

chromosome synapsed intimately with the SAT chromosomes, thereby indicating that the SAT chromosome was present in triplicate.

Univalents were present in most PMC's of the two hybrids. In some PMC's, a supernumerary nucleolus was associated with a univalent, the latter ostensibly being the triplicated SAT chromosome. Univalents either migrated to the poles or remained near the equator. The laggards were later eliminated in the form of micronuclei in microspores or as miniature microspores.

The imbalance imparted by the extra chromosomes appears to promote precocious bivalent disjunction. Consider the situation in the sixfold trisomic. The mean number of univalents per PMC in this plant averaged 2.1 as compared to .2 in the euploid hybrids (3). The "excess" univalents were due, in part, to precocious dissociation of trivalents into bivalents and univalents or into three univalents. Precocious dissociation, if it is assumed that a bivalent remained intact, would contribute an average of only 1.4 univalents per PMC since an average of 4.6 chromosomes participated in trivalents which remain intact through diakinesis. The origin of univalents in this manner would account for only a portion of the excess univalents. If trivalents are considered to be the only source for the excess univalents, over 10 percent of the trivalents would have to desynapse completely in order to generate an adequate supply of univalents. Since this is most unlikely (1), bivalents must be serving as the "excess" univalent source.

It is evident that the two aneuploids are similar in a number of ways, in spite of their different chromosome numbers. The most striking common feature is the fact that each extra chromosome is different, and thus each represents a distinctive triplication. The SAT chromosome was triplicate in each plant, and, on statistical grounds, there is a likelihood that at least one other chromosome is shared. The degree of trivalent retention through diakinesis was high in both plants. In the six-chromosome trisomic, 75 percent of the trivalents remained intact as did 80 percent in the four-chromosome trisomic.

The origin of the multiple trisomics remains an enigma. The plants could be products of an ascending aneuploid series, but the less imbalanced forms have yet to be found. The plants could be products of a descending aneuploid

series beginning at the triploid level. This alternative is less plausible than the first, for polyploidy is unknown in *L. aspera* and *L. spicata*. On the other hand, it is conceivable that the plants are not steps in a series, but arose directly from euploid parents in which meiotic irregularities yielded grossly imbalanced gametes.

Regardless of the mode of origin, one-half of the gametes involved in the formation of the aneuploids must have carried at least two extra chromosomes in the case of the four-chromosome trisomic, and at least three extra chromosomes in the case of the six-chromosome trisomic. Therefore, gametes can be viable and effectual in

spite of 20 to 30 percent duplication. Equally surprising is the fact that an organism can develop in a normal and robust fashion in spite of 40 to 60 percent triplication of its genome. Perhaps the toleration of chromosomal novelties is related in some manner to the hybridity of the plants in question.

DONALD A. LEVIN

Department of Biological Sciences,
University of Illinois at Chicago
Circle, Chicago 60680

References and Notes

1. C. R. Burnham, *Discussions in Cytogenetics* (Burgess, Minneapolis, 1962), pp. 139-203.
2. D. A. Levin, *Brittonia* 19, 248 (1967).
3. ———, *Evolution*, in press.
4. Supported in part by NSF grant GB-6743.

27 May 1968

Lateralized Suppression of Dichotically Presented Digits after Commissural Section in Man

Abstract. *Right-handed patients with surgical disconnection of the cerebral hemispheres cannot report verbal input to the left ear if different verbal stimuli have been channeled simultaneously to the right ear. With monaural stimulation, they show equal accuracy of report for the two ears. These findings highlight the dominance of the contralateral over the ipsilateral auditory projection system. Suppression of right-ear input is obtained in nonverbal tests. Dissociation between verbal and left-hand stereognostic responses indicate a right-left dichotomy for auditory experience in the disconnected hemispheres.*

It has been shown (1) that when the main commissures joining the two cerebral hemispheres of man are sectioned [as has been done to relieve intractable epilepsy (2)], the surgically disconnected hemispheres continue to function normally to a large extent; but only one, the left in the typical right-hander, appears capable of propositional speech and writing. The minor, right hemisphere does show some rudimentary verbal comprehension but emits few if any words. Hence the commissurotized patient is able to tell us in any detail only about sensory information that has reached his verbally dominant left hemisphere. For example, such a patient cannot name or describe objects flashed in his left visual field, but only those flashed on the right, because each field projects solely to the contralateral hemisphere. Nor can he name objects palpated with the left hand, although he manipulates them appropriately with that hand, and is able to remember and select the same object when it is placed among a collection of other items.

In audition, with which this report deals, the anatomical situation is quite different from that in vision or somes-

thesis. Each ear is represented bilaterally at every stage of the afferent pathway, from the cochlear nucleus to the auditory cortex in the temporal lobe, and therefore sound input cannot be restricted to one cerebral hemisphere; either hemisphere is able to hear through either ear. Yet, by presenting different verbal stimuli to the two ears simultaneously, we have been able to demonstrate, in commissurotized patients, a complete or near-complete suppression by the left or speaking hemisphere of input from the left ear.

We have tested seven patients with presumed complete midline section of the cerebral commissures, including the corpus callosum, the anterior and hippocampal commissures and, in at least two cases, the massa intermedia. These operations had been carried out at the White Memorial Hospital, Los Angeles, by Dr. Philip Vogel and his associates to help control severe convulsive disorders. The patients (five male, two female) were examined from 6 months to 4 years after operation, at which time their ages ranged from 14 to 44 years, with a mean age of 26 years. Below, their results on the auditory task are compared with those of 32

normal control subjects (student nurses and laboratory technicians), and with the performance of 30 patients at the Montreal Neurological Institute who had undergone a unilateral temporal lobectomy from 2 to 3 weeks previously, also for the relief of epilepsy. Twenty temporal lobectomies were in the right, or minor hemisphere, ten in the dominant left hemisphere. These patients were included in this analysis because in all cases the transverse gyri of Heschl (the primary auditory cortex in man) were said to have been completely excised in the temporal lobectomy.

The task used was Kimura's adaptation of the dichotic-listening procedure devised by Broadbent (3). Different digits are presented simultaneously to the two ears by means of a dual-channel tape recorder with stereophonic earphones. The digits are presented in groups of three pairs, with either a ½-second or a 1½-second interval between successive pairs. After each group of six digits, the subject is required to report all the numbers that he has heard, in any order. In the monaural (control) condition, all six digits are presented to one ear, with a half-second interval between successive digits. Three groups of six digits are presented to the left ear and three to the right, in a balanced order. The earphones are reversed for half the subjects, to cancel out the effect of any discrepancy between the two input channels.

Figure 1 shows the mean number of digits correctly reported for each ear, for the different groups. Normal subjects show a slight but significant superiority on the right ear. The effect of a temporal lobectomy is to decrease the efficiency of report for the ear contralateral to the lesion. Because this is a verbal task, patients with left temporal lobectomy in the dominant hemisphere for speech show a slight impairment on the test as a whole, but those with right temporal lobectomy merely show an accentuation of the right-ear superiority found in normal subjects (4). In the case of the commissurotomy patients, the ear-difference is far more striking. Deprived of all input from the right hemisphere (not merely from the right temporal lobe), they report very few digits from the left ear. Five of the seven subjects with callosal section obtained near-zero scores for the left ear, and complained that they could hear nothing in the left ear, although they had been expecting to hear numbers in

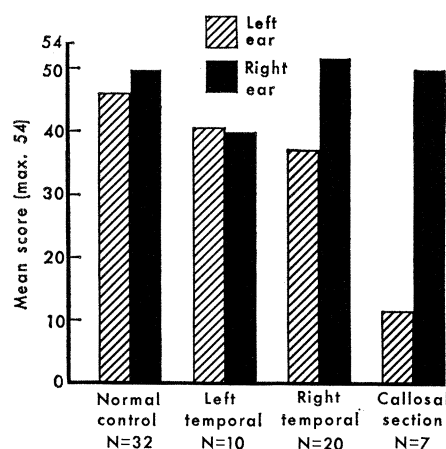


Fig. 1. Mean number of digits correctly reported for each ear, when different digits are simultaneously presented to the two ears. The results are for normal control subjects and for three different patient groups.

both ears. The remaining two subjects reported about a third as many digits for the left ear as for the right. A simple analysis of variance on the difference in score between the two ears for the various groups yielded an F -value of 11.1 ($P < .001$), and the difference in score between the left and right ears for the commissurotomy patients was significantly greater than that seen after right temporal lobectomy ($t = 4.98$; $P < .001$).

In contrast to the suppression of the input from the left ear under dichotic stimulation, under monaural conditions the callosal patients correctly reported 87 percent of the numbers channeled to the left ear and 90 percent of the numbers channeled to the right ear, with no patient showing any abnormal difference in performance for the two ears. Two subjects with zero scores for the left ear under the dichotic condition made 100-percent correct responses when all six digits were directed to the left ear.

Many factors influence performance on the dichotic-listening task after callosal section. These include the nature, locus, and extent of the preoperative epileptogenic lesion, the age of the patient at the time of operation as well as time elapsed since operation, and, perhaps most important, the amount of experimental sophistication the patient has acquired in the course of other testing (1). All the commissurotomy patients in the present study were being exposed to such auditory testing for the first time; nevertheless the only two patients to achieve some success in reporting digits presented to the left ear under the dichotic condition were both very experienced examinees with re-

spect to other sense modalities. In the more successful of the two, 4 years had elapsed since the commissural section, which was the longest postoperative follow-up period in the group; the other was a young boy with little evidence of preexisting brain damage.

The fact that all the commissurotomy patients were able to report digits presented to the left ear without difficulty, when there was no competing input from the right ear, shows that the ipsilateral pathway could be utilized. The suppression of ipsilateral input in the presence of a competing stimulus from the contralateral ear provides clear behavioral evidence of the dominance of the contralateral auditory projection system in man, a finding for which there is by now considerable electrophysiological (5) and some behavioral (6) support from work with lower species.

Whether a similar and reciprocal suppression of the right ear input in favor of the left might obtain in the right hemisphere could not be determined with the same verbal tests. Accordingly another stereo tape was prepared containing 27 pairs of competing instructions for simultaneous presentation to right and left ears. Each unilateral instruction named one or two objects to be retrieved by touch from among a collection of nine objects screened from sight. The subject was told to pick up with the left hand the named objects, in any order. For example the right ear might receive the message "Now pick up the paper clip" at the same time that the left ear received the words "Now find us the eraser."

Scores for left-hand retrieval under these conditions showed a strong preference for objects named through the left ear, with a partial to complete neglect of items named through the right ear. When asked to name the left-ear items picked up with the left hand, the subjects commonly misnamed the objects, using the names that were presented simultaneously through the right ear. The degree to which the right-ear stimuli could be retrieved with the left hand varied in different subjects under different conditions (7).

BRENDA MILNER
L. TAYLOR

Montreal Neurological Institute,
McGill University,
Montreal, Canada

R. W. SPERRY

Division of Biology,
California Institute of Technology,
Pasadena 91109

References and Notes

1. R. W. Sperry and M. S. Gazzaniga, in *Brain Mechanisms Underlying Speech and Language*, F. L. Darley, Ed. (Grune and Stratton, New York, 1967), p. 108; M. S. Gazzaniga and R. W. Sperry, *Brain* 90, 131 (1967); R. W. Sperry, in *The Harvey Lecture, Series 62* (Academic Press, New York, 1968), p. 293; R. W. Sperry, M. S. Gazzaniga, J. E. Bogen, in *Handbook of Clinical Neurology*, P. J. Vinken and G. W. Bruyn, Eds. (North-Holland, Amsterdam, in press).
2. J. E. Bogen and P. J. Vogel, *Bull. Los Angeles Neurol. Soc.* 27, 169 (1962); J. E. Bogen, E. D. Fisher, P. J. Vogel, *J. Amer. Med. Ass.* 194, 1328 (1966).
3. D. Broadbent, *Quart. J. Exp. Psychol.* 8, 145 (1956); D. Kimura, *Canad. J. Psychol.* 15, 166 (1961).
4. D. Kimura, *ibid.*, p. 156.
5. A. R. Tunturi, *Amer. J. Physiol.* 147, 311 (1946); M. R. Rosenzweig, *ibid.* 167, 147 (1951); J. L. Hall II and M. H. Goldstein, Jr., *J. Acoust. Soc. Amer.*, in press.
6. J. Kaas, S. Alexrod, I. T. Diamond, *J. Neurophysiol.* 30, 710 (1967).
7. A separate, more detailed report on these latter and related findings that bear on the right-left dichotomy in auditory experience is in preparation.
8. Supported by the National Institute of Mental Health (grant MH-07332 to R.W.S.) and by the Medical Research Council of Canada. We thank Drs. P. J. Vogel and J. E. Bogen for permission to study their patients.

1 May 1968

Human Brain: Left-Right Asymmetries in Temporal Speech Region

Abstract. We have found marked anatomical asymmetries between the upper surfaces of the human right and left temporal lobes. The planum temporale (the area behind Heschl's gyrus) is larger on the left in 65 percent of brains; on the right it is larger in only 11 percent. The left planum is on the average one-third longer than the right planum. This area makes up part of the temporal speech cortex, whose importance is well established on the basis of both anatomical findings in aphasic patients and cortical stimulation at operation.

It is generally accepted that the preponderance of the human left hemisphere in speech functions is not associated with significant structural differences between the two halves of the brain (1). We reinvestigated this problem on an extensive sample and found highly significant differences between the left and right hemispheres in an

area known to be of significance in language functions.

Our material consisted of 100 adult human brains, obtained at postmortem, and free of significant pathology (2). The hemispheres were divided, and then the upper surface of the temporal lobe (supratemporal plane) was exposed on each side by a cut made in

the plane of the Sylvian fissure. Figure 1, a drawing of a typical specimen, illustrates the anatomical landmarks. Figure 2 is a photograph of a specimen which demonstrates the typical left-right asymmetries. The posterior border of the planum temporale slopes backward more sharply on the left, while the anterior border of the planum (formed by the sulcus of Heschl) slopes forward more sharply on the left; both effects combine to produce a larger planum temporale on the left. A sharper backward slope was found on the left in 57 percent and on the right in 18 percent ($P < .001$), with equality on the two sides in 25 percent of the brains examined. A sharper anterior slope was found on the left in 40 percent and on the right in 24 percent ($P < .05$), with equality in 36 percent. The planum temporale was larger on the left in 65 percent and on the right in 11 percent ($P < .001$), with equality in 24 percent of our specimens.

The length of the outer border of the planum temporale ($x-y$, Fig. 1) was 3.6 ± 1.0 cm on the left and 2.7 ± 1.2 cm on the right ($P < .001$); the planum was 0.9 cm or one-third longer on the left than on the right. These measurements are compatible with observations (1, 3) that the left Sylvian fissure in man is on the average longer than the right. Our data show that this difference is accounted for by the increased length of the left planum tem-

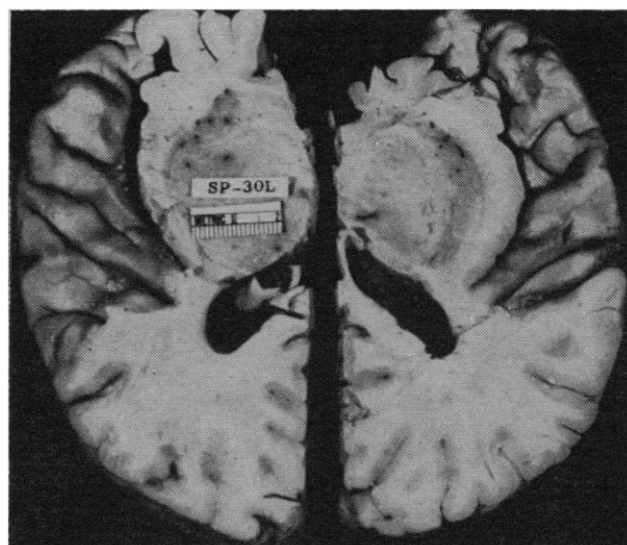
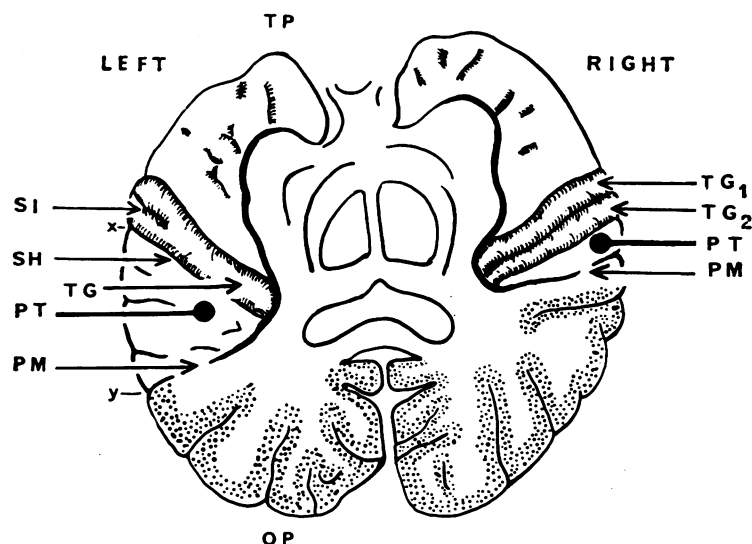


Fig. 1 (left). Upper surfaces of human temporal lobes exposed by a cut on each side in the plane of the Sylvian fissure; anatomical landmarks and typical left-right differences are shown. The posterior margin (PM) of the planum temporale (PT) slopes backward more sharply on the left than on the right, so that end y of the left Sylvian fissure lies posterior to the corresponding point on the right. The anterior margin of the planum formed by the sulcus of Heschl (SH) slopes forward more sharply on the left. In this brain there is a single transverse gyrus of Heschl (TG) on the left, but two on the right (TG₁, TG₂). TP, Temporal pole; OP, occipital pole; SI, sulcus intermedius of Beck. Fig. 2 (right). Upper surfaces of temporal lobes exhibit typical right-left differences. Sharper backward slope of posterior margin and sharper forward slope of anterior margin of planum temporale on the left, larger planum on the left, and longer outer border of left planum are evident.