over a period of several days, a few months before our measurements, had confirmed the method of prediction. The rectangles in Fig. 1 give the results of this control measurement and show that the residuals are near the zero line as they should be. Although the frequency-switching technique effectively canceled the solar sidelobe radiation, it was important to evaluate any possible solar interference. Before 15 June, tests were made with the antenna pointed within 1 deg of Sun, with no noticeable degradation in performance of the system. Nevertheless there remains a possibility that Sun's radiation affects the equipment in an unpredicted way. The near-occultation observations commenced on 10 June. Taurus A was observed for several hours daily for 5 days before and after the solar approach. The residuals (observed minus calculated frequencies) are plotted in Fig. 1; each point is the average of about 20 individual data points, the scatter being represented by an error bar. There appears to be a decrease of about 150 hertz in frequency near closest approach; however, on the basis of statistical analysis, the probability that this is a real decrease is only 90 percent.

An experiment (*4*) in which the frequency of radar pulses reflected from Venus and Mercury was measured sets an upper limit of 1/70 on the constant K of Fürth's theory (as was presented by Fürth; that is, with a $1/r$ dependent). In order to reconcile the Venus experiment with the apparent decrease of 150 hertz found by us one would have to assume that the effect is proportional to $1/r^2$. In this case the experiment of Shapiro *et al.* (*4*) could not detect the effect as the radar pulses passed some 80 solar radii away from Sun. A $1/r^2$ dependence is also indicated by the shape of the plot in Fig. 1. On the other hand, the $1/r^2$ dependence does not agree with red-shift measurements of the Na lines from the limb of Sun. The gravitational red shift should amount to

$$\Delta\nu/\nu = 2 \times 10^{-6}$$

and was experimentally found (*9*) to agree with the predicted value within 10 percent. If the effect found in our experiment depends on $1/r^2$ one should see the Na line red-shifted by

$$\Delta\nu/\nu = (150 \times 5^2)\ (1.4 \times 10^9 \times 2) = 1.3 \times 10^{-6}$$

(Our experiment showed a shift of 150 hertz, out of 1.4×10^9 hertz, when the rays passed at five solar radii. The Na lines are emitted from one solar radius but are affected by Sun only half as much as is the 21-cm line.) This shift, added to the gravitational red shift, should become

$$\Delta\nu/\nu = 3.3 \times 10^{-6}$$

which is inconsistent with the $2 \times 10^{-6} \pm 0.2$ found experimentally.

In conclusion, a possible decrease in frequency of the 21-cm line was observed, with an indicated dependence of $1/r^2$. This decrease could be of great significance, as it indicates a red shift for waves passing near a mass, but a higher degree of statistical confirmation is needed. The general relativistic effect could not be tested by use of the 21-cm line from Taurus A. Using the largest antenna and the best equipment available one could measure the shift within 1 hertz, which degree is still an order of magnitude greater than the effect. However, if a narrow and intense line were found near the ecliptic, the gravitational shift could be detected. Oxygen-hydrogen emission regions could provide such lines, but the accuracy of the measurement depends on (i) the width of the line, (ii) the intensity of the line, and (iii) the distance of the source from the ecliptic. Although the OH lines are much narrower than the hydrogen line, we could not find a line that was sufficiently intense and close enough to Sun.

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References and Notes

1. I. I. Shapiro, *Phys. Rev. Letters* **13**, 789 (1964).
2. D. K. Ross and L. T. Shiff, *Phys. Rev.* **141**, 1215 (1966).
3. A shift in frequency in the radar echoes from a planet, as a test for general relativity, was proposed by D. Sadeh [*Phys. Letters* **8**, 316 (1964)] and ——— and I. I. Shapiro [*Tech. Rept. 368* (Lincoln Laboratory, Lexington, Mass., 1964)]; J. R. Richard [*Tech. Rept. 628* (Univ. of Maryland)] calculated the effect from a purely general relativistic argument.
4. I. I. Shapiro, M. E. Ash, M. J. Tausner, *Phys. Rev. Letters* **17**, 933 (1966).
5. The relation between dl/dt and the orbital velocity V of Earth around Sun is $dl/dt = V \sin \tan^{-1} Vt/d$, where d is the distance from the center of Sun to the line Earth–Taurus A at the time of closest approach, and t is the time after closest approach. The maximum that dl/dt can attain is $0.7\ V = 20.7$ km/sec.
6. The value $(\Delta\nu/\nu)\,p$ is correct only within an order of magnitude as the plasma changes during the solar cycle; therefore the value 1.45 is only a crude estimate.
7. R. Fürth, *Phys. Letters* **13**, 221 (1964).
8. S. H. Knowles, in preparation.
9. J. E. Blamont and F. Roddier, *Phys. Rev. Letters* **7**, 437 (1961); Brault, thesis, Princeton Univ. (1962).
10. Supported by NSF grant GS 6823. Dror Sadeh, who is on leave from the University of California, Los Angeles, and the University of Tel Aviv, thanks W. F. Libby for constant support.

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Binocularly Driven Neurons in Visual Cortex of Split-Chiasm Cats

Abstract. *In cats with midsagittal section of the optic chiasm, some visual cortex neurons can be driven not only by the ipsilateral eye, through the direct geniculocortical pathways, but also by the contralateral eye, through the opposite visual cortex and corpus callosum. The receptive fields and the response characteristics observed upon stimulation of the contralateral eye are very similar to those observed upon stimulation of the ipsilateral eye; the two monocular receptive fields of a given cell lie in corresponding points of heteronymous halves of the visual field in close contact with the vertical meridian, thus adding in visual space and forming a binocular receptive area which crosses the vertical meridian and extends equally on either side of it.*

In mammals, the connections between the eyes and the brain are such that each half of the visual field is projected to the contralateral hemisphere only. Perceptual unity of the cerebral hemispheres in the act of seeing is thought to result largely from the activity of commissural pathways, especially the corpus callosum (*1*). Electrophysiological searches for the mechanisms by which the corpus callosum allows the cerebral hemispheres to share their private visual information have shown that:

1) Units of the posterior third of the corpus callosum are activated by visual stimuli much in the same way as the cells of the visual cortex in general, but only when the stimuli are presented along the vertical meridian of the visual field (*2*).

2) Callosal impulses elicited by visual stimulation arrive at the contralateral visual cortex and therein excite units situated at the boundary between areas 17 and 18 (*3*). This region is connected to the vertical meridian of the visual field also by its geniculocortical projections (*4*).

Given these facts, the question remains open as to what spatial relationships in the visual field the callosal and geniculocortical inputs to the same visual cortical cell bear to each other, and how these two inputs are integrated by the target unit in the visual cortex. The most likely hypothesis advanced thus far has been that the "geniculocortical" and "callosal" receptive fields of a visual cortex cell are strictly contiguous, the vertical meridian being the imaginary line of division between the two fields (*3, 5, 2*). As a result of this, the total receptive area of a cortical neuron provided with the two inputs would cross the vertical meridian and extend somewhat into both halves of the field of vision.

Working with cats with intact visual pathways, Hubel and Wiesel (*5*) found visual cortex neurons with receptive fields which seemed to have an extension into the ipsilateral half of the visual field, but the evidence was not decisive because of the difficulty in obtaining a sharp definition of the vertical meridian.

The "split-chiasm" animal (*6*) is a suitable preparation for distinguishing between the callosal and the geniculocortical inputs to the visual cortex. In this preparation, because of the section of the crossed optic fibers in the chiasm, the visual cortex of each side may be excited through either the geniculocortical or the callosal input, by stimulating, respectively, the ipsilateral or the contralateral eye (*7*). In the present investigation we have mapped the receptive fields of single visual cortex neurons of split-chiasm cats, looking for binocularly driven units. Experiments were performed in curarized midpontine pretrigeminal cats (*8*), whose optic chiasm had been midsagittally sectioned through a buccal approach from 2 weeks to 1 month before the experiment. Single-unit recordings from the visual cortex in the lateral gyrus were carried out by means of tungsten microelectrodes inserted through the unopened dura. Brain pulsations were minimized by hydraulically closing the skull defect with a saline-filled chamber covered at the top with paraffin. Stationary or moving stimuli were presented to one eye at a time (the other eye being tightly occluded with cotton), by projecting various geometrical patterns of light (circles, bars, slits, and so on) on a white, hemispheric screen 1 m in radius, positioned at 1 m from the cat's eyes. The pupils were maximally dilated with atropine and the corneas were protected with plastic contact lenses. Background illumination of the screen, measured at the cat's eyes, was 60 lux; stimuli were 0.2 log unit brighter than the background. The projections on the screen of the optic disk, area centralis, and vertical meridian of each eye were assessed by using a special ophthalmoscope and referring to the available data on the cat's optics (*9*). The completeness of optic chiasm section and the position of recording electrodes, marked in vivo on occasions by electrolytic lesions, were verified on histological slides, stained according to the Weil and Nissl methods. A more detailed description of the methods is given elsewhere (*2*).

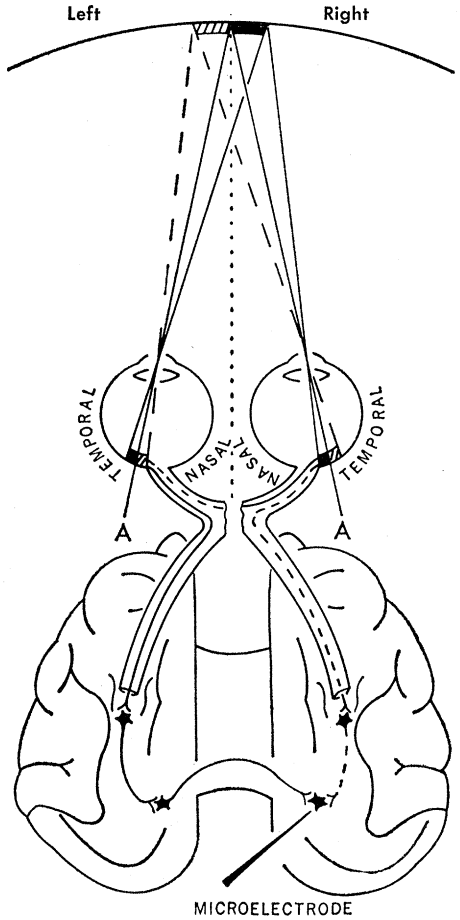

Fig. 1. A recorded neuron in the *right* visual cortex of a split-chiasm cat can be activated through both eyes by a visual stimulus crossing the vertical meridian of the visual field. The part of the stimulus lying in the *left* half of the visual field will excite the *right* temporal hemiretina (hatched area), the *right* uncrossed geniculocortical pathway (interrupted line) and the *right* visual cortex with the recorded neuron; the part of the stimulus lying in the *right* half of the visual field will excite the *left* temporal hemiretina (black area), the *left* uncrossed geniculocortical pathway (continuous line) and the *left* visual cortex, whereby excitation will be carried over to the recorded neuron in the right visual cortex via the corpus callosum. The half images of the object falling on the nasal hemiretinas (hatched area in the left eye, black area in the right eye) will be ineffective because of the section of the optic chiasm. Line *A* indicates the division between temporal and nasal hemiretinas in each eye.

In six cats, nine units, out of 70 which were driven from the ipsilateral eye, could be activated also by stimuli delivered to the other eye. A good "aroused" state of the preparation, as indicated by persistent electroencephalographic (EEG) desynchronization, and vigorous following eye movements before curarization (see *8*), was found to be of the utmost importance for the detection of visual cortical responses to contralateral eye stimulation. Several other cats had to be discarded because they displayed continuous EEG synchronization, absence of eye movements prior to curarization, and, as a consequence, little if any cortical response to contralateral eye stimulation.

In accord with typical properties of visual cortex cells (*5*), all units were excited only by stationary or moving stimuli of adequate size and form presented in appropriate points of the visual field. However, signs of atypical behavior, such as absence of response to stationary stimuli in cells of area 17, or lack of directional sensitivity in cells of area 18, were frequently encountered. Most units were also sluggish and fatiguable in responding. All these effects can be interpreted as the expression of a partial disorganization of the specific synaptic input to the visual cortex, resulting from the surgical interruption at the chiasm of at least 65 percent of the optic fibers. To this same cause seems best attributed also the

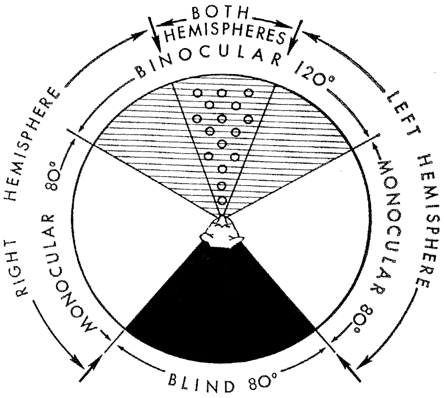

Fig. 2. The visual field of the cat and its relationships with the eyes and the cerebral hemispheres. The figure is partially imitated from Duke-Elder (*12*). The visual callosal mechanisms described in Fig. 1 allow both hemispheres to receive projections from an area of the visual field extending 20° on either side of the vertical meridian. The extension of the bihemispheric region of the visual field is inferred from the data of Berlucchi *et al.* (*2*) showing that some visual receptive fields of callosal units are as large as 20°.

finding, incidental to this study, of some visual cortex neurons totally unexcited by visual stimuli.

In accord with the data of Choudhury *et al.* (*3*) the nine units which were binocularly driven were found in a cortical strip that, following the cortical maps of Otsuka and Hassler (*10*), was at the boundary between areas 17 and 18. With each binocularly driven unit, the visual receptive field mapped upon stimulation of the contralateral, "callosal" eye was remarkably similar to that mapped upon stimulation of the ipsilateral, "geniculocortical," eye. Both receptive fields lay at the same longitude on the nasal side of the vertical meridian, which actually marked the temporal border of each field; as a result, the binocular receptive field of each one of these units covered an area across the vertical meridian, whose surface equaled the sum of the surfaces of the two monocular receptive fields. These units had receptive fields within or in the close neighborhood of the areas centralis up to approximately 10° along the vertical meridian. The size, orientation, and organization of the "callosal" receptive fields were also very similar to those of the corresponding "geniculocortical" fields. Monocular field sizes of these units varied from approximately 1° by 2° to 9° by 9°. All the binocularly driven cells showed field and response characteristics of the "complex" type (see *5*), displaying, however, some abnormalities, as mentioned above. Responses to stimulation presented in the "callosal" field were in general less brisk and more fatiguable than responses to equal "geniculocortical" stimuli. Simultaneous presentation of appropriate stimuli in both receptive areas of a binocular unit resulted in a response more intense than that obtained by stimulation of either area alone.

Although nine units are too small a sample to allow exclusion of other possible callosal-geniculocortical interactions, the results definitely show that some visual cortex neurons are linked with the eyes not only through the specific geniculocortical pathway, but also through an indirect callosal pathway.

Further, there is an orderly arrangement between specific and commissural inputs to the same visual cortex neuron, so that the receptive fields resulting from them, besides sharing the same organizational properties, add in visual space and give origin to a functionally homogeneous receptive area crossing the vertical meridian.

Figure 1 shows the experimental situation in the present study. It demonstrates how a visual cortical cell could be activated from both eyes, through a direct geniculocortical pathway and an indirect geniculocortico-callosal route, respectively.

Figure 2 presents a schematization of the relationships between visual space, eyes, and brain, taking into account the callosal mechanisms presented here.

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References and Notes

1. R. W. Sperry, *Sci. Amer.* **210**, 42 (1964); ———, in *Brain and Conscious Experience*, J. C. Eccles, Ed. (Springer, New York, 1966), p. 298.
2. G. Berlucchi, M. S. Gazzaniga, G. Rizzolatti, *Arch. Ital. Biol.* **105**, 583 (1967).
3. B. P. Choudhury, D. Whitteridge, M. E. Wilson, *Quart. J. Exp. Physiol.* **50**, 214 (1965).
4. S. A. Talbot and W. M. Marshall, *Amer. J. Ophthalmol.* **24**, 1255 (1941).
5. D. H. Hubel and T. N. Wiesel, *J. Neurophysiol.* **28**, 229 (1965).
6. R. E. Myers, *J. Comp. Physiol. Psychol.* **48**, 470 (1955).
7. It has been suggested (*11*) that in the cat, callosal fibers reaching the visual cortex originate not only from contralateral visual cortical areas, but also from contralateral lateral geniculate bodies. The existence of such crossed geniculocortical pathways has not been confirmed in a recent anatomical investigation [M. E. Wilson and B. G. Cragg, *J. Anat.* **101**, 677 (1967)]. The callosal visual interactions between the hemispheres revealed by recent electrophysiological work (*2*, *3*) appear to be mediated by a corticocortical pathway only.
8. C. Batini, G. Moruzzi, M. Palestini, G. F. Rossi, A. Zanchetti, *Arch. Ital. Biol.* **97**, 1 (1959).
9. P. O. Bishop, W. Kozak, G. J. Vakkur, *J. Physiol.* **163**, 466 (1962).
10. R. Otsuka and R. Hassler, *Arch. Psychiat. Z. Neurol.* **203**, 212 (1962).
11. M. Glickstein, J. Miller, O. A. Smith, *Science* **145**, 159 (1964); M. Glickstein, R. A. King, J. Miller, M. Berkley, *J. Comp. Neurol.* **130**, 55 (1967).
12. S. Duke-Elder, *System of Ophthalmology, The Eye in Evolution* (Kimpton, London, 1958), vol. 1, p. 673.
13. Supported by the Air Force Office of Scientific Research, through the European Office of Aerospace Research, EOAR, U.S. Air Force, under contract F6-1052-67-C-0028.

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Tetraploid DNA Content of Purkinje Neurons of Human Cerebellar Cortex

Abstract. *Microspectrophotometric analysis of single cells in Feulgen preparations revealed tetraploid amounts of DNA in Purkinje neurons of human cerebellar cortex.*

A brief preliminary report of the finding of tetraploid quantities of DNA in Purkinje neurons of normal human cerebellum has been published (*1*). This study was based on microspectrophotometric measurements of Feulgen preparations by the conventional plug technique. (I use "tetraploid" only with reference to DNA content, since the true status of the chromosomes is unknown.) I now report later measurements on the same cell type with a Deeley-type Barr and Stroud integrating microdensitometer (*2*). This instrument incorporates a scanning device that minimizes distributional error; extinction is summated as the scanning progresses, so that a direct measurement of total absorption is provided in arbitrary units for a single whole nucleus.

Material consisted of tissue blocks from cerebellar hemispheres of five brains obtained at necropsy from cadavers demonstrated to be free of evidence of neurologic disease; it was fixed in a 1 : 3 mixture of glacial acetic acid and 95-percent ethanol. After 4 to 6 hours of fixation, tissues were dehydrated and embedded in paraffin. For measurement of DNA content in Purkinje cells, sections were cut at 18 μ in order to ensure whole nuclei in sufficient numbers. A 10-μ section was prepared for measurement of gran-