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Recommended Citation

Zatorre, Robert J.; Halpern, Andrea R.; Perry, David W.; Meyer, Ernst; and Evans, Alan C.. "Hearing in the mind's ear: A PET investigation of musical imagery and perception." *Journal of Cognitive Neurosciences* (1996) : 29-46.

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Hearing in the Mind's Ear: A PET Investigation of Musical Imagery and Perception

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Abstract

■ Neuropsychological studies have suggested that imagery processes may be mediated by neuronal mechanisms similar to those used in perception. To test this hypothesis, and to explore the neural basis for song imagery, 12 normal subjects were scanned using the water bolus method to measure cerebral blood flow (CBF) during the performance of three tasks. In the control condition subjects saw pairs of words on each trial and judged which word was longer. In the perceptual condition subjects also viewed pairs of words, this time drawn from a familiar song; simultaneously they heard the corresponding song, and their task was to judge the change in pitch of the two cued words within the song. In the imagery condition, subjects performed precisely the same judgment as in the perceptual condition, but with no auditory input. Thus, to perform the imagery task correctly an internal auditory representation must be accessed. Paired-image subtraction of the resulting pattern of CBF, together with matched MRI for ana-

tomical localization, revealed that both perceptual and imagery tasks produced similar patterns of CBF changes, as compared to the control condition, in keeping with the hypothesis. More specifically, both perceiving and imagining songs are associated with bilateral neuronal activity in the secondary auditory cortices, suggesting that processes within these regions underlie the phenomenological impression of imagined sounds. Other CBF foci elicited in both tasks include areas in the left and right frontal lobes and in the left parietal lobe, as well as the supplementary motor area. This latter region implicates covert vocalization as one component of musical imagery. Direct comparison of imagery and perceptual tasks revealed CBF increases in the inferior frontal polar cortex and right thalamus. We speculate that this network of regions may be specifically associated with retrieval and/or generation of auditory information from memory. ■

INTRODUCTION

When asked to imagine the appearance of a tiger, the sound of wind chimes, or the smell of popcorn, many people report an experience similar to that of actually viewing the tiger, hearing the wind chimes, or smelling the popcorn. Subjectively, this experience seems fundamentally different in character from memory retrievals involving factual information, such as recalling the capital of China or the Pythagorean Theorem. Whereas these latter experiences do not appear to be tied to any particular modality, the "imagine" experiences seem to be more directly linked to the sensory system originally involved in encoding the information.

The question this informal comparison evokes is an important one for cognitive psychology: Do different

kinds of mental representations exist, or are all cognitive operations fundamentally alike? If the latter is true, then perhaps differences in subjective experiences might arise solely due to interpretative processes or to our use of language that has inaccurate terms for mental experiences [or to use Pylyshyn's (1981) term: "epiphenomenal"]. As one route to answer this question, many investigators have tried to document whether some cognitive experiences share characteristics with perceptual experiences. Similarities between perception and imagery would support the argument that humans, at least at some important level of description, generate different kinds of mental representations depending on the stimulus to be coded.

Another fundamental question related to that of the functional similarity between perception and imagery is

their neural substrate. Considerable knowledge has accumulated about the cerebral areas that underlie perceptual processing. This knowledge can be applied to try to understand the processes involved in imagery. For example, Farah (1988) has argued that there is a shared neural basis for perception and imagery, on the basis of neuropsychological evidence. However, the research to date has concentrated almost exclusively on visual imagery, thus limiting the generality of any conclusions that might be drawn. In the present study we examined cerebral blood flow (CBF) changes associated with auditory perceptual and imagery tasks using PET, thus allowing us to test directly the hypothesis that functional similarities exist generally between perceptual processes and imagery, and to examine the contribution of specific anatomical regions to the performance of these tasks. Before presenting the background and specific rationale of the present experiment, however, we will briefly review the cognitive literature on visual and auditory imagery.

Visual Imagery

Subjective reports are of limited use to assess the characteristics of cognitive representations. Therefore, in recent years, psychologists have tried to find more objective means of evaluating the similarity of perception and imagery. One type of objective evidence is behavioral: To what extent are tasks performed similarly when perceiving versus imagining a stimulus? To cite some examples, Bagnara, Simion, Tagliabue, and Umiltà (1988) found similarly fast "same" responses in a letter-matching task whether the first letter was actually shown or was generated by participants upon receipt of a cue. In both conditions, response latency decreased similarly as a function of feature dissimilarity between the letters. Farah (1989) found that after generating an image of a letter, people were swifter to detect an actual target that would have been on the letter (had it been really presented) than off the letter, suggesting that the image and percept shared representational format at some level. Finke (1985) reviewed a large body of behavioral evidence suggesting that objective indices such as response latencies and accuracy reflect similar performance on perceptual and imagery tasks.

However, as both critics and proponents of an imagery view have pointed out (Finke, 1985; Pylyshyn, 1981), behavioral indices are not immune from criticisms that they may be vulnerable to extraexperimental influences, such as experimenter expectancies, demand characteristics of the experimental situation, or tacit knowledge that subjects have about how their own mental processes work or ought to work. In response to this challenge, a number of researchers have turned to physiological evidence to support the notion that imagery and perception share actual neural mechanisms, and, by extension, cognitive structures. As reviewed by Farah (1988), physiological evidence includes recording brain

electrical or metabolic activity during perception and imagery tasks, as well as looking for parallel functional deficits in imagery and perception after specific types of brain damage. This type of evidence is relatively immune to the criticisms just noted, in that it is unlikely that people have any knowledge of the neuroanatomical loci of their cognitive activities, or can alter physiological indices in just such a way as to mimic perception-imagery concordances.

A recent study by Kosslyn et al. (1993) is one example of the physiological approach, using PET to measure CBF during visual perceptual and imagery tasks. Subjects performed a task similar to that used by Kosslyn, Ball, and Reiser (1978), and originally devised by Podgorny and Shepard (1978): A letter was shown or imagined on a grid, followed by a target dot. The task was to decide if the target fell within the letter in the perceptual task, or would fall within the letter in the imagery task. CBF in the perception condition was subtracted from that in the imagery condition to see which brain areas may be uniquely involved in imagery. One of the main results of Kosslyn et al. (1993) was that the imagery task activated a number of secondary visual cortical areas and possibly part of the primary visual area as well, over and above the subtracted perception task. The location of the activation was sensitive to the size of the image in ways similar to that found for size of perceived objects. In other words, even when no visual input was provided, the act of imagining caused activation in cortical areas known to subserve visual perception, and even engaged particular brain areas heretofore thought only to be sensitive to actual perceptual qualities.

Auditory Imagery

As noted above, the imagery literature has concentrated on the visual domain. However, many questions remain that cannot be answered without examining imagery processes across modalities. Is the visual system unique in using similar anatomical networks for both perception and imagery, or is this a more general feature of cognitive processes? Perhaps the nervous system has evolved in such a way that all sensory processing areas, which are normally responsive to environmental input, can also be activated endogenously, i.e., in the absence of external stimulation. If so, then at least a preliminary explanation of the neural basis for imaginal processing would be at hand.

Several studies have recently investigated auditory imagery, particularly as related to music. Many people, musically trained or not, report a strong subjective experience of being able to imagine music or musical attributes. Behavioral evidence is consistent with this subjective impression. For instance, Farah and Smith (1983) found that imagining a high (low) tone prior to presentation of an actual high (low) tone facilitated detection of the presented tone. This was taken to mean

that pitch can be represented in images. Hubbard and Stoeckig (1988) played or asked subjects to form an image of a musical chord and then played a real chord for a same/different judgment. In both perception and imagery, accuracy and reaction time were best when the chords were identical and worst when the chords were musically related. The authors concluded that harmonic information was preserved in the image. Crowder (1989) found that pitch matching was facilitated when two tones were played on the same instrument (shared a musical timbre), and was similarly facilitated when participants imagined the timbre of only the first note. For example, imagining a flute playing an A, as cued by a sine wave, decreased reaction time to say "same" when a flute A was actually presented, relative to having imagined a trumpet playing an A. Crowder concluded that aspects of timbre were preserved in the auditory image.

In addition to these elemental musical attributes, Halpern has presented evidence that aspects of tunes as a whole are preserved in auditory images, including the tempo of the melody (Halpern, 1988b) and the approximate absolute pitch range (Halpern, 1989). Most relevant to the task we will present in the current study, Halpern (1988a) asked musically untrained subjects to compare the pitch of two lyrics from a familiar, imagined song. For instance, is the pitch corresponding to "sleigh" higher or lower than that of "snow" in the song "Jingle Bells"? She varied the distance (number of beats) between the target lyrics chosen, as well as the distance from the beginning of the song of the first lyric of the pair. Response latencies increased systematically as a function of both factors, suggesting that subjects were "mentally scanning" the tune to compare the imagined pitches. Thus, she concluded that the temporal pace and ordering of the notes in the real song were preserved in analogous fashion in the image of the song. This result is similar to the conclusion that real-world spatial characteristics are preserved in visual images (Kosslyn et al., 1978).

In a previous study (Zatorre & Halpern, 1993), we examined whether auditory imagery and perception may share similar neural mechanisms by presenting a modification of Halpern's (1988a) tune scanning task to patients having undergone right or left temporal-lobe excision for the relief of intractable epilepsy. A perceptual version of the task was devised in which the listener made pitch judgments while actually hearing the song. Our reasoning was as follows: It is well-established anatomically and physiologically that cortical regions within the superior temporal gyrus are important for perceptual processing of auditory information (Brugge & Reale, 1985; Celesia, 1976; Penfield & Perot, 1963). Furthermore, unilateral lesions of the temporal lobe, especially on the right, result in impairments on such musical processing tasks as melody discrimination (Milner, 1962; Zatorre, 1985; Samson & Zatorre, 1988; Peretz, 1993), perception of the pitch of the missing fundamental (Zatorre, 1988), timbre discrimination (Milner, 1962; Samson

& Zatorre, 1994), and retention of pitch information in working memory (Zatorre & Samson, 1991). Thus, we predicted that if imagery and perception for familiar tunes share neural structures, then we should see similar deficits after temporal lobectomy in both tasks, relative to nonoperated controls. We also predicted that right temporal lobectomy would have more deleterious effects than left temporal lobectomy.

The results of that study were very clear and striking. While all subjects did better on the perception task compared to imagery, patients with left-temporal excisions showed no deficits relative to normal controls, whereas those with damage to the right temporal area were significantly worse than the other groups on both tasks, and by about the same amount on each task. We concluded that structures in the right temporal lobe were crucial for successful performance of both imagery and perception tasks, suggesting the same kind of neuroanatomical parallelism (and by extension functional parallelism) shown by Farah (1988), Kosslyn et al. (1993), and others for visual imagery and perception.

Although the data from Zatorre and Halpern (1993) allowed us to make some initial conclusions about the role of the temporal lobe in musical imagery and perception, the methodology of lesion studies leaves some questions unanswered. First, the design of the study allowed us to investigate the participation of only one region of the brain in our experimental tasks. While we demonstrated that the right temporal lobe is involved in performing the tasks, we have no information on the role of other brain areas in the actual or imagined pitch comparison. Second, our previous study was necessarily anatomically imprecise in that the patients tested had relatively large excisions. Thus we had no definitive information on which parts of the temporal neocortex might be active in our tasks. And finally, although we observed deficits in both imagery and perception tasks among the patients with right temporal-lobe excision, we could not say with certainty which specific subcomponents of our task were the most impaired by the excision.

PET Studies of Auditory Processing

The current study takes advantage of functional brain imaging technology to address the concerns just noted. We used paired-image subtraction with PET to isolate the contribution of specific brain regions to particular mental operations. This approach has been applied to various aspects of perception and cognition by a growing number of investigators. Several studies have reported that auditory stimulation with spoken words results in bilateral activation of superior temporal cortex, in agreement with data cited above (Petersen, Fox, Posner, Mintun, & Raichle, 1988; Wise et al., 1991; Demonet et al., 1992; Zatorre, Evans, Meyer, & Gjedde, 1992). Most of these studies also report asymmetric CBF changes in the

left posterior temporal region when subjects listen to speech sounds. A dissociation between primary and secondary cortical regions was also observed by Zatorre et al. (1992), as a function of the type of stimulus used (noise bursts vs. speech syllables).

In a more recent PET experiment, Zatorre, Evans, and Meyer (1994) reported that a region within the right anterior superior temporal gyrus was activated by "passive" listening to unfamiliar tonal melodic sequences (relative to noise bursts acoustically matched to the tones for total amplitude, duration, and amplitude envelope), supporting the existence of hemispheric processing asymmetries. In two further conditions subjects were required to compare the pitch of two tones within the melodic sequence; this could either involve little working memory capacity (comparison of the first two tones), or could require a greater working memory load (comparison of the first and last tones). When compared to the passive listening condition, a number of different regions, including dorsolateral and inferior right frontal areas, were activated in both tasks. This finding confirmed a similar result obtained with pitch judgments of syllables (Zatorre et al., 1992), and is also consistent with the finding that lesions of the right frontal lobe disrupt pitch retention (Zatorre & Samson, 1991). The judgment of first and last tones also resulted in a CBF increase in the right temporal lobe, above and beyond any CBF increase already accounted for by the passive listening condition. These findings, taken together, were interpreted as evidence for a functional network, involving right temporal and right frontal cortices, in the processing and maintenance of pitch information in working memory.

The Present Investigation

PET methodology allows us to study the neural processes of normal subjects, with more anatomical precision compared to many other physiological techniques, including lesion studies. Current PET techniques allow a spatial localization accuracy of about 5 mm, so that specific areas within the temporal lobe and other regions may be distinguished from one another. Precision is further enhanced in our case by superimposing PET activation on averaged MRIs of the actual test partici-

pants (Evans, Marrett, Torrescorzo, Ku, & Collins, 1991a), thereby providing excellent structure-function correlation, and avoiding problems associated with anatomical uncertainty that arise when direct structural information is missing. Finally, the logic of using multiple scans in PET methodology allows one to gain some insight as to the particular task components responsible for activation on any one scan. By subtracting activation engendered in one task from activation on a related task, the activation due to the unique components on either task can be examined.

For the present study, we presented three tasks to all participants, a *visual baseline* condition and two active tasks, one termed *perception* and the other *imagery* (see Table 1). The latter two were similar to those used by Zatorre and Halpern (1993): Two words from a familiar tune were presented on a screen, and the task was to decide if the pitch corresponding to the second word was higher or lower than the pitch corresponding to the first word. In the perceptual task, participants actually heard the song being sung, while in the imagery task they carried out the task with no auditory input. The visual baseline task was always given first; in this control task participants saw two words on the screen and they had to decide if the second word was longer or shorter than the first. The words were the same as those used in the musical tasks, but re-paired so that no image of a song would be evoked.

By subtracting the activation in the visual baseline from both the perception and imagery tasks, we should, in principle, eliminate cerebral activity related to non-specific processes shared by the two tasks, such as reading words on a screen, making a forced-choice decision, pressing a response key, etc. Thus, any CBF changes still remaining must be due to the unique demands of listening to a tune or imagining it, and making a pitch comparison. Direct comparison of the PET data obtained in the perceptual task with that of the imagery task should identify any brain regions uniquely active in retrieving and/or generating musical images.

Predictions

Several levels of prediction were made. The overall prediction, in keeping with the general hypothesis that

Table 1. Experimental Conditions^a

<i>Condition</i>	<i>Auditory stimulus</i>	<i>Visual stimulus</i>	<i>Judgment required</i>	<i>Percent correct</i>
Visual baseline	None	Pairs of words	Word length	100
Perceptual task	Familiar songs	Pairs of words	Pitch change of cued words	85
Imagery task	None	Pairs of words	Pitch change of cued words	73

^a Summary of paradigm, showing stimuli presented and responses elicited during each of the three experimental conditions. Note that all three tasks involved similar visual input, but only the perceptual task involved true auditory input. Both perceptual and imagery tasks required the identical judgment of pitch change as cued by the visual words.

imagery and perception share common underlying neural mechanisms, was that at least some of the regions activated by the perceptual judgment task would also be activated in the imagery task, and vice versa. Therefore, the CBF changes elicited by comparing the perceptual task to the visual baseline task should overlap to a considerable extent with the regions showing CBF changes when comparing the imagery task to the visual baseline task.

Several more anatomically specific predictions were also made. First, stimulation in the perceptual condition should elicit bilateral CBF increases in the superior temporal gyrus as compared to the silent visual baseline. Second, and more importantly, regions within the temporal neocortex should also demonstrate bilateral increases in CBF in the imagery task as compared to the visual baseline, even though no sound is actually presented. In both cases we hypothesized that bilateral activation would be observed, since the song stimuli contain both tonal and phonetic information, but we expected a right-sided asymmetry on the basis of the previous lesion and PET literature, since a pitch judgment is required. Third, we predicted that regions within the right frontal lobe would be involved in both tasks, insofar as they require pitch comparison of either real or imagined tonal information (Zatorre et al., 1992, 1994). Finally, we predicted that direct comparison between imagery and perceptual conditions should yield changes uniquely associated with image retrieval and generation. Although the substrate for this aspect of auditory imagery is unknown, we had speculated in our earlier study that this comparison would reveal activation of frontal-lobe areas.

RESULTS

Results of Behavioral Testing

All 12 subjects indicated in debriefing that they were familiar with the song materials used. Although performance varied considerably across individuals, all subjects reported that—with more or less difficulty—they had been able to generate the song internally during the imagery task.¹ None of the subjects reported thinking about or imagining songs during the visual baseline condition, although some of them indicated that the words presented to them reminded them of related themes (e.g., Christmas or church hymns).

Performance data, shown in Table 1, indicated compliance with the instructions and good comprehension and execution of both tasks. In keeping with our previous experience with similar tasks (Zatorre & Halpern, 1993), the imagery condition was significantly more difficult than the perceptual condition (all but two subjects performed better on the perceptual task).

Response latencies were also collected on-line. Because relatively few trials were presented to each participant and only latencies from correctly answered trials

are interpretable, too few data points were available to enable formal analyses. We will simply note that in both tasks, median time to answer increased as a function of how many beats (2, 4, or 6) separated the two queried lyrics in the real tune (the Stepsize variable, see Methods): 5251 to 8044 to 8430 msec in the perception task, and 3592 to 4866 to 4647 msec in imagery. Similar response latency increases were observed as a function of how many beats (0, 2, or 4) intervened from the beginning of the tune to the first queried lyric (the Startpoint variable, see Methods): 5642 to 7693 to 9059 msec in the perception task, and 3722 to 4609 to 4647 msec in imagery. These patterns correspond to those found in our previous investigations of auditory imagery (Halpern, 1988a; Zatorre & Halpern, 1993), and are consistent with the notion that subjects are, in the perception task, following instructions to wait until the second note is presented before answering, and in the imagery task, retrieving a memory of the tune that represents the unfolding of real time.

Results of PET Scanning

The PET results are presented in Tables 2, 3, and 4, and in Figure 1. Tables 2 and 3 list all regions that demonstrated significant CBF increases or decreases, respectively, in the perceptual-visual baseline subtraction and in the imagery-visual baseline subtraction (see Methods for details of statistical analysis). Table 4 lists all areas showing CBF changes in the comparison of the perceptual and imagery tasks to each another. The tables also list the stereotaxic coordinates for each focus, based on the brain atlas of Talairach and Tournoux (1988). Identification of brain regions and Brodmann areas was based on inspection of the averaged MRI scan information, and by reference to the atlas; where the atlas and the MRI information diverged, the latter was taken as correct.

Results of Perceptual and Imagery Tasks Relative to Visual Baseline: CBF Increases

The most striking finding in Table 2 is the fact that for nearly every region demonstrating CBF change in one condition, there is a corresponding CBF peak in the other condition, often within a few millimeters. As predicted, CBF increases were found bilaterally in the temporal lobes, in both conditions, and in the right frontal lobe. In addition, we observed areas of activation in both tasks in the left frontal and parietal lobes, as well as in supplementary motor area (SMA) and midbrain. The findings within each of these regions are presented in greater detail below; CBF increases are discussed first, followed by CBF decreases.

Temporal-Lobe Areas

As expected, highly significant CBF increases were found within the superior temporal gyrus bilaterally when sub-

Table 2. Regions Activated in Perceptual and Imagery Tasks as Compared to Visual Baseline Task (Blood Flow Increases)^a

Region	Task	Brodmann area	Coordinates			<i>t</i> -value
			<i>x</i>	<i>y</i>	<i>z</i>	
Right temporal lobe						
1. Posterior STG	Per	22/42	59	-23	6	9.11
2. Posterior STG	Per	22	59	-18	3	9.38
3. Posterior STG	Ima	22	43	-37	8	2.68
4. Anterior STG	Ima	21/22	52	6	-15	3.18
Left temporal lobe						
5. Posterior STG	Per	22/42	-55	-18	5	10.18
6. Posterior STG	Ima	22	-48	-44	11	2.73
7. Mid-STG	Ima	22	-60	-9	3	2.73
8. Posterior MTG	Ima	21	-50	-42	-2	3.23
Right frontal lobe						
9. Mid-frontal	Per	45/9	36	24	18	2.87
10. Mid-frontal	Ima	45/9	36	17	22	3.03
11. Mid-frontal	Per	44	51	13	31	2.81
Left frontal lobe						
12. Mid-frontal	Per	45/9	-35	24	22	4.62
13. Mid-frontal	Ima	45/9	-34	24	22	3.73
14. Ant-inf frontal	Per	10/47	-29	42	3	3.07
15. Ant-inf frontal	Ima	10/47	-29	46	2	3.78
Left parietal lobe						
16. Supramarginal gyrus	Per	40	-32	-45	35	4.95
17. Supramarginal gyrus	Ima	40/7	-28	-49	33	4.03
Other regions						
18. Right SMA	Per	6	7	5	60	2.74
19. Right SMA	Ima	6	4	5	58	3.73
20. Midbrain	Per	—	4	-30	-13	3.81
21. Midbrain	Ima	—	4	-21	-13	3.43

^a Activation foci (blood flow increases) for subtraction of the perceptual and imagery conditions minus the visual baseline condition. In this and subsequent tables, stereotaxic coordinates are derived from the human brain atlas of Talairach and Tournoux (1988), and refer to medial-lateral position (*x*) relative to midline (positive = right), anterior-posterior position (*y*) relative to the anterior commissure (positive = anterior), and superior-inferior position (*z*) relative to the commissural line (positive = superior). Designation of Brodmann numbers for cortical areas, based on this atlas, is approximate only. Significance level is given in *t*-test units; reported *t*-values in the range 2.68 to 3.5 were deemed significant by directed search (see Methods for details). STG, superior temporal gyrus; MTG, middle temporal gyrus; SMA, supplementary motor area.

jects were processing the auditory stimuli for the perceptual task, as compared to the baseline task, in which no auditory stimulation was provided (Fig. 1, panel D). More interesting is the finding that regions within the superior temporal gyrus were also activated, albeit at a much weaker level (significant according to the directed search; see Methods), when subjects imagined hearing the stimulus, again as compared to the baseline condition (Fig. 1, panel D). Note that this latter subtraction entails two entirely silent conditions, so that positive

CBF changes in the superior temporal gyri (associative auditory cortices) cannot be due to any external stimulation, but are most likely attributable to endogenous processing.

Although CBF increases were found within the superior temporal gyrus in both subtractions, these were not in identical, symmetrical locations. In the perceptual task, two of the peaks (numbers 1 and 5 in Table 2, on the right and left, respectively) are located near the primary auditory cortex, and appear to extend into it, as well as

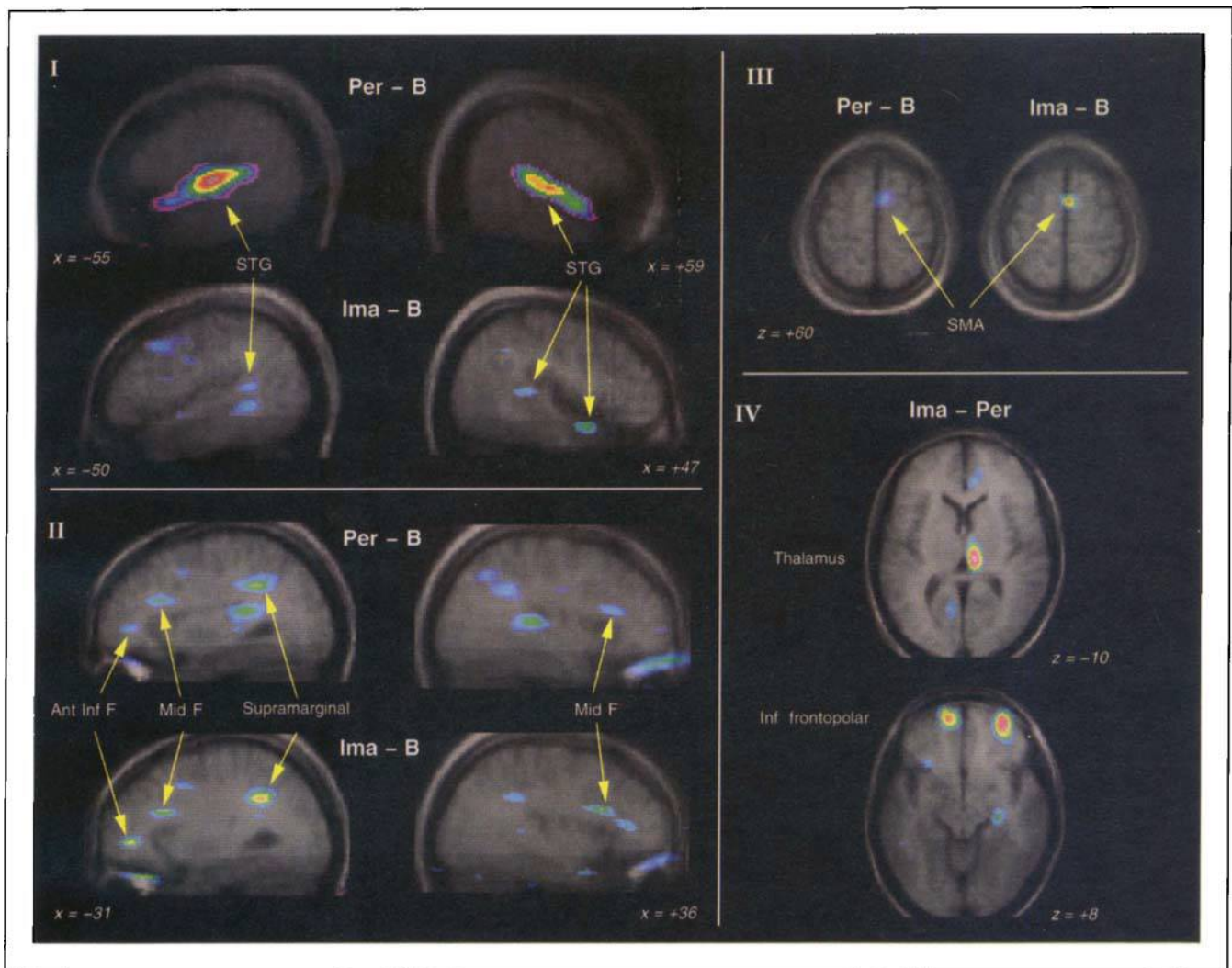


Figure 1. Averaged PET subtraction images are shown superimposed upon the averaged MRI scan for the 12 subjects tested. Subtraction of the control from activated state in each case yielded the focal changes in blood flow shown as a *t*-statistic image. The range of *t*-values for the PET data is coded by a color scale ranging from blue for the lowest values to white for the highest (see Tables 2–4 for precise *t*-values of each focus). Stereotaxic coordinates, in millimeters, are derived from the human brain atlas of Talairach and Tournoux (1988), and refer to medial-lateral position (*x*) relative to midline (positive = right), anterior-posterior position (*y*) relative to the anterior commissure (positive = anterior), and superior-inferior position (*z*) relative to the commissural line (positive = superior). Areas of apparent activation located in extracerebral space, near the orbit, are likely artifactual, and have been attenuated in the figures for reasons of clarity. I. The superior temporal gyrus (STG) activation foci in the perception task relative to the visual baseline (Per-B), and comparable areas of the STG activated in the imagery task minus baseline (Ima-B). The top two images correspond to sagittal sections of the left and right hemispheres (*x* = -55, focus 5; and *x* = 59, foci 1 and 2, respectively), and illustrate the strong CBF increases throughout the STG in the perception condition. The second pair of sagittal sections show the placement of STG foci in the imagery condition (on the left side, *x* = -50, foci 6 and 8; on the right side, *x* = 47, foci 3 and 4). All of the latter foci were found to be significantly activated via directed search; therefore, only regions of CBF increase located within the temporal lobes can be interpreted in this figure, as the directed search was confined to this volume. II. The similar pattern of activation in the perception-baseline subtraction (above) and the imagery-baseline subtraction (below). In the two left-hemisphere sagittal views (*x* = -31), inferior frontal foci (numbers 14 and 15) and mid-frontal foci (numbers 12 and 13) can be seen, together with foci in the supramarginal area (numbers 16 and 17). The two right-hemisphere sagittal views (*x* = 36) show the activation foci in the right mid-frontal lobe that were uncovered in the directed search of this area (numbers 9 and 10). The activation visible just below the supramarginal area in the Per-B subtraction represents a portion of the CBF increase in primary and secondary auditory cortices, shown in the more lateral sagittal sections of panel I. III. Two horizontal views (*z* = 60) illustrating CBF increases in the supplementary motor area in each subtraction (foci 18 and 19). IV. Data from the direct comparison of imagery and perception tasks to one another. The first horizontal section (*z* = 8) illustrates the activation in the right thalamus. The second horizontal section (*z* = -10) shows the two inferior frontopolar sites that were activated in this subtraction. Also visible in this slice is a possible focus in the right hippocampal area (see text).

throughout the superior temporal gyrus (see panel D), whereas the peak CBF increases in the imagery task are all outside of the primary area, either anteriorly (foci 4 and 7) or posteriorly (foci 3, 6, and 8). Furthermore, there appears to be a degree of lateral asymmetry in the results of the imagery task, since the CBF increase in the right anterior superior temporal gyrus (focus number 4 in Table 2; see right side of panel D) is located more anteriorly than any of the left-sided areas of CBF increase. These left temporal-lobe areas (foci 6 and 8; visible on the left side of panel D) are localized to the posterior portion of the superior temporal gyrus and to the middle temporal gyrus, respectively, approximately within the boundaries of classically defined Wernicke's area.

Left Frontal-Lobe Areas

Two regions within the left frontal lobe, one inferior and one mid-frontal, were consistently activated in both perception-baseline and imagery-baseline subtractions. Their correspondence is quite close comparing across the two subtractions, in which the peak CBF increases are within 1 mm of each other in the midfrontal area (foci 12 and 13 in Table 2), and within 4 mm in the anterior inferior frontal area (foci 14 and 15). Figure 1, panel II (left side) shows the similar location of these regions in each of the two task subtractions. Foci 12 and 13 fall most likely near the border between Brodmann's areas 45 and 9, whereas foci 14 and 15 are localized to the border of areas 10 and 47.

Right Frontal-Lobe Areas

These regions of CBF increase were found following the directed search described in the Methods section. Two regions were observed in the perceptual task, one mid-frontal most likely within the depth of the inferior frontal sulcus (focus 9; shown on the right side of panel II), and the other more posterior, probably within the superior portion of the inferior frontal gyrus (focus 11; not shown). A single mid-frontal area (focus 10; shown in panel II) was identified in the imagery task, close to focus 9 in the perception task, and falling near the border between cytoarchitectonic areas 45 and 9 according to Talairach and Tournoux (1988). Foci 9 and 10 are probably contralateral homologues of foci 12 and 13 in the left hemisphere, given their nearly symmetrical positions.

Other Areas of CBF Increase

The remaining regions showing CBF increases in the perceptual and imagery conditions, as compared to the baseline condition, were located in the left parietal lobe, supplementary motor area (SMA), and midbrain.

The left parietal-lobe CBF increases (foci 16 and 17 in Table 2), which are within 6 mm of one another across

conditions, fall most likely in the depths of the supramarginal gyrus. This activation is visible in Figure 1, panel II (left side) in both subtractions.

The SMA foci are visible in panel III of Figure 1, in two horizontal sections. Within the SMA the correspondence was also close across conditions (foci 18 and 19 in Table 2). Although both SMA foci are localized to the right of midline by a few millimeters, it is difficult to be certain that this represents a true lateralization, since this region is located medially, and the resolution of PET might not be sufficient to distinguish unilateral from bilateral activation.

The location of the midbrain areas in the perceptual-baseline and imagery-baseline comparisons (foci 20 and 21; not shown in the figure) is somewhat ambiguous. Judging by the MRI, however, it is possible that these foci may lie within a portion of the inferior colliculus.

Results of Perceptual and Imagery Tasks Relative to Visual Baseline: CBF Decreases

Locations of regions of decreased blood flow in perception-baseline and imagery-baseline are given in Table 3. CBF decreases were consistently noted in occipitotemporal regions bilaterally, in the vicinity of the left angular gyrus, the right mid insula, and various regions within the dorsal frontal lobes, as detailed below. The correspondence across subtraction conditions in these CBF decreases is also close, just as it was with the CBF increases. CBF decreases are not shown in the figure.

Occipitotemporal and Occipitoparietal Regions

These regions, listed in Table 3 (foci 1 through 8), demonstrated blood flow decreases in both perception-baseline and imagery-baseline subtractions. In other words, these were areas that were relatively more active during the visual word length judgment task than during either of the other two tasks. The peaks in the occipitotemporal region were found bilaterally, and all fell within portions of the ventral fusiform gyrus. The occipitoparietal regions, however, were only detected on the left side, and can be localized to the posterior aspect of the angular gyrus (foci 7 and 8), near the junction of the parietal and occipital lobes.

Opercular and Frontal Areas

Two other sets of blood flow decreases are shown in Table 3. One set (foci 9-11) was localized to the frontal opercular or immediately adjacent insular cortex, on the right side only. Once again, the correspondence across subtractions was quite close. Another set of regions that demonstrated significant CBF decreases fell within the anterior superior frontal gyrus, mostly to the left of midline. Most of these regions were active in the perceptual-baseline comparison only, with only a single peak

Table 3. Regions Activated in Perceptual and Imagery Tasks as Compared to Visual Control Task (Blood Flow Decreases)^a

Region	Task	Brodmann area	Coordinates			t-value
			x	y	z	
Left occipitotemporal						
1. Fusiform gyrus	Per	37/19	-34	-52	-15	2.96
2. Fusiform gyrus	Ima	37/19	-32	-49	-15	3.97
3. Fusiform gyrus	Ima	37/19	-34	-52	-13	3.92
Right occipitotemporal						
4. Fusiform gyrus	Per	37/19	40	-50	-15	5.17
5. Fusiform gyrus	Ima	37/19	38	-47	-15	4.17
6. Fusiform gyrus	Ima	37/19	39	-68	-13	3.87
Left occipitoparietal						
7. Angular gyrus	Per	39/19	-43	-74	24	4.37
8. Angular gyrus	Ima	39/19	-44	-80	24	2.72
Right frontal opercular/insula						
9. Mid insula/opercular	Per	—	40	8	8	4.10
10. Mid insula/opercular	Per	—	40	-2	13	4.10
11. Mid insula/opercular	Ima	—	38	-4	11	4.37
Left and right frontal lobe						
12. Superior frontal	Per	8	-17	42	45	4.03
13. Superior frontal	Per	8	-8	37	56	4.03
14. Superior frontal	Per	8	-5	30	60	3.70
15. Superior frontal	Ima	8	-7	36	57	3.32
16. Superior frontal	Per	9	-28	49	26	3.83
17. Superior frontal	Per	10	8	60	21	3.63

^a Activation foci (blood flow decreases) for subtraction of the perceptual and imagery conditions minus the visual baseline condition. For other details see footnote to Table 2.

(focus 15) identified in the imagery-baseline condition (this one peak is very close, however, to focus 13 identified in the perceptual comparison). The only region in the right frontal cortex (found in the perceptual comparison, focus number 17) is notable for being more anterior and inferior than all the rest, and likely falls within Brodmann area 10 of the frontal polar cortex.

Results of Direct Comparison Between Perceptual and Imagery Conditions

To explore the specific differences between the perception and imagery tasks, the PET data from each of these conditions were subtracted from one other. The results are shown in Table 4 and panel IV of Figure 1. Only 7 regions of CBF change were identified statistically in the perception-imagery subtraction. Two regions of CBF increase were found within the inferior frontopolar cortex, one in each hemisphere (foci 1 and 2 in Table 4; visible in the second horizontal section of panel IV at $z = -10$).

These regions are not quite symmetrically located, as the right-side peak is more laterally placed than the left-sided one, but they both likely extend into the frontopolar cortex of area 10. In addition to these areas, two further regions were also significantly activated in this comparison, one in the right posterior thalamus (visible in the first horizontal view of panel IV, at $z = 8$) and the other medially located in the subcallosal portion of the cingulate gyrus (not visible in the figure).

Two further areas were weakly activated. The first lies within the right hippocampus (visible in panel IV in the horizontal section at $z = -10$; x, y, z , coordinates: 28, -23, -11, $t = 2.88$), and the other in the right uncus (not visible in the figure; coordinates 27, 10, -26; t -value 3.00). Neither of these regions is reported in the table since they fell below the statistical criterion established by our exploratory search, and since they had not been specifically predicted (see discussion).

Regions of CBF decrease in this subtraction were limited to the superior temporal gyrus bilaterally, extend-

Table 4. Regions Activated in Imagery Task as Compared with Perceptual Task^a

Region	Brodmann area	Coordinates			t-value
		x	y	z	
Blood flow increases					
1. Left inferior frontopolar	10/11	-12	60	-8	4.22
2. Right inferior frontopolar	10/11	34	53	-11	3.99
3. Right posterior thalamus	—	9	-23	8	4.17
4. Subcallosal gyrus	25	3	12	-15	4.05
Blood flow decreases					
5. Left posterior STG	22/42	-50	-21	5	10.54
6. Right posterior STG	22	59	-16	2	8.96
7. Right posterior STG	42	55	-26	11	8.67

^aActivation foci (blood flow increases and decreases) for subtraction of imagery condition minus perceptual condition. For other details see footnote to Table 2.

ing to the vicinity of the primary auditory cortex. This result is to be expected, as real auditory input was provided during the perceptual task, whereas no such input was present in the imagery task. Thus, CBF decreases in this context simply reflect the presence of auditory stimulation in the perceptual condition. As expected, no areas in the visual cortices demonstrated significant CBF changes, since the visual stimulation was identical in both conditions, and no specific visual judgment was required in either one.

DISCUSSION

To summarize the results, the PET data obtained in this study strongly support the prediction that imagery processes share a substantial neural substrate with corresponding perceptual processes, since many of the same cortical and subcortical regions were activated in the perceptual task as in the imagery task. More specifically, we found evidence that auditory imagery for songs is associated with bilateral neuronal activity in the secondary auditory cortices within the superior temporal gyri, as expected based on the notion that processes within these regions underlie the phenomenological impression of imagined sounds. The results are also in accord with the prediction that regions of the right frontal lobe participate in judgments involving pitch comparisons. Other areas engaged in both perception and imagery tasks include areas in the left frontal and parietal lobes, as well as the supplementary motor area, which will be discussed in greater detail below.

Hearing a real sound is not, of course, identical to imagining it. Thus, even though comparison of perceptual and imagery tasks to the control task showed many similarities, the direct comparison of perceptual and imagery tasks enabled us to look at differences between these two conditions. The results of this comparison

suggest a unique aspect of auditory imagery for songs involving the contribution of regions in the subcallosal area and inferopolar aspect of both frontal lobes.

Contribution of Temporal Neocortex to Auditory Imagery

The fact that CBF increases within the superior and middle temporal gyri could be detected in the imagery-visual baseline condition is notable in that no overt auditory input was present in either condition. Cortical neurons within the superior aspect of the temporal lobe are known to be responsive to external auditory stimulation, based not only on physiological studies with animals (Brugge & Reale, 1985), and electrical stimulation studies in humans (Penfield & Perot, 1963), but also on PET studies using various types of auditory stimuli (Démonet et al., 1992; Petersen et al., 1988; Wise et al., 1991; Zatorre et al., 1992, 1994). It is therefore reasonable to conclude that in the absence of exogenous input, CBF increases in these areas reflect endogenous auditory processing (i.e., imagery).

It should be emphasized, however, that the temporal-lobe activation in the perceptual-visual baseline comparison incorporated primary auditory cortex and extended well into association cortical regions (see Fig. 1, top of panel D). In contrast, this was not the case for the imagery-baseline comparison (see Fig. 1, bottom of panel D): CBF increases in that case occurred exclusively in association cortex (and were of lower relative magnitude). This distinction may be important, and supports the idea that primary sensory regions are responsible for extracting stimulus features from the environment, while secondary regions are involved in higher-order processes, which might include the internal representation of complex familiar stimuli.

The finding that CBF changes occurred bilaterally, in

both the perception-visual baseline and imagery-visual baseline comparison, would be consistent with the fact that the songs to be generated contained both phonetic and tonal information. From cortical stimulation studies, it has been reported that various types of musical sensations, including sung speech, can be elicited from stimulation of either the left or right superior temporal gyrus (Penfield & Perot, 1963). There is also experimental evidence from research with temporal-lobe patients that recognition memory for the tonal component of a song can be affected by resection in either left or right temporal lobe (Samson & Zatorre, 1991). It seems likely, therefore, that temporal neocortex in both hemispheres participates in the internal representation of sung speech.

Notwithstanding the foregoing comments, it is important to emphasize that the peak CBF increases were asymmetrically distributed across the left and right temporal areas in comparison of the imagery task to the baseline condition (see bottom of panel D). The left temporal regions fell posteriorly, roughly within the boundaries of Wernicke's area (e.g., as defined from cortical stimulation data by Penfield & Roberts, 1959), with no CBF increases detected in the anterior portion of the left superior temporal gyrus. On the other hand, areas of CBF increase were found both posteriorly and anteriorly in the right superior temporal area (foci 3 and 4 in Table 2). It is tempting to speculate that this asymmetry may be related to different aspects of imagery for sung speech, with the left posterior regions contributing more to the speech-specific (e.g., phonetic) representation, while the regions in the right temporal lobe could be associated with the pitch information. This conjecture must remain just that until direct evidence can be adduced in its favor, but it would be consistent with a great deal of evidence (summarized in the introduction) supporting the importance of right temporal-lobe mechanisms in various aspects of pitch processing. The complementary role of left posterior temporal areas in speech-specific processes is also supported by data from several PET studies (Wise et al., 1991; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Paulesu, Frith, & Frackowiak, 1993), all of whom reported left posterior temporal CBF increases during verbal tasks with no auditory input (silent verb generation and visual word rhyme judgments).

The difference in location between left and right temporal-lobe activations may also be relevant to explaining a difference between the findings of the present study and those of Zatorre and Halpern (1993). The latter investigation reported that right temporal-lobe resection impaired pitch judgments of real or imagined songs but that similar left-side resection had no deleterious effect. Both experiments point to the role of the right temporal lobe in imagery for songs, and so to that extent they are in good agreement. However, based on the lesion study one might conclude that the left temporal cortex plays

no role in such judgments, and that it therefore should not have shown any CBF increases under the present conditions. One explanation of this apparent inconsistency is that left temporal cortex may participate in the task, but is not essential to its correct accomplishment; thus, it is activated, even though a lesion there has no effect on performance.

Another possible explanation for the partial discrepancy is that the extent of cortical excision in the epileptic patients tested in the previous study was confined to the anterior portion of the temporal lobe (typically 5 to 6 cm back from the temporal pole). Thus, resection would have included that portion of the right superior temporal gyrus activated in the imagery condition, but would have spared the more posterior regions of the left temporal lobe that demonstrated CBF increases in the present study. If our hypothesis is correct that the activation of the anterior right temporal region reflects imagined pitch processing, then excision of this area would be expected to lead to pitch imagery deficits, whereas excision of the corresponding area in the left temporal lobe, which was not activated, would not.

Role of Frontal Cortical Mechanisms in Song Perception and Imagery

Based on previous studies, we had made the prediction that judgments requiring subjects to process pitch information and to hold it in working memory would include a contribution from right frontal-lobe regions. This prediction was partially upheld by the results of the directed search, which yielded two such areas in the perceptual task, and one in the imagery task (see Table 2). These regions are not identical to those observed in a pitch memory task by Zatorre et al. (1994), particularly with respect to the most inferior right frontal peaks observed in that study (within area 47). However, some of the mid-frontal regions described by Zatorre et al. (1994) are within reasonable proximity (< 2 cm) of the mid-frontal foci obtained in the present study. Similarly, the right frontal-lobe CBF increases documented by Zatorre et al. (1992) during judgments of pitch of spoken syllables were also within 2 cm of the foci found in the present study.

Increased CBF in area 46 and adjacent area 9 has been linked to the active monitoring of information within auditory-*verbal* working memory (Petrides, Alivisatos, Meyer, & Evans, 1993). Increases in the same region, but with a rightward asymmetry, have been observed in auditory-*tonal* working memory tasks: during a tone monitoring task (Perry et al., 1993) and during pitch judgments within novel melodies (Zatorre et al., 1994). The present results for pitch judgments within familiar melodies show increases that are located more inferiorly, probably within the depth of the inferior frontal sulcus, at the border of areas 45 and 9, and, more posteriorly, probably within area 44. Pitch judgments within familiar

melodies do not require the active monitoring of a series of unpredictable events (as does monitoring novel melodies), but rather allow reference to a representation stored in long-term memory. Thus, the present results are compatible with a hierarchical view of working memory, in which more inferior lateral frontal areas are important for maintaining sensory information, whereas more superior frontal areas are required only when higher-level functions such as monitoring must be applied to the contents of this working memory store (Petrides, 1991).

In addition to the predicted areas of activation in the right frontal lobe, several regions were also identified in the left frontal lobe in both the perception and imagery subtractions (panel II, left side). The mid-frontal region seen in these subtractions is approximately symmetrical to the mid-frontal foci observed in the right hemisphere (panel II, right side). However, contrary to our predictions, CBF increases appeared to be equally or even more reliable within the left than within the right frontal lobe in the present study. This bilateral activation in area 45/9 may be related to the processing of the integrated linguistic and melodic content of songs.

The left anterior inferior frontal region that was also activated in both subtractions (foci 14 and 15 in Table 2) falls at the anterior border between area 47 and frontopolar area 10, and is not matched by a symmetrical region in the right hemisphere (see panel II). The left-sided asymmetry of these inferior frontal foci leads us to propose that they are intimately related to linguistic function. In fact, both imagery and perception tasks require the generation and/or monitoring of the text of the song based upon the two visual words presented as cues. Several previous PET studies have reported left inferior frontal activation in this general vicinity during tasks that require generating a semantically associated response based upon a single visual or auditory word (Petersen et al., 1988, 1989; Raichle et al., 1994). More recent data (Klein, Milner, Zatorre, Myers, & Evans, 1995) also indicate that generating a verbal response, whether semantically or phonologically related, activates regions within the left inferior frontal gyrus. Putting these facts together, therefore, we tentatively conclude that the engagement of cortical areas in the left inferior frontal lobe may reflect aspects of the linguistic processing that is inherent to both song imagery and perception tasks.

Similarity Between Activation Patterns for Perception and Imagery

Apart from the presence of frontal and temporal-lobe activation in both perceptual and imagery tasks, a number of other areas also showed significant CBF increases in both conditions. Although we had not made specific anatomical predictions about these regions, it is notable that almost every region activated in one subtraction was also found to be present in the other (Table 2).

Among these is a region in the left parietal lobe, in the

vicinity of the supramarginal gyrus, which was consistently identified (Fig. 1, panel II). These areas may be involved in a number of different subprocesses necessary to complete our perceptual and imagery task. For example, since the pitches to be compared were cued by visual words, it seems clear that some relatively complex cross-modal mechanism would be called into play. It is possible that the left parietal region represents part of this process, since parietal cortex may subservise certain types of multimodal operations.

Two other sets of regions also showed increased CBF in both real and imagined pitch judgment conditions, one in the SMA and the other in the midbrain. The activation of the SMA (Fig. 1, panel III) is particularly interesting, given its role in motor processes. This region has consistently shown CBF increases during various types of motor tasks, including speech production tasks (Petersen et al., 1988, 1989). Of greatest relevance to the present study, SMA is also involved when a motor task is only imagined, rather than overtly executed (Roland, Larsen, Lassen, & Skinhoj, 1980; Rao et al., 1993); moreover, conditions under which subjects generate internal speech have also yielded clear CBF increases in the SMA (Paulesu et al., 1993; Wise et al., 1991). The present finding of SMA activation may therefore be taken as evidence that there is a motor component to the song imagery task. This area was also activated in the perceptual task (but at a much lower magnitude); motor processes may therefore also be involved even when subjects are actually hearing the stimulus. Recent findings from our laboratory (Perry et al., 1993) on simple and complex tonal vocalization tasks also support a role for the SMA in the vocalization of sung pitches. This result implies that the SMA is part of a substrate for both overt and covert vocalization, and therefore supports the idea that imagery for songs includes not only an auditory component ("hearing the song in one's head") but also a subvocal component ("singing to oneself").

The midbrain areas activated in these subtractions are difficult to interpret in a straightforward manner, as many small nuclei are located close together in this portion of the midbrain. One possibility is that they represent activation of deep layers of the inferior colliculus. Virtually identical midbrain foci observed by Zatorre et al. (1994) during comparison of the first and last notes of novel melodies were attributed to collicular activity. Perry et al. (1993) also reported similar midbrain activation in a simple vocalization task. The spatial resolution of PET does not permit a definitive resolution of these issues. However, both previous studies that found midbrain activity, as well as the present one, involved processing of auditory inputs. It may therefore be most parsimonious to assume that the CBF increases in this region indeed reflect neuronal activity in the inferior colliculus, which receives strong afferent auditory input as well as efferents from auditory cortex (Aitkin, 1986). Furthermore, the theoretically interesting finding in the present study

is that both perception and imagery tasks resulted in similar midbrain CBF changes, implying a functional similarity in the contribution of this region to both tasks.

Processes Uniquely Associated with Musical Imagery

As already mentioned, although many of the same regions appear to be involved in making judgments about tonal patterns, whether imagined or real, this does not imply that the underlying mechanisms are identical. Indeed, both psychological models and common sense dictate that imagery must entail at least some different processes. These differences are best understood in light of our findings in the direct comparison between imagery and perception (Table 4). First, we note that except for primary auditory areas, none of the regions identified in Tables 2 and 3 shows CBF changes in this subtraction, presumably because they have been subtracted away. The CBF decreases that were found in primary and surrounding auditory cortices are not surprising, given that there was real auditory input in one condition but not in the other. The most salient new result in this subtraction is that two inferior frontopolar regions showed significant CBF increases in imagery over perception (Fig. 1, panel IV). It would be premature to assign a definitive functional role to these areas based upon our present limited knowledge. However, as an initial hypothesis, it is logical to propose that this activation pattern may reflect some aspects of retrieval and/or generation of auditory information from long-term memory.

Functional analysis of the two tasks would suggest that one major difference between them is that in the perceptual task the sensory information upon which to base the pitch judgment is presented to the subject, whereas in the imagery task this information must be sought from a memory store, and then "played out in the mind's ear" to make the pitch judgment. In our task, the song titles, together with the target words presented on each trial, would act as direct cues for subjects to retrieve the appropriate stored representation and then generate it. There is scant evidence in the neuropsychological literature with respect to the neural substrate for this specific type of process. Nonetheless, many investigators have reported that inferomedial frontal lesions result in serious memory difficulties under many circumstances (Talland, Sweet, & Ballantine, 1967; Volpe & Hirst, 1983; Whitty & Levin, 1960), although this has not been observed in all individuals with such damage (Eslinger & Damasio, 1985). Experimental data from monkeys with ventromedial frontal lesions have also demonstrated impairments in visual recognition memory (Bachevalier & Mishkin, 1986).

The relevance of such data to the present findings is indirect, but they do support the idea that these regions of the prefrontal cortex form part of a circuit underlying

memory processes. In fact, it is particularly interesting to note the neuroanatomical connections between inferomedial frontal areas and other regions known to participate in memory, particularly certain nuclei of the thalamus, which in turn receive inputs from amygdala and hippocampus (Goldman-Rakic & Porrino, 1985; Russchen, Amaral & Price, 1987). This pattern has led to the notion that the ventromedial prefrontal cortex, including the subcallosal area, constitutes a major component of a limbic system underlying memory (Bachevalier & Mishkin, 1986; Petrides, 1989).

To return to our findings (Table 4; Fig. 1, panel IV), we note that the activation pattern in this case supports this notion reasonably well: not only was there bilateral CBF increase in the inferior frontal poles, but also in the subcallosal area and in the thalamus, both to the right of midline. Moreover, the areas in the right hippocampus and uncus that were weakly activated may well be relevant, although they fell below the statistical criterion established by our exploratory search. If such results are replicable, they would add further evidence favoring the view that imagery may entail, among other things, retrieval processes from long-term memory (since any working memory component is subtracted out) that engage the proposed inferomedial frontal-hippocampal-thalamic network.

Recent PET data examining verbal memory are also partly in accord with our interpretation of these data. Shallice et al. (1994) observed right prefrontal and thalamic activation when subjects generated previously learned paired-associate words in response to a cue word, as compared to a task in which they simply repeated words. This generation task requires memory search and retrieval based upon a cue, and is thereby similar in this respect to our task, since our imagery condition requires the subject to retrieve learned information (the song) upon reading the cue words. A similar argument has recently been advanced by Haxby, Martin, Maisog, Keil, and Ungerleider (1994) for the retrieval of face memory information.

Blood Flow Decreases in Comparisons with Visual Baseline Task

A series of regions were identified to have higher CBF in the visual baseline task than in either the perceptual or imagery conditions; these are reflected as CBF decreases (Table 3), since the baseline task was subtracted from the other two. All three tasks included essentially identical visual input (see Table 1), and so it is reasonable that no regions involved in primary visual processes were found to be activated. However, since the visual baseline condition included a judgment of word length, which neither of the other two conditions did, the CBF decreases shown in Table 3 likely reflect some aspects of this process. In particular, the strong bilateral activation of inferior occipitotemporal cortex is probably re-

lated to the visual processing required to make the word length judgment (cf. Corbetta, Miezin, Shulman, & Petersen, 1993). In addition, it is interesting that areas near the left angular gyrus were activated, since this region may be involved in various aspects of decoding written text. Although reading per se would be involved in both the visual baseline task and the musical judgment tasks, the latter were considerably more difficult, and it seems likely that subjects would have devoted more resources to performing the tonal processing aspect of the task than concentrating on the visual reading component.

Conclusions

We conclude our discussion by considering how our data have illuminated our understanding of auditory imagery, as raised in our introductory comments. The striking similarities in brain areas activated by our perception and imagery tasks lead us to propose that the two tasks also share functional similarities. While we agree with Farah (1988) that this sort of investigation cannot directly address the question of the format of mental images, and it is possible that different functional representations could coexist in the same physical substrate, our data suggest that it is unlikely that auditory images exist solely as abstracted entities divorced from their perceptual origins. And as mentioned earlier, the involvement of SMA in both our tasks, but especially the imagery task, is consistent with the proposal that we engage output as well as input mechanisms when engaging in at least some kinds of "purely" mental operations.

One major area our study invites for future research is the means whereby images of familiar tunes are actually generated and maintained. Our imagery-perception subtraction suggests that bilateral frontal areas and right hippocampal and thalamic areas are related to image generation. Would these areas be involved in generation of other, nonverbal auditory representations, or in generating images in other modalities? To the extent that image generation across diverse stimuli engage similar mechanisms, we would have evidence for generalized image-generation processes, and, of course, the opposite would obtain should type of stimulus largely determine areas of activation. Also, in our study we cannot differentiate between image retrieval, generation, and maintenance; distinguishing between these on an anatomical level might help us understand how dissociable these processes are on the cognitive level.

Another area we hope to clarify in future research is the extent to which our current results were influenced by the activation of verbal as well as musical representations in our task. We are currently developing a version of our pitch comparison task that would not require reference to song lyrics, and thus could be used with familiar tunes that do not have words. Under these conditions, we might find the greater contribution of structures in the right hemisphere previously found in

musical perception tasks, compared to the mostly bilateral activation patterns we found here.

Thus we conclude that while many questions remain about how the mind internalizes the auditory world, at least to a first approximation we have evidence that hearing in the figurative mind's ear utilizes similar neuronal processes as hearing via the actual ear.

METHODS

Subjects

Twelve healthy right-handed McGill University students participated in the study after giving informed consent. Mean age of the group was 22 years, and both sexes were equally represented. Musical background varied, but none of the subjects was a professional musician. Most of them had had some musical training, typically in the form of instrumental lessons during their years of elementary or secondary education.

Stimulus Materials

The first phrase of three songs familiar to most people in North America provided the trials for the musical judgment tasks ("Jingle Bells," "Battle Hymn of the Republic," 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). Choice of stimulus trials followed the same logic as previously used by Halpern (1988a). 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 trial types. These requirements constrained the choice of songs to those with a sufficient number of unique words falling unambiguously on the required beats. The two lyrics in each pair always had different pitches.

Four trials were chosen from each of the three different songs, for a total of 12 experimental trials in each condition. Different trial types (with varying startpoints and stepsizes) were distributed across all three songs, with no systematic bias. The second pitch was higher in seven trials, and lower in the remaining five; average distance between the two pitches was 4.9 semitones. The first phrase of each song was sung in the soprano range by one of the authors, recorded, and digitized at 20 kHz on a 16-bit digital/analog converter on a Compaq 386 personal computer for later presentation.

For the visual baseline task, the same words chosen from the three songs were also used. However, they were scrambled with respect to their original order, such that no two words within a trial came from the same song. Half of the trials contained a longer word on the left, and vice versa.

Procedure

Three separate conditions were run during each of the three scanning periods (see Table 1): visual baseline, perception, and imagery, always in that order. Although each scan lasted only 60 sec, the tasks were always begun several seconds before scanning commenced, and continued after scanning, until all 12 trials had been presented. Performance data were collected on each subject on-line during scanning. The total duration of each test condition was approximately 2 min, 40 sec. Typically, scanning commenced during the third or fourth trial, and ended approximately after five or six trials had been completed.

In the visual baseline condition, words were presented on an NEC monitor suspended above the subject. On each trial, the subject viewed a pair of words positioned horizontally, and was asked to judge which word was longer (contained more letters). Subjects responded by pressing one of two keys with their right hand as soon as they had made their decision. The words were chosen from the same set as were used in the two other conditions, but were scrambled across songs such that on any given trial the words did not belong to the same song. For example, the words "SLEIGH" and "JOY," presented together on one trial for visual length judgment, belong to two different songs. To match precisely the visual input in this condition to the others, in which titles were necessary (see below), a single word was presented in the center of the screen before every four trials; this word required no response. Timing of trials in the baseline condition was adjusted to match exactly the timing of trials in the other two conditions. A total of 12 trials was presented. Several practice trials were also given prior to scanning to ensure adequate comprehension of the task. To prevent any musical associations or uncontrolled use of musical imagery during this control condition, subjects were not informed as to the nature of the subsequent conditions until after the baseline test had been completed.

In the perceptual judgment condition, subjects viewed pairs of words, this time drawn from the same song, and simultaneously listened to the song excerpt in question, presented binaurally over Eartone 3A insert earphones. Subjects were instructed to listen carefully to the song excerpt while reading the two words, and then to judge if the pitch corresponding to the second word was higher or lower than the pitch corresponding to the first word. Responses were by means of a key press with the right hand. Prior to performing the actual task, subjects were familiarized with all three stimulus songs by listening to each one several times; they then performed 12 practice trials on the pitch judgment. On each trial subjects were instructed to respond as soon as possible after the second word had been presented, even if the song was still playing. In all cases, however, the entire song excerpt was played. Thus, duration of each trial was

the same for a given song, but response latencies reflect the time for decision, and are not related to total duration of the song. Average trial duration across the three songs was 10.7 sec, with a 2-sec intertrial interval. Words appeared simultaneously with onset of the song excerpt, and disappeared when the song excerpt finished playing. The three different songs were presented in blocks of four trials each; order of songs was counterbalanced across subjects. To indicate to the subjects which song was to be heard on each block of trials, a single-word title appeared in the center of the screen prior to the four trials for that song. The title required no response, and disappeared from the screen after 2 sec.

In the imagery condition, subjects once again viewed pairs of words identical to those used in the preceding condition. This time they were instructed to perform the same pitch judgment they had made previously, but no auditory input was provided. Instead, subjects were encouraged to imagine the song, and to perform the pitch decision based on that. To preserve the identical timing of stimuli and trials as in the other two conditions, the words remained on the screen during each trial for the same length of time as had been required to play the song excerpt in the perceptual condition. Subjects were instructed to respond as soon as they knew the correct answer, however. Twelve practice trials were performed prior to scanning, followed by the 12 trials during which scanning was conducted. As in the other conditions, titles were presented prior to the four trials for each song. In this condition the titles were of particular importance, since they allowed the subject to select the appropriate song to imagine on each trial.

Note that the visual input was essentially identical in all three conditions, as was the motor response. Note also that the nature of the judgment (pitch higher or lower) was identical in the last two conditions, the only difference being that in the perceptual condition the judgment is made on a real auditory input, whereas in the imagery condition the judgment must be based upon some internally generated representation.

PET and MRI Scanning

PET scans were obtained using the Scanditronix PC-2048 system, which produces 15 brain image slices at an intrinsic resolution of $5.0 \times 5.0 \times 6.0$ mm (Evans, Thompson, Marrett, Meyer, & Mazza, 1991b). Using the bolus $H_2^{15}O$ methodology (Raichle et al., 1983) without arterial blood sampling (Fox & Raichle, 1984), the relative distribution of CBF was measured in each of the three conditions described above. Individual high-resolution MRI studies (63 slices, 2 mm thick) were obtained from a Philips 1.5T Gyroscan and coregistered with the PET data (Evans et al., 1991a). An orthogonal coordinate frame was then established based on the anterior-posterior commissure line as identified in the MRI volume (Evans et al., 1992). These coordinates were used to

apply a linear resampling of each matched pair of MRI and PET datasets into a standardized stereotaxic coordinate system (Talairach & Tournoux, 1988). PET images were reconstructed using a 20-mm Hanning filter to overcome residual anatomical variability, normalized for global CBF and averaged across subjects for each activation state. The mean state-dependent change image volume was then obtained, and converted to a *t*-statistic volume by dividing each voxel by the mean standard deviation in normalized CBF for all intracerebral voxels (Worsley, Evans, Marrett, & Neelin, 1992). Individual MR images were subjected to the same averaging procedure, such that composite images volumes sampled at $1.34 \times 1.72 \times 1.50$ mm in *x*, *y*, and *z* dimensions were obtained for both *t*-statistic and MRI volumes. Anatomical and functional images were merged to allow direct localization on the MR images of regions with high *t*-values.

Statistical Analysis

To evaluate the predictions, two levels of statistical threshold were used, corresponding to exploratory (data-driven) vs. directed (hypothesis-driven) search. First, the exploratory search was performed on all three subtractions. The presence of significant focal changes in CBF was tested by a method based on 3-D Gaussian random field theory (Worsley et al., 1992). Values equal to or exceeding a criterion of $t = 3.5$ were deemed statistically significant ($p < 0.0004$, two-tailed, uncorrected). Correcting for multiple comparisons, a *t*-value of 3.5 yields a false positive rate of 0.58 in 200 resolution elements (each of which has dimensions $20 \times 20 \times 7.6$ mm), which approximates the total volume of cortex scanned.

Two types of directed searches, one resulting from anatomically based predictions and the other from functionally based predictions, were then undertaken to test several separate hypotheses, as described above. The first two analyses involved searches within specific anatomically defined areas, in accord with the predictions made a priori. The hypothesis of temporal-lobe activation during the imagery task (as compared to the visual baseline) was tested by applying a *t*-threshold of 2.68. This threshold corresponds to an uncorrected *p*-value of 0.02, which yields a false-positive rate of 1 per total volume scanned within the temporal lobes [which account for approximately 23% of all cortex (Blinkov & Glezer, 1968), or fewer than 50 resolution elements]. The same *t*-threshold was used to search within the right frontal lobe for the presence of predicted CBF increases.

The logic behind the second type of directed search requires elaboration. Recall the hypothesis we wished to test: that perception and imagery share similar neural substrates; we reasoned, therefore, that for any given region activated in the perception-baseline comparison, there should also be a corresponding region activated in the imagery-baseline subtraction, and vice-versa. This

approach enabled us to generate local predictions: based upon examination of the regions activated above the 3.5 *t*-threshold in one subtraction, we searched for the presence of equivalent regions in the other subtraction, using the same *t*-cutoff of 2.68 that was used in the first directed search. The presence of any such matched peak locations would then support the prediction of functional equivalence across conditions.

Acknowledgments

We thank the technical staff of the McConnell Brain Imaging Unit and of the Medical Cyclotron Unit for their invaluable assistance, and P. Neelin and S. Milot for their technical expertise. This research was funded in part by Grants MT 11541 and SP-30 from the Medical Research Council of Canada, by a Chercheur-Boursier award to the first author from the Fonds de la Recherche en Sante du Quebec, and by the McDonnell-Pew Cognitive Neuroscience Program.

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Note

1. Results reported in this paper are for all 12 participants. A separate analysis of the PET activation data was also undertaken for the nine subjects who performed best on the imagery task (mean performance of this subgroup was 82% correct), in an attempt to remove any noise that might be contributed by those whose performance was poor, and who therefore might not have been performing the task as intended. This analysis revealed a pattern of results virtually identical to that of the group as a whole, and therefore will not be discussed further.

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