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RESEARCH ARTICLE

Common cortical areas involved in both auditory and visual imageries for novel stimuli

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Abstract
We examine cross-modality commonalities in visual and auditory imageries during fMRI scanning in a sample of healthy young adults. In a visual task combining viewed and imagined stimuli, 28 participants were asked to imagine novel scenes related to the other images, and in a similar auditory task combining heard and imagined stimuli, to imagine novel sentences spoken by individuals they had heard speaking previously. We identified a common set of regions in medial and lateral Brodmann area 6, as well as inferior frontal gyrus (BA 44/45), partially supporting previous meta-analytic results. Comparing individuals with high or low reported imagery ability, we replicated a previous result showing individuals with lower visual imagery ability showed greater activation in the cerebellum, frontal and dorsolateral prefrontal cortex, while there was no relationship with auditory imagery ability in this sample. The emphasis on imagining novel stimuli, rather than familiar or previously experienced stimuli, confirms the role of the supramodal imagery network underlying creative imagery.

Keywords Imagination · Auditory imagery · Visual imagery · fMRI · Imagery ability

Introduction

Sufficient neuroimaging studies of mental imagery have been performed to identify a "general imagery network" (McNorgan 2012), that comprises self-referential and autobiographical memory areas such as the anterior medial prefrontal cortex, the posterior cingulate regions of the default mode network (DMN), episodic and visuospatial memory areas such as the hippocampus, supplementary motor areas (pre-SMA/BA 6), and lateral ventral prefrontal cortex (BA 46/47). Auditory imagery usually recruits secondary auditory areas (BA 22), while visual imagery activates visual association areas (BA 19), though that may depend on the specifics of what is being imagined.

An event can be imagined with varying degrees of vividness, with some seeming faint and indistinct, and others sharp and compelling. Fulford et al. (2018) reviewed the results of imagery activations in fMRI studies in relationship to imagery vividness as measured using the Vividness of Visual Imagery Questionnaire (VVIQ). The VVIQ asks individuals to imagine a familiar person or setting, and to rate various aspects of the visual imagery on how vivid they are, from "Perfectly clear and as vivid as normal vision" to "no image at all." While the results of visual imagery activation across multiple studies are not entirely consistent, areas of activation during imagined visual objects related to VVIQ scores often included secondary visual areas (BA 19 and 18), posterior cingulate (BA 30), medial temporal areas such as the perirhinal cortex, and the precuneus (BA 7). Of note, many of these studies used familiar objects or previously seen objects as the stimuli to be imagined.

In contrast, studies of auditory imagery abound (Hubbard 2010) but studies of the relationship of neural activation with the imagery vividness are less common. Using auditory imagery of familiar tunes, Herholz and colleagues (Herholz et al. 2012) found auditory imagery ability related to increased activations in superior temporal gyrus and the dorsolateral prefrontal cortex. A rare study of both visual and auditory imageries in the same subjects was done by Zvyagintsev and colleagues (Zvyagintsev et al. 2013), in which they asked subjects to imagine a familiar melody or object,

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and asked for vividness ratings after each MRI session. They found networks which were specific to each modality, as well as a common ("supramodal") set of regions, and imagery vividness for the imagined stimuli were related to largely non-overlapping areas across modalities. They asked subjects to imagine the same self-selected object or melody each time; however, this makes it difficult to separate imagination from memory, which may account for the wide-spread fronto-parietal activation found in the supramodal imagery network.

In the current study, we test whether unfamiliar imagined pictorial event actions or novel auditory sentences activate the same brain regions for external and internally generated stimuli. We examine the brain response during the experience of externally and internally generated auditory and visual stimuli, and relate it to measures of auditory and visual imagery vividness in the same individuals. We expect a common imagery network as in McNorgan (2012) and Zvyagintsev et al. (2013) during imagination events across both modalities, and some overlap in each modality with modality-specific secondary sensory areas. We attempt to replicate the visual imagery analyses (Fulford et al. 2018) and extended the analysis into auditory imagery.

Materials and methods

Participants

The joint Georgia Tech/Georgia State Institutional Review Board approved the protocol of this study. All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Twenty-eight participants (17 females, 11 males; mean age = 21.4 years old) were recruited from the undergraduate population at GSU. Subjects were excluded if they had a history of loss of consciousness, severe head injury or were physically incapable of undergoing an MRI scan. Volunteers had normal or corrected vision. Informed consent was obtained from all individual participants included in the study.

Materials and procedure

VVIQ: the Vividness of Visual Imagery Questionnaire (VVIQ) consists of 16 items which are imagined and then rated for vividness (Marks 1973) (e.g. imagine the exact contour of the face, head, shoulders, and body of your mother) followed by their rating of the vividness of the image on a 5-point scale. The VVIQ is a reliable measure of imagery vividness used in numerous behavioral studies, with a Cronbach's alpha 0.87 (Borst and Kosslyn 2010) and has been associated with differential brain activation in fMRI (Cui et al. 2007). The total VVIQ scores were calculated by adding the ratings of all 16 items. The VVIQ scores for these participants ranged from 29 to 76 out of a max of 80 ($M = 60.40$ and $SD = 11.09$).

BAIS: the Bucknell Auditory Imagery Scale (BAIS) consisted of 14 different auditory scenarios, including music, conversations, and the environment (e.g., "Consider the beginning of the song 'Happy Birthday.'") The BAIS is a reliable measure of mental imagery suggestibility with a Cronbach's alpha of 0.91 (Pfordresher and Halpern 2013). Participants rate the similarity between each scenario and real experience on a 0–7 scale. The BAIS scores for this study ranged from 14 to 97 out of a max of 98 ($M = 61.73$, $SD = 20.73$).

Imaging protocol

Scanning was performed using a 3T Siemens TIM Trio scanner at the GSU/GA Tech Center for Advanced Brain Imaging, using a 12-channel head coil and default sequences. A T1-weighted structural scan was collected using an MPRAGE protocol, with isometric 1-mm voxels. The functional images were collected with a single-shot echoplanar gradient-echo pulse sequence (TR = 2.25 s, TE = 4.18 ms, flip angle = 77 degrees, field of view = 220 mm, 32 slices, 3.4 × 3.4 × 4.0 mm voxels). The auditory imagery task was collected in a single run of 405 frames, while the visual included 473.

fMRI tasks

Before scanning, all subjects received training in the tasks, including practice in imagining example stimuli and reporting details and vividness of the created image (practice images were not later used in the task). For the visual task, training included seeing examples and reading descriptions of visual scenes like the ones used in the task, and imagining and reporting scene details.

The visual task in the scanner was a 15-min visually imagined and experienced action slideshow of a hair stylist and a mechanic performing corresponding actions according to their occupation, and imagined actions where the jobs are switched to be inconsistent with expectations, to reduce the effect of memory schemata (Drivdahl and Zaragoza 2001; Kleider et al. 2008) (an example of a picture presentation is shown in Fig. 1). Each scan included 18 sets of three action displays, 18 sets of three blurred displays, 81 crosshair slides lasting between 2 and 4 s, 18 non-imagined sentences, and 8 attentional response slides. The 108 total displays are grouped into three-slide sequences to lend continuity to the action (e.g., the hair stylist using a blow dryer), as well as

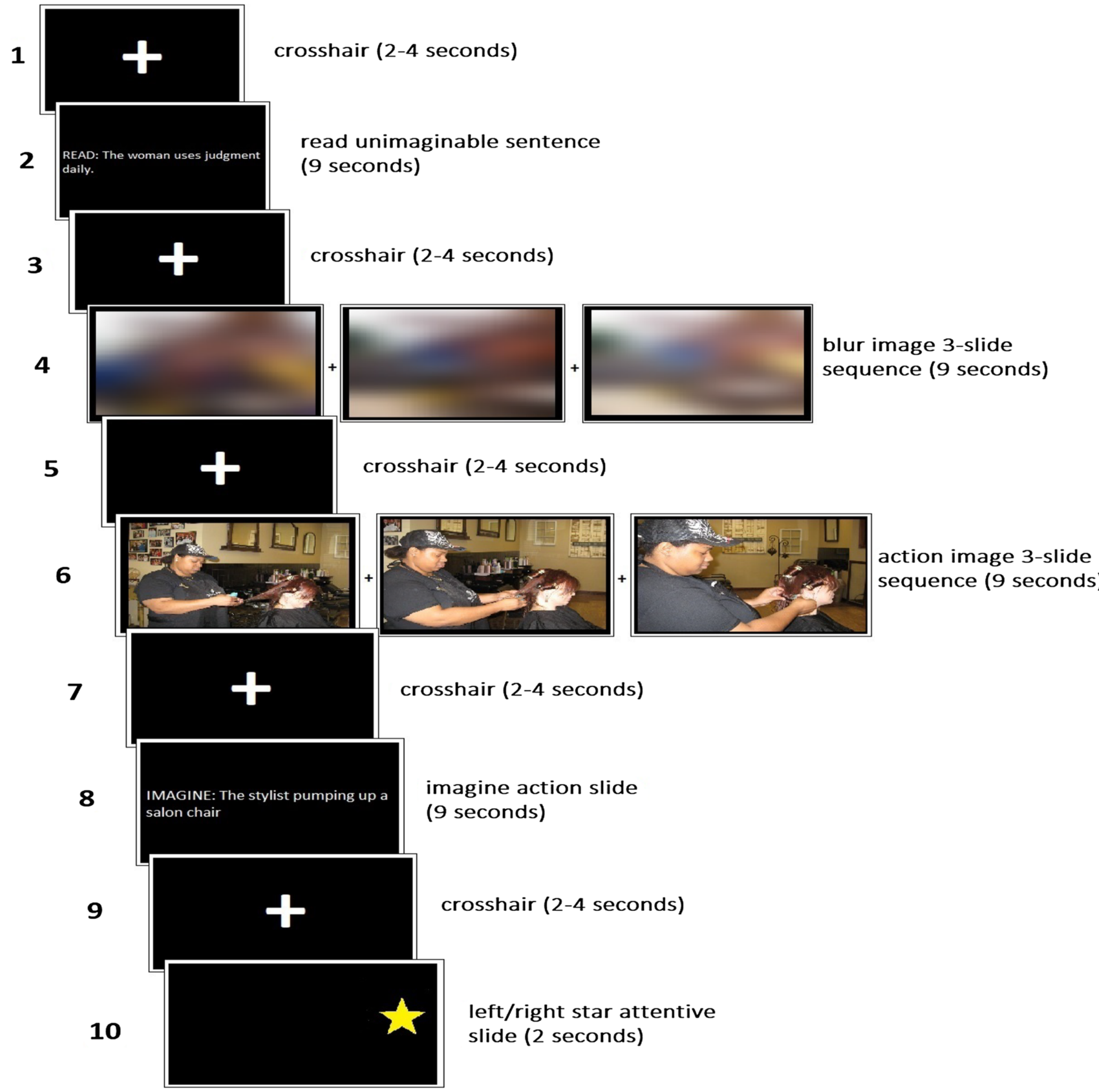

Fig. 1 Visual Encoding Slideshow Layout (**a**). Example of the order of the visual slideshow and timing presentation of the stimuli, crosshairs and button response as seen by the participants during the time in the scanner

blurred images in three-slide sequences. There are nine sections in each task. Each section is separated by a left/right attentive slide that lasts for 2 s and requires the participants to respond with the button box indicating what side of the screen the cross or star is located. In each section of the task, a crosshair lasting between 2 and 4 s is displayed before every read, imagine, action and blurred stimuli. For example, the participant may see a 3-s crosshair, then an unimaginable sentence to be read (e.g., "the woman uses judgment daily."), another crosshair, followed by a three-image slideshow of either the mechanic or the hair stylist performing an action lasting a total of 9 s for each slideshow. The order in which the participant receives the stimuli changes between each section. Two counterbalanced orderings of the different conditions: picture, blur, imagine, and read were used across subjects. The actor performing an action was counterbalanced across the different versions.

For the auditory task, the training prior to scanning included hearing the same text passage being read for a few minutes by each of the two people who had recorded the task stimuli, "Joe" and "Jill", along with some background information about Joe and Jill; and practicing imagining Joe's voice and Jill's voice. The auditory task (an example is in Fig. 2) was based on Sugimori et al. (Sugimori et al. 2014): 32 short sentences presented either audibly or visually, each repeated twice over the course of the task; half were cued each time by "Listen to Joe reading this sentence" (or Jill) before the stimuli

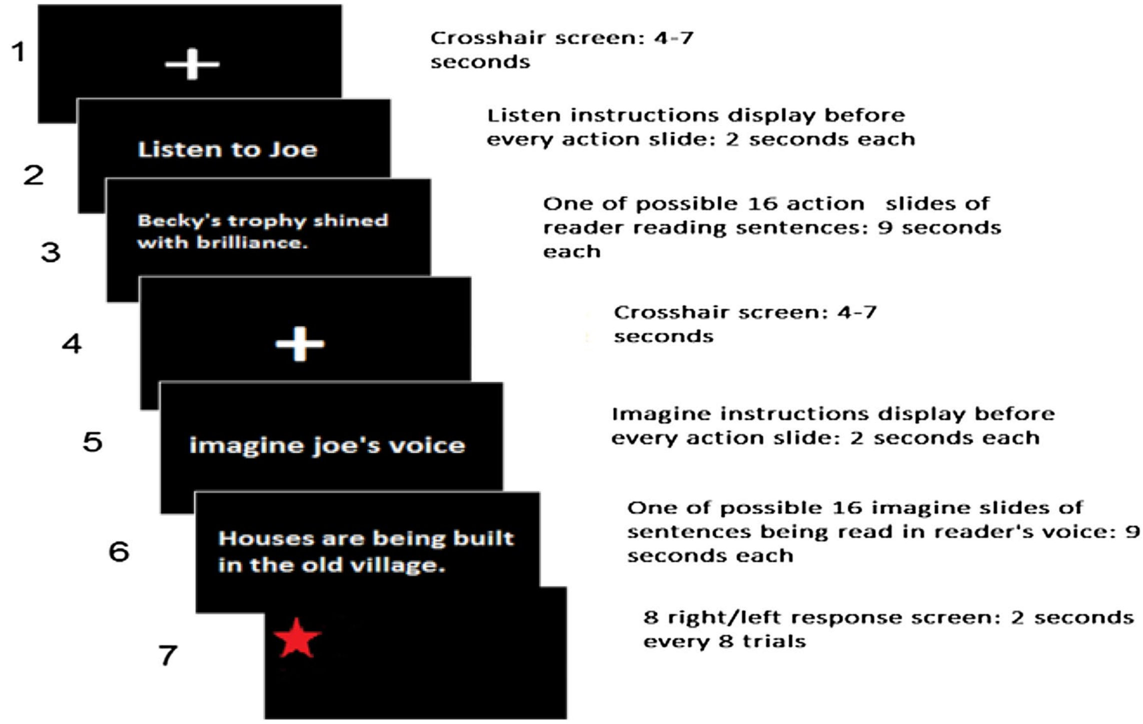

Fig. 2 Auditory Encoding Slideshow Layout. The order of the auditory slideshow and timing presentation of the stimuli, crosshairs and flasher images as seen by participants in the scanner

are presented. The remaining half was cued each time by "Imagine Joe reading this sentence" (or Jill) before the stimuli were presented. Both the heard and imagined conditions were displayed for 9 s per sentence. The conditions of hearing or imagining Joe or Jill for a given sentence were counterbalanced across participants. The sentences were standardized in length, and vocabulary difficulty [similar to (Frishkoff et al. 2010)]. Every eight trials, the auditory task used the same attentive response slides used in the visual session.

Quality controls

Scanning data were excluded if the subject showed no BOLD signal changes during the experienced stimuli presentation ('seen' and 'heard' contrasts) at a $p<0.05$ corrected for family wise error (FWE). Data were also screened for excessive head movement above 3 mm, and to confirm subjects responded to the occasional left/right stimuli. A total of 23 subjects' scanning data passed the criteria for both auditory and visual tasks. Three subjects did not complete the visual imagery scale, with a total of 20 suitable datasets for the analyses comparing activation with VVIQ scores.

Preprocessing

The DICOM data were preprocessed with DPARSF software (Chao-Gan and Yu-Feng 2010), advanced edition. The preprocessing pipeline included slice timing, motion correction, segmentation and normalization to the MNI template by using the $T1$ image-unified segmentation method, as well as nuisance covariate regression (six parameters of rigid-body motion), reslicing to $2\times2\times2$, and smoothing by FWHM of 6 mm.

Imaging analysis

All first- and second-level analyses were run using SPM8 (https://www.fil.ion.ucl.ac.uk/spm/). For individual subject data, the auditory design matrix included imagined and heard conditions; the visual analyses included seen images, imagined, blurred, and read conditions. Framewise displacement (Power et al. 2014) was used as a regressor in all task analyses, with the default 128 s used in the high-pass filter and autoregressive (AR1) modeling. The contrasts of interest were the imagine condition vs baseline for both sensory tasks, as well as imagined greater than seen stimuli, and imagined greater than heard. For the visual session, we also examined the contrast of imagined greater than reading conditions.

The Threshold Free Cluster Enhancement (TFCE) analyses were run using FSL's tool, randomise, for nonparametric permutation inference on neuroimaging data (Winkler et al. 2014). The TFCE process is described in detail in the related article (Smith and Nichols 2009). This nonparametric test was performed at the group level, with subjects that passed encoding exclusion criteria (23 visual encoding and 23 auditory encoding). A variance smoothing with a sigma of 5-mm option was added to increase power in the overall randomise command. FSL's randomise program generates 5000 permutations of the data when building up the null distribution. The cluster option is then run to extract clusters and local maxima at $p < 0.05$ FWE corrected.

High vs low imagery comparisons

We attempted to replicate the findings from Fulford et al. (2018) comparing individuals with high and low VVIQ, during imagination and experienced stimuli. VVIQ scores and BAIS scores were split by the median into 'high'- and 'low'-scoring groups (above and below 61 for the VVIQ, 65 for the BAIS), with means for high and low of 70 and 53 for the VVIQ groups, and 78 and 47 for the BAIS. The imagination and experienced (vs baseline) contrasts were compared across groups using a two-sample t test. Fulford et al. used a clusterwise threshold of $p < 0.001$ and a minimum cluster of 20, so for these comparisons we used the same thresholds. Given the liberal nature of these thresholds, we also examined the TFCE threshold results on the median split, as well as for a regression against the VVIQ measures. The results are shown in the Supplemental Material.

Results

Table 1 and Fig. 3 show the results of the visual task analyses, showing increased activation in visual imagination in comparison with rest, reading, and seen stimuli. Similar analyses are shown for auditory imagination in Table 2 and Fig. 4, with auditory imagination vs rest overlaid on auditory imagination > heard.

Brodmann's area (BA) 6, the medial precentral gyrus/supplementary motor area, consistently showed activity in both imagination conditions. The overlap of significant areas for imagination > rest for both modalities is shown in Fig. 5, in BA 6 (laterally in left precentral gyrus and a separate cluster medially in supplementary motor areas), and left BA 47 and 45 (left inferior frontal gyrus).

Visual imagination in comparison with reading text also showed significant activation from the fusiform into the bilateral primary and secondary visual areas (BA 17 and 18), and the inferior and middle temporal lobes. The activation in BA 22 in the middle temporal lobe, and in the fusiform gyrus, overlapped with the same areas as the imagination > rest effects in the auditory imagery conditions. In comparison with either reading alone or seeing an image, visual imagination of a scene activated largely overlapping areas in the left and right inferior frontal cortex, left lateral frontal cortex, bilateral putamen and caudate, and bilateral mid temporal cortex in BA 21 (see Fig. 3).

The results for auditory imagination vs the heard stimuli did not reach the threshold for cluster-wise significance, but showed a maximum activation in the left inferior frontal opera

Table 1 All regions identified in the visual task as showing peak cluster activation for imagination > rest, Imagination > read, and imagination > seen contrasts in a whole brain TFCE analysis

Brodmann's area	Anatomical area	MNI coordinates (mm)	Cluster extent (in voxels)
Imagination > rest			
6	Precentral L	−45 3 54	118
6	Supp motor area L	−6 15 54	141
45	Frontal inf Tri L	−48 27 21	489
47	Frontal inf Orb L	−45 27 −9	
Imagination > read			
37	Fusiform L	−27 −33 −21	10,026
6	Supp motor area R	3 12 57	
45	Frontal inf tri L	−51 30 21	
22	Mid temporal R	54 −48 12	575
22	Sup temporal R	66 −45 21	
39	Mid temporal R	48 −60 18	
45	Frontal inf Tri R	57 27 12	797
47	Frontal inf Orb R	33 33 −9	
45	Frontal inf Tri R	54 33 0	
Imagination > seen			
32	Supp motor area L	−3 12 51	4630
32	Cingulum mid L	−6 24 36	
32	Cingulum mid R	6 18 39	
48	Insula R	39 15 0	502
–	Sup temporal Pole R	51 12 −9	
46	Frontal mid R	36 51 18	324
23	Cingulum mid L	−3 −15 27	
21	Mid temporal L	−51 −42 −3	666
39	Supra marginal L	−51 −51 30	
48	Supra marginal L	−57 −45 27	
48	Heschl R	45 −15 9	104
48	Sup temporal R	48 −15 0	
39	Angular R	51 −60 48	

Peak cluster activation was found by masking the t stat output image with the significant voxels from the corrected p value output. Clusters and local maxima are then extracted from the threshold tstat output image. Voxel location coordinates are converted into MNI space using FSLeyes and loading the MNI T1 1-mm template. MNI coordinates are shown for peak clusters of activation

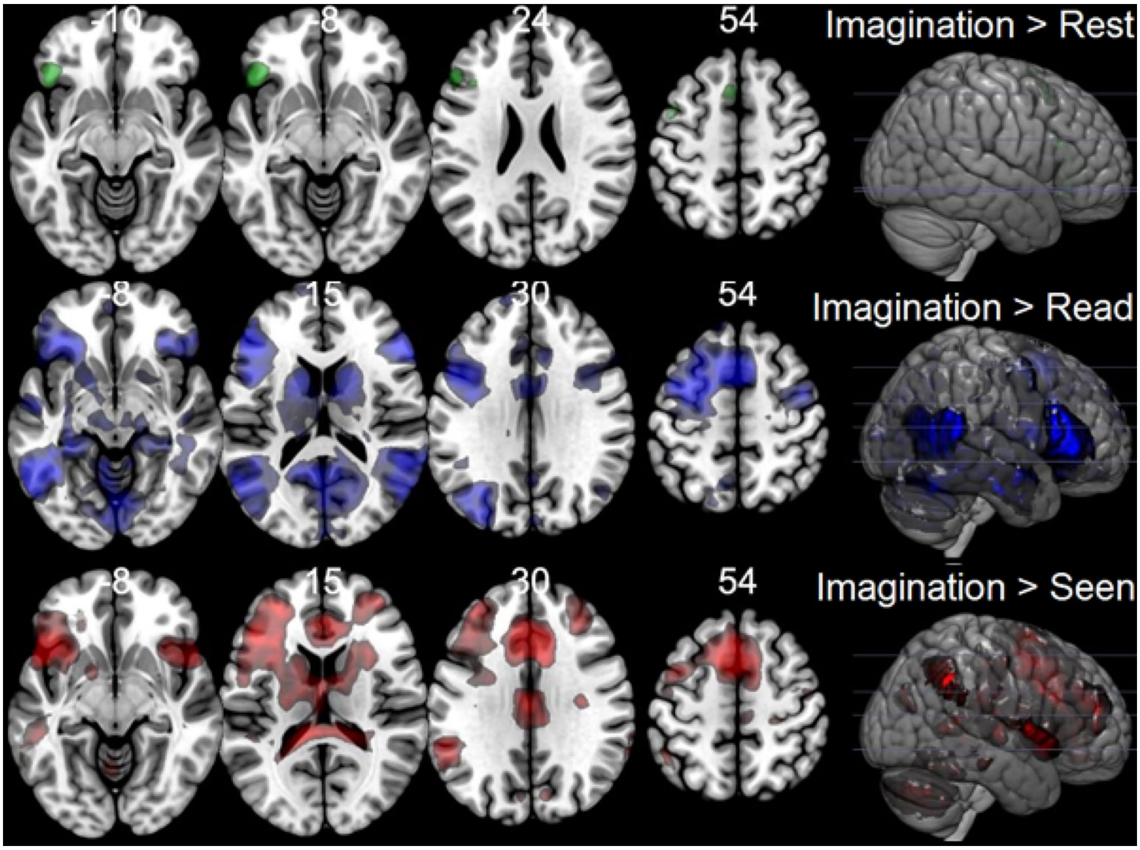

Fig. 3 Regions exhibiting significant activation, starting from the top, for visual imagination vs rest (green), visual imagination vs seen (red) and visual imagination vs read (blue). The images are displayed thresholded at $p < 0.05$ FWE from the TFCE output. The left side of the image corresponds to the left side of the brain

gyrus near the BA 6/B44 border, at the smaller extent threshold of $p < 0.0001$ uncorrected, at (−54,9,15), voxel cluster = 24.

In the comparison of high vs low imagery groups in the visual task, the low group showed greater activation than the high group as shown in Table 3, with the largest clusters in bilateral BA 9/46. No significant effects were found for the high > low comparison, similar to the findings of Fulford et al. In the analysis of seen contrasts, or the analysis of low vs high BAIS subjects in imagery or hearing conditions, no results passed the extent threshold (maximal statistical value was $t(21) = 4.99$, $p < 0.0001$). The TFCE and regression results are in Supplemental Figures S3 and S4, and Tables S1 and S2. The results largely agree for the parametric and TFCE methods, with the single area of agreement across regression and median split being the left mid Frontal gyrus, in BA 10.

Discussion

In this study of both auditory sentences and visual scene imagination in the same participants, we confirmed a "supramodal" imagery network in the frontal cortex consisting of medial and lateral BA 6/SMA and left middle and inferior frontal regions including BA 45/47/48. While the visual task yielded no regions of modality-specific activation, auditory imagery-specific regions included BA 21, BA 22, and BA 40/7.

These findings across modalities in the same subjects support what was found in a meta-analysis across modalities (McNorgan 2012). The precise areas depend on active or passive baselines, but both lateral and medial BA 6 are replicated. These regions of BA 6 have been repeatedly found in visual imagery tasks (Winlove et al. 2018), as well as musical and auditory imagery (Lima et al. 2016). In one study of auditory hallucinations compared to imagining the hallucination, SMA was selective for imagination (Raij and Riekki 2012). Given its role in motor planning and processing, these imagery activations are often interpreted in terms of subvocalizations or imagined motor processing (Zvyagintsev et al. 2013). We cannot rule out subvocalizations in the auditory imagery task we used, nor covert movements in the visual task. Nevertheless, our findings highlight the importance of these regions for imagination per se, as the imagined stimuli in our study did not require re-playing a remembered

Table 2 Regions identified in the auditory task as showing peak cluster activation for imagination > rest and imagination > heard contrasts in a whole brain TFCE analysis

Brodmann's area	Anatomical area	MNI Coordinates (mm) x y z	Cluster extent (in voxels)
Imagination > rest			
18, 19	Lingual L	− 18 − 93 − 12	1612
18	Lingual R	21 − 93 − 6	
19	Occipital inf L	− 39 − 84 − 12	
6	Precentral L	− 48 0 51	527
44	Frontal inf oper L	− 51 15 18	
6	Supp motor area L	− 6 9 63	108
22	Mid temporal L	− 57 − 9 − 9	173
40	Parietal inf L	− 30 − 54 42	125
40,7	Parietal sup L	− 33 − 57 54	
Imagination > heard			
48	Inf oper frontal L	− 45 12 6	20
6	Sup motor area L	− 9 6 60	14

Peak cluster activation was found by masking the *t* stat output image with the significant voxels from the corrected *p* value output. Clusters and local maxima are then extracted from the threshold tstat output image. Voxel location coordinates are converted into MNI space using FSLeyes and loading the MNI T1 1-mm template. MNI coordinates are shown for peak clusters of activation

experience of an object or sound, but focused on imagining scenes or sentences not previously experienced.

The auditory imagery results for these stimuli-imagining novel sentences said by an unfamiliar person highlighted very similar areas to the consensus results from McNorgan (2012) and from Herholz et al. (2012), including BA 22, ventrolateral frontal regions, fusiform gyrus and the inferior parietal lobule. The peak results are largely in the left hemisphere, with the exception of the lingual gyrus; this left-lateralization is common in imagery studies (McNorgan 2012), but it may also reflect that we did not include pitch or melody variation as many auditory imagery studies have which found right or bilateral activation, nor did we focus on well-known sounds, but focused on imagining novel but not unusual spoken sentences.

Perhaps surprisingly, we found only BA 7/40 for auditory imagery, unlike the meta-analysis which found those in common across modalities. The parietal lobe is one of the most common findings in imagery studies, particularly visual; in their recent meta-analysis of visual imagery studies, Winlove and colleagues (Winlove et al. 2018) found it active in almost every study. However, the vast majority of these studies focused on imagining a single, familiar object, rather than a novel but not unusual imagined scene. Our visual stimuli perhaps called on less working memory demands and more ideas of creative action, hence leading to

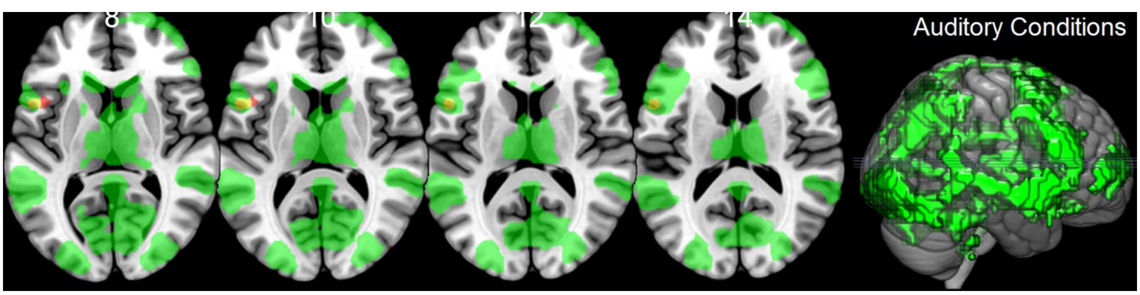

Fig. 4 Neural Activation for Auditory Imagination vs rest condition shown in green. The image is thresholded at $p < 0.05$ FWE from the TFCE output. In red is Auditory imagination greater than heard (uncorrected $p < 0.001$), with overlap in yellow (BA 6/44 boundary). The left side of the image corresponds to the left side of the brain

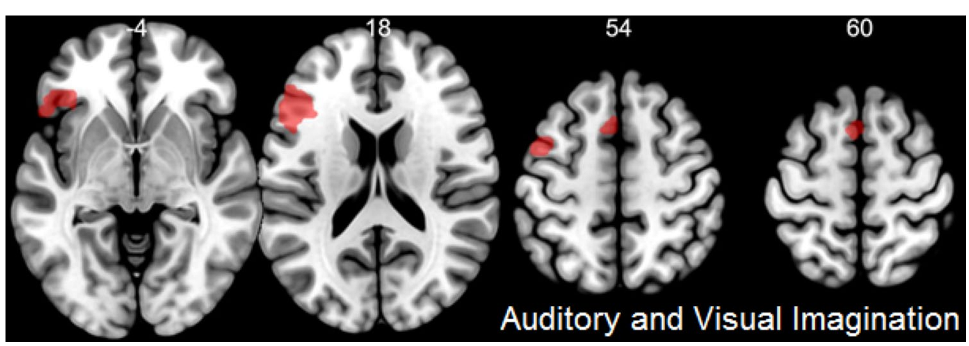

Fig. 5 Overlap of imagery across modalities in the same subjects; an inclusive mask of the visual imagination is added to the auditory imagination to show similar regions of activation in the inferior and medial frontal cortex

Table 3 Areas where lower VVIQ group > higher VVIQ group in the visual conditions with an uncorrected threshold of $p < 0.001$ and an extent threshold of $k = 20$ voxels

Brodmann area	Anatomical area	MNI coordinates (mm)	T (19) statistic	Cluster extent (in voxels)
Imagination > rest				
	Cerebellum R	15 − 39 − 18	6.28	20
	–	3 0 − 3	6.03	66
	Caudate L	− 9 15 − 6	4.62	
	Putamen L	− 15 9 − 9	4.16	
9/46	Frontal mid L	− 21 45 30	5.82	112
10	Frontal mid L	− 30 57 12	4.93	
10	Frontal sup medial L	− 12 57 18	4.84	
46	Frontal mid R	24 42 27	5.72	31
	Cerebellum crus1 R	33 − 75 − 30	5.48	36
	Cerebellum crus2 R	27 − 72 − 39	3.88	
	Vermis	6 − 51 − 12	5.32	23
38	Temp. pole sup L	− 48 15 − 15	5.25	24
10	Frontal med orb L	− 12 45 − 9	5.15	21
	Cerebellum crus2 R	15 − 78 − 39	4.84	21
	Cerebellum crus1 R	15 − 78 − 27	4.49	
	Putamen R	21 21 − 9	4.34	30
	Caudate R	12 18 − 3	4.12	
	Putamen R	24 9 − 9	3.75	
Seen > rest				
30	Hippocampus/para-hippocampus, L	− 12 − 27 − 9	5.45	44
27	Lingual L	− 9 − 36 0	4.97	
29/27	Cingulum post L/precuneus L	− 6 − 42 6	4.45	
7	Superior parietal R	27 − 63 57	5.20	33
7	Precuneus R	6 − 57 60	3.69	
	Putamen R	27 6 − 12	4.45	26

Analysis masked with a gray matter mask. Group level results of 19 subjects in a two-sample analysis of low vs high scorers of the Visual Vividness Imagery Questionnaire (VVIQ). MNI coordinates are shown for major clusters for each area of activation. The major anatomical regions and Brodmann's area numbers are listed starting with the location of the greatest cluster and extending from there

the increased BA6 and premotor areas involvement, without the parietal involvement.

We replicated some of the previous results examining relationships with imagery vividness, in that those with lower VVIQ showed more activation in BA 10, BA 9/46, BA 25 (left caudate), and the cerebellum during visual imagery as in Fulford et al. (2018). It is possible that those with lower VVIQ were more cognitively engaged in trying to imagine the scenes, emphasizing the dorsolateral prefrontal cortex—however, the same was not seen for auditory imagination vividness as measured by the BAIS. The VVIQ and the BAIS both ask about the vividness of imagining familiar experiences—your mother's face, the song "Happy Birthday"—and it is possible that the vividness as measured from these memory-driven experiences does not correlate strongly with imagination vividness for novel stimuli.

These results add to the understanding of imagery interactions by comparing auditory and visual imageries for novel stimuli in the same population. We emphasize the role of Brodmann area six and supplemental motor areas in imagery, regardless of modality.

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