Uncertainty and Surprise Jointly Predict Musical Pleasure and Amygdala, Hippocampus, and Auditory Cortex Activity

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Summary

Listening to music often evokes intense emotions [1,2]. Recent research suggests that musical pleasure comes from positive reward prediction errors, which arise when what is heard proves to be better than expected [3]. Central to this view is the engagement of the nucleus accumbens – a brain region that processes reward expectations – to pleasurable music and surprising musical events [4–8]. However, expectancy violations along multiple musical dimensions (e.g., harmony and melody) have failed to implicate the nucleus accumbens [9–11], and it is unknown how music reward value is assigned [12]. Whether changes in musical expectancy elicit pleasure has thus remained elusive [11]. Here, we demonstrate that pleasure varies nonlinearly as a function of the listener's uncertainty when anticipating a musical event, and the surprise it evokes when it deviates from expectations. Taking Western tonal harmony as a model of musical syntax, we used a machine-learning model [13] to mathematically quantify the uncertainty and surprise of 80,000 chords in US Billboard pop songs. Behaviourally, we found that chords elicited high pleasure ratings when they deviated substantially from what the listener had expected (low uncertainty, high surprise), or conversely, when they conformed to expectations in an uninformative context (high uncertainty, low surprise). Neurally, we found using fMRI that activity in the amygdala, hippocampus, and auditory cortex reflected this interaction, whilst the nucleus accumbens only reflected uncertainty. These findings challenge current neurocognitive models of music-evoked pleasure, and highlight the synergistic interplay between prospective and retrospective states of expectation in the musical experience.

Keywords:

aesthetics, amygdala, emotions, fMRI, information theory, nucleus accumbens, prediction, predictive coding, reward, syntax

Results

Humans use structured sound sequences known as music to express and evoke emotions [1]. Manipulating the listener's expectations is a key mechanism through which music elicits pleasure [1,2,14–16]. A fundamental concept and characteristic feature of Western music is tonal harmony, which describes the syntactic regularities of how simultaneous pitches are combined into chords, and how chords are related to other chords in a progression [17]. In this study, we directly addressed whether musical pleasure depended on the expectancy of individual chords in a progression (Experiment 1), and how that was reflected in human brain activity (Experiment 2).

Quantifying uncertainty and surprise with information theory

As music unfolds in time, the listener continuously forms expectations on upcoming temporal and acoustic features [3,13,18]. This implies the presence of two temporally dissociable states through which the expectancy of a chord can evoke pleasure: the uncertainty when anticipating what the next chord could be before it occurs, and the surprise elicited when the actual chord deviates from expectations [16,19]. In contrast, the existing literature has almost exclusively focussed on surprising musical events [19,20] and found inconclusive effects on musical pleasure [6,11].

To mathematically quantify uncertainty and surprise, we employed an unsupervised statistical-learning model [13] that learnt the statistical regularities of over 80,000 chord progressions from a corpus of 745 pop songs listed in the US Billboard 'Hot 100' chart between 1958 and 1991 [21]. Our model uses these learnt statistical regularities to simulate a listener's prediction for novel chord sequences using Shannon's entropy and information content (see Figure 1 and STAR Methods). Entropy reflects how uncertain a listener is when anticipating an upcoming chord given only the portion of the song heard so far. Information content, or

surprisal, reflects how surprised the listener is once actually hearing the chord. These two established information-theoretic measures have been extensively applied to natural language processing [22], but only recently to harmony [23] in music. Our data-driven approach is superior to traditional designs for three reasons. First, we quantify uncertainty and surprise as continuous variables as opposed to comparing a small number of discrete categories (e.g., violation/no-violation) predefined by the experimenter [6,9,23–27]. Second, our chord stimuli are taken directly from the corpus to ensure conformity to stylistic conventions, as opposed to artificial chord progressions used in prior studies (e.g., [9,25,26]). Third, instead of examining pleasure elicited by a musical piece overall (e.g., [4,5,7]), we investigate how expectancy differences on a chord-to-chord-level affect musical pleasure.

Experiment 1: Joint effects of uncertainty and surprise on musical pleasure

In Experiment 1, healthy adults (n = 39) listened to 1039 chords in 30 chord progressions (Table S1) selected from the 745 pop songs and rated the pleasantness of each chord using a mechanical slider. We only kept the chord progressions from the original songs (and removed the melody and rhythm) to ensure that our isochronous chord stimuli were not confounded by effects of other musical dimensions and familiarity (songs were confirmed to be unidentifiable by our subjects). We used a linear mixed model to analyse the extent to which uncertainty and surprise, and their interaction, predicted pleasantness of chords taken from the commercially successful pop songs. To account for temporal autocorrelations in the slider ratings, we used a first-order autoregressive covariance structure to model the relationship between successive chords in each stimulus. To disambiguate probabilistic processing of expectations from sensory processing, we controlled for low-level acoustic features (i.e., sensory dissonance, spectral centroid, and spectral complexity) in the model (see Table S3 for correlations with chord uncertainty and surprise).

We found that the pleasure rating of a chord was significantly predicted by main effects of uncertainty and surprise, as well as their interaction (Figure 2 and Table 1; see Table S2 for correlation of random effects). In other words, pleasantness depended on joint effects of the precision of the listener's predictions, and the probability of the chord given the tonal harmonic context. Since the generation of an expectation precedes its deviation, we interpret this interaction as the modulatory effect of uncertainty on the effect of surprise on musical pleasure. When the uncertainty of the harmonic context was low (e.g., towards the end of a musical section), chords with higher surprise (i.e., those that were less probable) were rated as more pleasant than those with lower surprise. Conversely, when uncertainty was high (e.g., in chord progressions atypical of the listener's musical experience), subjects rated chords that were less surprising as more pleasant (Figure 2B).

In fact, the regression surface (Figure 2C) resembled a saddle, where the multiplicative effect of uncertainty and surprise along the two diagonals predicted pleasantness in a parabolic (U/inverted-U) manner. This is reminiscent of Berlyne's [28] influential model in empirical aesthetics, which postulated an inverted-U relationship between pleasure and variables such as exposure and complexity. Critically, however, our findings paint a more complicated and multifaceted picture of musical pleasure. Our findings imply that isolated effects of individual variables alone cannot fully explain the musical experience, as it is likely to be a nonlinear function of multiple interacting factors.

Furthermore, consistent with prior work [29–33], the low-level acoustic features also showed significant effects on pleasure (but were controlled for in the model). The magnitude of standardised beta estimates in our model (see Table 1) indicated that when the uncertainty of the chord was at its mean, the effect of surprise was 30% larger than sensory dissonance, and this marginal effect became twice as large when chord uncertainty was increased to 1.5 SD above the mean.

Experiment 2: Neural basis of uncertainty and surprise in music-evoked pleasure

To directly assess the underlying brain regions whose activity correlated with uncertainty and surprise, another group of subjects (n = 40) listened to the same isochronous chord stimuli and were instructed to pay attention to how the chords fitted together in the progression whilst undergoing fMRI scanning in Experiment 2. As before, we confirmed that our stimuli were unfamiliar to the subjects. Despite the sluggishness of the blood-oxygen-level dependent (BOLD) response, the long duration of each chord (2.4 s) meant that metabolic changes could still be measured on a chord-to-chord level. We also used multiband echo-planar imaging (EPI) [34,35] to allow for a sub-second temporal resolution whilst maintaining good spatial coverage. We focussed our analysis on brain regions previously shown to be implicated in music-evoked emotions across multiple studies [1]: the bilateral amygdala and adjacent anterior hippocampus, bilateral auditory cortex, right nucleus accumbens, left caudate nucleus, and the pre-supplementary motor area. Given that musical pleasure depends on joint effects of uncertainty and surprise, we hypothesised that the underlying brain regions would also show the same interaction.

Consistent with our behavioural findings, we found in Experiment 2 (Figure 3; see Table S4 for parameter estimates) that the interaction between uncertainty and surprise significantly modulated the BOLD response in the bilateral amygdala and hippocampus (left: $\beta = -0.116$, corrected 95%-CI = [-0.201, -0.0445], sign test: $s = 11$, corrected $p = 0.0450$; right: $\beta = -0.140$, corrected 95%-CI = [-0.238, -0.0410], one-sample t-test: $t(39) = -4.02$, corrected $p = 0.00181$; see also Figure S1). This is in line with prior studies implicating the amygdala in surprises in tonal harmony and changes in musical tension [26,27], as well as the hippocampus in encoding the uncertainty of sequences [36,37], and forming memory associations during music listening [5].

Furthermore, this interaction modulated activity in the bilateral auditory cortex (left: β = -0.182, corrected 95%-CI = [-0.288, -0.0766], t(39) = -4.90, corrected p = 0.000120; right: β = -0.128, corrected 95%-CI = [-0.220, -0.0355], t(39) = -3.93, corrected p = 0.00234), with stronger effects in the left compared to the right (see Figure S2). In line with our observed interaction, pitch deviants in melodies [38] and timing deviants in rhythm [39] evoke reduced auditory mismatch responses for stimuli with increased uncertainty (although pleasantness was not investigated in those studies; see [16] for a discussion). The established role of the auditory cortex in processing sound, as well as the amygdala and hippocampus in processing emotions, suggest that the pleasure evoked by expectations in music rests on a close link between perceptual analysis and affective evaluation [1,3,40].

Remarkably, neither a significant interaction between uncertainty and surprise, nor a main effect of surprise were detected in the nucleus accumbens or caudate (all corrected p > 0.993). We instead detected a positive main effect of uncertainty in the right nucleus accumbens (β = 0.242, corrected 95%-CI = [0.0720, 0.412], t(39) = 4.04, corrected p = 0.00170), and left caudate (β = 0.281, corrected 95%-CI = [0.0661, 0.496], t(39) = 3.71, corrected p = 0.00447). This means striatal activity was increased when the tonal harmonic context was less informative in revealing what the ensuing chord could be, and decreased when more informative. In a post-hoc analysis, we found comparable results in the contralateral nucleus accumbens and caudate with no evidence of laterality (Figure S3). Our data therefore suggest that striatal activity encodes the uncertainty of an expectation, irrespective of the magnitude of surprise. Finally, the pre-supplementary motor area likewise only showed a significant positive modulation to uncertainty (β = 0.358, corrected 95%-CI = [0.145, 0.570], t(39) = 4.78, corrected p = 0.000176).

Discussion

Our results contribute direct evidence in support of an expectancy mechanism in evoking musical pleasure [2,14–16,18,41]. We showed that surprise, a retrospective response, alone cannot fully explain the link between expectations in music and pleasure. Our data demonstrate that uncertainty, a prospective state of expectation, is another crucial dimension needed to describe this relationship. Pleasantness ratings to isochronous chord progressions taken from commercially successful Western pop music indicated high pleasure in two situations: when a chord with high surprise had been predicted with low uncertainty, or conversely, when a chord with low surprise had been predicted with high uncertainty. This interaction effect was reflected by metabolic changes in the amygdala, anterior hippocampus, and auditory cortex, but not the nucleus accumbens. Uncertainty and surprise are in fact key components of an influential predictive-coding model of neuronal message-passing across the cortical hierarchy [16,20,42]. In this model, music perception is construed as an active process where the brain continuously updates its generative model of the environment to minimise variational free-energy [16,20]. Music may therefore elicit pleasure by encouraging the listener to continuously generate and resolve expectations as the piece unfolds in time [16,20]. The importance of the temporal dimension in evoking pleasure sets music apart from the static visual objects that are traditionally studied in empirical aesthetics [43,44].

Unlike prior studies [4,7,8,45] which appealed to the established role of the nucleus accumbens in reward expectation [46,47] as evidence supporting an expectancy mechanism of musical pleasure, we directly addressed how predictability in our stimuli modulated pleasantness. These studies also left unexplained which musical dimensions constituted an expected musical reward, and how reward value is assigned to musical events [12]. In contrast, our results indicate that musical pleasure comes from manipulating both the uncertainty of the listener's expectations before hearing an event, and the surprise that follows when such

expectations are not met. Here, these events are chords represented on the symbolic level and objectively quantified using information theory. These chord expectations are likely generated, at least partly, in the inferior frontal gyrus, a region shown to process expectation deviations in musical structure [9,18,48], and passed top-down to the auditory cortex [16,20,41]. Since the uncertainty and surprise of a chord were derived independently from its acoustic characteristics and solely on its conditional probability of occurrence, the same chord will have a different level of uncertainty and surprise depending on the combination of chords prior in the progression. Combined with the control of low-level acoustic regressors, we can rule out that our results were driven by sensory-acoustic features.

Activity in the nucleus accumbens and caudate did not show significant modulation to the effect of chord surprise and its interaction with uncertainty. Given the central role of the nucleus accumbens in reward prediction, this might be seen as at odds with our behavioural finding that pleasantness is predicted by the joint effect of uncertainty and surprise. Instead, we found that uncertainty positively modulated striatal activity. Our results suggest that the striatum performs a facilitatory, although important, role in generating musical pleasure – that of modulating incentive salience, or the motivation or 'wanting' of subsequent information that resolves uncertainty [41,46]. In addition to reward expectation, the nucleus accumbens is argued to play a significant role in integrating cognitive and affective information to direct attention and modify actions towards motivationally relevant stimuli through dopaminergic pathways [47]. In line with this and consistent with our findings, dopamine is assumed to encode the precision (the inverse of uncertainty) of prediction errors in the free-energy principle [16,20]. Indeed, causal studies on musical pleasure [45,49] do not claim that striatal dopaminergic neurons induce pleasurable emotions per se, but highlight their necessity in regulating affective responses to music. Taken together, we suggest that a role of the nucleus accumbens in musical pleasure is to modulate attention deployment, depending on uncertainty,

in the amygdala, hippocampus, and auditory cortex. In line with this, the nucleus accumbens has shown increased functional connectivity with the amygdala, hippocampus, auditory cortex, and the inferior frontal cortex for music that was more pleasant [4,6].

Our study has certain limitations. First, our auditory stimuli consisted of computer-generated isochronous chord progressions taken from original pop songs. Although this allowed us to isolate effects of harmonic expectancy by controlling for confounds such as rhythm, melody, familiarity, dynamics, and instrumentation, the expectancy of these other dimensions and the dimensions themselves are also likely to influence pleasure [2,8,15,50,51]. Second, the parametric values of uncertainty and surprise derived from our computational model are constrained by the corpus from which the statistical regularities are computed. In other words, a highly surprising chord predicted with low uncertainty here is only relative to other chords present in the McGill Billboard corpus of commercially successful pop songs [21]. Third, listeners' experiences shape their internal model of the statistical regularities of chords in a progression [13]. This means that factors such as culture, genre, and style affect how surprising a chord is, and with how much precision it can be expected [13]. Whether our results extend to other musical styles (see e.g., [52] for a discussion on atonal music), and the extent to which enculturation, expertise, and individual differences shape our preferences and emotional responses to music thus remain open questions.

In summary, we show with the help of an unsupervised statistical-learning model that musical pleasure depends on the dynamic interplay between prospective and retrospective states of expectation. We demonstrate that this joint effect is reflected by metabolic changes in the amygdala, hippocampus, and the auditory cortex, and is likely mediated through dopaminergic incentive salience signals in the nucleus accumbens – which instead showed a positive modulation to uncertainty. Our fundamental ability to predict [16,20] is therefore an

important mechanism through which abstract sound sequences acquire affective meaning and transform into a universal cultural phenomenon that we call ‘music’ [15].

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Author Contributions:

V.K.M.C., & S.K. conceived the study. V.K.M.C., S.K., P.M.C.H., M.T.P., L.M., & J.D.H. conceptualised the study. V.K.M.C., S.K., L.M., P.M.C.H., J.D.H., & M.T.P. developed the experimental paradigm. P.M.C.H, & M.T.P. developed the computational model. V.K.M.C., & P.M.C.H. developed the stimuli. L.M., S.K., M.T.P., & J.D.H. supervised the research. V.K.M.C. collected and analysed the data, prepared the figures, and wrote the original draft of the manuscript. V.K.M.C., S.K., P.M.C.H., L.M., M.T.P., & J.D.H. reviewed and edited the manuscript.

Declaration of Interests:

The authors declare no competing interests.

Figure Titles and Legends:

Figure 1. Quantifying uncertainty and surprise of a chord.

(A) An unsupervised statistical-learning model was trained on a corpus of 745 US Billboard 'Hot 100' pop songs to derive the uncertainty (red) and surprise (blue) of chords (here: 'Knowing Me, Knowing You' by ABBA, refer to Audio S1). Uncertainty is the lack of a clear expectation when anticipating an event *before* it is heard, whilst surprise occurs when what is *actually* heard deviates from expectations. Uncertainty of chord e_i is quantified by its entropy, or expected negative log-probability, taken across the set of all chords S in the corpus and conditional on the previous context of chords $\{e_1, \ldots, e_{i-1}\}$ in the progression. Surprise of chord e_i is quantified by its information content, and is the negative log-probability of the actual chord conditional on the context. Grey bars indicate points of high uncertainty but low surprise, and low uncertainty but high surprise. Subjects (n = 79) were asked to either rate the pleasantness of each chord (2.4 s) from 30 pop song chord progressions behaviourally, or to listen attentively and to focus on how they fitted together in the context whilst undergoing fMRI scanning. (B) & (C) Scatter plot and marginal densities of the uncertainty and surprise for all chords in the McGill Billboard corpus [21] (circles, n = 80,943) and in our chord stimuli (triangles, n = 1039; see Table S1).

Figure 2. Uncertainty and surprise jointly shape the pleasure rating of a chord.

(A) Standardised pleasure ratings to a chord progression taken from 'Knowing Me, Knowing You' by ABBA (Audio S1). Diamonds indicate mean pleasantness ratings for each chord. Filled circles indicate fitted values from a linear mixed model with chord uncertainty, surprise, and their interaction as predictors. Error bars indicate 95%-confidence intervals (95%-CI). Low-level acoustic parameters were also included as covariates to control for sensory confounds. (B) Contour plot demonstrating how pleasantness ratings jointly depend on

uncertainty and surprise. When the tonal harmonic context does not allow for a prediction with high precision (i.e., when uncertainty is high), the pleasantness of a surprising chord is low. However, when the uncertainty is low, surprising chords are highly pleasurable. (C) Data from B replotted in 3D. Although reminiscent of the characteristic inverted-U response from empirical aesthetics, the regression surface is in fact a saddle for which pleasantness varies nonlinearly across different levels of uncertainty and surprise.

Figure 3. Neural basis of uncertainty and surprise in music-evoked pleasure.

(A) Model-based fMRI revealed that BOLD activity in the bilateral amygdala and neighbouring anterior hippocampus (Amyg/Hipp), as well as the bilateral auditory cortex (AC) is significantly modulated by the interaction of chord uncertainty and surprise. (B) The right nucleus accumbens (NAcc), left caudate (CN), and pre-supplementary area (pre-SMA) instead only showed significant positive modulations to chord uncertainty. See also Figures S1-S3 and Table S4. Box plots show parameter estimates for the effect of uncertainty, surprise, and their interaction in each region of interest (n = 40; filled-circles: data points; solid line: median; diamond: mean; notches: 95%-CI of the median; hinges: IQR; whiskers: 1.5*IQR; statistical inferences were made using one-sample t-tests (two-tailed) or sign tests (for non-normal data) and Bonferroni-corrected for multiple comparisons (n.s.: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$).

Tables:

Fixed-effect predictor	Standardised β	95%-CI	Deviance	p
Intercept	0.0219	[-0.0740, 0.118]	0.200	0.655
Uncertainty	-0.143	[-0.186, -0.0989]	40.2	2.33×10^{-10} ***
Surprise	-0.327	[-0.418, -0.236]	29.2	6.57×10^{-8} ***
Uncertainty × Surprise	-0.124	[-0.183, -0.0644]	13.4	0.000246 ***
Sensory dissonance	-0.251	[-0.345, -0.158]	19.3	1.41×10^{-5} ***
Spectral centroid	0.0719	[0.0244, 0.119]	8.77	0.00306 **
Spectral complexity	0.224	[0.147, 0.300]	23.0	1.65×10^{-6} ***
Overall pleasantness of sequence	0.171	[0.032, 0.309]	5.28	0.0215 *
Overall arousal of sequence	-0.0321	[-0.160, 0.0956]	0.242	0.623

Marginal R^2 = 0.476; Conditional R^2 = 0.654; *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$

Table 1. Parameter estimates of the linear mixed model in Experiment 1.

Subjects (n = 39) continuously rated the pleasantness of 1039 chords in 30 chord sequences using a mechanical slider. The pleasantness of a chord depended on not only the amount of surprise evoked, but also the uncertainty in anticipating the chord before it was actually heard. Low-level acoustic effects were also introduced as covariates (see Table S3 for correlations with chord uncertainty and surprise) to disambiguate probabilistic processing from low-level sensory processing. Deviance here denotes twice the difference in log-likelihood between the full model and a restricted model with the effect omitted. Significance of individual fixed effects were determined using the likelihood-ratio test after a full-null model comparison [53,54]. Marginal and conditional R^2 values for the model were estimated according to [55]. See Table S2 for correlation of random effects.

STAR Methods

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Stefan Koelsch (stefan.koelsch@uib.no). This study did not generate new unique reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

A total of 83 healthy human adults took part in the study. Data from one male subject in Experiment 1 was excluded due to non-compliance with the experimental procedure. Functional MRI data from two subjects (1 female, 1 male) in Experiment 2 were excluded due to data-handling errors, and one further female subject was excluded as her overall music reward score (see below) was over 3 standard deviations below the population mean. Subjects took part in either the behavioural or fMRI experiment, but not both to ensure that the stimuli were novel to the subjects.

For Experiment 1, data were analysed from 39 subjects with diverse levels of musical training (21 females, age: M = 24.1 y, SD = 3.80, general musical sophistication: M = 71.5, SD = 16 (corresponding to the 31st percentile of 147,633 self-selected subjects in the 'How musical are you?' test on the BBC website) from the Goldsmiths Musical Sophistication Index (Gold-MSI) [56], musical training subscale of the Gold-MSI: M = 23.4, SD = 10.3, range = 7–41 (corresponding to the 1st and 86th percentile), overall music reward: M = 48.6, SD = 8.53 (population M = 49.98 and SD = 10.01 based on a sample of 857 young-adult subjects) from the Barcelona Music Reward Questionnaire (BMRQ) [57]).

For Experiment 2, data were analysed from 40 subjects also with diverse levels of musical training (20 females, age: M = 25.2 y, SD = 4.16, general musical sophistication: M = 72.2, SD = 19.9 (corresponding to the 32nd percentile), musical training: M = 23.6, SD = 11.5,

range = 7– 48 (corresponding to the 1st and 100th percentile), overall music reward: M = 47.9, SD = 10.3).

No significant differences in age (Mann-Whitney U = 888, p = 0.290), general musical sophistication (Welch's t-test t(74.38) = 0.175, p = 0.861), musical training (Mann-Whitney U = 779, p = 0.996), or overall music reward (Mann-Whitney U = 817, p = 0.720) were observed between subjects from the behavioural experiment (Experiment 1) and fMRI experiment (Experiment 2). No sex-specific analyses were conducted as we were interested in effects general to the population.

All subjects were self-reported right-handed, with normal hearing, had normal or corrected-to-normal vision, and reported no known history of psychological or neurological disorders. Written informed consent was obtained from each subject prior to the experiment, and the study was approved by the Ethical Committee of the Medical Faculty at Leipzig University.

METHOD DETAILS

Information Dynamics Of Music model

We used the Information Dynamics Of Music (IDyOM) model [13,58] to derive the surprise and uncertainty of every chord in the McGill Billboard Corpus [21]. This unsupervised statistical-learning model computes the Shannon information content and entropy [59] of a chord by prospectively generating a probability distribution for each chord in a song (or more generally, symbols in a sequence) conditioned on its previous context and the prior experience of the model.

At the core of IDyOM is the PPM algorithm, a variable-order Markov model introduced by Cleary and Witten [60] and subsequently updated by Moffat [61] and Bunton [62]. The PPM algorithm reads a sequence one symbol at a time, and generates a probability distribution for

the symbol by blending together predictions from n-gram models of different orders. An n-gram model of order n–1 is a Markov model that generates the probability of a symbol by conditioning on the previous context of n–1 symbols. Thus, given the set of all chords S and a chord progression $\{e_1, \ldots, e_i, \ldots, e_N\}$, the n-gram probability of chord e_i is given by $p(e_i \mid e_{i-(n-1)}, \ldots, e_{i-1})$. The information content of chord e_i is defined as the negative logarithm of its conditional probability, i.e.,

$$I(e_i) = -\log_2 p(e_i \mid e_{i-(n-1)}, \ldots, e_{i-1}),$$

whilst the entropy of chord e_i is the expected information content of chord e_i. This is obtained by multiplying the conditional probability of all possible chords in S by their information contents then summing together, giving

$$H(e_i) = -\sum_{e \in S} p(e_i = e \mid e_{i-(n-1)}, \ldots, e_{i-1}) \log_2 p(e_i = e \mid e_{i-(n-1)}, \ldots, e_{i-1}).$$

Previous work has demonstrated the superiority of IDyOM over fixed order n-gram models in modelling listeners' probabilistic expectations of musical events [19,58].

IDyOM incorporates both a short-term model and a long-term model. The short-term model is trained incrementally on the current progression, thereby learning statistical regularities specific to the current stimulus. The long-term model is trained on all stimuli in a representative corpus of musical compositions, simulating the listener's prior musical exposure; here we used the McGill Billboard pop music corpus as it reflects a musical style that is popular and widely accessed by listeners of Western tonal music, and contains the most common chord progressions in pop music. We also applied 10-fold cross-validation to avoid overfitting to individual songs. IDyOM combines the short- and long-term models using a geometric weighted mean [63], where each model is inversely weighted by the entropy of its predictions. This model configuration, termed 'BOTH' in [64], has proved to be useful both for modelling musical style [65] and for modelling music perception (e.g., [19,66–69]). Consequently, IDyOM captures both stylistic regularities (from the training corpus) and local

regularities (from the portion of the song heard so far) to improve its ability to generate successful predictions.

Although previous applications of IDyOM have mostly been limited to the melodic domain [19,58,66–69], there is emergent interest in applying the model to harmonies [23]. In melodic applications, an important aspect of IDyOM is the use of viewpoints to embody different psychological and music-theoretic principles (e.g., relative pitch, tonality). Comparable viewpoint systems have yet to be established in the harmonic domain (although see [70] for initial work in this direction). We therefore used IDyOM in a single-viewpoint configuration, where the symbolic alphabet consisted of chord symbols present in the training corpus and included scale degree, chord type, and inversions.

Stimuli

Stimuli consisted of 30 unique auditory chord progressions (see Table S1) selected from 745 songs listed on the US Billboard 'Hot 100' chart between 1958 and 1991 in the McGill Billboard Corpus [21], resulting in a total of 1039 chords. The duration of each chord was 2.4 s, and each progression contained 30-38 chords (M = 34.6). These parameters were chosen to optimise signal-to-noise ratio of the data given the long rise time (~6 s until peak after stimulus onset) and sluggishness of the BOLD response in fMRI. Each chord progression was also transposed to C major to further reduce the possibility of familiarity effects. No significant correlations between the uncertainty and surprise of chords were detected in the stimulus set ($r = -0.0218$, $p = 0.482$; see Figure 1C and Table S3).

Chord sequences were chosen by first generating all possible (494,807) chord progressions containing 30-38 chords for every song in the corpus, and imposing the criteria that 1) each progression must begin on the tonic root position and end on a perfect or plagal cadence (as in most Western tonal compositions), 2) each progression must contain at least one

chord that belongs to each quadrant of the product [high/low informational content] × [high/low entropy] (where high and low respectively denote the upper and lower 40th percentile of chords in the corpus), and occurs at least five chords after onset and before the end of each progression, 3) each progression must contain at least unit variance in entropy and log(information content) (to adjust for skewness in the distribution) in each progression, and that 4) each sub-sequence of at least five chords must only repeat after a gap of at least two chords and not repeat more than three times (including the first presentation) consecutively. Note that the quadrant boundaries are constrained by the set of chords in the corpus, and may thus be conservative within the broader spectrum of musical styles beyond pop music. We then selected exactly one progression from the remaining songs that minimised the ordinal relationship between information content and 1-lagged entropy (i.e., the entropy of the subsequent chord) using Kendall's tau. This final step was carried out for another study with a different research question.

All chords were initially generated as MIDI files using the MIDI-Toolbox [71] in Matlab R2013b (MathWorks, Natick, MA, USA) and rendered as wav files (44100 Hz sampling rate) with a synthetic timbre composed of a jazz guitar, an acoustic guitar, and a marimba using Pro Tools (Avid Technology, Burlington, MA, USA). All instruments played the full chords together in every stimulus. Three separate background rhythms with a synthetic drum-kit timbre were made using GarageBand for iOS (Apple Inc., Cupertino, CA, USA), and superposed on the sound waves in Matlab. Each rhythm spanned the duration of each chord, was in quadruple time (regardless of the time signature of the original song), and was repeated throughout each stimulus. These background rhythms were introduced to enhance the momentum of the stimuli given the relatively slow tempo of the chord progressions. Reverberation and damping were adjusted to ensure that the waveform of each chord and

rhythm did not spill over to the subsequent chord. The auditory stimuli were then normalised in loudness using ReplayGain in Audacity (https://audacityteam.org).

Procedure for Experiment 1

Subjects gave pleasantness ratings to chords in auditory chord sequences using a custom-built 10 cm analogue mechanical slider in a soundproof cabin. The slider was held with the left hand and placed on the lap perpendicular to the body, whilst the right thumb was used to move the slider pot. Moving the pot away from the body indicated a higher rating, and vice versa. The highest rating was 'sehr angenehm' (very pleasant), and the lowest was 'nicht angenehm' (not pleasant). Each trial began with the subject resetting the slider to the lowest rating as the first chord was identical for all stimuli (ratings from the first chord were excluded from the analysis), and the stimulus was presented 2 s afterwards. Subjects rated the pleasantness of each chord in the auditory sequence by moving the slider pot to its corresponding position, and were explicitly told to give at most one rating for every chord. They were encouraged to use the full range of the slider, and to select extreme ratings at least 5 times throughout the entire experiment as in prior work [72]. Once the chord progression was over, subjects were given two 3 s time-windows to rate the overall pleasantness and arousal of the progression (order pseudo-randomised) on a 1-6 scale using the top number keys on a computer keyboard. Subjects were then prompted to begin the next trial as before.

The 30 auditory isochronous chord progressions were presented in a pseudo-random order, with the three background rhythms evenly assigned to the stimuli and counterbalanced across participants. The experiment was delivered using PsychToolbox 3 [73] in Octave 4.0.0 [74], and stimuli were presented using supra-aural headphones (Beyerdynamic DT 770 PRO) at a comfortable volume. The slider was connected to an Arduino Micro microcontroller that acted as a digital-analogue converter with a 20 Hz sampling rate. Subjects practised on three

trials (with a different set of stimuli) prior to the experiment to ensure they understood the task. At the end of the experiment, subjects were asked whether the chord progressions in the stimuli were familiar to them, and if possible, to name the possible artist or song. No subjects mentioned the relevant artist or song featured in our stimuli, except for one subject who suggested the possibility of a chord progression by The Beatles without actually identifying the song.

Procedure for Experiment 2

The fMRI experiment was divided into five runs, and the procedure was similar to the behaviour experiment. Each trial began with the instruction asking subjects to close their eyes, then the presentation of an auditory chord progression ensued after a 10 s pause. Subjects' task was to listen attentively to the chord progressions and to pay attention to how each chord fits in with the previous chords in the progression. A 1 s-sine wave tone (C5 = 523.25 Hz) then informed subjects to open their eyes 1 s after the end of stimulation. Following a 1 s pause, subjects were given two 3 s time-windows to rate overall pleasantness and arousal of the stimulus using a 1-6 scale (order randomised to minimise motor preparation) on an MR-compatible button box in each hand. They were then instructed to close their eyes again and the next trial began.

In each run, six auditory sequences (two of each rhythm, counterbalanced across subjects) were pseudo-randomly selected from the 30 stimuli and presented without replacement. The experiment was delivered using PsychToolbox 3 in Octave 4.0.0, and stimuli were presented using noise-isolating earphones (Sensimetrics S14) at a comfortable volume. Foam pads were placed around the head to minimise movement, and the scanner was stopped for a pause of approximately 60 s at the end of each run. Subjects practiced on three trials (with a different set of stimuli) outside the scanner prior to the experiment to ensure they understood

the task. At the end of the experiment, subjects were asked whether the chord progressions in the stimuli were familiar to them, and if possible, to name the possible artist or song. No subjects mentioned the relevant artist or song featured in our stimuli.

fMRI data acquisition for Experiment 2

Brain imaging data were acquired on a 3T Magnetom Skyra scanner (Siemens Healthcare, Erlangen, Germany) with a 32-channel head coil and a multiband EPI sequence [34,35] (TR = 500 ms, TE = 24 ms, flip-angle = 45°, FoV = 204 mm, in-plane matrix = 68×68, slice thickness = 3.2 mm, inter-slice gap = 0.32 mm, phase-encoding = A/P, multiband acceleration factor = 4, 7/8 partial-Fourier sampling, pre-scan normalisation enabled, 1241 volumes per run, 5 runs in total). Slices were oriented along the axial plane parallel to the AC-PC line and covered the whole neocortex (with partial coverage of the cerebellum and brainstem). Six dummy scans were acquired and discarded by the scanner for steady-state magnetisation at the start of each run.

QUANTIFICATION AND STATISTICAL ANALYSIS

Behavioural data analysis for Experiment 1

To obtain pleasure ratings for all chords, the pleasantness time series for every chord progression was first smoothed using a moving median filter with a fifth-order symmetric window to reduce analogue noise. The mode of the smoothed signal was then sampled in a time window from one second after each chord onset until its end to account for delays in moving the slider. The first chord of each progression was discarded since each trial began by resetting the slider.

Stationarity of each uncertainty and surprise sequence (derived using IDyOM) was examined using the Augmented Dickey-Fuller (ADF) test and Kwiatkowski-Phillips-Schmidt-Shin (KPSS) test, and suggested that no differencing was required.

We then fitted a linear mixed model using the package glmmTMB [75] in R 3.5.1 using RStudio (RStudio, Inc., Boston, MA, USA). The response variable was the pleasantness rating of each chord (averaged across subjects), and the predictors of interest were chord uncertainty, surprise, as well as the interaction between the two variables. This interaction is given by the element-wise product of uncertainty and surprise. As previous work suggested that sensory dissonance, spectral complexity, and spectral centroid also affect pleasure ratings in music [29–32,76], we extracted the mean value of these low-level acoustic features for every chord using Essentia 2.1 [77] and entered them as covariates in the model. We also added overall pleasantness and overall arousal ratings of each excerpt as covariates. Furthermore, stimulus-specific random effects were included for the intercept, surprise, interaction between uncertainty and surprise, sensory dissonance, and spectral complexity. These were selected following the suggestion of Barr and colleagues [78], where all fixed effects predictors were initially also entered as random effects, and then dropped as random effects until the model converged. A first-order autoregressive covariance structure was also used to model the autocorrelation between each subsequent chord rating in a given stimulus. All predictors and the response variable were moreover standardised before entering into the model. Parameters were estimated using maximum likelihood for model comparison. Model residuals were visually inspected for homoscedasticity and normality. Subject-specific random effects were not included as the model residuals became severely heteroscedastic.

We further fitted a null model for a full-null model comparison to guard against inflated Type I errors [53,54]. This null model was formed by dropping from the full model our predictors of interest (i.e., uncertainty, surprise, and their interaction), and the random effect of

surprise (due to convergence issues). After establishing the overall significance of the full model over the null model (likelihood-ratio test: $\chi^2(8) = 225$, $p < 2.20 \times 10^{-16}$) using a significance threshold of $p < 0.05$, the significance of each fixed effect in the full model (see Table 1) was tested against reduced models (where effect is dropped) using the likelihood ratio test. Here, we report Wald 95%-confidence intervals.

fMRI data preprocessing for Experiment 2

Functional MRI images were analysed using SPM12 (Wellcome Centre for Human Neuroimaging, London, UK) version 7219 in Matlab 2017b. After conversion to Nifti format, acquired images were despiked using 3dDespike in AFNI [79], then motion-corrected, co-registered to subjects' T1-weighted structural image, normalised to MNI space and resampled to the native voxel resolution [80], before smoothing with a 6×6×6.4-mm (corresponding to twice the voxel size) FWHM Gaussian kernel. Slice-timing correction was not applied given the fast repetition time of the acquisition sequence.

fMRI data analysis for Experiment 2

We analysed our model-based fMRI [81] data using a two-stage mixed effects model [82]. A linear model was first fitted on the subject level with one boxcar function modelling the stimulation of each chord progression, and standardised parametric modulators coding uncertainty, surprise, interaction between uncertainty and surprise, sensory dissonance, spectral centroid, and spectral complexity of each chord, as well as valence and arousal ratings for each progression. These regressors were convolved with the canonical haemodynamic response function and its temporal derivative. Each parametric modulator was separately orthogonalised with respect to the task-regressor to correctly assign signal variance to the main stimulus regressor [83]. Six rigid-body transformation regressors were further introduced as

covariates to reduce motion-induced artefacts. Effects of temporal autocorrelation were modelled with a FAST-autoregressive model, and a high-pass filter with a 128-s cut-off was applied to remove low-frequency scanner drifts. Individual means and variances were then pooled into a group-level model for population inferences. As we aimed to identify the neural correlates of chord uncertainty and surprise in brain regions previously implicated in music-evoked emotions, we took all seven significant clusters from a meta-analysis on anatomical regions implicated in music-evoked emotions [1]. These consisted of the bilateral amygdala and a restricted portion of the anterior hippocampal formation adjacent to the amygdala (including the hippocampal-amygdaloid transition area, hippocampus proper, and the subiculum), right ventral striatum (including the nucleus accumbens), left caudate nucleus, bilateral auditory cortex, and the pre-supplementary motor area.

Population inferences (see Figure 3 and Table S4) were made on the mean parameter estimates obtained with MarsBar version 0.44 [84] using two-tailed one-sample and paired t-tests (as suggested in [85]). If data deviated from normality according to the Shapiro-Wilk test, sign tests or Wilcoxon signed-rank tests were instead conducted with 95% bootstrap confidence intervals of the median on 10000 permutations. P-values and confidence intervals were Bonferroni-corrected according to the number of regions tested in a given analysis.

DATA AND SOFTWARE AVAILABILITY

Data supporting findings of this study are available from the Lead Contact upon request. Code for the IDyOM model is available at Sound Software: https://code.soundsoftware.ac.uk/projects/idyom-project. The McGill Billboard corpus dataset is available at DDMAL: https://ddmal.music.mcgill.ca/research/The_McGill_Billboard_Project_(Chord_Analysis_Dataset)/

Legend for Supplemental Audio S1:

Audio S1. Example stimuli. Related to Figure 1 and Figure 2.

A chord progression taken from ‘Knowing Me, Knowing You’ by ABBA (see Figure 1 and Figure 2) and transposed to C major. Each chord progression stimulus had three different background rhythm versions that were counterbalanced across participants.

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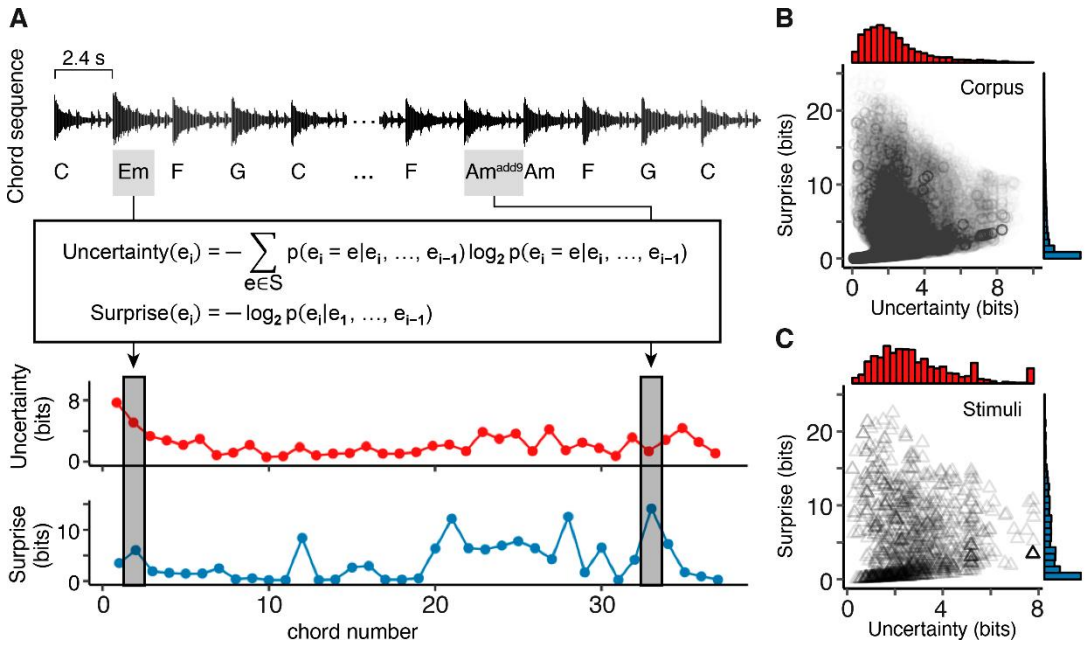
A
2.4 s
Chord sequence
C Em F G C ... F Am^add9 Am F G C
Uncertainty(e_i) = − Σ_{e∈S} p(e_i = e|e_i, …, e_{i−1}) log_2 p(e_i = e|e_i, …, e_{i−1})
Surprise(e_i) = − log_2 p(e_i|e_1, …, e_{i−1})
Uncertainty (bits)
Surprise (bits)
chord number
B
Corpus
Surprise (bits)
Uncertainty (bits)
C
Stimuli
Surprise (bits)
Uncertainty (bits)

FIGURE 1

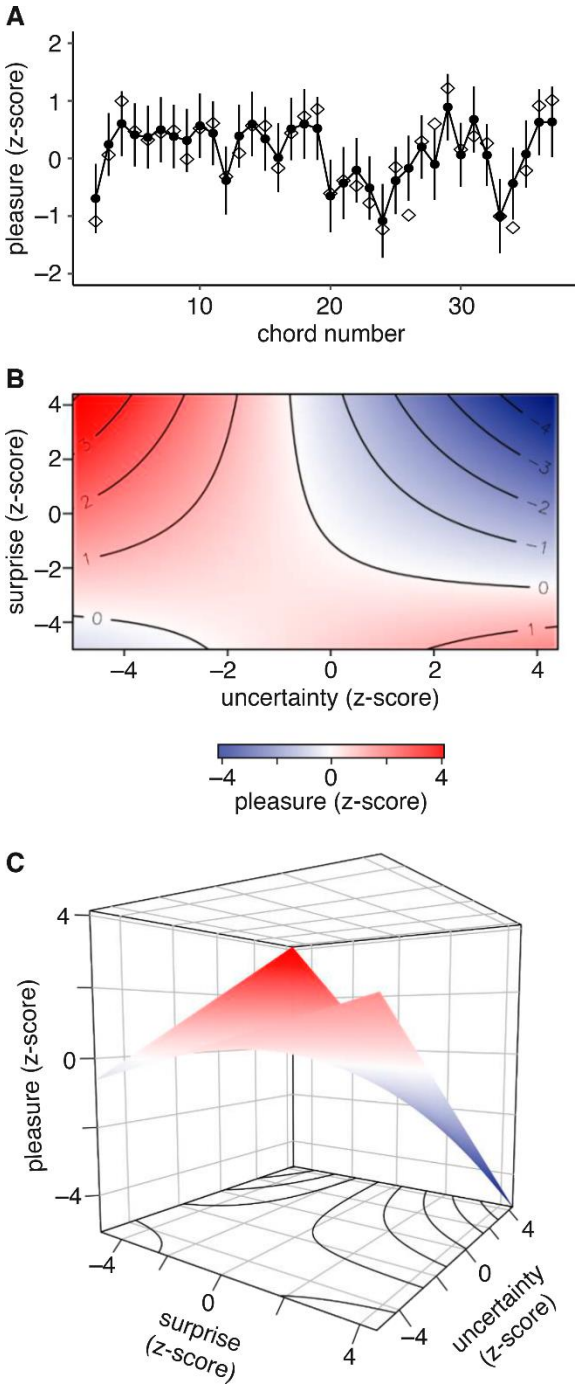
A
pleasure (z-score)
chord number
B
surprise (z-score)
uncertainty (z-score)
pleasure (z-score)
C
pleasure (z-score)
surprise (z-score)
uncertainty (z-score)

FIGURE 2

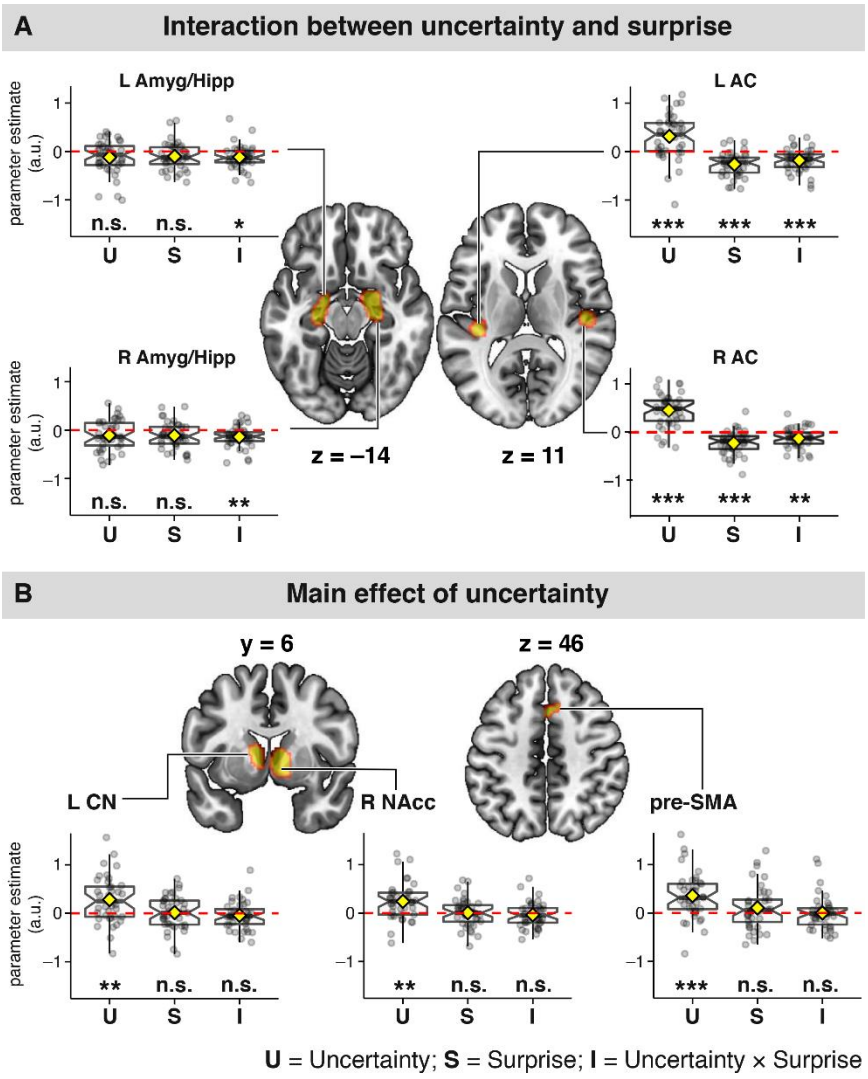
A
Interaction between uncertainty and surprise
L Amyg/Hipp
L AC
R Amyg/Hipp
R AC
parameter estimate (a.u.)
n.s. n.s. *
*** *** ***
n.s. n.s. **
*** *** **
U S I
z = –14
z = 11
B
Main effect of uncertainty
y = 6
z = 46
L CN
R NAcc
pre-SMA
** n.s. n.s.
** n.s. n.s.
*** n.s. n.s.
U = Uncertainty; S = Surprise; I = Uncertainty × Surprise

FIGURE 3