Generating New Musical Preferences from Multi-level Mapping of Predictions to Reward

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Abstract

Learning to make predictions is an intrinsically rewarding process for human minds. Yet how we map these learned predictions to liking and pleasure remains unclear, particularly in the case of abstract rewards, such as music. Here we show that musical preference can be generated *de novo* without extrinsic rewards. To test this, we used digital music technology to create novel melodies in the Bohlen-Pierce scale, which is an alternative tuning system different from acoustic principles of any established musical culture. Across eight studies (n = 1005 total) we showed that systematically manipulating predictions for music composed in this new scale affected self-report liking ratings. Participants preferred more frequently-presented items that adhered to rapidly-learned scale structure, suggesting multiple levels of relationships between familiarity and preference. These learning trajectories depended on an individual's music reward sensitivity, and were similar for USA and Chinese participants. Furthermore, fMRI showed that while auditory cortical activation reflects predictions, functional connectivity between auditory and reward areas encodes preference. Collectively, the results provide a cognitive mechanism by which musical sounds become rewarding, through multiple levels of prediction learning process. This mechanism, in turn, may underlie the success of music-based interventions for multiple clinical populations.

Keywords: new music, auditory learning, statistical learning, medial prefrontal cortex, dopamine

Introduction

Why do we love music? In contrast to other pleasures in life, such as food and sex, music has no obvious adaptive value; yet an attraction to music is ubiquitous across cultures and across the lifespan. Indeed, both listening to and performing music ranks highly among life's greatest pleasures [1] and reliably engages the dopaminergic reward system [2-4]. One hypothesis for the allure of music is that it co-opts a ubiquitous feature of the central nervous system that underlies perception, action, and emotion: the continuous learning of reward signals from prediction and prediction error [5-8]. Recent findings have converged on the hypothesis that the rewarding effect of music comes from making successful predictions and minimizing prediction errors, known as the predictive coding of music (PCM) model [9, 10]. Musical predictions can unfold in multiple levels, whether they be structural (melody, tonality), temporal (rhythm, meter), and/or acoustic (pitch, timbre); and these predictions emerge from repeated exposure, which imparts implicit knowledge of statistical properties (frequencies and transitional probabilities) of stimulus sequences commonly encountered within one's own culture [11, 12]. The human ability to recognize and learn transitional probabilities has been posited to underlie language learning [13, 14] and decision-making [15]. This same statistical learning mechanism is also used to learn transitional probabilities in tone sequences [16]. Repeated exposure to sound sequences with predictable statistical probabilities can change preferences for those sound sequences [17], resulting in a classic inverted-u model that relates preference to familiarity [Chmiel & Schubert, 2017]. However, the precise relationships between exposure, prediction and error learning, and to preference has remained unclear, and the relationship between exposure and prediction to activity in the reward system is yet to be quantified. Nor do we know how this relationship varies across cultures, or with individual differences in reward sensitivity to music. Understanding the relationship between predictive coding and the reward system will provide a mechanistic account not only for why people enjoy music, but also the circumstances under which our ability to predict leads to reward, a concept that underlies much of motivated behavior [18].

A fundamental challenge in understanding how predictability inherently relates to learning and reward comes from the fact that most stimuli that we encounter, even for the first time, makes use of overlearned predictions to which we may have been exposed throughout our lives. This is especially the case with musical structures, such as common sets of pitches or musical scales that we have implicitly acquired from lifelong exposure [19]. As a concrete example of such knowledge, most listeners within the Western culture show implicit knowledge of, and preference for, common-practice Western musical scale structures based around the octave, which is a doubling of acoustic frequency [20]. As we become exposed to musical sounds throughout the lifespan, the brain continuously and automatically learns to form predictions for sounds that will likely come next, and the implicit learning of these predictions and minimization of prediction errors forms one's body of knowledge, including of music within the culture.

We circumvent this challenge of overlearned predictions by incorporating a unique and unfamiliar musical system: the Bohlen-Pierce (B-P) scale, which is based on a tripling of acoustic frequency, thus differing acoustically and statistically from the world's existing musical systems [21]. Here we test the multi-level organization of mapping between predictions and reward using naturalistic music composed in grammatical structures defined in the B-P scale [17]. In Study 1-4, we ask the degree to which self-reported liking ratings reflect high-level predictions (through repeated exposure to full pieces) as well as low-level predictions (through alterations to the endings of exposed melodies). In Study 5, we test the effects of musical reward sensitivity, as well as both congenital and acquired music anhedonia, on this mapping between predictions and reward. In Study 6, we test the effects of culture on statistical learning by comparing groups from the US and China. In Study 7, we reversed the presentation of altered and original melodies to ensure that the effects were due to statistical exposure rather than to some surface features of the melodic stimuli. Finally, in Study 8, we evaluate brain activation in the reward system during the process of learning statistical probabilities and preference-formation using fMRI. The stimuli are available on https://osf.io/n84d5/, along with the preregistration for this study.

Results

Analysis Plan

For all studies, participants provided familiarity and liking ratings for melodies composed in a predefined grammatical structure in the B-P scale that were either 1) presented a variable number of times in an exposure phase (*effect of number of presentations*, a manipulation of prediction strength), or 2) altered to have a different ending than the original, grammatical melodies that were presented during exposure (*effect of alterations*, i.e. a prediction error). Familiarity ratings were used as the outcome variable to quantify prediction learning, and liking ratings were used as the outcome variable to quantify reward. To investigate the effects of number of presentations and alterations on these post-exposure familiarity and liking ratings, we constructed linear mixed-effect models using the R package *lme4* [22]. We included melody alteration (original vs. altered) as an interaction term in these models, which was effect-coded such that the main effect of number of presentations represents the average effect across both original and altered melodies, and the interaction term represents the difference between this effect across conditions. This modeling allowed us to separately investigate 1) the effect of prediction strength (main effect of number of presentations), 2) the effect of prediction error (main effect of melody alteration), and 3) the effect of prediction error on the exposure-familiarity/liking trajectory (the interaction between number of presentations and melody alteration). We specified by-participant random slopes (including the interaction term) and intercepts and by-item (melody) random intercepts. Continuous predictor and dependent variables were standardized before being entered into the model. Significance of fixed effects (number of presentations and melody alteration) was determined using the Satterthwaite method to approximate the degrees of freedom with the *lmerTest* package [23].

Study 1

Participants listened to 8 monophonic musical melodies composed in the B-P scale during the exposure phase. The number of presentations varied for each melody (either 2, 4, 8, or 16 times with two melodies in each condition). After exposure, participants made familiarity and liking ratings for each melody, along with two melodies not heard in the exposure phase (thus, presented 0 times during exposure), as well as altered versions of the 10 melodies, which were identical except for an unexpected ending. For familiarity ratings, there was a significant interaction between number of presentations and melody alteration ($\beta = 0.01$, $t(1883) = 3.99$, $p < 0.001$): the effect of number of presentations (main effect: $\beta = 0.33$, $t(171) = 21.23$, $p < 0.001$) was stronger for the original melodies compared to the altered ones. Original melodies were also rated as more familiar than their altered counterparts (main effect: $\beta = 0.16$, $t(1169) = 6.33$, $p < 0.001$). For liking ratings, there was also a significant interaction between number of presentations and melody alteration (β = 0.05, t(1200) = 2.27, p = 0.02): the effect of number of presentations on liking ratings (main effect: β = 0.03, t(1169) = 2.05, p = 0.04) was stronger for original compared to altered melodies. Original melodies were rated as more liked compared to altered melodies (main effect: β = 0.11, t(1793) = 4.94, p < 0.001). Thus, the overall pattern of liking ratings mirrored that of the familiarity ratings, with increased predictability at both levels mapping onto reward as operationalized by liking ratings.

Study 2

In Study 2, we extended the findings from Study 1 to determine the degree to which changing the specific numbers of presentations during the exposure phase affected liking ratings. In a new group of participants, we replicated Study 1 but with melodies that were presented either 0, 2, 4, 6, 10, or 14 times. For familiarity ratings, there was again a significant interaction between number of presentations and melody alteration (β = 0.06, t(3411) = 2.81, p = 0.005): the effect of number of presentations (main effect β = 0.3, t(163) = 15.71, p < 0.001) was stronger for the original melodies. Original melodies were rated as more familiar than altered ones (main effect β = 0.14, t(1545) = 5.87, p < 0.001). For liking ratings, we again found a significant main effect of number of presentations (β = 0.02, t(163) = 2.1, p = 0.04). Original melodies were more liked compared to altered melodies (β = 0.02, t(171) = 2.1, p < 0.001). We did not detect an interaction between melody alteration and number of presentations (β = 0.13, t(3179) = 1.06, p = 0.29). Thus, changing the specific numbers of presentations from Study 1 removed the previously-observed interaction for liking ratings, such that ungrammatical melodies/prediction errors still resulted in a similar-sized mere exposure effect as grammatical/original melodies as number of presentations increased.

Studies 3 and 4

Studies 3 and 4 were designed to replicate the findings from Studies 1 and 2 with a new sample. Study 3 used the same numbers of presentation as Study 1 (0, 2, 4, 8, 16) and Study 4 used the same numbers of presentation as Study 2 (0, 2, 4, 6, 10, 14). For familiarity ratings in Study 3, there was a significant interaction between number of presentations and melody alteration (β = 0.07, t(2305) = 2.79, p = 0.005): again, the effect of number of presentations (main effect β = 0.33, t(168) = 18.81, p < 0.001) was stronger for the original melodies. Original melodies were also rated as more familiar than their altered counterparts (β = 0.14, t(1168) = 5.81, p < 0.001). For liking ratings, we also replicated the main effect of number of presentations (β = 0.06, t(169) = 3.66, p < 0.001). Again, original melodies were preferred over altered melodies (β = 0.07, t(1507) = 3.15, p = 0.002). There was no interaction between melody alteration and number of presentations (β = 0.01, t(1434) = 0.56, p = 0.57). For familiarity ratings in Study 4, we replicated the main effect of number of presentations on familiarity ratings (β = 0.34, t(163) = 19.62, p < 0.001). Again, original melodies were rated as more familiar than altered melodies (β = 0.17, t(1923) = 7.08, p < 0.001). We did not detect a melody alteration X number of presentations interaction (β = 0.04, t(2026) = 1.66, p = 0.1). For liking ratings in Study 4, we replicated the significant effect of number of presentations (β = 0.03, t(162) = 2.14, p = 0.03). Original melodies were once again rated as more liked than altered melodies (β = 0.09, t(3316) = 4.67, p < 0.001). There was no interaction between melody alteration and number of presentations (β = 0.02, t(1801) = 0.87, p = 0.38). Together, these four studies consistently show that main effects of presentation and alteration were robust for both familiarity and liking, but the interaction was much more variable especially for liking. Since Studies 1 through 4 used different samples of participants but the same stimuli with different numbers of presentations, we proceeded to combine the data from these studies for a mini meta-analysis to evaluate the effects of alteration and number of presentations on familiarity and liking across a larger sample.

Mini Meta-Analyses of Studies 1-4

Prediction shows a logarithmic relationship with number of presentations

When considering the shape of the relationship between number of presentations and familiarity, we expected that familiarity ratings would show a logarithmic relationship with number of presentations, (i.e. participants would learn the stimuli after a certain amount of presentations, after which subsequent presentations do not make them more familiar), as opposed to a more linear relationship (i.e. ratings continue to increase with the number of presentations). We compared the fit between logarithmic and linear models for combined data across Studies 1-4 (n = 667). These models had the same random effects structure as previous models. Results from this mini meta-analysis showed both main effects of number of presentations and alterations, as well as significant interactions between alterations and number of presentations, in both linear and logarithmic models. Following the suggestion of Zuur et al. [24], parameters were estimated using maximum likelihood, and Akaike's Information Criteria (AIC) was compared across these models to compare their fit. This revealed that a logarithmic model (AIC = 31575) was a better fit compared to a linear model (AIC = 33986) to model the relationship between number of presentations and familiarity ratings (see Table 1 and Figure 1).

Liking ratings show a quadratic relationship with number of presentations

We used the same approach to best describe the relationship between liking ratings and number of presentations. However, as the trajectory between exposure and liking typically shows an inverse-U relationship (see Chmiel & Schubert, 2017 for a review), we compared model fits of a linear and quadratic model using a Likelihood Ratio test. Both linear and quadratic models showed significant main effects of number of presentations and alterations, as well as significant interactions between the two. The quadratic model was found to best describe the relationship between number of presentations and liking ratings ($\chi^2(13) = 127.03$, $p < 0.001$; see Table 1 and Figure 1).

A) Familiarity Ratings

Model:	**Linear**		**Logarithmic**	
Effect	β	p	β	p
Number of Presentations	0.33	<0.001	0.41	<0.001
Number of Presentations * Alteration (Original > Altered)	0.07	<0.001	0.08	<0.001
Alteration (Orignal > Altered)	0.15	<0.001	0.15	<0.001
R² (Conditional, Marginal):	0.11, 0.49		0.17, 0.58	

B) Liking Ratings

Model:	**Linear**		**Quadratic**	
Effect	β	p	β	p
Number of Presentations	0.04	<0.001	0.05	<0.001
Number of Presentations²			-0.01	0.11
Number of Presentations * Alteration (Original > Altered)	0.03	0.02	0.03	0.01
Number of Presentations² * Alteration (Original > Altered)			-0.01	0.39
Alteration (Original > Altered)	0.1	<0.001	0.11	<0.001
R² (Conditional, Marginal):	0.004, 0.61		0.004, 0.62	

Table 1. *Standardized Beta coefficients, associated p-values, and R^2 values for each model fit for familiarity (A) and liking (B) ratings.*

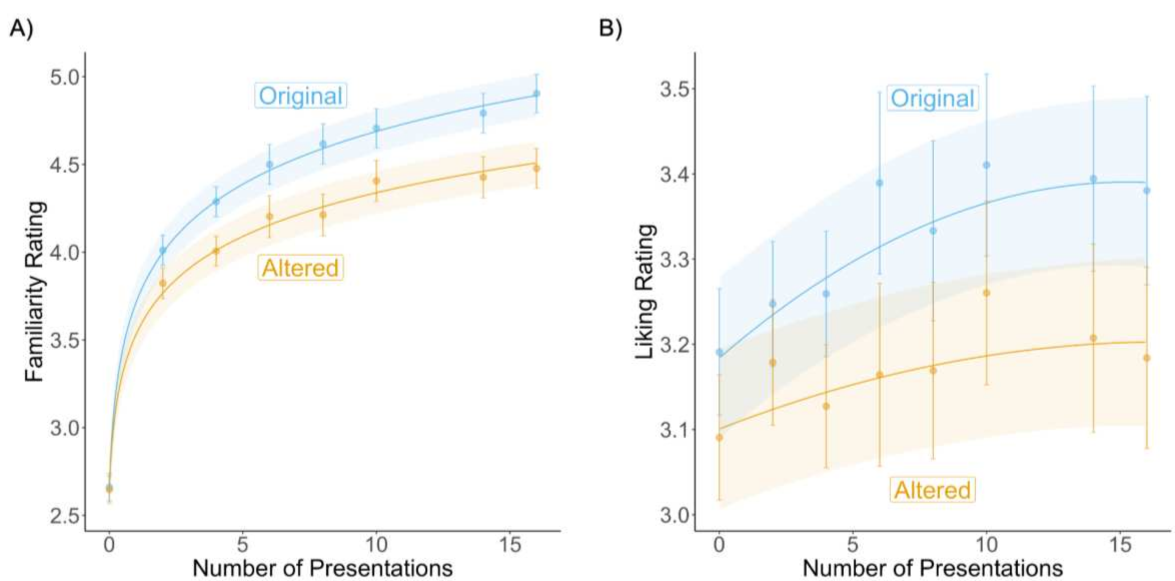

Figure 1. *Best-fit model predictions of familiarity (A) and liking (B) ratings as a function of number of presentations and alteration across Studies 1 to 4. Points and associated error bars indicate mean ratings and 95% confidence intervals.*

Music reward sensitivity influences the learning trajectory

With the aggregated data from 667 participants across Studies 1-4, we then tested the hypothesis that individual differences in music reward sensitivity may be due, in part, to an inability to translate statistically-learned predictions into a reward response. Following past work (Martinez-Molina et al., 2016), we split our sample into tertiles using the Barcelona Music Reward Questionnaire (BMRQ), a measure of music reward sensitivity [25]. These tertiles represent relatively high (hyperhedonics, BMRQ = 86-100), medium (hedonics, BMRQ = 76-85), and low sensitivity (anhedonics, BMRQ = 26-75) to music reward in our sample. To test this hypothesis, we added an interaction term for music reward sensitivity to our best fitting models (logarithmic for familiarity ratings; quadratic for liking ratings). For these analyses, this variable was dummy-coded to treat the hedonic group as the reference level. We interpreted any interaction between number of presentations and music reward sensitivity as evidence that the relationship between familiarity and/or liking ratings and number of presentations differed across groups.

For familiarity ratings, there were no differences in ratings across the three tertiles. Further, there were no significant two-way interactions between music reward sensitivity and number of presentations or alteration, and no significant three-way interaction between music reward sensitivity, number of presentations, and alteration (for all results, see Table 2, Figure 2).

For liking ratings, there was a significant difference across groups: the hedonic group rated melodies as more liked than the anhedonic group ($\beta = 0.17$, $t(663) = 2.36$ $p = 0.02$). There were no significant linear interactions between number of presentations and music reward sensitivity, and there were not any interactions between alteration and music reward sensitivity. There was no significant three-way interaction between music reward sensitivity, number of presentations, and alteration. We did, however, detect an interaction between the quadratic number of presentations term and music reward sensitivity (interaction $\beta = 0.06$, $t(649) = 3.05$, $p = 0.002$): while the anhedonic group showed a significant inverse-U relationship between number of presentations and liking ratings ($\beta = -0.04$, $t(650) = -3.12$ $p = 0.002$), the hedonic group did not ($\beta = 0.02$, $t(649) = 0.24$) (for all results, see Table 2, Figure 2).

A) Familiarity Ratings

Effect	Tertile Contrast	β	p
Music Reward Sensitivity	Hyperhedonic > Hedonic	0.06	0.26
	Hedonic > Anhedonic	0.02	0.66
Music Reward Sensitivity * Number of Presentations	Hyperhedonic > Hedonic	0.01	0.6
	Hedonic > Anhedonic	-0.008	0.75
Music Reward Sensitivity * Alteration (Original > Altered)	Hyperhedonic > Hedonic	0.008	0.78
	Hedonic > Anhedonic	-0.005	0.86
Music Reward Sensitivity * Number of Presentations * Alteration (Original > Altered)	Hyperhedonic > Hedonic	0.03	0.34
	Hedonic > Anhedonic	-0.005	0.85
R^2 (Conditional, Marginal):	0.17, 0.59		

B) Liking Ratings

Effect	Tertile Contrast	β	p
Music Reward Sensitivity	Hyperhedonic > Hedonic	0.06	0.4
	Hedonic > Anhedonic	0.17	0.02
Music Reward Sensitivity * Number of Presentations	Hyperhedonic > Hedonic	0.02	0.47
	Hedonic > Anhedonic	-0.02	0.38
Music Reward Sensitivity * Number of Presentations^2	Hyperhedonic > Hedonic	-0.03	0.14
	Hedonic > Anhedonic	0.06	0.002
Music Reward Sensitivity * Alteration (Original > Altered)	Hyperhedonic > Hedonic	-0.01	0.79
	Hedonic > Anhedonic	0.03	0.37
Music Reward Sensitivity * Number of Presentations * Alteration (Original > Altered)	Hyperhedonic > Hedonic	0.0006	0.99
	Hedonic > Anhedonic	0.02	0.5
Music Reward Sensitivity * Number of Presentations^2 * Alteration (Original > Altered)	Hyperhedonic > Hedonic	0.007	0.81
	Hedonic > Anhedonic	-0.003	0.91
R^2 (Conditional, Marginal):	0.02, 0.62		

Table 2. *Standardized Beta coefficients and associated p-values for the three-way (music reward sensitivity X number of presentations X alteration) interaction models built on (A) familiarity and (B) liking ratings. Only music reward sensitivity terms are shown.*

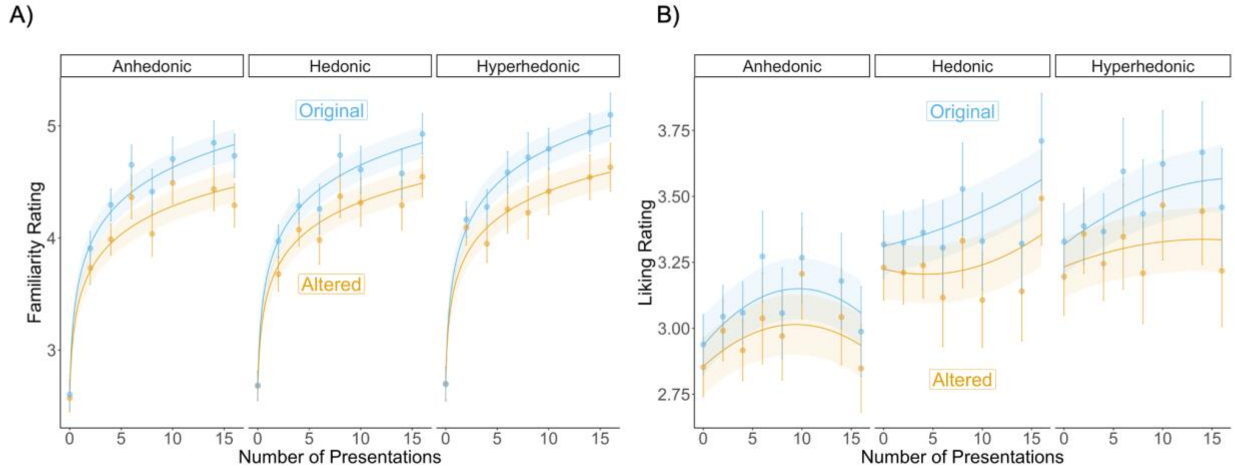

Figure 2. *Model-predicted familiarity (A) and liking (B) ratings as a function of number of presentations, alteration, and music reward sensitivity (tertile split on BMRQ: anhedonic, hedonic, and hyperhedonic groups). Points and associated error bars represent 95% confidence intervals.*

Study 5

Study 5 consisted of two case studies that include participants with congenital and acquired music-specific anhedonia, a condition in which listeners derive no pleasure from listening to music [26]. Both participants underwent a streamlined version of our study paradigm, with melodies presented 0, 4, 10, and 14 times, and only one melody per condition. We calculated the mean squared error (MSE) for liking and familiarity ratings of both the original and altered versions of these melodies using model predictions from the three-way (number of presentations X alteration X music reward sensitivity) interaction models at all three levels of music reward sensitivity. For familiarity ratings, the model prediction at the hyperhedonic level best matched music-specific anhedonics' responses (i.e. the model showed the lowest MSE of 18.13 at the hyperhedonic level), followed by the hedonic (19.95) and anhedonic (20.18) levels. In contrast, for liking ratings, the model had the lowest MSE (3.66) from the anhedonic level when predicting the music-specific anhedonics' data, compared to both the hedonic (4.97) and hyperhedonic (5.01) levels. These case studies provide further support for the idea that both cases of congenital and acquired musical anhedonia had difficulty mapping predictions to reward.

Study 6

Study 6 extends the findings from Studies 1-4 to investigate possible cultural effects on the process of learning musical structure and subsequent reward. To this end, we recruited 156 participants from China to complete the identical procedure as Study 4. For familiarity ratings, there was a significant interaction between number of presentations and melody alteration (β = 0.08, t(1758) = 3.13, p = 0.002): the effect of number of presentations (main effect: β = 0.3, $t(154) = 14.9$, $p < 0.001$) was stronger for original compared to altered melodies.Original melodies were rated as more familiar than altered melodies (main effect β = 0.11, $t(2437) = 4.49$, $p < 0.001$). For liking ratings, we replicated the significant effect of number of presentations (β =

0.06, t(155) = 4, p = 0.001). Again, original melodies were rated as more liked than their altered counterparts (β = 0.12, $t(189) = 5.29$, $p < 0.001$). There was no interaction between melody alteration and number of presentations (β = 0.007, t(971) = 0.32, p = 0.75).

To further test whether familiarity and liking rating trajectories matched that of the US sample, we again fit two classes of models (logarithmic and linear for familiarity ratings; linear and quadratic for liking ratings) to these data. This revealed that, again, a logarithmic model best fit familiarity ratings (linear model AIC = 8958.3; logarithmic model AIC = 8376.9). A likelihood ratio test also indicated that a quadratic model fit to the liking rating data was better fit than a linear model ($\chi^2(13) = 127.03$, $p < 0.001$; see Figure 3).

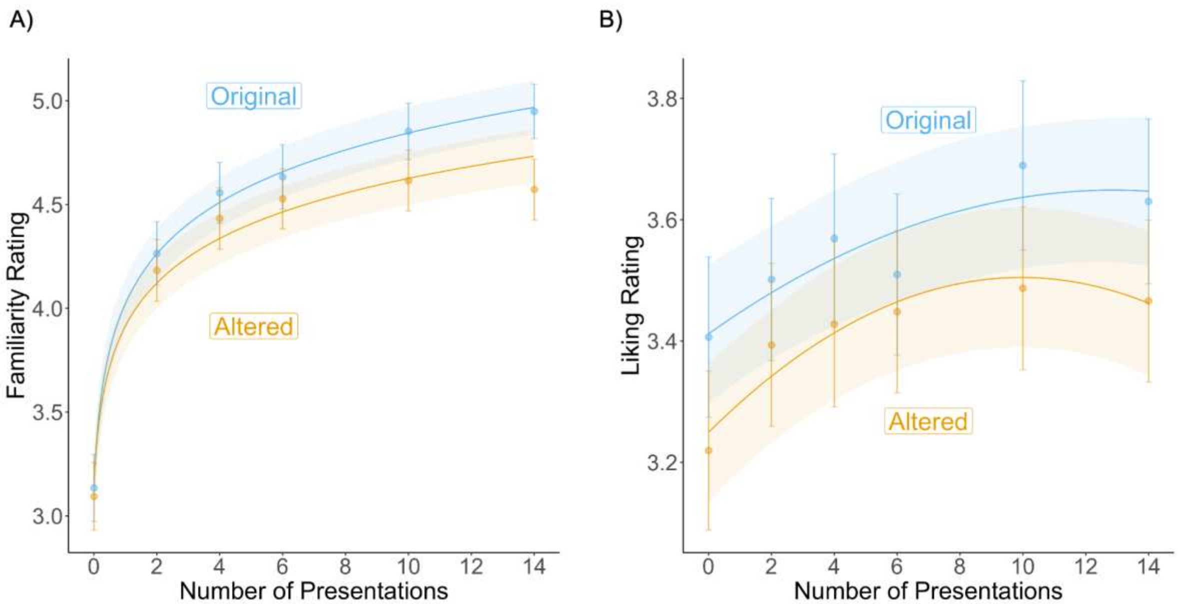

Figure 3. *Cross-cultural replication of the effects of alterations and number of presentations on familiarity and liking ratings. Best fitting model predictions with mean ratings and 95% confidence intervals.*

Study 7

To ensure that our results regarding the effects of alteration were due to statistical exposure to the original melodies and their underlying harmonic or grammatical structure (as opposed to specific features of these melodies), we ran an additional follow-up study in which the altered melodies were presented in the exposure phase (at 0, 2, 4, 8, and 16 times) and the original melodies were presented in the post-exposure rating phase. For familiarity ratings, we replicated the significant effect of number of presentations (β = 0.31, $t(161) = 15.19$, $p < 0.001$), but no main effect of alteration (β = 0.01, $t(2129) = 0.48$, $p = 0.63$) and no interaction between melody alteration and number of presentations (β = -0.04, $t(2786) = -1.77$, $p = 0.08$). For liking ratings, there was again a significant effect of number of presentations (β = 0.03, $t(159) = 2.36$, $p = 0.02$) and altered melodies were preferred over original melodies (β = 0.05, $t(2595) = 2.27$, $p = 0.02$).

We did not detect a melody alteration X number of presentations interaction (β = -0.007, $t(2519)$ = -0.31, p = 0.75). This study suggests that the grammatical structure underlying the original melodies aided with predictions, leading to increased familiarity and liking for grammatical melodies. Repeatedly presenting the ungrammatical, altered melodies led to increased familiarity of those melodies, but not to differential learning of their structure or stronger mapping of those structures to reward.

Study 8

In Study 8, we relate prediction learning to fMRI activity in the reward system. 21 young adults participated in the same study design as in Study 6 outside of the scanner, and then listened to the 8 melodies during fMRI as part of a larger-scale study in the lab looking at effects of music-based interventions in young adults and older adults (Quinci et al, 2022). Whole-brain, univariate analyses showed greater activation for original vs. altered melodies in the right Heschl's gyrus (Figure 4A), suggesting that the auditory cortex is sensitive to the predictions.

The functional connectivity between auditory and reward areas was quantified by correlating the time series of beta-values extracted from Heschl's gyrus (the same ROI as in Figure 4A) and reward-sensitive regions including the nucleus accumbens and the medial prefrontal cortex (see Materials and Methods). A two-way within-subjects ANOVA with the dependent variable of auditory-reward functional connectivity, with the factors of alterations and number of presentations, showed a significant main effect of alteration ($F(1,20) = 5.24$, $p = .033$, $\eta_p^2 = .21$) and a significant main effect of number of presentations ($F(3,60) = 3.31$, $p = .026$, $\eta_p^2 = .14$). Figure 4B shows a linear relationship for original melodies as well as the effect of alteration. The same pattern was not observed for functional connectivity between Heschl's gyrus and the nucleus accumbens (alteration: $F(1,20) = 1.61$, $p = .22$, $\eta_p^2 = .074$; number of presentations: $F(3,60) = .30$, $p = .83$, $\eta_p^2 = .015$.)

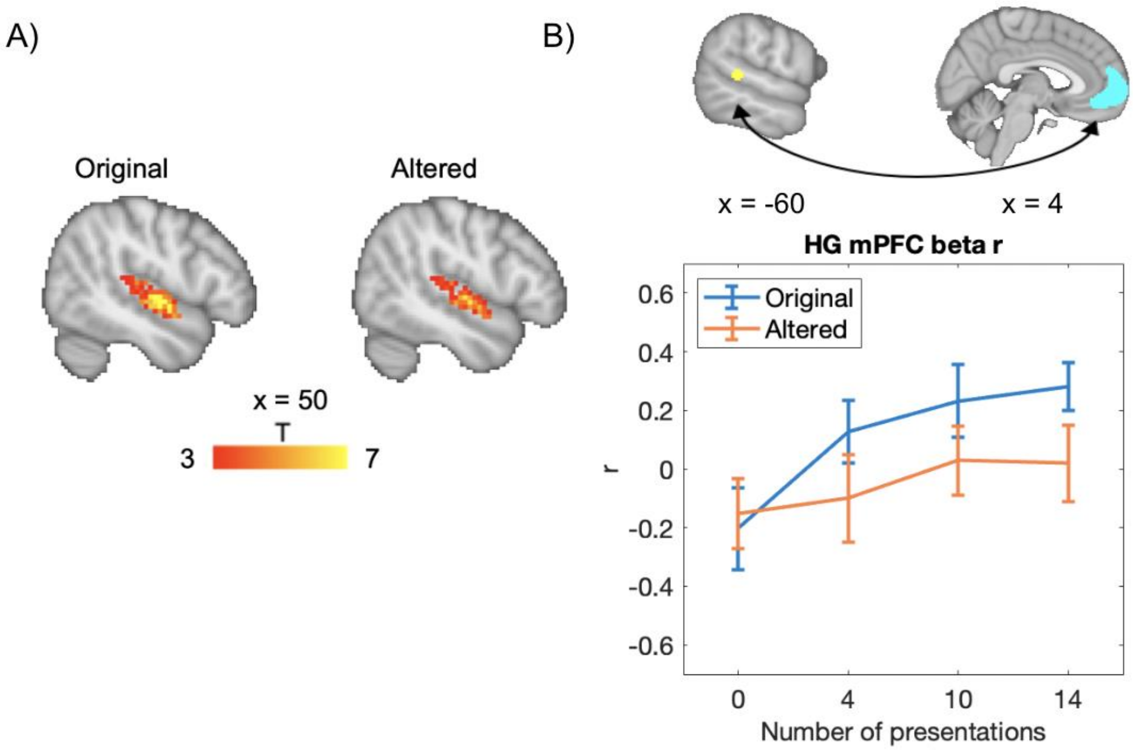

Figure 4. *fMRI results. A) Greater activation for original than for altered melodies in Heschl's gyrus, confirming that auditory regions implement predictions. B) Higher functional connectivity, as quantified by correlations in beta-series, between auditory regions (Heschl's gyrus) and reward regions (mPFC) for original melodies than for altered melodies (B) which increases with number of presentations for original but not for altered melodies.*

Discussion

Across eight studies, we showed that listeners from two different cultures can rapidly learn multiple levels of predictions in novel music, and that this learning subsequently maps onto liking, is conserved across cultures and is related to the reward system of the brain. In Studies 1-4, we established that changing the number of presentations (prediction strength) and altering the endings of melodies (prediction errors) both changed predictions in ways that affected self-report preferences for music. Meta-analysis across Studies 1-4 and neuropsychological results from Study 5 confirmed that individuals with musical anhedonia formed predictions in the same way as controls, but did not derive preferences from predictions in the same way as their more hedonic counterparts. Study 6 established that both Chinese and American participants were affected by prediction strength and prediction errors in this system that was unfamiliar to both cultures. Study 7 showed that reversing the exposure to altered versions reversed the liking ratings for altered and original melodies, but did not change the effect of number of presentations. Finally, Study 8 ties this relationship between prediction and reward to increasing functional connectivity between the auditory and reward system.

Taken together, results provide support for the PCM model, while extending it in three key directions: 1) towards its applicability to prediction and reward in the case of unfamiliar, statistically and probabilistically novel music; 2) towards its relevance in more culturally-independent context via a cross-cultural comparison, and 3) towards its specific disruption in the special case of musical anhedonia.

The PCM model proposes that musical expectations can form from learning statistical regularities and patterns in music (schematic expectations) as well as familiarity with a particular piece of music or genre of music (veridical expectations; [10, 11]). However, the degree to which these two types of expectations influence musical reward has been difficult to assess, given that adult humans are usually overexposed to particular musical genres that follow the same statistical patterns. Here we explicitly test the influence of different types of predictions on musical reward and preference by using novel melodies written in an unfamiliar musical key, and simultaneously manipulating prediction errors and prediction strength. Participants' consistent preference for original over altered melodies and those which were presented more often demonstrate the importance of the confirmation of these expectations following brief exposure. The fact that participants in Study 7 preferred altered melodies heard during the exposure phase (which were grammatically invalid) over their original counterparts in Study 7 suggests the effect of alteration identified in Studies 1-4 and 6 arose not only because these alterations violated our predefined grammatical structure (i.e. schematic expectation violation), but also because they ended differently than the these melodies (i.e. veridical expectation violation). Unlike in the meta-analysis of Studies 1-4 and the cross-cultural replication in Study 6, there was no main effect of melody alteration on familiarity ratings in Study 7, nor was there a melody alteration X number of presentations interaction (as in Studies 1-3 and 6), however there was a main effect of number of presentations. This suggests that when the melodies in the exposure phase adhere to an artificial grammar (as they do in Studies 1-4 and 6), there is an effect of grammatical regularities (i.e. an effect of schematic expectations) in generating musical predictions. Though the evidence of a melody alteration X number of presentations interaction on liking ratings is mixed across Studies 1-4, results from our meta-analysis indicate that a significant interaction does exist, such that the linear effect of number of presentations is stronger for original compared to altered melodies. This provides further evidence that, along with prediction error and strength, the presence of artificial harmonic regularities in novel musical melodies does impact reward.

Furthermore, while the PCM model posits that the brain's ability to make real-time predictions in music depends on prior experience, cultural background, musical competence, and individual traits, the degree to which these factors contribute to musical reward is not yet clear. Our results show that predictive learning of music occurs across cultures when using novel musical stimuli that are unfamiliar to both cultures. Both American and Chinese participants showed the same effect of local and global manipulations on preference ratings, suggesting that the influence of culture on music reward learning may apply in situations in which there are differences in implicit knowledge of familiarized musical structure.

Individual differences in reward sensitivity to music, on the other hand, does seem to be an important factor in the process of linking predictive coding with musical reward, in that participants who experience less pleasure from music in general did not continue to like pieces after more presentations. While familiarity ratings were not affected by individual differences in music reward sensitivity, liking ratings were strongly affected, suggesting that the musical anhedonics' differential exposure-liking trajectory was not due to an inability to form predictions, but rather to a difference in mapping predictions to reward. The fact that musical anhedonics still preferred original over altered melodies, despite not showing effects of number of presentations, suggests that the pleasure they derive listening to music is sensitive to prediction errors, but not to prediction strength. As an additional follow-up to the individual differences approach, we also found evidence that musical sophistication (as assessed by the Goldsmith Musical Sophistication Index [34]) impacted the trajectory of post-exposure liking ratings (see Supplemental Materials). Further research, possibly an fMRI study with a large population of musical anhedonics, will be needed to isolate the key mechanism by which the mapping between predictive coding and reward is altered in individuals with musical anhedonia.

Importantly, our study is the first to show that forming predictions of novel music de novo is associated with changes in the reward circuitry of the brain. Electrocortical (EEG and ECoG) recordings have demonstrated that cortical signal in the middle Heschl's gyrus is sensitive to melodic expectations [27], and fMRI studies have found that auditory and reward-related areas of the brain (including the amygdala, hippocampus, and ventral striatum) show increased activation during musical prediction errors [9] as well as during unexpected and/or unpredictable chord sequences [28]. However, as previous studies used familiar musical stimuli rooted in the Western musical tradition with exclusively Western participants, it was not possible to determine when in the process of statistical and reward learning the auditory and reward systems of the brain become engaged. Here, we observed that predictions emerge specifically in the middle Heschl's gyrus, which showed sensitivity to melodic alterations, thus extending previous EEG/ECoG results. Furthermore, increased functional connectivity between the Heschl's gyrus and mPFC was observed when listening to pieces that were presented more frequently, suggesting that the influence of repeated exposure on liking is subserved by changes in communication between the auditory and reward network.

Several outstanding questions stem from these studies that warrant future exploration. First, it remains to be seen whether preference ratings would continue to increase with more than 16 exposures. It is quite possible that the positive relationships found between presentation and liking is reflective of the positive side of a quadratic function, and that if we were to extend the number of repetitions in this paradigm, we would see preference ratings begin to decrease at an inflection point. Given that we chose to optimize for longer, more dynamic pieces of music, it was not feasible to increase the number of presentations beyond 16 without altering other key aspects of the design, introducing fatigue or habituation, or otherwise increasing cognitive demand in ways that would confound the study. Future studies with shorter stimuli may be able to assess the full extent of the relationship between liking and repetition in B-P stimuli and the degree to which relative frequencies (14 relative to 10 vs 14 relative to 2) play a part.

Second, while the current fMRI study shows sensitivity to prediction in the reward system, it is not sufficiently powered to assess possible individual differences in neurobiology between musical anhedonics and hedonics. Previous neuroimaging studies that included participants with musical anhedonia have shown reduced structural and functional connectivity between auditory cortex, reward and emotion-processing areas of the brain in musical anhedonics [29, 30] and that alterations of fronto-striatal pathways can lead to either increases or decreases in subjective liking ratings of music [31]. Future neuroimaging studies are needed in this special population, and also across cultures, to establish the role of this auditory-subcortical-prefrontal network in the mapping between musical prediction and reward.

In sum, we developed an innovative paradigm to assess prediction-reward learning of music de novo across cultures and in special populations. Our results are the first to show the multiple levels by which predictions and prediction errors in music generate reward, and provide strong evidence for this learning process across cultures. Individuals with musical anhedonia did not show the same pattern of reward learning, offering a testable mechanism by which the human brain learns to predict sounds from our environment and to map those predictions onto reward. As the relationship between predictions and reward underlie much of motivated behavior [7, 8, 18], examining the emergence of this relationship during the course of a study may provide a better understanding of how these foundational neurocognitive systems may go awry in a variety of psychiatric and neurological diseases.

Materials and Methods

Stimuli

The stimuli used in all studies were composed in the Bohlen-Pierce Scale. While most musical systems around the world are based around the octave, which is a 2:1 ratio in frequency, the B-P scale is based on a 3:1 ratio (*tritave* rather than octave) that is divided into 13 logarithmically even steps. This 13-tone scale can be used to generate musical intervals and chords which have low-integer ratios and are perceived as psychoacoustically consonant (Mathews, 1988). While music in B-P scale is known to some composers, performers, conductors and scholars, it is considered “non-standard music” (Hajdu, 2015) and has not been adopted into any mainstream musical culture to date. Monophonic melodies were composed in the B-P scale by a musician and research assistant in the lab (E.Z.) in the digital audio workstation Ableton Live on a Korg nanoPAD2 USB MIDI and played on a MIDI clarinet instrument from the plugin library Xpand!2 by Air Music Tech. The clarinet was chosen because its timbre has higher energy at odd harmonics than at even harmonics; this spectral distribution is easier to learn due to its congruence with the B-P scale [21]. In total, 14 20s Bohlen-Pierce melodies were composed that followed the same artificially-derived harmonic structure from past studies [17]. Light compression and reverb were applied to all stimuli to bring them to the same volume, and were subsequently exported as 44.1kHz .mp3 files. To generate melodies that contained an error in local prediction, an altered version of each melody was also created, which was identical to the original piece except for the ending, which was changed to violate the musical structure of the B-P scale. Specifically, violations consisted of deviations from the chordal tones of the last chord [17, 32, 33], such that they disrupt the harmonic structure of the established melody. The original and altered melodies are available online at https://osf.io/n84d5/. In all studies, the altered melodies were presented only once, during the post-exposure phase. Finally, two of the melodies were used only as part of the perceptual cover task (during the exposure phase). A vibrato effect was added to a single note in these two melodies and during the task, participants were asked to press a key whenever they heard the vibrato note. To decrease expectations, we created six versions of each, where the location of this vibrato note varied across each version.

Study 1

Participants

A priori power analysis using pilot data (n = 46) indicated that a sample size of 165 would achieve 0.80 power to detect a medium effect size (Cohen's $f = 0.27$) of the effect of the number of presentations on liking ratings at a significance level of 0.05. Participants were Prolific workers in the United States between the ages of 18-65. We recruited 234 participants for Study 1, of which 66 participants were excluded for failing our perceptual cover task (see Procedure below), resulting in a final sample size of N = 169 (104 female; mean age = 32.03).

To measure individual differences in music reward sensitivity and identify musical anhedonics, participants completed the BMRQ, a 20-item questionnaire based on five factors: musical seeking, emotion evocation, mood regulation, sensory-motor, and social reward. Participants also completed the Goldsmith Musical Sophistication Index (Gold-MSI), a self-report measure of musical skills and behaviors [34], the Revised Physical Anhedonia Scale (PAS), a self-report measure of general anhedonia [35], and the Ten-Item Personality Inventory (TIPI), a brief measure of the Big-Five personality traits [36]. All scales were scored in accordance with the original publication.

Procedure

After consenting, participants were screened using an online headphone check [37] to ensure that they were using headphones and could hear our stimuli properly before undergoing the three phases of our study. In phase 1 (pre-exposure), participants listened to 8 of the B-P melodies, one at a time, and provided liking ratings, using a Likert-scale ranging from 1('strongly dislike') to 6 ('strongly like') and familiarity ratings, from 1 ('not familiar at all') to 6 ('very familiar') for each melody. As the pre-exposure ratings are intended for a different analysis on the effects of novelty rather than reward learning, they will be presented in a separate report; here we focus on post-exposure ratings.

In phase 2 (exposure), the 8 melodies heard in phase 1 were played for participants a varying number of times (either 2, 4, 8 or 16 with two melodies in each condition). The specific melodies in each of the 4 exposure conditions was counterbalanced across participants. Furthermore, the presentation order was pseudorandomized so that no melody was heard consecutively. During this phase, participants were asked to complete a perceptual cover task, in which they were instructed to listen for notes that contained a "warble" sound (vibrato) and to press the "v" key on their keyboard as soon as they heard one. Six of the trials (created from two different B-P melodies) heard in the exposure phase contained vibrato notes, with the vibrato occurring at different points of the melody. In total, participants heard 66, 20s melodies during phase 2, resulting in an exposure phase that lasted 22 minutes.

During phase 3, participants heard each of the 8 melodies again (without vibrato), along with 2 new melodies that they had not heard in phase 1 or 2 (0 presentation condition) as well as the altered versions (different endings) of these ten melodies. Participants provided liking and familiarity ratings for each of these 20 trials, using the same scale as in phase 1.

After completing phase 3, participants were redirected to an online survey where they provided demographic information and completed individual difference measures including the BMRQ and PAS.

Exclusion criteria

Participants who did not accurately perform the surface task of identifying the warble/vibrato notes during exposure were removed from all subsequent analyses. Specifically, for each participant, we calculated d-prime from the total number of hits (number of vibrato melodies for which a 'v' was pressed), misses (number of vibrato melodies for which a 'v' was not pressed), false alarms (number of vibrato melodies for which a 'v' was not pressed) and correct rejections (number of non-vibrato melodies for which a 'v' was not pressed). D-prime was calculated from the difference between z-transformed hit and false-alarm rates, with the adjustment where 0.5 errors were assumed for participants who made no errors [38]. The d-prime measure therefore indicates how well participants could discriminate between a warble note and a non-warble note and was used to remove participants who did not follow instructions for the surface task. Any participant who had a d-prime measure of less than 1 was removed from subsequent analyses [38], as was specified in our pre-registration. However, in follow-up analyses we did explore whether keeping the participants who did not reach the d-prime criterion changed the results; these exploratory analyses are included in Supplementary Materials.

Study 2

Participants

To maintain consistency, we used the same target sample size from our a priori power analysis for Study 1 for Studies 2-4. We recruited 221 participants. 57 participants were excluded for failing a perceptual cover task, resulting in a total sample size of 164 (93 female, mean age = 32.67).

Procedure

Participants underwent the same procedure as in Study 1, with the exception that 10 melodies were presented either 0, 2, 4, 6, 10, or 14 times during the exposure phase (2 melodies in each condition).

Study 3

Participants

We recruited 214 participants, 45 of whom were excluded for failing our perceptual cover task, resulting in a total sample size of 169 (89 female; mean age = 32.27).

Procedure

Participants underwent the exact same procedure as in Study 1, with the exception that the order of melodies heard in the pre-exposure phase was completely randomized.

Study 4

Participants

We recruited 222 participants, 57 of whom were excluded for failing our perceptual cover task, resulting in a total sample size of 165 (83 female; mean age: 31.78).

Procedure

Participants underwent the exact same procedure as in Study 2, with the same 10 melodies during exposure phase, with the exception that the order of melodies heard in the pre-exposure phase were randomized and counterbalanced across participants.

Study 5

Participants

The congenital music specific anhedonic (initials BW, 58-year-old male) had participated in a previous case study in our lab [30]. The acquired music specific anhedonic (initials NA, 53-year-old female) had reached out to the final author after self-reporting a loss in pleasure derived from music listening after having received rTMS treatment for depression after the death of a loved one. As both of these cases were self-identified as musically anhedonic, rather than recruited online using Prolific, they were treated as separate case studies rather than included in the same group for Studies 1 through 4. Both of these cases had low scores on the extended BMRQ (eBMRQ BW = 30; NA = 43; [39] but normal PAS scores (PAS-auditory: BW = 8, NA = 4; PAS-non-auditory: BW = 14, NA = 15).

Stimuli

We used a subset of four non-altered melodies which were rated, on average, the highest in post-exposure liking ratings across Studies 1-4 for Study 5. These, along with their altered versions, resulted in eight unique melodies presented to participants in this study. Participants also completed an updated version of the BMRQ: the extended Barcelona Music Reward Questionnaire (eBMRQ), which includes an additional sixth factor consisting of 4 additional items which measures experiences of absorption in music listening [39].

Procedure

Participants underwent the same procedure as previous studies, with the exception that melodies were presented either 0, 4, 10, or 14 times during the exposure phase and that there was only one melody assigned to each condition.

Study 6

Participants

Participants were recruited via WeChat, a Chinese instant messaging app. A poster containing a QR code was sent in several group messages of students of Beijing Normal University, who subsequently shared this code via word of mouth and personal WeChat messages. We recruited 216 participants. 56 were excluded for failing our perceptual cover task and 4 for completing the task twice, for a total of 156 (106 female; mean age: 23.09).

Stimuli

The same stimuli used in Studies 2 and 4 were used in Study 6. Participants in Study 6 also completed the eBMRQ instead of the BMRQ.

Procedure

The QR code led to a questionnaire that recorded participants' name and email address. An email was then sent to the address participants provided, which contained a link to the experiment. This link redirected participants to our experiment, in which they subsequently underwent the same Procedure as Study 3.

Study 7

Participants

We recruited 279 participants, 116 of whom were excluded for failing our perceptual cover task, resulting in a total sample size of 163 (64 female; mean age: 35.46).

Procedure

Participants completed the same procedure as in Study 1, with the exception that altered melodies were presented in the pre-exposure and exposure phase of the study. Along with this, original melodies were only presented in the post-exposure phase.

Stimuli

The same stimuli used in Studies 1 and 3 were used in Study 8. Participants in Study 7 also completed the eBMRQ instead of the BMRQ.

Study 8

Participants

Participants in this study were either undergraduates at Northeastern University who completed the study (both the online task and an in-person fMRI scan) for course credit or young adults recruited via word-of-mouth from the Boston area. A total of 21 participants (15 female, mean age = 19.8) completed the fMRI version of our task.

Stimuli

The same stimuli and materials that were used in Study 6 were used in Study 7, including the eBMRQ.

Procedure

Participants underwent the same procedure as in Study 6 as well as an fMRI scan immediately after completing the online behavioral study. During the scan, participants listened to 24 clips of music once. Eight of the clips were Bohlen-Pierce melodies that participants had heard previously during the task (at 0/4/10/14 presentations; both original and altered melodies). The remaining trials acquired were not in the Bohlen-Pierce scale and were not used in the analysis for the present study. Each trial consisted of 20s of passive listening, followed by 2s to rate the melody for liking (on a scale of 1-4), and 2s to rate the melody for familiarity (also 1-4 scale).

fMRI Data Acquisition

Images were acquired using a Siemens Magnetom 3T MR scanner with a 64-channel head coil at Northeastern University Biomedical Imaging Center. fMRI data were acquired as echo-planar imaging (EPI) functional volumes covering the whole brain in 48 axial slices (fast TR = 475 ms, TE = 30 ms, flip angle = 60°, FOV = 240mm, voxel size = 3 x 3 x 3 mm^3, slice thickness = 3 mm, anterior to posterior, z volume = 14.4 mm) in a continuous acquisition protocol of 1440 volumes for a total acquisition time of 11.4 minutes. T1 images were also acquired using a MPRAGE sequence, with one T1 image acquired every 2400 ms, for approximately 7 minutes. Sagittal slices (0.8 mm thick, anterior to posterior) were acquired covering the whole brain (TR = 2400 ms, TE = 2.55 ms, flip angle = 8°, FOV= 256, voxel size = 0.8 x 0.8 x 0.8 mm^3). As part of the existing protocol we also acquired resting state and DTI sequences, but these were not used for this study.

fMRI Data Analysis

Pre-processing. fMRI data were preprocessed using the Statistical Parametric Mapping 12 (SPM12) software [40] with the CONN Toolbox [41]. Preprocessing steps included functional

realignment and unwarping, functional centering, slice time correction, outlier detection using the artifact detection tool, functional and structural segmentation and normalization to MNI template, and functional smoothing to an 8mm gaussian kernel [42]. Denoising steps for fMRI data included white matter and cerebrospinal fluid confound correction [43], and bandpass filtering to 0.008– 0.09 Hz.
First-level analysis. First- and second-level analyses were completed in SPM12. For each participant, data were converted from 4D to 3D images, resulting in 1440 scans. The model was specified using the following criteria: interscan interval = 0.475 seconds, microtime resolution = 16, microtime onset = 8, duration = 42. Only data from the time while the participant was listening to the musical excerpt were included in this model. Each of the 8 trial types (0/4/10/14 presentations of both original and altered melodies) was modeled separately, and trials during which participants were listening to non-BP melodies were included as a separate, condition so as to be regressed out of the model's intercept. The resulting first-level contrasts were then analyzed using a one-sample t-test across all participants at the second level. Whole-brain results were rendered to a standard MNI brain. Results from the second-level analyses were statistically corrected using a voxel threshold of $p < 0.05$ (FDR-corrected) through CONN Toolbox. Beta-weights for ROIs in the Heschl's gyrus (HG) and medial prefrontal cortex (mPFC) were extracted from participants' first-level SPM.mat files using the CONN Toolbox atlas and correlated separately for each trial to test for the effects of alteration and number of presentations on the functional connectivity between auditory and reward-sensitive regions.

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