Consciousness and Cognition 35 (2015) 66–77

Contents lists available at ScienceDirect

Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog

Tunes stuck in your brain: The frequency and affective evaluation of involuntary musical imagery correlate with cortical structure

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ARTICLE INFO

Article history:
Received 21 November 2014
Available online 16 May 2015

Keywords:
Music
Imagery
Involuntary
Cortical thickness
Voxel-based morphometry

ABSTRACT

Recent years have seen a growing interest in the neuroscience of spontaneous cognition. One form of such cognition is involuntary musical imagery (INMI), the non-pathological and everyday experience of having music in one's head, in the absence of an external stimulus. In this study, aspects of INMI, including frequency and affective evaluation, were measured by self-report in 44 subjects and related to variation in brain structure in these individuals. Frequency of INMI was related to cortical thickness in regions of right frontal and temporal cortices as well as the anterior cingulate and left angular gyrus. Affective aspects of INMI, namely the extent to which subjects wished to suppress INMI or considered them helpful, were related to gray matter volume in right temporopolar and parahippocampal cortices respectively. These results provide the first evidence that INMI is a common internal experience recruiting brain networks involved in perception, emotions, memory and spontaneous thoughts.

1. Introduction

It is a common experience to have music looping in one's head, a phenomenon colloquially termed "earworms", as well as "stuck song syndrome", or, more formally, involuntary musical imagery (INMI, Liikkanen, 2008). INMI appears spontaneously and without conscious control. As a spontaneous cognitive phenomenon, INMI can be considered alongside other self-generated thoughts (SGT) such as mind wandering or daydreaming, which are known to occupy a substantial proportion of mental life (Killingsworth & Gilbert, 2010; Klinger & Cox, 1987).

INMI is prevalent in the general population (Liikkanen, 2008) and several diary and behavioral studies have shed light on the phenomenon. INMI is typically triggered by recent musical exposure (Bailes, 2007; Byron & Fowles, 2013; Halpern & Bartlett, 2011; Hyman et al., 2013), as well as low attention states and memory associations (Williamson et al., 2011). Individuals who are musically trained or who actively engage with music in other ways, experience INMI more frequently (Beaty et al., 2013; Liikkanen, 2011; Müllensiefen et al., 2014). INMI episodes are mostly pleasant but can also be disturbing (Beaman & Williams, 2010; Williamson, Liikkanen, Jakubowski, & Stewart, 2014), while recent data suggests that the

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http://dx.doi.org/10.1016/j.concog.2015.04.020
1053-8100/

occurrence of musical imagery (both involuntary and voluntary) is influenced by mood states (Beaty et al., 2013; Williamson et al., 2011). Personality traits such as obsessive–compulsive traits (Müllensiefen, Fry, et al., 2014), neuroticism and openness to experience (Beaty et al., 2013; Floridou, Williamson, & Müllensiefen, 2012) are associated with more frequent INMI, while individual differences in mental control and schizotypy predict difficulty in the suppression of INMI (Beaman & Williams, 2013). Finally, there is evidence that the occurrence of INMI depends on availability of cognitive resources (Hyman et al., 2013), as is the case for other forms of SGT (Forster & Lavie, 2009).

In contrast to the behavioral literature that has emerged over recent years, no study to date has focused on the neural basis of INMI. This may, in part, relate to the lack of predictability of INMI, such that episodes of INMI would likely prove elusive in a functional scanning paradigm, or unsuitable for typical neuroimaging designs. Nonetheless, it is of considerable interest to examine the cerebral basis of INMI, not least because the experience is very common, can be vivid and complex, and may have the capacity to positively influence moods and emotions, akin to instances of actual music listening (Fritz, Halfpaap, Grahl, Kirkland, & Villringer, 2013; Koelsch, 2014; Schellenberg, Nakata, Hunter, & Tamoto, 2007; Shifriss, Bodner, & Palgi, 2014).

A potentially fruitful approach to a neurological investigation of INMI is one based on individual differences, i.e., investigating whether discrete aspects of the INMI experience systematically co-vary with regional differences in brain structure. A new measure, the Involuntary Musical Imagery Scale (IMIS) (Floridou, Williamson, Stewart, & Müllensiefen, 2015) captures multiple facets of the INMI experience, including questions relating to frequency, as well as evaluative, sensorimotor and self-reflective aspects of the experience. The measure has been tested on 2315 participants, and has been demonstrated to have good validity using exploratory and confirmatory factor analysis (Cronbach's alpha for the factors ranged from 0.76 to 0.91), as well as good test–retest reliability (all significant test–retest correlations ranging from 0.65 to 0.79). This makes the IMIS a valuable tool for establishing whether variation in any of these aspects of the INMI experience is reflected in systematic differences in brain structure. In formulating our hypotheses regarding a potential relationship between INMI and brain structure, we consider three bodies of literature, pertaining to the neural bases of deliberate auditory imagery, emotional response to music, and self-generated thought.

Voluntary musical imagery, or more generally auditory imagery, has been previously described in the psychological and neuroscientific literature (Halpern, 2001; Herholz, Halpern, & Zatorre, 2012; Hubbard, 2010; Zatorre, Halpern, Perry, Meyer, & Evans, 1996) and has been shown to recruit brain areas similar to those involved in music perception and performance, including the primary and secondary auditory cortices (Halpern & Zatorre, 1999; Linke & Cusack, 2015; Zatorre & Halpern, 2005; Zatorre et al., 1996) and the supplementary motor area (SMA) (Halpern, Zatorre, Bouffard, & Johnson, 2004). Voluntary musical imagery also relies on interactions between auditory areas and the right inferior frontal gyrus (rIFG) (Herholz et al., 2012), the latter being recruited in working memory for pitch processing (Albouy et al., 2013; Hyde, Zatorre, & Peretz, 2011; Hyde et al., 2007) and both auditory perception and imagery (Herholz et al., 2012).

Recent research on the neural correlates of music-evoked emotion has shown that music can elicit widespread activity in the brain's emotional circuitry (Koelsch et al., 2004). Intense pleasure, fear and joy evoked by music activates deep regions involved in reward such as the nucleus accumbens, amygdala, striatum and hypothalamus (Blood & Zatorre, 2001; Koelsch et al., 2013; Pehrs et al., 2013; Zatorre & Salimpoor, 2013). Furthermore, a wide range of cortical areas contribute to the affective evaluation of music, such as the orbitofrontal cortex (OFC), ventromedial prefrontal cortex and anterior cingulate cortex (ACC) (Alluri et al., 2013; Blood & Zatorre, 2001; Lehne, Rohrmeier, & Koelsch, 2013), as well as the parahippocampal cortex (PHC) (Engelien et al., 2006; Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006). Whether these brain networks are also implicated in the affective evaluation of musical imagery has not yet been addressed.

Brain networks involved in endogenous processes such as mind wandering may also contribute to aspects of the INMI experience, such as frequency of episodes, linking them with personal concerns, or forming an evaluative judgment. The generation of SGT may rely on spontaneous activity in the Default-Mode Network (DMN), a set of brain areas which are more active when participants are not focusing on a task (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Buckner, Andrews-Hanna, & Schacter, 2008; Callard, Smallwood, Golchert, & Margulies, 2013; Fox, Nijeboer, Solomonova, Domhoff, & Christoff, 2013; Kucyi & Davis, 2014). This network includes the medial prefrontal cortex, the posterior cingulate cortex, the PHC, and the ventral ACC. While generating undirected thoughts, the DMN may be also coupled with the executive network and decoupled from sensory areas (Christoff, 2012), while the internal train of thought could emerge from interactions between the DMN and fronto-parietal networks (Smallwood, Brown, Baird, & Schooler, 2011). It appears that the form and content of SGT are reflected in spontaneous fluctuations during resting state in perigenual cingulate cortex, primary visual cortex, the insula and the cerebellum (Gorgolewski et al., 2014), as well as the medial OFC. Accordingly, it was found that patterns of activations in the medial OFC during task and rest encode the affective content of SGT (Tusche, Smallwood, Bernhardt, & Singer, 2014). Finally, in a structural MRI study of SGT it was found that midline brain areas mediate task unrelated thoughts; the tendency to engage in SGT during low cognitive load correlates with cortical thickness in the medial prefrontal cortex, the ACC and lateral prefrontal opercular cortex (Bernhardt et al., 2013).

A recent review has emphasized the potential of structural MRI to uncover brain–behavior relationships (Kanai & Rees, 2011). Here, we use two common methods to study covariation between brain structure and behavior, namely voxel-based morphometry (VBM, Ashburner & Friston, 2000) and cortical thickness. These two measures provide different insights into brain morphology, as VBM measures local variations in gray matter volume (GMV), while cortical thickness measures the distance between the gray–white matter interface and the pial surface. Typically, cortical thickness is measured by modelling the surface of the cortical sheet. This surface model can subsequently be used to derive measurements of cortical thickness, as well as cortical surface area and surface-based GMV. Here, we first perform whole-brain analysis of VBM and cortical thickness to identify structure–function relationships with the IMIS. Such an approach does not require an *a priori* hypothesis regarding the spatial location of the effects, while the use of the two measures provides complementary information on function–structure relationships. Next, we use regions of interest with the surface model in an exploratory analysis to test the convergence between the VBM and cortical thickness results. Specifically, we tested whether results observed in whole-brain VBM analysis could be related to local ROI-based analysis of surface area, surface-based GMV and cortical thickness in order to understand which morphological feature (cortical area or thickness) might be driving variations in GMV.

The previously mentioned literature provides a starting point for our hypotheses regarding the neural basis of INMI. We hypothesize that (1) individual differences with respect to auditory and temporal aspects of the INMI experience (such as the frequency and length of INMI episodes) will correlate with structural variation in areas including the IFG, the SMA and auditory areas, (2) evaluative aspects of INMI will rely on brain regions recruited in music-evoked emotions, such as the OFC, the ACC and the PHC and (3) networks involved in SGT, such as the DMN, will be involved in both the affective evaluation and the frequency of INMI episodes.

2. Methods

2.1. Participants

44 healthy subjects (23 women) who took part in previous neuroimaging studies at the Cambridge Medical Research Council's Cognition and Brain Sciences Unit between 2009 and 2012 were selected for this study. Their ages ranged from 25 to 70 years old and there was no history of neurological damage, hearing loss or tinnitus. 70% of the subjects were aged between 20 and 40, and the remaining were aged above 65. Seven participants were undergraduate students in the Cambridge area, and the rest were not currently in education. All participants spoke British English, though 5 spoke it as a second language. We measured participants' musical training using the Goldsmiths Musical Sophistication Index (Gold-MSI, see Section 2.2). Eight participants played one or more instruments, but none were expert musicians. Participants were all right-hand dominant, and all of them had normal or corrected-to-normal vision. Online consent was obtained from the subjects conforming to the Declaration of Helsinki, and ethical approval for MRI was obtained from the Cambridge Psychology Research Ethics Committee.

2.2. Behavioral testing

Participants were invited to fill in an online survey, which comprised two pre-existing questionnaires: the Involuntary Musical Imagery Scale (Floridou et al., 2015), and the Goldsmiths Musical Sophistication Index (Gold-MSI, Müllensiefen, Gingras, Musil, & Stewart, 2014). The Involuntary Musical Imagery Scale (IMIS) consists of four factors that assess (1) the extent to which people negatively evaluate the INMI experience (*Negative Valence* factor), (2) the extent to which people move in time to their INMI (*Movement* factor), (3) the degree to which people are helped in their everyday activities by INMI (*Help* factor), and (4) the extent to which INMI reflects the content of personal matters, worries, or concerns (*Personal Reflections* factor). The IMIS also includes three additional questions regarding the overall frequency of INMI occurrence, the typical length of the section of music that is experienced as INMI (subsequently referred to as INMI section length), and the average length of an INMI episode (subsequently referred to as INMI episode length). Finally, the *Active Engagement* and *Musical Training* subscales of the Gold-MSI were included to control for individual differences in participants' musical backgrounds. The *Active Engagement* subscale measures engagement with music, including questions on concert attendance, amount of time spent listening and writing about music, and income spent on music-related activities. The *Musical Training* subscale measures formal training on a musical instrument, music theory training, and time spent practicing an instrument. The order of presentation of the two questionnaires was randomized and the whole survey took approximately 20 min to complete. All participants were financially compensated for their time.

2.3. MRI data acquisition

All images were acquired on the same Siemens 3T Tim Trio scanner (Siemens Medical Systems, Erlangen, Germany) with a 12-channel head coil. During the period the scans were acquired there were no significant upgrades to the scanner hardware; only minor changes in software were made that Siemens state would not affect the sequences used here. T1-weighted structural images were acquired for each participant using an MPRAGE sequence (TR = 2250 ms, TE = 2.99 ms, flip angle = 9°, FOV = 256 mm × 240 mm × 160 mm, voxel size = 1 mm × 1 mm × 1 mm).

2.4. VBM analysis

All images were processed using SPM8 (Wellcome Trust Centre for Neuroimaging, London, UK) and the AA pipeline version 4.1 (Cusack et al., 2015, https://github.com/rhodricusack/automaticanalysis). The Dartel VBM8 pipeline was used, and has been described in detail elsewhere (Peelle, Cusack, & Henson, 2012). We will summarize here the main processing steps. Each individual's T1-weighted image was first co-registered using normalized mutual information to the ICBM152-space (i.e., MNI-space) template distributed with SPM8. Bias-corrected structural images were created to reduce the influence of intensity inhomogeneity on segmentation. These images were then segmented into tissue classes using unified segmentation (Ashburner & Friston, 2005) as implemented in the "new segment" option of SPM8. The volume of the resulting gray matter was determined from the segmented images by integrating over all voxels and multiplying by voxel size to provide an estimate of total gray matter volume (TGM). The tissue class images created during segmentation were then used to generate a custom template using a diffeomorphic method known as DARTEL (Ashburner, 2007; Ashburner & Friston, 2009). Individual images were transformed to template space, the DARTEL template was registered to the tissue probability maps using an affine transformation, and this transformation was then incorporated into the warping process. Images were smoothed using isotropic Gaussian kernel of full-width half-maximum 8 mm during the final normalization to MNI space. Voxel intensities during normalization were scaled by the determinant of the Jacobian transformation matrix at each voxel, in order to account for the local change in volume due to warping (Peelle et al., 2012).

A whole-brain general linear model was used to identify covariation between local GMV and measures of interest (INMI frequency and the four factors of the IMIS), which were tested in separate models. All models included age, gender and TGM as covariates of no interest. Cluster extent was corrected for non-stationarity and inhomogeneity (Hayasaka, Phan, Liberzon, Worsley, & Nichols, 2004). The reported effects were significant at $p < .05$ at the cluster level, corrected for multiple comparisons using family-wise error (FWE), except where stated otherwise.

2.5. Cortical thickness analysis

FreeSurfer (5.1.0; http://surfer.nmr.mgh.harvard.edu) was used to generate models of the cortical surface and cortical thickness from the T1-weighted images. The processing steps have been described in detail elsewhere (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999; Han et al., 2006). In brief, MRI data first underwent a series of pre-processing steps that involved intensity normalization, removal of non-brain tissue, tissue classification, and surface extraction. Following surface extraction, sulcal and gyral features across individual subjects were aligned by morphing each subject's brain to an average spherical representation, which allows for accurate matching of cortical thickness measurement locations among participants while minimizing metric distortion. For each subject, the entire cortex was visually inspected and segmentation inaccuracies (such as inclusion of veins or dura matter in gray matter boundaries) were manually corrected. Cortical thickness was calculated as the closest distance from the gray/white boundary to the gray/CSF boundary at each vertex on the tessellated surface. For whole-brain analysis, thickness data were smoothed on the tessellated surfaces using a 10 mm full-width-at-half-maximum Gaussian kernel prior to statistical analysis. Selecting a surface-based kernel reduces measurement noise but preserves the capacity for anatomical localization, as it respects cortical topological features (Lerch & Evans, 2005). Cortical thickness data were analyzed using the SurfStat toolbox for Matlab (available at http://www.math.mcgill.ca/keith/surfstat). Linear regression models were used to assess effects of the covariates of interest on cortical thickness at each vertex. Covariates of interest (INMI frequency and all factors of the IMIS) were tested in separate models and all models included age and gender as covariates of no interest. Findings from surface-based analysis were controlled for multiple comparison using random field theory for non-isotropic images (Worsley, Andermann, Koulis, MacDonald, & Evans, 1999), with a cluster formation threshold of $p < .001$ and a family-wise error (FWE) threshold of $p < .05$ at the cluster level.

2.6. Post-hoc region of interest analysis

In order to assess the convergence between effects observed in local GMV measured using VBM and surface-based measures, we performed an exploratory post hoc analysis using regions of interest (ROI) from the Desikan Killiany Atlas (Desikan et al., 2006). ROIs were selected in order to include significant clusters previously found in the VBM whole-brain analysis. Cortical surface area, GMV and cortical thickness values were averaged in ROIs using Freesurfer, and averaged ROI values were tested in linear regressions with respective covariates of interest, and including age, gender and total gray matter as covariates of no interest.

3. Results

3.1. Behavioral results

All participants except one reported having INMI (Table 1). In the remaining 43 subjects, descriptive statistics of scores on the IMIS factors, section length and episode length, as well as Gold-MSI scores, are displayed in Table 1.

As expected based on the IMIS validation study (Floridou et al., 2015), subjects with high scores on the Gold-MSI *Musical Training* subscale had more frequent INMI ($r = .338$, $p < .05$), and subjects with high scores in Gold-MSI *Active Engagement* had higher scores on the *Negative Valence* factor of the IMIS ($r = .466$, $p < .01$), as well as the *Help* factor ($r = .391$, $p < .05$) and the *Movement* factor ($r = .321$, $p < .05$). In view of these correlations, which are consistent with similar

Table 1
Descriptive statistics of the questionnaire data. Description of the scores for INMI frequency, section length and episode length are indicated in Fig. 2. As one subject reported never having INMI, all other scores and questions of the IMIS are based on the remaining sample.

	Median (IQR)	*N*
Temporal aspects of INMI		
IMIS – Frequency	4 (2)	44
IMIS – Section Length	2 (1)	43
IMIS – Episode Length	2 (2)	43
	Mean (Std)	*N*
IMIS Factors and G-MSI Scores		
IMIS – Negative Valence	13.4 (4.2)	43
IMIS – Movement	6.7 (2.6)	43
IMIS – Personal Reflections	5.1 (2.1)	43
IMIS – Help	4.4 (1.6)	43
G-MSI – Musical Training	35.3 (10.0)	44
G-MSI – Active Engagement	20.2 (11.7)	44

findings in the literature, in subsequent analyses we included models where the two Gold-MSI scores were defined as covariates of no interest.

3.2. VBM results

3.2.1. IMIS 'Negative Valence' factor

The *Negative Valence* score of the IMIS was positively correlated with GMV in a cluster located in the right temporal pole (TP, $x = 34$, $y = 9$, $z = -22$, $p < .05$) (see Table 2 and Fig. 1A, where fitted values of GMV estimates are plotted against IMIS *Negative Valence* scores). Neither the significance nor the location of this cluster was affected when controlling for Gold-MSI *Active Engagement* ($x = 34$, $y = 8$, $z = -22$, $p < .05$).

3.2.2. IMIS 'Help' factor

The *Help* factor of the IMIS was positively correlated with GMV in a cluster centered in the right PHC ($x = 27$, $y = -34$, $z = -18$, $p < .01$), and negatively correlated with a sub-threshold cluster in the left middle frontal gyrus (MFG, $x = -42$, $y = 8$, $z = 38$, $p = .07$, cluster level, FWE corrected) (see Table 2 and Fig. 1B, where fitted values of GMV are plotted as a function of the IMIS *Help* factor). The significance and location of these two clusters was not affected after controlling for Gold-MSI *Active Engagement* score.

No significant clusters relating GMV to INMI frequency, episode length or section length were found. Similarly, the *Personal Reflections* and *Movement* factors of the IMIS were not systematically related to variation in GMV (see Table 2).

Unthresholded VBM statistical maps of reported contrasts are avalaible on Neurovault (Gorgolewski et al., 2015) at the following address: http://neurovault.org/collections/59/.

3.3. Cortical thickness results

Subjects with more frequent INMI showed reduced cortical thickness in four significant clusters after FWE correction (Table 3 and Fig. 2A). In the right hemisphere, INMI frequency was negatively related to a cluster in the IFG pars triangularis ($x = 46$, $y = 25$, $z = 7$, $p < .05$) and in Heschl's Gyrus (HG) ($x = 57$, $y = -15$, $z = -4$, $p < .05$). In the left hemisphere, INMI frequency was negatively related to clusters in the Angular Gyrus (AG, $x = -38$, $y = -55$, $z = 18$, $p < .05$) and the ACC ($x = 6$, $y = 48$, $z = -5$, $p < .05$). Clusters where cortical thickness was significantly related to INMI frequency were not modified in significance or location when controlling for the Gold-MSI *Musical Training* score. For the four IMIS factors, no clusters were significant after FWE correction. Finally, INMI section length was negatively related to a cluster in the right ACC (Fig. 2B; $x = -8$, $y = 42$, $z = 2$, $p < .01$), and INMI episode length was negatively related to a cluster in the left superior frontal gyrus (SFG) (Fig. 2C; $x = -5$, $y = 23$, $z = 58$, $p < .01$).

In an attempt to confirm that the observed significant effects were not driven by age-related cortical thinning, we performed an additional exploratory analysis including only subjects younger than 40 years old, thus yielding a more restricted age distribution ($N = 32$). This resulted in clusters of cortical thickness at the same locations and directionality as with the full sample, that were significant at an uncorrected threshold ($p < .01$).

3.4. ROI analysis results

In an exploratory post hoc analysis testing the convergence between the VBM results and surface-based measures, we selected ROIs based on the significant VBM clusters (see Section 3.1) associated with the *Help* and *Negative Valence* factors of the IMIS respectively. In the right PHC ROI, scores in the *Help* factor were related to cortical surface area ($p < .05$, $R^2 = 0.29$), as well as GMV ($p < .05$, $R^2 = 0.34$) but not to cortical thickness. In the left MFG ROI (rostral MFG), no significant relationship

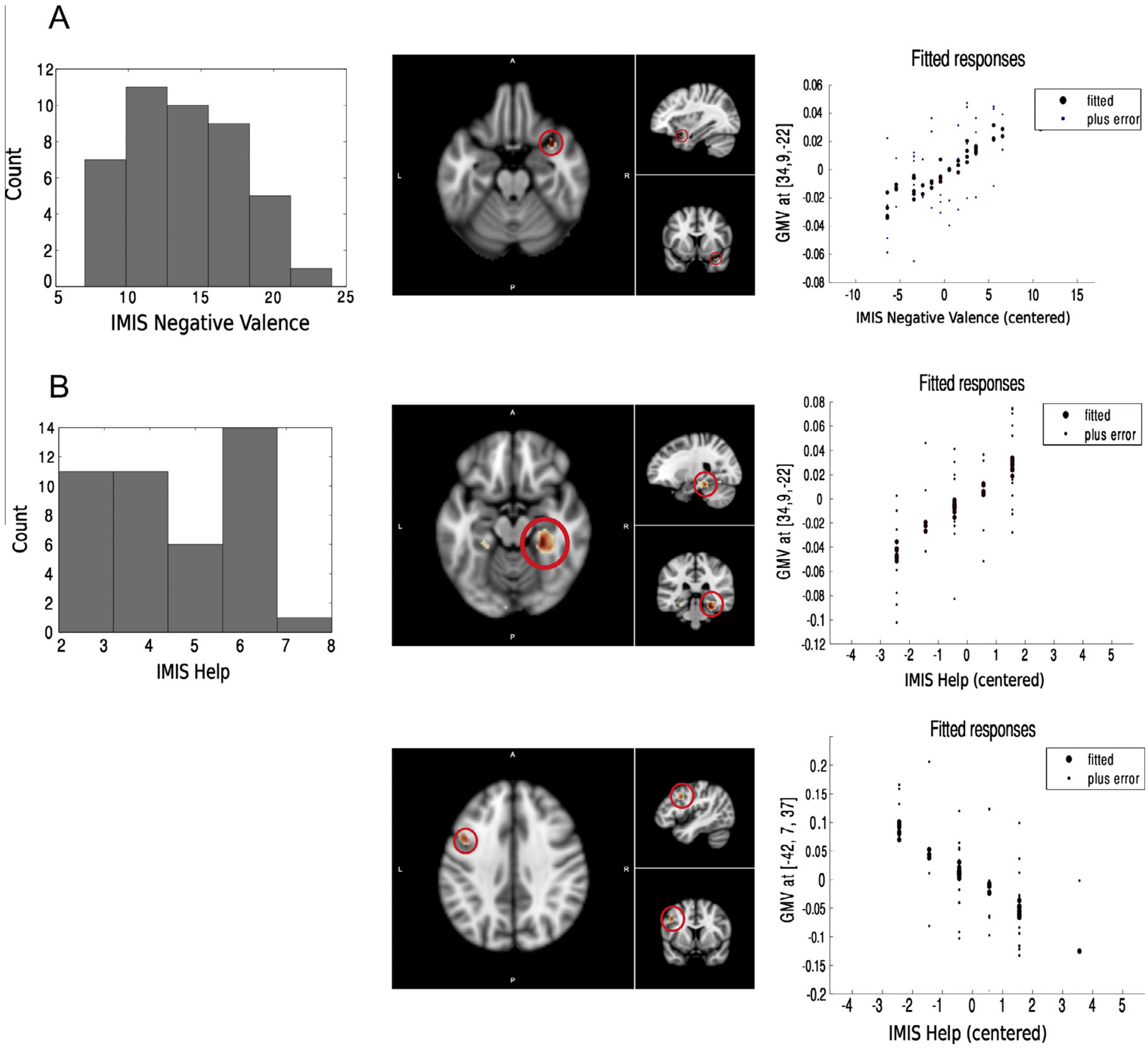

Fig. 1. Relationships between GMV and IMIS *Negative Valence* (A) and *Help* (B) factors. Left column depicts the distribution of scores. Middle column represent the location of significant clusters after FWE correction and non-stationarity of cluster extent ($p < 0.05$). Right column depicts fitted and predicted values of GMV (normalized voxel intensities) against covariates of interest (centered by removing the mean).

Table 2
Relationships between GMV and IMIS factors. Directions are indicated inside parentheses. *T* value is reported at the voxel level, and *p* value is reported at the cluster level, corrected using FWE and non-stationarity of cluster extent.

IMIS factor (Direction)	*T* Value	Cluster extent (Resel)	*p* Value (FWE)	*X*	*Y*	*Z*	Location
Negative valence (+)	4.47	0.789	.022	34	9	−22	Right TP
Help (+)	5.19	1.348	.005	27	−34	−18	Right PHC
Help (−)	4.6	0.456	.07	−42	8	38	Left MFG

was found between the *Help* factor and GMV, surface area or thickness. In the right temporal pole ROI, the *Negative Valence* factor was marginally related to cortical surface area ($p = .06$, $R^2 = 0.39$) and to GMV ($p = .08$, $R^2 = 0.18$) but not to cortical thickness. Overall, these results indicate that the effects observed in VBM of covariations between GMV and the IMIS factors may be driven by cortical surface area, independently of cortical thickness.

Additionally, to further investigate the link between the frequency of INMI episodes and cortical thickness in both the right STG and IFG, we tested interregional cortical thickness correlations between these areas. Interregional cortical thickness correlations have been used before in studies on brain structure in musicians (Bermudez, Lerch, Evans, & Zatorre, 2009). We computed Pearson partial correlation between the thickness of the right STG and right IFG ROIs, with age, total gray matter volume, gender, frequency of INMI episodes (as it modulated cortical thickness in both these regions) and GMSI-training as covariates, and found a significant positive correlation ($r = .34$, $p < .05$).

Table 3
Relationships between CT and IMIS temporal aspects. All are negative relationships. *T* value is reported (when significant at the peak level), and *p* value is reported at the cluster level (all clusters were significant), corrected using FWE.

Factor	*T* Value (Peak)	Cluster extent (Resel)	*p* Value (FWE)	*X*	*Y*	*Z*	Location
Frequency	NA	1.42	.012	−38	−55	18	Left AG
Frequency	NA	1.16	.029	46	25	7	Right IFG
Frequency	NA	1.10	.037	57	−15	−4	Right HG
Frequency	NA	1.09	.038	6	48	−5	Left ACC
Section length	NA	2.00	.002	−8	42	2	Right ACC
Episode length	5.3	1.49	.001	−5	23	58	Left SFG

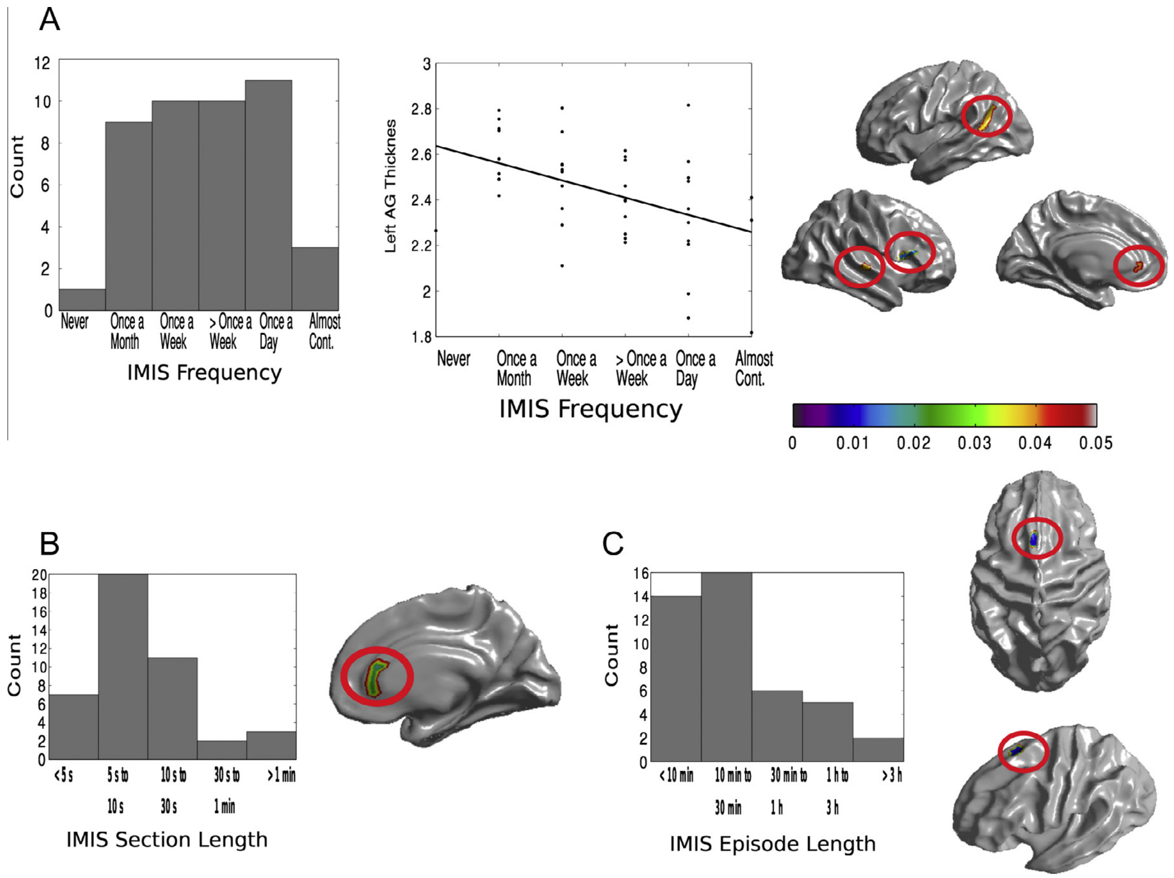

Fig. 2. Relationship between CT and INMI temporal aspects. (A) IMIS frequency and CT. Left column depicts the distribution of frequency scores. Middle column represents fitted and predicted values of CT in the left AG against INMI frequency. Right column represents the location of significant clusters of CT on a standard surface template (fsaverage5). (B) and (C) Distribution of scores and locations of clusters for IMIS section length and episode length.

4. Discussion

This study examined the covariation of brain structure and aspects of involuntary musical imagery using a validated self-report measure (IMIS) (Floridou et al., 2015) and two measures of brain structure: VBM and cortical thickness. The current results show relationships between aspects of the INMI experience and gray matter volume/cortical thickness in temporal, inferior frontal, parietal, parahippocampal and anterior cingulate areas. We discuss these findings within the framework of the literature on voluntary musical imagery, self-generated thoughts and music-evoked emotions.

4.1. Covariation of cortical thickness with the frequency and length of INMI episodes

The present study found that the frequency of INMI episodes correlated with cortical thickness in the right HG and right IFG. The former region has been strongly implicated both in auditory perception (Griffiths & Warren, 2002) and voluntary musical imagery (Halpern, 2001; Halpern & Zatorre, 1999; Zatorre et al., 1996), while the latter region is held to have a role in pitch memory (Albouy et al., 2013; Hyde & Peretz, 2004; Hyde et al., 2007) and is activated in both auditory perception and imagery (Herholz et al., 2012). Thus, our results suggest that the involvement of fronto-temporal regions also extends to non-volitional forms of musical imagery. In addition, the IFG may also play a role in suppressing unwanted INMI episodes due to its role in inhibitory mechanisms (Aron, Robbins, & Poldrack, 2004, 2014). Reduced cortical thickness in the right IFG may be linked to less inhibition of spontaneous auditory activity in superior temporal areas, possibly explaining the negative relationship between the thickness of the IFG and the frequency of INMI episodes. Furthermore, we found that reduced cortical thickness of the right HG was related to more frequent INMI, a finding that appears somewhat contradictory with previous results that have revealed thicker superior temporal cortices in musical experts compared to non-musicians (e.g. Bermudez et al., 2009). This contradiction may stem from methodological issues or complex underlying biological processes (see Limitations), or it may reflect the simultaneous influence of several factors that modulate cortical structure. While it might be difficult to interpret this result when considering the STG in insolation, a perspective accounting for covariation between several areas might be more informative. Interestingly, we found that cortical thickness in the right STG and IFG were strongly correlated independently of INMI frequency, thus replicating previous results (Bermudez et al., 2009) and suggesting further evidence of interdependency between these two areas. Further studies will be needed using both structural and functional MRI, in order to better inform on the functional contribution of the frontotemporal pathway to non-volitional forms of musical imagery.

Additional areas of covariation with aspects of the INMI experience show parallels with regions implicated in studies of self-generated thought (SGT) (Andrews-Hanna et al., 2010; Gorgolewski et al., 2014; Smallwood et al., 2011). Specifically, we found a relationship between the frequency of INMI episodes and cortical thickness of a cluster in the left AG, notably, the ventral part, which is functionally connected to the PHC and medial prefrontal cortex (Mars et al., 2011), and lies within the DMN (Buckner et al., 2008; Seghier, 2013). In addition, greater frequency and longer section length of INMI episodes were both associated with reduced cortical thickness in ventral parts of the left and right ACC, which is also a core component of the DMN. A recent study demonstrated a relationship between cortical thickness of the ACC and the proportion of task-unrelated thoughts in situations of low cognitive load (Bernhardt et al., 2013) providing some convergence with our data, although the directionality of the effects are not consistent. Nethertheless, the structural covariation found between the frequency of INMI episodes and two regions of the DMN (AG and ACC) provides evidence of shared mechanisms with other forms of SGT.

4.2. Covariation of gray matter volume with the evaluative aspects of INMI

We proposed that regions that have been implicated in SGT would also be involved in the self-reflective and evaluative aspects of INMI (*Help*, *Negative Valence* and *Personal Reflections* factors of the IMIS). In addition, we predicted that evaluative aspects would be correlated with regions involved in music-evoked emotions such as the OFC and the PHC. We found that local GMV in regions of the right medial temporal lobe, namely the right parahippocampal region (comprising the PHC and TP), as well as the left MFG, correlated with factors of the IMIS representing both the negative evaluation of INMI and the extent to which participants find INMI episodes helpful. Specifically, GMV in right TP was greater for people who reported higher disturbance by their INMI episodes (IMIS *Negative Valenc*e factor). The TP has been suggested as part of a network for affective processing (Royet et al., 2000), and projects white matter tracts to the Superior Frontal Gyrus, the OFC and other emotion-related areas (Blaizot et al., 2010; Fan et al., 2013). The role of the OFC in affective processes is indicated in several prior studies on emotions induced by sensory stimuli such as the human voice (Belin et al., 2008; Brück, Kreifelts, & Wildgruber, 2011), music (Alluri et al., 2013; Koelsch, 2014; Lehne et al., 2013), or body movement (Jacob et al., 2012), as well as SGT (Tusche et al., 2014). This last study is of particular interest to our results, as it shows that the OFC may have an affective role in the internal mentation of unconstrained SGT in the absence of sensory input. As a consequence, a link between the structure of the right TP and the disturbance of INMI episodes is in line with two of our prior hypothesis, namely that INMI might share neural resources with other forms of SGT, and may involve networks responsible for music-evoked emotions comprising the TP and the OFC. These results suggest that the tendency to be disturbed by INMI may be linked to the inability to inhibit negative emotions associated with the experience of INMI, as shown by structural properties in brain regions involved in affective processing and inhibition. This view is further supported by behavioral evidence that high neuroticism is associated with disturbance of imagery episodes (Beaty et al., 2013).

The IMIS *Help* factor measures how much participants feel their INMI episodes help them to get things done and to focus on their current task (Floridou et al., 2015). Participants scoring highly on the IMIS *Help* factor had greater GMV in the right PHC and less GMV in the left MFG. Both regions are important for memory retrieval, and recent fMRI studies have reported that the PHC is activated in both the voluntary and involuntary recall of episodic memories (Hall, Gjedde, & Kupers, 2008; Hall et al., 2014). There is strong evidence from the fMRI literature highlighting an important role of the PHC in music-evoked emotions (Blood & Zatorre, 2001; Koelsch, 2014; Koelsch et al., 2006; Trost, Ethofer, Zentner, & Vuilleumier, 2012) which has been interpreted in the more general context of emotional processing and social functions of music (Koelsch, 2014). In particular, parahippocampal volume is increased in individuals with a higher tendency to experience positive emotions related to music listening (Koelsch, Skouras, & Jentschke, 2013), which is congruent with our findings of increased GMV in the PHC in subjects with high scores on the *Help* factor. In addition, activity in the MFG has been found to correlate with the degree of autobiographical salience of musical excerpts (Janata, 2009). The opposite directions of these relationships between the Help factor and GMV in the PHC and the MFG suggest that these regions may have different roles to play with respect to the relationship between INMI and other ongoing tasks: while greater GMV in the PHC may facilitate retrieval of memories or emotions related to the INMI episode (or the music associated with it), less GMV in the MFG may lead to reduced salience of retrieved memories, thus preventing interference of the memory with the task at hand. Parallel findings from the SGT literature suggest task performance can be helped or hindered as a function of the content of SGT (Ruby, Smallwood, Sackur, & Singer, 2013) and working memory capacity (Levinson, Smallwood, & Davidson, 2012).

4.3. Methodological comments

It is worth noting that our approach, in the present paper, was to use two common methods to measure gray matter structure, namely VBM and cortical thickness, in an unconstrained approach using whole brain analysis. Such an approach does not require an *a priori* hypothesis on the spatial location of the effects, at the cost of reduced statistical sensitivity due to a large number of comparisons. As a consequence, it is possible that our analysis failed to detect other areas of covariation between facets of the INMI experience and brain structure. In addition, as VBM and cortical thickness reflect distinct features of the actual gray matter geometry (the former being related to volume, while the latter is a one-dimensional measure), we expected our analysis to uncover several facets of structure–function relationships not necessarily reflected at the same spatial locations in both measures. In a post hoc exploratory analysis using ROIs, we found that most effects found in the whole brain VBM analysis were observable in cortical surface area, and tended to be reflected in local GMV as well, but not in cortical thickness. This suggest that some of the relationships we observed between GMV and INMI facets are driven by changes in cortical surface area rather than cortical thickness, a view which is consistent with recent methodological findings on gray matter morphometry (Kong et al., 2014; Lemaitre et al., 2012; Meyer, Liem, Hirsiger, Jäncke, & Hänggi, 2014; Winkler et al., 2010). As a consequence, the selective differences observed between facets of INMI and either cortical surface area, GMV or cortical thickness might indicate distinct underlying cellular substrates (Zatorre, Fields, & Johansen-Berg, 2012). The complex relationship between MRI-derived measurements and these cellular substrates is still poorly understood, and observed individual differences might be driven by either genetic or developmental/training factors (Kanai & Rees, 2011). Accordingly, interpreting the directionality of function–structure relationships is subject to caution, as reduced cortical thickness can also be interpreted as a more efficient cortical organization, as discussed in detail in recent literature (Meyer et al., 2014). In order to decide between different interpretations of function–structure relationships, future studies could measure the same subjects with structural or functional MRI, and a task targeting a psychological process putatively related to INMI. A related example can be found in the mind-wandering literature; in Bernhardt et al., 2013, cortical thickness in the medial prefrontal cortex was related to both the tendency to engage in task-unrelated thoughts, and in the ability to delay gratification of monetary rewards (Bernhardt et al., 2013). Testing for similar overlaps between individual differences in INMI facets, brain structure and domain-general psychological processes (such as inhibitory mechanisms or auditory short-term memory) may prove to be particularly informative to understanding the phenomenology of INMI.

5. Conclusions

We have used structural MRI in order to study individual differences in cortical structure related to the experience of INMI. To the best of our knowledge, this study is the first to investigate the neural basis of INMI. Our results link several facets of INMI with the variability of cortical structure, providing evidence that the structure of fronto-temporal, cingulate and parahippocampal areas contribute to both the occurrence and evaluative processing of the spontaneous internal experience of music.

Acknowledgments

This project was funded by a Grant from the Leverhulme trust [RPG-297] awarded to L.S.

Additionally, we wish to acknowledge Sofie Valk for her advice on the analysis of cortical thickness data using SurfStat, as well as Roberto Toro for his help regarding general issues in structural MRI. We are also grateful to Georgina Floridou for designing and sharing the IMIS, and Jonathan Smallwood for his feedback on the interpretation of the data. We also wish to thank two anonymous reviewers, whose very constructive comments have greatly improved the paper. Finally, we are thankful to Robert P. Carlyon, Alex Billig, and the MRC Cognition and Brain Sciences Unit, Cambridge for their help in organizing the study and collecting the MRI data.

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