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fMRI-based Multivariate Pattern Analyses Reveal Imagery Modality and Imagery Content Specific Representations in Primary Somatosensory, Motor and Auditory Cortices

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Abstract

Previous studies have shown that the early visual cortex contains content-specific representations of stimuli during visual imagery, and that these representational patterns of imagery content have a perceptual basis. To date, there is little evidence for the presence of a similar organization in the auditory and tactile domains. Using fMRI-based multivariate pattern analyses we showed that primary somatosensory, auditory, motor, and visual cortices are discriminative for imagery of touch versus sound. In the somatosensory, motor and visual cortices the imagery modality discriminative patterns were similar to perception modality discriminative patterns, suggesting that top-down modulations in these regions rely on similar neural representations as bottom-up perceptual processes. Moreover, we found evidence for content-specific representations of the stimuli during auditory imagery in the primary somatosensory and primary motor cortices. Both the imagined emotions and the imagined identities of the auditory stimuli could be successfully classified in these regions.

Key words: auditory cortex, decoding, mental imagery, MVPA, somatosensory cortex

Introduction

Mental imagery is the ability to generate, represent and manipulate objects and events that are not physically present. It is an important cognitive function that plays a role in a multitude of everyday processes. During development, internal representations of the world are sustained in the brain to interpret sensory input and are gradually refined over time to correspond to the structure of the environment (Berkes et al. 2011). This refinement process leads to an increased similarity between evoked and internally generated neuronal activity.

As argued in predictive coding theory, the higher order regions in which internal representations are maintained provide predictions about the environment to the early sensory regions on the basis of internal models (Rao and Ballard 1999; Friston 2012; Naselaris et al. 2015). For example, as shown by de Borst et al. (2012) and Mechelli et al. (2004), during visual imagery, frontal regions mediate activity in category selective regions in occipital-temporal cortex, as well as early visual areas, through (content-specific) feedback connections. These feedback connections allow for mediation and interpretation of visual input

by the calculation of prediction errors, and may drive the early visual cortex to represent features of objects or scenes during mental content generation. This makes mental imagery an essential part of cognition as it plays a strong modulatory role during perception and is at the heart of several core human functions such as learning, memory, planning, and perspective taking (Kosslyn et al. 1995; Cohen et al. 1996; Jackson et al. 2006).

Traditionally, much of the research devoted to unravelling the neuro-biological basis of mental imagery focused on the visual domain. Analogous to the distinction between the ventral "what" and the dorsal "where" cortical processing streams in visual perception (Ungerleider and Haxby 1994), neuroimaging research showed that a dichotomy exists between object and spatial imagery (Cohen et al. 1996; Mellet et al. 1996; Tagaris et al. 1996; Ishai et al. 2000; O'Craven and Kanwisher 2000; Trojano et al. 2000; Formisano et al. 2002; Ishai et al. 2002). For example, Ishai et al. (2000) showed that the category-selective regions in occipito-temporal cortex were re-activated during imagery in a category-specific manner. Similarities between perception and imagery have also been found in other modalities, such as the modulation of somatosensory cortex activity during tactile imagery (Schmidt et al. 2014) and the involvement of the superior temporal gyrus during auditory imagery (Halpern and Zatorre 1999). However, compared to visual and motor imagery, mental imagery research in the tactile and auditory domains is still sparse. The lack of research in these areas is remarkable, as the investigation of both tactile and auditory imagery has significant clinical relevance. Trauma patients often report repetitive mental representations of the traumatic event that include tactile sensations and sounds (McCann and Pearlman, 1990). Auditory hallucinations are the most frequent hallucinations in psychotic disorders such as schizophrenia, and tactile hallucinations occur in 15% of the cases (Lewandowski et al. 2009). Hallucinations are strongly associated with mental imagery, yet they are differentiated by the lack of voluntary control (Linden et al. 2011). Auditory imagery also plays an important role during other cognitive processes, such as inner vocalizations during reading. Therefore, additional contributions to the investigation of the neuro-biological underpinnings of tactile and auditory imagery and their possible perceptual bases are relevant.

One major point of discussion in the mental imagery literature has been whether mental representations rely on similar neural mechanisms as those used for perception and whether these representations include primary sensory cortices. Research on the role of the primary sensory cortices during mental imagery has given mixed results in the past. In the visual domain, several visual imagery studies reported primary visual cortex activation (Kosslyn et al. 1993, 1999; Klein et al. 2000; Ishai et al. 2002; Ganis et al. 2004), while others did not (Mellet et al. 1996; Ishai et al. 2000; Knauff et al. 2000; Mellet et al. 2000; Trojano et al. 2000; Formisano et al. 2002). It has been suggested that the involvement of early visual cortex in visual imagery relies on the mental representation of fine-grained details rather than the spatial properties of objects or scenes (Mellet et al. 2000; Kosslyn and Thompson 2003). In other modalities, especially the motor domain, the role of the primary sensory cortex in mental representations has also been discussed. Several neuroimaging studies found that the primary motor cortex (areas 4a and 4p) was activated during motor imagery (Roth et al. 1996; Guillot et al. 2008; Sharma et al. 2008; Sharma and Baron 2013). However, other studies found contradicting results (Gerardin et al. 2000; Kasess et al.

2008). Also for motor imagery, these contradicting findings might relate to the specific task requirements. Although tactile imagery has not been investigated very frequently, the results of a few studies suggested that tactile imagery may drive primary somatosensory cortex (Yoo et al. 2003; Savini et al. 2012; Schmidt et al. 2014). In auditory imagery tasks on the other hand, activation of the auditory cortex was usually restricted to the secondary and association areas and did not include the primary auditory cortex (Halpern and Zatorre 1999; Halpern et al. 2004; Bunzeck et al. 2005; Kleber et al. 2007; Daselaar et al. 2010; Zvyagintsev et al. 2013).

More recently, several functional MRI (fMRI) studies investigated the similarities between perception and imagery in a more detailed way using multivariate analyses to decode the perceptual and imagined neural representations of two stimuli (Reddy et al. 2010; Stokes et al. 2011; Albers et al. 2013; Vetter et al. 2014; de Borst et al. 2016). These studies followed upon similar investigations in the domain of visual working memory (Harrison and Tong 2009; Xing et al. 2013). Most studies trained a classifier on the difference between activity patterns of two stimuli during a perceptual task and tested the classifier on the activity patterns during a similar imagery task. In the visual domain, the successful classification of imagery conditions, when trained on perception conditions, indicated that imagery and perception rely on similar neural codes (Reddy et al. 2010; Stokes et al. 2011; Albers et al. 2013; Vetter et al. 2014; de Borst et al. 2016). In the motor domain, one imagery study trained and tested a classifier on distinguishing different imagined hand movements. They found, among other results, that the primary motor cortex could decode these imagined hand movements. However, they did not directly test the similarity between these imagery patterns and multi-voxel patterns during perception (Pilgramm et al. 2016). So far, limited research on the representational similarities between perception and imagery has been performed in the tactile and auditory domains. Similarly, little is known about whether the somatosensory and auditory cortices contain content-specific representations of stimuli during imagery, even though this has been shown for the early visual cortex. Neuroimaging studies have mainly looked at univariate similarities between tactile perception and tactile imagery (Yoo et al. 2003; Savini et al. 2012; Schmidt et al. 2014) or auditory perception and auditory imagery (Halpern and Zatorre, 1999; Daselaar et al. 2010; Zvyagintsev et al. 2013). While these studies point to the utilization of primary and secondary sensory cortex during tactile imagery and the utilization of secondary sensory cortex during auditory imagery, the results do not tell us whether the underlying neural representations between imagery and perception are similar, nor whether these cortices represent imagery content. As pointed out by Albers et al. (2013), it could be the case that bottom-up and top-down signals are encoded differently in the early sensory cortices.

In this study we addressed two main questions: what are the unique fine-grained multi-voxel patterns in the brain that differentiate: (1) *imagery modalities,* such as tactile versus auditory imagery of a stimulus, and (2) *imagery content,* such as imagery of stimulus identity 1 versus 2. Moreover, we specifically addressed whether (A) the primary sensory cortices discriminate imagery modality and imagery content, and whether (B) these imagery modality and imagery content discriminative patterns also have a perceptual basis, i.e. do they share information with perception modality and perception content discriminative patterns. To address these questions, participants learned to associate four different 3D-printed figures (two identities × two emotions) with four different vocal

expressions. During fMRI measurements the participants perceived and imagined these tactile and auditory stimuli in a slow event-related design. We performed whole-brain Search Light Mapping analyses (WB-SLM; Kriegeskorte et al. 2006) to obtain information on the patterns of imagery modality and imagery content across the brain. In WB-SLM, several neighboring voxels contained in a moving sphere are considered in a decoding analysis. By centering this sphere on every voxel a whole-brain map of decoding accuracies is obtained. We found wide-spread patterns in somatosensory, motor, auditory and visual cortices from which imagery modality could be decoded. We found that the emotion of auditory mental images could be decoded from intraparietal sulcus. To investigate whether the early sensory cortices represented imagined modality information and imagery content we used an anatomical region-of-interest (ROI)-based classification approach, which considers only the voxels within the ROI for the decoding analysis. We found that we could successfully classify imagery modality in all task-specific early sensory cortices (somatosensory, motor, and auditory cortex), as well as in the visual cortex. Imagery content could be successfully discriminated in primary somatosensory and motor cortex for auditory emotions and auditory identities. Finally, we trained a classifier on discriminating perception modalities and perception content and tested whether the classifier could discriminate imagery modalities and imagery content in both the WB-SLM and the ROI-based classification analyses. While we did not find any evidence for a perceptual basis of imagery content, our results did show that the imagery modality information patterns have a perceptual basis in primary somatosensory, primary motor, and primary visual cortices.

Materials and Methods

Participants

Twelve healthy right-handed volunteers (seven females, five males, mean age 30.17 years; range 20–52) participated in this study. All participants had normal or corrected-to-normal vision and gave their informed consent. The study was approved by the local ethical committee.

Stimuli

The stimuli consisted of four audio files of human voices, two audio files of tones, and four 3D printed figures. The human voices were recorded from two male speakers, who were each expressing two emotions by wailing (fear) or growling (anger) without speech for 4.5 seconds (s). Additionally, two 0.5 s tones of 400 and 1200 Hz were used as cues. The 11 cm 3D figures were printed in-house using white thermoplastic material that was sanded afterwards to create a smooth surface. The 3D printed figures consisted of two male identities expressing the same emotions as the auditory stimuli. The fearful emotion was expressed by the figure with open hands held in front of him, arching backwards, while the angry emotion was expressed with a forward bend and with fists clenched in front of him (Fig. 1). The identities were distinguishable by body shape, as one male was skinnier (ID 1), while the other one was plumper (ID 2), and their clothing was different.
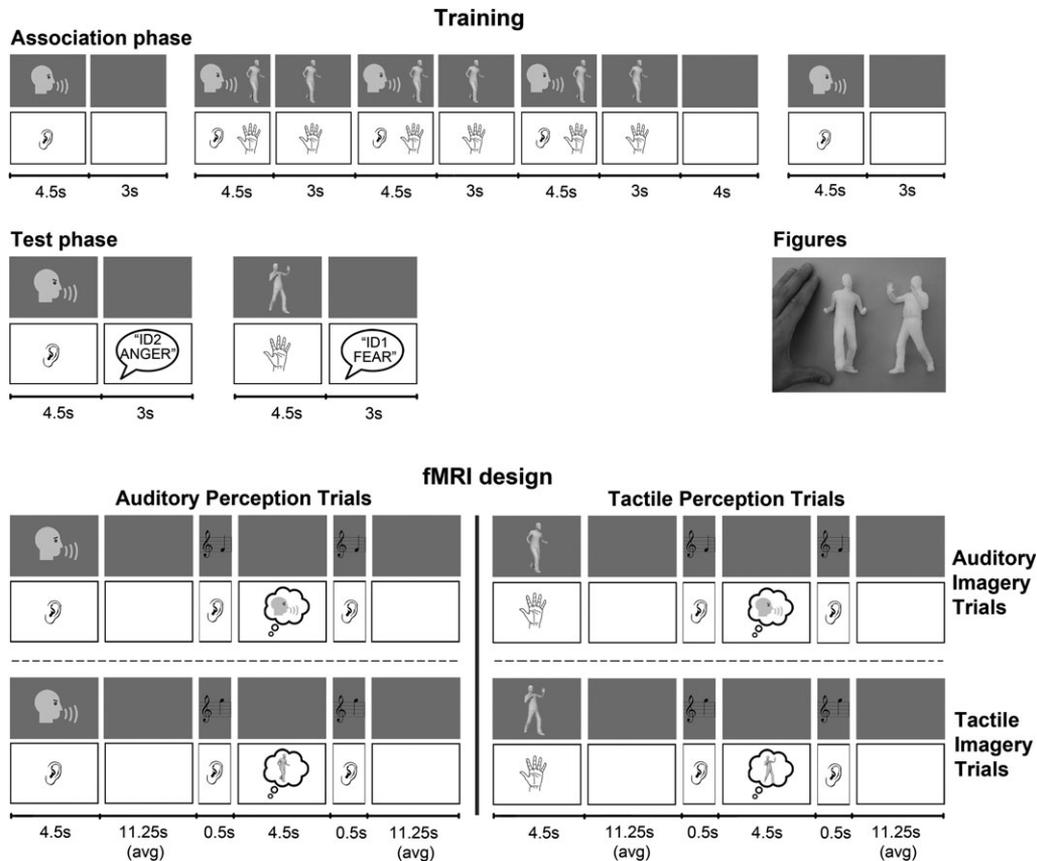
Task

Before the start of the fMRI session, the participants were trained on associating the four different 3D printed figures with the four different voices (Fig. 1 top). The participants were blind-folded throughout the training. First, the participants listened to each of the auditory stimuli once, with a 3 s inter-stimulus interval. Then, each auditory stimulus was presented three times in a row, with a 3 s inter-stimulus interval, while the blind folded participants were exploring the corresponding tactile stimulus. Each set of identical stimuli was followed by a 4 s inter-stimulus interval. After the last auditory and tactile stimuli were presented simultaneously, the auditory stimuli were all presented once more, again with a 3 s inter-stimulus interval. After this association phase, the participants entered a test phase in order to verify whether they could distinguish all stimuli. For the test phase 16 trials of auditory stimuli (4 stimuli × 4 repetitions, in randomized order) were presented. Each trial consisted of one 4.5 s stimulus presentation and a 3 s inter-stimulus interval. The participants had to name the identity and emotion of the voice as fast as possible. If after 16 stimuli they did not have at least eight in a row correct, the procedure was repeated until they did. The same procedure was performed with the tactile stimuli.

During fMRI measurements participants were blindfolded, while keeping their eyes open. The slow-event related experiment was divided into three functional runs. In each run the perception conditions were presented in a block (Fig. 1 bottom, auditory perception trials, and tactile perception trials). Within a block, trials consisted of the same perception condition followed by tactile or auditory imagery conditions. In the auditory perception block (Fig. 1 bottom left) each trial consisted of an affective voice (4.5 s), rest (11.25 s average), start cue (0.5 s), imagery (4.5 s), end cue (0.5 s), and rest (11.25 s average) (Fig. 1). The auditory stimulus indicated which identity and emotion the subject had to imagine. The start cue indicated the modality in which the subject had to imagine (low 400 Hz tone: auditory imagery, high 1200 Hz tone: tactile imagery). The tactile blocks (Fig. 1 bottom right) were identical to the auditory blocks, except for the first stimulus in each trial, which was tactile perception of the 3D figure. The 3D figures were manually presented to the participants' right hand by the experimenter, after which the participant could explore the figure with both hands. After 4.5 s the figure was removed. Thus, independent of the perceptual modality, participants always performed trials of auditory (50%) and tactile imagery (50%) in each block. The participants always imagined the emotion and the identity of the stimulus simultaneously.

Design

The experiment contained 16 different experimental conditions: Auditory Perception of Fearful ID 1 (APF1), Auditory Perception of Fearful ID 2 (APF2), Auditory Perception of Angry ID 1 (APA1), Auditory Perception of Angry ID 2 (APA2), Auditory imagery of Fearful ID 1 (AIF1), Auditory Imagery of Fearful ID 2 (AIF2), Auditory Imagery of Angry ID 1 (AIA1), Auditory Imagery of Angry ID 2 (AIA2), Tactile Perception of Fearful ID 1 (TPF1), Tactile Perception of Fearful ID 2 (TPF2), Tactile Perception of Angry ID 1 (TPA1), Tactile Perception of Angry ID 2 (TPA2), Tactile Imagery of Fearful ID 1 (TIF1), Tactile Imagery of Fearful ID 2 (TIF2), Tactile Imagery of Angry ID 1 (TIA1), and Tactile Imagery of Angry ID 2 (TIA2). In the multivariate analyses on imagery modality (auditory vs. tactile imagery) certain conditions were collapsed to create overarching conditions (i.e. their trials were analysed together). The condition Auditory Perception was created by collapsing conditions APF1, APF2, APA1, and APA2. Similarly, the conditions Auditory Imagery (AIF1, AIF2, AIA1, AIA2 collapsed), Tactile Perception (TPF1,

Figure 1. Task design of the study. Top: Training phase, in which participants were first familiarized with the stimuli and associated the auditory stimuli with the tactile stimuli (e.g. ID 1 angry voice with ID 1 angry body). Subsequently, they were tested on how well they could identify the stimuli (separate for auditory and tactile stimuli). Bottom: fMRI design, in which the auditory perception trials and the tactile perception trials are indicated on the left and right. On half of the trials the participants perform auditory imagery (top), while in the other half they perform tactile imagery (bottom), equally divided over both types of perception trials. The (average) duration of each stimulus is indicated below in seconds.

TPF2, TPA1, TPA1 collapsed), and Tactile Imagery (TIF1, TIF2, TIA1, TIA2 collapsed) were created. In the other multivariate analyses on imagery content (emotion and identity) the regular 16 conditions were used for analyses.

Each of the three functional runs contained two blocks. Each block consisted of 16 trials, making a total of 96 trials for the whole experiment. Each of the 16 conditions was presented four times per run (2 conditions per trial). The duration of the rest periods was 9, 10.5, 12, or 13.5 s. The combined duration of the two rest periods in each trial always added up to 22.5 s in order to keep the overall trial length identical. Therefore, the duration of the two rest periods within one trial was always assigned in pairs (9 s & 13.5 s, 13.5 s & 9 s, 10.5 s & 12 s and 12 s & 10.5 s). The order of the trials, stimuli, and the duration of the rest periods were pseudo-randomized for each participant, so that every pair of rest periods occurred an equal amount of times with every perceptual stimulus.

Data Acquisition

A 3T Siemens MR scanner (MAGNETOM Prisma, Siemens Medical Systems, Erlangen, Germany) was used for imaging. Functional scans were acquired with a multiband Gradient Echo Echo-Planar Imaging sequence with a Repetition Time (TR) of 1500 milliseconds (ms) and an Echo Time (TE) of 30 ms. For each functional run 687 volumes were acquired comprising

57 slices (matrix = 800×800, 2 mm isotropic voxels, inter slice time = 26 ms, flip angle = 77°). After the three functional runs high resolution T1-weighted structural images of the whole brain were acquired with an MPRAGE with a TR of 2250 ms and a TE of 2.21, comprised of 192 slices (matrix = 256×256, 1 mm isotropic voxels, flip angle = 9°).

Data Analyses

Functional MRI Preprocessing

The fMRI data were analyzed using fMRI analysis and visualization software BrainVoyager QX version 2.8.4 (Brain Innovation B.V., Maastricht, the Netherlands) and Matlab version R2013b, 8.2.0.701 (The Mathworks Inc., Natick, Massachusetts, USA). Functional data were 3D motion corrected (sinc interpolation), corrected for slice scan time differences and temporally filtered (high pass, GLM-Fourier, 2 sines/cosines). The data were not spatially smoothed to preserve all information for the multivariate analyses. The anatomical data were corrected for intensity inhomogeneity (Goebel et al. 2006) and transformed into Talairach space (Talairach and Tournoux 1988). The functional data were then aligned with the anatomical data and transformed into the same space, to create 4D volume time-courses (VTCs). The anatomical data were used for surface reconstruction (Goebel et al. 2006). The multivariate analyses were performed in the volume space, not on the surface.

The surface reconstructions of one subject were used for displaying results.

Region of Interest Definition

For the ROI-based classification analyses we extracted probabilistic cyto-architectonic maps from the SPM Anatomy Toolbox (Version 2.1, Forschungszentrum Jülich GmbH; Eickhoff et al. 2005). We extracted all available sub-regions of primary auditory cortex (Te1.0, Te1.1, Te1.2) (Morosan et al. 2001), primary somatosensory cortex (Area 1, 2, 3a, 3b) (Geyer et al. 2000; Grefkes et al. 2001), primary motor cortex (Area 4a, 4p) (Geyer et al. 1996) and visual regions up to V5/MT (V1, V2, V3, V4, V5) (Amunts et al. 2000; Wilms et al. 2005; Malikovic et al. 2007). Each voxel in a probabilistic region reflects the cyto-architectonic probability (10–100%) of belonging to that region. We followed the procedure of obtaining maximum probability maps as described in Eickhoff et al. (2006), as these are thought to provide ROIs that best reflect the anatomical hypotheses. This meant that all voxels in the ROI that were assigned to a certain area were set to "1" and the rest of the voxels were set to "0". We also extracted the Colin27 anatomical data to help verify the subsequent transformations. In order to transform the Colin27 anatomical data and the regions from MNI space to Talairach space (as used for the other analyses), we imported the ANALYZE files in Brainvoyager, flipped the *x*-axis to set the data to radiological format, and rotated the data –90° in the *x*-axis and +90° in the *y*-axis to get a sagittal orientation. Subsequently, we transformed the Colin27 anatomical data to Talairach space and applied the same transformations to the ROIs. On the basis of these anatomical ROIs we defined volumes of interest (VOIs) that were used as an input for the multivariate analysis (see next section).

Multivariate Analyses

For the prediction of imagery modality (auditory vs. tactile imagery) and imagery content (imagery of ID 1 vs. ID 2 and imagery of fear vs. anger) we employed two types of multivariate analyses. First, we performed multivariate pattern analyses (MVPA) using a WB-SLM approach and secondly we performed multivariate analyses in anatomically defined ROIs using support vector machine (SVM) classification (ROI-SVM). To investigate the perceptual basis of the representational patterns that underlie imagery modality and imagery content WB-SLM and ROI-SVM analyses were conducted using a classifier that was trained on perception trials and tested on imagery trials. The multivariate analyses were performed for each subject individually. The resulting prediction accuracies and voxel maps were subsequently used for calculating group results.

For the single trial estimation of the MVPA mean values were extracted in the imagery intervals (2–8 volumes from onset) and the perception intervals (2–8 volumes from onset) relative to baseline (–1 till 0 s before onset, % signal change) (Brainvoyager QX 2.8 MVPA Toolbox). For the WB-SLM analyses a whole-brain mask (from averaged VTC over all 12 subjects) was used to extract voxels. On the estimated trials a SLM approach was applied to find the local patterns with the most discriminative voxels for the two classes (In-house Matlab scripts; Kriegeskorte et al. 2006). A leave-one-run-out strategy was then used for training and testing of the data using SVM classification. In the perception-trained classification we used a leave-one-run-out cross validation as well. We considered a run (e.g. run 3) and excluded its perception trials from the training dataset and subsequently performed testing on the imagery

trials of that run. The procedure was repeated for all the runs. For the WB-SLM a searchlight of 33 voxels with a radius of 3 (including the center) was used. The resulting search light maps were averaged over runs in each individual. We tested whether the average accuracy of a searchlight across subjects was significantly higher than chance. In order to determine the significance level, we considered the accuracies obtained in all the subjects and, using a resampling approach, computed the probability of obtaining the observation under the null hypothesis that the mean population accuracy is 50% (balanced two-class classification). Under the null hypothesis, the likelihood of the observations is symmetric around chance (if a subject is at chance level, 40% and 60% accuracies are equally likely), and it is therefore possible to build an empirical estimate of the null distribution by performing all the possible switches of the observed accuracies around chance (Good 2005, Section 3.2.1). With N = 12 subjects, the total number of permutations was 2^{12} (4096) and it was therefore feasible to employ an exact permutation test. The correction for multiple comparisons was done using cluster threshold estimation based on the permutations: we set an initial uncorrected threshold of $\alpha = 0.01$ and, for each permutation, we tagged as significant those searchlights whose accuracy across subjects was larger than the $(1-\alpha)$ quantile. For each permutation we estimated the extent of the largest cluster of significant searchlights, and built a distribution of cluster sizes. Clusters of significant searchlights in the observed data larger than the 95% quantile of such distribution were considered significant, with $p < 0.05$. The significant searchlights extracted for the group map of imagery-trained classification of imagery modality are shown in Figure 2A and of perception-trained classification of imagery modality in Figure 3A. The significant searchlights extracted for the group map of imagery-trained classification of imagery content are shown in Figure 4A.

For the ROI-SVM classification the same single trial estimations of the MVPA mean values in the imagery and perception intervals were used as during the WB-SLM analyses. The voxels were extracted within each ROI (see section "Region of Interest Definition"). On the estimated trials a ROI-based approach was applied to discriminate response patterns within specific brain regions. A leave-one-run-out strategy was used for training and testing of the data using SVM classification. Similar to the WB-SLM analyses, we used a leave-one-run-out cross validation in the perception-trained classification as well. A single classification accuracy was obtained for each region per subject and run. These accuracies were then averaged over runs. We tested whether the average accuracy of a region across subjects was significantly higher than chance. Using the above described methods (but using "subjects by regions" instead of "subjects by voxels"), we tested the accuracies against an empirical null distribution and corrected for multiple comparisons using an FDR correction with $p < 0.05$ (Benjamini and Hochberg 1995). The results of the ROI-SVM analyses of imagery modality (average accuracies and standard error) are shown in Figure 2B (imagery-trained classification) and Figure 3B (perception-trained classification). The results of the ROI-SVM analyses of imagery content are shown in Figure 4B, C, D and Table 1 (imagery-trained classification).

Results

Classification of Imagery Modality

First, we tested whether we could successfully discriminate the imagery of touch versus sound from local patterns in

(A) Whole-brain analysis

(B) Region of Interest analysis
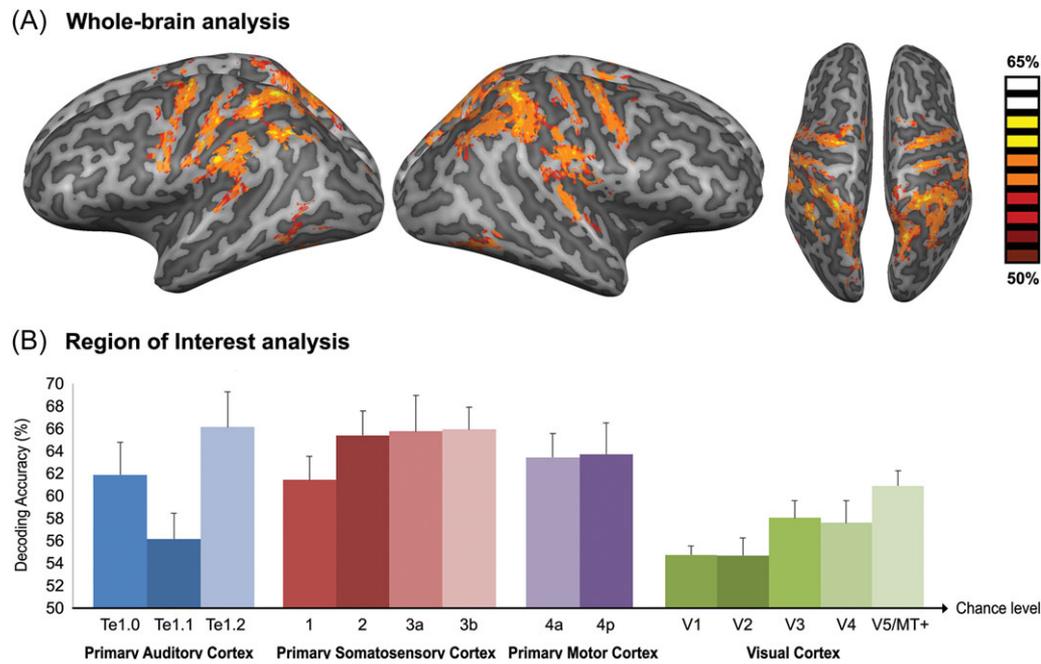
Figure 2. Imagery-trained classification of auditory versus tactile imagery. (*A*) Searchlights that contain significant information about imagery modality on the group level (*p*[corrected] < 0.05) are superimposed on an inflated cortical surface of a single subject. The color coding (red to white) reflects the average classification accuracy in each searchlight. (*B*) The classification accuracies and standard errors of anatomical regions that contain significant information (*p*[corrected] < 0.05) about imagery modality on the group level are shown.

(A) Whole-brain analysis
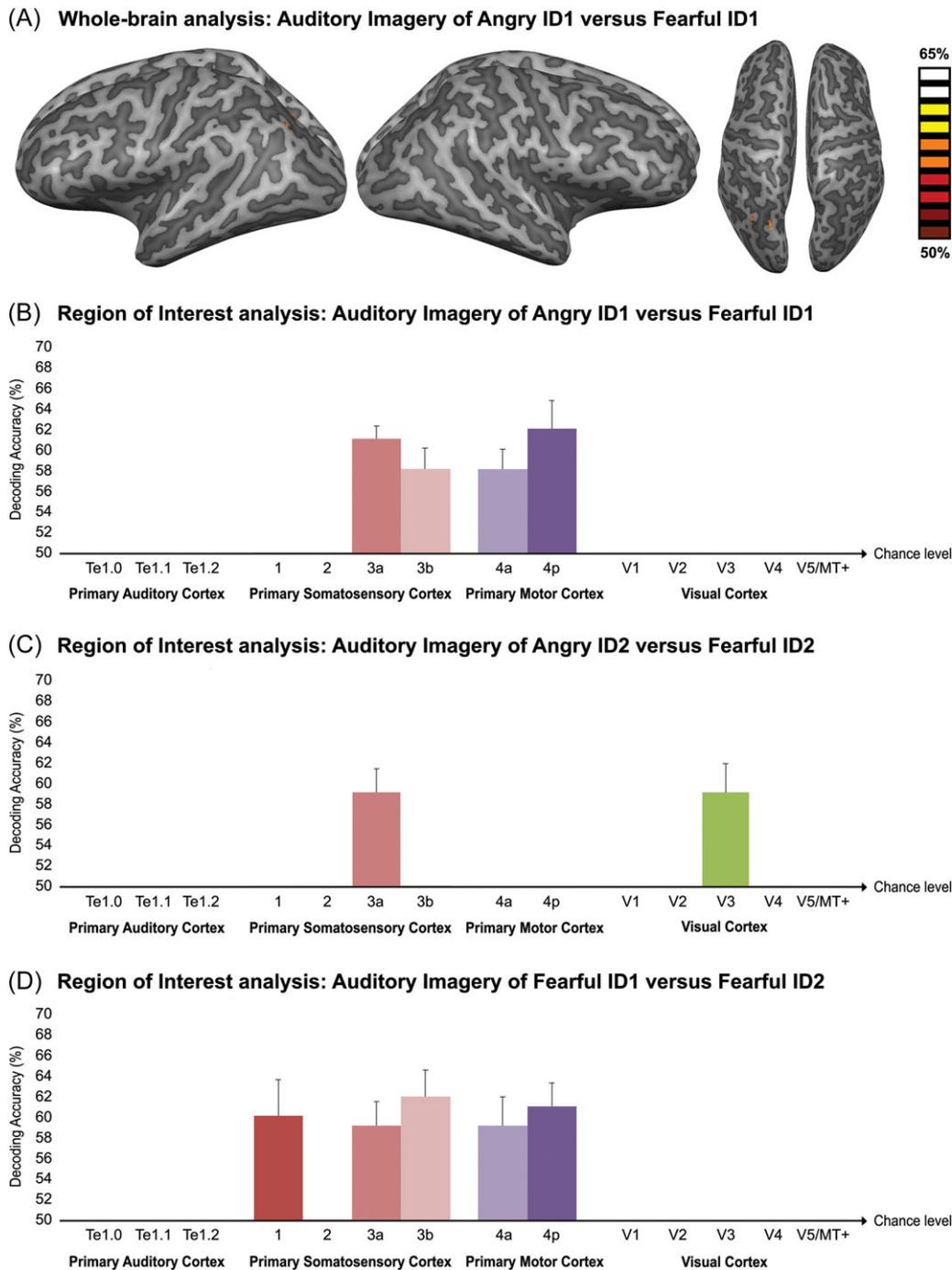

(B) Region of Interest analysis
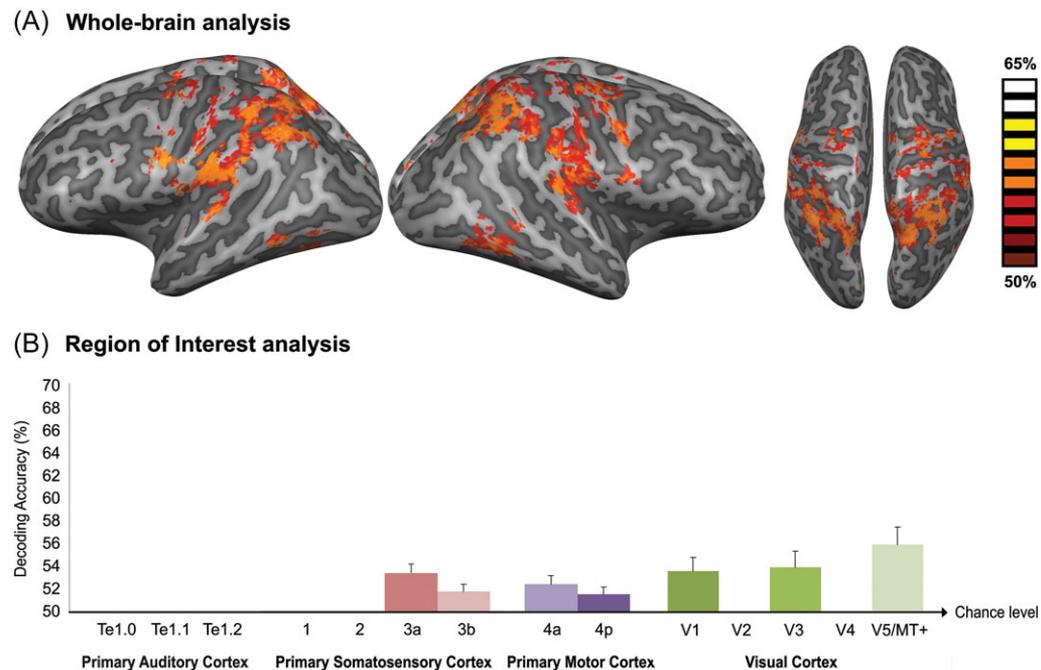
Figure 3. Perception-trained classification of auditory versus tactile imagery. (*A*) Searchlights that contain significant perception-based information about imagery modality on the group level (*p*[corrected] < 0.05) are superimposed on an inflated cortical surface of a single subject. The color coding (red to white) reflects the average classification accuracy in each searchlight. (*B*) The classification accuracies and standard errors of anatomical regions that contain significant perception-based information (*p*[corrected] < 0.05) about imagery modality on the group level are shown.

the brain. We investigated this using a whole-brain searchlight mapping approach and, subsequently, for pre-defined anatomical ROIs, which included the primary sensory cortices.

Training and Testing on Imagery: Whole-Brain Searchlight Mapping Analysis

We decoded auditory versus tactile imagery from local patterns in the brain using an imagery-trained classifier and a

(A) Whole-brain analysis: Auditory Imagery of Angry ID1 versus Fearful ID1

(B) Region of Interest analysis: Auditory Imagery of Angry ID1 versus Fearful ID1

(C) Region of Interest analysis: Auditory Imagery of Angry ID2 versus Fearful ID2

(D) Region of Interest analysis: Auditory Imagery of Fearful ID1 versus Fearful ID2

Figure 4. Imagery-trained classification of imagery content. (A) Searchlights that contain significant information about auditory imagery of angry versus fearful ID 1 on the group level (p[corrected] < 0.05) are superimposed on an inflated cortical surface of a single subject. The color coding (red to white) reflects the average classification accuracy in each searchlight. (B) The classification accuracies and standard errors of anatomical regions that contain significant information (p[corrected] < 0.05) about auditory imagery of angry versus fearful ID 1 on the group level are shown. (C) The classification accuracies and standard errors of anatomical regions that contain significant information (p[corrected] < 0.05) about auditory imagery of angry versus fearful ID 2 on the group level are shown. (D) The classification accuracies and standard errors of anatomical regions that contain significant information (p[corrected] < 0.05) about auditory imagery of fearful ID 1 versus fearful ID 2 on the group level are shown.

leave-one-run-out cross-validation approach. We subsequently verified whether these patterns included early somatosensory and early auditory cortex. We found that the sensory modality could be successfully predicted from the brain activity during the imagery period (mean decoding accuracy = 57%, p[corrected] < 0.05). As displayed in Figure 2A, primary

somatosensory cortex (SI, postcentral gyrus) contained information about the imagery modality, as did the somatosensory association cortex (superior parietal lobe, intraparietal sulcus) and the primary motor cortex (precentral gyrus). In the auditory cortex (see Fig. 2A) information about imagery modality pertained to the auditory association cortex in the left hemisphere

Table 1 Imagery-trained classification of imagery content in regions of interest (ROI)

Identity	AIA1 vs AIA2		AIF1 vs AIF2		TIA1 vs TIA2		TIF1 vs TIF2	
Region	Accuracy	p(FDR)	Accuracy	p(FDR)	Accuracy	p(FDR)	Accuracy	p(FDR)
Te1.0	49 ± 3.4	0.78	53 ± 3.7	0.44	49 ± 3.9	0.71	49 ± 3.2	0.90
Te1.1	52 ± 3.6	0.48	52 ± 3.3	0.48	50 ± 3.0	0.71	48 ± 2.7	0.90
Te1.2	48 ± 3.1	0.78	53 ± 3.1	0.43	51 ± 4.0	0.70	47 ± 3.5	0.90
PSC1	52 ± 2.3	0.48	**60 ± 3.7**	**0.045**	50 ± 1.6	0.70	50 ± 2.1	0.90
PSC2	47 ± 2.7	0.79	50 ± 3.2	0.58	52 ± 4.3	0.70	46 ± 3.6	0.90
PSC3a	55 ± 3.2	0.41	**59 ± 2.5**	**0.008**	54 ± 2.5	0.42	50 ± 2.2	0.90
PSC3b	52 ± 3.4	0.48	**62 ± 2.7**	**0.005**	49 ± 2.3	0.71	52 ± 2.0	0.90
PMC4a	53 ± 3.3	0.48	**59 ± 3.1**	**0.008**	51 ± 2.8	0.70	50 ± 1.8	0.90
PMC4p	54 ± 3.1	0.41	**61 ± 2.3**	**0.003**	51 ± 2.0	0.70	46 ± 2.7	0.90
V1	48 ± 3.0	0.78	50 ± 3.6	0.58	48 ± 3.1	0.71	47 ± 3.4	0.90
V2	50 ± 2.7	0.70	51 ± 2.8	0.51	49 ± 2.7	0.71	51 ± 3.5	0.90
V3	55 ± 2.7	0.41	48 ± 3.2	0.71	49 ± 2.8	0.71	52 ± 3.3	0.90
V4	52 ± 3.8	0.48	46 ± 1.8	0.94	47 ± 3.7	0.72	49 ± 3.5	0.90
V5	52 ± 1.9	0.41	51 ± 3.9	0.52	57 ± 2.9	0.33	45 ± 2.7	0.90
Emotion	AIA1 vs AIF1		AIA2 vs AIF2		TIA1 vs TIF		TIA2 vs TIF2	
Region	Accuracy	p(FDR)	Accuracy	p(FDR)	Accuracy	p(FDR)	Accuracy	p(FDR)
Te1.0	53 ± 3.5	0.35	52 ± 3.9	0.30	48 ± 4.9	0.77	44 ± 3.6	0.91
Te1.1	56 ± 3.1	0.13	55 ± 4.5	0.21	47 ± 3.8	0.77	48 ± 2.8	0.82
Te1.2	58 ± 4.1	0.13	49 ± 3.2	0.63	50 ± 4.0	0.77	47 ± 4.3	0.82
PSC1	52 ± 3.1	0.38	57 ± 3.5	0.10	56 ± 3.9	0.43	47 ± 2.9	0.82
PSC2	48 ± 3.4	0.71	56 ± 2.6	0.06	48 ± 3.7	0.77	51 ± 2.4	0.82
PSC3a	**61 ± 1.2**	**0.003**	**59 ± 2.4**	**0.003**	50 ± 3.5	0.77	50 ± 3.1	0.82
PSC3b	**58 ± 2.1**	**0.008**	56 ± 3.3	0.10	57 ± 3.2	0.42	51 ± 4.6	0.82
PMC4a	**58 ± 2.0**	**0.009**	53 ± 2.8	0.17	52 ± 2.3	0.49	51 ± 3.1	0.82
PMC4p	**62 ± 2.8**	**0.008**	48 ± 3.9	0.69	48 ± 3.3	0.77	50 ± 3.5	0.82
V1	52 ± 3.2	0.38	54 ± 2.0	0.10	52 ± 3.1	0.77	49 ± 2.8	0.82
V2	53 ± 2.6	0.23	54 ± 2.5	0.11	53 ± 2.5	0.43	49 ± 3.6	0.82
V3	49 ± 2.0	0.66	**59 ± 2.9**	**0.048**	49 ± 3.0	0.77	48 ± 4.0	0.82
V4	49 ± 3.4	0.66	56 ± 2.4	0.06	48 ± 3.2	0.77	53 ± 3.9	0.82
V5	49 ± 3.3	0.66	54 ± 2.6	0.11	50 ± 3.5	0.77	48 ± 3.6	0.82

All average classification accuracies, standard errors and corrected p values are shown per ROI for each of the four analyses of imagery-trained classification of imagined identities and each of the four analyses of imagery-trained classification of imagined emotions. The regions with significant accuracies (p[FDR] < 0.05) are indicated in bold.

(superior temporal gyrus), but included searchlights in Heschl's sulcus in the right hemisphere. Also the multi-modal region supramarginal gyrus contained information about imagery modality. The results of this first analysis confirmed earlier findings that early somatosensory cortex is involved in tactile imagery (Yoo et al. 2003; Savini et al. 2012; Schmidt et al. 2014) and showed that tactile imagery may also involve primary motor cortex. In the auditory cortex we found that brain activity during trials of auditory versus tactile imagery could be successfully discriminated in auditory association cortex, in line with previous research (Halpern and Zatorre 1999; Daselaar et al. 2010), as well as in primary auditory cortex (see also the next section). In addition to these sensory-specific regions we also found that imagery modality could be successfully predicted from searchlights in, amongst others, the left superior temporal sulcus, right middle frontal gyrus and the inferior temporal gyrus. We found these MVPA results in the absence of any significant univariate differences between tactile and auditory imagery. We also performed four WB-SLM analyses for the separate auditory versus tactile conditions: AIA1 versus TIA1, AIA2 versus TIA2, AIF1 versus TIF1 and AIF2 versus TIF2. These results can be found in the Supplementary Materials (Supplementary Fig. 1).

Training and Testing on Imagery: ROI-SVM Classification

Next, we directly tested our second research question – do the primary sensory cortices differentiate mentally imagined tactile information from auditory information – by performing ROI-SVM classification analyses on the basis of anatomical probability maps (see Fig. 2B). In the primary somatosensory cortex, we were able to successfully decode imagery modality in area 1 (accuracy 61%, p(FDR) < 0.001), area 2 (accuracy 65%, p(FDR) < 0.001), area 3a (accuracy 66%, p(FDR) < 0.001), and area 3b (accuracy 66%, p(FDR) < 0.001). In the primary auditory cortex, we were able to successfully decode imagery modality in areas Te1.0 (accuracy 62%, p(FDR) < 0.005), Te1.1 (accuracy 56%, p(FDR) < 0.05), and Te1.2 (accuracy 66%, p(FDR) < 0.005). In primary motor cortex, we were able to successfully decode imagery modality in area 4a (accuracy 66%, p(FDR) < 0.001) and area 4p (accuracy 65%, p(FDR) < 0.001). These results show that in the somatosensory and the auditory domain mental imagery representations also extend to the modality-specific early sensory cortices.

In addition to the task-specific sensory regions, we also investigated whether we could decode the imagery modality from non-task-specific sensory regions in visual cortex. We could successfully decode imagery modality from all visual

regions, including V1 (accuracy 55%, p(FDR) < 0.01), V2 (accuracy 55%, p(FDR) < 0.05) V3 (accuracy 58%, p(FDR) < 0.005), V4 (accuracy 58%, p(FDR) < 0.005), and V5/MT (accuracy 61%, p(FDR) < 0.001).

Thirdly, we addressed whether the discriminative patterns of tactile versus auditory imagery are perceptual in nature, using a WB-SLM analysis and ROI-SVM classification analyses.

Training on Perception, Testing on Imagery: Whole-Brain Searchlight Mapping Analysis

We tested whether we could successfully decode imagery modality from local patterns in the brain on the basis of a *perception*-trained classifier, in order to identify whether the imagery representations had a perceptual basis. To do this, we used a classifier that was trained on discriminating the brain activity during the perceptual conditions, in which the participant touched the 3D printed figures and heard the vocalizations, and then tested the classifier on the ability to discriminate the brain activity during the imagery conditions, in which the participant imagined touching the 3D figures and hearing the vocalizations. Similar to the imagery-trained classification of imagery modality, we used a leave-one-run-out cross-validation approach. The perception-trained classifier could successfully predict imagery modality from brain activity during the imagery period (mean decoding accuracy = 55%, p[corrected] < 0.05). As shown in Figure 3A, the voxel patterns of the perception-trained classifier in which the imagery modality could reliably be discriminated strongly resembled the significant voxel patterns of the imagery-trained classifier (Fig. 2A). The results revealed that the representations of imagery modality were similar to representations of perception modality, although overall classification accuracies were lower. This was not only clear in the different sensory association areas, but also in primary somatosensory cortex, primary motor cortex and primary visual cortex. We further tested similarities between perception and imagery in the early sensory cortices with the ROI-SVM analyses described below. We also performed four WB-SLM analyses of perception trained classification of auditory versus tactile imagery separate for each emotion-identity condition. These results can be found in the Supplementary Materials (Supplementary Fig. 2).

Training on Perception, Testing on Imagery: ROI-SVM Classification

We investigated specifically whether the imagery modality information contained in the early sensory cortices was similar to the perceptual modality information. These analyses would help us understand whether the representational similarities between perception and imagery also pertained to the early sensory cortices. We performed ROI-SVM classification analyses on the basis of the anatomical probablity maps, where we trained the classifier on discriminating the tactile and auditory perception conditions and tested on the tactile and auditory imagery conditions. In the primary somatosensory cortex (see Fig. 3B), we were able to successfully decode imagery modality in area 3a (accuracy 53%, p(FDR) < 0.005) and area 3b (accuracy 52%, p(FDR) < 0.005), but not in area 1 (accuracy 51%, p(FDR) < 0.5), or area 2 (accuracy 51%, p(FDR) < 0.5). In the primary auditory cortex, we were not able to decode imagery modality in any of the areas Te1.0 (accuracy 52%, p(FDR) < 0.3), Te1.1 (accuracy 51%, p(FDR) < 0.3), or Te1.2 (accuracy 53%, p(FDR) < 0.2). In primary motor cortex, we were able to successfully decode imagery modality in area 4a (accuracy 52%, p(FDR) < 0.01) and area 4p (accuracy 52%, p(FDR) < 0.05).

Moreover, we could successfully decode imagery modality from visual regions V1 (accuracy 54%, p(FDR) < 0.05), V3 (accuracy 54%, p(FDR) < 0.05), and V5/MT (accuracy 56%, p(FDR) < 0.01), but not from regions V2 (accuracy 52%, p(FDR) < 0.2), and V4 (accuracy 51%, p(FDR) < 0.2). These results indicate that although imagery modality could be predicted from brain activity in the primary auditory cortex (Fig. 2B), that these representations were not similar to perceptual modality representations (Fig. 3B). For the primary somatosensory, primary motor and primary visual cortex on the other hand, the representations of imagery modality did show similarities with perception.

Classification of Imagery Content

Finally, we addressed our second main research question by testing whether we could successfully discriminate imagery content, e.g. two imagined stimulus emotions or two imagined stimulus identities, from local patterns in the brain using WB-SLM analyses and ROI-SVM classification analyses.

Training and Testing on Imagery: Whole-Brain Searchlight Mapping Analysis

For the classification of imagined anger versus fear, four separate WB-SLM analyses were performed per imagery modality and identity: AIA1 versus AIF1, AIA2 versus AIF2, TIA1 versus TIF1, and TIA2 versus TIF2. We used an imagery-trained classifier and a leave-one-run-out cross-validation approach. Emotion could be successfully predicted from brain activity in the left posterior intraparietal sulcus during the auditory imagery of ID 1 (mean decoding accuracy = 60%, p[corrected] < 0.05, see Fig. 4A). For the other whole-brain emotion classification analyses no searchlights showed accuracies that were significantly above chance. Four separate WB-SLM analyses were performed for the classification of imagined ID 1 versus ID 2, per imagery modality and emotion: AIA1 versus AIA2, AIF1 versus AIF2, TIA1 versus TIA2, and TIF1 versus TIF2. We found that in none of the four analyses the identities of the imagined stimuli could be predicted significantly above chance on the group level.

Training and Testing on Imagery: ROI-SVM Classification

Subsequently, we tested whether primary sensory cortices represent mentally imagined auditory and tactile content by performing ROI-SVM classification analyses on the basis of anatomical probability maps. As in the WB-SLM analyses, we classified each separate set of conditions for imagined emotion and identity. For imagined emotion, we could successfully decode auditory imagery of emotion. Auditory imagery of fearful ID 1 versus angry ID 1 (see Fig. 4B) could be decoded in somatosensory and motor areas PSC3a (accuracy 61%, p(FDR) < 0.005), PSC3b (accuracy 58%, p(FDR) < 0.01), PMC4a (accuracy 58%, p(FDR) < 0.01), and PMC4p (accuracy 62%, p(FDR) < 0.01). Auditory imagery of fearful ID 2 versus angry ID 2 (see Fig. 4C) could be successfully decoded in somatosensory area PSC3a (accuracy 59%, p(FDR) < 0.005) and visual area V3 (accuracy 59%, p(FDR) < 0.05). We could not successfully decode tactile imagery of emotion for ID 1 or ID 2 in any of the ROIs (see Table 1). For identity imagery we were able to successfully decode (see Fig. 4D) auditory imagery of fearful ID 1 versus fearful ID 2 in somatosensory and motor areas PSC1 (accuracy 60%, p(FDR) < 0.05), PSC3a (accuracy 59%, p(FDR) < 0.01), PSC3b (accuracy 62%, p(FDR) < 0.01), PMC4a (accuracy 59%, p(FDR) < 0.01), and PMC4p (accuracy 61, p(FDR) < 0.005). In none of the

other three ROI-SVM analyses we could successfully predict the imagined identity (see Table 1).

Training on Perception, Testing on Imagery: Whole-Brain Searchlight Mapping Analysis

Using WB-SLM we could not successfully predict the emotion from the perception conditions split into identity and imagery modality, nor the identity from the perception conditions split into emotion and imagery modality. Therefore, we did not perform any prediction of imagery conditions on the basis of a perception-trained classifier for these comparisons.

Training on Perception, Testing on Imagery: ROI-SVM Classification

Since for the perception content we could only successfully predict auditory perception of fearful ID 1 versus ID 2 in Te1.1 (accuracy 58%, p(FDR) < 0.05), we conducted the perception-to-imagery ROI-SVM classification for this stimulus pair in all ROIs. None of the ROIs showed significant accuracies for auditory perception-to-imagery classification of the fearful identities.

Discussion

While it has been shown that the early visual cortex contains content-specific representations of stimuli during visual imagery, and that these representational patterns of imagery content have a perceptual basis, there is little evidence to date that this is also the case for the auditory and tactile domains. In this study we aimed to find the unique fine-grained multi-voxel searchlight patterns in the brain that (1) discriminate between imagery modalities: tactile versus auditory imagery and (2) discriminate between imagery content in the auditory and tactile domains: imagined stimulus ID 1 versus ID 2 and imagined fear versus anger. Moreover, we addressed whether these patterns (A) pertained to early sensory cortices and (B) had a perceptual basis. Using multivariate analyses we addressed whether the primary somatosensory cortex, primary auditory cortex and other regions in the brain show content and modality specific representations of imagined stimuli. We found that tactile versus auditory imagery could be successfully predicted from primary somatosensory, primary auditory and primary motor cortices as well as from early visual areas. These patterns also extended beyond the primary sensory regions, into the auditory and somatosensory association areas in lateral occipito-temporal cortex, supramarginal gyrus, superior parietal lobe, and intraparietal sulcus. Moreover, most of these modality-specific imagery searchlight patterns resembled those evoked by tactile and auditory perception, with the exception of patterns in the primary auditory cortex. Primary somatosensory and primary motor cortices showed content-specific representations of imagery content, both for the classification of auditory emotions and auditory identities. Moreover, for ID 2, auditory imagery of emotion could also be successfully classified in visual area V3. For ID 1, auditory imagery of emotion could be successfully predicted from the intraparietal sulcus using a whole-brain classification approach. We found no evidence for a perceptual basis of content-specific imagery patterns in this study.

Representations of Imagery Modality

The imagery-trained classification of tactile versus auditory imagery revealed a widespread network of searchlights that could accurately decode the imagery modality. These classification results indicate which regions were most discriminative for auditory versus tactile imagery, not whether these regions underlie auditory or tactile imagery specifically. Nevertheless, based on the literature, we will discuss the different regions in the context of their known functionalities. The results of the WB-SLM analysis, as well as the ROI-SVM classification analyses, showed that the regions which contained information about imagery modality included the primary sensory cortices. For the tactile domain we could see that both the primary somatosensory and the primary motor cortex had high decoding accuracies for imagery modality (Fig. 2). The involvement of primary somatosensory cortex during tactile imagery is in line with previous research (Yoo et al. 2003; Savini et al. 2012; Schmidt et al. 2014). Moreover, the results suggest that the participants not only imagined how the touch of the 3D printed figures felt, but likely also imagined the motor movements during touch. As can be seen from Figure 2A, the imagery modality searchlights in the somatosensory cortex mostly pertained to the middle section, around the area that is responsive during perception and observation of touch to the fingers (Pihko et al. 2010; Sanchez-Panchuelo et al. 2012; Kuehn et al. 2014). In the motor cortex on the other hand, the searchlights extended over a larger portion of the cortex, likely due to imagination of movements of the fingers, wrists and arms, which were involved in the manipulation of the figure. However, searchlights that were discriminative for auditory versus tactile imagery could also be observed in the lateral portions of the pre- and postcentral gyrus, in the area of the face and lips. As discussed later on, the primary somatosensory and motor cortices could also discriminate between the imagined auditory emotions and the auditory identities, suggesting that these areas contain specific auditory imagery content. These results indicate that auditory and tactile imagery both drove the motor and somatosensory cortices, but in differentiated regions, or to a different extent.

In the auditory cortex we saw that most of the modality information was localized to the auditory association areas, but that imagery modality could also be successfully predicted from the primary auditory areas. This was especially true for areas Te1.0 and Te1.2, which correspond to the middle and lateral portions of the primary auditory cortex. Most univariate fMRI studies reported that only the secondary auditory cortex and not the primary auditory cortex was involved during auditory imagery (Halpern and Zatorre 1999; Halpern et al. 2004; Bunzeck et al. 2005; Kleber et al. 2007; Daselaar et al. 2010; Zvyagintsev et al. 2013). Two univariate studies did report primary auditory cortex activation during auditory imagery (Yoo et al. 2001; Oh et al. 2013), but their experimental design either lacked a control condition or placed the imagery conditions in close proximity with perceptual stimuli. Our results, obtained using multivariate methods, indicated that brain activity during trials of auditory versus tactile imagery could be discriminated in the primary auditory cortex, even in the absence of univariate effects. These effects seemed to be mostly driven by auditory versus tactile imagery of fearful identities (Supplementary Fig. 1 bottom), as the imagery modality WB-SLM results for angry identities did not show significant classification accuracies in primary auditory cortex (Supplementary Fig. 1 top). It should be taken into account though, that for the ROI-SVM analyses we did not perform individual localizations to map the primary auditory cortex, but instead used anatomical probabilistic maps to identify the regions. Nevertheless, the WB-SLM results of imagery-trained classification of imagery modality also revealed significant

searchlights in right Heschl's sulcus. The fact that many studies failed to find primary auditory cortex activation during auditory imagery may reflect the difficulty for most participants to form accurate auditory mental representations that would drive the primary auditory cortex. Moreover, the involvement of the primary auditory cortex may also relate to the imagery task, as in some studies participants may have imagined words or movements rather than sounds (Kleber et al. 2007), or the simultaneous presentation of visual information may have suppressed the primary auditory cortex (Bunzeck et al. 2005). In visual imagery, the involvement of primary visual cortex seems to depend on the imagination of fine-grained details. The representation of these small details would need support from neurons that encode specific visual features, such as orientation or spatial frequency. A similar mechanism could be at work in the auditory cortex. Only when the task requires the participant to imagine specific auditory features, such as the different formats, the mental representations would drive the primary auditory cortex. For example, in the perceptual domain, Formisano et al. (2008) have shown that the discrimination of vowels relied much more on patterns near Heschl's gyrus than the discrimination of speakers. This suggests that the neural patterns in the auditory cortex directly relate to the transformation of specific acoustic features, which could also be the case during imagery. Regardless, even though some studies focussed their imagery task on specific acoustic features, they still did not find activity in primary auditory cortex (Halpern and Zatorre 1999; Halpern et al. 2004). In our study, participants needed to imagine both the pitch and the prosody of the auditory stimuli, which may have supported the neural representation of these features in auditory cortex. However, neither the imagined emotion nor the imagined identity of the auditory stimuli could be decoded from primary auditory cortex, thus providing no evidence for the mental representation of specific acoustic properties in primary auditory cortex during this task. Our results for the prediction of auditory imagery content, discussed later on, hint towards participants having used an inner vocalization strategy for the auditory imagery task. Therefore, the mental representations during auditory imagery may have contained more feature-specific details in primary motor and somatosensory cortex than in primary auditory cortex.

The results of the ROI-SVM classification analyses additionally revealed that imagery modality could be successfully decoded in the primary visual area V1. The presence of imagery modality information in early visual cortex may stem from the fact that during tactile imagery of the figures participants were more likely to perform additional visual imagery of the shape of the figures. Brain activity during auditory processing on the other hand often shows a negative correlation with the visual modality – when activity in auditory cortex is increased, activity in visual cortex is decreased and vice versa – which could relate to the allocation of resources to the relevant sensory cortex (Amedi et al. 2005; Azulay et al. 2009). These differences may have contributed to the successful classification of imagery modality in V1.

Not only did the primary sensory cortices contain information about tactile versus auditory imagery, but the imagery modality discriminative searchlights extended into several of the somatosensory, auditory, and visual association cortices. The superior parietal cortex, intraparietal sulcus (somatosensory association area) and the superior temporal gyrus (secondary auditory cortex) have often been reported as involved in the mental representation of touch or sound (Halpern and Zatorre 1999; Yoo et al. 2003; Halpern et al. 2004; Bunzeck et al. 2005; Kleber et al. 2007; Daselaar et al. 2010; Savini et al. 2012; Zvyagintsev et al. 2013; Schmidt et al. 2014). While it was suggested that the lateral parietal cortex relates to modality-independent imagery (Daselaar et al. 2010), in this study and in earlier work (de Borst et al. 2016), we could discriminate our two imagery modalities in the intraparietal sulcus and the superior parietal lobe. Tactile and visual imagery may evoke the mental representation of spatial properties much more than auditory imagery, and thus activate the posterior parietal cortex more strongly (Cohen et al. 1996; Mellet et al. 1996; Tagaris et al. 1996; Sathian et al. 1997; Trojano et al. 2000; Formisano et al. 2002). However, our results of imagery content classification indicate that auditory emotion can be predicted from the intraparietal sulcus, suggesting a relevant role for auditory imagery as well.

The superior temporal gyrus has been shown to process higher level properties of sound, such as prosody or speaker identity (Formisano et al. 2008; Bonte et al. 2014). Although the superior temporal gyrus was discriminative for imagery modality, we did not find any evidence for differential activations during imagery of speaker identity or emotion. An additional association area, the supramarginal gyrus, also contained imagery modality information. The supramarginal gyrus is a multimodal region, where input arrives from auditory, somatosensory and visual cortex. It is involved in identifying postures and gestures of other people, as shown by case studies of apraxia and tactile agnosia (Reed and Caselli 1994; Kareken et al. 1998), but also in phonological and articulatory processing of words and sounds. The temporo-parietal junction (TPJ), which is overlapping with the supramarginal gyrus, is known to be involved in body perception, self-other distinction and multimodal integration (Saxe and Kanwisher 2003; Blanke et al. 2005; Sinke et al. 2010; Ionta et al. 2011; Cazzato et al. 2015; Ganesh et al. 2015). In this study the supramarginal gyrus might have re-activated under top-down influence of the formation of mental representations of postures, as part of the task involved in the imagination of specific postures of the 3D printed figures, or may have linked auditory and somatosensory processes. Moreover, even though subjects were blindfolded with eyes open, we could successfully predict imagery modality from visual areas V1–V5. In seeing individuals, tactile imagery is often accompanied by visual imagery. As has been shown before, visual imagery can activate the visual association areas as well as the primary visual cortex (Kosslyn et al. 1993, 1999; Klein et al. 2000; Ishai et al. 2002; Ganis et al. 2004). In our study, the classification accuracy is especially high in visual area V5/MT. As the participants moved and rotated the 3D-printed figure in their hands during the tactile perception condition, participants may have imagined rotating the figure as well. Alternatively, given the overlap between area V5/MT and the extrastriate body area (EBA), participants may have also mentally represented the figures' bodies (Ferri et al. 2013). We also found significant searchlights in the occipito-temporal cortex, around the lateral occipital complex (LOC), which might further underlie the mental representation of shape (Pietrini et al. 2004; Peltier et al. 2007).

Representations of Imagery Content

Furthermore, we investigated what brain regions were discriminative for specific imagery content, such as the imagined emotions or the identities of the voices and figures. We found that the primary somatosensory and primary motor cortices

were discriminative for the imagined emotions of the voices, as well as for the imagined identities of the fearful voices. The primary somatosensory and motor cortices being discriminative for imagined auditory content, rather than the auditory cortex, suggests that participants were using an inner vocalization strategy to imagine the voices. Although participants were instructed to imagine how the voices sounded, they may have been using their "inner voice" rather than their "inner ear" for imagery. Earlier work by de Borst et al. (2016) on film professionals and non-experts also revealed that non-experts are more likely to use some form of inner speech as an auditory imagery strategy. Similar to the execution of vocalizations, such as speech or singing, inner speech during imagery has shown to activate the primary motor cortex and the somatosensory cortex (Ozdemir et al. 2006; Kleber et al. 2007). Also during the imagery of non-vocal sounds, such as the melody of a tune, activation of the motor and parietal cortices has been reported (Halpern and Zatorre 1999).

Interestingly, both imagined voice emotions and voice identities could be discriminated in the primary motor and somatosensory cortices. The perception of emotion in combination with memory retrieval has been strongly linked to the dorsal pathway, including motor and parietal regions (de Gelder 2006). For example, an fMRI-based TMS study showed that left intraparietal sulcus is involved in identifying emotionally negative pictures compared to neutral pictures (Kaffenberger et al. 2008). We found similar results in left intraparietal sulcus for auditory fear versus anger imagery. Other research showed that perception of emotional compared to neutral prosody evoked larger N1 responses in parietal cortex (Iredale et al. 2013) and that different emotional utterances could be discriminated in parietal cortex (Wildgruber et al. 2002), suggesting the presence of an intonational store in inferior parietal cortex. Earlier work also suggested that the inferior parietal lobe contains a working memory circuit for processing vocalizations (Aboitiz and Garcia 1997). Our results support this idea by showing that certain auditory features that underlie the representation of imagined (negative) emotions can be discriminated in motor and parietal cortex, and in the left intraparietal sulcus in specific.

Moreover, we could predict the fearful voice identity from primary motor and primary somatosensory cortex. Previously, brain activity in pre- and postcentral gyrus has been reported during auditory frequency discrimination (Weeks et al. 1999), speaker and syllable identification (Dijkstra et al. 2015; Evans and Davis 2015) and memory maintenance of voice identity (Rama et al. 2004). In other work, searchlights in pre- and postcentral gyrus showed high correlation with the syllable identity model (Evans and Davis 2015). Similar to the representation of imagined voice emotion, the representation of imagined speaker identity in motor and somatosensory cortex could also relate to imagined articulatory aspects of the stimuli. In speech perception, Hickok and Poeppel (2000) suggested a strong link between the auditory and articulatory processes in auditory and motor cortex, through an auditory–motor interface system in parietal cortex. These systems may also be in place during mental imagery of voice identity and emotion.

Although we could successfully classify the fearful identities from brain activity during mental imagery trials, we could not do the same for the angry identities. Most likely, imagery of the identities of the fearful stimuli could be better predicted because they were more dissimilar in pitch than the angry voices. Furthermore, we could neither predict imagined auditory emotion nor imagined auditory identity from the primary auditory cortex. This is in line with auditory perception

research which showed that the discrimination of perceived voice identities does not involve the primary auditory cortex, but is more localized to a region in the superior temporal gyrus (Formisano et al. 2008; Dijkstra et al. 2015). Since we mainly included primary sensory cortices in our ROI-SVM analyses, we could not investigate imagery content discrimination in secondary regions. Nevertheless, we also did not find any discriminative searchlights in superior temporal gyrus using the WB-SLM approach. This might be explained by the fact that when using all conditions separately, rather than merged into overarching conditions, too little trials were available for training. This, in combination with stricter multiple comparisons corrections on the whole-brain level than for the ROIs, might indicate why we could not successfully predict imagined voice identity and emotion in other brain regions using the WB-SLM approach. Although this could also be an explanation for the null-results on our tactile imagery trials of identity and emotion, an additional issue with the tactile representations could be that the participants imagined touching the figure, rather than forming a mental imagine of the shape, which is less differentiating for the specific identity and emotion. This could explain why auditory and tactile imagery could be discriminated across the cortex, but no regions that were discriminative for imagery of tactile identity or emotion were found.

Perceptual Basis of Imagery

While several studies have now shown support for the perceptual nature of visual imagery and the representation of imagery content in early visual cortex, there is so far little research on whether this also pertains to other imagery modalities. Here we showed that auditory versus tactile imagery of affective voices and bodies could be discriminated in primary somatosensory cortex, primary auditory cortex, primary motor cortex, and primary visual cortex. Moreover, primary somatosensory and primary motor cortex could discriminate auditory imagery content. Subsequently, we investigated whether the neural representations discriminative for imagery modality or imagery content were similar to neural representations discriminative for modality and content during bottom-up perception. We found that we could decode imagery modality, but not imagery content, with a classifier that was trained on perception trials, in regions very similar to the results of the imagery-trained classification. Predictably, the overall accuracy during perception-trained classification was lower. This could reflect that perception and imagery processes are similar, but not identical, making it more difficult to classify imagery modality on the basis of perception modality. It is remarkable though that we found almost the same regions that could successfully decode imagery modality on the basis of perception conditions as we did on the basis of imagery conditions in the WB-SLM analysis. We would have expected the sensory regions to show strong similarities between perception and imagery, as they do, but also had expected some regions to show little resemblance to perception. Mental imagery after all activates an extensive network that includes regions that are found to be more active during imagery than during perception, such as the medial superior frontal gyrus and the premotor cortex (de Borst et al. 2012). However, as the imagery-trained WB-SLM analyses focussed on classifying auditory versus tactile imagery, these could be best discriminated in sensory regions rather than regions that support both imagery modalities. Additionally, one can observe in Figure 3A that the accuracies of discriminating tactile and auditory imagery on the basis of perception were

highest in the association areas, such as supramarginal gyrus, superior parietal lobe, and intraparietal sulcus. The ROI-based results showed that in the primary sensory cortices, perception-trained classification of imagery modality was significant in primary somatosensory cortex, primary motor cortex and primary visual cortex (Fig. 3B). For the primary auditory cortex this was not the case. None of the primary auditory regions showed classification accuracies significantly above chance. Although our results suggested that the primary auditory cortex does discriminate between the auditory and tactile imagery trials, we could not confirm that the local representations were similar to perception. As the perception-trained decoding accuracies of imagery modality in the primary auditory regions were in a similar range as the decoding accuracies in the other primary cortices and were close to chance level, the results may reflect a larger inter-subject variability in auditory cortex. The WB-SLM analyses did indicate that perception-to-imagery decoding was successful in other auditory regions along the STG and the lateral sulcus. However, also during the classification of imagery content we found that the primary somatosensory and primary motor cortices and not the primary auditory cortex discriminated between the imagery trials of affective voices and voice identities.

Conclusions

In this study we found that the primary somatosensory and auditory cortices could discriminate between imagery of touch and imagery of sound. The discrimination of imagery modality was further supported by the somatosensory association areas, superior parietal cortex and intraparietal sulcus, and the auditory association areas, superior temporal gyrus and supramarginal gyrus. Moreover, also primary sensory cortices that were not directly related to the task, the primary motor cortex and the primary visual cortex, could discriminate between tactile and auditory imagery. Most of these imagery-discriminative patterns showed similarities with perception-discriminative patterns, suggesting that top-down modulation of the somatosensory, motor and visual cortices rely on similar neural representations as bottom-up perceptual processes. The exception to this was the primary auditory cortex, where perception-trained decoding of imagery modality did not reach significance. Moreover, we found evidence for content-specific representations of the stimuli during auditory imagery in the primary somatosensory and primary motor cortices. Both the imagined emotions and the imagined identities of the voices could be successfully classified in these regions.

Supplementary Material

Supplementary material can be found at: http://www.cercor. oxfordjournals.org/.

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Notes

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