Beyond auditory cortex: working with musical thoughts

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Musical imagery is associated with neural activity in auditory cortex, but prior studies have not examined musical imagery tasks requiring mental transformations. This paper describes functional magnetic resonance imaging (fMRI) studies requiring manipulation of musical information. In one set of experiments, listeners were asked to mentally reverse a familiar tune when presented backwards. This manipulation consistently elicits neural activity in the intraparietal sulcus (IPS). Separate experiments requiring judgments about melodies that have been transposed from one musical key to another also elicit IPS activation. Conjunction analyses indicate that the same portions of the IPS are recruited in both tasks. The findings suggest that the dorsal pathway of auditory processing is involved in the manipulation and transformation of auditory information, as has also been shown for visuomotor and visuospatial tasks. As such, it provides a substrate for the creation of new mental representations that are based on manipulation of previously experienced sensory events.

Keywords: musical imagery; mental transformations; intraparietal sulcus; fMRI

Introduction

Mental imagery takes many forms and can have various functions. Perhaps the most familiar form of imagery involves evocation of previously experienced information. This aspect of imagery is most closely tied to memory recall, and can serve to enhance information retrieval. But from the earliest cognitive studies of imagery it became evident that imagery could also involve a component of manipulation or modification. For example, one of the clearest demonstrations of visual imagery required volunteers to mentally transform viewed objects from one, seen orientation to another, imagined one.[1] This ability to transform an internal representation to arrive at an answer to a question, or to solve a problem, raises many questions about the mechanisms by which such processes take place, and of their functional significance. In the domain of music, a number of studies have pointed to the utility of auditory imagery to accomplish specific musical goals: for example, in the study of a written score,[2] as a way to ensure accurate intonation during a performance,[3] or as an aid to learning.[4] There is in

fact good evidence that mental practice—which no doubt includes more than just an auditory imagery component—can be beneficial to musicians,[5,6] and can even result in changes in cortical functional organization.[7] These studies confirm the utility (and hence the psychological reality) of musical imagery for musicians and performers, but do not clarify to what extent the imagery required for the task may involve manipulation of existing representations as opposed to evocation of those memory traces. Yet it seems clear that in order for creativity to exist, it would be necessary for musicians, especially composers or improvisers, to have the ability to recombine or juxtapose previously experienced musical events into novel combinations.

Experimental studies of musical imagery have tended to focus more on its perceptual aspect, rather than on active manipulation of information, in contrast to studies in the visual domain (e.g., Ref. 8). For example, tasks typically used to study musical imagery require a volunteer to imagine a familiar tune and make a judgment about it;[9] such procedures tap into retrieval and experiential aspects of the imagery process fairly well, but do not require

anything beyond that. More recently, investigators have become interested in how musical imagery can be used in a more active way (see the other contributions in this volume for examples of these approaches). This idea leads to the studies that I will describe in this paper, which focus on the neural substrates of mental manipulation of musical information.

Previous research into the neural basis of musical imagery has primarily been carried out in the context of the more passive tasks just alluded to. The aim has mostly been to identify the neural structures that are implicated in people's ability to imagine music, usually well-known tunes. Among the first experimental approaches to this phenomenon was a study in which Andrea Halpern and I investigated the ability of people with unilateral temporal-lobe excisions to make judgments about the pitch of imagined versus heard melodies.[10] We found that patients with removals within the right temporal lobe performed more poorly on both perception and imagery tasks than did those with left temporal excision or controls. The "common fate" of the two tasks paralleled findings in the visual imagery domain in which damage to visual cortex led to deficits in both visual imagery and perception.[11] Furthermore, the result was consistent with many previous experiments with this patient population, indicating that damage to auditory cortical regions—especially those within the right temporal lobe—resulted in tonal processing deficits.[12]

A series of functional neuroimaging studies using positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and magnetoencephalography (MEG) followed that consistently implicate auditory cortex in a variety of musical imagery tasks. We and others have now documented increases in neural activity in auditory cortical regions while volunteers perform imagery tasks that include judging the pitch change of two syllables within an imagined tune;[13] imagining the continuation of a familiar melody when cued with its opening tones;[14] comparing the similarity of two imagined instrumental timbres;[15] imagining a familiar tune during gaps in its presentation;[16] and judging if a sounded tone is a correct continuation of an imagined melody.[17] The important contribution of auditory cortex to musical imagery is thus well established, but the question remains about how this system might be implicated in more active

forms of imagery, and whether additional neural resources might be needed for tasks that require more than evocation of a previously experienced auditory event.

Clues to this question arise from two sources: first, from a consideration of the neural pathways associated with processing of auditory information, and second, from the literature on manipulation and transformation of perceptual information in nonauditory domains. A large body of neurophysiological and neuroanatomical studies in monkeys, coupled with functional imaging and other types of studies in humans, have led to the view that there are (at least) two processing pathways originating in auditory cortex. One is more ventrally directed, leading along the superior and middle temporal gyri with eventual targets inferior frontal cortex; and another is more dorsally directed, going to parietal, premotor, and ultimately dorsolateral frontal cortices.[18] The functional significance of these processing streams has often been discussed in terms of spatial versus nonspatial processing, or in terms of language-specific processes.[19] The relevant concept here, however, is that there are hierarchically organized information-processing loops that might be expected to play a role in tasks requiring processing of auditory representations, such as those that might be involved in active imagery. This idea, in turn, meshes well with a wealth of evidence from other domains in which the dorsal stream, specifically regions within the posterior parietal cortex, is implicated in tasks requiring manipulation of information. For example, parietal cortex, especially the intraparietal sulcus (IPS), is known to be recruited by visual mental rotation tasks,[20] as well as visuo-motor tasks,[21] and tasks requiring manipulation (as opposed to monitoring) of items in working memory.[22] There is scant evidence for an involvement of these areas in auditory tasks, although some studies have reported relevant findings.[23] Furthermore, the posterior parietal cortex receives inputs from auditory cortex in the temporal lobe.[24,25] It is thus reasonable to investigate whether active musical imagery tasks might also involve portions of these same networks.

The foregoing gives the background to a recent fMRI study from our lab[26] in which we sought to create a musical imagery task that would involve a manipulation component, and not simply evocation as had been the case in prior studies. Our
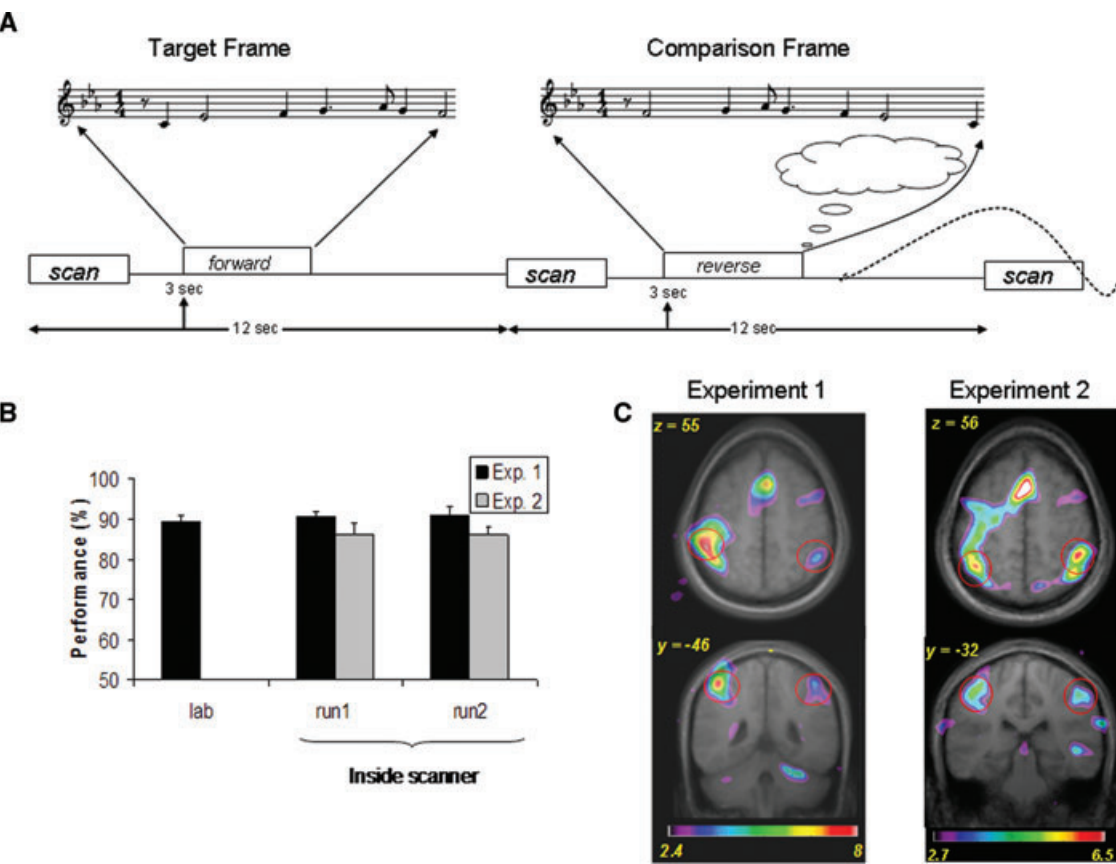
Figure 1. (A) Timeline of a trial in the fMRI mental reversal experiment (experiment 1 of Ref. 26). Each trial contained two 12-sec frames. The target stimulus (in this example, "Greensleeves") was sounded in the first frame, and was followed in the second frame by a comparison stimulus that was either a true or incorrect temporal reversal of that melody. The mental event of interest (depicted by the "cloud") presumably occurs sometime between the end of the reversed melody presentation and the scan. The dotted line illustrates the presumed hemodynamic function associated with performing the mental reversal task. The fMRI volume acquisitions were clustered as shown within the sparse-sampling paradigm so as to maximize the likelihood of capturing the BOLD signal associated with the mental reversal. Experiment 2 was similar but only a visual tune title was given in the first frame. (B) Behavioral performance on the tasks in experiments 1 and 2, collected first in the laboratory, and subsequently during fMRI scanning. Note the high levels of performance. (C) fMRI results from the two experiments. The top (horizontal) and bottom (coronal) sections illustrate BOLD signal increases within the intraparietal sulcus (circled) when contrasting the reverse condition to a control condition containing matched acoustical stimulation.

prediction was that there would be activation of auditory regions to a greater extent when manipulation was required than when it was not, but we also expected that extra-auditory regions might also be recruited. We developed a task requiring temporal reversal, or reordering of tones in time from front to back (Fig. 1A). This task is artificial in the sense that the circumstances where a listener would need to perform a mental reversal are essentially nil in normal musical listening (although retrograde permutations are occasionally used as a compositional device). Our aim in any case was not to mimic nor-

mal listening, but to create a controlled situation requiring the mental reorganization of auditory material. This task is arguably a good way to achieve this goal, and also is similar to some classic tasks used in neuropsychology (e.g., digit repetition backwards).

Because identification of a tune presented in reverse order would prove too difficult for most people, we opted for a comparison task in which a familiar tune is first presented in its normal form, and is then followed by a reversed form; this latter may or may not be an exact reversal, and the listener's task is to mentally reorder the second pattern to

determine whether it matches the target tune or not. On those trials in which the second pattern was not identical to the first, any changed notes were chosen from the same key and from the same range as those in the target tune in order not to provide any obvious cues. This is a mental manipulation that musicians can perform, but it can still be argued that it could be carried out without any mental reversal because one could, in principle, create some sort of inventory of tones present in the two stimuli and then compare them without needing to reorder. We judged this highly unlikely based on our own intuitions, but as a test of this potential issue (and to satisfy some pesky reviewers) we carried out a control behavioral task in which the incorrect note in the reversed melody was systematically varied in position. We reasoned that if reversal were in fact taking place as we claimed, it should take longer to judge the incorrect item when it occurred at the beginning than at the end. That is, if the reversed tune is represented by tones 6, 5, 4, 3, 2, 1, and note 5 is incorrect, it will take longer to judge than if note 2 is incorrect, assuming that the listeners are following the instructions and mentally replaying the tones in the normal 1–6 order. This is indeed what we observed, with response latencies differing by close to 200 ms in the two conditions. These type of chronometric behavioral data are quite important in validating the task, and fits with other behavioral studies both in the auditory[27] and visual[28] domains, indicating that the intended mental transformation was taking place.

Having developed the task, we were now in a position to examine the pattern of brain activity associated with the mental reversal. We selected from among a group of musically trained listeners 12 individuals who on average were able to perform the task at between 80 and 90% correct (Fig. 1B). The fMRI paradigm was set up so that we could analyze the activity after the target tune separately from the brain activity associated with the comparison tune—the one requiring reversal. We also implemented a control stimulus that was acoustically similar to the tunes. When we contrasted the reversal condition to either the control or forward conditions we observed increases in blood-oxygenation signal in a number of cortical and subcortical regions. The most prominent of these included the IPS, dorsolateral and ventrolateral frontal cortex, and the anterior cingulate (Fig. 1C). We did not ob-

serve the expected recruitment of auditory cortical areas, as had been seen in prior studies, although when we looked for blood oxygen level–dependent (BOLD) activity that correlated with individual differences in imagery vividness, as measured via an off-line questionnaire, we did see a significant correlation in the right planum temporale. One reason for the lack of auditory cortex activity in the contrast analysis is that the scanning sequence was set up to pick up the brain activity from imagery but not from the sounded stimulus; to do so necessitated placing the acquisition rather late in the trial, perhaps resulting in the wrong timing to detect the (very likely weak) auditory cortex activity. To remedy this situation, we carried out a second experiment in which the trial time was shortened; in addition, we removed the sounded stimulus from the "forward" condition replacing it by the title of the to-be-imagined tune. This way we avoided any potential contamination of the BOLD signal in auditory cortex to the real stimulus as opposed to the imagined one. The results mirrored the data from the first experiment in that similar areas of parietal and frontal cortex were activated; in addition, we did observe some BOLD activity in the right superior temporal sulcus area, albeit weak in magnitude.

The clearest finding in this study was the recruitment of dorsal-pathway structures in the reversal task. In both experiments, the findings consistently indicated large changes in BOLD signal in the IPS, along with dorsolateral frontal and anterior cingulate regions. The expectation that we would observe enhanced auditory cortex activation was not borne out very clearly, although there was some evidence in experiment 2, and also in experiment 1 in relation to individual variability in auditory imagery vividness. Although most prior auditory imagery studies have reported clear auditory cortex recruitment, as mentioned above, this is not universally the case.[29] Although this issue is not resolved to our satisfaction, we can put it aside for the moment and turn our attention instead to the robust finding of IPS activation. In part, this change of focus was motivated by an unrelated series of experiments being carried out at the same time in our lab, which were initially motivated by different questions. We had been interested for some time in the processing of melodies outside the context of imagery, and had recently been pursuing behavioral probes that would be sensitive to individual differences in the ability to
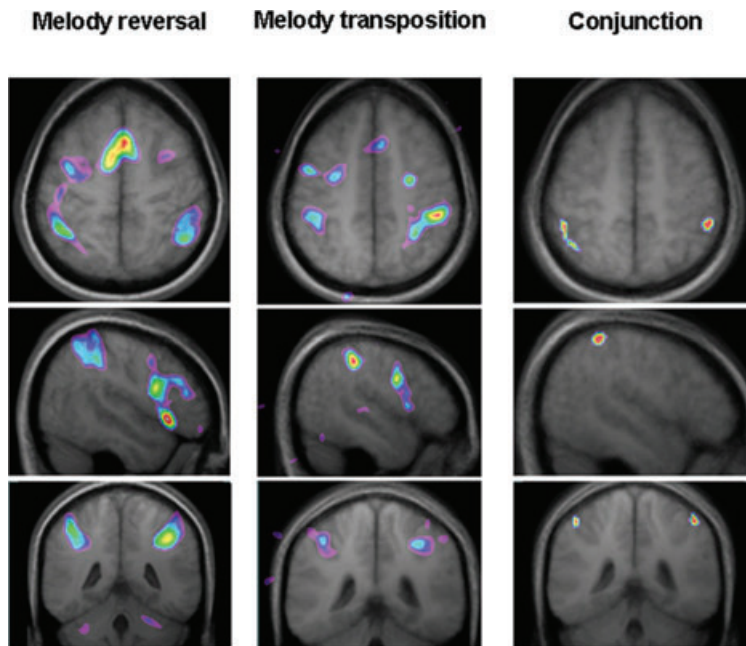
Melody reversal   **Melody transposition**   **Conjunction**

Figure 2. Comparison of melody reversal and melody transposition tasks. Each column shows, from top to bottom, horizontal, sagittal, and coronal sections through the IPS region. The left column shows BOLD signal increases in a contrast of reverse versus forward conditions; the middle column shows BOLD signal increases in a contrast of transposed versus untransposed conditions; the right column shows the conjunction analysis of the data from the first two columns. Note that the principal region showing significant conjunction is within the IPS.

encode and recognize melodic patterns. To accomplish this aim we developed a discrimination task using novel, unfamiliar melodies, in which the second item in a discrimination pair is either transposed to a different musical key or not.[30] The listener's instruction is to determine whether the two patterns are identical or if there is a single changed tone in the second item. On trials in which the second melody is transposed relative to the first, the task would then require that the pitch intervals between successive tones be abstracted because the absolute pitch values would all be different. This task met several criteria relevant to our needs because (1) it is sensitive to musical training, but does not require musical training for successful execution (indeed, nonmusicians find the concept intuitive even if they also often find the task itself challenging); and (2) it elicits a wide range of scores from near-chance to near-perfect. The latter feature was important to us because we were attempting to capture the population variance in this aspect of auditory processing.

When we compared brain activity measured with fMRI in the transposition condition to the non-transposition condition, we observed strong activa-

tion within the IPS.[30] This activity was also stronger during transposition than it was during other, control tasks with similar cognitive demands (including, in particular, working memory load), such as a rhythm discrimination task and a phoneme discrimination task. None of these control tasks required anything akin to the transposition. The argument that IPS activity is directly linked to the specific demands of transposition was strengthened by an additional finding: when we ran an analysis taking each individual's behavioral score as a regressor and then looking throughout the entire brain volume for voxels whose activity was predictive of success, we observed that the peak response was located in the right IPS. In other words, IPS activity was directly linked to performance on the transposition task.

If the two tasks we have studied, musical transposition and musical reversal, are indeed related to similar underlying processes, then we should be able to demonstrate that the same subregion within the IPS is in fact involved. One simple way to do this is to superimpose the findings from the two experiments, to see whether there is overlap. A

conjunction analysis allowed us to do just that, and we did observe significant conjunction in a number of voxels within the IPS when comparing the images derived from the reversal and transposition tasks (Fig. 2). This finding is suggestive but not sufficient to demonstrate that the same specific subregion is in fact involved. To do so, we need to demonstrate that there is overlap in individual brains, else the effect could be attributed to averaging and smoothing artifacts; this could only be done if the same people were tested with the two tasks. Moreover, the two tasks in question had not been designed to be compared because they used quite different materials (familiar vs. unfamiliar tunes; different timbres; different durations), and also different control conditions. In order to allow a direct comparison, we therefore implemented a new study in which identical stimulus materials were used for both a reversal and a transposition task, allowing us to test these on the same individuals. As expected, each task yielded strong activation within the IPS, thus replicating each of the two prior studies. More importantly, when we conducted a group conjunction analysis we found overlapping voxels across the two tasks. Most critically of all, we conducted separate conjunctions in each individual data set without any spatial smoothing, and this confirmed that there was significant overlap in nine out of 10 individual brains. We are confident, therefore, in the conclusion that these two tasks share an underlying neural substrate.

This conclusion raises a further question: what do these two tasks have in common that they should recruit similar neural structures? At first glance these sets of findings might seem to be so disparate as to be unrelated. In fact, the IPS has been implicated in a wide range of tasks,[21] and it is therefore reasonable to assume that there is a wide range of processes that take place within this complex cortical region. This is no doubt partly the case given that there are gradients within the IPS in terms of its anatomical features, such as its connectivity.[31] Yet, the various tasks that have been linked to the posterior parietal cortex in general, and the IPS in particular, do share some underlying computational features. In some general sense, they can all be said to involve transformations of some kind, often from one reference frame to another. This is the most accepted model in the visuomotor domain, for example, where work from both monkeys and humans indicates that the

IPS is a critical link in a network involved in operations such as eye movements to a target, reaching, and grasping.[31,32] On a cognitive level, it has already been remarked that the IPS is important for visual mental rotation[20] and for working memory tasks requiring manipulation[22] as opposed to monitoring.

We would propose that just as the quite varied visuospatial, visuomotor, and cognitive operations mentioned previously all require some kind of transformation, this is also the case for musical reversal and transposition. In both cases, it is the relationship between the individual elements (tones) that must be abstracted, rather than their absolute values (temporal order or pitches) in order for the transformation to be applied (reordering in time, or raising/lowering in pitch). These operations bear a formal similarity, we argue, with the required computations in rotating an object in visual space, or even reaching a target, in that sensory information has to be represented in a sufficiently abstract form to allow the required action. Although the IPS has traditionally been viewed as an interface for visual inputs, it does receive inputs from many modalities, including auditory in both monkeys[24] and humans.[25] It is therefore well-situated to be involved in carrying out the type of transformation operations we have discussed here.

To come back to the topic of imagery, then, what have we learned? The main conclusion we draw is that, in order to understand more active aspects of imagery, we must move beyond neural representations that involve auditory cortex alone. Instead, we propose that the sensory-motor pathways that are critical for other aspects of auditory processing, especially the dorsal pathway, are critical to the ability to work with musical thoughts. The interaction between sensory representations within auditory cortical areas and the manipulation mechanisms involving parietal (and frontal) cortices are the substrate that allows for representations of previous events to be generated internally, and then manipulated to create novel structures. In this way of thinking, then, we may have the beginnings of a model to explain some aspects of creative thinking.

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Conflicts of interest

The author declares no conflicts of interest.

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