

Predictive processing, cognitive control, and tonality stability of music: An fMRI study of chromatic harmony

Chia-Wei Li ^a, Fong-Yi Guo ^b, Chen-Gia Tsai ^{c,d,*},¹

^a Department of Radiology, Wan Fang Hospital, Taipei Medical University, Taipei, Taiwan

^b Graduate Institute of Brain and Mind Sciences, National Taiwan University, Taipei, Taiwan

^c Graduate Institute of Musicology, National Taiwan University, Taipei, Taiwan

^d Neurobiology and Cognitive Science Center, National Taiwan University, Taipei, Taiwan

ARTICLE INFO

Keywords:

fMRI
Frontoparietal network
Hierarchical processing
Music
Prediction error
Working memory

ABSTRACT

The present study aimed at identifying the brain regions which preferentially responded to music with medium degrees of key stability. There were three types of auditory stimuli. *Diatonic music* based strictly on major and minor scales has the highest key stability, whereas *atonal music* has the lowest key stability. Between these two extremes, *chromatic music* is characterized by sophisticated uses of out-of-key notes, which challenge the internal model of musical pitch and lead to higher precision-weighted prediction error compared to diatonic and atonal music. The brain activity of 29 adults with excellent relative pitch was measured with functional magnetic resonance imaging while they listened to diatonic music, chromatic music, and atonal random note sequences. Several frontoparietal regions showed significantly greater response to chromatic music than to diatonic music and atonal sequences, including the pre-supplementary motor area (extending into the dorsal anterior cingulate cortex), dorsolateral prefrontal cortex, rostralateral prefrontal cortex, intraparietal sulcus, and precuneus. We suggest that these frontoparietal regions may support working memory processes, hierarchical sequencing, and conflict resolution of remotely related harmonic elements during the predictive processing of chromatic music. This finding suggested a possible correlation between precision-weighted prediction error and the frontoparietal regions implicated in cognitive control.

1. Introduction

Predictive processing is inherent in a wide range of mental activities, including perception, cognition, action, emotion, and social interaction (Bastos et al., 2012; Clark, 2013; Friston, 2012; Lupyán & Clark, 2015; Seth & Friston, 2016; Tamir & Thornton, 2018). In the field of music cognition, researchers have been increasingly adopting theories of predictive processing to explain various listening experiences of music (Agres, Abdallah, & Pearce, 2018; Gold, Pearce, Mas-Herrero, Dagher, & Zatorre, 2019; Huron, 2006; Koelsch, Vuust, & Friston, 2019; Schaefer, Overy, & Nelson, 2013; Vuust & Kringelbach, 2010). It is posited that structural regularities of prior musical passages enable a listener to build a predictive model that generates ensuing musical possibilities. A mismatch between musical prediction and auditory input results in prediction error. Electrophysiological studies have found neural correlates of prediction error signals during music listening (Koelsch,

Jentschke, Sammler, & Mietchen, 2007; Lumaca, Haumann, Brattico, Grube, & Vuust, 2019; Maess, Koelsch, Gunter, & Friederici, 2001; Omigie et al., 2019; Steinbeis, Koelsch, & Sloboda, 2006; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009). These findings represented evidence of neural involvement in the predictive processing of music.

Rhythm perception provides a promising model for understanding the role of predictive processing in the induction of emotional and bodily responses to music. The brain's predictive model of metrical structure assigns relative probabilities to notes and rests of a pattern according to prior information of temporal regularities, and a syncopation occurs when these predictions are violated (Vuust & Witek, 2014). Based on a hierarchical Bayesian inference framework (Friston, 2010), Vuust et al. (2018) proposed a model for predictive coding of rhythmic incongruity (PCRI), in which the rhythm is the auditory input and the meter is a predictive model for temporal events. In this hierarchical inference framework, top-down information flows provide lower

* Corresponding author at: Graduate Institute of Musicology, Neurobiology and Cognitive Science Center, National Taiwan University, Taiwan.

E-mail address: tsaichengia@ntu.edu.tw (C.-G. Tsai).

¹ No.1, Sec. 4, Roosevelt Road, Taipei 106, Taiwan.

levels with prior expectations about rhythm, whereas bottom-up information flows carry prediction errors that update posterior expectations in higher levels. This PCRI model successfully explained that listeners' ratings of subjective pleasure and desire for body-movement are inverted U-shaped functions of the degree of syncopation (Witek, Clarke, Wallentin, Kringsbach, & Vuust, 2014). The brain's perception of syncopation depends on prediction errors due to rhythmic incongruity and their precision due to metrical certainty. Listeners experience stronger pleasure and desire for body-movement in response to rhythms with medium degrees of syncopation compared to rhythms with low and high degrees of syncopation, because the precision-weighted prediction error is highest at medium degrees of syncopation. On the other hand, rhythms with lowest degrees of syncopation lead to minimal prediction errors, and rhythms with highest degrees of syncopation lead to minimal precision because the meter is quite uncertain (Vuust et al., 2018).

Following the insights of these syncopation studies, the present study addressed the brain's predictive model for musical pitch: tonality. Music with tonality or "in a key" is called tonal music. A majority of human music is tonal, although the clarity/stability of tonality varies considerably. Most notes in a passage of tonal music are members of a specific set of notes, which is the *scale* of the key of this passage. A scale has a tonal center or tonic, which is the most stable note of the key. When a melody is in F major, for example, most notes of this melody belong to the F major scale, with the tonic of F major—F—being the center of attraction. For a harmonic progression, the center of attraction is the tonic chord rooted on the tonic, and musical phrases ending with the progression of the dominant chord (rooted on the fifth degree of the scale) to the tonic chord give a feeling of conclusion to listeners who are familiar with Western tonal music. Tonality in Western music implicates a hierarchy of notes, chords, and keys on the basis of a dominant-tonic relationship (Koelsch, Rohrmeier, Torrecuso, & Jentschke, 2013; Carol L. Krumhansl, 1990; Moss, Neuwirth, Harasim, & Rohrmeier, 2019).

In Western music, there could be an inverted U-shaped relationship between key stability in music and perceived tension aroused by precision-weighted prediction error in the predictive model of tonality. In diatonic music based strictly on major and minor scales, prior notes establish a key and a predictive pitch set, from which all ensuing notes are drawn. On the other hand, there is no predictive model of tonality in atonal music, which has the lowest key clarity/stability. Between these two extremes of key clarity/stability, chromatic music is characterized by sophisticated uses of notes foreign to the seven-tone diatonic (i.e., major and minor) scales. To explore more complex and tonally more ambiguous sonorities, composers of Western classical music in the 19th century developed rich vocabularies of chromatically altered chords, which refer to chords with out-of-key notes. Musicological research suggests that chromatic music has profound and distinguished expressive power (Agawu, 1986; Baker, 1990; Bass, 1988; Bribitzer-Stull, 2006; McCreless, 1983; Somer, 1995). In science-fiction and fantasy films, chromatic music is typically used to emphasize mysterious events or supernatural power (Heine, 2018). A type of chromatic harmony in the *Star Wars* can give 'the impression that only a very powerful sorcerer, perhaps only a god, could animate these chords thus, could make them progress so against their tonal nature (Buhler 2000, p. 47).' This suggests a possible link between the complicated affective responses to chromatic music and the cognitive processing of its unpredictability. In light of the aforementioned syncopation studies, it is tempting to speculate that the precision-weighted prediction error of tonal processing may be an inverted U-shaped function of key stability. The reason for this is that chromatic music with intermediate degrees of key stability would lead to the highest precision-weighted prediction error, whereas diatonic music would lead to minimal prediction errors of the tonality model, and atonal music would lead to minimal precision because tonality does not exist.

Some chromatically altered chords appear as the result of *tonicization*, which is a means to embellish harmonic progressions by temporarily elevating a diatonic chord to the status of a tonic chord (noted as

"I"). For example, the third degree of the F major scale is A, and the minor chord rooted on A is noted "III" in F major. To embellish the III, one can insert the dominant chord (noted as "V") of A minor immediately before this III, as shown in Fig. 1. The dominant-tonic progression on the tonicized A gives a momentary feeling of A minor within the broader context of F major. The dominant chord of the III in F major, noted as "V of III", belongs to the most common type of chromatically altered chords: secondary dominant chord, which refers to a dominant chord resolving to a scale degree other than the tonic (Piston & DeVoto, 1978). Tonicizations in music are similar to relative clauses in language: a tonicized chord temporarily becomes a tonic chord, much in the same way that a noun temporarily becomes the subject in a relative clause.

There is an intriguing link between tonicization and the hierarchical PCRI model (2018). In the above example, the "V of III" contains two notes foreign to the F major scale, namely, G-sharp and B-natural. These two notes are unlikely to cause an instantaneous collapse of the predictive model of F major. Instead, the associated prediction error is fed forward from a lower level to higher levels to update the model's "beliefs" about tonality—in a manner similar to when the prediction error induced by syncopated notes is fed forward from a lower level to higher levels to update the model's "beliefs" about meter (Vuust et al., 2018). Based on top-down feedback from the higher levels, important harmonic progressions in a few keys and predicted sounds of chords would be activated as posterior expectations in the middle and lower levels, respectively. Then, the auditory input of [III → II → I] prompts an updating of tonality model in the higher levels. After integrating the information of [[V of III → III] → II → I] over a relatively larger temporal scale, the higher levels could interpret the chromatically altered chord "V of III" in the context of the invariant key of F major.

The above example of the secondary dominant suggests that there is not a black and white dichotomy that separates syntactically irregular chords from syntactically regular chords. A number of neuroimaging studies used an event-related approach in which the final chord of a trial was either a diatonic chord in accordance with the harmonic syntax or a chromatically altered chord "violating" the harmonic syntax (Koelsch et al., 2007; Maess et al., 2001; Omigie et al., 2019; Steinbeis et al., 2006). However, if a chromatically altered chord is appropriately resolved by ensuing chords, this chromatically altered chord is syntactically regular in a global tonal context. Chromatic music is characterized by chromatically altered chords and diverse ways of their resolution. While chromatically altered chords are widely used in Western classical, jazz, pop/rock, and film music, research on neural responses to chromatic music is surprisingly scant. The aim of the present study was to compare the neural responses to diatonic music, chromatic music, and atonal random note sequences. Chromatic music with medium degrees of key stability was expected to be associated with the highest involvement of regions linked to higher-order hierarchical processing of harmonic syntax, because the cognition of chromatically altered chords and tonicization relies on the hierarchy of keys (e.g., the hierarchy of F major and A minor in Fig. 1). This is in contrast to diatonic music based solely on the hierarchy of notes and chords.

In the present study, the majority of chromatically altered notes stem from secondary dominant chords and tonicization, while a few chromatically altered notes stem from borrowed chords, Neapolitan chords, augmented sixth chords, appoggiatura chords, and tension notes. In each stimulus of chromatic music, chromatically altered chords and related keys are resolved in the context of the tonic key, with the exception of the last chord. The novelty of the present study lies in the possibility to examine the neural correlates of higher-order hierarchical organizations that are presumably required for the integration of distantly related harmonic elements in chromatic music. Previous functional magnetic resonance imaging (fMRI) studies on harmonic syntax mainly focused on unresolved chromatically altered chords, consistently observing enhanced activity in the inferior frontal gyrus (IFG) in response to irregular harmonic progressions (Bianco et al., 2016; Perani et al., 2010; Seger et al., 2013). Given a gradient of

A

F: I IV V I III II I

B

F: I IV V I V of III III II I

a: V I

Fig. 1. Tonicization and secondary dominant in Western tonal harmony. All notes of the diatonic harmonic progression in F major (A) are in-key notes. In its modified version (B), a secondary dominant chord “V of III” is added to embellish “III”. This secondary dominant chord is a chromatically altered chord, because it contains two out-of-key notes, i.e., notes that are not in the scale of F major. The shadowed area indicates the progression of [V of III → III], which is the dominant- tonic progression on the tonicized A. It is very common to tonicize a diatonic chord through its dominant chord, and this process makes the tonicized chord sound like a tonic chord for a short period of time.

abstraction along the anterior-posterior axis of the lateral frontal cortices (Badre, 2008; D’Esposito & Postle, 2015), the contrast of chromatic music minus diatonic music in our study would show more anterior activation clusters in the lateral frontal cortices compared to those observed in previous fMRI studies on harmonic irregularities in diatonic music.

In addition to the frontal cortices, the inferior parietal lobule (IPL) is likely to support the predictive processing of music. A recent study showed greater activity in the IPL and prefrontal cortex in response to medium complexity rhythms compared to high complexity rhythms, suggesting their involvement in generating and updating stimuli-based expectations (Matthews, Wittek, Lund, Vuust, & Penhune, 2020). In the present study, the IPL could play a role in representing important harmonic progressions in a few keys that are useful for predicting the continuation of chromatic music, while the frontal cortices might employ higher-order operations on these memories according to the hierarchical relationship between chords and keys. On the other hand, listeners tend to load harmonic progressions in a single key in working memory when predicting the continuation of diatonic music, and no predictive model of pitch is available for atonal random note sequences. Taken together, it seems reasonable to suspect an inverted U-shaped relationship between key stability in music and activity in the frontal cortices and IPL, which might support the working memory processes underlying the more complicated predictive processing of chromatic music compared to diatonic music and atonal sequences.

2. Material and methods

2.1. Participants

Twenty-nine young adults (average age 22.8 ± 2.4 years, 2 left-handed, 19 females) participated in the fMRI experiment, in which two fMRI scanning runs for the present study on key stability alternated with three fMRI scanning runs for another study on discrimination of musical pitch intervals. This design was used to minimize habituation and learning effects that could occur with repeated exposures to the same music within a short period of time. The selection and recruitment of participants are mentioned in the next two paragraphs. Other methods and results of the study on discrimination of musical pitch intervals are not mentioned further in this paper.

Volunteers were recruited via a public announcement on the internet, which stated the requirement of excellent relative pitch, namely, an ability to evaluate relations among pitches. All volunteers completed two pre-scan online tests. The first test was a modified

version of the interval-discrimination task of the other study, and the second test was a modified version of the key-stability-rating task in the present study. The interval-discrimination test involved four conditions, varying two factors of the size of reference pitch interval (large versus small) and the deviation size of pitch interval (large vs. small). In each question “3–1” or “3–4” (musical scores with numerical notation) were presented visually to indicate a reference interval of the minor sixth or the minor second. Then, a tone pair was presented auditorily twice. The interval size of this tone pair was either larger or smaller (50% probability for each, randomly presented) by either 1 or 0.5 semitone than the visually presented reference interval. Volunteers were asked to answer whether the interval of the tone pair was larger or smaller than the reference interval. There were eight questions in each of the four conditions, and all 32 questions were randomly presented in this test. Volunteers were only enrolled in the neuroimaging portion of this study if they gave more than 75% correct answers for each condition.

The pre-scan key-stability-rating test included four questions. For each question, the volunteer was presented with a stimulus of diatonic music and a stimulus of chromatic music (in random order). He/she was asked to identify the one with higher key stability. At the beginning of this test, two examples of diatonic music labeled as high key stability and two examples of chromatic music labeled as low key stability were provided to facilitate volunteers’ understanding of key stability. Volunteers were only enrolled in the neuroimaging portion of this study if they correctly identified diatonic music in all four questions.

A total of 274 volunteers took the pre-scan online tests. Thirty-seven volunteers met the inclusion criteria. Twenty-nine of them completed the fMRI experiment. They were all native Mandarin speakers, and had no history of neurological or psychiatric disorder. All of the 29 participants had studied musical instruments for 2 years or more (average 8.43 ± 3.79 years). The participants were compensated with approximately 20 USD after the completion of the fMRI scan. Written informed consent was obtained from each participant prior to participation in the study. All research procedures were performed in accordance with a protocol approved by the Institutional Review Board of National Taiwan University (201812HM063). This study was conducted in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Tasks and stimuli

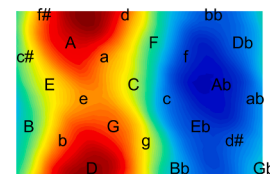
There were two tasks during the fMRI scans: an interval-discrimination task and a key-stability-rating task. The present study only involved the key-stability-rating task. There were three types of

auditory stimuli for this task: diatonic music, chromatic music, and atonal note sequence. Nine stimuli were generated for each type by a composer and the corresponding author of this article. These stimuli were scored for four voices, three bars (6 s) in length, with 4/4 time signature and 120 bpm, as shown in Fig. 2 (see [Supplementary Material](#) for all stimuli). All notes of these stimuli were in the range of F2 to C6. Only diatonic triads and the dominant seventh chord were used in diatonic music. The stimuli of diatonic music covered eight major-mode tonalities: C major, D major, E \flat major, E major, F major, G major, B \flat major, and B major. Each stimulus of chromatic music was generated through “chromatizing” a stimulus of diatonic music, namely, using more complex chords with notes foreign to the diatonic scale while keeping the bass notes on the first and third beats unchanged. A majority of chromatically altered chords were regularly or irregularly resolved. For example, we used a regular resolution of [V of V \rightarrow V] and an irregular resolution of [V of V \rightarrow II of VI] in the chromatic stimuli. Eight of nine chromatic stimuli end with a chromatically altered chord, which is not resolved. The process of chromatizing considerably reduced key stability, and there were 10–13 (20.83–28.08%) out-of-key notes in each stimulus of chromatic music. Each stimulus of atonal note sequence was generated by randomly selecting musical notes in the natural ranges of four voices. Tone sequences were coded in MIDI (musical instrument digital interface) and converted to WAV files using Reason 8.0 (Propellerhead, Inc.) with a virtual musical instrument named “BRIGHTPIANO.”

We used the MIDI Toolbox (Eerola & Toiviainen, 2004) to estimate key stability of the stimuli. Calculation of key strength of MIDI files in MIDI Toolbox is based on cross-correlation of its pitch class distribution with the distribution associated with a key (Temperley, 2001). Fig. 2 shows the key strength of 24 keys (12 major-mode keys and 12 minor-mode keys) of examples of three stimulus types on the key map derived from the tonal hierarchies (Krumhansl & Kessler, 1982). It can be seen that the example of diatonic music has the clearest peak of key strength, whereas the example of atonal sequence has the least clear peak of key strength. The value of maximal key strength is an indicator of key stability.

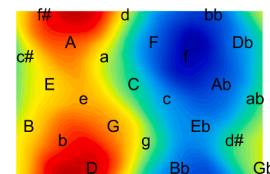
Diatonic Music

D: I IV IV II V I V V I V I I



Chromatic Music

D: VI IV V of II VII of II II VII of V V III V of IV IV VII of II II



Atonal Sequence

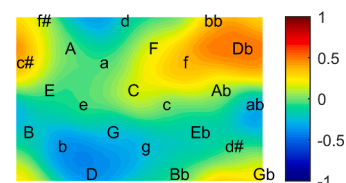


Fig. 2. Examples of three types of auditory stimuli. The left panel shows musical scores, while the right panel shows the profiles of key strength on the key map. As the number of accidentals increases across diatonic music, chromatic music, and atonal sequence, the clarity of the peak of key strength decreases.

2.3. Procedure

On the day of neuroimaging, participants underwent a practice session outside the scanner to become familiar with the tasks. There were 30 trials for the interval-discrimination task and 18 trials for the key-stability-rating task in this practice session. For the key-stability-rating task, there were six trials for each of three stimulus types. All 18 trials were presented in a random order. This practice session lasted approximately 25 min.

The neuroimaging portion of this study began with an anatomic scan of the whole brain. There were five fMRI scanning runs separated by 30–60 s rest intervals. In total, the anatomic and functional scanning runs lasted approximately 50 min. For the two key-stability-rating scanning runs, each trial began with a silence (3 s) and warning noise (pink noise, 0.5 s). A fixation cross was presented during the presentation of warning noise. Then, an auditory stimulus was presented from the 4th s onwards. After this auditory presentation, a four-point rating scale (very stable–very unstable) was visually presented, and the participants were instructed to rate key stability by button pressing within 5 s (Figure S1). There were 18 trials for each of the three conditions, and each trial was 15 s in length. The 54 trials were randomly distributed into two tonal-stability-rating scanning runs. Each run consisted of 27 trials and lasted 6.75 min.

All auditory stimuli were presented through scanner-compatible headphones (Resonance Technology, Van Nuys, CA, USA). Participants wore earplugs to reduce the scanner noise by 15–25 dB. During structural scanning, the experimenter presented an example of diatonic music a few times and adjusted the auditory volume according to participants' feedback. Participants adapted to listening to music in the presence of scanner noise during this volume-adjusting test. No stimuli in the pre-scan test, practice session, and volume-adjusting test were presented in the neuroimaging portion of this study.

2.4. MRI data acquisition

Functional and structural image were acquired on a 3 Tesla MR

system (MAGNETOM Prisma, Siemens, Erlangen, Germany) and a 20-channels array head coil at the Imaging Center for Integrated Body, Mind, and Culture Research, National Taiwan University. In the functional scans, about 2.5 mm slices of axial images were acquired using a gradient echo planar imaging (EPI) with the following parameters: time to repetition = 2500 ms, echo time = 30 ms, flip angle = 87° , in-plane field of view = 192×192 mm, and acquisition matrix = $78 \times 78 \times 45$ to cover whole cerebral areas. For spatial individual-to-template normalization in preprocessing, a Magnetization Prepared Rapid Gradient Echo T1-weighted imaging with spatial resolution of 0.9 mm isotropic was acquired for each participant.

2.5. Data analysis

The values of maximal key strength (an objective indicator of tonality stability) and the subjective rating scores of key stability for each stimulus were computed and averaged across participants. Shapiro tests were used to assess normality of the data distribution of the maximal key strengths and key stability rating for three stimulus types. Subsequently, either paired *t*-tests or Wilcoxon signed-rank tests were conducted on these values to evaluate significant contrasts between stimulus types. Correlation analysis was carried out to examine the relationship between the maximal key strength and key stability rating.

Preprocessing and statistical analysis of the fMRI data was performed using the SPM12 toolbox (Wellcome Trust Centre for Neuroimaging, London, UK). The first four volumes of each run were discarded to exclude T1 saturation effects. The functional images were corrected for differences in slice-acquisition time to the first volume and were realigned to the first volume in each scanning run using affine transformation. Coregistered images were normalized to the standard Montreal Neurological Institute (MNI) average template and resampled to a 2-mm isotropic voxel size. Normalized images were spatially smoothed with a Gaussian kernel of 5-mm full width at half maximum.

Data from each participant were entered into a general linear model using a block-designed procedure. The three conditions for this task were modeled using a box-car function convolved with the canonical hemodynamic response function. In each block, every stimulus was presented for 6 s (Figure S1). The resulting model coefficients for individual participants were subjected to second-level analysis, in which a one-way ANOVA and pairwise comparisons were applied to all voxels to examine whether they showed differential activation across three conditions. All activation was thresholded at FDR corrected $p < 0.05$, with a minimum cluster size of 50 voxels.

3. Results

The data of maximal key strength for each stimulus type were normally distributed. Therefore, we used paired *t*-tests to evaluate if there was significant difference in maximal key strength across three stimulus types. Due to non-normality of the distribution of rating scores of key stability for each stimulus type, we used Wilcoxon signed-rank tests to evaluate if there was significant difference in key stability rating across three stimulus types. Fig. 3A and Fig. 3B show the results of maximal key strength and key stability rating, respectively. The maximal key strength of diatonic music was significantly higher than that of chromatic music ($df = 8$, Cohen's $d = 0.25$, $p < 0.01$); the maximal key strength of chromatic music was significantly higher than that of atonal sequences ($df = 8$, Cohen's $d = 2.01$, $p < 0.01$). The key stability rating of diatonic music was significantly higher than that of chromatic music (z -score = 4.71, $p < 0.01$); the key stability rating of chromatic music was significantly higher than that of atonal sequences (z -score = 4.71, $p < 0.01$). Scatterplots for the correlation analysis is shown in Fig. 3C. There was a significant positive correlation between the maximal key strength and key stability rating ($r = 0.89$, $p < 0.01$).

The results of fMRI data analysis for the contrasts between chromatic music, diatonic music, and atonal sequence conditions were summarized by Tables 1, 2, and 3, respectively. Compared to the diatonic music condition, the chromatic music condition was associated with significantly increased activity in the dorsal premotor cortex, pre-supplementary motor area (preSMA) extending into the dorsal anterior cingulate cortex (dACC), rostralateral prefrontal cortex (RLPFC), dorsolateral prefrontal cortex (DLPFC) extending into IFG, intraparietal sulcus (IPS), and precuneus; on the contrary, decreased activity was shown in several regions, including the primary motor area, anterior insula, anterior cingulate cortex, lateral temporal regions, striatum, and amygdala (Figure S3). Compared to the atonal sequence condition, the chromatic music condition was associated with significantly increased activity in the dorsal premotor cortex, IFG, preSMA/ACC, DLPFC/IFG, RLPFC, angular gyrus, precuneus, caudate nucleus, and cerebellum; on the contrary, decreased activity was shown in several regions, including the primary motor area, medial superior frontal gyrus, anterior cingulate cortex, posterior cingulate cortex, middle frontal gyrus, lateral temporal regions, and amygdala (Figure S4). When comparing diatonic music to atonal sequences, significant enhanced activation was found in a number of regions, including the postcentral gyrus, preSMA/dACC, lateral temporal regions, anterior insula, thalamus, striatum, and cerebellum, while significant decreased activity was found in the primary motor area, superior parietal lobule, IPL, SMA, striatum, middle temporal pole, precuneus, and cerebellum (Figure S5).

The intersections of chromatic music versus diatonic music and

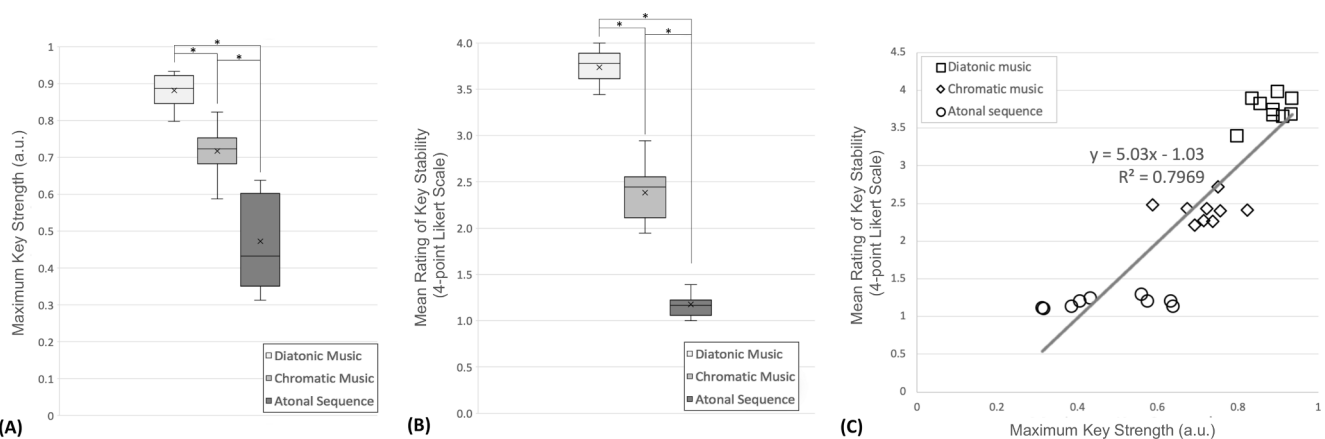


Fig. 3. Statistical results of the tonality stability of three stimulus types. (A) Objective measurement of tonality stability (estimated by the maximal key strength using MIDI toolbox). (B) Mean rating of key stability. ($* p < 0.01$). (C) Scatterplot with correlation between the maximal key strength and mean rating of key stability.

Table 1

Activation clusters for the contrasts between chromatic music and diatonic music.

Volume information	Peak location			t-value	Cluster (voxel)
	X	Y	Z		
<i>Chromatic music > Diatonic music</i>					
Precentral gyrus, postcentral gyrus	34	-22	50	7.28	986
Intraparietal sulcus	-38	-54	42	5.87	491
Precuneus	-4	-72	46	5.72	656
Middle frontal gyrus (dorsal premotor cortex)	-36	10	54	5.38	107
Medial superior frontal gyrus (pre-supplementary motor area), dorsal anterior cingulate cortex	-4	26	46	5.15	167
Middle frontal gyrus (dorsolateral prefrontal cortex), inferior frontal gyrus	48	28	32	4.51	103
	-38	22	30	4.06	122
Intraparietal sulcus	40	-54	44	3.82	54
Inferior frontal gyrus (rostromedial prefrontal cortex)	-34	56	8	3.58	83
<i>Diatonic music > Chromatic music</i>					
Precentral gyrus, postcentral gyrus	-40	-20	60	10.26	6385
	66	-4	18	3.87	74
	40	-6	46	5.66	445
Cerebellar lobule IV-VI	14	-48	-18	8.65	1166
Anterior insula	-26	-8	0	7.49	1843
Anterior cingulate cortex	6	48	12	6.21	652
Superior temporal gyrus, supramarginal gyrus, superior temporal pole	50	-42	18	5.25	800
	-56	-6	-8	5.06	317
	48	-22	-6	4.97	368
	56	6	-10	4.71	112
Caudate nucleus	4	4	-4	4.61	52
Cerebellar lobule VIII-IX	10	-64	-42	4.60	59
Amygdala, parahippocampal gyrus	22	-2	-18	4.57	94
Cerebellar lobule Crus I	-22	-82	-32	4.56	135
Supramarginal gyrus	56	-32	28	4.31	116
Medial superior frontal gyrus	12	52	42	4.16	145
Lingual gyrus	18	-72	-8	3.73	58

chromatic music versus atonal sequences were presented in Table 4, Table 5, and Fig. 4. The beta values of some activation clusters of these intersections were extracted to highlight the activation variations related to the processing of tonality. Activity in the preSMA/dACC, DLPFC/IFG, RLPC, IPS, and precuneus showed inverted U-shaped profiles with the key stability of music. By contrast, activity in the middle temporal gyrus, medial superior frontal gyrus, medial orbito-frontal cortex, and amygdala showed U-shaped profiles with the key stability of music.

4. Discussion

Harmonic syntax in music provides a window into the neural mechanisms underlying predictive processing. Diatonic chords in music establish and confirm the predictive model of tonality, whereas chromatically altered chords result in prediction errors of this model and reduce key stability. An overarching goal of the current study was to specify the neural underpinnings of the hierarchical organization of keys involved in the predictive processing of chromatic music. In line with our hypothesis, the results show that activity in a few frontal and posterior parietal regions implicated in working memory processes was significantly greater during exposure to chromatic music, relative to diatonic music and atonal sequences.

When comparing harmonic irregularities to harmonic regularities, significant activity in the posterior IFG has been repeatedly observed in previous fMRI studies (Bianco et al., 2016; Perani et al., 2010; Seger et al., 2013), which did not take into consideration the resolution of harmonic irregularities. On the other hand, we found that the DLPFC and anterior IFG preferentially responded to chromatic music, in which a majority of chromatically altered chords were resolved in a global tonal context.

Table 2

Activation clusters for the contrasts between chromatic music and atonal sequence.

Volume information	Peak location			t-value	Cluster (voxel)
	X	Y	Z		
<i>Chromatic music > Atonal sequence</i>					
Medial frontal gyrus (pre-supplementary motor area), dorsal anterior cingulate cortex	-4	12	52	5.74	688
Anterior insula, inferior frontal gyrus	34	22	0	5.69	284
	-32	20	0	5.34	215
Cerebellar lobule IV-V	18	-52	-22	5.56	63
Inferior frontal gyrus, middle frontal gyrus	52	30	26	5.18	858
	-42	42	-2	5.17	170
	-40	20	26	3.76	127
Postcentral gyrus	-36	-26	54	4.66	291
Caudate nucleus	16	14	0	4.53	136
Precuneus	10	-68	50	4.42	96
Intraparietal sulcus	-32	-52	34	4.12	148
Cerebellar lobule Crus I	-8	-76	-26	4.04	66
Middle frontal gyrus (dorsal premotor cortex)	-26	-4	70	4.04	52
<i>Atonal sequence > Chromatic music</i>					
Precentral/postcentral gyrus, dorsal anterior cingulate cortex, medial frontal cortex, precuneus, posterior cingulate cortex	36	-22	54	8.43	5197
Medial superior frontal gyrus, anterior cingulate cortex, middle frontal gyrus	-4	54	26	7.06	5228
Amygdala, parahippocampal gyrus	22	-2	-18	6.13	498
	-18	-2	-24	6.03	332
Angular gyrus, middle temporal gyrus, supramarginal gyrus	-58	-58	26	5.90	1574
Cerebellar lobule IV-VI	-20	-50	-26	5.63	506
Inferior temporal gyrus, temporal pole	-42	4	-38	5.61	1234
	42	-6	-34	5.30	230
Middle temporal gyrus	48	-32	-8	5.22	50
Posterior insula, supramarginal gyrus, middle temporal gyrus	46	-16	18	5.18	1476
Medial frontal gyrus	-14	6	70	4.74	121
Middle temporal gyrus	66	-18	-14	4.63	206
Rolandic operculum	58	4	6	4.50	72
Olfactory gyrus	4	8	-8	4.36	52
Middle temporal gyrus	-66	-42	6	4.29	132
Inferior temporal gyrus	36	24	-20	4.17	61

During the task of judging key stability, activity in participants' DLPFC and posterior parietal cortices (left IPS and precuneus) for chromatic music was more pronounced than for diatonic music and atonal sequences. Co-activation of these regions has been reported in neuroimaging studies of working memory (Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Crottaz-Herbette, Anagnoson, & Menon, 2004; Diwadkar, Carpenter, & Just, 2000; Veltman, Rombouts, & Dolan, 2003). Posterior parietal cortices may be in charge of representations and manipulations of verbal, numerical, and visuo-spatial working memory (Andin, Fransson, Ronnberg, & Rudner, 2015; Lamp, Alexander, Laycock, Crewther, & Crewther, 2016; Zago et al., 2008). IPS activity tends to increase along with the amount and complexity of working memory (Pammi, Miyapuram, AhmedSamejima, Bapi, & Doya, 2012; Todd & Marois, 2004; Xu & Chun, 2006). In the present study, the left IPS might support the representations of important harmonic progressions of the tonic key and temporary foreign keys in service of predictive processing of chromatic music. Simultaneous maintenance of harmonic progressions of these keys could place heavy demands on working memory resources. This is in contrast to the facts that the predictive processing of diatonic music is associated with the maintenance of harmonic progressions in a single key, and that no predictive model of tonality is available for atonal sequences.

A recent fMRI study of rhythm perception provides novel insight into the neural mechanisms underlying predictive processing of music.

Table 3

Activation clusters for the contrasts between diatonic music and atonal sequence.

Volume information	Peak location			t-value	Cluster (voxel)
	X	Y	Z		
<i>Diatonic music > Atonal sequence</i>					
Precentral/postcentral gyrus, superior/inferior parietal lobule	-34	-26	54	12.80	4124
	52	8	48	4.81	445
	-52	-20	18	4.81	73
Cerebellar lobule VI, lingular gyrus	18	-52	-22	11.69	1462
	-34	-68	-24	4.60	124
Medial frontal gyrus, superior frontal gyrus, dorsal anterior cingulate cortex	-4	-20	52	6.24	666
Cerebellar lobule VIII	6	-68	-34	6.17	261
Putamen	-32	-16	-4	5.31	330
Rolandic operculum, anterior insula	-42	-4	12	4.92	136
Superior temporal pole	56	6	-10	4.89	74
	-52	8	-8	4.55	60
Anterior insula	40	20	8	4.48	207
Thalamus	-18	-24	6	4.44	104
Superior temporal gyrus	60	-18	-2	4.26	52
Medial superior frontal gyrus	4	26	54	4.13	52
Anterior insula	-36	22	2	3.90	79
<i>Atonal sequence > Diatonic music</i>					
Precentral/postcentral gyrus, middle frontal gyrus, superior/inferior parietal lobule	36	-22	54	13.68	3446
Cerebellar lobule IV-VI	-18	-52	-20	8.04	466
Medial frontal gyrus	8	0	52	6.07	393
Medial superior frontal gyrus	-10	58	28	5.65	741
	14	56	30	3.76	170
Putamen	32	-10	-2	5.50	51
Rolandic operculum	44	-16	18	4.52	82
Inferior temporal gyrus	-42	4	-42	4.42	80
Angular gyrus	-58	-60	26	4.41	155
Inferior parietal lobule	-38	-78	42	4.36	178
Middle temporal pole	-50	12	-32	4.29	88
Precuneus	0	-58	44	3.41	74

Table 4

Activation clusters for the intersection of chromatic music minus diatonic music and chromatic music minus atonal sequence.

Volume information	Center location			Cluster (voxel)
	X	Y	Z	
<i>Chromatic music > Diatonic music ∩ Chromatic music > Atonal sequence</i>				
Medial frontal gyrus (pre-supplementary motor area), dorsal anterior cingulate cortex	0	26	40	161
Intraparietal sulcus	-32	-58	42	105
Precuneus	6	-70	40	95
Middle frontal gyrus (dorsolateral prefrontal cortex), inferior frontal gyrus	42	34	22	95
	-42	22	18	61
Inferior frontal gyrus (rostrolateral prefrontal cortex)	-44	42	0	34

Matthews et al. (2020) found greater activity in the bilateral dorsal IPL or IPS in response to medium complexity rhythms compared to high complexity rhythms. The authors evaluated the role of bilateral IPS in relation to the processing of motor-driven temporal predictions and sensory input (Rauschecker, 2011; Rimmele, Morillon, Poepfel, & Arnal, 2018). This view is reminiscent of the suggestion put forward by Vickery and Jiang (2009) that during uncertain decision-making, the IPS may contribute to the construction of an internal model, which would be continuously updated by the bottom-up information. During exposure to medium complexity rhythms, listeners' model of meter is somewhat uncertain because it is continuously challenged by the bottom-up information of syncopations, and the top-down predictions need to be assessed and updated (Matthews et al., 2020; Vuust et al., 2018). During

Table 5

Activation clusters for the intersection of diatonic music minus chromatic music and atonal sequence minus chromatic music.

Volume information	Center location			Cluster (voxel)
	X	Y	Z	
<i>Diatonic music > Chromatic music ∩ Atonal sequence > Chromatic music</i>				
Medial orbitofrontal gyrus, anterior cingulate cortex	-8	40	-16	482
Mid-anterior cingulate cortex, paracentral lobule	-8	-26	34	239
Superior/middle temporal gyrus, supramarginal gyrus, inferior parietal lobule	62	-58	8	329
	-60	-52	18	163
	54	-14	-18	62
	-60	-12	-20	31
Medial superior frontal gyrus	12	46	30	111
Supramarginal gyrus	58	-32	24	65
Parahippocampal gyrus, amygdala	20	-4	-22	53
	-20	-6	-30	47

exposure to chromatic music (with medium key stability), listeners' model of tonality is also uncertain because it is continuously challenged by out-of-key notes. Our finding that the left IPS preferentially responded to chromatic music provides further evidence for a critical role of the IPS in the processing of precision-weighted prediction error. This finding accords with a previous study that found correlation between ramping activity in the posterior parietal cortex and the precision of sensory prediction errors (FitzGerald, Moran, Friston, & Dolan, 2015).

The preSMA/dACC exhibited greater activity in response to chromatic music compared to diatonic music. This finding substantiates earlier studies on musical syntax showing enhanced activity in the SMA/preSMA during exposure to unexpected harmonic progressions (Seeger et al., 2013), uncertain harmonic progressions (Cheung et al., 2019), and music with low key clarity (Alluri et al., 2012). We extended previous studies to atonal random sequences, reporting greater activity in the preSMA/dACC for chromatic music than for atonal random sequences, in which tonality does not exist. The SMA/preSMA is recognized as a key structure for preparation and initiation of voluntary actions, prediction of the sensory consequences of actions, error/conflict processing, and sequence processing (Bonini et al., 2014; Cona & Semenza, 2017; Moore, Ruge, Wenke, Rothwell, & Haggard, 2010; Nachev, Wydell, O'Neill, Husain, & Kennard, 2007; Russo et al., 2020). In addition to motor functions, the preSMA is also implicated in comprehension and predictive processing of language and music (Babajani-Feremi, 2017; Dietrich, Hertrich, Seibold, & Rolke, 2019; Siman-Tov et al., 2019). Increased preSMA activity in response to chromatic music, as reported here, might reflect its role in sequence processing of harmony. Evidence has accumulated to indicate that IFG and preSMA may work in tandem to support domain-general processing of hierarchical sequences (Bahlmann, Schubotz, Mueller, Koester, & Friederici, 2009; Cona & Semenza, 2017; Wiener, Turkeltaub, & Coslett, 2010). Moreover, the DLPFC and preSMA/dACC play a major role in cognitive control under conditions of uncertainty (Taren, Venkatraman, & Huettel, 2011; Wu et al., 2019). In a study of visuo-motor sequences, Pammi et al. (2012) suggested that the IPS may be involved in building (encoding) representations of individual chunks, while the preSMA and DLPFC may be involved in concatenating chunks and in the online maintenance of chunks to enable execution. Based on these previous studies and our findings, we propose that during exposure to chromatic music, formation of the representations of short harmonic progressions in the left IPS may be under the guidance of the preSMA and DLPFC/IFG, which contribute to hierarchical sequencing and cognitive control in an uncertain tonal context.

In the present study, the RLPFC is the most rostral area that preferentially responded to chromatic music. This region has been found to be active when there is conflict between simultaneous stimuli, representations, or response tendencies. Novick et al. (2005) posited that the left RLPFC supports general cognitive control mechanisms for the detection

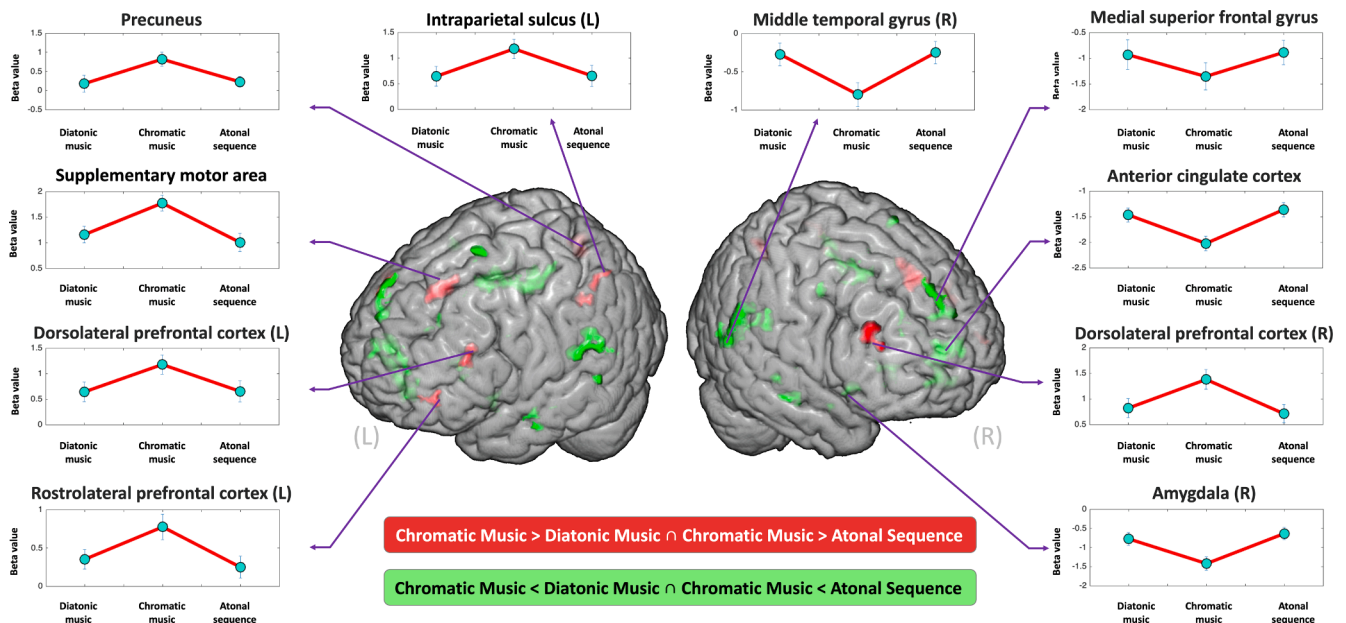


Fig. 4. Activation maps of intersections of chromatic music versus diatonic music and chromatic music versus atonal sequences. Error bars represent standard errors. The threshold was set at FDR-corrected $p < 0.05$ with a minimum cluster size of 50 voxels.

and resolution of incompatible linguistic items and representations, implementing reanalysis in the face of misinterpretation. In support of this idea, previous studies observed that the left RLPFC displayed significantly increased activation for ambiguous versus unambiguous sentences (Vitello, Warren, Devlin, & Rodd, 2014) and for ambiguous versus unambiguous words (Grindrod, Garnett, Maljutina, & den Ouden, 2014). It is interesting to note that the RLPFC is engaged in processing musical ambiguity as well. Polyrhythms in music, which create tension or conflict between a counter pulse and the main pulse, have been found to activate the RLPFC (Vuust, Roepstorff, Wallentin, Mouridsen, & Ostergaard, 2006; Vuust, Wallentin, Mouridsen, Ostergaard, & Roepstorff, 2011). The RLPFC also showed greater activity in response to diatonic than unresolved chromatically altered chords (Bianco et al., 2016). Here we report that when comparing chromatic music to diatonic music, significant activation was found in the RLPFC. A chromatically altered chord not only challenges the predictive model of tonality and elevates musical tension, its resolution by the ensuing harmonic progression may lead to a reinterpretation of this chord. For example, the chromatic altered chord in Fig. 1 could be recognized as the dominant chord of A minor, giving rise to a feeling that the key is moving from F major to A minor. However, the ensuing harmonic progression makes the listener to reinterpret this chromatic altered chord as a secondary dominant chord of the invariant key of F major. We propose that during exposure to chromatic music, the RLPFC may mediate conflict resolution of remotely related harmonic elements, updating the semantic representations of chromatically altered chords in a broad, superordinate context of the tonic key. This view is in accordance with Raposo et al. (2012), who suggested that during the processing of superordinate concepts, the left RLPFC may exert extra semantic control for coordinating information that is less shared by other members of the category level, compared to basic level concepts.

We demonstrated that activity in the DLPFC/IFG, RLPFC, and preSMA/dACC preferentially responded to chromatic music with medium key stability. One framework that may be helpful in considering their roles is the model of hierarchical cognitive control recently addressed by Badre and Nee (2018). Based on the previous view of a functional gradient along the anterior-posterior axis of the lateral frontal cortex (Badre, 2008; D'Esposito & Postle, 2015), Badre and Nee (2018) distinguished three zones in the lateral frontal areas. The most rostral zone of RLPFC is implicated in schematic control, which is based on

superordinate or model-based knowledge encoded in schemas. This schematic-control zone tends to be active when participants track hypothetical strategies, goals, and pending states. The mid-lateral zone encompassing DLPFC is implicated in contextual control, which is based on internally maintained context representation. The most caudal zone of motor/premotor cortices is implicated in sensory-motor control of effector movements. Akin to the lateral frontal cortices, the dorsomedial prefrontal cortex can also be fractioned into subdivisions, with progressively rostral areas computing progressively abstract signals (Badre & Nee, 2018). We propose that during exposure to chromatic music, the RLPFC may be recruited to integrate remotely related harmonic elements for tracking the hypothetical goal of an invariant tonic key, while the DLPFC/IFG and preSMA/dACC may work in concert to process resolutions of chromatic altered chords under a continuously changing tonal context. In light of a hierarchical error representation model (Alexander & Brown, 2015), error signals generated by the preSMA/dACC may be used to modulate prediction error representations in the DLPFC/IFG, and the representations of important harmonic progressions in relevant keys may serve to contextualize subsequent error calculations and predictions carried out by the preSMA/dACC.

Our findings provide a new angle to explore the parallel relationship between language and music. In an fMRI study of sentence-level semantic integration, the left IPS, precuneus, bilateral DLPFC/IFG, and preSMA/dACC showed a monotonic increase in activity as a function of semantic integration load, which was parametrically manipulated with high cloze probability, low cloze probability, and semantically violated sentences (Zhu et al., 2013). In present study, the stimuli of diatonic music may be characterized by high cloze probability, whereas the stimuli of chromatic music may be characterized by low cloze probability and semantic violation. We observed greater activity in the bilateral IPS, precuneus, bilateral DLPFC/IFG, and preSMA/dACC for chromatic than for diatonic music. Moreover, Lee and Newman (2010) reported that the bilateral IPS, precuneus, bilateral IFG, and preSMA were significantly more active during comprehension of sentences containing object-relative clauses compared to simple active sentences. Considering similar activation patterns across these three studies, we suggest that future investigations should elucidate the relations between the processing of chromatic music, sentence-level semantic processing, and relative clause processing.

With regard to emotional effects of music, we observed significantly

increased activity in the amygdala in response to diatonic music and atonal sequences compared to chromatic music. This result might reflect that diatonic music and atonal sequences elicited emotion in a relatively straightforward manner, while emotional responses to chromatic music were subtle and elusive. Perhaps future research could obtain a more detailed picture of affective effects of various chromatically altered chords.

5. Conclusions

The results of the current study have indicated that several frontal and posterior parietal regions in experienced music listeners respond preferentially to chromatic music, which is characterized by remotely related harmonic elements and medium degrees of key stability. We have provided preliminary evidence that there is an inverted U-shaped relationship between the key stability of music and activity in these frontoparietal regions, which are recently implicated in predictive coding processes (Siman-Tov et al., 2019). Our finding also supports the proposal that cognitive control is involved in processing tonal ambiguity (Slevc & Okada, 2015) and expands upon previous studies on the predictive processing of musical rhythms (Matthews et al., 2020; Vuust et al., 2018; Vuust & Witek, 2014; Witek et al., 2014). Predictive processing of chromatic music relies on the hierarchy of keys and representations of important harmonic progressions in several keys. Domain-general cognitive control implemented in the frontoparietal regions is necessary for working memory processes, hierarchical sequencing, and conflict resolution of remotely related harmonic elements during exposure to chromatic music, and this frontoparietal network is sensitive to precision-weighted prediction error. Given the diverse evidence of associations between music training and cognitive abilities (Dumont, Syurina, Feron, & van Hooren, 2017; Jaschke, Eggermont, Honing, & Scherder, 2013; Silvia, Thomas, Nusbaum, Beaty, & Hodges, 2016), we think it would be interesting for future research to evaluate whether listening skills with chromatic music have beneficial effects on cognitive functioning.

Funding

This research was supported by the grant from the Ministry of Science and Technology, Taiwan (grant number: MOST 108-2410-H-002-216). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

CRedit authorship contribution statement

Chia-Wei Li: Software, Data curation, Visualization, Writing - original draft, Formal analysis. **Fong-Yi Guo:** Software, Investigation, Data curation, Formal analysis. **Chen-Gia Tsai:** Conceptualization, Methodology, Investigation, Supervision, Project administration, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors have declared that no competing interests exist.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandc.2021.105751>.

References

- Agawu, V. K. (1986). Mahler's tonal strategies: A study of the song-cycles. *Journal of Musicological Research*, 6(1–2), 1–47.
- Agres, K., Abdallah, S., & Pearce, M. (2018). Information-theoretic properties of auditory sequences dynamically influence expectation and memory. *Cognitive Science*, 42(1), 43–76.

- Alexander, W. H., & Brown, J. W. (2015). Hierarchical error representation: A computational model of anterior cingulate and dorsolateral prefrontal cortex. *Neural Comput*, 27(11), 2354–2410.
- Alluri, V., Toivainen, P., Jaaskelainen, I. P., Gleason, E., Sams, M., & Brattico, E. (2012). Large-scale brain networks emerge from dynamic processing of musical timbre, key and rhythm. *Neuroimage*, 59(4), 3677–3689.
- Andin, J., Fransson, P., Ronnberg, J., & Rudner, M. (2015). Phonology and arithmetic in the language-calculation network. *Brain Lang*, 143, 97–105.
- Babajani-Feremi, A. (2017). Neural mechanism underlying comprehension of narrative speech and its heritability: Study in a large population. *Brain Topogr*, 30(5), 592–609.
- Badre, D. (2008). Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends Cogn Sci*, 12(5), 193–200.
- Badre, D., & Nee, D. E. (2018). Frontal cortex and the hierarchical control of behavior. *Trends Cogn Sci*, 22(2), 170–188.
- Bahlmann, J., Schubotz, R. L., Mueller, J. L., Koester, D., & Friederici, A. D. (2009). Neural circuits of hierarchical visuo-spatial sequence processing. *Brain Res*, 1298, 161–170.
- Baker, J. M. (1990). The limits of tonality in the late music of Franz Liszt. *Journal of Music Theory*, 34(2), 145–173.
- Bass, R. (1988). Prokofiev's technique of chromatic displacement. *Music Analysis*, 7(2), 197–214.
- Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., & Friston, K. J. (2012). Canonical microcircuits for predictive coding. *Neuron*, 76(4), 695–711.
- Bianco, R., Novembre, G., Keller, P. E., Kim, S. G., Scharf, F., Friederici, A. D., et al. (2016). Neural networks for harmonic structure in music perception and action. *Neuroimage*, 142, 454–464.
- Bonini, F., Burle, B., Liegeois-Chauvel, C., Regis, J., Chauvel, P., & Vidal, F. (2014). Action monitoring and medial frontal cortex: Leading role of supplementary motor area. *Science*, 343(6173), 888–891.
- Bribitzer-Stull, M. (2006). The Aflat-C-E complex: The origin and function of chromatic major third collections in nineteenth-century music. *Music Theory Spectrum*, 28(2), 167–190.
- Buhler, J. (2000). Star Wars, music, and myth. In J. Buhler, C. Flinn, & D. Neumeier (Eds.), *Music and Cinema* (pp. 33–57). Hanover, NH: Wesleyan University Press.
- Bunge, S. A., Ochsner, K. N., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (2001). Prefrontal regions involved in keeping information in and out of mind. *Brain*, 124(Pt 10), 2074–2086.
- Cheung, V. K. M., Harrison, P. M. C., Meyer, L., Pearce, M. T., Haynes, J. D., & Koelsch, S. (2019). Uncertainty and surprise jointly predict musical pleasure and amygdala, hippocampus, and auditory cortex activity. *Curr Biol*, 29(23), 4084–4092 e4084.
- Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav Brain Sci*, 36(3), 181–204.
- Cona, G., & Semenza, C. (2017). Supplementary motor area as key structure for domain-general sequence processing: A unified account. *Neurosci Biobehav Rev*, 72, 28–42.
- Crottaz-Herbette, S., Anagnoson, R. T., & Menon, V. (2004). Modality effects in verbal working memory: Differential prefrontal and parietal responses to auditory and visual stimuli. *Neuroimage*, 21(1), 340–351.
- D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annu Rev Psychol*, 66, 115–142.
- Dietrich, S., Hertrich, I., Seibold, V. C., & Rolke, B. (2019). Discourse management during speech perception: A functional magnetic resonance imaging, fMRI study. *Neuroimage*, 202, Article 116047.
- Diwadkar, V. A., Carpenter, P. A., & Just, M. A. (2000). Collaborative activity between parietal and dorso-lateral prefrontal cortex in dynamic spatial working memory revealed by fMRI. *Neuroimage*, 12(1), 85–99.
- Dumont, E., Syurina, E. V., Feron, F. J. M., & van Hooren, S. (2017). Music interventions and child development: A critical review and further directions. *Front Psychol*, 8, 1694.
- Eerola, T., & Toivainen, P. (2004). *MIDI toolbox: MATLAB tools for music research*. Finland: University of Jyväskylä.
- FitzGerald, T. H. B., Moran, R. J., Friston, K. J., & Dolan, R. J. (2015). Precision and dynamical dynamics in the human posterior parietal cortex during evidence accumulation. *Neuroimage*, 107, 219–228.
- Friston, K. (2010). The free-energy principle: A unified brain theory? *Nat Rev Neurosci*, 11(2), 127–138.
- Friston, K. (2012). Prediction, perception and agency. *Int J Psychophysiol*, 83(2), 248–252.
- Gold, B. P., Pearce, M. T., Mas-Herrero, E., Dagher, A., & Zatorre, R. J. (2019). Predictability and uncertainty in the pleasure of music: A reward for learning? *J Neurosci*, 39(47), 9397–9409.
- Grindrod, C. M., Garnett, E. O., Malyutina, S., & den Ouden, D. B. (2014). Effects of representational distance between meanings on the neural correlates of semantic ambiguity. *Brain Lang*, 139, 23–35.
- Heine, E. (2018). Chromatic mediant and narrative context in film. *Music Analysis*, 37(1), 103–132.
- Huron, D. B. (2006). *Sweet anticipation music and the psychology of expectation*. Cambridge, MA: MIT Press.
- Jaschke, A. C., Eggermont, L. H., Honing, H., & Scherder, E. J. (2013). Music education and its effect on intellectual abilities in children: A systematic review. *Rev Neurosci*, 24(6), 665–675.
- Koelsch, S., Jentschke, S., Sammler, D., & Mietschen, D. (2007). Untangling syntactic and sensory processing: An ERP study of music perception. *Psychophysiology*, 44(3), 476–490.

- Koelsch, S., Rohrmeier, M., Torrecuso, R., & Jentschke, S. (2013). Processing of hierarchical syntactic structure in music. *Proc Natl Acad Sci U S A*, 110(38), 15443–15448.
- Koelsch, S., Vuust, P., & Friston, K. (2019). Predictive processes and the peculiar case of music. *Trends Cogn Sci*, 23(1), 63–77.
- Krumhansl, C. L. (1990). *Cognitive foundations of musical pitch*. New York: Oxford University Press.
- Krumhansl, C. L., & Kessler, E. J. (1982). Tracing the dynamic changes in perceived tonal organization in a spatial representation of musical keys. *Psychol Rev*, 89(4), 334–368.
- Lamp, G., Alexander, B., Laycock, R., Crewther, D. P., & Crewther, S. G. (2016). Mapping of the underlying neural mechanisms of maintenance and manipulation in visuo-spatial working memory using an n-back mental rotation task: A functional magnetic resonance imaging study. *Front Behav Neurosci*, 10, 87.
- Lee, D., & Newman, S. D. (2010). The effect of presentation paradigm on syntactic processing: An event-related fMRI study. *Hum Brain Mapp*, 31(1), 65–79.
- Lumaca, M., Trusbak Haumann, N., Brattico, E., Grube, M., & Vuust, P. (2019). Weighting of neural prediction error by rhythmic complexity: A predictive coding account using mismatch negativity. *Eur J Neurosci*, 49(12), 1597–1609.
- Lupyan, G., & Clark, A. (2015). Words and the world: Predictive coding and the language-perception-cognition interface. *Current Directions in Psychological Science*, 24(4), 279–284.
- Maess, B., Koelsch, S., Gunter, T. C., & Friederici, A. D. (2001). Musical syntax is processed in Broca's area: An MEG study. *Nat Neurosci*, 4(5), 540–545.
- Mathews, T. E., Witek, M. A. G., Lund, T., Vuust, P., & Penhune, V. B. (2020). The sensation of groove engages motor and reward networks. *Neuroimage*, 214, Article 116768.
- McCreech, P. (1983). Ernst Kurth and the analysis of the chromatic music of the late nineteenth century. *Music Theory Spectrum*, 5, 56–75.
- Moore, J. W., Ruge, D., Wenke, D., Rothwell, J., & Haggard, P. (2010). Disrupting the experience of control in the human brain: Pre-supplementary motor area contributes to the sense of agency. *Proc Biol Sci*, 277(1693), 2503–2509.
- Moss, F. C., Neuwirth, M., Harasim, D., & Rohrmeier, M. (2019). Statistical characteristics of tonal harmony: A corpus study of Beethoven's string quartets. *PLoS One*, 14(6), Article e0217242.
- Nachev, P., Wydell, H., O'Neill, K., Husain, M., & Kennard, C. (2007). The role of the pre-supplementary motor area in the control of action. *Neuroimage*, 36(Suppl 2), T155–T163.
- Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cogn Affect Behav Neurosci*, 5(3), 263–281.
- Omigie, D., Pearce, M., Lehongre, K., Hasboun, D., Navarro, V., Adam, C., et al. (2019). Intracranial recordings and computational modeling of music reveal the time course of prediction error signaling in frontal and temporal cortices. *J Cogn Neurosci*, 31(6), 855–873.
- Pammi, V. S., Miyapuram, K. P., AhmedSamejima, K., Bapi, R. S., & Doya, K. (2012). Changing the structure of complex visuo-motor sequences selectively activates the fronto-parietal network. *Neuroimage*, 59(2), 1180–1189.
- Perani, D., Saccuman, M. C., Scifo, P., Spada, D., Andreolli, G., Rovelli, R., et al. (2010). Functional specializations for music processing in the human newborn brain. *Proc Natl Acad Sci U S A*, 107(10), 4758–4763.
- Piston, W., & DeVoto, M. (1978). *Harmony* (4th edition). New York: W.W. Norton.
- Raposo, A., Mendes, M., & Marques, J. F. (2012). The hierarchical organization of semantic memory: Executive function in the processing of superordinate concepts. *Neuroimage*, 59(2), 1870–1878.
- Rauschecker, J. P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hear Res*, 271(1–2), 16–25.
- Rimmele, J. M., Morillon, B., Poeppel, D., & Arnal, L. H. (2018). Proactive sensing of periodic and aperiodic auditory patterns. *Trends Cogn Sci*, 22(10), 870–882.
- Russo, A. A., Khajeh, R., Bittner, S. R., Perkins, S. M., Cunningham, J. P., Abbott, L. F., et al. (2020). Neural trajectories in the supplementary motor area and motor cortex exhibit distinct geometries, compatible with different classes of computation. *Neuron*, 107(4), 745–758 e746.
- Schaefer, R. S., Overy, K., & Nelson, P. (2013). Affect and non-uniform characteristics of predictive processing in musical behaviour. *Behav Brain Sci*, 36(3), 226–227.
- Seeger, C. A., Spiering, B. J., Sares, A. G., Quraini, S. I., Alpetter, C., David, J., et al. (2013). Corticostriatal contributions to musical expectancy perception. *J Cogn Neurosci*, 25(7), 1062–1077.
- Seth, A. K., & Friston, K. J. (2016). Active interoceptive inference and the emotional brain. *Philos Trans R Soc Lond B Biol Sci*, 371(1708), 20160007.
- Silvia, P. J., Thomas, K. S., Nusbaum, E. C., Beaty, R. E., & Hodges, D. A. (2016). How does music training predict cognitive abilities? A bifactor approach to musical expertise and intelligence. *Psychology of Aesthetics, Creativity, and the Arts*, 10(2), 184–190.
- Siman-Tov, T., Granot, R. Y., Shany, O., Singer, N., Hendler, T., & Gordon, C. R. (2019). Is there a prediction network? Meta-analytic evidence for a cortical-subcortical network likely subserving prediction. *Neurosci Biobehav Rev*, 105, 262–275.
- Slevc, L. R., & Okada, B. M. (2015). Processing structure in language and music: A case for shared reliance on cognitive control. *Psychon Bull Rev*, 22(3), 637–652.
- Somer, A. (1995). Chromatic third-relations and tonal structure in the songs of Debussy. *Music Theory Spectrum*, 17(2), 215–241.
- Steinbeis, N., Koelsch, S., & Sloboda, J. A. (2006). The role of harmonic expectancy violations in musical emotions: Evidence from subjective, physiological, and neural responses. *J Cogn Neurosci*, 18(8), 1380–1393.
- Tamir, D. I., & Thornton, M. A. (2018). Modeling the predictive social mind. *Trends Cogn Sci*, 22(3), 201–212.
- Taren, A. A., Venkatraman, V., & Huettel, S. A. (2011). A parallel functional topography between medial and lateral prefrontal cortex: Evidence and implications for cognitive control. *J Neurosci*, 31(13), 5026–5031.
- Temperley, D. (2001). *The cognition of basic musical structures*. Cambridge, Mass.: MIT Press.
- Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, 428(6984), 751–754.
- Veltman, D. J., Rombouts, S. A., & Dolan, R. J. (2003). Maintenance versus manipulation in verbal working memory revisited: An fMRI study. *Neuroimage*, 18(2), 247–256.
- Vickery, T. J., & Jiang, Y. V. (2009). Inferior parietal lobule supports decision making under uncertainty in humans. *Cereb Cortex*, 19(4), 916–925.
- Vitello, S., Warren, J. E., Devlin, J. T., & Rodd, J. M. (2014). Roles of frontal and temporal regions in reinterpreting semantically ambiguous sentences. *Front Hum Neurosci*, 8, 530.
- Vuust, P., Dietz, M. J., Witek, M., & Kringelbach, M. L. (2018). Now you hear it: A predictive coding model for understanding rhythmic incongruity. *Ann N Y Acad Sci*.
- Vuust, P., & Kringelbach, M. L. (2010). The pleasure of making sense of music. *Interdisciplinary Sci Rev*, 35(2), 166–182.
- Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predictive coding of music-brain responses to rhythmic incongruity. *Cortex*, 45(1), 80–92.
- Vuust, P., Roepstorff, A., Wallentin, M., Mouridsen, K., & Ostergaard, L. (2006). It don't mean a thing... Keeping the rhythm during polyrhythmic tension, activates language areas, BA47. *Neuroimage*, 31(2), 832–841.
- Vuust, P., Wallentin, M., Mouridsen, K., Ostergaard, L., & Roepstorff, A. (2011). Tapping polyrhythms in music activates language areas. *Neurosci Lett*, 494(3), 211–216.
- Vuust, P., & Witek, M. A. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythm and meter perception in music. *Front Psychol*, 5, 1111.
- Wiener, M., Turkeltaub, P., & Coslett, H. B. (2010). The image of time: A voxel-wise meta-analysis. *Neuroimage*, 49(2), 1728–1740.
- Witek, M. A., Clarke, E. F., Wallentin, M., Kringelbach, M. L., & Vuust, P. (2014). Syncopation, body-movement and pleasure in groove music. *PLoS One*, 9(4), Article e94446.
- Wu, T., Chen, C., Spagna, A., Wu, X., Mackie, M. A., Russell-Giller, S., et al. (2019). The functional anatomy of cognitive control: A domain-general brain network for uncertainty processing. *J Comp Neurol*.
- Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, 440(7080), 91–95.
- Zago, L., Petit, L., Turbelin, M. R., Andersson, F., Vigneau, M., & Tzourio-Mazoyer, N. (2008). How verbal and spatial manipulation networks contribute to calculation: An fMRI study. *Neuropsychologia*, 46(9), 2403–2414.
- Zhu, Z., Feng, G., Zhang, J. X., Li, G., Li, H., & Wang, S. (2013). The role of the left prefrontal cortex in sentence-level semantic integration. *Neuroimage*, 76, 325–331.