Generating New Musical Preferences from Hierarchical Mapping of Predictions to Reward

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Abstract
Prediction learning is considered a fundamental feature of biological systems that underlies perception, action, and reward. For cultural artifacts like music, isolating the genesis of reward from prediction is challenging, since predictions are acquired implicitly throughout life. Here, we examined the trajectory of listeners' preferences for melodies in a novel musical scale, where local and global predictions were independently manipulated. Across seven studies (n = 842 total) in two cultures, participants preferred melodies that were presented more during exposure (globally predictable) and that followed schematic expectations (locally predictable). Learning trajectories depended on music reward sensitivity. Furthermore, fMRI showed that while auditory cortical activation reflects predictions, functional connectivity between auditory and reward areas encodes preference. The results are the first to show a hierarchical, relatively culturally-independent process by which predictions map onto reward. Collectively, our findings propose a novel mechanism by which the human brain links predictions with reward value.

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

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 (Dube & Le Bel, 2003) and reliably engages the dopaminergic reward system (Ferreri et al., 2019; Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011; Salimpoor et al., 2013). One hypothesis for the allure of music is that it coopts 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 (Clark, 2013; Engel, Fries, & Singer, 2001; Friston, 2010; Schultz, 2000). 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 Gold, Pearce, Mas-Herrero, Dagher, and Zatorre (2019); (Vuust, Heggli, Friston, & Kringelbach, 2022). Musical predictions can be structural (melody, tonality), temporal (rhythm, meter), and/or acoustic (pitch, timbre), and 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 (Huron, 2006; Margulis, 2014). The human ability to recognize and learn transitional probabilities has been posited to underlie language learning (Saffran, Aslin, & Newport, 1996) and decision-making (Haruno et al., 2004). This same statistical learning mechanism is also used to learn transitional probabilities in tone sequences (Saffran, Johnson, Aslin, & Newport, 1999). While repeated exposure to sound sequences with predictable statistical probabilities can change preferences for those sound sequences (Loui, Wessel, & Hudson Kam, 2010), we do not know the trajectory by statistical learning of predictions and minimizing prediction error relates to preference, or to activity in the reward system. Nor do we know how this relationship varies across culture, 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 (Schultz, 2015).

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 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. We circumvent this challenge by incorporating a unique and unfamiliar musical system: the Bohlen-Pierce (B-P) scale, which differs acoustically and statistically from the world's existing musical systems (Loui, 2022). Here, we test the hierarchical organization of mapping between predictions and reward using naturalistic music composed in the B-P scale. 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. Finally, in Study 7, we evaluate brain activation in the reward system during the process of learning statistically probabilities and preference-formation using fMRI.

Results

For all studies, participants provided familiarity and liking ratings for melodies in the B-P scale that were either 1) presented a variable number of times in an exposure phase (*effect of number of presentations*, i.e. global, veridical, high-level manipulation), or 2) altered to have a different ending than the original melodies that were presented during exposure (*effect of alterations*, i.e. a local, schematic, moment-by-moment, low-level manipulation, which generates a prediction error that varies by the number of presentations). 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 effect of number of presentations on these post-exposure familiarity and liking ratings, we constructed linear mixed-effect models using the R package *lme4* (Bates, Mächler, Bolker, & Walker, 2015) with an interaction term to account for the effect of alterations. We specified random intercepts for each participant and counterbalanced melody assigned to each condition. Significance of fixed effects (number of presentations and melody alteration, both treated as categorical variables) was determined by an analysis of variance (ANOVA) using the Satterthwaite method to approximate the degrees of freedom with the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017). The stimuli are made available on https://osf.io/n84d5/, along with the preregistration for this study.

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, we found significant main effects of number of presentations ($F(4, 3164.4) = 341.64$, $p < 0.001$, $\eta_p^2 = 0.3$) and alterations ($F(1, 3164.4) = 46.17$, $p < 0.001$, $\eta_p^2 = 0.01$): participants were more familiar with original, non-altered melodies, as well as those which were presented more within the exposure phase. The effect of number of presentations was stronger for the non-altered melodies than for the altered one, as supported by an ordinal interaction between the two factors ($F(4, 3164.4) = 6.03$, $p < 0.001$, $\eta_p^2 = 0.008$). For liking ratings, we found significant main effects for both number of presentations ($F(4, 3158.3) = 3.45$, $p = 0.008$, $\eta_p^2 = 0.004$), and alterations ($F(1, 3158.3) = 19.40$, $p < 0.001$, $\eta_p^2 = 0.007$): participants preferred both non-altered melodies and those which were presented more during the exposure phase. The interaction between the number of presentations and melody manipulation was marginal ($F(4, 3158.2) = 2.17$, $p = 0.07$, $\eta_p^2 = 0.003$).

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. As expected, we found significant main effects of number of presentations ($F(5, 3740.1) = 3215.45$, $p < 0.001$, $\eta_p^2 = 0.22$) and alterations ($F(1, 3740) = 36.49$, $p < 0.001$, $\eta_p^2 = 0.01$) on familiarity ratings, indicating that participants were more familiar with unaltered melodies and those that were presented more during the exposure phase. The interaction between the number of presentations and alterations was also significant ($F(5, 3740) = 2.57$, $p < 0.001$, $\eta_p^2 = 0.003$). For liking ratings, we again found significant main effects for both number of presentations ($F(5, 3718.1) = 3.05$, $p = 0.009$, $\eta_p^2 = 0.004$) and alterations ($F(1, 3158.3) = 39.21$, $p < 0.001$, $\eta_p^2 = 0.01$), such that participants preferred both non-altered melodies and those which were presented more during exposure. We did not detect an interaction effect ($F(5, 3718.1) = 1.45$, $p = 0.2$, $\eta_p^2 = 0.002$).

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). In Study 3, we replicated the significant main effects on familiarity ratings of number of presentations ($F(4, 3180.2) = 323.83$, $p < 0.001$, $\eta_p^2 = 0.29$) and alterations ($F(1, 3180) = 37.31$, $p < 0.001$, $\eta_p^2 = 0.01$), as well as the interaction between the two ($F(4, 3180) = 2.95$, $p = 0.02$, $\eta_p^2 = 0.004$). Similarly, for liking ratings, we replicated main effects of number of presentations ($F(4, 3164.4) = 9.16$, $p < 0.001$, $\eta_p^2 = 0.01$), and alterations, ($F(1, 3164.1) = 9.7$, $p = 0.002$, $\eta_p^2 = 0.003$). Again, we did not detect an interaction ($F(4, 3164.4) = 0.7$, $p = 0.59$, $\eta_p^2 = 0.001$).

In Study 4, we replicated the significant main effects on familiarity ratings of number of presentations ($F(5, 3754.2) = 274.49$, $p < 0.001$, $\eta_p^2 = 0.29$) and alteration ($F(1, 3754.1) = 54.03$, $p < 0.001$, $\eta_p^2 = 0.01$), but not the interaction between the two ($F(5, 3754.1) = 1.43$, $p = 0.2$, $\eta_p^2 = 0.002$). For liking ratings, we again replicated the effect of number of presentations ($F(5, 3729.1) = 2.62$, $p = 0.02$, $\eta_p^2 = 0.004$), and alterations ($F(1, 3729.1) = 20.58$, $p < 0.001$, $\eta_p^2 = 0.005$).The interaction between number of presentations and melody alteration was not significant ($F(5, 3729.1) = 0.46$, $p = 0.81$, $\eta_p^2 = 0.001$).

Meta Analyses of Studies 1-4

<u>Prediction shows a logarithmic relationship with liking and familiarity</u>

To determine the magnitude of the effect of prediction on liking and familiarity ratings, we collapsed data across Studies 1-4 and treated the number of presentations as a continuous variable, using the same linear mixed-effects models as above. We specifically tested three classes of models: whether liking and familiarity ratings continued to increase with the number of presentations (linear relationship), increased to a maximum and then decreased (quadratic relationship), or increased rapidly with lower numbers of presentations and then leveled off (logarithmic relationship). To this end, we compared fits of models with quadratic and logarithmic transformations of number of presentations as the predictor variable to that with no transformation (a linear model). Each model was constructed using an effect coding contrast. Following the suggestion of Zuur, Ieno, Walker, Saveliev, and Smith (2009), parameters were estimated using maximum likelihood, and Akaike's Information Criteria (AIC) was computed and compared across different models. As shown in Table 1, logarithmic models resulted in the best fit for both familiarity and liking ratings (see Figure 1).

A) Familiarity Ratings

	Linear		Logarithmic		Quadratic	
Effect	β	p	β	p	β	p
Number of Presentations	0.33	< 0.001	1.15	< 0.001	0.48	< 0.001
Alteration	0.15	< 0.001	-0.11	0.411	0.19	0.164
Number of Presentations * Alteration	0.07	< 0.001	0.23	< 0.001	0.09	< 0.001
Number of Presentations (Quadratic term)					-0.23	< 0.001
Number of Presentaitons (Quadratic) * Alteration					-0.04	0.006
AIC	49331		**47943**		48210	

B) Liking Ratings

	Linear		Logarithmic		Quadratic	
Effect	β	p	β	p	β	p
Number of Presentations	0.04	< 0.001	0.13	< 0.001	0.05	< 0.001
Alteration	0.1	< 0.001	0.006	0.006	0.11	0.004
Number of Presentations * Alteration	0.03	0.02	0.09	0.018	0.03	0.15
Number of Presentations (Quadratic term)					-0.01	0.056
Number of Presentaitons (Quadratic) * Alteration					-0.001	0.43
AIC	40140		**40137**		40140	

Table 1. Standardized Beta coefficients, associated p-values, and AIC for each model fit for familiarity (a) and liking (b) ratings. AIC for the best-fitting models are shown in bold.

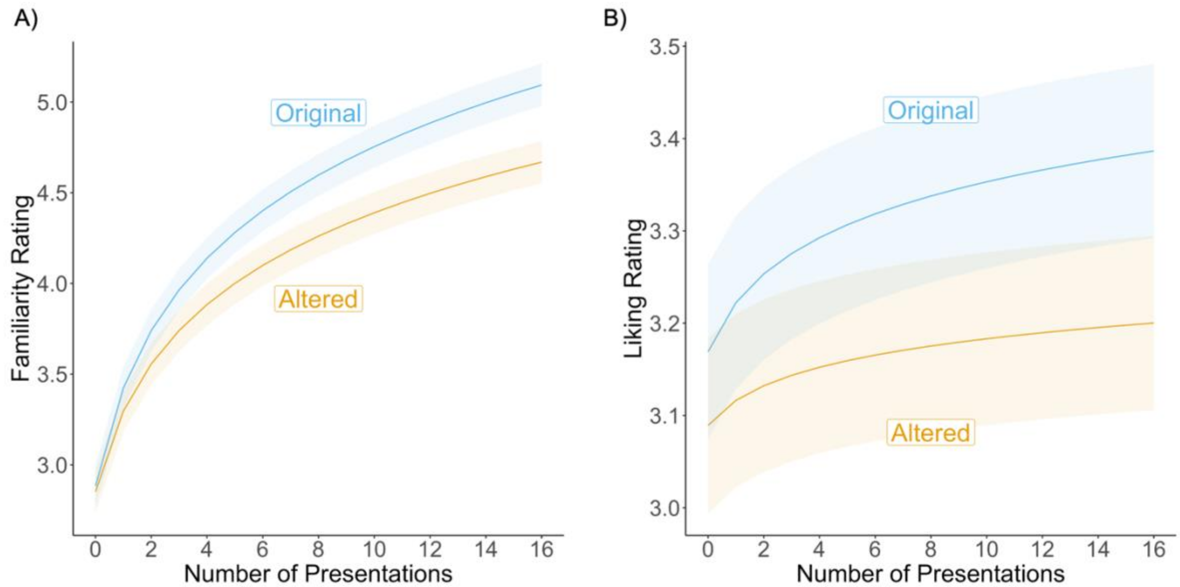

Figure 1. Meta-analysis of Studies 1 to 4, showing effects of alterations and number of presentations on familiarity and liking ratings.

<u>Music reward sensitivity influences the learning trajectory</u>

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. Using the Barcelona Music Reward Questionnaire (BMRQ), a measure of music reward sensitivity (Mas-Herrero, Marco-Pallares, Lorenzo-Seva, Zatorre, & Rodriguez-Fornells, 2013), we divided our sample from Studies 1-4 into tertiles representing high (hyperhedonics, BMRQ = 86-100), medium (hedonics, BMRQ = 76-85), and low sensitivity (anhedonics, BMRQ = 26-75) to music reward. As in Studies 1-4, we ran the same linear mixed-effects model (treating number of presentations as a categorical variable) with an additional interaction term for music-reward sensitivity and tested for significance of fixed effects with an ANOVA. For familiarity ratings, this revealed a main effect of number of presentations (F(7, 13934.6) = 719.3, $p < 0.001$, $\eta_p^2 = 0.27$) and alteration (F(1, 13838.3) = 196.12, $p < 0.001$, $\eta_p^2 = 0.01$), but not music-reward sensitivity (F(2, 674.3) = 1.18, $p = 0.31$, $\eta_p^2 = 0.004$). Furthermore, we detected two-way interactions between number of presentations and music-reward sensitivity (F(14, 13959.1) = 2.42, $p = 0.002$, $\eta_p^2 = 0.002$) and number of presentations and alteration (F(7, 13838.2) = 7.12, $p < 0.001$, $\eta_p^2 = 0.004$), but not between music-reward sensitivity and alteration (F(2, 13838.2) = 0.28, $p = 0.76$, $\eta_p^2 = 0.00004$). The three-way interaction between music-reward sensitivity, alteration, and number of presentations was not significant (F(14, 13838.2) = 0.58, $p = 0.88$, $\eta_p^2 = 0.0006$).

For liking ratings, we found main effects for number of presentations (F(7, 13849) = 9.43, $p <$ 0.001, $\eta_p^2 = 0.005$), alteration (F(1, 13770.2) = 94.6, $p < 0.001$, $\eta_p^2 = 0.007$), and music-reward sensitivity (F(1, 3729.1) = 20.58, $p < 0.001$, $\eta_p^2 = 0.02$). Furthermore, there was a significant two-way interaction between number of presentations and music-reward sensitivity (F(14, 13857.3) = 2.23, $p < 0.01$, $\eta_p^2 = 0.002$), though no significant two-way interactions between alteration and music-reward sensitivity ($F(2, 13770.2) = 1.13$, $p = 0.32$, $\eta_p^2 = 0.0002$) nor between number of presentations and alteration ($F(7, 13770.2) = 1.58$, $p = 0.14$, $\eta_p^2 = 0.001$). Again, a three-way interaction between number of presentations, alteration, and music-reward sensitivity was not found ($F(14, 13770.2) = 0.33$, $p = 0.99$, $\eta_p^2 = 0.0003$).

To further probe the detected interaction between music-reward sensitivity and number of presentations on both liking and familiarity ratings, we applied the same approach of fitting a linear, quadratic, and logarithmic model from our first meta-analysis to each tertile separately, while treating number of presentations continuously. For familiarity ratings, a logarithmic model performed best for all three music-reward sensitivity groups (see Table 2). Hyperhedonics had the highest beta value for the logarithmic model, followed by hedonics and anhedonics, respectively. This, combined with the significant two-way interaction between number of presentations and music reward sensitivity, suggests that hyperhedonics were more ready to rate pieces presented fewer times as familiar (see Table 3, Figure 2).

For liking ratings, the best fit model differed across groups: A linear model showed the best fit for predicting liking ratings from the hyperhedonic and hedonic groups, whereas a quadratic model showed the best fit for predicting liking ratings from the anhedonic group (see Figure 2). While hedonics and hyperhedonics's liking ratings increased with more presentations, anhedonics' liking ratings showed an inverse-U curve, decreasing as the number of presentations increased after 10 presentations. Additional model fits for the altered melodies also support the inverse-U curve relationship between number of presentations and liking in the anhedonic group, as shown in the Supplementary Materials (Figure S1).

We additionally found evidence that individual differences in musical exposure and experience influenced the learning trajectory. These results are presented in the Supplementary Materials (Table S1).

A) Familiarity Ratings

	Anhedonic			**Hedonic**			**Hyperhedonic**		
Model	β	p	AIC	β	p	AIC	β	p	AIC
Linear	0.36	< 0.001	8618.8	0.35	< 0.001	8700.4	0.37	< 0.001	7911.4
Logarithmic	1.26	< 0.001	**8324.9**	1.22	< 0.001	**8417**	1.31	< 0.001	**7680.6**
Quadratic	0.53 (linear) -0.26 (quadratic)	< 0.001 < 0.001	8376.1	0.51 -0.25	< 0.001 < 0.001	8466	0.53 -0.24	0.09 0.55	7743.2

B) Liking Ratings

	Anhedonic			**Hedonic**			**Hyperhedonic**		
Model	β	p	AIC	β	p	AIC	β	p	AIC
Linear	0.04	0.005	6895.4	0.06	< 0.001	**7177.3**	0.06	< 0.001	**6798.9**
Logarithmic	0.14	< 0.001	6889.2	0.19	< 0.001	7182.4	0.18	< 0.001	6800.1
Quadratic	0.07 (linear) -0.05 (quadratic)	< 0.001 0.001	**6886.1**	0.05 0.01	0.59 0.41	7178.6	0.06 -0.01	0.09 0.55	6800.5

Table 2. Standardized Beta coefficients, associated p-values, and AIC for each model fit for familiarity (a) and liking (b) ratings across music reward sensitivity. AIC for the best-fitting model for each group is shown in bold.

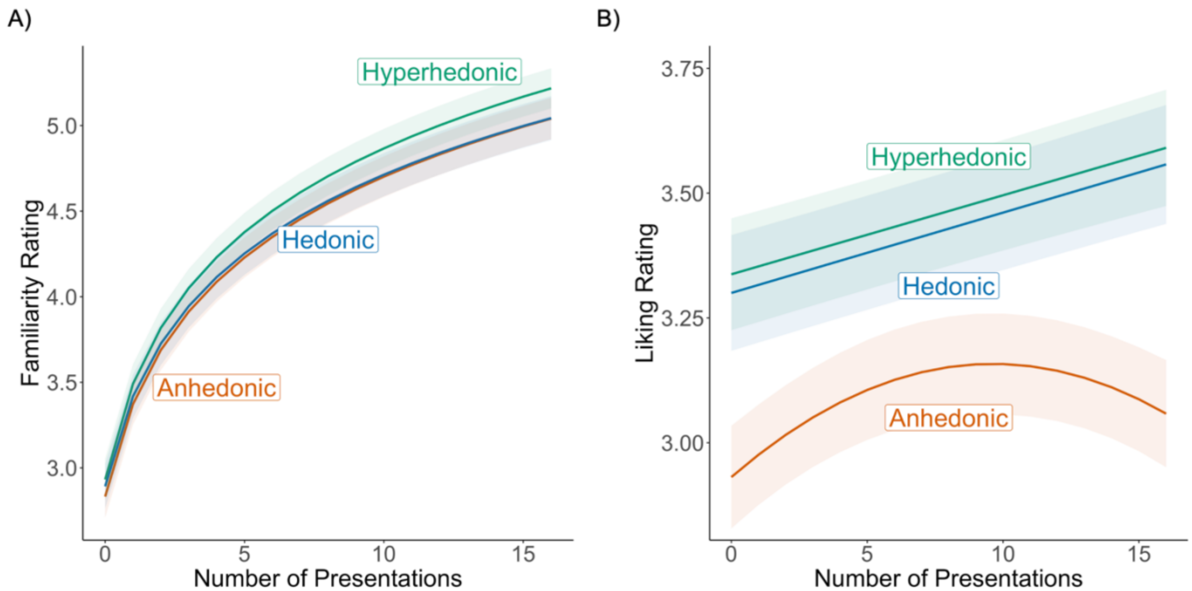

Figure 2. Meta-analysis of Studies 1 to 4 showing best-fit models for the effect of number of presentations on familiarity and liking, separated by music reward (tertile split on BMRQ: hyperhedonic, hedonic, and anhedonic groups).

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 (Mas-Herrero, Zatorre, Rodriguez-Fornells, & Marco-Pallares, 2014). 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 rating of the non-altered melodies using predictions from the best fit models of musical anhedonics, hedonics, and hyperhedonics in Study 4. For familiarity ratings, the hyperhedonics' model best predicted music-specific anhedonics' responses (i.e. the hyperhedonic model showed the lowest MSE of 7.93), followed by the anhedonic (8.66) and hedonic (8.71) models. In contrast, for liking ratings, our anhedonic model had the lowest MSE (2.35) when predicting the music-specific anhedonics' data, compared to both the hedonic (4.05) and hyperhedonic (3.59) models. 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, we detected significant main effects of number of presentations ($F(5, 3558) = 221.17$, $p < 0.001$, $\eta_p^2 = 0.24$) and alteration ($F(1, 3557.9) = 21.33$, $p < 0.001$, $\eta_p^2 = 0.006$), such that original melodies and those heard more during the exposure phase were rated as more familiar by participants. The interaction between the number of presentations and alteration was marginal ($F(5, 3557.9) = 2.2$, $p = 0.05$, $\eta_p^2 = 0.003$). For liking ratings, we replicated the significant main effects for both number of presentations ($F(5, 3540.1) = 8.5$, $p < 0.001$, $\eta_p^2 = 0.01$), and for alterations ($F(1, 3450) = 28.11$, $p < 0.001$, $\eta_p^2 = 0.008$), such that participants preferred both non-altered melodies and those which were presented more during the exposure phase (Figure 3). We did not detect an interaction effect ($F(5, 3540.1) = 0.57$, $p = 0.73$, $\eta_p^2 = 0.001$).

For results showing the influence of music-reward sensitivity on liking and familiarity ratings in the Chinese population, see Supplementary Materials.

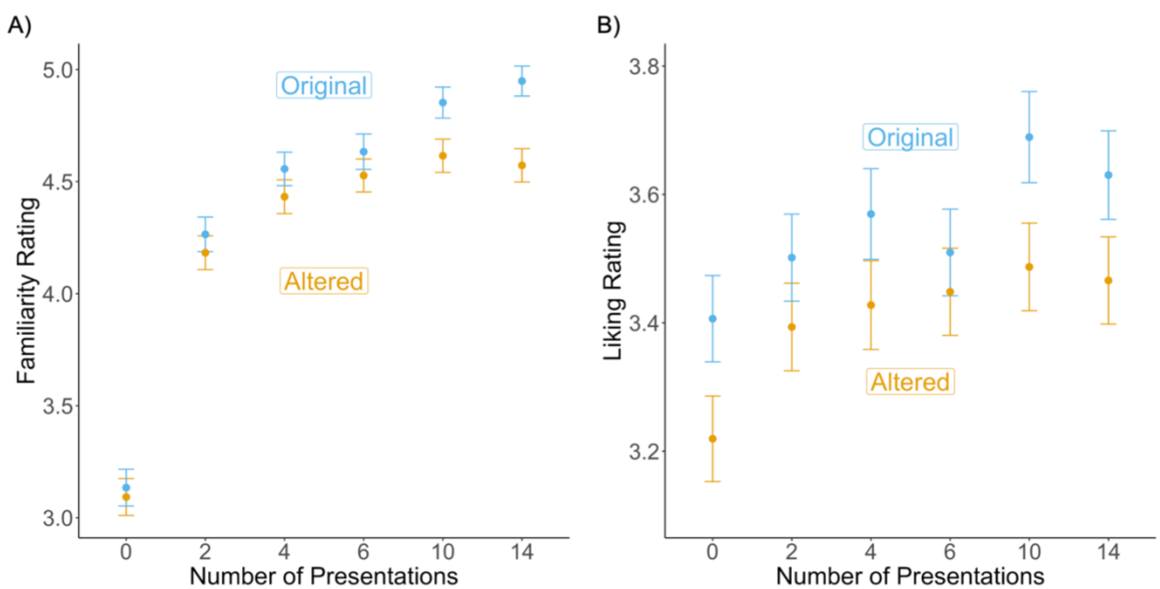

Figure 3. Cross-cultural replication of the effects of alterations and number of presentations on familiarity and liking ratings. Error bars represent +/- 1 Standard Error.

Study 7

In Study 7, we relate prediction learning to activation in the reward system of the brain in an fMRI study. 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. Whole-brain, univariate analyses showed greater activation for original vs. altered melodies in auditory regions, specifically the right Heschl's gyrus. A follow-up within-subjects ANOVA on the dependent variable of beta-values in the Hesch's gyrus confirmed a significant main effect of alteration ($F(1, 18) = 6.0$, $p = 0.025$, $\eta_p^2 = 00.25$, Figure 4A). This suggests 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 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 ($F(1,18) = 10.43$, $p = .005$, $\eta_p^2 = .367$) and a significant main effect of number of presentations ($F(1,18) = 5.275$, $p = .034$, $\eta_p^2 = .227$). Figure 4B shows a linear relationship for original melodies as well as the effect of alteration. For results using the ventral striatum as the seed-region of the reward network, see the Supplementary Materials.

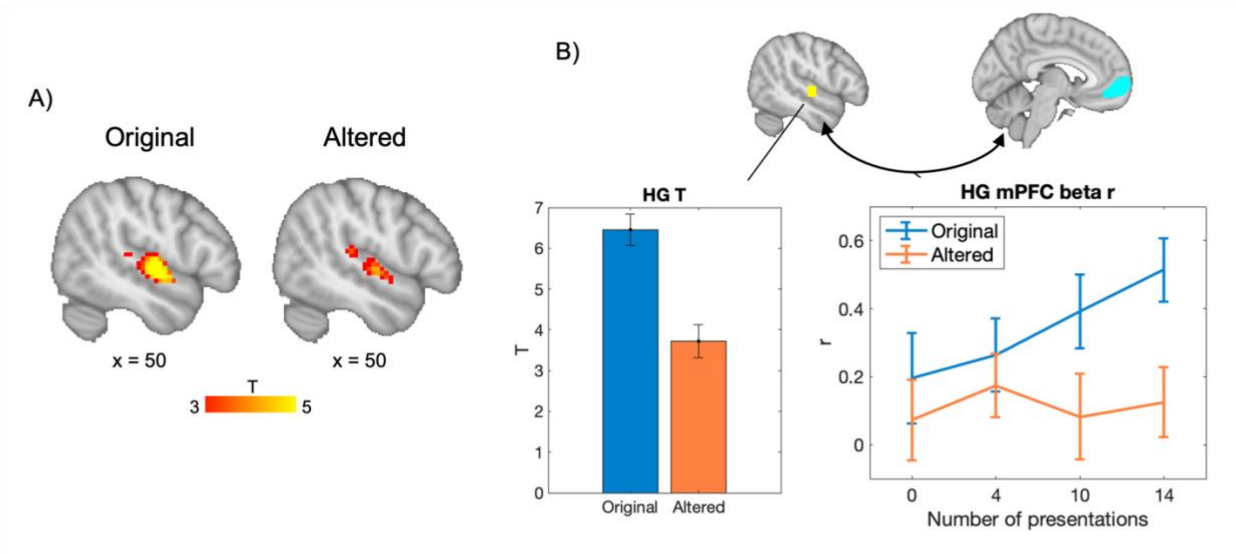

Figure 4. fMRI results. A) Greater activation for original than for altered melodies in Heschl's gyrus, confirming that auditory regions implement predictions. B) Higher functional connectivity, as quantified by correlations in beta-series, between auditory regions (Heschl's gyrus) and reward regions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

Discussion

Across seven studies, we showed that listeners from two different cultures can rapidly learn both local and global predictions in novel musical pieces and that this learning subsequently maps onto liking and changes in the reward system of the brain. In Studies 1-4, we established that changing the number of presentations (global prediction learning) and altering the endings of melodies (local prediction learning) both independently changed predictions in nested but orthogonal 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 results were similar in both Chinese and American participants. Finally, Study 7 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, 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. PCM 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; (Huron, 2006; Vuust et al., 2022). 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. Using novel melodies written in an unfamiliar musical key, and manipulating expectations in two different ways, circumvents this issue and allows us to disentangle the influence of different types of predictions on musical reward and preference. The fact that participants liked melodies that they heard more during the exposure phase, as well as altered versions of those same melodies, suggests that both types of expectations contribute to musical reward.

Furthermore, while the PCM argues 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 argue that cultural background plays a minimal to non-significant role in predictive learning of music when using novel musical stimuli that do not come from any existing culture. 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 repetitions. In addition, there was a significant interaction between BMRQ and number of presentations on familiarity ratings, in that participants with lower reward sensitivity to music rated the pieces they heard more during exposure as less familiar than hyperhedonics. The difference in liking ratings associated with BMRQ could therefore be due to motivation, in that people who are less sensitive to musical rewards were less motivated to learn from the task. However, the fact that musical anhedonics still show differences in liking ratings when local predictions were manipulated (original vs. altered versions) suggests that they are able to learn some aspects of statistical regularities in the music. 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 (Di Liberto et al., 2020), 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 (Gold et al., 2019) as well as during unexpected and/or unpredictable chord sequences (Cheung et al., 2019). 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 is unclear from the existing data 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, it remains unclear the specific mechanism by which the mapping between implicit learning and musical reward becomes aberrant in participants with musical anhedonia. While the current fMRI study shows sensitivity to prediction in the reward system, it is not sufficiently powered to assess possible neurobiological differences 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 (Loui et al., 2017; Martínez-Molina, Mas-Herrero, Rodríguez-Fornells, Zatorre, & Marco-Pallarés, 2019) and that alterations of fronto-striatal pathways can lead to either increases or decreases in subjective liking ratings of music (Mas-Herrero, Dagher, Farrés-Franch, & Zatorre, 2021). Future neuroimaging studies will therefore be needed to determine the possible role that this auditory-subcortical-prefrontal network plays 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 hierarchical organization by which predictions and prediction errors in music map on to reward, and provide strong evidence that this hierarchical learning process emerges similarly 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 (Clark, 2013; Friston, 2010; Schultz, 2015), 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 (Loui, 2022). In total, 14 20s Bohlen-Pierce melodies were composed that followed the same artificially-derived harmonic structure from past studies (Loui et al., 2010). 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 (Loui, Li, & Schlaug, 2011; Loui et al., 2010; Loui, Wu, Wessel, & Knight, 2009), 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 (Müllensiefen, Gingras, Musil, & Stewart, 2014), the Revised Physical Anhedonia Scale (PAS), a self-report measure of general anhedonia (Chapman, Chapman, & Raulin, 1976), and the Ten-Item Personality Inventory (TIPI), a brief measure of the Big-Five personality traits (Gosling, Rentfrow, & Swann, 2003). All scales were scored in accordance with the original publication.

Procedure

After consenting, participants were screened using an online headphone check (Woods, Siegel, Traer, & McDermott, 2017) 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 (Wickens, 2001). The d-prime measure therefore indicates how well participants could discriminate between a warble note and a nonwarble 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 (~69% correct) was removed from subsequent analyses (Wickens, 2001), 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 which 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 which 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 (Loui et al., 2017). The acquired music specific anhedonic (initials NA, 53-year-old female) had reached out to 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; (Cardona, Ferreri, Lorenzo-Seva, Russo, & Rodriguez-

Fornells, 2022) 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 (4 additional items) which measures experiences of absorption in music listening (Cardona et al., 2022).

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 Beijing college students, 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 3 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

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 (Penny, Friston, Ashburner, Kiebel, & Nichols, 2011) with the CONN Toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012). 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 (Friston et al., 1995). Denoising steps for fMRI data included white matter and cerebrospinal fluid confound correction (Behzadi, Restom, Liau, & Liu, 2007), 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. 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 auditory and reward networks, as defined by previous work in our lab (Wang, Belden, Hanser, Geddes, & Loui, 2020), were extracted from participants' first-level SPM.mat files using the CONN Toolbox 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 regions.

Acknowledgments

Supported by NSF-CAREER award #1945436 and NIH R21AG075232 to PL. We thank Milena Quinci, Odessa Deng, the NUBIC team, and all our participants.

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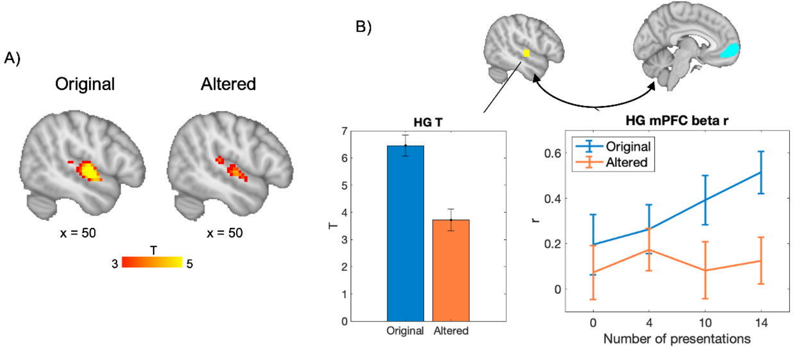
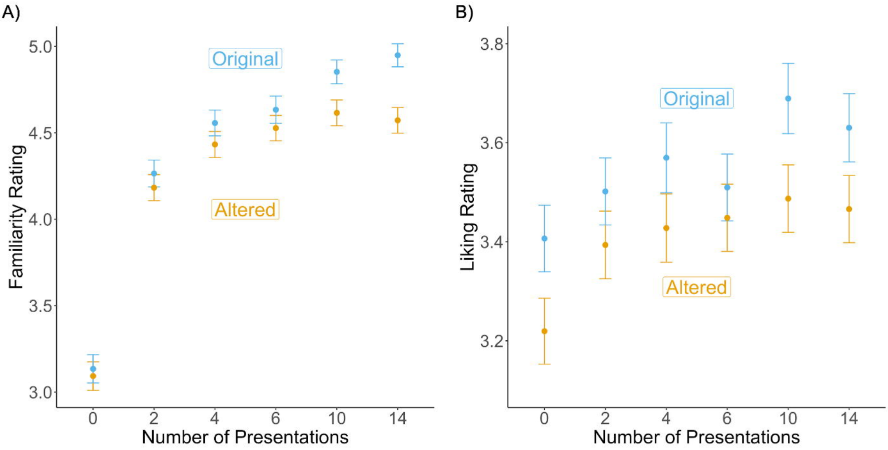

A)
Original
Altered
x = 50
x = 50
T
3
5
B)
HG T
7
6
5
4
3
2
1
0
T
Original
Altered
HG mPFC beta r
Original
Altered
0.6
0.4
0.2
0
r
0
4
10
14
Number of presentations



A)
Familiarity Rating
5.0
4.5
4.0
3.5
3.0
Original
Altered
0
2
4
6
10
14
Number of Presentations
B)
Liking Rating
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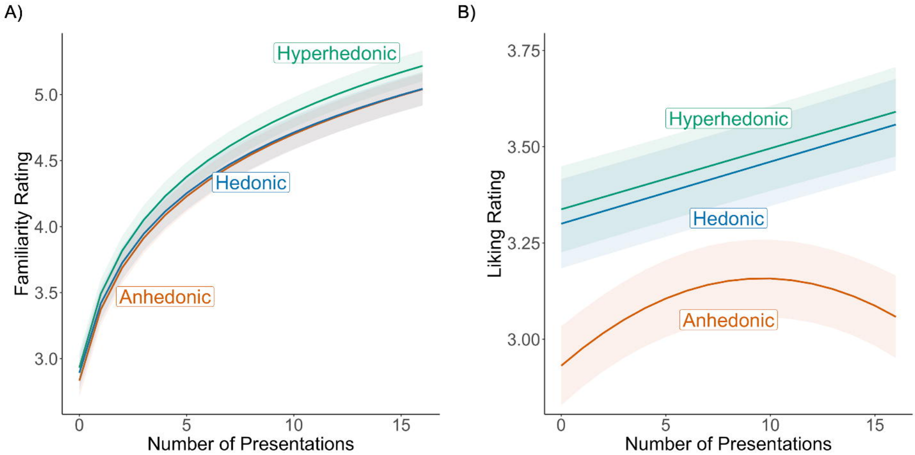
3.6
3.4
3.2
Original
Altered
0
2
4
6
10
14
Number of Presentations



A)
Hyperhedonic
Hedonic
Anhedonic
Familiarity Rating
5.0
4.5
4.0
3.5
3.0
0
5
10
15
Number of Presentations
B)
Hyperhedonic
Hedonic
Anhedonic
Liking Rating
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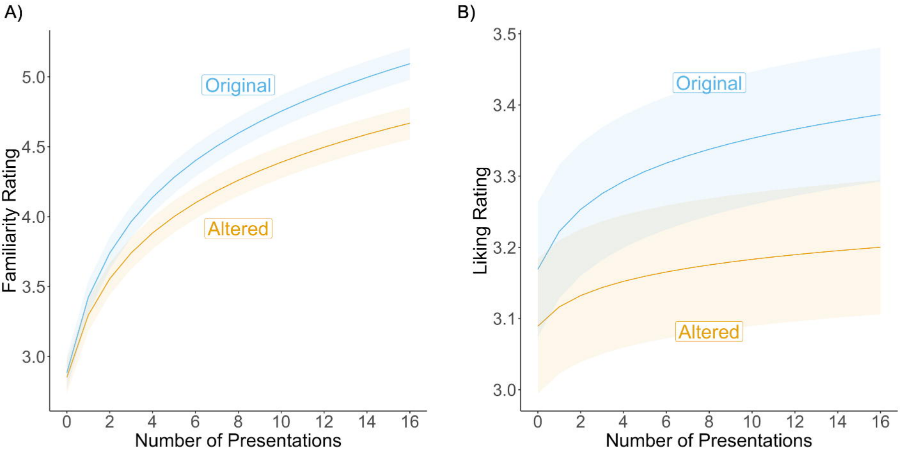
3.50
3.25
3.00
0
5
10
15
Number of Presentations



A)
Familiarity Rating
5.0
4.5
4.0
3.5
3.0
Original
Altered
0
2
4
6
8
10
12
14
16
Number of Presentations
B)
Liking Rating
3.5
3.4
3.3
3.2
3.1
3.0
Original
Altered
0
2
4
6
8
10
12
14
16
Number of Presentations

A) Familiarity Ratings

Effect	Linear		Logarithmic		Quadratic	
	β	p	β	p	β	p
Number of Presentations	0.33	< 0.001	1.15	< 0.001	0.48	< 0.001
Alteration	0.15	< 0.001	-0.11	0.411	0.19	0.164
Number of Presentations * Alteration	0.07	< 0.001	0.23	< 0.001	0.09	< 0.001
Number of Presentations (Quadratic term)					-0.23	< 0.001
Number of Presentaitons (Quadratic) * Alteration					-0.04	0.006
AIC	49331		**47943**		48210	

B) Liking Ratings

Effect	Linear		Logarithmic		Quadratic	
	β	p	β	p	β	p
Number of Presentations	0.04	< 0.001	0.13	< 0.001	0.05	< 0.001
Alteration	0.1	< 0.001	0.006	0.006	0.11	0.004
Number of Presentations * Alteration	0.03	0.02	0.09	0.018	0.03	0.15
Number of Presentations (Quadratic term)					-0.01	0.056
Number of Presentaitons (Quadratic) * Alteration					-0.001	0.43
AIC	40140		**40137**		40140	

A) Familiarity Ratings

Model	Anhedonic			Hedonic			Hyperhedonic		
	β	p	AIC	β	p	AIC	β	p	AIC
Linear	0.36	< 0.001	8618.8	0.35	< 0.001	8700.4	0.37	< 0.001	7911.4
Logarithmic	1.26	< 0.001	**8324.9**	1.22	< 0.001	**8417**	1.31	< 0.001	**7680.6**
Quadratic	0.53 (linear)	< 0.001	8376.1	0.51	< 0.001	8466	0.53	0.09	7743.2
	-0.26 (quadratic)	< 0.001		-0.25	< 0.001		-0.24	0.55	

B) Liking Ratings

Model	Anhedonic			Hedonic			Hyperhedonic		
	β	p	AIC	β	p	AIC	β	p	AIC
Linear	0.04	0.005	6895.4	0.06	< 0.001	**7177.3**	0.06	< 0.001	**6798.9**
Logarithmic	0.14	< 0.001	6889.2	0.19	< 0.001	7182.4	0.18	< 0.001	6800.1
Quadratic	0.07 (linear)	< 0.001	**6886.1**	0.05	0.59	7178.6	0.06	0.09	6800.5
	-0.05 (quadratic)	0.001		0.01	0.41		-0.01	0.55	