

Neural responses to nostalgia-evoking music modeled by elements of dynamic musical structure and individual differences in affective traits

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ABSTRACT

Nostalgia is an emotion that is most commonly associated with personally and socially relevant memories. It is primarily positive in valence and is readily evoked by music. It is also an idiosyncratic experience that varies between individuals based on affective traits. We identified frontal, limbic, paralimbic, and midbrain brain regions in which the strength of the relationship between ratings of nostalgia evoked by music and blood-oxygen-level-dependent (BOLD) signal was predicted by affective personality measures (nostalgia proneness and the *sadness* scale of the Affective Neuroscience Personality Scales) that are known to modulate the strength of nostalgic experiences. We also identified brain areas including the inferior frontal gyrus, substantia nigra, cerebellum, and insula in which time-varying BOLD activity correlated more strongly with the time-varying tonal structure of nostalgia-evoking music than with music that evoked no or little nostalgia. These findings illustrate one way in which the reward and emotion regulation networks of the brain are recruited during the experiencing of complex emotional experiences triggered by music. These findings also highlight the importance of considering individual differences when examining the neural responses to strong and idiosyncratic emotional experiences. Finally, these findings provide a further demonstration of the use of time-varying stimulus-specific information in the investigation of music-evoked experiences.

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1. Introduction

Nostalgia is a positive emotional experience that is characterized by memories that feature the self in social contexts (Batcho, 2007; Wildschut et al., 2006). Nostalgia plays a functional role in maintaining personal wellbeing by increasing self-positivity (Hart et al., 2011), self esteem (Wildschut et al., 2006), and accessibility of positive self-attributes (Vess et al., 2012). Socially relevant benefits of nostalgic experience include increased feelings of social connectedness (Hart et al., 2011) and perceived social support (Zhou et al., 2008), often through reviving the memory of meaningful relationships (Wildschut et al., 2010). Thus, nostalgia may act as an indirect compensatory mechanism that can foster positive affect and a sense of social proximity in the face of emotional stressors through the recall of positive autobiographical memories (Wildschut et al., 2010).

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Triggers of nostalgia include loneliness, sadness, existential threat (Routledge et al., 2008; Wildschut et al., 2006), and music (Zentner et al., 2008). Nostalgia is often evoked by personally salient music (Barrett et al., 2010; Janata et al., 2007) and music that expresses sadness (Taruffi and Koelsch, 2014).

However, nostalgia is an idiosyncratic experience that varies between individuals in frequency and intensity. Affective personality measures such as trait-level sadness and neuroticism (Barrett et al., 2010), neural measures such as baseline right-cortical asymmetry, a neural correlate of withdrawal-related motivation (Tullett et al., 2015), and naturally, a self-report questionnaire measure of nostalgia proneness (Sedikides et al., 2008; Barrett et al., 2010), predict individual differences in proneness to nostalgia.

Neuroimaging investigations have identified limbic, paralimbic, and medial prefrontal regions as critical to recall of emotional memories (LaBar and Cabeza, 2006) and engagement of socially relevant emotions (e.g. Britton et al., 2006; Kross et al., 2011). Musical stimuli that evoke emotions characterized by low arousal and positive valence (among them nostalgia) have been shown to increase brain activity in limbic and medial prefrontal areas (Trost

et al., 2012). Nostalgic experience while listening to music that was neither familiar nor memory-evoking was differentiated from other low-arousal positively valenced emotions not by limbic or prefrontal activity, but by increased cuneus and precuneus activity (Trost et al., 2012). Nevertheless, stimulus familiarity and autobiographical salience have been shown to predict the strength of music-evoked nostalgia (Barrett et al., 2010). It is therefore unclear whether there are different neural correlates of nostalgia that is evoked by familiar and autobiographically salient music.

The experiencing of music-evoked autobiographical memories elicited by familiar and personally salient music has been shown to activate prefrontal, limbic (anterior cingulate), and reward-related subcortical regions (substantia nigra) to a degree relative to the reported strength of positive affect experienced during these music-evoked memories (Ford et al., 2011; Janata, 2009). However, these studies did not examine the neural correlates of nostalgic experience, nor have they considered whether the degree of recruitment of brain areas related to emotional memory experiences (especially nostalgia) is associated with measures of traits (such as sadness, or nostalgia proneness) that predict inter-individual differences in the experience of emotional memories.

We used music to evoke nostalgic experiences and we used measures of trait affect to investigate individual differences in neural response during these nostalgic experiences. Use of music as a nostalgia-eliciting stimulus allowed us to also utilize a stimulus-specific analysis method (*tonality tracking analysis*, using the Tonal Space Model) to gain greater insight into brain regions that supported music-evoked nostalgic experience.

1.1. The tonal space model of dynamic musical structure

Music comprises complex time-varying auditory signals that are structured along a number of feature dimensions varying from lower-level sensory/acoustic descriptors to higher-level cognitive schema. Examples of sensory or acoustic features are timbral features such as roughness, brightness, and spectral flux, or simple tonal features such as pitch height. More cognitive musical dimensions comprise relationships among discrete music events in time and in tonal space, and give rise to rhythm, meter, and tonality. We focus on tonality, and the concept of tonal space because the importance of this cognitive schema to the perception and appreciation of music has been well established across many psychological and neuroscientific studies.

Tonal space comprises the system of major and minor keys in Western tonal music in which the melodies and chord (harmony) changes in pieces of music create time-varying trajectories (Collins et al., 2014; Janata, 2003; Janata et al., 2007; Krumhansl, 1990; Toiviainen and Krumhansl, 2003). Multiple levels of perceptual and cognitive processing shape tonal expectations during music listening (Bigand et al., 2014; Collins et al., 2014), as has been shown using computational models of the perceptual representation-cognitive schema continuum (Collins et al., 2014; Toiviainen and Krumhansl, 2003). Models of tonal space (which more closely reflect musical cognitive processes rather than sensory processes) have been shown to drive melodic and harmonic expectations for strongly primed musical events, and have been shown to explain variance in response times to strongly primed musical events above and beyond the variance explained by models of acoustic features of music (which more closely reflect sensory rather than cognitive mechanisms of music perception; Collins et al., 2014).

The way in which a piece of music moves through tonal space constitutes a unique structural signature of that piece of music. This property has been exploited in analyses of brain activity recorded during music listening in order to infer which brain areas contribute to the time-varying experiencing of that piece of music

(Janata et al., 2002; Janata, 2005; Janata, 2009). Among the time-varying experiences people have with music are the patterns of tension and relaxation that are generated by the generation, violation, and resolution of tonal expectations (Huron, 2006; Steinbeis et al., 2006; Lerdahl and Krumhansl, 2007). Another type of time-varying experience associated with music is the unfolding of a personal memory evoked by the music (Janata, 2009). In the case of tonal tension, there is a direct relationship between a trajectory through tonal space and the emotional experience of tension. In the case of music-evoked memories, the relationship is not as direct. We postulate that as music plays and is perceived in time, autobiographical memories (and other thoughts) will be triggered and play out in time alongside the dynamic perception of the music. These parallel but interacting experiential processes should therefore lead to some degree of observed coupling between the dynamic descriptor of the stimulus and brain areas that are supporting various facets of the perceptive, mnemonic and emotional experiences that are enabled by the stimulus in the moment.

We have previously labeled this type of stimulus/brain coupling *tonality tracking* (Janata et al., 2002). It is easy to construe this label exclusively in terms of an analytical process, accomplished by some brain region, whereby the most likely tonal center of the moment is identified, e.g. a passage in B-major. While the identification of tonal center certainly qualifies as tonality tracking, and this is how it was used originally in a study that identified the rostral aspects of the medial prefrontal cortex as a brain area that was most consistently sensitive to movements of a melody in tonal space during target detection tasks (Janata et al., 2002), we believe it is more appropriate to think of tonality tracking in broader terms as some form of coupling between the tonal dynamics of a musical stimulus and the brain areas that support the specific psychological states that a person is experiencing in association with that stimulus (as evidenced by statistically significant correlations of time-series).

Tonality tracking analyses have demonstrated that an array of extra-sensory cortical regions, including temporal lobe and prefrontal regions, varied in the degree to which measured blood-oxygenation-level-dependent (BOLD) signal in these regions coupled with the dynamic movement of a piece of music in tonal space. The degree of coupling depended on whether the music was memory-evoking or not (Janata, 2009). We used the same approach to identify those brain areas that coupled preferentially to music excerpts that accompanied nostalgic experiences.

We note that time-varying acoustic features of music have also been used to examine the inter-individual consistency in the loci of brain responses to such features (Alluri et al., 2012, 2013; Burunat et al., 2016; Toiviainen et al., 2013). These studies have either focused on one piece of music (a tango by Astor Piazzolla) or a small collection of pieces without regard for their familiarity to participants. They have mainly found consistent activations of auditory cortices in response to low-level timbral features, but more spatially variable and inconsistent activations for higher-level tonal and rhythmic features. Thus, while these studies support the general approach of using time-varying acoustic and musical features to identify brain areas that couple with those time-varying patterns, they don't provide an adequate basis for thinking about how brain regions might couple with dynamic acoustic features during emotional remembering experiences. We thus restricted our use of musical features to tonality tracking.

1.2. Aims of the current study

In the current study, we applied an established music-evoked autobiographical memory task (Barrett et al., 2010; Janata et al., 2007) in a functional neuroimaging context to identify the brain regions involved in affective and mnemonic processes during

music-evoked nostalgia. We used personality measures associated with nostalgic experience (Barrett et al., 2010) to predict individual differences in neural activity during music-evoked nostalgia. We then utilized unique time-varying tonal signatures of musical selections (Janata et al., 2002; Janata, 2005; Janata, 2009) to identify the areas of the brain that tracked moment-to-moment changes in musical structure more strongly during the presentation of nostalgic compared to non-nostalgic stimuli.

2. Methods

2.1. Tasks and materials

2.1.1. Music listening task

Participants listened to a total of 30 musical excerpts, each 20 s in duration, during two 13 min and 20 second music listening tasks (15 stimuli per task period). Each participant's stimuli were selected from a database of over 3600 samples downloaded before 2009¹ from the Billboard Top-100 Pop, Hip Hop, and R&B lists on the Apple iTunes Music Store, and randomly sampled from stimuli that were released when a given participant was between 7 and 19 years old, with the distribution peaking at age 15 and negatively skewed, using the *Ensemble* experiment management system (Tomic and Janata, 2007). Previously, this algorithm yielded a high percentage of music-evoked nostalgic (Barrett et al., 2010) and autobiographical (Janata et al., 2007; Janata, 2009) memories. A total of 318 unique stimuli were used.

After each musical excerpt, participants heard auditory response cues that prompted them to rate, separately, the degree to which they experienced nostalgia, happiness, sadness, autobiographical salience, arousal, and stimulus familiarity while listening to that excerpt. Ratings were provided on a 5-point rating scale (1 = "not at all", 2 = "weakly", 3 = "moderately", 4 = "strongly", 5 = "extremely"). There was no time limit for providing responses. A jittered inter-stimulus-interval of 1–5 s was introduced between the end of each response period and the beginning of the following stimulus.

2.1.2. Emotion localizer tasks

Participants completed five separate seven-minute emotion induction tasks: two facial emotion localizer tasks (positive affect and negative affect; Schneider et al., 1994) and three lexical emotion localizer tasks (positive, negative, and neutral affect; Velten et al., 1968). During each task, participants were presented with a series of self-paced stimuli and instructed to use each stimulus to internally generate the emotion expressed by that stimulus. Facial stimuli consisted of monochrome images of male and female Caucasian actors portraying either happy (N=40) or sad (N=40) expressions of varying intensity (Erwin et al., 1992; Schneider et al., 1994). Lexical stimuli consisted of 30 self-referential statements of increasing emotional intensity for each valence category (Colibazzi et al., 2010; Velten, 1968). The results of these tasks will not be reported here.

2.1.3. Southampton nostalgia scale (SNS)

The SNS (Sedikides et al., 2008) is a self-report measure of one's tendency to experience nostalgia (nostalgia proneness). We used the total score from the SNS to predict individual differences in brain activity recorded during the presentation of nostalgic and non-nostalgic stimuli, since this measure has predicted strength of

music-evoked nostalgia (Barrett et al., 2010).

2.1.4. Affective neuroscience personality scales (ANPS)

The ANPS are theory-driven measures developed to assess behavioral traits related to six primary neural affective systems (play, seek, care, fear, anger, and sadness systems; (Davis et al., 2003; Davis and Panksepp, 2011; Panksepp, 1998). Sadness scale scores were used to predict individual differences in brain activity recorded during the presentation of nostalgic and non-nostalgic stimuli because this measure predicted individual differences in proneness to experiencing nostalgia (Barrett et al., 2010).

2.2. Participants and procedure

In order to identify and recruit individuals for whom our stimulus selection algorithm reliably triggered nostalgic experiences, participants completed the music-listening task as a pre-screening measure. Twelve participants (age $M=22.4$, range 19–33; 8 females) from undergraduate and graduate psychology courses at the University of California, Davis who reported at least moderate nostalgia (a rating of at least 3, "moderately") during at least 30% of prescreening stimuli were recruited for the main study. Participants completed a series of music listening, resting state, and emotion localizer tasks while blood-oxygenation level-dependent (BOLD) signal was recorded in a magnetic resonance imaging (MRI) scanner. The experiment structure is described in Fig. 1. Stimuli heard by the participant during the pre-screening were not presented to the participant during the main experiment.

Participants provided responses in the MRI scanner using a 5-button MR-safe response pad (Lumitouch; Photon Control Inc., Burnaby, Canada). Visual stimuli were projected onto a screen and viewed over the feet through a mirror attached to the head coil. Musical stimuli were presented via electrostatic headphones (MR Confon GmbH, Magdeburg, Germany). Subjects also wore foam earplugs. Prior to scanning, the volume was set to a comfortable level that was louder than the scanner but that did not distort the audio.

2.3. fMRI data acquisition and preprocessing

Data were collected on a 3T Siemens Trio system at the Imaging Research Center on the UC Davis Medical Center campus. Echo-planar image (EPI) volumes measuring BOLD signal consisted of 34 slices (4 mm thick, no skip; in-plane resolution: 3.4×3.4 mm; TR = 2.0 s; TE = 25 ms; flip angle = 90°) and were corrected for distortion using a point-spread function and the native Siemens distortion correction algorithms. A high-resolution structural image (field of view = 256×256 mm, 192 slices, resolution = $1 \times 1 \times 1$ mm, time repetition [TR] = 2.5 s, time echo [TE] = 4.82 ms, flip angle = 7°) and a "coplanar" structural T1-weighted axial image (slice positions and orientations identical to EPIs; TR = 600 ms, TE = 8.6 ms, flip angle = 70° , in-plane resolution: 0.86×0.86 mm) were also acquired for each participant.

SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm5/>) was used to preprocess the imaging data in the following steps: realignment of EPI volumes to the first volume of the first EPI run (the reference EPI), coregistration of the reference EPI to the participant's high-resolution structural image through the "coplanar" volume, and spatial normalization of the high-resolution volume to the MNI251 T1 template with propagation of the normalization parameters to the coplanar and EPI volumes. Normalized images were resliced (2 mm³ voxels), smoothed (5 mm FWHM), and the image time-series was high-pass filtered (1/120 Hz cutoff). Preprocessed EPI data were analyzed using the Janata Lab Music Toolbox (<http://atonal.ucdavis.edu/resources/software/jlmt/>), custom MATLAB scripts, and random-effects general linear modeling

¹ Data for this study were collected between 2008 and 2009. Stimuli in the 3600 sample database included stimuli that were contemporary to study participants when they were between 7 and 19 years old.

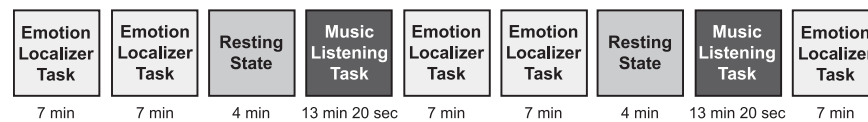


Fig. 1. Experiment structure. Participants completed nine task scans during which we collected echoplanar images. The fourth and eighth scans were music listening tasks that each lasted 13 min and 20 s each. The third and sixth scans were four-minute resting-state periods, during which participants were asked to remain still with their eyes closed. All other scans were emotion localizer tasks that each lasted 7 min. Results from these emotion localizer tasks are not presented in this report. The order of specific emotion localizer tasks was counterbalanced across participants. Resting-state periods were included before each music-listening scan to give a washout period during which any emotional effects of the localizer procedures could dissipate.

in SPM5. Anatomical locations reported in MNI coordinates for each analysis were derived using the Anatomy Toolbox in SPM5 (Eickhoff et al., 2005). Neurosynth (www.neurosynth.org) was used to identify anatomical labels for all loci that were not assigned a label in the Anatomy Toolbox. Labels were corroborated and corrected as necessary using the (Duvernoy, 1999) atlas, matching atlas sections against the average normalized high-resolution structural anatomical image from our sample.

2.4. Statistical analysis: parametric block analysis of brain activity during music-evoked nostalgia

A “base model,” including motion parameter estimates from the image realignment preprocessing stage, linear trends across each scan, the mean signal intensity of each scan, and regressors representing button presses and response cue onsets, was estimated for music listening task EPI data. The residuals from this base model were submitted to a parametric block analysis which included a block regressor to indicate music listening periods (Fig. 2: “music-playing”) and a set of regressors that parametrically modulated the music-playing regressor given a participant’s ratings of each stimulus (self-report regressors; Fig. 2: “nostalgia”, “happiness”, “sadness”, and “arousal”; exclusion of “autobiographical salience” and “familiarity” regressors is addressed in the *Results* subsection titled “Parametric block analysis of brain activity during music-evoked nostalgia”). Contrast images were submitted to second-level random-effects analysis using one-sample *t*-tests, thereby identifying clusters meeting the minimum voxel-wise significance of $p < 0.05$ (using whole-brain false discovery rate, or FDR, correction) and minimum extent of 20 voxels (320 mm³).

To identify brain areas that responded differentially to music-evoked nostalgia based on an individual’s nostalgia proneness or affective personality traits, random-effects models were fit, regressing fixed-effects contrast estimates for the strength-of-nostalgia variable on either the SNS total scale scores or the *sadness* scale of the ANPS. The same thresholding criteria were used for reporting significant effects.

2.5. Tonality tracking

2.5.1. Generation of tonality tracking regressors from raw audio

Tonality tracking regressors were generated using a set of custom MATLAB scripts (the Janata Lab music toolbox, or *jlm*²). We first decomposed the raw audio for each musical stimulus into periodicity pitch images,³ and projected those periodicity pitch images into tonal space (major/minor key relationship represented on a toroidal surface) through a custom-trained Kohonen self-organizing map (using the same toroidal projection map used in Janata et al., 2002 and Janata, 2009). Change in toroidal tonal space over time collectively describes the change over time in tonal center of a musical selection (Collins et al., 2014; Janata et al.,

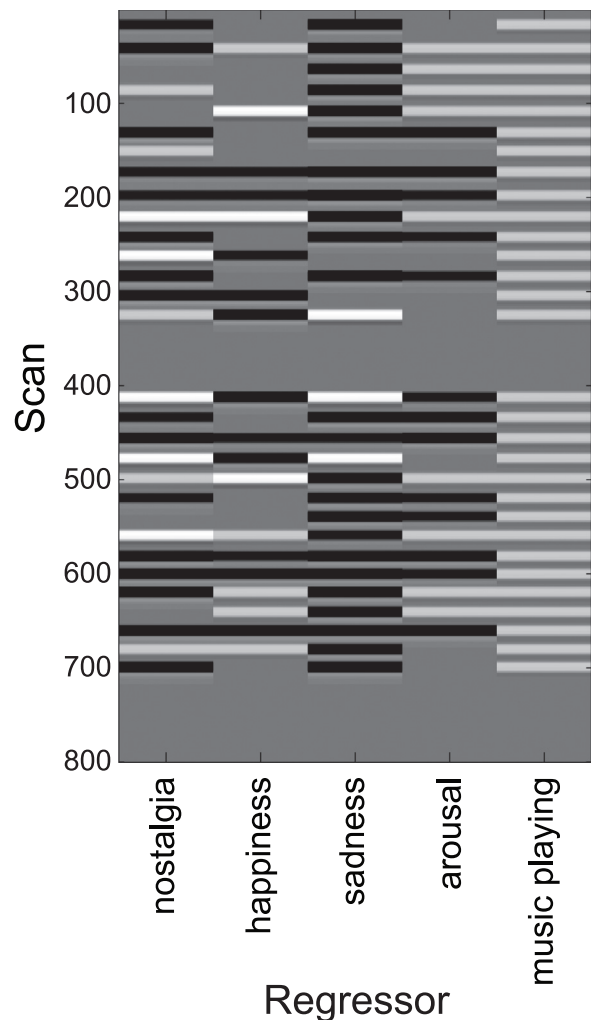


Fig. 2. An example subject-level design matrix depicting the parametric block analysis. The grayscale values in the design matrix code the regressor values, with black representing the most negative values and white the most positive. The ubiquitous gray represents zero. The columns along the abscissa represent separate parametric regressors, and the rows along the ordinate represent individual scan volumes (sampled at a rate of 1 volume every 2 s). For the music playing regressor (the fifth column from the left), light gray periods mark scans during which a musical excerpt was presented. Each of the other regressors in the design matrix (nostalgia, happiness, sadness, and arousal) represent parametric modulations of each music listening period, where the height of that period is modulated by the response provided by the participant after listening to the given song. For the first four columns, black bars represent song excerpts that were rated as a 1 (not at all) on nostalgia, happiness, sadness, and arousal ratings, whereas white bars represent songs that were rated as 5 (extremely) on these dimensions.

2002; Janata, 2005; Janata et al., 2007; Janata, 2009; Krumhansl, 1990; Toiviainen and Krumhansl, 2003).

From the tonal space representation, we extracted 34 toroidal surface basis functions for each stimulus that then became the regressors in the neuroimaging models (Janata et al., 2002). A set of regressors was generated for songs that were marked at least

² <http://atonal.ucdavis.edu/resources/software/jlmt>

³ <http://www.ipem.ugent.be/Toolbox/>

moderately nostalgic (3 or greater on the 5-point rating scale for nostalgia), and a second set of regressors was generated for songs that were marked not at all or weakly nostalgic (ratings of 1 or 2 on the 5-point rating scale).

2.5.2. Subject-level analysis

The residuals of the parametric block analysis model described above were used in a random-effects regression in SPM 5, with subject-level data regressed on a design matrix that included the TT regressors for both nostalgic and non-nostalgic stimuli (68 regressors total). Monte Carlo simulation was used at the subject level to identify voxels in which a significant amount of variance was predicted by the entire set of TT regressors (Janata, 2009).

For each TT model, we conducted an F-test for each subject to identify the subset of voxels in which a significant amount of variance was explained across the set of TT regressors (at $p < 0.05$, corrected for family-wise error rate, FWE). The order of songs for each participant was then randomly shuffled in each of a series of alternate models, and the alternate models were evaluated for each voxel in the subset. A null distribution was generated from the residual mean square errors (RMSE) of these alternate models. A Gaussian function was fit to the null distribution after each iteration. Iterations continued until the mean of the standard deviations of RMSE from the fitted Gaussian function across all voxels over the last 10 iterations steps was less than 0.001, with a minimum of 10 total iterations. Voxels from the veridical model were labeled TT voxels if the RMSE in that voxel was in the smallest 5% of the values in the null distribution.⁴

2.5.3. Group-level analysis

To identify brain areas that showed TT at a group level we used a cluster mass threshold method (Bullmore et al., 1999; Hayasaka and Nichols, 2004). This method estimates the likelihood that the mass of a given cluster (mass = # of voxels in a cluster \times sum of voxel heights within the cluster) of potential TT voxels exceeded the mass of clusters expected by chance (i.e. when the spatial locations of tonality tracking voxels in individuals subjects was randomized). The maximum cluster mass method allows us to combine voxel intensity and cluster extent information in our thresholding procedure, thus enabling identification of small clusters that demonstrate TT in a large number of subjects, as well as larger clusters that demonstrate TT in fewer subjects, while controlling for family-wise error rate (Hayasaka and Nichols, 2004).

The specific implementation of the cluster-mass thresholding procedure was as follows. First, we estimated a voxel intensity threshold corresponding to the number of subjects expected to show tonality tracking in a voxel by chance alone. A binary mask indicating those voxels that exhibited TT (thresholded at the subject-level using the Monte Carlo simulations described above) was generated for each subject. These maps were then summed across subjects, yielding a veridical map of the number of subjects that showed TT in any given voxel. This map was then statistically thresholded using a Monte Carlo simulation to estimate the number of subjects that would be expected to show tonality tracking in a given voxel by chance. For each subject, the location of TT voxels was randomly distributed within a brain volume that

was defined as the intersection of all brain volume masks from individual subjects. These randomized TT images were summed across subjects to obtain the number of subjects hypothetically activating each voxel by chance alone. A histogram was constructed from all these voxel values to indicate how many voxels were expected to be activated by N subjects, where N ranges from 0 to 12. This procedure was repeated 500 times, and the resulting 500 histograms were averaged and normalized to obtain a final histogram showing the expected distribution of numbers of voxels showing TT for N subjects. The probability of observing N subjects in any voxel by chance alone was then calculated, and a cutoff of $p < 0.05$ yielded a threshold of at least 3 subjects ($p = 0.048$). A minimum threshold of 3 participants was slightly more liberal than the estimated group-level threshold of 4 used previously (Janata, 2009). Thresholding with a smaller criterion number of subjects led to massive, implausible clusters during simulation that covered most or all of the measured brain space.

To combine the voxel height and cluster extent information, we constructed a null distribution of the maximum TT cluster mass at each of 1000 iterations using the thresholded image from the first step. On each iteration, the voxels in the thresholded image for each subject (from the subject-level analysis) were randomly distributed throughout a brain volume defined by the intersection of a gray matter mask and the intersection of all brain volume masks from all subjects. On each iteration, these randomized TT images were summed across participants, and the mass of each contiguous cluster of voxels was calculated by summing the number of subjects across voxels in the cluster. Tonality tracking clusters in the veridical group-level image were labeled as tonality tracking if their mass was greater than 95% of maximum cluster masses in the null distribution.

2.5.4. Tonality tracking bias analysis

Preference (bias) of a voxel for tonality tracking during the presentation of nostalgic (a rating of 3 or greater on the 5-point rating scale for nostalgia) versus non-nostalgic (ratings of 1 or 2 on the 5 point rating scale) stimuli was assessed by calculating the ratio of the F-statistics of nostalgic and non-nostalgic sets of tonality regressors in each subject-level model, adjusted for the number of songs rated as nostalgic or non-nostalgic by a given participant. Average tonality tracking bias across participants was calculated in each significant group-level TT cluster.

3. Results

Fig. 3 shows the distribution of nostalgia ratings across all stimulus presentations. Of 360 stimulus presentations, 211 (59%) were rated as being at least weakly nostalgic (a rating of at least 2 on the 5 point nostalgia rating scale), and 144 (40%) were rated as being at least moderately nostalgic (a rating of at least 3 on the 5-point nostalgia rating scale). The mean nostalgia rating for stimuli rated at least weakly nostalgic (at least 2 on the 5 point nostalgia rating scale) indicated that on average, when stimuli were rated as some level of nostalgic, stimuli were rated moderately nostalgic or higher ($M = 3.21$, $SD = 1.07$). Each participant rated between four (4/30, or 13.3%) and 22 (22/30, or 73.3%) stimuli as at least moderately nostalgic (median = 12, or 40%). This represents a higher rate of nostalgia responding within the current sample than within our previously reported sample (Barrett et al., 2010), and reflects the impact of our pre-screening procedure that identified individuals for whom our stimulus selection algorithm identified stimuli that were rated as nostalgic.

Nostalgia proneness (SNS) scores were fairly high on average ($M = 5.93$, $SD = 0.725$) compared to scores in recent reports (Seehusen et al., 2013), but were normally distributed

⁴ In the previous application of this modeling scheme (Janata, 2009), the author used 100 iterations of simulation at the subject level, and imposed a minimum extent threshold of 40 voxels on tonality tracking clusters that were entered into and retained within the second-level model. It is likely that for some subjects, a representative null distribution is available at well under 100 iterations, but this may not be the case for all subjects. Thus, we used an improved simulation procedure at the subject level that minimizes the necessary number of permutation steps at this level.

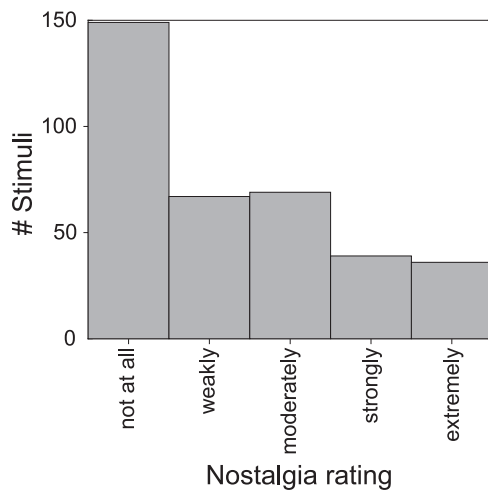


Fig. 3. The distribution of nostalgia ratings across all participants and stimuli. A nostalgia rating was provided after each stimulus presentation using a 5-point rating scale (from “not at all” to “extremely”).

(Kolmogorov-Smirnov statistic = 0.203, $p = 0.634$) and evenly distributed across a wide range (4.4–7, out of a possible range of 1–7). The correlation between nostalgia proneness (SNS) scores and the number of stimuli rated by each individual as being at least moderately nostalgic was not statistically significant ($r = -0.171$, $p = 0.596$). Nearly identical results were observed when correlating SNS scores with the number of stimuli rated by each individual as at least weakly, at least strongly, and extremely nostalgic. SNS scores were also not significantly correlated with the mean nostalgia rating across all stimuli for each individual ($r = -0.190$, $p = 0.554$).

Scores on the ANPS Sadness scale ($M = 2.98$, $SD = 0.53$) were within range of published norms (Barrett, Robins, & Janata, 2013), and were normally distributed (Kolmogorov-Smirnov statistic = 0.146, $p = 0.929$). Sadness scores were not significantly correlated with the number of stimuli rated by each individual as being at least moderately nostalgic ($r = -0.073$, $p = 0.821$), nor were Sadness scores correlated significantly with the mean nostalgia ratings across all stimuli for each individual ($r = -0.104$, $p = 0.748$), and Sadness scores were not significantly correlated with SNS scores ($r = -0.374$, $p = 0.230$).

3.1. Parametric block analysis of brain activity during music-evoked nostalgia

Consistent with previous reports (Barrett et al., 2010), nostalgia ratings for stimuli in our sample were highly correlated with ratings of stimulus familiarity ($r = 0.7817$, $p < 0.0001$) and autobiographical salience ($r = 0.7829$, $p < 0.0001$). Therefore, familiarity and autobiographical salience regressors were excluded from analysis. Separate linear contrasts were fit for each remaining self-report regressor (nostalgia, happiness, sadness, and arousal).

Table 1

Summary of loci at which changes in BOLD signal positively correlated with ratings of happiness.

Location	Left Hemisphere						Right Hemisphere					
	xmm	ymm	zmm	No. of Voxels	T	p (FDR)	xmm	ymm	zmm	No. of Voxels	T	p (FDR)
Middle frontal gyrus	-38	12	58	228	6.179	0.014						
Anterior cingulate cortex	-10	30	-4	902	6.256	< 0.001						
Thalamus	-4	-8	10	251	5.046	0.013						

3.1.1. Contrasts for self-report regressors

No voxels were associated with ratings of nostalgia, sadness, or arousal as main effects in the parametric block analysis at the group level. Activity in the left-lateral middle frontal gyrus, anterior cingulate cortex, and thalamus (Table 1) was positively associated with ratings of happiness during music listening.

3.1.2. Interactions between self-report regressors and personality measures

Individual differences in the relationship between BOLD signal and ratings of nostalgia correlated negatively with SNS scores in the bilateral superior frontal gyrus, right temporal pole, the left midbrain, and in two regions implicated in affect and reward processing: a midbrain cluster including the substantia nigra and ventral tegmental area, and a cluster in the left amygdala (Table 2; Fig. 4). In other words, among those individuals less prone to nostalgia, activity in these areas increased when they experienced music-evoked nostalgia, whereas among those individuals more prone to nostalgia, activity in these areas decreased as the strength of reported nostalgia increased.

Similarly, ANPS sadness scores predicted a negative relationship between BOLD signal and ratings of nostalgia in the anterior cingulate, whereas they predicted a positive relationship between BOLD signal and ratings of nostalgia within a brainstem region (Table 3; Fig. 5). Thus the SNS and ANPS sadness interactions show modulation of the recruitment of emotion and reward processing regions during nostalgia by personality measures previously shown to predict the strength of nostalgic experience (Barrett et al., 2010).

3.2. Tonality tracking analyses

We identified brain areas (Table 4; Fig. 6A) in which, across participants, the time-varying activity was significantly correlated with the time-varying tonal structure of the music they heard. TT regressors that explained at least 25% more variance in BOLD signal (with a mean TT bias ratio of at least 1.25) during nostalgic (with a rating of 3 or greater on the 5-point nostalgia rating scale) compared to non-nostalgic (a rating of 1 or 2 on the 5-point scale) stimulus presentations included the right IFG, right anterior insula, a cluster including the substantia nigra and periaqueductal gray matter, the cerebellum, and a region in the brainstem (Table 4, bold typeface; Fig. 6B).

4. Discussion

In this study, we evoked nostalgic experiences by exposing participants to familiar music that was popular during their adolescent and teenage years. Nostalgia is necessarily an idiosyncratic experience, and variability in the self-reported strength of nostalgic experience in response to a trigger such as music can be predicted by individual differences in nostalgia proneness and trait-level affect (Barrett et al., 2010). To our surprise, we found no significant main effects of nostalgia ratings on BOLD signal that were consistent in their localization across participants. However,

Table 2

Summary of loci where the correlation between changes in BOLD signal and ratings of nostalgia were negatively predicted by the SNS.

Location	Left hemisphere						Right hemisphere					
	xmm	ymm	zmm	No. of Voxels	T	p (FDR)	xmm	ymm	zmm	No. of Voxels	T	p (FDR)
Superior frontal gyrus	-12	48	20	123	-6.691	0.016	20	38	26	394	-9.079	< 0.001
Temporal pole							40	8	-20	87	-5.393	0.048
amygdala	-30	0	-14	278	-5.915	< 0.001						
Midbrain (ventral tegmental area/substantia nigra)* ^a	0	-22	-10	532	-7.019	< 0.001						
Midbrain	-12	-32	-34	107	-6.626	0.025						

Notes: Regions indicated with an asterisk (*) were not assigned in the anatomy toolbox, and were identified using NeuroSynth.

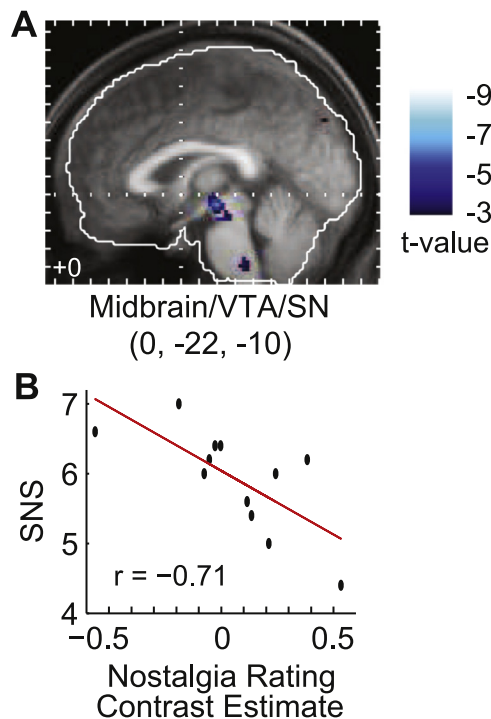
^a The midbrain cluster extends laterally into the ventral tegmental area and the substantia nigra, as identified using NeuroSynth.

Fig. 4. Nostalgia activations that varied as a function of nostalgia proneness in the midbrain/NTA/SN cluster (0, -22, -10). (A) The sagittal section ($x = 0$) shows the cluster in the midbrain region in which (B) individual differences in the relationship between changes in BOLD signal and nostalgia ratings were predicted by scores on the Southampton Nostalgia Scale (SNS). Tick marks indicate 10 mm spacing along the y (rostral-caudal) and z (ventral-dorsal) dimensions. The white outline surrounding the brain indicates the boundaries of an EPI inclusion mask. The scatterplot (B) shows the relationship between SNS scores for each individual and the contrast value for each individual from the nostalgia contrast of the parametric block analysis for the peak voxel in the identified cluster. The red line indicates the line of best fit through these data, and r denotes the zeroth-order Pearson product moment correlation between SNS score and nostalgia rating contrast estimate.

we did find that the relationship between the strength of music-evoked nostalgic experience and activity in brain areas involved in emotion processing interacted with personality traits. Examination of the distribution of contrast estimates for nostalgia ratings in these areas (Figs. 4 and 5) showed that these values were

distributed equally around zero, strongly suggesting that the specific neural response to nostalgic experience may vary widely between individuals, and also explaining why in regions like this the group-level analysis would not yield an estimate significantly different from zero. Overall, our analyses revealed that scores on measures of affective personality, including nostalgia proneness and trait-level *sadness*, predicted individual differences in the relationship between ratings of nostalgia and BOLD signal in prefrontal, temporal, limbic, and paralimbic regions.

4.1. Nostalgia, autobiographical salience, and familiarity of stimuli

Self-relevant nostalgia, as a psychological construct, is a special case of autobiographical memories (Wildschut et al., 2006; Barrett et al., 2010; Wildschut et al., 2010). As a continuation of our previous work on the topic (Barrett et al., 2010), we were interested in understanding the neural correlates of this self-relevant nostalgia. In our data, and consistent with previous reports (Barrett et al., 2010; Janata et al., 2007), ratings of nostalgia were highly correlated with ratings of familiarity and autobiographical salience. Such correlations raise the question of whether familiarity, autobiographical salience, and nostalgia can be considered separable constructs. We conducted secondary analyses to investigate the distribution of ratings of nostalgia ratings for stimuli that were rated as extremely familiar or autobiographically salient.

We identified 80 stimulus presentations (out of the total of 360 presentations) that were identified as extremely familiar (a rating of 5 on a 5-point familiarity rating scale). Of these stimulus presentations, 13 were rated as “not at all” or “weakly” nostalgic, 15 were rated as “moderately” nostalgic, 22 that were rated strongly nostalgic, and 30 that were rated extremely nostalgic. We also identified 31 stimulus presentations (out of the total of 360 presentations) that were extremely autobiographically salient (a rating of 5 on a 5-point autobiographical salience rating scale). Of these stimulus presentations, 4 were rated as “not at all” or “weakly” nostalgic, 2 were rated as “moderately” nostalgic, 7 that were rated strongly nostalgic, and 18 that were rated extremely nostalgic.

When restricting analyses to only these stimuli (either extremely familiar or extremely autobiographical), we did not have sufficient power to identify regions of the brain that were differentially sensitive to nostalgia. However, such distributions of

Table 3

Summary of loci for which the correlation between changes in BOLD signal and ratings of nostalgia were predicted by scores on the ANPS Sadness trait.

Location	Left hemisphere						Right hemisphere					
	xmm	ymm	zmm	No. of Voxels	T	p (FDR)	xmm	ymm	zmm	No. of Voxels	T	p (FDR)
Brainstem							2	-40	-30	165	6.186	0.022
Anterior cingulate cortex							2	36	28	223	-4.805	0.003

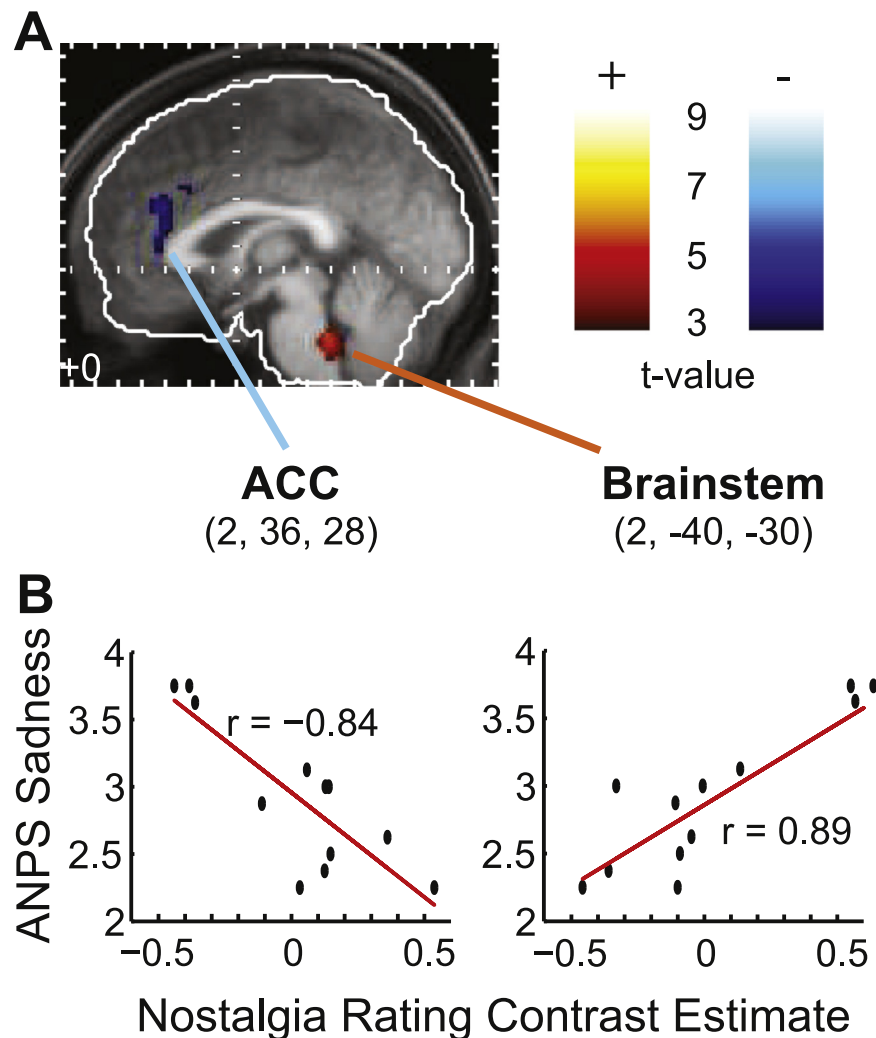


Fig. 5. Nostalgia activations that varied by trait *sadness*. (A) The sagittal section shows brain locations where (B) individual differences in the relationship between changes in BOLD signal and ratings of nostalgia were predicted by scores on the *sadness* scale of the Affective Neuroscience Personality Scales. Coordinate labels and tick marks as in Fig. 4. The scatterplots (B) show the relationship between *sadness* scores for each individual and the contrast value for each individual from the nostalgia contrast of the parametric block analysis for the peak voxel in a cluster identified in the personality interaction analysis. Best-fit lines and correlation labels as in Fig. 4.

responses (and the separation of nostalgic and autobiographical ratings) give us confidence that participants were able to differentiate between the constructs and that we are reporting on effects of nostalgia and not simply effects of familiarity or autobiographical salience.

4.2. Nostalgia and individual differences in personality

We found activity in brain areas (including the temporal pole and superior frontal gyrus) in which activity was previously shown to correlate with ratings of autobiographical salience of musical selections (Janata, 2009) to correlate with ratings of nostalgia during music listening to different degrees, depending on a measure of the proneness of an individual to experiencing nostalgia (the Southampton Nostalgia Scale, or SNS). These brain regions have also been identified as nodes of general autobiographical memory networks (Svoboda et al., 2006).

Subcortical interactions between personality and the relationship between BOLD signal and nostalgia ratings were unexpected. The substantia nigra and ventral tegmental area (VTA; in the mesolimbic dopaminergic system) play a central role in reward processing (Haber and Knutson, 2010), and the substantia nigra in particular has been associated with the experience of positive affect during music listening (Janata, 2009). The amygdala plays a

central role in the detection of emotionally salient stimuli. Activity in both the amygdala and mesolimbic dopaminergic regions is involved in the experience of music-evoked pleasure (Koelsch, 2014).

Our data suggest that there may be a negative relationship between ratings of nostalgia and BOLD activity in both the substantia nigra/VTA and amygdala for those who score highly on the SNS, whereas there may be a positive relationship between BOLD activity in these regions and ratings of nostalgia for those who score low on the SNS. This means that when individuals who are prone to experiencing nostalgia experience music-evoked nostalgia, the activity in these areas decreases as the strength of the experienced nostalgia increases, whereas the activity in these areas increases as the strength of experienced nostalgia increases in those less prone to experiencing nostalgia.

A possible functional interpretation of this result is that listeners who experience nostalgia less frequently experience less negative affect and more positive affect when a piece of music evokes nostalgia, whereas the opposite is true for those who experience nostalgia more frequently. As a preliminary test of this interpretation, we conducted a post-hoc analysis of ratings of sadness that individuals provided after listening to stimuli that they rated as at least moderately nostalgic (rated at least 3 on a 5-point nostalgia rating scale). Individuals who scored in the

Table 4
Summary of tonality tracking clusters.

		Left Hemisphere						Right Hemisphere					
Region	Location	xmm	ymm	zmm	# of voxels	# of indiv at peak	Mean TT bias ratio	xmm	ymm	zmm	# of voxels	# of indiv at peak	Mean TT bias ratio
Pre/Frontal													
	IFG (<i>pars orbitalis</i>)							40	40	-6	129	8	1.25 (1.23–1.27)
	IFG (<i>pars opercularis</i>)							48	16	16	57	6	1.35 (1.33–1.37)
	Medial orbital gyrus	-22	24	-14	20	9	1.10 (1.07–1.13)						
	Posterior orbital gyrus							28	26	-6	33	6	1.12 (1.07–1.17)
	Pre-SMA							12	14	56	24	6	0.98 (0.93–1.03)
	Precentral gyrus							52	-4	48	26	6	1.22 (1.20–1.25)
Temporal													
	Middle temporal gyrus							50	-16	-18	45	6	1.20 (1.18–1.21)
	Superior temporal gyrus	-62	-18	4	23	6	1.16 (1.11–1.20)						
	Middle temporal gyrus	-48	-24	-12	353	7	1.18 (1.16–1.19)						
	Parahippocampal gyrus							40	-40	-8	38	6	1.07 (1.04–1.10)
Parietal													
	Precuneus	0	-58	68	28	8	1.05 (1.02–1.09)						
	Supramarginal gyrus							56	-24	26	53	6	1.12 (1.11–1.14)
	Precentral gyrus							54	-2	22	62	6	1.08 (1.06–1.10)
	Precuneus							14	-46	44	32	6	1.12 (1.10–1.15)
Occipital													
	Superior occipital gyrus	-20	-78	30	24	5	0.91 (0.89–0.93)	28	-72	18	34	6	1.00 (0.99–1.02)
	Middle occipital gyrus	-40	-82	2	42	7	1.14 (1.11–1.17)						
	Middle occipital gyrus	-40	-86	20	27	7	1.16 (1.12–1.20)						
	Cuneus	2	-72	20	21	6	1.21 (1.19–1.24)						
	Lingual gyrus							4	-72	4	43	7	1.19 (1.16–1.21)
	Fusiform gyrus	-36	-44	-16	132	7	1.09 (1.07–1.11)						
Insula													
	Mid insula	-34	2	-2	61	6	1.08 (1.06–1.09)						
	Anterior insula*							32	32	2	29	6	1.30 (1.25–1.34)
	Insula							38	-12	14	25	5	1.21 (1.19–1.23)
	Insula							40	-20	16	20	5	1.15 (1.14–1.17)
Cingulate													
	Mid cingulate cortex	-10	-2	34	47	6	1.13 (1.12–1.15)						
	Mid cingulate cortex	0	-4	40	80	7	1.11 (1.10–1.12)						
	Mid cingulate cortex	-2	-16	42	41	6	1.12 (1.09–1.14)	16	6	40	20	6	1.13 (1.11–1.15)
	Mid cingulate cortex	-8	-38	40	60	7	1.10 (1.07–1.12)						
	Anterior cingulate cortex							6	22	24	49	6	1.19 (1.16–1.22)
Cerebellum													
	Cerebellum (crus 1)	-26	-62	-36	43	7	1.21 (1.16–1.27)	40	-72	-36	41	6	1.06 (1.04–1.08)
	Cerebellum (VI)	-10	-60	-18	79	7	1.18 (1.15–1.22)						
	Cerebellum (VII)	-36	-62	-46	24	6	1.11 (1.03–1.18)						
	Cerebellum							20	-34	-34	44	7	1.27 (1.25–1.29)
	Cerebellum							16	-46	-38	36	6	1.11 (1.09–1.14)
	Cerebellar vermis							0	-76	-18	33	7	1.07 (1.04–1.10)
	Cerebellar vermis							6	-66	-24	41	7	1.02 (0.99–1.05)
	Cerebellar white matter							18	-58	-34	69	7	1.13 (1.10–1.16)
Subcortical													
	Thalamus	-8	-30	14	43	6	1.12 (1.11–1.13)	26	-18	24	25	5	1.14 (1.08–1.20)
	Thalamus	-6	-12	12	35	6	1.21 (1.20–1.23)						
	Caudate nucleus							18	-8	24	22	6	1.17 (1.14–1.19)
	Pons*							8	-22	-30	46	7	1.24 (1.22–1.27)
	Brainstem*	-6	-38	-36	47	6	1.36 (1.34–1.38)						
	SN/PAG*^a							0	-24	-12	386	7	1.25 (1.24–1.26)
White Matter													
		-16	22	-10	24	7	1.14 (1.08–1.20)						
								28	24	26	41	6	1.15 (1.11–1.20)
								32	-64	10	49	7	1.08 (1.05–1.10)

Note: Regions indicated with an asterisk (*) were not assigned in the anatomy toolbox, and were identified using NeuroSynth. Clusters with a mean TT bias ratio of 1.25 or greater are identified in bold typeface. The distributions of TT bias ratios for clusters with a mean TT bias ratio of 1.25 or greater are presented in Fig. 6. # of voxels = the number of voxels in each cluster. # of indiv at peak = the number of individuals demonstrating tonality tracking at the peak voxel in the cluster. Mean TT bias ratio = the mean across all voxels (with 95% confidence intervals around the mean) within the identified cluster of the tonality tracking bias ratio, which is defined for each voxel as the ratio of the F-statistic for nostalgic tonality tracking variables to the F-statistic for non-nostalgic tonality tracking variables. IFG = inferior frontal gyrus. SN = substantia nigra. PAG = periaqueductal gray matter. SMA = supplementary motor area.

^a The periaqueductal gray matter cluster extends bilaterally into the substantia nigra.

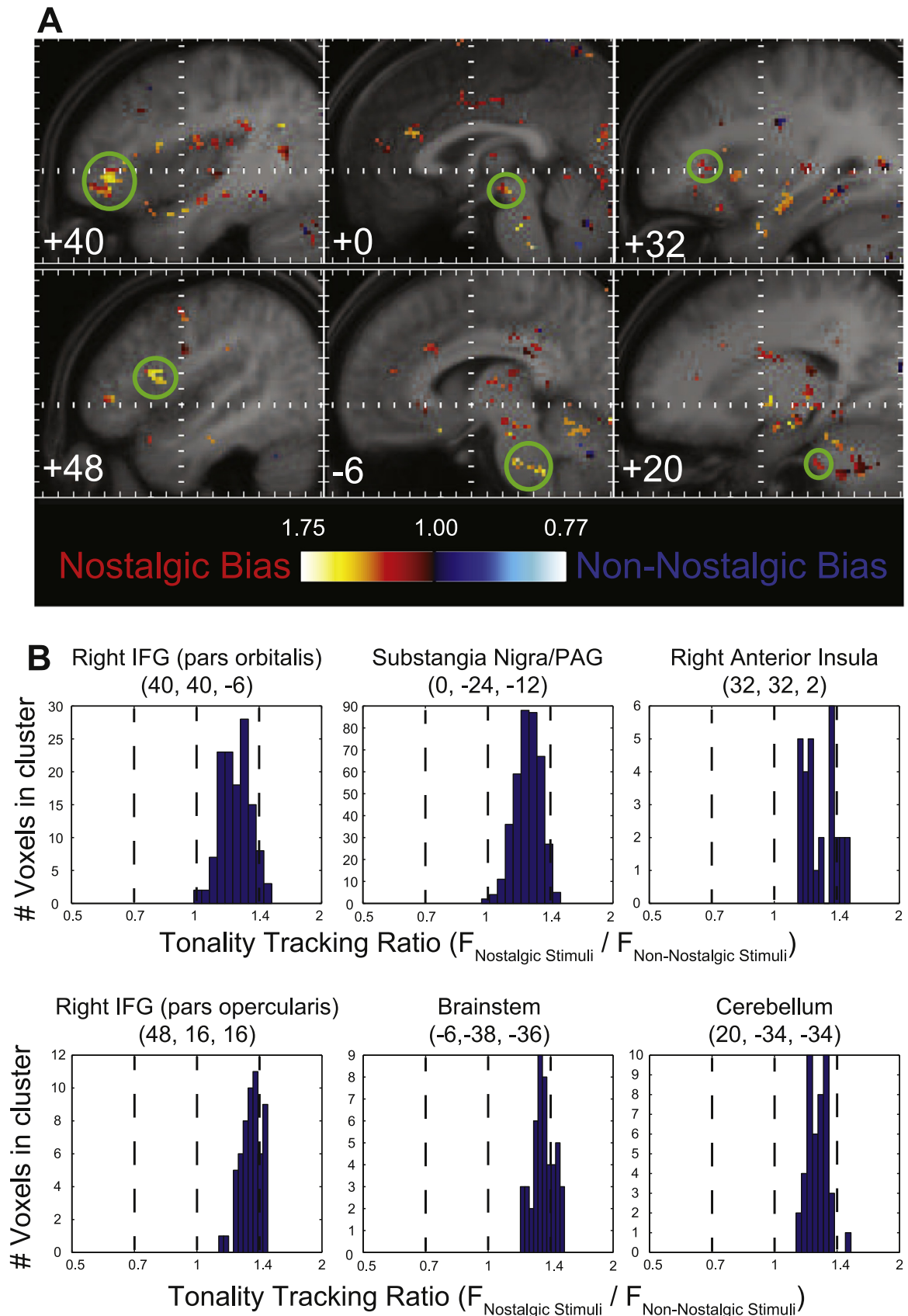


Fig. 6. Brain areas tracking the time-varying tonal structure of music in nostalgic and non-nostalgic contexts. A) Values in the legend indicate the ratio of variance explained by tonality tracking (TT) regressors for nostalgic stimuli to variance explained by TT regressors for non-nostalgic stimuli (corrected for the number of stimuli in each category). Variance explained by either nostalgic or non-nostalgic TT regressors was assessed using an F-test. Yellow to red regions indicate a greater amount of variance explained by TT regressors in nostalgic than in non-nostalgic stimuli. Light to dark blue regions indicate a greater amount of variance explained by TT regressors in non-nostalgic than in nostalgic stimuli. Green circles indicate the cluster whose TT bias ratio distribution is presented in the matching panel in Fig. 6B. B) Each axis presents the TT bias ratio distributions for the TT cluster in the matching panel in Fig. 6A. Values on the x-axis indicate the ratio of variance explained by TT regressors for nostalgic stimuli to variance explained by TT regressors for non-nostalgic stimuli (corrected for the number of stimuli in each category). Variance explained by either nostalgic or non-nostalgic TT regressors was assessed using an F-test. A value of 1 indicates that voxels with that bias ratio tracked nostalgic and non-nostalgic stimuli equally well, and a value larger than 1 indicates that voxels with that bias ratio tracked nostalgic stimuli more strongly than non-nostalgic stimuli. Numbers in parentheses following the anatomical label indicate the x, y, and z coordinates (in mm) of the voxel that was activated by the greatest number of participants. IFG = inferior frontal gyrus. PAG = periaqueductal gray matter.

lowest tercile on the SNS experienced less sadness on average ($M = 1.2083$, $SE = 0.0663$, where the sadness rating scale ranged from 1 to 5) than individuals who scored in the highest tercile on the SNS ($M = 1.4593$, $SE = 0.1337$). This effect approached significance at the 5% alpha level with a one-tailed t -test ($p = 0.0527$, $t = 1.6355$, $df = 90$). A similar analysis of happiness ratings trended towards the opposite effect, whereby individuals who scored in the lowest tercile on the SNS gave higher happiness ratings ($M = 3.4792$, $SE = 0.1297$) than did those who scored in the highest tercile on the SNS ($M = 3.2273$, $SE = 0.1200$) following stimuli that were rated as at least moderately nostalgic ($p = 0.0838$, $t = 1.3915$, $df = 90$). Though this combination of neural and behavioral results needs replication in a larger sample, it sheds some light on how individual differences in experience, mediated by personality traits, may manifest themselves at a neural level during the experiencing of a mixed valence emotion such as nostalgia.

Other regions showing effects of personality on reactivity to nostalgia-evoking music (including the anterior cingulate) have been shown to play a role in cognitive and affective regulation processes (Botvinick et al., 2004). In individuals exhibiting high levels of trait level sadness, activity in this brain area decreased as the amount of experienced nostalgia increased. Of possible significance, is the fact that the section of the anterior cingulate in which we observed this effect is apposed to section of the medial prefrontal cortex that plays a role in social cognition (Van Overwalle, 2009; Amodio & Frith, 2006), and music-evoked autobiographical remembering (Janata, 2009; Ford et al., 2011).

Modulation of activity in distributed reward and emotion regions by nostalgia is consistent with proposed functions of nostalgia as counteracting sadness with socially-relevant, personally meaningful memories that lead to increased positive affect (Hart et al., 2011; Wildschut et al., 2006). Our findings suggest that individual differences in nostalgia proneness may predict individual differences in the engagement of emotion and reward processes during music-evoked nostalgia, whereas individual differences in the personality trait of *sadness* may predict individual differences in the engagement of emotion and conflict regulation processes during music-evoked nostalgia. More broadly, our findings underscore the importance of considering individual differences when investigating neural correlates of memory and affect, especially idiosyncratic experiences such as music-evoked nostalgia.

4.3. Nostalgia and tonality tracking

The time-varying tonal structure of music has been used to identify brain areas that couple with this structural signature of music in time (Janata et al., 2002; Janata, 2005) and in different psychological contexts (i.e. autobiographical recall vs. no autobiographical recall) (Janata, 2009). In order to better understand how the time-varying structure of nostalgia-evoking stimuli couples with time-varying brain activity, we used a tonality tracking (TT) analysis to identify brain areas that coupled preferentially to either nostalgic or non-nostalgic music. The first report of TT during music-evoked remembering found that about twice the amount of variance in BOLD activity in the left IFG was explained by TT regressors during autobiographical music listening than during non-autobiographical music listening (Janata, 2009). We observed a TT bias towards nostalgic music listening in the right IFG, with an average of 25–35% more variance explained in the IFG by nostalgic compared to non-nostalgic stimuli. The TT cluster in the right IFG ($x = 40$, $y = 40$, $z = -6$) is very close to a region ($x = 41$, $y = 43$, $z = -4$) where activity has been shown in separate samples to correlate with tonality processing (Hyde et al., 2006).

While previous TT studies found recruitment of nodes in an internally directed attention network (the default mode network, or DMN) during music listening (Janata et al., 2002) and music-

evoked autobiographical memories (Janata, 2009), we did not observe such effects here. The absence of both TT and general linear modeling effects in the dorsal medial prefrontal cortex was particularly conspicuous. Post-scan debriefing indicated that participants in the current study, when experiencing an autobiographical memory, were generally more focused on attending to the music than they were to attending on the evoked memories. This differs from the self-reports of participants in the previous study, in that participants in the previous study reported more attention to memories than the music (Janata, 2009). Overall, the task demands across our entire experimental session directed attention to the emotional qualities of the stimuli. In the non-musical emotion induction tasks that participants encountered during scanning (which comprised 5 of the 9 total task periods), we asked participants to focus on the content of a particular stimulus (faces or sentences) and use this content to drive their emotional experience. In other words, our experimental context, in terms of non-music-listening tasks, involved attention directed outward towards emotional stimuli. It may be that this type of stimulus focus carried over for most participants into the music-listening task period, where participants were primed to attend more closely to musical stimulus features rather than their inner mnemonic experience. It is possible that attentional focus provides a strong psychological context, in addition to nostalgic or autobiographical experiences, that shapes which brain areas couple more strongly to structural properties of the musical stimulus. This particular hypothesis must be tested with a prospectively designed study.

Notably, we found TT bias for nostalgic stimuli in areas in which TT has not been reported previously, including the anterior insula and a midbrain region that spans the substantia nigra and ventral tegmental area. The insula, which is believed to code representations of subjective feelings and interoceptive or visceral states (Critchley et al., 2004), and the substantia nigra and ventral tegmental area, involved in reward processing (Haber and Knutson, 2010), are both reasonable targets for engagement during emotional music listening. Our results provide initial evidence that activity in these areas couples with time-varying structural properties of pieces of music. In particular, this is consistent with recent evidence that core reward processing regions, including the ventral tegmental area (in the mesolimbic dopaminergic system), are activated during music-evoked pleasure (Koelsch, 2014). This points to a possible mechanism whereby structural aspects of a complex auditory stimulus induce affective responses within a complex emotion such as nostalgia.

Right cortical asymmetry of power in the alpha band as recorded during rest using EEG was recently found to predict nostalgia proneness (Tullett et al., 2015). Our findings are consistent with a right-lateralized processing model of nostalgia. All cortical brain regions that showed biased TT during nostalgic experience were right-lateralized.

While not showing bias in tonality tracking for either nostalgic or non-nostalgic stimuli, a number of occipital regions demonstrated general tonality tracking (Table 4). Occipital activation has been previously reported during music listening (Alluri et al., 2013; Trost et al., 2012), and specifically with tonality tracking analysis (Janata, 2009). This has previously been interpreted in a similar way to occipital activity during eyes-closed self-directed visual imagery (e.g. Pearson et al., 2015). Mental imagery has been interpreted as a form of top-down perception that can drive activity in occipital cortex regions. A plausible account of occipital activation during eyes-closed music listening, identified in tonality tracking analyses, would propose that top-down activation of the visual system is being driven during nostalgic and autobiographical memory recall, and resulting visual imagery is unfolding in the same time-frame as the time-varying tonal structure

of music (Janata, 2009). While our interpretation is still speculative, it is consistent with the literature on mental imagery.

4.4. Limitations and future directions

Given previous reports of the relationship between personality and nostalgic experience (e.g. Barrett et al., 2010), we anticipated that individual differences in affective personality might be useful for investigating the neural basis of music-evoked nostalgia. However, we did not anticipate just how important they would be. While the current study reveals striking relationships between neural processes underlying nostalgic experience and individual differences in affective personality traits, we acknowledge the small sample size. Given the clear importance of individual differences for studying music-evoked nostalgia, repeating this study in a larger, more focused and homogenous samples of participants selected to vary specifically in nostalgia proneness and/or sadness is warranted. Such an approach would allow for extension of the personality interaction analysis to identify TT networks that are biased both in psychological context (nostalgic vs non-nostalgic context) and individual trait context (personality traits), thus revealing nostalgia proneness or *sadness*-specific nostalgic-biased TT networks. Similarly, explicitly manipulating attentional set (instructing participants to focus attention on the memories versus structural aspects of the stimulus) could allow one to examine whether TT networks are indeed configured by attentional biases, as post-scan ratings in this and a previous study (Janata, 2009) suggest they might be.

Ratings of familiarity, autobiographical salience, and nostalgia were correlated strongly in the current sample. However, there was not sufficient power to examine the relationship between brain activity and nostalgia ratings within stimuli that were matched for familiarity or autobiographical salience. Future studies should provide greater experimental control of the relationship between familiarity, autobiographical salience, and nostalgia.

We have demonstrated that nostalgic experience recruits brain areas that are involved in affective processing. It may be that these areas are engaged in social ameliorative processes that are associated with nostalgia, such as increasing social connectedness, self-positivity, and feelings of social proximity. Can we use music-evoked nostalgia paradigms to develop evidence for the neural bases of increased specific social affective processing during nostalgia? Future work could address this question by adding manipulations that specifically evoke individual triggers of nostalgia such as loneliness, sadness, and social threat, in order to investigate the more specific recruitment of brain areas involved in music-evoked nostalgia when counteracting these negative states. Thus, music-evoked nostalgia could be used as a tool to study the neural basis of increased feelings of social connectedness, self-positivity, and other such experiences.

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