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. 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, as a way to ensure accurate intonation during a performance, or as an aid to learning. 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, and can even result in changes in cortical functional organization. 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; such procedures tap into retrieval and experiential aspects of the imagery process fairly well, but do not require
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Previous research into the neural basis of musical

imagery has primarily been carried out in the con-

text of the more passive tasks just alluded to. The

aim has mostly been to identify the neural struc-

tures that are implicated in people’s ability to imag-

ine music, usually well-known tunes. Among the

first experimental approaches to this phenomenon

was a study in which Andrea Halpern and I investi-

gated 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 do-

main in which damage to visual cortex led to deficits

in both visual imagery and perception.11 Furthe-

more, 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 magne-
toencephalography (MEG) followed that consis-
tently 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 fa-
miliar tune during gaps in its presentation;16 and

judging if a sounded tone is a correct continuation

of an imagined melody.17 The important contribu-

tion 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 re-

sources 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 neurophys-

iologicial 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 an-
other is more dorsally directed, going to parietal,

premotor, and ultimately dorsolateral frontal cor-
tices.18 The functional significance of these process-
ing 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 orga-
nized information-processing loops that might be

expected to play a role in tasks requiring process-
ing 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, specifi-
cally regions within the posterior parietal cortex, is

implicated in tasks requiring manipulation of infor-

mation. 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 mem-

ory.22 There is scant evidence for an involvement of

these areas in auditory tasks, although some stud-

ies 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 im-

agery tasks might also involve portions of these same

networks.

The foregoing gives the background to a recent

fMRI study from our lab26 in which we sought to

create a musical imagery task that would involve

a manipulation component, and not simply evo-

cation as had been the case in prior studies. Our
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 normal 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 data are quite important in validating the task, and fits with other behavioral studies both in the auditory 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 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.

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...
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. 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 activation within the IPS. 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

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.
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, 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. 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. On a cognitive level, it has already been remarked that the IPS is important for visual mental rotation and for working memory tasks requiring manipulation 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 and humans. 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.

References
