1993

Effect of unilateral temporal-lobe excision on perception and imagery of songs

R.J. Zatorre

Andrea Halpern
Bucknell University, ahalpern@bucknell.edu

Neuropsychologia, Vol. 31, No. 3, pp. 221–232, 1993.
Printed in Great Britain.

0028-3932/93 $6.00 + 0.00

EFFECT OF UNILATERAL TEMPORAL-LOBE EXCISION ON PERCEPTION AND IMAGERY OF SONGS

ROBERT J. ZATORRE* and ANDREA R. HALPERN†

*Montreal Neurological Institute, McGill University, Montreal, Quebec, Canada and †Department of Psychology, Bucknell University, Lewisburg, PA, U.S.A.

(*Received* 16 *June* 1992; *accepted* 22 *September* 1992)

Abstract—Auditory imagery for songs was studied in two groups of patients with left or right temporal-lobe excision for control of epilepsy, and a group of matched normal control subjects. Two tasks were used. In the perceptual task, subjects saw the text of a familiar song and simultaneously heard it sung. On each trial they judged if the second of two capitalized lyrics was higher or lower in pitch than the first. The imagery task was identical in all respects except that no song was presented, so that subjects had to generate an auditory image of the song. The results indicated that all subjects found the imagery task more difficult than the perceptual task, but patients with right temporal-lobe damage performed significantly worse on both tasks than either patients with left temporal-lobe lesions or normal control subjects. These results support the idea that imagery arises from activation of a neural substrate shared with perceptual mechanisms, and provides evidence for a right temporal-lobe specialization for this type of auditory imaginal processing.

INTRODUCTION

INVESTIGATIONS into mental imagery have suggested that functional similarities exist between perception and imagery [5, 8, 15], and that a common neural substrate may underlie both imaginal and perceptual processes. One may hypothesize that, to the extent that the two types of processes make demands on the same neural mechanism, they should suffer a common fate after damage has occurred. For example, it has been found that lesions that cause visual neglect also result in failure to access one side of imagined visual scenes [2]. Also, complementary data from event-related potential studies implicate posterior cortical areas in both visual imagery and visual perception (for a review see FARAH [5, 6]).

The issue of how imagery and perceptual processing interact in the brain is of considerable importance in understanding how externally and internally driven neural processes operate. However, the relevant research to date has concentrated nearly exclusively on visual imagery; converging evidence from non-visual tasks has not been available, thereby limiting the generality of the conclusions that can be drawn. The purpose of the present investigation was to examine auditory perception and imagery, and their potentially common neural substrate.

Contemporary imagery research has sought to identify empirically reliable behavioral indices that are consistent with the existence of mental imagery. The goal has generally been to identify regularities in subjects' performance that can be parsimoniously explained by inferring an internal imaginal representation that shares certain properties with the real event. In the visual domain, for example, KOSSLYN *et al.* [16] reported that it takes longer to scan two points in an image that are far from one another than it does to scan near points. Such evidence has been taken as implying an internal representation that contains information about the continuity of space and/or processes that use that continuity in an analogous way to perceptual scanning. Similar conclusions can be drawn from other types of tasks, such as those thought to require mental rotation of a visually presented stimulus, (see Ref. [4]). These data also fit with the subjective impressions of visual imagery, which are typically described as having visual-like characteristics.

Auditory imagery—the experience of "hearing" music or speech in the absence of a proximal stimulus—is at least as compelling subjectively as visual imagery. Auditory imagery has been studied in several ways by cognitive psychologists. For instance, FARAH and SMITH [7] had subjects imagine a high or low tone during an auditory signal detection task. Intensity thresholds were lower if prior to signal presentation, subjects imagined the same tone as that used in the trial, compared to imaging a different tone. This facilitation was interpreted as evidence that frequency information is represented in images. As another example, HUBBARD and STOECKIG's [14] subjects formed an image of a chord and then heard a played chord (target) for a same/different comparison. The target was either identical, different but musically related, or different and musically unrelated to the imagined chord. Accuracy and reaction times were best for the identical, then unrelated, then related targets. Because this pattern is also observed when the first chord is actually played, Hubbard and Stoeckig concluded that musical percepts and musical images share processing mechanisms.

The study of musical imagery seems particularly promising because of the complexity of musical representations, and the importance of music within most human cultures. In addition, musical imagery appears to be nearly ubiquitous, even among people without formal musical training. HALPERN [11–13] has established in normal subjects that the phenomenon of musical imagery can be measured in an objective and experimentally rigorous fashion. Her interest was in demonstrating that internal representations of songs preserve some of the features of real songs, the most important being the temporal extent and ordering of the notes of the song. In the study of greatest relevance here, HALPERN [11] tested musically unselected subjects in a task in which they mentally compared pitches corresponding to two words in a familiar song. Results showed a systematic increase in reaction times as a function of the temporal distance between words (the stepsize), regardless of instructions to use imagery or not. In addition, reaction times were longer when the first word was drawn from the latter part of the song, than when it was drawn from near the beginning (the startpoint). These results, which are analogous to the visual scanning studies mentioned above, suggest that subjects mentally scan the song in real time, and further suggest that songs have analog representations with temporal-like characteristics.

In the present study, we applied the technique developed to study musical imagery to subjects with discrete, focal damage to one temporal lobe. The neuropsychological and neurophysiological literature indicates that perceptual processing of auditory information is closely linked to the function of the temporal lobes. This conclusion is supported by anatomical [9, 10], electrophysiological [3, 17], and blood flow activation studies [20, 30] indicating that primary and secondary auditory cortices are located within the superior aspect of the temporal lobes. Furthermore, lesions of the temporal cortex result in various types of auditory processing deficits. Specifically, right temporal lobectomy leads to deficits in tonal processing tasks, including discrimination of melodies [18, 22, 26] perception of the pitch of the missing fundamental [27], and short-term retention of pitch information [29]. However, a role for the left temporal lobe is also suggested in some instances, particularly for recognition memory tasks, and for songs in which the tune is mediated via the text of the song [23, 24].

Given the foregoing neuropsychological evidence for the privileged role of the right temporal cortex in many aspects of musical perception, and based on the hypothesis that perceptual and imaginal processing share an underlying neural substrate, we predicted an association between the breakdown of musical imagery and musical perceptual skills following right temporal-lobe damage. If so, one may be more confident that imagery and perception share cognitive operations in neurologically intact people. The alternative hypothesis, i.e. a dissociation between perceptual and imaginal deficits, would imply at least partially separate mechanisms in these two functions. Such an alternative is feasible, in that mental imagery might call upon more complex cognitive functions than those involved in direct perceptual processing. If this hypothesis were correct, one would expect different effects of right temporal-lobe damage on the two tasks.

We tested the prediction by developing analogous perceptual and imagery tasks using familiar songs, modeled on HALPERN's [11] study. The judgment required in both tasks was a simple pitch comparison, the only difference between the tasks being that in one case the song was actually presented, whereas in the other the subject had to generate the tones internally based upon the visually presented text. Groups of patients who had undergone left or right temporal-lobe excision for the relief of intractable epilepsy were tested, together with neurologically intact subjects, and we predicted a parallel deficit in perception and imagery following right but not left temporal resection.

METHOD

Subjects

Twenty-eight patients who had undergone unilateral temporal-lobe excision (14 on each side) for the treatment of epilepsy participated in the study, together with 14 normal control subjects, approximately matched for age, and educational level (see Table 1). Musical training was approximately balanced across groups, with only a few subjects in each group having had formal music lessons. All subjects spoke English, and were familiar with the songs selected (see below).

Table 1. Characteristics of subjects: mean age, education, and neuropsychological test data for patient groups

	Group		
	Normal control	Left temporal	Right temporal
Age (years)	31.0	33.4	31.8
Education (years)	14.5	15.4	13.1
IQ Scores*			
Verbal	—	101.6	98.6
Performance	—	110.1	99.1
Verbal memory†			
Immediate	—	7.8	10.4
Delayed		5.6	8.1
Visuospatial memory‡			
Copy score	—	27.7	27.3
Delayed recall	—	17.5	15.8

*From the Wechsler Adult Intelligence Scale—Revised.

†Average of scores for two verbal passages from the Wechsler Memory Scale in immediate and 90-min delayed recall conditions (Max = 22).

‡Scores for copy and 45-min delayed recall of Rey Osterreith complex figure (Max = 36).

In all patients retained for study the pre-operative cerebral lesion, which usually dated from birth or early life, had been well-lateralized and was of a static and atrophic nature. Patients were excluded from study if they presented atypical speech representation, had known damage outside the region of surgical excision, had a fast-growing tumor, or had a Full-Scale WAIS R IQ under 75. The surgical removals involved the anterior part of the temporal neocortex, and included portions of the amygdala, uncus, parahippocampal gyrus and varying amounts of the hippocampus itself. The excision did not extend into any portion of the transverse gyri of Heschl, except for two cases in the RT group who had a partial removal within this zone. Testing was carried out either 2 weeks following surgery (21 patients: 10 LT and 11 RT) or in follow-up, one or more years after undergoing operation (seven patients: four LT and three RT). An illustration of a right temporal-lobe excision is given in Fig. 1, which shows magnetic resonance images of a representative case.

Neuropsychological test data available for the patients (Table 1) indicate WAIS—R IQ ratings in the average range in both groups, with no significant difference between either Verbal or Performance scales [$F(1, 24) = 2.44$, $P > 0.10$]. Thus, the groups are well-matched with respect to overall intellectual function. However, the patients in the LT group did demonstrate a specific verbal memory deficit, as expected based on the neuropsychological literature. Both immediate and delayed recall of verbal passages from the Weschler Memory Scale were impaired as compared to the performance of subjects in the RT group [$F(1, 23) = 4.42$, $P < 0.05$]. No significant difference between groups was observed, however, in the copy or recall of the Rey–Osterreith Complex Figure [$F(1, 23) < 1$].

Materials

The first phrase of seven songs familiar to English speakers in North America provided the trials (examples include "Jingle Bells", "Puff the Magic Dragon" and "Joy to the World"). The experiment required a pool of trials each consisting of two lyrics ("lyric" here always refers to a monosyllabic word, or the first syllable of a two-syllable word). The first lyric began on beat 1, 3 or 5 of the first phrase of the song (the variable known as "startpoint"). The second lyric occurred 4, 6 or 8 beats away from the first lyric (the variable known as "stepsize"), forming nine main trial types. These requirements constrained the choice of songs to those with a sufficient number of unique words falling unambiguously on the required bests. The two lyrics in each pair always had different pitches.

It proved impossible for each song to provide all nine trial types. Instead, each trial type was represented by four to six trials from different songs, for a total of 45 main trials. In addition, six filler trials from startpoints and stepsizes outside this scheme were included to approximately equalize the number of trials where the second pitch was higher (26) with trials where it was lower (25). The filler trials also helped equalize the average interval distance between the pitches in the higher and lower trials (5.34 and 5.72 semitones, respectively).

To summarize, a total of 51 trials were used for both the perceptual and imagery task. Of these, 45 were distributed among the nine trial types resulting from a combination of the three startpoints and three stepsizes. The filler trials were included in accuracy analyses but excluded from reaction time analyses because startpoint and stepsize were unique to each filler trial.

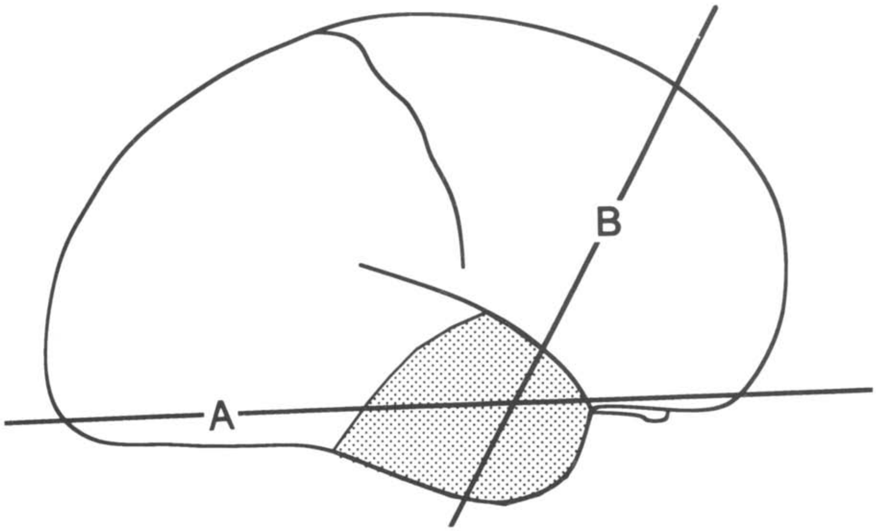
The first phrase of each song was sung in the soprano range by one of the authors (AH), a competent amateur singer. Each tune was recorded and digitized for later presentation on a Compaq 386 personal computer. Trials were blocked by song, and presented in the same pseudorandom order for each subject, but a different order was used for the perceptual and imagery tasks.

Procedure

Subjects were initially screened for familiarity with the seven songs by presenting them with the titles and lyrics of each, and verifying that they were indeed familiar. A second screening procedure was then undertaken to exclude any subject who had difficulty with judgements of pitch. For this purpose a brief test was prepared in which two tones of different pitch were presented on each trial (2 sec duration, 1 sec interstimulus interval), and the subject had to indicate if the second tone was higher or lower than the first. All subjects retained for study scored at least 15 out of 16 trials correct; only one subject had to be excluded for failing the screening test.

The main experiment was conducted in two parts: first the perceptual task, followed by the imagery task. Prior to beginning the perceptual task, two practice trials were given for each of the seven songs. During a trial the subject heard the song over headphones and simultaneously viewed the full text on the computer screen. Two lyrics within the text were capitalized, and the subject was instructed to indicate if the pitch corresponding to the second capitalized lyric was higher or lower than the pitch of the first syllable. For example, in the case of a trial such as "dashing through the SNOW in a one-horse open SLEIGH, o'er the fields we go, laughing all the way" the pitch corresponding to SLEIGH is higher than that of SNOW, and so the correct answer is "higher". Subjects responded by pressing a key on a computer keyboard. Reaction times were collected from the onset of the song, but the song continued playing to the end of the excerpt even if the subject responded before it had finished. Subjects were instructed to listen carefully and to press the key as soon as they had made the pitch judgment. No feedback was given after the practice trials had ended. The songs were presented in a blocked fashion; i.e. all trials for each song were completed before going on to the next one.

For the imagery task, the procedure was identical except that no auditory stimulus was provided. The subjects were instructed to make the pitch judgement according to the text on the screen, but to rely on their own internal



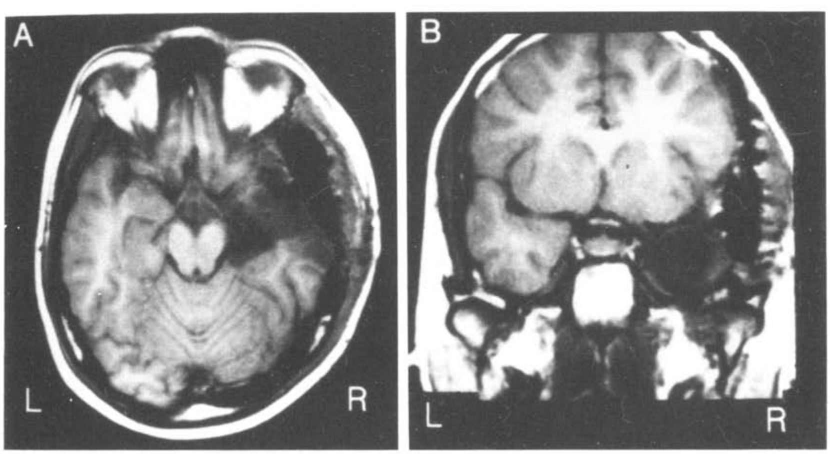


Fig. 1. Diagram illustrating a typical removal in the right temporal lobe (stippled area) based on the neurosurgeon's drawing, together with magnetic resonance images taken through the area of excision in the horizontal (A) and coronal (B) planes. The removal in this case included the amygdala, and most of the hippocampus and parahippocampal gyrus, as well as temporal neocortex. Note the resection in the right superior temporal gyrus, seen in both horizontal and coronal views, as contrasted with the intact left temporal lobe.

auditory image of the song. They were not permitted to sing the song out loud or to hum it, and were encouraged to guess if not sure of the correct answer. The experimental session lasted about 45 min.

RESULTS

The accuracy results are presented in Fig. 2 as overall percent correct for each task for each group of subjects. It is clear from the figure that the imagery task was more difficult than the perceptual task for all subject groups, but that performance following right temporal excision was impaired on both tasks. This conclusion was borne out by a two-way analysis of variance which yielded significant effects of task [$F(1, 39) = 25.22$, $P < 0.0001$], and group [$F(2, 39) = 6.04$, $P < 0.005$], with no significant interaction. The latter main effect was due entirely to the performance of the right temporal group, which performed significantly more poorly than either the left temporal or normal control groups ($P < 0.01$ by a Newman–Keuls test), who in turn did not differ from one another. Two patients within this group had received an excision encroaching onto Heschl's gyrus; however, their performance on both tasks was not particularly distinct from the other subjects in this group, and both of their means fell near the average range for the group as a whole.

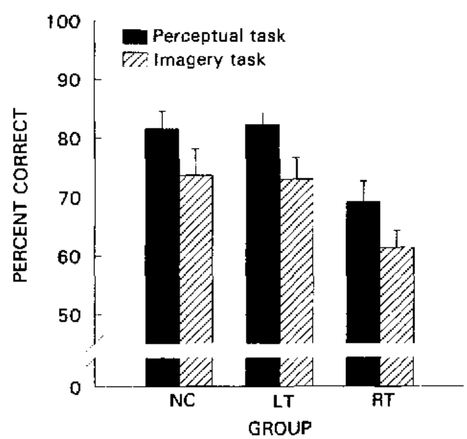


Fig. 2. Mean percent correct for normal control subjects (NC), patients with left temporal-lobe excision (LT), and patients with right temporal-lobe excision (RT) in perceptual and imagery tasks ($N = 14$ in each group). Error bars indicate one standard error of the mean. Fifty percent represents chance performance.

The poor performance of the right temporal group precludes complete analysis of their reaction time data, since many subjects performed near chance levels on the imagery task, and only correct trials yield interpretable reaction time data. However, in order to be able to make some comparison, we examined the reaction time data of those subjects who performed well enough to permit meaningful analysis. We established a criterion of 55% correct as near-chance performance, excluding any subject who did not attain this level on the imagery task, and then analyzed the reaction time results (correct trials only) for the selected subgroups whose performance exceeded this level. This yielded nine subjects in the right temporal group (average % correct 67.5) and 12 in the left temporal group (average % correct 76.6), along with all 14 of the normal control subjects.

The reaction time data were then analyzed separately for the perceptual and imagery task, and also examined separately for stepsize effects and for startpoint effects. (Analysis was also performed on logarithmically transformed reaction time values, but are not reported as the results were essentially identical to those reported here for untransformed values.)

For the perceptual task the mean reaction times for each stepsize and startpoint are shown in Table 2, together with the associated error rates. Analysis of variance on the reaction times demonstrated a highly significant main effect of stepsize [$F(2, 64) = 190.8$, $P < 0.0001$], as well as of startpoint [$F(2, 64) = 142.6$, $P < 0.0001$], but no other significant effects. This outcome confirms that reaction times increase as a function of increasing stepsize and startpoint, and that all groups behaved in a similar manner with respect to these variables.

Table 2. Mean reaction times (in msec) and standard deviation (in parentheses), together with % error rate (in bold face) as a function of stepsize and startpoint in perceptual task

	Stepsize			Startpoint		
	4	6	8	1	3	5
Group						
NC	7813	9782	10,601	7973	9647	10,577
	(1598)	(1642)	(1452)	(1175)	(1703)	(1814)
	13.1	**17.6**	**22.0**	**24.3**	**14.8**	**13.7**
LT	7409	9261	10,262	7688	9063	10,181
	(1377)	(1267)	(1685)	(1333)	(1369)	(1627)
	12.9	**17.8**	**16.3**	**15.0**	**17.2**	**14.7**
RT	7324	9207	9872	7646	8795	9962
	(1432)	(1366)	(1613)	(1430)	(1188)	(1794)
	24.3	**26.7**	**25.7**	**35.6**	**28.1**	**13.0**

Note: Data for patient groups includes only selected subjects who performed above 55% correct (see text).

For the imagery task, the reaction time and error rate data are shown in Table 3. An analysis of variance for group by stepsize of the reaction times yielded a significant group effect [$F(2, 32) = 3.80$, $P < 0.05$], as well as a significant stepsize effect [$F(2, 64) = 13.86$, $P < 0.0001$], but no interaction of the two factors. Inspection of the means (Table 3) indicated that the right temporal group was faster overall, and that all subjects tended to increase their reaction time for larger stepsizes.

The data for the startpoint effect were more equivocal. In this analysis there was also a significant group effect [$F(2, 32) = 3.96$, $P < 0.03$], and there was also a group by startpoint interaction [$F(4, 64) = 3.83$, $P < 0.01$]. The latter interaction seems to be primarily due to the behaviour of the normal control subjects, who did not show a consistent increase in reaction time as a function of startpoint (see Table 3). As in the previous analysis, the reaction times of the right temporal group are faster than those of the other two.

The possibility that the fast performance on the imagery task by the right temporal subjects was due to a speed–accuracy trade-off was tested by examining the relation between mean performance on the imagery task and overall speed across the nine subjects retained for this part of the analysis. No evidence in favour of this trade-off was found, since there was no significant correlation ($r = -0.57$, $P > 0.10$) between % correct and average reaction time. In fact, the trend is in the opposite direction, since subjects who performed best tended also to have the fastest reaction times.

Table 3. Mean reaction times (in msec), and standard deviation (in parentheses), together with % error rate (in bold face) as a function of stepsize and startpoint in imagery task

	Stepsize			Startpoint		
	4	6	8	1	3	5
Group						
NC	8747	10,543	11,133	10,306	10,613	9505
	(3442)	(3696)	(3546)	(4121)	(3622)	(2940)
	18.0	**28.1**	**27.5**	**22.9**	**30.0**	**20.8**
LT	8522	9704	10,213	8033	9474	10,932
	(3928)	(3399)	(4052)	(2962)	(3745)	(4672)
	26.9	**30.3**	**28.6**	**31.5**	**30.9**	**23.4**
RT	6174	7305	7264	6622	6820	7302
	(1354)	(1805)	(1690)	(1670)	(1519)	(1661)
	32.8	**40.4**	**42.2**	**45.3**	**43.1**	**27.0**

Note: Data for patient groups includes only selected subjects who performed above 55% correct (see text).

DISCUSSION

The pattern of results supports the initial hypothesis that imagery and perception share a common neural locus, at least in part, since right temporal lobectomy resulted in reduced performance on both types of tasks. The strongly lateralized effect was predicted, and is in keeping with the literature on the importance of right temporal-lobe structures to melodic processing [28].

The deficit we describe appears to be specific to structures within the right temporal lobe, insofar as lesions of the left temporal neocortex did not produce any decrement at all on either task. As is clear from the data in Table 1, damage to the left temporal lobe does have deleterious effects on verbal memory, but it did not result in impaired performance on our tasks. It is also of interest to note that visual imagery has been reported to be intact following unilateral temporal-lobe excision. ALIVISATOS [1] used a visual mental-rotation task modeled after that of COOPER and SHEPARD [4] with groups of patients very similar to those tested in the present study, and found normal functions relating reaction time to stimulus orientation. Thus, although other aspects of visual imagery have not been studied, we may tentatively conclude based on current knowledge that the present results are modality-specific.

The normal performance of the left temporal-lobe group in the present study may be somewhat surprising in view of SAMSON and ZATORRE's [23] evidence that such lesions do impair memory for songs. In that study, the tune recognition deficit was confined to the right temporal group when the tunes were presented separately from words (i.e. tunes without words vs spoken words). However, for sung text, recognition of both the tune and the lyrics was disturbed following either left or right temporal excision. In the present study, the pitch judgement was based on acoustic information actually carried by the sung words (in the perceptual task), or at least indexed by the visual words (in the imagery task); given this verbal component, one might have expected a deficit following left temporal excision. We believe that these seemingly conflicting results can be reconciled, however, if the familiarity of the songs is taken into account. Whereas SAMSON and ZATORRE [23] used novel materials, the present study used highly familiar, overlearned songs. It seems likely that in such songs, after many listenings, the tune has become abstracted from the text to a large extent, and can be accessed independently from it. Furthermore, in the course of the experiment, the subjects saw the text 12–18 times across trials; this additional practice may compensate for any residual verbal processing deficits. In any case, the intact performance of the left temporal group argues strongly against any influence of the verbal component of the task on pitch processing.

The reaction time results allow us to make additional inferences about how subjects were performing the tasks. In the perceptual task the results clearly showed that most subjects took longer to make judgements about lyrics that were distant from one another within the song, as compared to those that were close in time (stepsize effect). This effect is not surprising, as it simply reflects the fact that subjects were waiting to hear the second pitch before making their judgement. The obtained pattern demonstrates that subjects understood the task and were able to follow the instructions.

We also found a similar pattern of reaction time changes according to stepsize in the imagery task in all three groups, replicating HALPERN's [11] results. This finding supports our interpretation that the task actually requires access to some internal representation that preserves temporal characteristics analogous to those of the real stimulus. This reasoning is most strongly supported for the NC and LT group because their high accuracy makes them comparable to the subjects in Halpern's previous research. Thus in general, the similarity of NC and LT groups suggests that the LT lesion has neither a quantitative nor qualitative effect on the auditory imagery task.

Interpretation of the reaction time data from the right temporal group must be undertaken with caution due to their overall poor performance. Recall that we selected only the subgroup of right temporal patients whose performance was sufficiently above chance to permit analysis, which is not necessarily a representative sample. Nonetheless, we observed the same stepsize effect in this group as in the others on the trials they did perform correctly. This finding suggests that the right temporal patients who were able to perform the task were using strategies similar to those of the other groups, but perhaps less frequently or less successfully.

The overall faster performance of the right temporal group on the imagery task is more puzzling. Although we do not believe this reflects a simple speed accuracy trade-off for the reasons outlined above, we cannot completely reject the possibility either. Furthermore, even among the subjects retained, interpretation of the reaction time data is difficult, since we cannot tell for any given trial whether a correct answer was given as the outcome of a relevant cognitive decision, or as a "lucky guess".

Unlike HALPERN's [11] results, we did not observe any systematic reaction time changes with the various startpoints used. This may have been due to our use of the complete text of the song excerpt on the screen, and to our blocking of trials so that one song was tested at a time. In the previous study, subjects saw only two lyrics, and had to access a different song on each trial, making it more likely that they had to scan from the beginning to find the right place within the song. In the present study, however, it was probably much easier to jump to the first lyric given the additional information provided by the full text. The fact that the NCs were the least affected by the startpoint manipulation may simply show that they were most able to use this efficient strategy.

Let us now consider which specific cognitive operations may be adversely affected by the excision from the right temporal area. Three obvious candidates are (i) generating the tune image from long-term memory, (ii) remembering the pitches to be compared, and (iii) actually comparing the pitch of the two tones. A deficit in this last stage is least likely, because all subjects passed our screening test of comparing the height of two sounded pitches, and also because previous research has found simple pitch discrimination to be unaffected by temporal-lobe damage [18, 27]. A deficit in tune generation may account for some part of the lowered performance in the RT group. However, the subjects in this group were deficient relative to the other groups even in the perceptual task, in which no tune generation was required. Thus, inability to generate tunes cannot be the sole cause of the deficit.

An inability to maintain a memory trace of a pitch would be consistent with previous work on the function of the right temporal lobe [29]. If this explanation is valid, it would implicate a deficit for retaining the pitch of *imagined* as well as real tones. This idea could be tested in future research by reducing the memory load for pitch comparison. If both imagery and perception tasks improve by the same amount with this reduced memory load, then we would have evidence for the major deficit being in the pitch memory component of our task. To the extent that the perception task might benefit more than the imagery task by the memory load reduction, we would have evidence for an additional deficit in tune image generation.

Finally, we consider how these findings fit within a broader neuropsychological model of musical function. Although we have emphasized the important role of the right temporal neocortex, there is little doubt that a complex function such as musical imagery depends on many separate but closely interrelated structures, probably in both cerebral hemispheres. It is of particular interest to consider the possible role of frontal-lobe mechanisms in this respect. Much of the prefrontal cortex receives direct anatomical input from the superior temporal gyrus [21], and there is evidence that the prefrontal cortex, especially in the right hemisphere, plays a role in pitch judgement tasks [29, 30]. In the type of task explored in the present study, one may hypothesize that frontal-lobe systems may contribute to image generation, given the neuropsychological evidence that frontal-lobe damage affects various aspects of response organization, selection and generation [19, 25]. It will be important, therefore for future research to focus on the effect of frontal-lobe damage on musical imagery.

Acknowledgements—We thank Drs A. Olivier, W. Feindel, R. Leblanc and J.-G. Villemure for access to their patients and for providing information regarding neurosurgical excisions. We also express our gratitude to the patients who participated in this study for their cooperation, and to Virginia Penhune and Pierre Ahad for their invaluable assistance. This research was supported in part by grant MA-9598 from the Medical Research Council of Canada, and by funds from the Fonds de la Recherche en Sante du Quebec.

REFERENCES

1. ALIVISATOS, B. The role of the frontal cortex in the use of advance information in a mental rotation paradigm. *Neuropsychologia* **30,** 145–159, 1992.
2. BISIACH, E., LUZZATTI, C. and PERANI, D. Unilateral neglect, representational schema and consciousness *Brain* **102,** 609 618, 1979.
3. CELESIA, G. Organization of auditory cortical areas in man. *Brain* **99,** 403–414, 1976.
4. COOPER, L. A. and SHEPARD, R. N. Chronometric studies of the rotation of mental images. In *Visual Information Processing*, W. G. CHASE (Editor), pp. 75–176. Academic Press, New York, 1973.
5. FARAH, M. J. Is visual imagery really visual? Overlooked evidence from neuropsychology. *Psychol. Rev.* **95,** 307–317, 1988.
6. FARAH, M. J. The neural basis of mental imagery. *Trends Neurosci.* **12,** 395–399, 1989.
7. FARAH, M. J. and SMITH, A. F. Perceptual interference and facilitation with auditory imagery. *Percept. Psychophys.* **33,** 475–478, 1983.
8. FINKE, R. A. Theories relating mental imagery to perception. *Pychol. Bull.* **98,** 236–259, 1985.
9. FITZPATRICK, K. A. and IMIG, T. J. Organization of auditory connections: The primate auditory cortex. In *Cortical Sensory Organization*, C. N. WOOLSEY (Editor), Vol. 3. Humana Press, Clifton, NJ, 1982.

10. GALABURDA, A. and SANIDES, F. Cytoarchitectonic organization of the human auditory cortex. *J. comp. Neurol.* **190,** 597–610, 1980.
11. HALPERN, A. R. Mental scanning in auditory imagery for songs. *J. exp. Psychol.: Learn. Mem. Cognit.* **14,** 434–443, 1988a.
12. HALPERN, A. R. Perceived and imagined tempos of familiar songs. *Music Percept.* **6,** 193–202, 1988b.
13. HALPERN, A. R. Memory for the absolute pitch of familiar songs. *Mem. Cognit.* **17,** 572–581, 1989.
14. HUBBARD, T. L. and STOECKIG, K. Musical imagery: generation of tones and chords. *J. exp. Psychol.: Learn. Mem. Cognit.* **14,** 656–667, 1988.
15. KOSSLYN, S. M. *Image and Mind.* Harvard University Press, Cambridge, MA, 1980.
16. KOSSLYN, S. M., BALL, T. M. and REISER, B. J. Visual images preserve metric spatial information: Evidence from studies of image scanning. *J. exp. Psychol.: Hum. Percept. Perf.* **4,** 47–60, 1978.
17. LIEGEOIS-CHAUVEL, C., MUSOLINO, A. and CHAUVEL, P. Localization of the primary auditory area in man. *Brain* **114,** 139–153, 1991.
18. MILNER, B. Laterality effects in audition. In *Interhemispheric Relations and Cerebral Dominance*, V. B. MOUNTCASTLE (Editor), pp. 177–195. Johns Hopkins Press, Baltimore, 1962.
19. MILNER, B. and PETRIDES, M. Behavioural effects of frontal-lobe lesions in man. *Trends Neurosci.* **7,** 403–407, 1984.
20. PETERSEN, S. E., FOX, P. T., POSNER, M. I., MINTUN, M. and RAICHLE, M. E. Positron emission tomographic studies of the cortical anatomy of single word processing. *Nature* **331,** 585–589, 1988.
21. PETRIDES, M. and PANDYA, D. N. Association fiber pathways to the frontal cortex from the superior temporal region in the rhesus monkey. *J. comp. Neurol.* **273,** 52–66, 1988.
22. SAMSON, S. and ZATORRE, R. J. Discrimination of melodic and harmonic stimuli after unilateral cerebral excisions. *Brain Cognit.* **7,** 348–360, 1988.
23. SAMSON, S. and ZATORRE, R. J. Recognition memory for text and melody of songs after unilateral temporal-lobe lesion: Evidence for dual encoding. *J. exp. Psychol.: Learn. Mem. Cognit.* **17,** 793–804, 1991.
24. SAMSON, S. and ZATORRE, R. J. Learning and retention of melodic and verbal information after unilateral temporal lobectomy. *Neuropsychologia* **30,** 815, 826, 1992.
25. STUSS, D. T. and BENSON, D. F. *The Frontal Lobes.* Raven Press, New York, 1986.
26. ZATORRE, R. J. Discrimination and recognition of tonal melodies after unilateral cerebral excisions. *Neuropsychologia* **23,** 31–41, 1985.
27. ZATORRE, R. J. Pitch perception of complex tones and human temporal-lobe function. *J. acoust. Soc. Am.* **84,** 566–572, 1988.
28. ZATORRE, R. J. Effects of temporal neocortical excisions on musical processing. In S. MCADAMS and I. DELIEGE (Editors), Music and the Cognitive Sciences. *Contemp. Music Rev.* **4,** 265–277, 1989.
29. ZATORRE, R. J. and SAMSON, S. Role of the right temporal neocortex in retention of pitch in auditory short-term memory. *Brain* **114,** 2403–2417, 1991.
30. ZATORRE, R. J., EVANS, A. C., MEYER, E. and GJEDDE, A. Lateralization of phonetic and pitch processing in speech perception. *Science* **256,** 846–849, 1992.