Pitch perception of complex tones and human temporal-lobe function[a]

Robert J. Zatorre

Montreal Neurological Institute and Hospital, McGill University, 3801 University Street, Montreal, Quebec H3A 2B4, Canada

Sixty-four patients with unilateral temporal-lobe excisions as well as 18 normal control subjects were tested in a missing fundamental pitch perception task. Subjects were required to indicate if the pitch of a pair of tones rose or fell. The excisions encroached upon Heschl's gyri in some cases, whereas, in others, this region was spared. All subjects included for study were able to perform well on a control task in which complex tones including a fundamental were presented. Stimuli for the experimental task, which was procedurally identical with the control task, consisted of several harmonic components spanning the same spectral range, but without a fundamental. Only subjects with right temporal lobectomy in whom Heschl's gyri were excised committed significantly more errors than the normal control group on this task. Patients with left temporal-lobe lesions or with anterior right temporal-lobe excisions were unimpaired. These results suggest that Heschl's gyri and surrounding cortex in the right cerebral hemisphere play a crucial role in extracting the pitch corresponding to the fundamental from a complex tone.

PACS numbers: 43.66.Hg, 43.63.Fv

INTRODUCTION

The perceived pitch of a periodic complex tone need not correspond to a harmonic partial physically present in the signal. Listeners typically perceive the pitch corresponding to the fundamental period of vibration, even when no energy is present at the fundamental. This phenomenon has been referred to as periodicity pitch, or the problem of the missing fundamental (Licklider, 1951; Schouten, 1938; cf. Green, 1976, for a review). Despite considerable research into the psychoacoustics of this phenomenon, very little has been established regarding the neural substrate that may be involved.

There is evidence, however, that central auditory mechanisms, particularly the auditory cortex, may play an important role in perception of missing fundamental pitch. Psychophysical results suggest a central locus for this phenomenon (Houtsma and Goldstein, 1972) because subjects are able to perceive the missing fundamental pitch even when two different harmonics are presented dichotically. This finding rules out the possibility that the fundamental may be reintroduced by peripheral mechanisms, involving interactions between harmonics at the cochlear level. There is also electrophysiological evidence (DeRibaupierre *et al.*, 1972) that some neurons in the primary auditory cortex of cats respond in a way that would allow coding of periodicity pitch. Finally, there have been some behavioral studies with animals (Symmes, 1966; Whitfield, 1980) in which it was found that bilateral lesions of the primary auditory cortex and surrounding regions impair the ability to respond to the fundamental pitch.

No studies have been carried out, to my knowledge, to assess the effects of unilateral focal cerebral lesions on perception of the pitch of the missing fundamental in humans. The present study was, therefore, carried out in order to examine pitch perception in patients with unilateral excisions in the temporal lobe, contrasting the perception of complex tones containing fundamental energy with those that do not. The patients included in this report are well suited to such study because the extent of the cortical removal (including or sparing Heschl's gyri) was known with considerable precision, and lesions of the left and of the right temporal lobe were comparable. This should, therefore, permit the possible contribution of the primary auditory cortex to perception of missing fundamental pitch to be examined in a detailed fashion.

I. METHOD

A. Stimuli

Two sets of stimuli were prepared. For the control task, complex tones were synthesized containing a prominent fundamental component plus eight harmonics. For the missing fundamental task, the complex tones consisted of consecutive harmonics of a given fundamental frequency, but contained no energy at the fundamental. Stimuli were created by digital synthesis using the MITSYN system (Henke, 1976) running on a PDP-11/34 computer. They were output through a 12-bit D/A converter at a 20-kHz sampling rate and recorded on audio tape after low-pass filtering at 7.8 kHz via a Rockland model 852 filter with a 48-dB/oct rolloff. Overall intensity of each complex tone was equated to within 3 dB before recording. Playback was binaural over

matched TDH-39 earphones at low intensity (<55-dB A-weighted sound-pressure level) in order to minimize the effects of distortion products. The desired spectral energy distribution was confirmed by Fourier analysis of the tape output.

For the missing fundamental task, pairs of stimuli were prepared such that the mean and range of spectral energy was identical within a pair, but the periodicity, or fundamental frequency, differed (Fig. 1). When perceived correctly, the effect in any given pair is to hear a change in pitch between the two tones. For both control and missing fundamental tasks, the stimuli in each pair were 500 ms long, with rise and fall times of 5 ms, and with no intertone interval. The intertrial interval in all cases was 3 s.

Although the two stimuli within a pair necessarily differed slightly in timbre, insofar as they differed in their harmonic composition, such a difference would be insufficient to perform the task correctly because the subject was required to indicate the direction of pitch change. This can only be accomplished if the pitch corresponding to the fundamental frequency is perceived, particularly since no examples or feedback were given during the missing fundamental task.

For both control and missing fundamental tasks, three frequency levels were created at a fundamental frequency corresponding to 200 vs 300 Hz, 400 vs 600 Hz, and 600 vs 900 Hz (see Fig. 1). In the missing fundamental task, tones at each of these frequency levels were presented in each of two spectral conditions, for a total of six different sets of trials. In the low-spectrum condition, one tone of the pair (the one with the lower fundamental frequency) contained the second through the fourth harmonics, and the other (the one with the higher fundamental frequency) contained the third through the sixth harmonics. Similarly, in the high-spectrum condition, one tone in the pair contained the fourth to the sixth harmonics, and the other contained the sixth through the ninth harmonics. In the control task, 18 pairs per frequency condition were presented, and, in the missing fundamental task, 24 pairs in each of the six conditions were presented. In all cases, the fundamental frequency rose in half the trials and fell in the other half.

B. Subjects

Sixty-four patients who had undergone unilateral temporal-lobe excisions at the Montreal Neurological Hospital for the relief of medically intractable epilepsy were tested, along with 18 normal control (NC) subjects. Subjects were matched approximately for age, intelligence quotients, and education (Table I), and gave their consent for testing. Most patients suffered from seizures dating from birth or early life. Epileptogenic lesions were static and atrophic in all cases except for four cases of low-grade astrocytoma, two cases of ganglioglioma, and four cases of angioma. Patients with neurological evidence of bilateral or diffuse lesions, or with high-
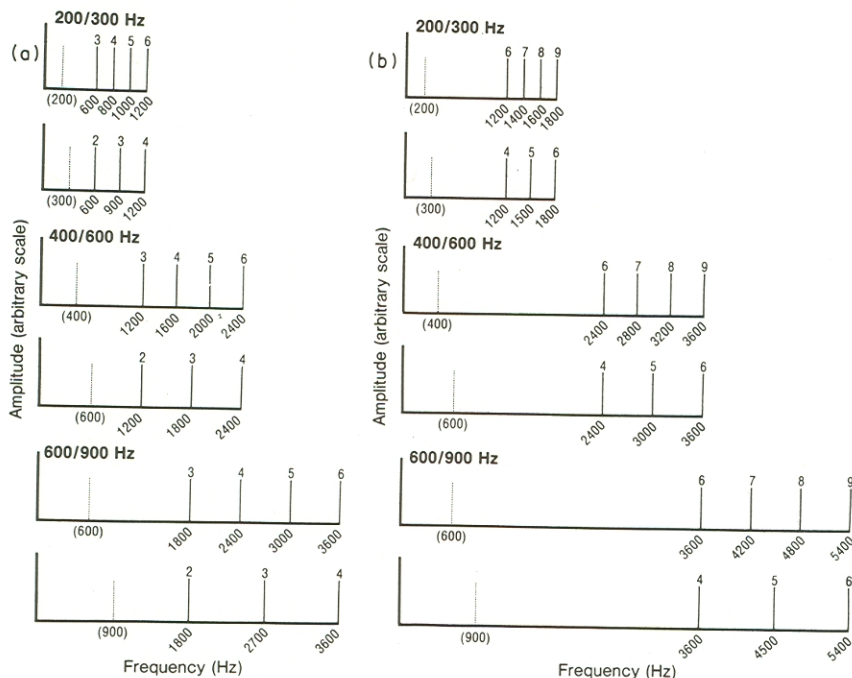

FIG. 1. Idealized stimulus spectra for stimuli used in missing fundamental task. Solid lines indicate components present in the stimulus, with corresponding harmonic numbers above each. Dotted lines indicate fundamental (not present in the stimulus) corresponding to each set of harmonics: (a) low-spectrum condition, (b) high-spectrum condition.

TABLE I. Characteristics of groups of subjects studied: number, sex distribution, mean age, mean number of years of education, mean Wechsler full-scale IQ scores, and mean extent of excision as measured from the temporal pole to the resection margin along the first temporal gyrus, and along the third temporal gyrus. Abbreviations: NC, normal control; LT, left temporal lobectomy; RT, right temporal lobectomy; A, partial or complete excision of primary auditory cortex (Heschl's gyri); a, sparing of primary auditory cortex.

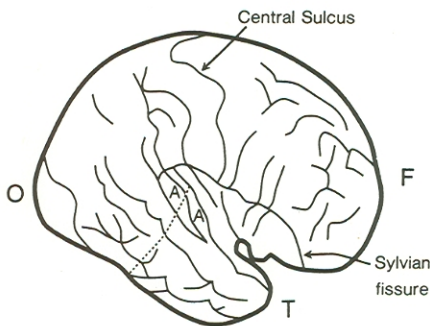| Group	N	Sex	Age (yr)	Educ. (yr)	IQ	Extent of excision (mm) 1st T.G.	3rd T.G.
NC	18	11M, 7F	25.1	13.6	...	...	...
LTa	15	9M, 6F	27.1	13.0	109.3	46	53
LTA	16	10M, 6F	25.4	13.0	104.9	53	55
RTa	15	6M, 9F	30.4	12.9	113.1	52	58
RTA	18	7M, 11F	30.9	11.9	102.5	59	66

FIG. 2. Schematic diagram showing lateral view of the right cerebral hemisphere with the Sylvian fissure opened to expose the upper bank of the temporal lobe. The dotted line indicates the posterior extent of excision in the right temporal lobe in a representative case in which the removal encroached onto Heschl's gyri (auditory cortex, marked by the letter A). Subjects in whom this region was spared would have a slightly more anterior resection margin. Other abbreviations: F, frontal pole; O, occipital pole; T, temporal pole.

grade neoplasms were not included in the study. Also excluded were patients whose postoperative electroencephalographic studies indicated significant epileptogenic activity contralateral to the excision, or beyond the resected region. Subjects were either presumed to have speech functions represented in the left cerebral hemisphere based on handedness and neuropsychological test data, or this was established directly by intracarotid sodium Amytal testing (Wada and Rasmussen, 1960; Branch et al., 1964). No subject had extensive musical training.

The patient groups were subdivided according to the side and extent of excision, as determined by the neurosurgeon at the time of surgery. In some cases, the excision included all or part of Heschl's gyri, whereas, in other cases, the removal was confined to the anterior part of the temporal lobe, sparing Heschl's gyri. Thirty-one patients underwent left-temporal lobectomy, of whom 15 had sparing of Heschl's gyri (LTa group), and 16 had a partial or complete resection in this region (LTA group). Of the 33 subjects who underwent right-temporal lobectomy, 15 had sparing of Heschl's gyri (RTa group), whereas 18 had an excision in this area (RTA group). Extent of cortical excision as estimated by the neurosurgeon varied across groups, as shown in Table I. Measurements are given from the temporal pole posteriorly along the first (superior) and third (inferior) temporal gyri. Medially, the resections always included the uncus and amygdala, but varying amounts of the hippocampus and parahippocampal gyrus were excised, and this was independent of the excision of Heschl's gyri. Figure 2 shows the approximate extent of removal in the right temporal lobe for a subject with an excision encroaching upon Heschl's gyri.

Forty-seven patients were tested approximately 2 weeks following surgery; the rest were seen in follow-up examination 1 or more years after surgery. Unilateral temporal lobectomy is not associated with permanent hearing loss in either ear (Jerger, 1960; Shankweiler, 1966). However, to avoid any confounding effects, data were excluded for any subject with pure-tone audiometric thresholds 15 dB or more below normal in the frequency range between 250 and 8000 Hz.

C. Procedure

On each trial, subjects heard a pair of tones and were required to make a judgment as to whether the pitch rose or fell. They indicated their choice by pointing to an answer sheet containing the words up and down, and arrows pointing in the appropriate directions. The control task was explained to the subject with examples, and with several practice trials if necessary. Any subject who committed more than 25% errors on any condition of the control task after practice was excluded from further study. All subjects were given the control task first, followed by the six conditions of the missing fundamental task. The order of presentation was fixed for all subjects, alternating between high- and low-spectrum conditions, with the 200/300-Hz frequency level first, 400/600-Hz frequency level second, and 600/900-Hz frequency level third. Having established an adequate level of performance on the control task, the purpose of this study was to determine if pitch perception would be impaired when the fundamental was missing. Therefore, neither practice nor feedback was given on the missing fundamental condition.

II. RESULTS

Preliminary analyses were performed to ensure that the patient groups were well matched on demographic variables. Analysis of variance indicated that none of the subject groups differed significantly in age [$F(4,74) = 1.98$, $p > 0.10$], in number of years of education [$F(4,72) = 1.25$, $p > 0.25$], nor in full-scale IQ scores [$F(3,60) = 2.50$, $p > 0.05$].

As shown in Fig. 3, all subjects retained for study were able to perform well on the control task. There were no significant differences between the normal control group and the patient groups on this task. The results of the missing

568   J. Acoust. Soc. Am., Vol. 84, No. 2, August 1988

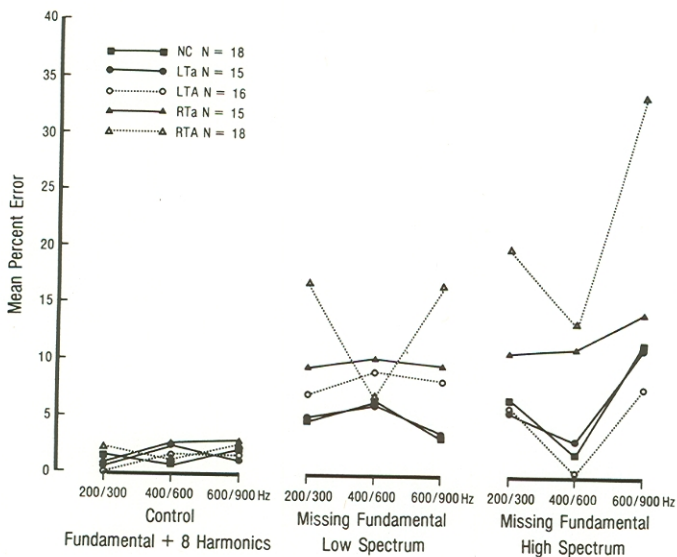Robert J. Zatorre: Pitch and temporal-lobe function   568

FIG. 3. Mean percent error rates (chance = 50%) in control and missing fundamental tasks for groups of subjects studied. Abbreviations as in Table I.

fundamental task are also shown in Fig. 3. The overall error rate was higher for the high-spectrum than for the low-spectrum condition across all groups of subjects (Wilcoxon signed-ranks test, $W = 946$, $p = 0.01$).

The distribution of error scores in the missing fundamental tasks was skewed, with the modal response tending toward zero errors for most subjects. Thus most subjects, with the notable exception of those in group RTA, performed nearly perfectly in most conditions. Given this generally high level of performance, and because of the relatively small number of trials per condition, the mean error rates were calculated for each subject across the three frequencies in each spectral condition in order to evaluate any group differences. These values were subsequently ranked, separately for the low- and high-spectrum conditions, and then submitted to Kruskal–Wallis analyses. For the low-spectrum condition, this analysis yielded a significant result ($H = 10.05$, $df = 4$, $p < 0.05$). Subsequent comparison by way of Mann–Whitney tests indicated that only group RTA was significantly impaired with respect to the NC group ($T = 395$, $p < 0.03$); the other groups did not differ significantly from normal. In the high-spectrum condition, there was also a significant difference in the ranks of the error scores ($H = 17.62$, $df = 4$, $p < 0.01$), and Mann–Whitney tests indicated once again that only group RTA showed a significant deficit as compared to group NC ($T = 412$, $p < 0.01$). The data suggest possibly better performance by several groups in the 400/600-Hz conditions, but this was not borne out statistically.

The Kruskal–Wallis and Mann–Whitney statistics were applied due to the highly skewed nature of the obtained distributions. Another approach to analyzing these data is to count the number of subjects falling above or below the mean error rate of the NC group. In the low-spectrum condition, 12 of the 18 RTA subjects scored worse than the 4.9% NC

error rate; this was the only group to show a significant difference from normal according to the Fisher exact test ($p = 0.02$). Similarly, in the high-spectrum condition, only the RTA group differed from normal, and once more 12 of these patients scored below the 6.7% NC error rate ($p = 0.02$). This subsidiary analysis, therefore, confirms the results obtained with the ranked scores.

III. DISCUSSION

Heschl's gyri have been identified as the primary auditory cortex in the human brain on the basis of their connections to the medial geniculate nucleus and the evoked responses recorded to auditory stimulation (Flechsig, 1896; Penfield and Perot, 1963; Celesia, 1976). Cytoarchitectonic criteria have also been used to delineate this region further (Galaburda and Sanides, 1980). Anatomical and electrophysiological evidence in primates and other animals suggests that the primary cortex is surrounded by numerous interconnected cortical fields which contain cells responsive to auditory stimulation, and that many of these fields are tonotopically organized (Brugge and Reale, 1985; Pandya and Yeterian, 1985; Woolsey, 1982). The temporal-lobe excisions of the patients studied in this report would probably destroy several of these fields, but the deficit appears only after a lesion invading Heschl's gyri on the right side. This result suggests that the right primary auditory cortex plays a crucial role in extracting the pitch corresponding to the fundamental frequency from a complex stimulus, a finding that is in clear agreement with animal studies (Symmes, 1966; Whitfield, 1980). However, because temporal lobectomy damages more than one auditory field, it must be concluded that the combined damage to the right primary auditory cortex along with surrounding regions is sufficient to produce a significant impairment.

The fact that all patient groups were able to perform very well with the control stimuli demonstrates that the cognitive demands of the task, including the concept of rising or falling pitch, had been understood, and that temporal lobectomy does not disrupt processing of complete complex tones. This result is also in agreement with numerous studies indicating that simple frequency discrimination (i.e., with pure tones, or with complex tones when the fundamental is present) is not permanently disrupted even by large bilateral ablations of auditory cortex in animals (Butler *et al.*, 1957; Kelly and Whitfield, 1971; Meyer and Woolsey, 1957; Thomson, 1960; Whitfield, 1980), nor by unilateral temporal-lobe lesions in humans (Milner, 1962; Berlin *et al.*, 1965). Whitfield's (1980) results are particularly interesting in this respect: He found that cats with bilateral auditory cortex ablations were unable to respond to the (missing) fundamental pitch of an anharmonic series, but they were able to relearn discrimination of individual pairs of stimuli. Transfer of learning from one complex to another was abolished, however, suggesting that the animals were responding on the basis of the individual frequency components, and not the fundamental pitch. The findings in the present study are similar insofar as discrimination of complete complex tones was unaffected, and this task could be accomplished on the basis of any or all of the individual frequency components in the stimuli. The deficit only arises when the task cannot be performed on this basis (i.e., when the individual components give no clue to the change in pitch). Under these circumstances, the fundamental pitch must somehow be extracted in order to respond correctly.

As expected on the basis of the psychoacoustic literature (Ritsma, 1967), stimuli in the high-spectrum condition elicited more errors overall than stimuli in the low-spectrum condition. There was no statistical evidence, however, for a more severe or a more consistent deficit in the RTA group in the high-spectrum condition as opposed to the low-spectrum condition. There was also no evidence for an effect of distortion products. The fact that group RTA performed poorly on most conditions contradicts the explanation that distortion products played any significant role.

Despite the significant deficit obtained, many of the subjects in group RTA did not approach random performance on most conditions. In fact, approximately one-third of these subjects performed at levels comparable to normal on at least one condition of the missing fundamental task. This finding is important in understanding the nature of the deficit. One possible explanation for this degree of spared function is that the lesions in group RTA did not destroy posterior temporal and parietal opercular areas known or thought to subserve important auditory function (Brugge and Reale, 1985; Galaburda and Sanides, 1980; Pandya and Yeterian, 1985). Another possible explanation which cannot be excluded at this time is that the auditory cortex in the left temporal lobe may, under some circumstances, be able to assume the function normally carried out by the right side. Future research will have to decide among these alternatives.

A number of psychoacoustic theories have been proposed to account for missing fundamental pitch perception (Goldstein, 1973; Terhardt, 1974; Wightman, 1973). These theories differ in detail, but they all propose some type of pattern-matching mechanism that assigns the fundamental pitch to a complex tone on the basis of partial information (i.e., in the absence of a fundamental component), according to certain algorithms. Neural models to account for this pattern-recognition process (Roederer, 1975; Whitfield, 1970; Wilson, 1974) generally propose that periodic signals initially undergo Fourier transformation at the peripheral level, resulting in a spectral analysis. The tonotopic organization of harmonic information at peripheral as well as central levels of the auditory system (Brugge and Reale, 1985; Woolsey, 1982) may represent such an analysis. The neural response pattern of the central "pitch processor" to a given stimulus would then allow the fundamental pitch to be computed. This approach is also fruitful in explaining pitch constancy, the ability to judge pitches as equivalent despite widely differing spectral information (e.g., two musical instruments playing the same note). The present results are compatible with the idea that the function of the central pitch processor is cortically mediated. According to this account, damage to Heschl's gyri and adjacent cortex in the right temporal lobe disrupts the pattern-matching process that must take place for successful pitch extraction to occur. However, when the fundamental is present, the task can be accomplished, presumably due to information processing at lower levels. It would be predicted, therefore, that lesions that disrupt missing fundamental pitch perception would also result in deficits in pitch matching of stimuli that differ in their spectral composition.

The deficit reported in the present study is also consistent with a number of findings that implicate structures in the human right cerebral hemisphere (especially the right temporal cortex), in the discrimination of timbre (Milner, 1962), or in matching the pitch of complex tones (Robin *et al.*, 1987; Sidtis, 1984; Sidtis and Volpe, 1981), tasks that probably depend in some way on the ability to analyze the spectral pattern. In the case of dichotic pitch-matching tasks (Sidtis, 1984; Sidtis and Volpe, 1981), it is interesting that deficits have been reported following large lesions of the right hemisphere, even with complex tones that include the fundamental. Furthermore, patients with section of the corpus callosum show strong left-ear preferences in such tasks (Sidtis and Gazzaniga, 1981), contrasting with the right-ear superiority elicited by verbal stimuli. Although these authors report deficits even when the fundamental is present, the findings are not necessarily contradictory to those obtained in the present experiment because the pitch of a complex tone may be primarily determined by the harmonics under certain circumstances, even if the fundamental is present (Plomp, 1967). Thus, in a pitch-matching task, especially one in which two complexes are heard simultaneously, analysis of the spectral pattern is probably important in arriving at the correct answer.

It is also of interest that unilateral lesions in the right hemisphere consistently produce these types of deficits in humans, whereas bilateral lesions in animals appear to be needed for similar impairments to emerge (although studies with unilateral lesions in animals are rare). This finding par-

allels many others in neuropsychology, underlining the important functional asymmetry between the two human cerebral hemispheres.

The findings in the present study are also relevant to deficits that have been described in both production and perception of speech prosody following right-hemisphere lesions (e.g., Shapiro and Danly, 1985; Weintraub *et al.*, 1981). This impairment is thought to relate, at least in part, to impaired processing of the fundamental frequency of the speech stream, and may be further evidence of the importance of right-hemisphere structures to pitch processing. However, the contribution of structures outside the auditory cortex to prosodic function is also likely to be important, so it is not necessarily the case that restricted temporal-lobe lesions would lead to impaired processing of prosodic aspects of language.

It is not yet clear how the type of deficit uncovered in this study may contribute to the widespread impairments in musical perception and production often observed following right temporal-lobe lesions as well as more extensive right-hemisphere damage (Benton, 1977; Marin, 1982; Zatorre, 1984). It should be pointed out that many of the musical processing deficits that have been reported following right-hemisphere lesions are probably not directly related to fundamental frequency extraction, but rather involve other pattern-matching processes, insofar as they appear even with sequences composed of sinusoidal waveforms (Zatorre, 1985). Nevertheless, it would appear that the loss of the ability to extract the fundamental pitch from a complex sound would constitute a serious obstacle for many musically relevant tasks.

ACKNOWLEDGMENTS

Benton, A. L. (**1977**). "The amusias," in *Music and the Brain*, edited by M. Critchley and R. A. Henson (Thomas, Springfield, IL), pp. 378–397.

Berlin, C. I., Chase, R. A., Dill, A., and Hagepanos, T. (**1965**). "Auditory findings in patients with temporal lobectomies," Am. Speech Hear. Assoc. **7**, 386.

Branch, C., Milner, B., and Rasmussen, T. (**1964**). "Intracarotid sodium Amytal for the lateralization of cerebral speech dominance," J. Neurosurg. **21**, 399–405.

Brugge, J. F., and Reale, R. A. (**1985**). "Auditory cortex," in *Cerebral Cortex*, edited by A. Peters and E. G. Jones (Plenum, New York), Vol. 4, pp. 229–271.

Butler, R. A., Diamond, I. T., and Neff, W. D. (**1957**). "Role of auditory cortex in discrimination of changes of frequency," J. Neurophysiol. **20**, 108–120.

Celesia, G. (**1976**). "Organization of auditory cortical areas in man," Brain **99**, 403–414.

De Ribaupierre, F., Goldstein, M. H., and Yeni-Komshian, G. (**1972**). "Cortical coding of repetitive acoustic pulses," Brain Res. **48**, 205–225.

Flechsig, P. E. (**1896**). *Gehirn und Seele* (Veit, Leipzig).

Galaburda, A., and Sanides, F. (**1980**). "Cytoarchitectonic organization of the human auditory cortex," J. Comp. Neurol. **190**, 597–610.

Goldstein, J. L. (**1973**). "An optimum processor theory for the central formation of the pitch of complex tones," J. Acoust. Soc. Am. **54**, 1496–1516.

Green, D. M. (**1976**). *An Introduction to Hearing* (Erlbaum, Hillsdale, NJ).

Henke, W. L. (**1976**). *An Interactive Dialogue Language for Time Signal Processing* (MIT Research Laboratory of Electronics, Cambridge, MA).

Houtsma, A. J. M., and Goldstein, J. L. (**1972**). "The central origin of the pitch of complex tones: Evidence from musical interval recognition," J. Acoust. Soc. Am. **51**, 520–529.

Jerger, J. F. (**1960**). "Observations on auditory behavior in lesions of the central auditory pathways," Arch. Otolaryngol. **71**, 797–806.

Kelly, J. B., and Whitfield, I. C. (**1971**). "Effect of auditory cortical lesions on discriminations of rising and falling frequency-modulated tones," J. Neurophysiol. **34**, 802–816.

Licklider, J. C. R. (**1951**). "A duplex theory of pitch perception," Experientia **7**, 128–134.

Marin, O. S. M. (**1982**). "Neurological aspects of music perception and performance," in *The Psychology of Music*, edited by D. Deutsch (Academic, New York), pp. 453–477.

Meyer, D. R., and Woolsey, C. N. (**1957**). "Effects of localized cortical destruction on auditory discriminative conditioning in the cat," J. Neurophysiol. **15**, 149–162.

Milner, B. (**1962**). "Laterality effects in audition," in *Interhemispheric Relations and Cerebral Dominance*, edited by V. B. Mountcastle (Johns Hopkins, Baltimore), pp. 177–195.

Pandya, D. N., and Yeterian, E. H. (**1985**). "Architecture and connections of cortical association areas," in *Cerebral Cortex*, edited by A. Peters and E. G. Jones (Plenum, New York), Vol. 4, pp. 3–61.

Penfield, W., and Perot, P. (**1963**). "The brain's record of auditory and visual experience: A final summary and discussion," Brain **86**, 595–696.

Plomp, R. (**1967**). "Pitch of complex tones," J. Acoust. Soc. Am. **41**, 1526–1533.

Ritsma, R. J. (**1967**). "Frequencies dominant in the perception of the pitch of complex sounds," J. Acoust. Soc. Am. **42**, 191–198.

Robin, D. A., Eslinger, P., Tyler, R., and Damasio, H. (**1987**). "Impaired pitch perception following focal right hemisphere damage," Neurol. **37** (Suppl. 1), 128.

Roederer, J. G. (**1975**). *Introduction to the Physics and Psychophysics of Music* (Springer, New York).

Schouten, J. F. (**1938**). "The perception of subjective tones," Konnkliijke Nederlandse Akademie van Wetenschappen Proc. **41**, 1086–1093.

Shankweiler, D. (**1966**). "Effects of temporal-lobe damage on the perception of dichotically presented melodies," J. Comp. Physiol. Psychol. **62**, 115–119.

Shapiro, B. E., and Danly, M. (**1985**). "The role of the right hemisphere in the control of speech prosody in propositional and affective contexts," Brain Lang. **25**, 19–36.

Sidtis, J. J. (**1984**). "Music, pitch perception and the mechanisms of cortical hearing," in *Handbook of Cognitive Neuroscience*, edited by M. S. Gazzaniga (Plenum, New York), pp. 91–114.

Sidtis, J. J., and Gazzaniga, M. S. (**1981**). "Complex pitch perception after callosal section: Further evidence for a right-hemisphere mechanism," J. Acoust. Soc. Am. Suppl 1 **69**, S119.

Sidtis, J. J., and Volpe, V. T. (**1981**). "Right hemisphere lateralization of complex pitch perception: A possible basis for amusia," Neurol. **31**, 101.

Symmes, D. (**1966**). "Discrimination of intermittent noise by macaques following lesions of the temporal lobe," Exper. Neurol. **16**, 201–214.

Terhardt, E. (**1974**). "Pitch, consonance, and harmony," J. Acoust. Soc. Am. **55**, 1061–1069.

Thompson, R. F. (**1960**). "Function of the auditory cortex of cat in fre-

quency discrimination," J. Neurophysiol. **23**, 321–34.

Wada, J., and Rasmussen, T. (**1960**). "Intracarotid injection of sodium Amytal for the lateralization of speech dominance: Experimental and clinical observations," J. Neurosurg. **17**, 266–282.

Weintraub, S., Mesulam, M.-M., and Kramer, L. (**1981**). "Disturbances in prosody. A right-hemisphere contribution to language," Arch. Neurol. **38**, 742–744.

Whitfield, I. C. (**1970**). "Neural integration and pitch perception," in *Excitatory Synaptic Mechanisms*, edited by P. Anderson and J. K. Jensen (Univ. forlaget, Oslo), pp. 277–285.

Whitfield, I. C. (**1980**). "Auditory cortex and the pitch of complex tones," J. Acoust. Soc. Am. **67**, 644–647.

Wightman, F. L. (**1973**). "The pattern transformation model of pitch," J. Acoust. Soc. Am. **54**, 407–416.

Wilson, J. P. (**1974**). "Psychoacoustical and neurophysiological aspects of auditory pattern recognition," in *The Neurosciences Third Study Program*, edited by F. O. Schmitt and F. G. Worden (MIT, Cambridge, MA), pp. 147–153.

Woolsey, C. N. (**1982**). *Cortical Sensory Organization* (Humana, Clifton, NJ), Vol. 3.

Zatorre, R. J. (**1984**). "Musical perception and cerebral function: A critical review," Music Percept. **2**, 196–221.

Zatorre, R. J. (**1985**). "Discrimination and recognition of tonal melodies after unilateral cerebral excisions," Neuropsychologia **23**, 31–41.