

Evidence Concerning Neurobiologic Basis of Speech Perception

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SUMMARY AND CONCLUSIONS

1. Miller (43) has proposed that "recognition of speech sounds is based on auditory-perceptual mechanisms common at least to mammals." As a measure of processing in auditory cortex we have used computer generated, sparse acoustic stimuli (SAS) containing only the first three formants of corresponding speech sounds. Parameters of SAS were duration, direction, and extent of second formant change, and frequencies of F_1 , F_2 , and F_3 , generating four sets of sounds. Subjects and patients classified SAS presented monaurally to each ear and binaurally. Classifications of these SAS were arranged in multidimensional contingency tables and tested for departure from homogeneity.

2. If a variable is systematically altered in graded steps, responses of normal subjects show regions of perceptual stability separated by areas of abrupt change in perception (transitions). The form and locus of transitions show short-term (minutes) and long-term (over 3 yr) stability, signifying exquisitely sensitive processing of rapidly changing sounds by the auditory cortex. Significant variation in loci of transition demonstrates that neither hand preference nor unilateral cerebral dominance for speech plays any role in classification of these SAS or in motor acts signifying classification.

3. After ablation of all auditory cortex in one hemisphere, inputs from the ipsilateral ear to the auditory cortex of the remaining hemisphere are insufficient to permit appro-

priate classifications. In the remaining hemisphere the auditory cortex shows altered connectivity due to loss of inter-hemispheric (callosal) inputs from ablated auditory cortex.

4. Ablating rostral area 22 and inter-hemispheric (anterior commissural) connections while preserving primary auditory cortex (areas 41 and 42) does not alter perception and classification of SAS. However, after such ablations, seizures arising in remaining auditory cortex reversibly alter perception of SAS.

5. Ablating premotor and prefrontal cortex and dividing the rostral two-thirds of the corpus callosum and anterior commissure does not alter perception of SAS or the motor acts signifying classifications. Interhemispheric traffic between homologous areas 41 and 42 and caudal area 22 employs the caudal one-third of the corpus callosum.

INTRODUCTION

Sufficient evidence has accumulated to encourage studying the perception of speech within the broader context of animal communication (4,61). Spectrography of speech sounds has permitted analysis in terms of the geometric, aerodynamic, and physical characteristics of the vocal tract. Speech contains narrow-band "colored" noise, rising or falling "frequency-modulated" tones, relatively unchanging "steady-state" sounds, and brief periods of silence (18, 58). The steady-state sounds contain harmonically related resonant components

(formants) whose generation can be characterized by a relatively elastic tube with variable constrictions at the ends and middle (lips, glottis, and tongue) excited by a "quasi-periodic acoustic source at the glottal end" (vocal cord vibration) (56). Such sounds are perceived as vowels. Stevens (56) has shown that this system has nonlinear or "quantal" features because "for some types of articulatory parameters, there are ranges of values . . . for which the acoustic signal has well-defined attributes, and these ranges are bounded by regions in which the properties of this signal are relatively sensitive to perturbations in the articulation." Stevens has used the term plateau-like to characterize an articulatory region in which considerable variation in the muscular contractions positioning the vocal tract yields the same sound and has proposed that plateau-like regions seem to define articulatory phonetic features of speech in all natural languages.

Such investigations have led to the synthesis of sparse acoustic stimuli (SAS), which contain only two or three formants and have long been used successfully in studying speech perception (7, 36). SAS have enough features of speech that they can be identified and classified in terms of speech counterparts. However, SAS are "prelinguistic" because they contain no semantic clues and "prephonetic" because they omit some acoustic components of natural speech. Such studies have yielded unexpected findings. If a variable, for example, duration of formant change, is systematically altered in graded steps and people are asked to classify the resulting sounds, regions of perceptual stability emerge, analogous to Stevens's plateau-like regions, separated by a zone of abrupt change in perception. These transitions have been interpreted in terms of phonetic characterization of speech and called phonemic boundaries (36). However, a growing body of evidence suggests that these perceptual alterations reflect acoustic rather than "phonetic" properties of the stimuli (8, 57, 58, 65). A parallel body of evidence indicates that many animals make equally precise discriminations of speech sounds. Dewson, Pribram, and Lynch (15) have shown that rhesus monkeys can dis-

criminate vowel sounds and that bilateral ablations of primary auditory cortex produce "an apparently complete inability to relearn a conditional discrimination between the vowel sounds [I] and [u] . . . [but only] a transient, slight deficit in the retention of a similar conditional discrimination between tone and noise. . . ." Burdick and Miller (5) have shown that chinchillas can discriminate [i] and [a] despite variations in loudness, pitch level, and voice qualities of male and female speakers. Another study showed that chinchillas discriminated aspirated and unaspirated plosive consonants as precisely as human subjects (32). On the evidence that cats, chinchillas, dogs, and monkeys can discriminate vowels, place-of-articulation in stop-consonants, and aspirated-unaspirated plosive consonants, Miller (43) has concluded that "recognition of speech sounds is based on auditory-perceptual mechanisms common at least to mammals." In the somatosensory system, studies by LaMotte and Mountcastle (33) have shown identical psychophysical functions for detection and discrimination of vibration in man and monkey, providing further evidence for co-extensive perceptual mechanisms in primates.

While some doubt remains about the precise organization of cortical auditory areas, evoked response studies have made clear that the primary auditory area (AI), lying on the superior temporal plane both in man and monkey, contains a topographic mapping of basilar membrane (6, 42) and that several other topographic mappings of basilar membrane exist in cortex surrounding AI. Evidence that in man the left superior temporal plane is larger than right (62) is paralleled by evidence for comparable asymmetry in the chimpanzee (66). Thus, morphologic, physiologic, and behavioral evidence indicate that the auditory cortex contains neuronal arrays that process the complex, rapidly changing acoustic signals that characterize both animal communication sounds and speech.

Many animals generate sound for communication using an unpaired vocal tract whose configuration changes with the synchronous and symmetric contractions of paired muscles. In nonhuman primates we

know relatively little about the role of cortical motor mechanisms in such paired movements (38); however, in man it has long been known that lesions in the left premotor area produce far more profound disruption in articulatory sequences (apraxia) than do lesions in right (27). Recently, evidence has emerged for analogous asymmetric motor control in several species of song birds (canary, chaffinch, white-crowned sparrow, and white-throated sparrow). In these birds lesions in the left hyperstriatum ventrale produce a more enduring disruption in conspecific learned songs than do lesions in right (46). Cross-grain to this predominantly unilateral control of bilateral articulatory movements, primates have evolved independent, increasingly refined control of distal upper-extremity movements, culminating in a cortical motor system that effects direct control of individual finger movements through a monosynaptic corticospinal system (34, 48). Studies of perception of speech can exploit this heterogeneity within cortical motor systems.

Marler (40) has argued that speech evolved from graded vocal utterances of nonhuman primates. A less stringent hypothesis is that speech exploits a phylogenetically widespread auditory-motor system. If either hypothesis is correct, SAS can be used to study the anatomicophysiological basis of speech perception. If neither assumption is correct, SAS still can be used to study processing of complex acoustic signals.

Previously, we have reported that SAS provide "a measure of central auditory processing" (9) and that lesions involving auditory cortex alter perception and classification of SAS (11). We have also described a statistical method in which classifications of SAS are arranged in multidimensional contingency tables and tested for departure from homogeneity (16). With this method we characterize perceptual alterations in individuals, compare individuals, and measure change across time. In 1875 Hughlings Jackson (26) proposed studying cerebral function through a "double plan" that compares the effects of "limited destroying lesions" with "discharging lesions of these parts." In this century, precise excision of epileptogenic foci in the cere-

bral cortex has become an accepted treatment for some patients with intractable epilepsy. This study reports the perceptions and classifications of SAS by normal persons and by patients who have undergone defined cortical resections of various location and extent for treatment of otherwise uncontrollable seizures.

METHODS

Among steady-state sounds with three or more formants, the frequencies and relative intensities of formants characterize sounds perceived as vowels (56, 58). In contrast, appropriate frequency modulation of formants creates sounds perceived as semivowels or consonants. The duration during which formant frequencies change distinguishes sounds perceived as semivowels from stop-consonants (36). Sounds that change slowly, over 80 ms or more, are perceived as semivowels [w] or [y]; sounds that change rapidly, 50 ms or less, as stop-consonants [b] or [g]. With duration held constant, the direction and extent of change in second formant (F_2) frequency characterize sounds perceived as stop-consonants differing in place or articulation: [b], [d], and [g]. The time between a stop-burst and onset of resonance in formants of the voiced portion of a vowel ("voice-onset time") distinguishes sounds perceived as voiced stop-consonants, [b], [d], and [g] from unvoiced stop-consonants [p], [t], and [k] (36, 58).

A sound synthesizer coupled with a special-purpose computer generates sets of sounds. In this study, we consider parameters of duration, direction, and extent of F_2 change using three sets of sounds; we also consider frequencies of F_1 , F_2 , and F_3 . With extent of change held constant, changes in duration of F_2 fall to steady-state yield set [ge]-[ye] (GY); with changes in duration of F_2 rise, set [be]-[we] (BW) (Fig. 1). With duration held constant, direction and extent of F_2 change yield set [be]-[de]-[ge] (BDG) (Fig. 2). In this set, falling F_2 frequencies are perceived as [ge], minimal F_2 change as [de], and rising F_2 frequencies as [be]. In sets BW and GY the time over which F_2 changed was systematically increased in 10-ms steps from 20 to 130 ms; in set BDG the extent of F_2 change was systematically increased in 100-Hz steps from 1,050 to 2,150 Hz, with appropriate compensatory change in F_3 . With duration held constant, altering center frequency of steady-state formants by increasing F_1 from 300 to 520 Hz in 12 20-Hz steps while decreasing F_2 and F_3 from 2,280 to 1,800 Hz and from 2,780 to 2,300 Hz, respectively, in 40-Hz steps yields a set of front vowels: [i]-[I]-[e] (ile).

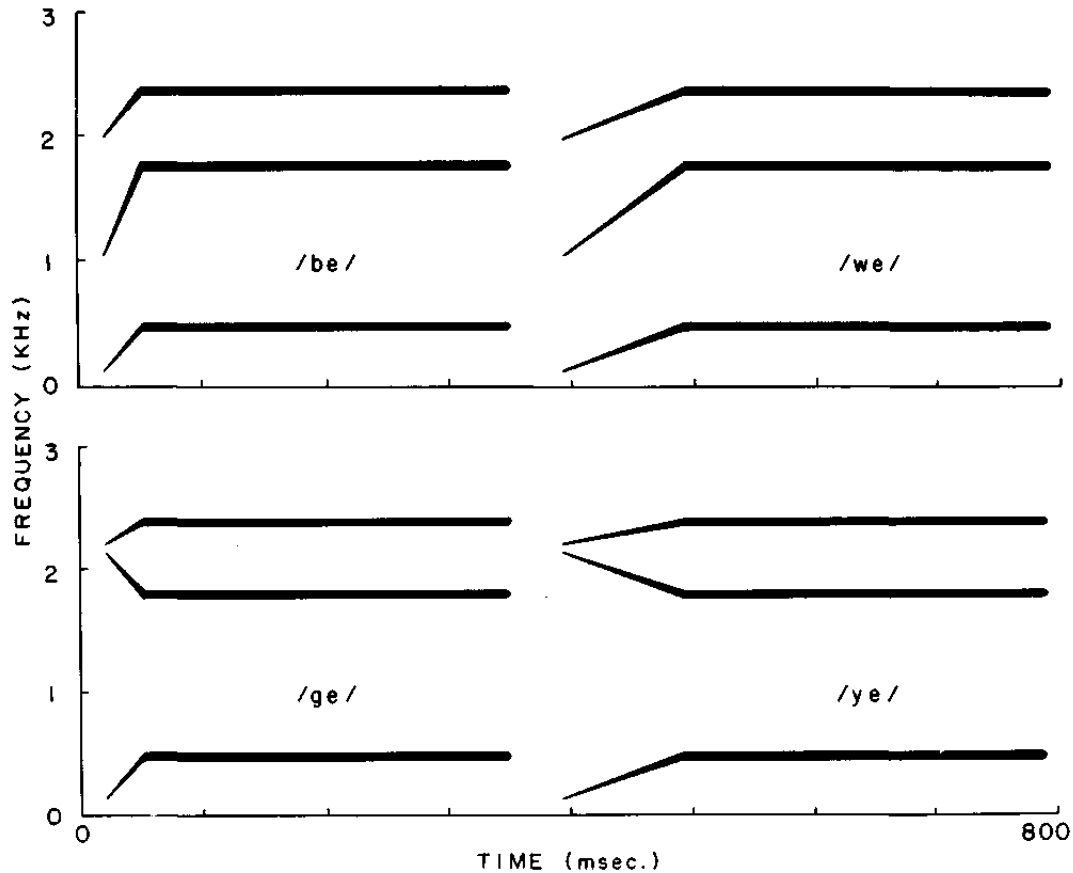


FIG. 1. Schematic diagram of changes in acoustic spectra for stimuli of set BW (upper portion) and set GY (lower portion). Fundamental frequency — 100 Hz; steady-state formants (F_1 , F_2 , and F_3 , labeled from below upward) are similar to those of vowel [e]. Extent of F_2 change held constant in each set; duration of change varies in 10-ms steps from 20 ms (stimulus value 1) to 130 ms (stimulus value 12).

Even in adults with normal hearing, transitions with isolated vowels are often less abrupt than with place-of-articulation stop-consonants: [b], [d], [g] (20, 59, 60). Sets of SAS consisting of four presentations of each of the 12 stimuli (48 stimuli per set; interstimulus interval, 4 s) were recorded in randomized sequences on audiotape using an Elcaset recorder (Sony ELS). During testing, subject listens to SAS presented monaurally to each ear and binaurally through headphones (Koss pro4AAA with matched drivers). Intensity levels between speech reception threshold (SRT) and 95 dB sound pressure level (SPL) have little effect on how subjects with normal hearing classify SAS; however, presentations above 95-dB SPL may impair perception. Mild-to-moderate sensory hearing loss does not impair perception if intensity level is above SRT and below 95 dB SPL; severe-to-profound sensorineural hearing loss may impair perception

of SAS because presentations above SRT often exceed 95 dB SPL (39, 50). In the present study all subjects save case 5 had hearing sensitivities within normal limits for speech range in both ears, normal hearing being defined as pure-tone thresholds less than 15 dB HL (re: 1969 ANSI) at octave frequencies from 250 Hz through 3 kHz, speech reception thresholds less than 15 dB HL, and CID W22 speech discrimination scores above 90%. Intensity of presentations, determined using a steady-state vowel generated with each set, was 65 dB SPL, a level each person found comfortable.

The subject listens to three different pairs of SAS (stimulus values 1-12, 2-10, 3-7) until able to distinguish between stimuli in pairs in at least one mode. For responses we have used a forced-choice identification paradigm. The subject uses a motor act to indicate classification of each SAS, pointing to one of several symbols

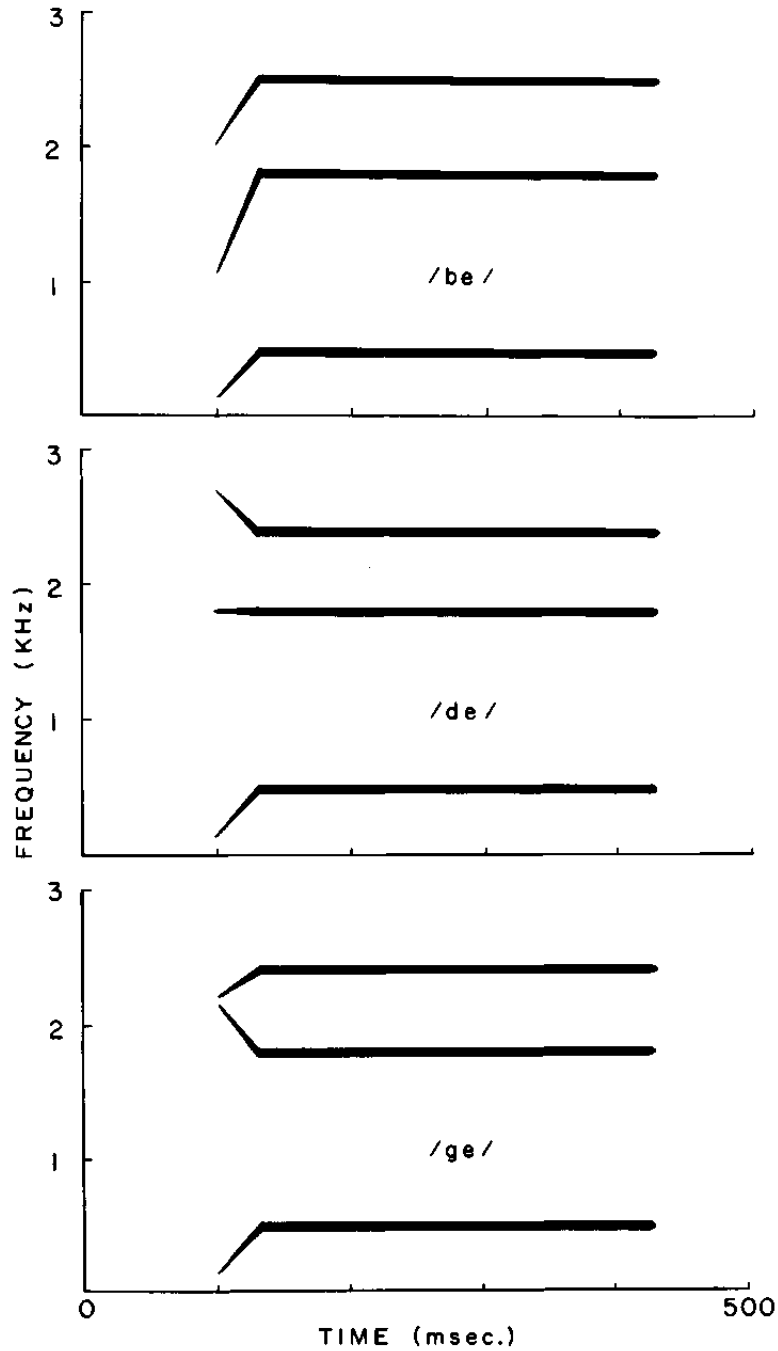


FIG. 2. Schematic drawing of changes in acoustic spectra for stimuli of set BDG. Duration of frequency change held constant (40 ms); extent of F_2 change varies in 100-Hz steps from 1,050 Hz (stimulus value 1) to 2,150 Hz (stimulus value 12) with F_3 change appropriate for rate of F_2 change.

printed on a card, e.g., for GY to a green circle 2.5 cm in diameter or printed "geh" for [ge], and to a yellow circle 2.5 cm in diameter or "yeh" for [ye].

Patients and subjects have been asked to classify the same set of SAS twice, indicating responses with right hand for one trial and left hand for another. In all testing, the order of

presentation of stimulus sets has been randomized with respect to parameters, for example, ear and hand. We have replicated phoneme-boundary effects described in other studies despite uncertainty about their presentation modes (20, 36, 59, 60, 65).

Statistical methodology

As described, each subject listens to four presentations of 12 stimulus values randomly ordered over the entire set of 48 presentations. After each presentation the subject must classify the stimulus as one of either two ([ge]-[ye] or [be]-[we]) or three ([be]-[de]-[ge] or [i]-[l]-[e]) SAS. At the end of each set, the subject has generated 12 either binomial or trinomial responses, each with samples of $n = 4$. Inasmuch as these 12 sets of binomial or trinomial responses are connected by a progression of specified formant changes, a 2 x 12 or 3 x 12 contingency table has been created. However, each table consists of 12 samples of size 4 instead of one sample of size 48.

Although analysis of contingency tables has not been so widely exploited as other measures of probability, several monographs document the analytic power of this method (2, 17, 19, 23, 41, 51). Our analyses exploit primarily two tests of homogeneity. The first type measures departures for a constant fraction of like classification across all stimulus values. Let n_{ij} be the number of classifications i at stimulus value j . For example, if the classification is [ge], let $i = 1$; and if [ye], $i = 2$. If the duration of formant frequency change is 10 ms, $j = 12$ when duration = 130 ms. Let also be the row, column and grand totals, respectively.

$$n_{i.} = n_{i1} + n_{i2} + \dots + n_{i12} \tag{1}$$

$$n_{.j} = n_{1j} + n_{2j} \tag{2}$$

$$\begin{aligned} n_{..} &= n_{.1} + n_{.2} = n_{.1} + n_{.2} + \dots + n_{.12} \\ &= n_{1.1} + n_{1.2} + \dots + n_{2.12} \end{aligned} \tag{3}$$

Then

$$\begin{aligned} G^2 &= 2\left[\sum_{i=1}^2 \sum_{j=1}^{12} n_{ij} \ln n_{ij} - \sum_{i=1}^2 n_{i.} \ln n_{i.}\right. \\ &= \sum_{j=1}^{12} n_{.j} \ln n_{.j} + n_{..} \ln n_{..} \end{aligned} \tag{4}$$

is a likelihood ratio χ^2 with degree of freedom, $df = 11$. If a subject is on the whole unable to differentiate between SAS for all 12 stimulus values, $G^2 = 0$. At the other extreme, classifying four presentations of the six shorter stimulus values one way [ge] and the six longer the other way [ye] yields a maximum: $G^2 = 96 \cdot \ln 2 = 66.54$; for 8 presentations, 133.08; for 12 presentations, 199.62. The average value of a χ^2 with $df = 11$ is 11 with a

standard error of $\sqrt{22} = 4.69$. Thus, a person whose classifications yield G^2 's approximating 55 or 60 differs significantly from another person whose classifications yield G^2 just above chance levels of 19.68 (at 0.05 level of significance) or 24.7 (at 0.01 level). It must be remembered that for trinomial (3 x 12) tables $df = 22$, and G^2 values change accordingly.

The second type of analysis tests homogeneity of different parameters, for example, ears, hands, or studies made at different times. This type of analysis can examine changes in classifications over time: the intervals between the testing for a given set may vary from minutes to months. The analysis provides additional rigor because it can test for changes in each parameter, for example, analysis of alterations in classifying presentations in left ear, right ear, or binaurally. Furthermore, because this type of analysis can also consider the parameter time, it can address whether appropriate (normal) classifications are homogeneous (stable) or heterogeneous (changing), as well as whether inappropriate (abnormal) classifications are homogeneous (unaltered) or heterogeneous (changing) toward more appropriate (improving) or less appropriate (deteriorating) states.

The number of like classifications now has three indexes, the third one indicating replication of the entire set either over time or some other variable. Let n_{ijk} be that frequency with $k =$ time of examination and i and j remaining as before. Then the likelihood χ^2 ratio is

$$\begin{aligned} G^2 &= 2\left[\sum_{i=1}^2 \sum_{j=1}^{12} \sum_{k=1}^K n_{ijk} - \sum_{i=1}^2 \sum_{j=1}^{12} n_{ij.} \ln n_{ij.}\right. \\ &\quad \left. - \sum_{k=1}^K n_{..k} \ln n_{..k} + n_{...} \ln n_{...}\right] \end{aligned} \tag{5}$$

with $df = 12$ for two 2 x 12 tables, and 24 for three 2 x 12 tables; $df = 24$ for two 3 x 12 tables, and 48 for three 3 x 12 tables.

In these studies we use both types of analysis to illuminate the perception of SAS by normal persons as well as altered perceptions experienced by some of our patients.

RESULTS

Persons with intact nervous system

Studies on normal subjects have provided considerable evidence concerning perception of speech sounds (36, 37, 50, 65). We present studies of two normal subjects that are representative (16) of our findings in a population of normal adults.

Case 1, a 30-yr-old right-handed man, showed normal thresholds with pure-tone and speech

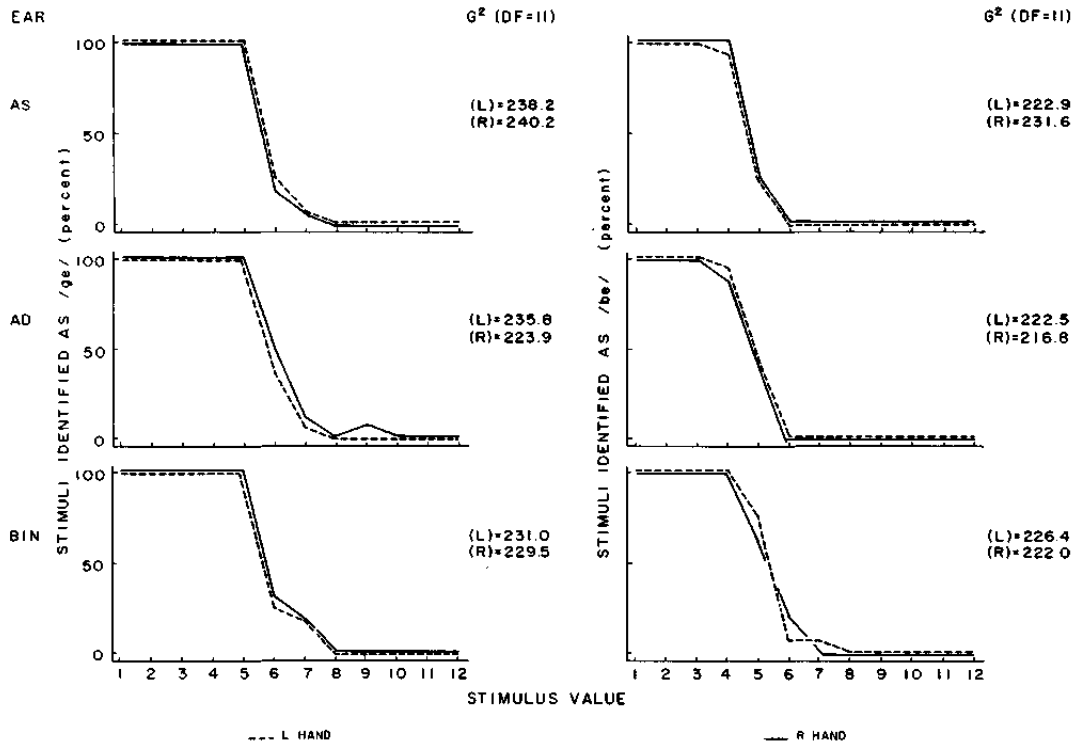


FIG. 3. Case 1 sets GY, B W. Graphs illustrating percent of stimuli identified in manner indicated as function of rate of formant change. Duration of F_2 change varies in 10-ms steps from 20 ms (stimulus value 1) to 130 ms (stimulus value 12). Ordinate: for GY (left portion), percent of stimuli identified as [ge]; for BW (right portion), as [be]. Abscissa: cardinal stimulus values. AS, left monaural presentations; AD, right monaural presentations; BIN, binaural presentations. L, left-hand responses; R, right-hand responses; df, degree of freedom.

audiometry and speech-discrimination scores within normal limits.

Figure 3 displays graphically results for GY and BW; Fig. 4, data for BDG. Table 1 records G^2 values for all sets during this single testing session. Within GY subject classifies all shorter duration stimuli as [ge] and all longer stimuli as [ye]. Subject classified less consistently stimuli of intermediate durations, the same stimulus sometimes being classified as [ge] and other times as [ye] (Fig. 3). Turning to Table 1, for all sets G^2 for ear and hand parameters exceeds df indicating heterogeneity for stimulus value, consonant with sharply defined transitions in perception (Figs. 3 and 4). The precipitous transitions indicate that forced-choice identifications do not result in consistent classification only at parametric extremes and random performance, "guessing," at intermediate stimulus values. Across parameters ear and hand

there is homogeneity for site and form of transitions for each set. In this testing session, the findings are based on a total of 16 presentations for each value of the stimulus; that is, the subject's response remained stable throughout a test period of about 7 h. Table 2 records G^2 values for each parameter during single 15-min test sessions and for the sum of repeated test sessions over a 3-yr interval. During this 3-yr interval the subject was tested with three different tapes, four different sets of headphones and four different tape recorders. Thus, these findings demonstrate a short- and long-term stability of responses.

Case 2, a 32-yr-old right-handed woman, had normal hearing as determined by pure-tone and speech audiometry.

Figure 5 displays graphically her classifications of GY and BW; Fig. 6, of BDG. Table 3 records G^2 values for all sets during

TABLE 1. *Case 1: GY, BW, and BDG results from single testing session shown in Figs. 3 and 4*

	AS	AD	BIN	Ears
GY				df = 24
L	238.2*	235.8*	231.0*	2.5†
R	240.2*	223.9*	229.5*	7.0†
df = 11				
Hands	0.8†	2.3†	0.2†	
df = 12				
BW				df = 24
L	222.9*	222.5*	226.4*	17.5 (0.825)
R	231.6*	216.8*	222.0*	16.4 (0.870)
df = 11				
Hands	1.4†	0.4†	3.2 (0.994)	
df = 12				
BDG				df = 48
L	397.4*	384.0*	382.6*	13.1†
R	394.7*	369.5*	392.1*	20.1†
df = 22				
Hands	16.0 (0.888)	6.9†	12.3 (0.980)	
df = 24				
ile				df = 48
L	361.0*	353.0*	364.8*	36.2 (0.990)
R	355.8*	376.9*	364.2*	16.5†
df = 22				
Hands				
df = 24	7.0†	5.1†	21.2 (0.710)	

AS, left monaural presentations; AD, right monaural presentations; BIN, binaural presentations. L, left-hand responses; R, right-hand responses, ears, AS vs. AD vs. BIN for hand indicated; hands, L hand vs. R hand for ear indicated, df, degrees of freedom. Numbers in parentheses are P . P = probability that χ^2 exceeds G^2 . See text for details. * $P < 10^{-3}$. † $P > 0.999$.

this single testing session. G^2 values for ear and hand parameters exceed df indicating heterogeneity for stimulus value, concordant with sharply defined transitions.

Inspection of Fig. 5 reveals variation in sites of transition. Because stimuli in the region of transition contribute to the numerical value, G^2 functions can provide measures of form and location of transitions across parameters and indicate if such variations are statistically significant. For GY, there is homogeneity of hands for left monaural (AS) presentations but not for right monaural (AD) or binaural (BIN) presentations. Considering ears, responses made with the left hand show homogeneity; in contrast, right-hand responses show heterogeneity. In BW, there is homogeneity of hands for AD and BIN presentations but not for AS. By contrast with GY, in BW there is no homogeneity for left-hand responses, but again there is heterogeneity for right-hand responses. For BDG there is

clear evidence for homogeneity of hands for AS and BIN presentations, but less striking evidence for AD presentations. There is homogeneity of ears for right- and left-hand responses. For ile, transitions in each mode are as well defined as the corresponding mode for BDG; moreover, there is homogeneity across hands and ears.

For GY and BW, we can now ask to what extent form and locus contribute to heterogeneity. Form of transition can be analyzed by aligning transitions independently of the absolute stimulus value, that is, by considering order but not cardinality of stimulus value; the minimum of G^2 values defines homogeneity of form. In GY considering form of transitions across hands, for AS presentations $G^2 = 2.9$; for AD, 2.1; and for BIN, 2.1. Considering BW across hands, for AS presentations $G^2 = 4.7$; for AD, 4.7; and for BIN, 6.3. These findings indicate homogeneity of form or "isomorphic" transitions. Thus, any heterogeneity must

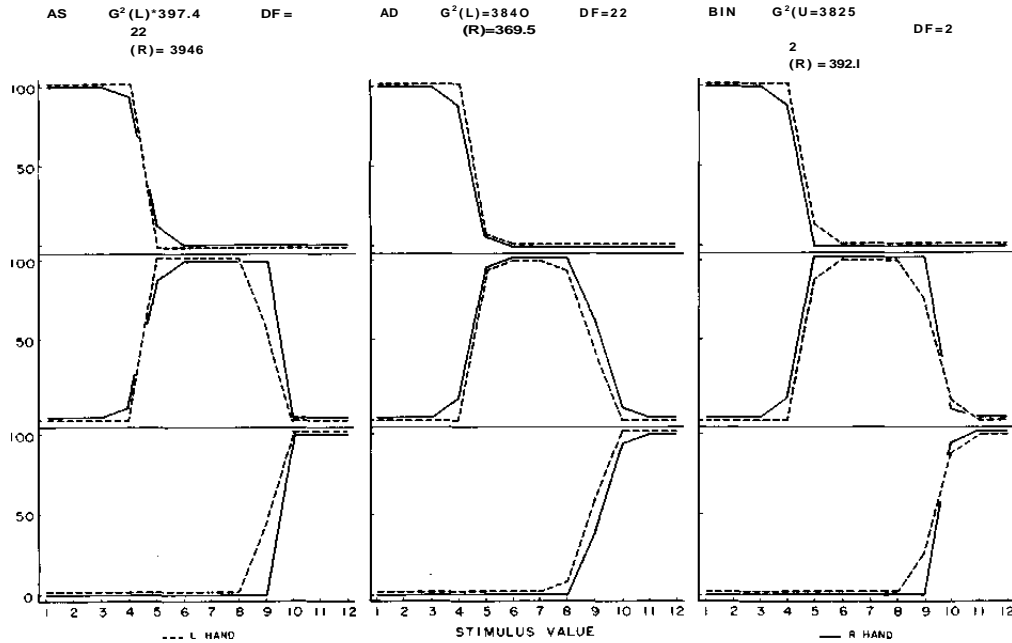


FIG. 4. Case 1, set BDG. Graphs illustrating percent stimuli identified in manner indicated as function of rate of formant change. Extent of F₂ change varies in 100-Hz steps from 1,050 Hz (stimulus value 1) to 2,150 Hz (stimulus value 12). Ordinate: percent of stimuli identified as [be] (upper portion), [de] (middle portion), and [ge] (lower portion). Abscissa: cardinal stimulus values.

arise from variations in locus of transitions. Figure 5 reveals that differences arise from loci of hand responses: for GY with left-hand responses, transitions occur at shorter duration stimulus values than with right-hand responses. For BDG, locus of transition is invariant across hands for AS and BIN presentations; in contrast with findings

in sets GY and BW, the relatively minor deviations from homogeneity for AD presentations apparently do not arise solely from variations in locus.

These findings illuminate several points. In case 1, form and locus of transitions have been homogeneous and invariant over 3 yr. In case 2, form of transitions

TABLE 2. Case 1: for GY, BW, and BDG, comparison of tabulated responses across four consecutive epochs during single 15-min test sessions and across summed episodic test sessions conducted over 3 yr

	AS		AD		BIN	
	15 min	3yr	15 min	3yr	15 min	3yr
GY	df = 36	df = 12	df = 36	df = 12	df = 36	df = 12
L	6.0*	5.1 (0.953)	4.1*	1.1*	4.1*	4.6 (0.970)
R	4.9*	3.6 (0.990)	5.6*	0.4*	6.2*	4.2 (0.980)
BW						
L	3.0*	1.2*	0.8*	1.3*	0.8*	4.1 (0.981)
R	0*	4.1 (0.981)	3.9*	1.0*	4.1*	0.2*
BDG	df = 72	df = 24	df = 72	df = 24	df = 72	df = 24
L	4.1*	1.6*	5.1*	3.0*	5.4*	4.7*
R	6.2*	12.0 (0.980)	6.6*	5.9*	5.4*	1.7*

Abbreviations as in Table 1. Numbers in parentheses are *P*.

* *P* > 0.999.

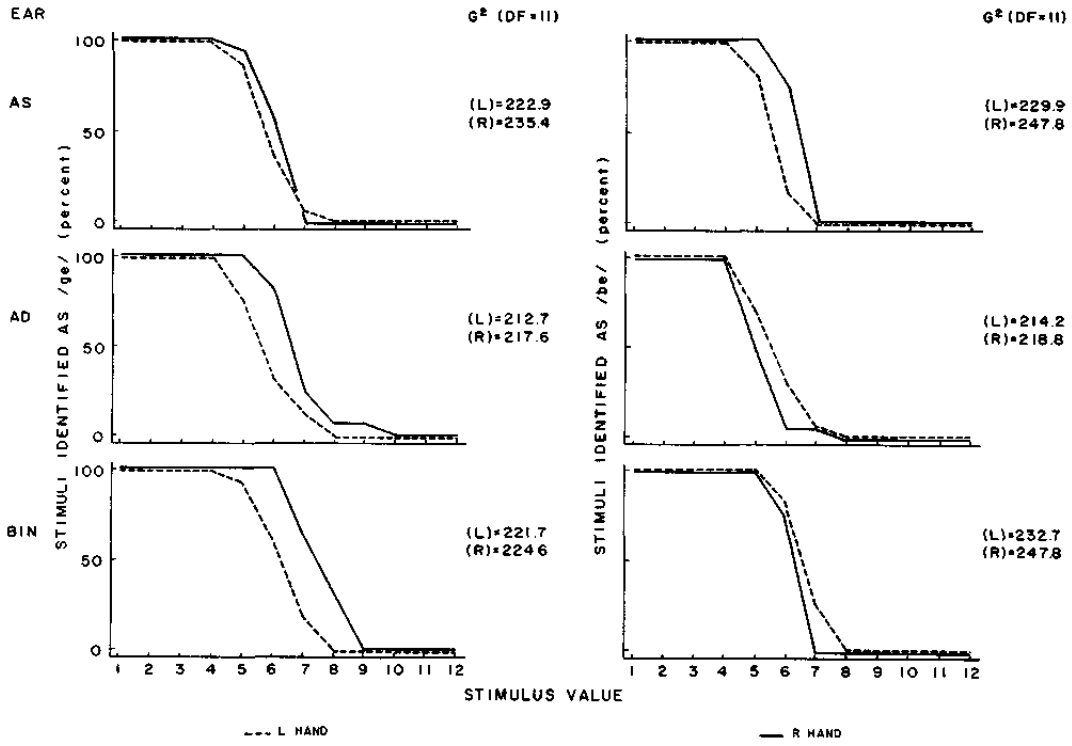


FIG. 5. Case 2, sets GY and BW.

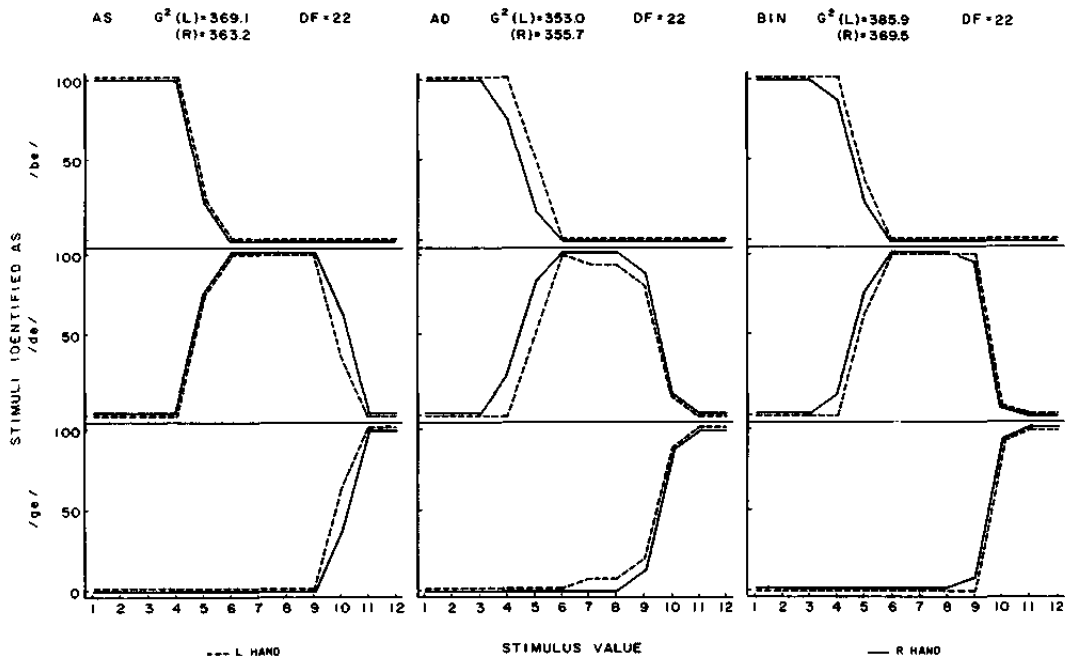


FIG. 6. Case 2, set BDG.

TABLE 3. Case 2: GY, BW, and BDG results from single testing session shown in Figs. 5 and 6

		AS	AD	BIN	Ears
GY					df = 24
	L	222.9*	212.7*	221.7*	7.1†
	R	235.4*	217.7*	224.6*	43.8 (0.004)
	df = 11				
	Hands	2.9 (0.996)	18.3 (0.108)	25.6 (0.012)	
	df = 12				
BW	L	229.9*	214.2*	232.7*	29.6(0.180)
	R	247.8*	218.9*	247.8*	46.3 (0.004)
	df = 11				
	Hands	15.3 (0.230)	4.7 (0.967)	6.3 (0.905)	
	df = 12				
BDG					df = 48
	L	369.2*	353.0*	385.9*	19.3†
	R	363.3*	355.8*	369.6*	24.6 (0.997)
	df = 22				
	Hands	2.0†	12.8 (0.975)	4.9†	
	df = 24				
ile	L	380.9*	398.4*	382.1*	9.3†
	R	386.7*	377.1*	366.6*	6.3†
	df = 22				
	Hands	3.7†	7.9†	12.5 (0.979)	
	df = 24				

Abbreviations as in Table 1. Numbers in parentheses are *P*.* $P < 10^{-4}$.† $P > 0.999$.

is invariant and homogeneous; heterogeneity arises largely from variations in locus of transition. Isomorphic transitions and variations in locus demonstrate that neither hand preference nor unilateral cerebral dominance for speech plays any role in classification of these SAS or the motor act signifying classification, findings consistent with the statement of Kimura (31)". . . that left hemisphere specialization of function cannot be characterized in terms of the acoustic correlates of speech . . ."

Unilateral ablation of auditory cortex

We report findings in two patients who had unilateral excision of auditory cortex incident to hemispherectomy.

Case 3, an 8-yr-old girl, had developed normally until age 4 when she showed symptoms of unilateral subacute hemispheric encephalitis. Because of intractable seizures, she underwent right hemispherectomy at age 4 yr, 10 mo.

Our first examinations were made 3 yr postoperatively. Figure 7 (right removal) shows her classification of GY. For AD and BIN presentations her responses are hetero-

geneous with clear evidence of transitions: for AD, $G^2 = 88.3$, $P = 0.0001$; and for BIN, $G^2 = 58.6$, $P = 0.0001$. We have found that normal children of this age show well-defined transitions, differing from adults in only minor degrees (12, 13, 16). For AS presentations her responses with the right hand are homogeneous ($G^2 = 1.2$, $P = 0.9997$) and with the left hand nearly homogeneous ($G^2 = 9.3$, $P = 0.593$) indicating random classifications. These findings have remained unchanged during each testing session and during repeated testing over 12 mo. She has also been tested and asked to speak aloud her identifications. She again showed homogeneity for AS presentations. Moreover, for binaural presentations with 8-dB interaural intensity differences, she showed less heterogeneity when AS > AD than when AD > AS, excluding a defect in hand guidance.

The patient's impressions merit comment. She did not hear AS presentations as undifferentiable sounds that she classified randomly; rather, she reported SAS sounded equally clear in each ear and believed she

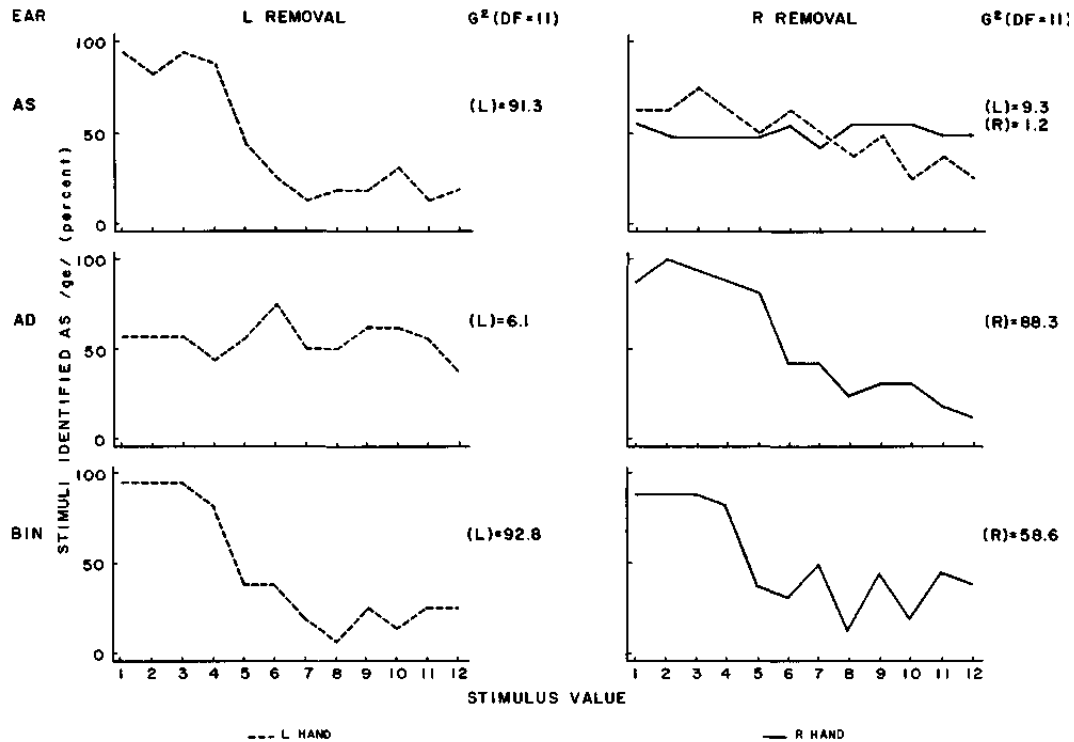


FIG. 7. Unilateral ablation of auditory cortex: set GY. Right removal, case 3; left removal, case 4. See text for details.

had classified them appropriately. She found BIN presentations "not as clear" as monaural except for intensities of AD > AS.

Because of hemispherectomy, her motor responses to SAS can reflect only activity in left motor cortex. Her classifications with AS presentations are essentially random regardless of whether motor responses employ the crossed corticospinal system (right hand) or the uncrossed corticobulbar system (left hand) (35). Thus, homogeneity only with AS presentations demonstrates that ipsilateral inputs to the left auditory cortex are insufficient to detect or resolve differences in these SAS.

Case 4, a 30-yr-old woman, had been born of prolonged and difficult labor resulting in extensive damage to left cerebral hemisphere and intractable seizures. Preoperative intracarotid amobarbital studies had shown that right cerebral hemisphere initiated speech. At 29 yr of age, she underwent left hemispherectomy.

Our initial examination was 6 mo postoperatively; 18 mo postoperatively, the

findings remained essentially unchanged. Because of severe spasticity, she could not make motor responses with the right arm. Figure 7 (left removal) shows her classifications of GY. AS and BIN presentations showed evidence of transitions: for AS, $G^2 = 91.4$ ($P < 10^{-4}$); and for BIN, $G^2 = 95.6$ ($P < 10^{-4}$). With AD presentations she classified at near-chance levels: $G^2 = 6.6$; $P = 0.828$. However, with BW, transitions appeared for ear: for AS presentation, $G^2 = 151.7$; for AD, 95.2; and for BIN, 150.1 ($df = 11$); for each, $P < 10^{-4}$. In contrast with GY, case 4 initially showed "practice effects" with BW. BW presentations were first made to AD; she reported all SAS as identical and "B's." Next AS presentations were made, and she recognized differences. Following this, AD presentations were repeated; she discriminated SAS but also reported that they were "different" from AS presentations. These AD presentations showed a transition similar in locus and form to AS, and a second transition

($P = 0.0001$) between stimulus values 11 and 12; she classified the extreme value as "beh." Despite repeated attempts, she never appropriately discriminated SAS in BDG: for AS presentations, $G^2 = 13.0$ ($P = 0.93$); for AD, 14.8 ($P = 0.87$); for BIN, 23.4 ($P = 0.38$). In this set she perceived AD presentations as "buzzes something like bees." She reported that in AS presentations she heard "beh's," "deh's," "meh's," and "neh's," but no "geh's." Phonetically [m], [n], and [ŋ] are nasal counterparts of [b], [d], and [g]; the presence of F_1 and F_2 resonance before FM is usually sufficient to permit distinguishing acoustically between nasals and voiced stops. She classified ile appropriately in each mode: for AS presentations $G^2 = 317.8$; for AD, 313.2; for bin, 296.2, all $P < 10^{-4}$. In this patient, transitions with monaural ile and BW presentations show that her near-chance performance with AD presentations of GY cannot reflect some non-specific perceptual deficit. The findings in this patient and in case 3 indicate that for certain SAS, inputs from the ear ipsilateral

to the remaining auditory cortex are not sufficient to detect or resolve differences in the induced motion of basilar membrane.

We next report findings in four patients who underwent limited cortical resections sparing auditory cortex.

Anterior temporal lobectomy

The usual anterior temporal lobectomy spares Brodmann's areas 41 and 42 (AI) and the posterior portion of area 22 (sometimes designated Tpt, and the only part of area 22 postulated to be an auditory area important in speech and language functions (21)). Even if carried out in the dominant hemisphere, anterior temporal lobectomy produces no permanent deficit in speech perception or language.

Case 5, a 26-yr-old man, underwent right anterior temporal lobectomy. Preoperative intracarotid amobarbital studies demonstrated left hemispheric dominance for speech. Preoperatively, pure-tone audiometry had shown bilateral, moderate, high-frequency sensorineural hearing loss (45 dB AD and 35 dB AS at and above 3,000 Hz). Speech reception thresholds

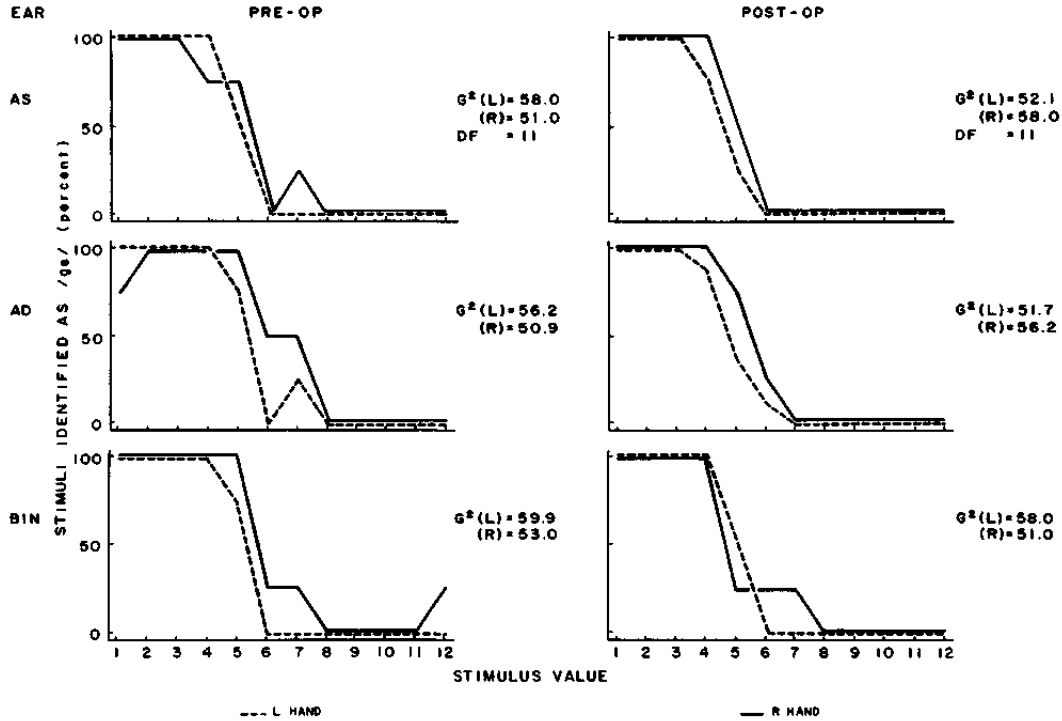


FIG. 8. Case 5, set GY. Preop, preoperative findings, Postop, postoperative findings.

were -2 dB in each ear; speech discrimination in AD was 96% at 42 dB SPL and in AS 88% at 38 dB SPL.

Figure 8 shows pre- and postoperative results for GY. If ear and hand parameters are combined and preoperative performance compared with postoperative, $G^2 = 60.4$ ($df = 132$), indicating highly significant homogeneity. Table 4 summarizes G^2 values for GY and BW: the findings for BW are consonant with those for GY. In BW relatively low G^2 values are seen in preoperative AS left-hand testing and postoperative BIN right-hand testing. In each instance the patient was tested immediately after a brief seizure; these values probably reflect postictal depression of auditory cortex function. In summary, for this patient anterior temporal lobectomy has not resulted in altered classification of SAS.

Case 6, a 45-yr-old woman, underwent left anterior temporal lobectomy at age 32. Preoperative amobarbital studies had shown left hemispheric dominance for speech. The resection

included temporal lobe neocortex, hippocampus, and white matter medially to the free edge of the tentorium. Postexcision electrocorticography showed spikes persisting in the gyri breves of the insula and the transverse gyrus of Heschl. The surgical procedure abolished major seizures, but she continued to have minor seizures originating in the left auditory cortex. During these, voices and sounds became "jumbled" and the environment appeared "unreal" or "dreamlike." These focal seizures were often followed by brief periods of confusion and amnesia (automatisms).

Table 5 shows G^2 values for sets GY, BW, and BDG. The values indicate sharply defined transitions for all ear and hand parameters. Thus, postoperative interictal studies showed no evidence of altered perception.

During testing sessions, spontaneous seizures permitted observation of the effects of ictus in the left auditory cortex. During one such seizure (Fig. 9), the patient ceased responding for about 3 min. After this automatism, testing was resumed using binaural

TABLE 4. Case 5: GY and BW results preoperatively, postoperatively, and comparisons preoperatively vs. postoperatively

		AS	AD	BIN	Ears
GY					$df = 24$
Preop	L	58.0*	56.2*	59.9*	3.1†
	R	51.0*	50.9*	53.0*	13.7 (0.953)
	Hands $df = 11$	3.6 (0.990)	7.1 (0.850)	6.1 (0.910)	
Postop	L	52.1*	51.7*	58.0*	3.5†
	R	58.0*	56.2*	51.0*	6.3†
	Hands $df = 11$	2.1†	2.1†	3.6 (0.990)	
Pre vs. Post	L	2.1†	5.2 (0.951)	0.5†	
	R	3.6 (0.990)	7.1 (0.850)	7.6 (0.816)	
	Hands $df = 12$				
BW					
Preop	L	26.5* (0.005)	48.9*	54.5*	25.0 (0.406)
	R	51.6*	46.8*	58.0*	10.0 (0.995)
	Hands $df = 11$	19.1 (0.082)	4.1 (0.982)	2.1†	
Postop	L	49.6*	51.6*	54.5*	12.9 (0.965)
	R			39.9*§	
	Hands $df = 12$				
Pre vs. Post	L	12.6 (0.402)	5.1 (0.953)	5.2 (0.951)	
	R			10.8 (0.545)	
	Hands $df = 12$				

Abbreviations as in Table 1. In each condition, number of presentations (n) per stimulus value = 4. Numbers in parentheses are *P*. * $P < 10^{-4}$. † $P > 0.999$. § Tested following seizure.

TABLE 5. Case 6: GY, BW, and BDG results from interictal testing

	AS	AD	BIN	Ears
GY				df = 24
L	57.2*	60.7*	51.7*	4.9†
R	57.2*	52.0*	61.3*	4.9†
df = 11				
Hands	3.1 (0.994)	3.1 (0.994)	3.6 (0.990)	
df = 12				
BW				
L	46.1*	52.1*	56.2*	12.7 (0.969)
R	46.5*	41.7*	52.3*	9.9 (0.995)
df = 11				
Hands	4.1 (0.981)	8.2 (0.769)	1.5†	
df = 12				
BDG				df = 48
L	79.6*	72.3*	91.3*	27.5 (0.995)
R	90.5*	84.0*	86.5*	24.4 (0.998)
df = 22				
Hands	13.2 (0.963)	13.0 (0.967)	13.5 (0.957)	
df = 24				

Abbreviations as in Table 1. In each condition $n = 4$. Numbers in parentheses are P . * $P < 10^{-4}$. † $P > 0.999$

presentations. When pointing with right hand, many of her responses differed from those she had made interictally to the same SAS. However, each time the right hand indicated an inappropriate response, the left hand immediately indicated the appropriate response. Afterward, she was amnesic for this interval.

Focal epileptic discharges in auditory cortex disrupt processing in animals (54) and man (13). Testing of this patient during intensive monitoring with telemetered EEG and simultaneous audiovisual recordings confirmed that postictally she consistently had transiently impaired processing in the left auditory cortex, whereas processing in right auditory cortex was intact. Bilateral epileptic discharges during the automatism caused postictal paralysis of the remaining right hippocampus, producing amnesia (63). Note that she did not use her right hand (left motor cortex) to indicate perceptions by her right auditory cortex.

The findings in these patients demonstrate that anterior temporal lobectomy does not alter perception of SAS.

Frontal lobectomy

During frontal lobectomy the motor strip (area 4), as determined by electrical stimulation, defines the posterior border of

excision. In the dominant hemisphere, the premotor area essential for speech is also preserved. Such resections produce no evident motor deficit; however, in monkeys ablation of the premotor area may produce alteration in visually guided reaching movements (44). We report findings in two patients who underwent frontal lobectomy.

Case 7, an 11-yr-old boy, had had left hemiparesis from birth. Preoperative amobarbital studies had shown left hemispheric dominance for speech. Surgery revealed that the right frontal lobe had been destroyed leaving a large porencephalic cyst. The remaining cortical tissue was resected and commissurotomy of the rostral two-thirds of the corpus callosum, including the genu, and the anterior commissure was carried out.

The patient was tested pre- and postoperatively. A severely spastic left arm limited preoperative testing to responses with the right hand. For BW well-defined transitions existed for ear parameter: preoperatively for AS, $G^2 = 52.1$; for AD, 43.4; for BIN, 48.9. Postoperatively, with right-hand responses values were essentially unchanged: for AS, 58.0; for AD, 54.4; and BIN, 46.8 (preop vs. postop AS, 5.1, $P = 0.954$; AD, 4.1, $P = 0.981$, BIN, 5.5, $P = 0.938$); with left-hand responses for AS $G^2 = 52.4$ and for AD, 49.0. For BDG

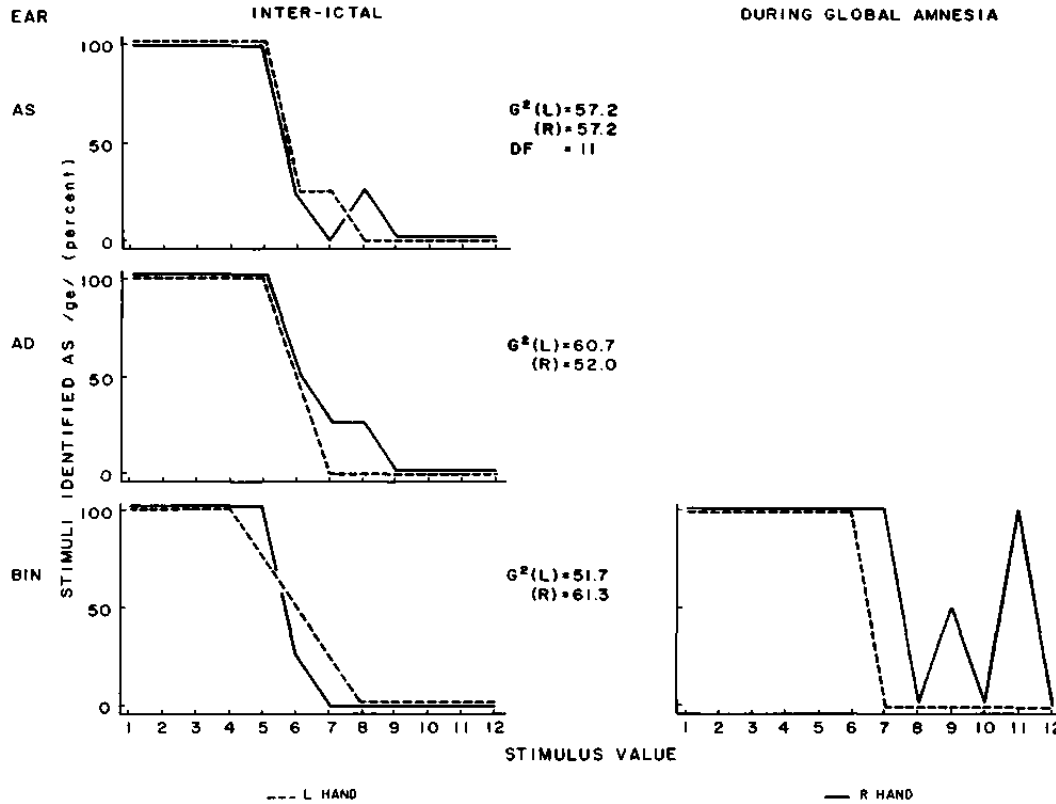


FIG. 9. Case 6, set GY. Interictal, classifications interictally with AS, AD, and BIN presentations both for R- and L-hand responses. During global amnesia, responses to BIN presentations postictally. See text for details.

transitions were well defined postoperatively: with right-hand responses for AS presentations $G^2 = 69.7$; for AD, 78.0; and for BIN, 65.4; with left-hand responses for AS, 82.4; for AD, 72.6; and for BIN, 89.5. Figure 10 shows results for GY. Preoperatively, he could not discriminate GY and reported that all SAS sounded like yeh regardless of ear parameter. Even after successfully performing BW, on subsequent trials he still could not discriminate GY. Postoperatively, spasticity in his left extremities had abated sufficiently that he could indicate responses with either hand; he discriminated SAS readily and his classifications showed well-defined transitions.

Case 8, a 35-yr-old right-handed woman, underwent resection of all the mesial surface and all the dorsolateral aspect of the left frontal lobe anterior to the motor area save for the inferior frontal convolution. Orbital cortex was preserved. Preoperatively the patient's only

symptom had been intractable seizures; however, an indolent, histologically low-grade glioma had caused the seizures. Postoperatively, she had no demonstrable motor or speech deficit.

The patient underwent several examinations during the 5 mo before surgery and has been tested at regular intervals since the operation. Figure 11 displays results for GY pre- and postoperatively. Table 6 summarizes G^2 values for BW. In preoperative testing G^2 values for AS presentations and AD right-hand responses are lower than those of normal subjects although still indicating significant ($P < 0.0001$) heterogeneity. Preoperatively she experienced frequent focal seizures and, at one time, clinical intoxication from phenytoin. As a result, testing sessions were limited by the circumstances of her illness. Despite phenytoin intoxication, the patient adequately classified SAS; however, impaired vigilance from intoxication may have con-

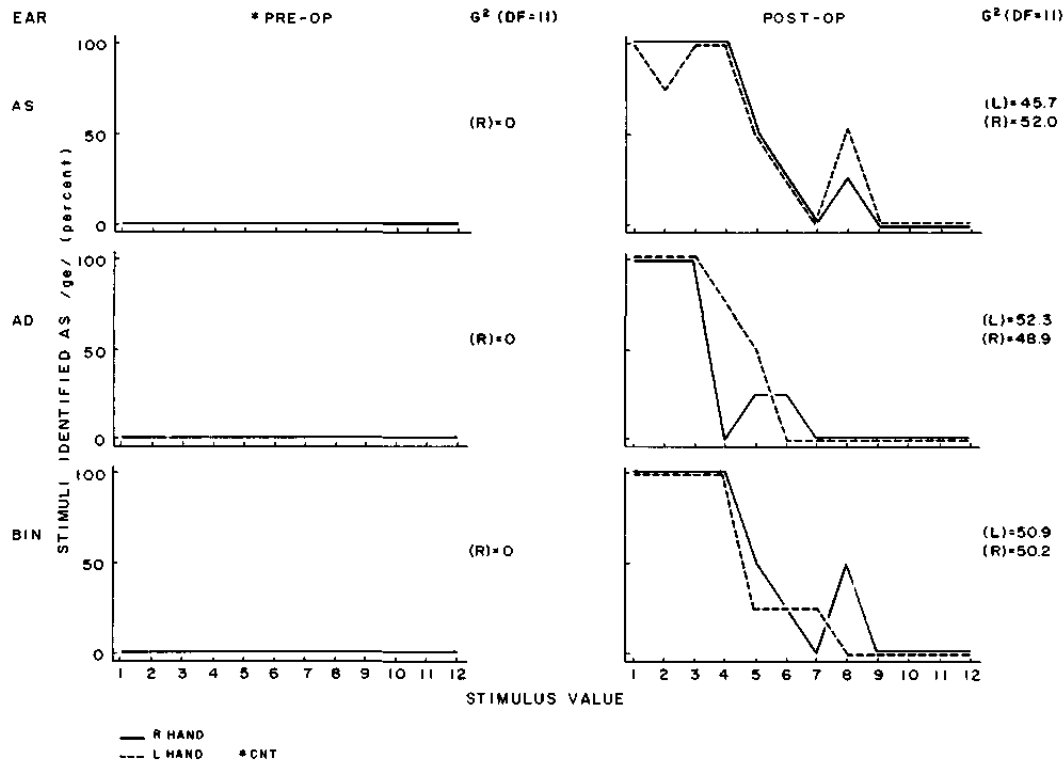


FIG. 10. Case 7, set GY. CNT, could not test. See text for details.

tributed to altered performance. Furthermore, although there was no evidence the tumor had displaced cerebral structures, unpredictable alterations in regional cerebral blood flow do occur in patients with brain tumor. Postoperatively, transitions were well defined and classifications with AS presentations consonant with AD and BIN. For BW, postoperative performance was comparable to GY.

In patients 7 and 8, postoperative findings of well-defined transitions indicate that unilateral frontal lobectomy does not alter

perception of these SAS. In case 7, the preoperative finding of fixed responses to GY may well have resulted from frequent seizures; in other patients we have observed such fixed responses during automatisms (10). Postoperatively in case 7, homogeneity of transitions across hands is significant in view of the extensive rostral resection of the corpus callosum.

DISCUSSION

In the cochlea the acoustic energy of sound is transformed into movements of the

TABLE 6. Case 8: BW results from preoperative and postoperative testing

		AS	AD	BIN
Preop	R	63.5*	79.2*	80.6*
Postop	R	57.9*	49.0*	60.0*
df = 11				
Pre vs. Post	R	10.1 (0.615)	8.1 (0.777)	6.4 (0.895)
df = 12				

Abbreviations as in Table 1. Numbers in parentheses are *P*. Preoperatively, *n* = 8; postoperatively, *n* = 4. * *P* < 10⁻⁴.

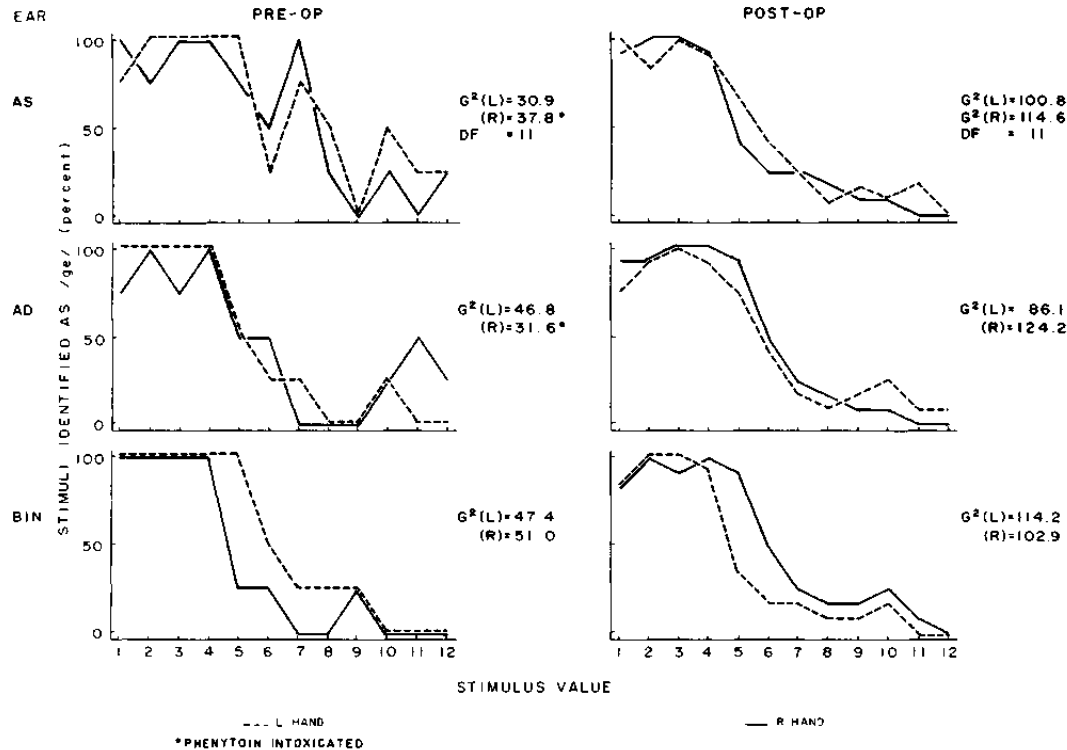


FIG. 11. Case 8, set GY. See text for details.

basilar membrane. In structure the membrane is a spiral helix in which the basal portion is narrower and more rigid than the apical portion. The cochlear apparatus transforms a pure tone into a traveling wave on the basilar membrane in which the site of maximum displacement signifies frequency (1, 68). The spectrum of frequencies is continuous, with higher frequencies represented in basal portions and lower frequencies in apical portions of the membrane. Chords consisting of two or more pure tones excite complex traveling waves (68, 69) and evoke apparently characteristic discharge patterns from primary (cochlear) neurons (22); similar results have been reported from psychophysical studies of ripple noise (25) and pitch strength of ripple noise (67). At the present time, little is known about the nature of the complex basilar membrane movements induced by constant frequency (CF) and frequency modulated (FM) components of speech sounds, or the representations of such movements (52).

Despite these limitations, study of the consequences of ablating auditory cortex can provide clues about neuronal processing in auditory cortex. Dewson et al. (14, 15) have demonstrated in monkey that only bilateral ablation of auditory cortex impairs ability to discriminate vowels [i] and [u]; consistent with these findings, case 4 classified ile appropriately in each mode. Further, case 4 discriminated SAS in BW, demonstrating that she could detect rapid FM changes and discriminate among movements induced in basilar membranes. She did report that monaural presentations of the same stimuli sounded differently in each ear although the nature of this difference remains uncertain.

Neither case 3 nor case 4 discriminated monaural presentations of GY in the ear opposite to cortical ablation. In light of the previous findings this cannot represent some general perceptual defect nor can it arise from inability to differentiate shorter from longer durations of FM change in these SAS. The view that in man unilateral

cortical lesions do not impair auditory perception has been refuted by Bocca, Calearo, and Cassinari (3) who presented lists of phonetically balanced words to patients with temporal lobe tumors. If speech was unfiltered, articulation (discrimination) functions were normal; however, after low-pass filtering, which drastically reduced frequencies above 1,000 Hz, articulation functions were distinctly lower in the ear contralateral to the tumor, findings consonant with our observations. Low-pass filtering essentially eliminates F_2 and higher formants and thus drastically alters acoustic information in the filtered speech.

An explanation of these findings may lie in the nature and representation of basilar membrane movements. Steady-state vowels induce a series of traveling waves with characteristic maxima and local perturbations. Rising frequencies in BW induce confluent traveling waves; in sequences these may cover decreasing extents of the basilar membrane. Falling frequencies in GY cause traveling waves to converge centrally and be "compressed" on the membrane; in sequences these may cover increasing extents of the membrane and may produce local (68) "discontinuities" on transition to steady state. Fundamental perturbations may become essentially co-extensive with briefer transitions of B than of G. Moreover, because primary cochlear neurons have asymmetric frequency-threshold sensitivities with more abrupt higher frequency "leading" edges and broader lower frequency "tails," discharge patterns for frequency-falling waves may show more abrupt onset than offset; thus, information can be "finer grained." The auditory system of some bats seems to exploit similar anatomic and neural constraints, at least in echolocation (55).

Phillips and Irvine (49) have studied the relative effects of contralateral (contra) and ipsilateral (ipsi) monaural inputs to single cells in AI of cats. They found "for each cell, the contra ear provides an excitatory input. . . . In contrast to the constant excitatory nature of the contra input to these cells, the ipsi input varied considerably, being quantitatively always smaller than contra or entirely lacking." These monaural

input patterns were stable over intensity. In cases 3 and 4 it seems possible that inputs to the remaining auditory cortex from the ipsilateral ear are sufficiently degraded that the auditory cortex cannot resolve appropriately the finer grained movements of the basilar membrane.

Hemispherectomy does not leave the remaining hemisphere unaltered (12). Using degeneration techniques, Pandya, Hallett, and Mukherjee (47) have studied interhemispheric connections of the primary auditory area (TC in their terminology) and auditory association areas (TA and TB). TC connects solely and only incompletely with TC of the other hemisphere via callosal fibers. TA can be divided into rostral and caudal portions which connect to homotypical areas; the rostral portion projects via the anterior commissure, while the caudal portion projects via the corpus callosum. Caudal TA and TB perhaps correspond to Tpt in area 22. Based on findings from these restricted ablations, one could anticipate altered connectivity in the remaining hemisphere of cases 3 and 4. For cases 3 and 4, classifications of GY presented monaurally to the ear opposite the remaining hemisphere were homogeneous ($G^2 = 4.6$, $P = 0.97$); BIN classifications were also homogeneous ($G^2 = 8.5$, $df = 12$). However, their classifications differed strikingly from those of normal subjects [for example, in GY comparing corresponding BIN classifications of case 3 with case 2, $G^2 = 92.8$; and for case 4 compared with case 2, $G^2 = 58.0$ ($df = 12$)]. Thus in cases 3 and 4, the function of the remaining hemisphere has been systematically altered but not in any manner attributable to the disease that involved the ablated hemisphere. Furthermore, in GY each patient classified monaural and binaural presentations homogeneously (for case 3, AD vs. BIN, $G^2 = 5.2$; for case 4, AS vs. BIN, $G^2 = 6.5$, $df = 12$), indicating that inputs to the remaining hemisphere from the ipsilateral ear did not substantially alter performance.

Turning to patients with anterior temporal lobectomy, after operation cases 5 and 6 showed appropriate classifications of SAS; however, seizures involving the auditory cortex altered their classifications. It ap-

pears reasonably certain that anterior temporal lobectomy destroys interhemispheric fibers traveling via the anterior commissure. Studies of case 6 during electrographic and clinical seizures yielded further evidence concerning the role of callosal fibers. Interictally, case 6 classified SAS appropriately and homogeneously across ears and hands. Postictally she indicated altered perceptions in the left auditory cortex (AD presentations) but intact perceptions in the right auditory cortex (AS presentations). For what reason did she not use the left motor cortex (right hand) to allow the right auditory cortex to correct in appropriate classifications made by the left? By studying visually guided hand movements in monkeys, Haaxma and Kuypers (24) have shown that visual information processed in one hemisphere is transferred in the caudal portion of corpus callosum to homologous visual areas of the opposite hemisphere and thence via intrahemispheric connections to motor cortex, and that the hand areas of the motor cortex share no callosal connections. Furthermore, Pandya et al. (47) have shown that auditory association areas of one hemisphere make only sparse connections with frontal and parietal areas of the opposite hemisphere. Thus, the right auditory cortex lacks direct connections to the left motor cortex and has only indirect connections via the callosum and left auditory association areas. On the basis of these observations it appears unlikely that in case 6 an intrahemispheric defect in guided hand movements caused altered indications of classification. Furthermore, we have also shown that random classifications of case 3 could not have resulted from defective hand guidance. Thus, the impairment must arise from altered perception and, because ipsilateral inputs are insufficient for appropriate classification of these sounds, the postictal alterations can only accurately reflect altered function in the left auditory cortex.

Findings in cases 7 and 8 support this account. Case 7 had section of both the anterior commissure and the rostral two-thirds of the corpus callosum. Postoperatively, he indicated classifications appropriately by either hand for AS and AD. Find-

ings in case 8 substantiate that unilateral ablation of premotor and prefrontal cortex need not interfere with appropriate classification of SAS.

The nature of the perceptual defect in these patients is illuminated by convergent lines of evidence. Studies in animals have demonstrated that unilateral ablation of the auditory cortex produces no permanent deficit in response to onset of tones or absolute threshold (29, 45); audiometric studies of our patients are in accord with this. Suga, O'Neill, and Manabe (61) have reported that "biosonar" signals of mustache bat contain up to four harmonics, each consisting of a long CF component followed by a short FM component. They have demonstrated that the auditory cortex of this bat contains separate areas for parallel processing of the CF and FM components and have argued "that biologically significant complex sounds may generally be processed by neurons sensitive to combinations of information-bearing elements. . . ." In an anatomical study of the hemispheric intracortical connections in the monkey, Jones and Powell (28) have concluded that "there is an orderly sequence of projections within each of the three intracortical sensory paths . . .," arguing for an underlying unity in functional organization of sensory systems. In analyzing the effects of lesions in the visual cortex, Weiskrantz (64) has pointed out that "discrete lesions of the visual cortex produce discrete visual defects, but nevertheless information can still be detected even in the very heart of the field defect . . ." and has speculated that "the behavioral capacities of the de-striated monkey are such as to suggest . . . that it may be using information normally involved in noticing and fixating of 'attention provoking' stimuli, and that it is deficient principally in the detailed examining of those stimuli once noticed." These findings may provide a context for understanding the inability of case 4 to discriminate appropriately set BDG even in monaural presentations to the ear opposite the remaining hemisphere: hemispherectomy has altered connectivity in the remaining hemisphere perhaps to the extent that the auditory cortex can no longer assemble appropri-

ately certain "combinations of information-bearing elements." Our investigation has shown that studies using SAS can not only contribute to understanding the perception of speech sounds, but can also provide a deeper understanding of cortical processing of biologically significant sounds. Our findings are consistent with the hypothesis that the "recognition of speech sounds is based on auditory-perceptual mechanisms common at least to mammals" (43). To study the function of auditory cortex, Scheich (53) has proposed (53) a threefold program in stimulus-design using: 1) a continuum of natural call variations, 2) "technical dissection" of natural calls, and 3) synthesis of complex acoustic com-

ponents into stimuli. Our findings in human beings justify using such a program in animal surrogates.

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