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Cerebral Substrates of Musical Imagery

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ABSTRACT: Musical imagery refers to the experience of “replaying” music by imagining it inside the head. Whereas visual imagery has been extensively studied, few people have investigated imagery in the auditory domain. This article reviews a program of research that has tried to characterize auditory imagery for music using both behavioral and cognitive neuroscientific tools. I begin by describing some of my behavioral studies of the mental analogues of musical tempo, pitch, and temporal extent. I then describe four studies using three techniques that examine the correspondence of brain involvement in actually perceiving vs. imagining familiar music. These involve one lesion study with epilepsy surgery patients, two positron emission tomography (PET) studies, and one study using transcranial magnetic stimulation (TMS). The studies converge on the importance of the right temporal neocortex and other right-hemisphere structures in the processing of both perceived and imagined nonverbal music. Perceiving and imagining songs that have words also involve structures in the left hemisphere. The supplementary motor area (SMA) is activated during musical imagery; it may mediate rehearsal that involves motor programs, such as imagined humming. Future studies are suggested that would involve imagery of sounds that cannot be produced by the vocal tract to clarify the role of the SMA in auditory imagery.

KEYWORDS: Musical imagery; Behavioral studies; Cognitive neuroscience

INTRODUCTION

Many people experience the sounds of music in two distinct but related manners. Listening to live or recorded music is, of course, the way we commonly think of enjoying music. However, many people also report that they can reexperience music by imagining it in their heads. This can be pleasurable or not, depending on the circumstances, but in either case, the experience appears to be a vivid one, even among people untrained in music. In fact, I am often asked how to “stop” a tune from obsessively intruding into everyday thoughts. Highly trained musicians report that they can use auditory imagery to help them in their everyday tasks, such as “hearing” music as they read musical notation.

In recent years, I have studied the characteristics of this auditory imagery experience, initially from a behavioral perspective and more recently from a cognitive neuroscientific perspective. I have been most interested in the auditory imagery experiences of untrained or moderately trained musicians, although many interesting questions derive from considering experts as well. My paradigms and experimental

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logic have been derived partly from the more extensive literature in visual imagery; other approaches have been created anew as the need arose. In studying any mental imagery, the challenge is to externalize what is essentially an internal experience to examine what it means to have, in the case of musical imagery, a “tune inside the head.”

BEHAVIORAL APPROACH

In the 1980s, I carried out an extensive series of experiments with young adult college students to explore how auditory imagery of music may be characterized. I explored the mental representation of *tempo*^{1,2} and *pitch*³ in familiar songs. To study representation of tempo, I asked participants to set their preferred tempo for a familiar tune being played on a computer. The program allowed continuous adjustments of tempo until the tune sounded right to the listeners. I then asked them to imagine the same tunes and set a metronome to the imagined tempo. Tempo settings were highly correlated in the perception and imagination tasks. I also showed that people can manipulate the tempo of an imagined song, within limits, to make it “sound” very fast or very slow. Finally, I showed that musicians showed impressive consistency when asked to tap out the tempo of an imagined song on one day and again two to five days later (average standard deviation = 1.4 metronome settings over four attempts), although nonmusicians were somewhat less consistent.

In the domain of pitch, I asked people to imagine familiar songs and hum the starting note corresponding to their auditory image of the song. In a second task, I asked people to think of the starting note of a familiar song and select that note from a piano keyboard (all the tunes were popular folk or children’s songs, unlikely to have been heard with any particular starting note in the past). Once again, consistency of pitch production or selection was impressive for musically unselected participants, even over a delay of several days (average standard deviation = 1.25 semitones for production, 2 semitones for selection over four attempts). Finally, I asked people to rate how similar a played note was to the opening note of a tune they had imagined and produced a few days earlier. The person’s own preferred note was rated quite highly, as were starting notes a major third lower, minor third higher, and a perfect fifth higher than the preferred notes (these are all musically coherent intervals). However, subjects rated notes only one semitone higher or lower than their preferred note as dissimilar to their imagined pitch, showing a fairly acute sense of pitch representation.

These behavioral tasks seem to show a veridical representation of characteristics particular to music. However, I also explored the *extension in time* that is characteristic of almost all auditory stimuli and thus ought to be captured in auditory imagery. I explored this temporal aspect in the subsequent cognitive neuroscientific studies of auditory imagery for music.

To begin, I modified a paradigm introduced in visual imagery by Kosslyn, Ball, and Reiser.⁴ In that study, they asked people to learn a map of an imaginary island. Pairs of features on the island were presented, and subjects had to “mentally scan” between them. Latencies to do so were highly correlated with actual distance between the features on the map, suggesting that the mental representation was preserving an analogue of space.

To extend this paradigm to musical imagery,⁵ I selected a number of familiar songs where unique lyrics fell on specified beats of the tune. For instance, the first line of the American national anthem, "The Star Spangled Banner," is, "Oh, say can you see by the dawn's early light?" In the most relevant study in that series, I presented the title of the song, followed by one lyric from the first line of the song, followed by the second lyric. The task was mental pitch comparison: Was lyric 2 higher or lower in pitch than lyric 1? No singing or humming was allowed. The lyrics were either close together ("Oh" and "can") or far apart in the actual tune ("Oh" and "dawn's"). I found that this was a difficult task for my musically unselected subjects; nevertheless, reaction times increased nearly linearly as the separation in beats between the two lyrics increased. Subjects reported using auditory imagery to accomplish the task, even though they were not instructed to do so. The consistency of reaction time data with this report strongly suggested to me that this task had captured the extension in time of auditory imagery for music.

COGNITIVE NEUROSCIENTIFIC APPROACH

The behavioral studies cited above have in common the logic that if responding to an imagined stimulus resembles responding to a perceived stimulus, we may conclude that imagery is a particularly vivid and veridical form of mental representation. However, this comparison between imagery and perception may be strengthened by examining the similarities in neural underpinnings of the two processes. This approach is complementary to the behavioral approach in that at least to some extent behavioral responses might be influenced by external influences such as demand characteristics or experimenter expectancies.⁶ However, it is unlikely that people can influence their own brain structures or activities. We may thus look to similarities in the brain loci involved in auditory imagery and perception to gain a better perspective on the processing of similarities and differences in the two types of tasks. An argument for this approach is well articulated by Farah⁷ for the visual domain.

The strongest hypothesis is of course that the brain areas would be identical in auditory imagery and perception. This may serve as a guiding null hypothesis, but we would not in reality expect this amount of overlap; people other than those hallucinating can tell the difference between imagining and hearing a song. However, the extent of overlap may tell us how similarly the brain processes hearing and imagining hearing. Brain areas uniquely active in imaging tasks can by extension inform us as to the additional or alternative processing demands imposed in imagery by having to, in effect, create as well as perceive the stimulus.

As noted above, the approach has been reasonably successful in the visual domain. For instance, Kosslyn *et al.*⁸ used positron emission tomography (PET) to measure brain activity during parallel perceptual and imagined visual tasks. They found quite a few areas activated in common, even to the extent that varying the size of the presented object and varying the size of an imagined object activated similar brain areas in similar ways. Few people have looked at auditory imagery using parallel perceptual and imagery tasks. However, the neural structures responsible for some aspects of musical perception are well defined. My partner for most of the studies described in the following sections has been Robert Zatorre. When we began our first study, he and Samson, among others, had already established that a number of

musical tasks are impaired after lesions in the right temporal neocortex.^{9–12} Thus our initial hypothesis was that the same region would be involved in musical imagery tasks that resembled musical perceptual tasks.

What follows are brief descriptions of a series of studies using three different cognitive neuroscience techniques to investigate the cerebral substrates of musical imagery. The first is a lesion study, which can give information about the necessary involvement of some brain areas in an activity. The next two studies use PET paradigms to investigate brain areas that are active in auditory imagery for verbal and nonverbal songs, respectively. Finally, I describe a study using transcranial magnetic stimulation (TMS) that returns to the logic of the lesion studies, in that a brain area in normal people is disrupted for a brief time and the ensuing decrements in performance are measured.

LESION STUDY

My first study with Zatorre¹³ examined the effect of right temporal lobectomy on performance of a mental pitch comparison task that I described earlier.⁵ Participants were patients having undergone surgical excision of the anterior portion of the right or left temporal lobe (excluding the primary auditory cortex) for relief of intractable epilepsy. We tested the patients either two weeks after surgery (approximately two-thirds of the patients), or at follow-up medical appointments a year or more after surgery. A control group consisted of age- and education-matched neurologically normal individuals. Preoperative testing insured that the patients had typical language representation. All participants were familiar with the songs we used, and they all passed a brief test of pitch discrimination ability.

The imagery task was essentially the one described earlier. Participants saw a title of a song, for instance, “Jingle Bells,” followed by the first line of the song, with two words in capital letters, such as “Dashing through the SNOW, in a one-horse open SLEIGH.” They decided if SLEIGH was higher or lower in pitch than SNOW, and pressed a button to answer. The parallel perception task, which was always presented first, was the same except that the song, sung with lyrics, was actually presented to participants from a digitized sound file while they made their judgment. Accuracy and reaction times were recorded. The reaction time pattern replicated the pattern I had shown earlier⁵ of increasing latency with increasing distance in beats between the lyrics, although accuracy turned out to be the measure of interest here.

Accuracy results are shown in FIGURE 1. It is clear that the imagery task was more difficult than the perception task, as expected. It is also clear that the right temporal lobectomy group was impaired relative to controls on both the imagery and perception tasks, to an equal extent, whereas the left temporal lobectomy group was impaired on neither.

This pattern was consistent with our hypothesis that the right temporal lobe is an important mediator of musical imagery, as it has been shown to be for musical perception. We considered which particular aspect of the task was most likely to have been subserved by the right temporal lobe. All participants passed a simple tone discrimination task, so a deficit in pitch comparison itself was unlikely to be the cause of the group’s impairment. Furthermore, this group was impaired in the perception task, when the tune did not need to be generated from memory, making memory re-

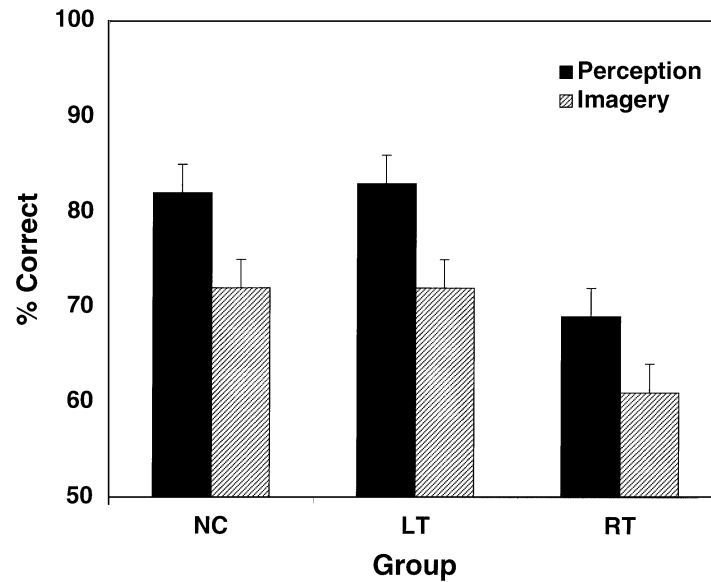


FIGURE 1. Mean percent correct, plus standard error, for normal control subjects (NC), patients with left temporal lobe excision (LT), and patients with right temporal lobe excision (RT) in perception and imagery tasks in the lesion study.

trieval unlikely to be the right temporal lobe's crucial contribution. Thus we concluded that the right temporal deficit is likely to be primarily due to a difficulty in remembering the (imagined) pitches to be compared.

PET STUDIES

Lesion studies allow one to draw conclusions about the areas *crucial* to perform certain tasks. They do not, however, allow any conclusions about what brain areas are *active* in the tasks, whether or not they are crucial. Lesion studies also are confined to the particular excisions made available by accidents of nature or deliberate surgery. If we want to study the somewhat broader question of what areas throughout the brain are active during imagery and perception tasks, then functional brain imaging technology is a useful addition to our investigations. Another advantage of brain imaging techniques is that neurologically normal participants can be studied, in contrast to the neurologically abnormal people studied, by definition, in lesion work. In our next study, Zatorre and I¹⁴ used positron emission tomography (PET) to observe the changes in cerebral blood flow (CBF) as participants performed musical imagery tasks similar to the ones already described.

In this approach, tasks are set up in a series so that more complex tasks include elements of the simpler tasks presented to subjects. Subtracting the activation observed in the simpler task from that observed in the more complex task allows one to isolate activation unique to the critical components of the more complex task. For

instance, in almost any cognitive task, the brain activation due to the simple registration of auditory or visual stimuli, and the motor activation involved in pressing buttons, are not of major interest. Therefore, control tasks are often presented that involve simply seeing or hearing a stimulus and pressing a button in response. Subtracting activation due to these lower-level components gives a better indication of the mental work involved in the tasks of more interest.

In our study, we presented the imagery and perception tasks that we used previously,¹⁴ except we presented single words instead of complete first lines from the songs. A third task was meant to control for such simpler tasks as visual perception and button pressing. This visual baseline presented pairs of words used in the imagery and perception task, but each pair member came from a different song. For each pair presented on the screen, participants had to judge which one was longer in length and press a button for their choice. Because the pairs were scrambled, we assumed listeners would not be reminded of songs; thus auditory imagery should not be activated. But over the course of the baseline condition, all words used in the main task would be seen. All songs were very familiar to the subjects, who were 12 healthy right-handed young adults. Most had some musical training but none were serious musicians.

All participants underwent a magnetic resonance imaging (MRI) scan in order to allow us to later localize CBF activity to the appropriate anatomy for each person. For the test session, the three tasks were explained and there was a short practice session. After being placed in the scanner, the subjects received an injection of radioactively labeled water ($H_2^{15}O$) required to index the CBF activity, and performed the visual baseline task. This was then repeated for the perception task and then the imagery task, in that order.

As expected, people were more accurate on the perception task than the imagery task, and once again reaction times in both imagery and perception increased as a function of distance between the lyrics in the real tunes. The analysis then proceeded by subtracting the activation shown in the baseline task from the perception task and also the baseline task from the imagery task. A graphic representation of the results is shown in panel I of FIGURE 2. Here we see in the upper part of panel I that the primary auditory area (located in superior temporal gyrus, or STG) is quite active when listening to sounds, as one would expect. More interesting is the fact that several areas of the STG adjacent to the primary auditory cortex (secondary auditory cortex) are also active when people were just imagining the sounds (lower part of panel I). Panel II shows several other areas of correspondence between the imagery and perception tasks: several areas in the frontal lobe were active in both tasks, as was one area in the parietal lobe. Panel III shows activity in the supplementary motor area (SMA, involved in motor planning) in both tasks, stronger in imagery than perception. When we subtracted the activity in the perception task from that in the imagery task, only four brain areas were unique to imagery, two of which are pictured in panel IV. These two areas, the thalamus and inferior frontopolar areas, are known to be involved in memory functions, and may be associated with the extensive memory demands attached to the imagery task.

The results of this study supported several of our earlier ideas but also raised new questions. Consistent with our lesion study,¹³ several areas of the temporal lobe classified as secondary auditory cortex were activated when people were carrying out

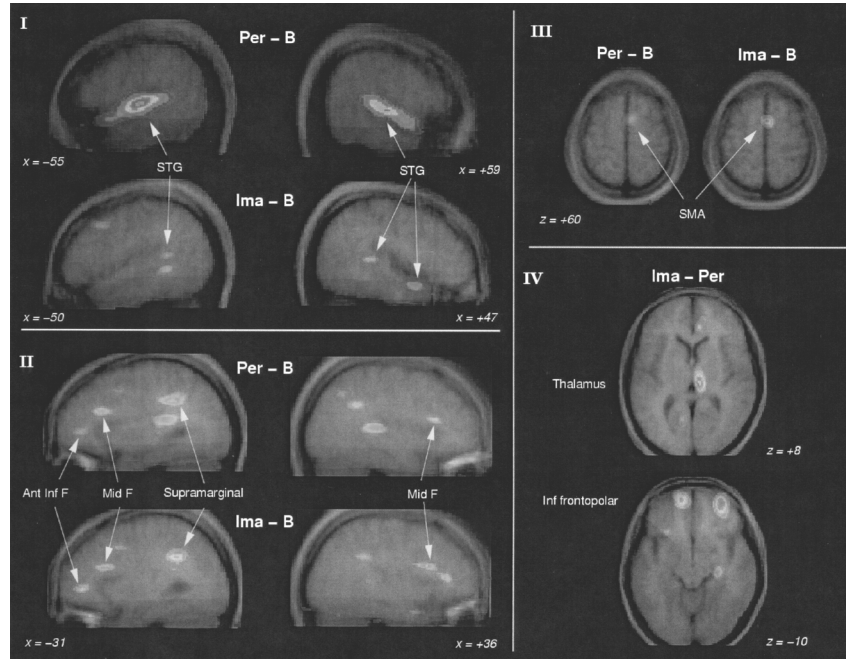


FIGURE 2. See Plate 2 in color section. Brain areas showing activation in the perception minus baseline, imagery minus baseline, and imagery minus perception conditions of the verbal tune PET study.

mental pitch comparisons, in the absence of any overt auditory stimulation. Thus we concluded that the right STG is both *active* during such tasks (shown by the PET study), as well as *necessary* for carrying out the task successfully (shown by the lesion study). We were also not surprised by the areas of activation in the frontal lobes. Activation in frontal areas similar to the ones seen here was found by Zatorre *et al.*¹⁵ in a PET study in which participants had to judge relative pitches of notes in novel (perceived) tunes, and in a study where the pitches of spoken syllables were compared.¹⁶

Two results were more unexpected. First, contrary to the literature cited earlier that consistently showed right-sided asymmetries in brain activation during music processing,¹⁵ and deleterious consequences of right-sided lesions for music processing,⁹⁻¹³ here almost all the activated areas were bilateral, except for right-sided activation in the thalamus. A second unexpected finding was the strong activation of the SMA during imagery even though subjects were not actually producing any motor movements. Both these findings might be related to the fact that the stimulus songs all had words, which participants had to access during the tasks. The left frontal regions have been implicated in various overt verbal tasks,^{17,18} so that the bilateral activation seen here might be reflecting the dual nature of the stimulus to be processed (words plus music). Activation of the SMA has been observed when subjects are asked to generate internal speech¹⁹ and to overtly vocalize music.²⁰ Thus

the SMA activation observed here in our imagery task may reflect a subvocal rehearsal process of either words or music to support performance on an otherwise difficult task.

In light of these issues, our next PET study²¹ used only nonverbal tunes. We were interested to see whether removing words from our task would lead to more right-sided activation than we saw earlier, consistent with various findings in the music perception literature. We also wanted to see if SMA would be active even when potential rehearsal devices would not involve words. Finally, we wanted to try a different type of imagery task to see if our results would generalize over paradigms.

To this end, we developed a stimulus pool of tunes that were familiar but did not have lyrics. These included movie and television themes, classical excerpts, and miscellaneous tunes such as the Westminster (Big Ben) chimes. In our main task (cue/imagery) we played the first few notes of a theme as a cue, and asked participants to imagine the theme to the end of its first phrase (this task and the materials had been presented to people in advance of scanning to familiarize them with task parameters). To have a behavioral index of auditory imagery, the played excerpts differed in length. If subjects were carrying out instructions as we intended, latency to press the button should increase from our shortest (2.2 s on average) to longest excerpts (6.2 s on average).

We also had some control tasks. For these, we took the first few notes of each real tune, and scrambled the note order so that the cue did not elicit a memory of any real tune. In the control task for simple listening and button pressing we presented these “fake” cues and simply had people press a button after each one (control). A second control task involved imagery but no retrieval from long-term memory. In this task, we presented the fake cue and asked for people to simply reimagine it immediately after presentation (control/imagery). The subtraction of interest for current purposes is the cue/imagery minus the control task.

As previously, PET scanning was undertaken in conjunction with an MRI to provide anatomical localization of CBF activation for each person. Eight healthy, right-handed young adults participated, who had from 3 to 16 years of musical training. The conditions were presented in order of control, cue/imagery, and control/imagery.

As predicted, the average time to press a button indicating imaging of the tune was complete in the cue/imagery condition varied proportionally to the length of the tune. Thus we are confident that subjects were following our imagery instructions. The results of the cue/imagery minus control subtraction are shown in FIGURE 3. As in our previous study,¹⁴ we found activation in the secondary auditory cortex (marked STG), although this time the activation was in the right but not left temporal lobe. We also found activation in several regions of the frontal lobe (inf F), most of which were more prominent on the right than the left side. Finally we once again found strong activation in the SMA.

We thus confirmed several findings from our study with verbal tunes:¹⁴ areas normally concerned with processing of auditory information are recruited even when the auditory information is internally generated. This occurred even with a different behavioral task and different songs than had been used earlier. We also confirmed the activity of the SMA in our task. The fact that this area was active even though no verbal rehearsal could logically have been taking place suggests that the SMA is involved with some kind of subvocal humming strategy during the imagery generation.

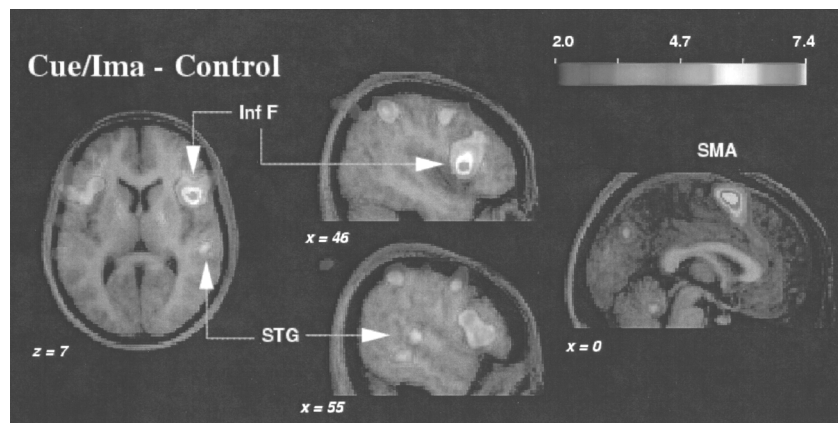


FIGURE 3. See Plate 3 in color section. Brain areas showing activation in the cue/imagery minus control subtraction in the nonverbal tune PET study.

The frontal areas activated here are also approximately the same as some of the frontal areas seen in our previous task. Because the current task did not require extensive involvement of working memory (mental pitch comparison was not required, merely internal scanning of the tune), it is likely that the areas in common in our two studies reflect retrieval from musical semantic memory rather than working memory.

The major new contribution here was that once words were removed from the stimulus and the task, we found prominent right-sided asymmetry in the areas active in the imagery task. The temporal lobe activation is consistent with our lesion study¹³ that showed similar decrements from right-sided temporal lobectomy in both imagery and perception tasks. Thus we conclude that this area is both active in and necessary to the support of musical imagery tasks. The second right-sided asymmetry involved a region in the frontal lobes. This area, on the left, has been implicated in retrieval from verbal semantic memory,²² suggesting that retrieval from semantic memory may be lateralized depending on the type of material. Another right-sided asymmetry was found in activation of the thalamus, a subcortical area involved in memory among other functions. In our earlier PET study,¹⁴ that activation was above our statistical threshold; here it was just below the threshold and thus was not pictured with our main results. However, we can take this as at least suggestive evidence that a circuit involving temporal, frontal, and subcortical areas on the right are important in imagined music processing.

TRANSCRANIAL MAGNETIC STIMULATION

The final study in the series I am reviewing is currently unpublished, and was conducted in partnership with Alvaro Pascual-Leone, Fumiko Maeda, and Gottfried Schlaug. Transcranial magnetic stimulation (TMS) is a noninvasive method of affecting underlying brain tissue by application of a magnetic pulse to the outside of the

skull. The pulse is discharged via a coil that can be placed on the skull overlying the brain area of interest, using external anatomical landmarks, or in our case an MRI of each subject, to locate the areas of interest. A high-frequency series of pulses (10–20 Hz) has been shown to excite the underlying brain tissue, and low-frequency (1-Hz) sequences have been shown to inhibit the underlying tissue.²³ The inhibition is temporary, and the technique is safe for most people, although some discomfort may be experienced by the tapping sound the coil makes. Precautions are taken to exclude people with a history of seizure, as well as people who would be excluded from any study involving MRI, such as anyone with metal implants in the skull. The excitatory aspect of TMS is of interest to clinicians and researchers in the treatment of mental illness such as depression.²⁴ The inhibitory function of low-frequency TMS is of interest to researchers in that a temporary “lesion” can be created in otherwise normal people, and subsequent effects on behavior can be studied.

TMS has already been used to investigate visual imagery. Kosslyn, Pascual-Leone, and colleagues²⁵ showed that an application of 10 min of 1-Hz TMS to the visual cortex impaired later performance of both a visual perception and equivalent visual imagery task. They took this as evidence, in accord with lesion logic, that the primary visual cortex is necessary for performance of the visual imagery task, strengthening the argument that visual perception and imagery are mediated by common structures.

In our TMS study, we selected three brain areas that had been shown to be active during auditory imagery in my previous work, plus one control area. We also wanted to look at auditory imagery for both verbal and nonverbal tunes, as some different brain areas were shown to be active for these two types of tasks. To this end, we needed an auditory imagery task that would be suitable for both types of tunes. We modified a task used by Smith,²⁶ in which participants are given the title of a familiar tune and then asked about a pitch relationship between two notes indexed by ordinal position. In our case, we asked participants to judge whether the second note of a given tune was higher or lower than its first note. Verbal and nonverbal tunes could both be tested, and we intermixed the two types in the test.

The general outline of a session was to administer the auditory imagery task as a pretest. We then determined each person’s motor threshold, or the lowest amount of energy that, when applied to the skull overlying the hand area of the motor cortex, just made the person’s finger twitch. Each person received TMS at 90% of that value. Administration of 10 min of 1-Hz TMS to a designated brain area ensued, followed immediately by another auditory imagery task as a posttest (using different tunes for pretest and posttest). When more than one brain area was investigated in a single session, 30 min of rest intervened between testing different brain areas, to allow the effects of the TMS to dissipate entirely.

Participants were nine right-handed adults with average age of 34, all of whom had some musical background (four were active musicians). Each person underwent an MRI scan before the TMS session. This allowed us to locate, using anatomical measurements, the areas of interest to us. The control area we selected was primary visual cortex (coil placed at the back of the skull), which had not been implicated in auditory imagery tasks before. The three experimental areas were the SMA (top of the skull a little more than midway towards the back), and the left and the right auditory cortex (above and slightly behind the top of the ear in most people). Because

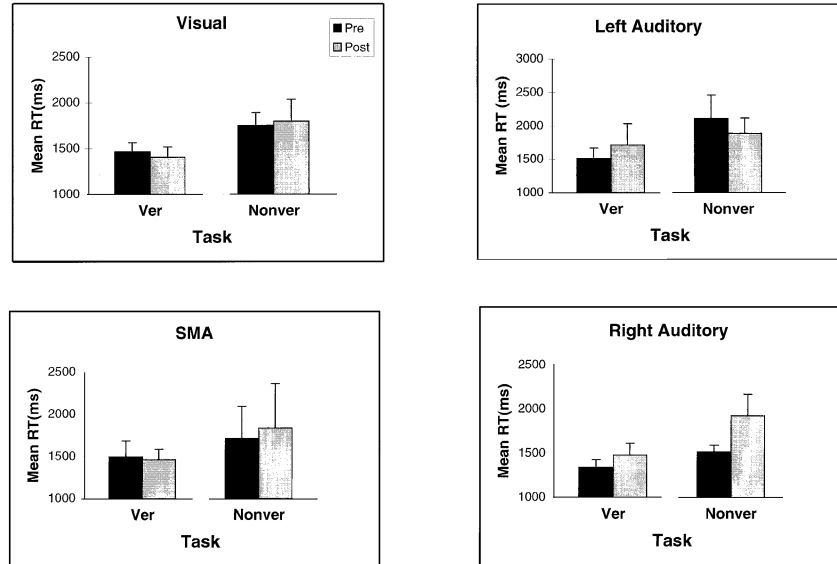


FIGURE 4. Mean reaction time before and after TMS for the verbal (Ver) and nonverbal (Nonver) imagery tasks, after application to the visual cortex, supplementary motor area (SMA), left auditory cortex, and right auditory cortex.

of the anatomy of the auditory cortex, we could not localize our coil placement exactly on secondary auditory cortex. We located the coil instead as near as possible on the primary auditory cortex, with the assumption that the TMS activation would also likely affect the secondary cortex that is immediately adjacent to that area. Our prediction was that after 10 min of low-frequency stimulation, performance overall (in accuracy and/or time) would decrease for the experimental but not for the control areas. We made a further prediction that both left and right auditory cortex stimulation would impair processing of verbal tunes, but that the right auditory cortex stimulation would only impair nonverbal tunes.

Brain areas were tested in different orders for each person. However, as early results seemed to indicate that stimulation to the SMA was showing no effect, three volunteers did not receive SMA stimulation, in an effort to reduce subject time and discomfort. Thus all results except those for SMA were based on nine subjects; those for SMA were based on six subjects.

Accuracy was quite high in the task, so results concentrated on reaction times. FIGURE 4 shows the results for each brain area for the verbal and the nonverbal tasks, both before and after TMS stimulation. The nonverbal tunes are a little less familiar to people, and thus they were responded to on average more slowly than the verbal tunes. Inspection of the four panels shows that in accord with the prediction, the TMS made no difference when applied to the visual cortex. But, surprisingly, TMS made no significant difference when applied to SMA and left auditory cortex. The

lower right panel does show a predicted effect: TMS applied to right auditory cortex slowed down responses to the imagery task, but only for the nonverbal tunes.

Stimulation to the two auditory areas were the most comparable in terms of subjective experience: the coil clicks were rather loud in the ear, and some jaw muscles were activated by the stimulation. Thus we compared those two areas statistically in an analysis of variance, using the three factors of tune (verbal, nonverbal), area (left, right auditory) and test (pre-, post-); all factors were within subjects. The main effect of tune was significant, $F(1,8) = 6.24$, $p < 0.05$, but the crucial three-way interaction of tune, area, and test just failed to reach significance, $F(1, 8) = 3.26$, $p = 0.10$. Because of the strong prediction about these areas, we made a specific comparison of the pre- and posttests after right auditory stimulation. The comparison was not significant for verbal tunes, but was for nonverbal tunes, Newman-Keul's $t = 4.173$, $p < 0.05$.

As far as I know, this study was the first use of TMS to investigate auditory areas. As mentioned above, the coil had to be localized over primary auditory cortex, which in my previous studies was not activated in auditory imagery tasks. Thus we were relying on the somewhat weaker collateral activation to the secondary auditory cortex to show inhibition in the areas of more interest to us. Therefore, although the results were not as statistically strong as we would like, the increase in latency to nonverbal tunes after nonverbal tunes only is consistent with the pattern of data shown in our PET study with nonverbal tunes.²¹ The isolation of this effect to nonverbal tunes is particularly notable, because the verbal tunes were tested in the same session with the same subjects, and did not elicit the inhibition.

The lack of effect after SMA stimulation, after strong activation of this area shown in two PET studies, is more puzzling. Null effects are always hard to interpret, but two possibilities suggest themselves. One is methodological: the neural fibers subserving SMA bend as they move ventrally from the skull surface, and it may be that our particular configuration of coil type and its placement simply did not activate the area sufficiently. On the other hand, it is possible that although SMA provides useful rehearsal mechanisms during auditory imagery tasks, it may not be an area that *must* be involved in such tasks. The task used here required retrieval of the tune once a title was given, but only the first two notes had to be retrieved. Perhaps SMA is more useful when auditory imagery tasks that extend more in time are required, such as "scanning" between two notes several beats apart¹⁴ or "playing" several seconds of a familiar tune inside one's head.²¹ Pilot versions of the TMS task, in fact, asked subjects to compare the first and third notes, which might involve SMA to a greater extent; this could be tried in the future (although accuracy rates would be lower, making interpretation of reaction times more problematic).

CONCLUSIONS AND DIRECTIONS

The studies just reviewed seem to converge on the general idea that parts of the cortex specialized for processing actual sound are also recruited to process imagined sound. Furthermore, the particular structures processing imagined music bear some similarity to those processing heard music. Specifically, the right temporal lobe has been shown to be active in, and necessary for, adequate performance on both per-

ceived and imagined pitch comparison tasks derived from previously known music. This structure may be especially important for processing music that does not have words, when the left temporal structures cannot be recruited for verbal processing.

The role of the SMA remains unclear, in several respects. Because of our failure to disrupt imagery processing with TMS inhibition, we are not sure if a fully functioning SMA is necessary for good performance on musical imagery tasks. The strong activation of SMA shown by PET in both verbal and nonverbal auditory imagery tasks suggests that "internal humming" may at least be helpful to maintain an auditory image over time.

This latter point can be subjected to test by devising auditory imagery tasks in which internal humming would not be helpful or even possible to support the task. One domain to investigate would be imagery for environmental sounds. Intons-Peterson²⁷ has shown that people can generate images of everything from volcanoes erupting to wind chimes tinkling, and make mental comparisons on subjective loudness of these sounds. As people cannot possibly produce most of these sounds, it would be useful to find a task that shows activation in secondary auditory areas (which we can, by now, use as a tentative correlate of the subjective state of auditory imagery) and see if SMA is also activated.

An alternative domain to explore might be that of timbre. Crowder²⁸ demonstrated in several behavioral paradigms that people asked to imagine timbres of different instruments can do so. He gave people a sine wave of a particular pitch and asked them to imagine it in an instrument timbre. A second tone was then presented in an actual timbre at the same or a different pitch and subjects had to say if the pitch was the same or different as the first note. People were slower to confirm that two pitches were the same if the imagined and perceived timbres did not match. As people cannot produce the sounds of guitars and clarinets, SMA support should not be necessary if it is providing a motor rehearsal program. Timbre imagery tasks would also have the advantage of providing us a lateralization hypothesis, as Samson and Zatorre¹¹ showed the importance of the right temporal lobe in timbre tasks. Thus brain imaging studies using either PET or functional magnetic resonance imaging in these domains should help us clarify the role of the SMA in auditory imagery tasks.

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