

1 **Pupil responses to pitch deviants reflect predictability of melodic sequences**

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11 **Keywords: music, melodies, contextual entropy, deviants, pupillometry**

12 **ABSTRACT**

13 Humans automatically detect events that, in deviating from their expectations, may signal prediction  
14 failure and a need to reorient behaviour. The pupil dilation response (PDR) to violations has been  
15 associated with sub- cortical signals of arousal and prediction resetting. However, it is unclear how the  
16 context in which a deviant occurs affects the size of the PDR. Using ecological musical stimuli that we  
17 characterised using a computational model, we showed that the PDR to pitch deviants is sensitive to  
18 contextual uncertainty (quantified as entropy), whereby the PDR was greater in low than high entropy  
19 contexts. The PDR was also positively correlated with the unexpectedness of notes. No effects of music  
20 expertise were found, suggesting a ceiling effect due to enculturation. These results show that the  
21 same sudden environmental change can lead to differing arousal levels depending on contextual  
22 factors, providing evidence for a sensitivity of the PDR to long-term context.

23 **Introduction**

24 The experience of surprise is very common in the sensory realm and often triggers automatic changes  
25 in arousal and attentional states that are fundamental to adaptive behaviours. Music is a ubiquitous  
26 and ecological example of a situation where changes in listeners' arousal and attention are  
27 intentionally manipulated. Composers may, for example, modulate the predictability of musical  
28 passages in order to achieve differing levels of tension in a listener. A great deal of empirical work has  
29 shown that surprising sounds are recognised by listeners in an effortless and automatic fashion  
30 (Pearce, 2018). This process is thought to be supported by a mismatch between the current  
31 unexpected input and the implicit expectations made possible by schematic and dynamic knowledge  
32 of stimulus structure (Huron, 2006; Krumhansl, 2015; Tillmann, Bharucha, & Bigand, 2000; Vuust &  
33 Witek, 2014). However, there is still rather little research examining mismatch responses under  
34 different degrees of uncertainty during passive listening.

35 Evidence of listeners experiencing events in music as unexpected comes from studies investigating  
36 behavioural (Marmel, Tillmann, & Delbé, 2010; Omigie, Pearce, & Stewart, 2012; Tillmann & Lebrun-  
37 Guillaud, 2006) and brain responses to less regular musical events (Bianco, Novembre, Keller, Kim, et  
38 al., 2016; Carrus, Pearce, & Bhattacharya, 2013; Koelsch, 2016; Koelsch, Gunter, et al., 2002; Maess,  
39 Koelsch, Gunter, & Friederici, 2001; Miranda & Ullman, 2007; Omigie, Pearce, Williamson, & Stewart,

40 2013; Pearce, Ruiz, Kapasi, Wiggins, & Bhattacharya, 2010). With regard to the former, priming  
41 paradigms have shown that a context allows perceivers to generate implicit expectations for future  
42 events, leading to facilitated processing (i.e., priming) of expected events. With regard to the latter,  
43 violation paradigms have shown increased brain responses to deviant events (out of key notes, or  
44 harmonically incongruent chords) within structured contexts as well as events which are musically  
45 plausible but more improbable in the given context. For example, Omigie et al. (2013) tested brain  
46 responses to melodies whose notes were characterised in terms of their predictability by a model of  
47 auditory expectations (Pearce, 2005). They showed that surprising events (more improbable notes)  
48 within melodies elicited a mismatch response – often termed the mismatch negativity, MMN (Garrido,  
49 Kilner, Stephan, & Friston, 2009; Näätänen, Paavilainen, Rinne, & Alho, 2007). This response decreased  
50 in amplitude for progressively more predictable events, as estimated by a computational model of  
51 melodic expectation. A similar parametric sensitivity to note unexpectedness has since also been  
52 observed in subcortical regions like the anterior cingulate and insula (Omigie et al., 2019). Moreover,  
53 sensitivity to music structure violation seems to emerge in all members of the general population that  
54 have had sufficient exposure to a given musical system (Bigand & Poulin-Charronnat, 2006; Pearce,  
55 2018; Rohrmeier, Rebuschat, & Cross, 2011), and this sensitivity is modulated by pre-existing  
56 schematic knowledge of music, as reflected in acquired levels of musical expertise (Fujioka, Trainor,  
57 Ross, Kakigi, & Pantev, 2004; Koelsch, Schmidt, & Kansok, 2002a; Tervaniemi, 2009; Vuust, Brattico,  
58 Seppänen, Näätänen, & Tervaniemi, 2012).

59 According to theoretical and empirical work framing perception in the context of predictive processing,  
60 the experience of surprise may be modulated by the predictability of a stimulus structure as it unfolds  
61 (Clark, 2013; Dean & Pearce, 2016; Friston, 2005; Ross & Hansen, 2016). Random or high entropic  
62 stimuli hinder the possibility of making accurate predictions about possible upcoming events, whilst  
63 stimuli characterized by familiarity or regular statistics will enable relatively precise predictions by  
64 permitting the assignment of high probability to a few possible continuations. Perceptually, it has been  
65 shown that listeners indeed experience high-entropic musical contexts with greater uncertainty  
66 compared to low entropy ones (Hansen & Pearce, 2014). Moreover, previous work has shown that  
67 neurophysiological signatures associated with auditory surprise display larger responses to a given  
68 deviant event when it is embedded in a low rather than high entropic context (Dean & Pearce, 2016;  
69 Garrido, Sahani, & Dolan, 2013; Hsu, Le Bars, Hamalainen, & Waszak, 2015; Ricardo Quiroga-Martinez,  
70 2018; Rubin, Ulanovsky, Nelken, & Tishby, 2016; Southwell & Chait, 2018). Therefore, research  
71 suggests that to understand whether and how surprising events modulate arousal and re-orient  
72 behaviours, the statistics of the proximal context must be considered.

73 A vast literature has used pupil dilation response (PDR) as a general marker of arousal, selective  
74 attention, and surprise (Aston-Jones & Cohen, 2005; Sara, 2009). Pupil dilation is associated with the  
75 locus coeruleus-norepinephrine (LCN) system (Laeng, Sirois, & Gredeback, 2012; Widmann, Schröger,  
76 & Wetzel, 2018), the activation of which results in wide spread norepinephrine release in the brain.  
77 Increase of the PDR has been extensively reported in response to violation of expectations or  
78 surprising/salient events in distracted listeners (Damsma & van Rijn, 2017; Liao, Yoneya, Kidani,  
79 Kashino, & Furukawa, 2016; Wetzel, Buttellmann, Schieler, & Widmann, 2016; Zhao et al., 2019), and  
80 when deviants are presented below participants' perceptual threshold (Fink, Hurley, Geng, & Janata,  
81 2018). Furthermore, a relationship between PDR and continuous ratings of surprisal in music  
82 (measured via a continuous slider) has been reported during passive listening (Liao, Yoneya, Kashino,  
83 & Furukawa, 2018). Other work has specifically associated the PDR to violations of statistical  
84 regularities in the sensory input even when these violations are behaviourally irrelevant (Alamia,

85 VanRullen, Pasqualotto, Mouraux, & Zenon, 2019; Zhao et al., 2019). These results provide supporting  
86 evidence for a role of norepinephrine in the tracking of abrupt deviations from the current predictive  
87 model of the world, and as a signal of prediction resetting that enables the discovery of new  
88 information (Dayan & Yu, 2006).

89 Music has the ability to play with our expectations, hence manipulating our arousal and emotions in  
90 an automatic fashion (Laeng, Eidet, Sulutvedt, & Panksepp, 2016; Meyer, 2001; Zatorre & Salimpoor,  
91 2013). Abrupt changes in register, texture and tonality are all examples of instances where the listener  
92 may have to reset or potentially abandon current models about the unfolding music. Such changes  
93 may however appear less surprising if embedded in high entropy contexts. Here, we use music as an  
94 ecological setting with which to study how the PDR to deviant musical events is modulated by structure  
95 of the stimulus context, specifically by its entropy. The growing field of computational musicology  
96 means that information in melodies can be statistically estimated. One particular model of auditory  
97 expectations – the Information Dynamics of Music, IDyOM (Pearce, 2005) – has been shown to model  
98 listeners’ experience of surprise and uncertainty. This unsupervised Markov model learns and  
99 estimates the conditional probability of each subsequent note in a melody based on a corpus on which  
100 it has been trained (long-term sub-model; extra-opus-learning) and the given melody as it unfolds  
101 (short-term sub-model; intra-opus learning). The model outputs information content and entropy  
102 values, which, respectively, reflect the experienced unexpectedness of a certain note after its onset  
103 and the experienced uncertainty in precisely predicting a subsequent note based on the preceding  
104 pitch probabilities.

105 We created novel melodies (Figure 1) that adhered to the principles guiding Western tonal melodic  
106 structure. We then created shuffled versions of these melodies to create stimuli that were higher in  
107 entropy albeit matched for pitch range, content and tonal space. The information theoretic properties  
108 of all stimuli were estimated using IDyOM (Pearce, 2005). Listeners were presented with these  
109 melodies either in their standard form or with a pitch deviant whilst PDR was measured. Participants  
110 were not informed about the presence of the pitch deviants, but asked to rate the unexpectedness of  
111 last note of each melody. We expected a larger PDR to deviant notes that are embedded in low rather  
112 than high entropy contexts, and that are higher in their unexpectedness – information content value  
113 – as estimated by the computational model. Also, we expected entropy of the melodies to predict  
114 subjective ratings of stimulus unexpectedness (Hansen & Pearce, 2014). Finally, based on evidence of  
115 greater brain response to musical violations in musicians than non-musicians (Vuust, Brattico,  
116 Seppänen, Näätänen, & Tervaniemi, 2012b), presumably reflecting expertise-related enhancement in  
117 the accuracy of predictive models, differences due to musical expertise (Müllensiefen et al., 2014) were  
118 also investigated.

## 119 **Methods**

### 120 *Participants*

121 Forty-seven participants (age:  $M=26.19$ ,  $SD=6.24$ , min.=20, max.=52, 68% female, representing 15  
122 nationalities) took part in the study. The sample scored relatively high on the general musical  
123 sophistication index, GoldMSI (Müllensiefen et al., 2014), with  $M=87.40$ ,  $SD=25.24$ , min.=32,  
124 max.=120. A big sample size was chosen based on a previous experiment using musical stimuli (Laeng  
125 et al., 2016) and to ensure statistical power. As a post-hoc confirmation of the adequacy of our sample-  
126 size, we quantified effect sizes of the difference between PDR to deviants in high vs. low entropy  
127 contexts. The power analysis was conducted in the G\*Power software package (version 3.1.9.2) with

128 the setting  $p = .05$  and  $N = 42$  and confirmed that our sample size was adequate ( $1 - \beta > .9$ ). Two  
129 participants reported ophthalmologic concerns or surgery prior to the experiment but were not  
130 excluded from participation as the pupil dilates even in blindsight participants (Weiskrantz, Cowey, &  
131 Barbur, 1999). Technical problems occurred during the recording of four participants, who were  
132 therefore excluded from the analysis. One subject was further excluded as blink gaps were too large  
133 to be interpolated. In sum, forty-two participants' data were analysed.

134 Ethical approval for this study was granted by the Research Ethics Committee of Goldsmiths, University  
135 of London. Participants were instructed as to the purpose of the study, and consented to participate  
136 (written informed consent). Participation was remunerated with 5 pounds.

### 137 *Stimuli*

138 One-hundred-twenty melodies were used in this study (thirty originally composed, thirty matched  
139 'shuffled' versions, and sixty corresponding versions with a deviant tone always as the 13<sup>th</sup> note). The  
140 melodic sequences comprised 20 tones, were 5 seconds long, isochronous (with an inter-onset-interval  
141 of 250 ms, 20/4 bar with 240 bpm), and had constant intensity and timbre (MIDI generated piano  
142 timbre).

143 The corpus of melodies was composed according to the principles of Western-tonal music and using  
144 all tones of the chromatic scale. Ambitus and tonal space varied across melodies. Interval size did not  
145 exceed a perfect fifth (Narmour, 2015) between adjacent notes. Thus, the original melodies were  
146 characterized by a smooth contour. To generate matched melodies that controlled for potential biases  
147 such as tonal space, pitch class, frequency range or ambitus, high entropy melodies were created from  
148 the original melodies by randomizing the order of constituent notes using MIDI processing tools (Eerola  
149 & Toivainen, 2004). Our manipulation of entropy, whereby notes in original melodies were randomly  
150 shuffled without constraint, necessarily resulted in the mean absolute interval size being greater in  
151 high entropy than in low entropy melodies [L vs. H:  $t(58) = -2.644$ ,  $p\text{-value} = .01$ ]. Corpus studies of  
152 western tonal music show that large interval sizes are much less common than small ones (Huron,  
153 2001). Thus, we anticipated that the presence of such large intervals would lead to the higher entropy  
154 levels desired for the high entropy condition.

155 Deviant notes were inserted in all 60 melodies (original and shuffled version) at the onset of the 13<sup>th</sup>  
156 note (3000ms on the salient onbeat) in order to create the corresponding set of *deviant melodies* (Fig.  
157 1). The deviant note was integrated into the second half of the melody in order to allow the  
158 establishment of an expectation-forming context before its occurrence. To ensure that differences in  
159 the PDR to the deviant notes between low and high entropy condition were not attributable to  
160 difference in the just preceding event, but to the context, the interval size between the deviant and  
161 the preceding 12th note was the same in matched pairs of high and low entropy melodies (see Fig. 1).  
162 However, interval size of the deviant varied between maj7 up/down, min9 up/down and aug11  
163 up/down as those intervals sound particularly unusual within a melodic progression. Larger interval  
164 size of the deviant was assigned to matched pairs with lower entropy differences. This allowed for a  
165 variety of deviant interval sizes (a range of unexpectedness) while ensuring salience of deviants even  
166 in melodies showing relatively smaller entropy differences.

167 Entropy values were assigned by the IDyOM model to each note of the melodies. The IDyOM model  
168 considered one pitch viewpoint, namely 'cpitch', whereby chromatic notes count up and down from  
169 the middle pitch number ( $C=60$ ) (Pearce, 2005). Through a process of unsupervised learning, the model  
170 was trained on a corpus (903 Western tonal melodies) comprising songs and ballads from Nova Scotia

171 in Canada, German folk songs from the Essen Folk Song Collection and chorale melodies harmonised  
172 by J.S. Bach. The probability of each note of the stimulus used here were then estimated based on a  
173 combination of the training set's statistics and those of the given melody at hand. The model outputs  
174 information content and entropy values. In mathematical terms, information content is inversely  
175 proportional to the probability of an event  $x_i$ , with  $IC(x_i) = -\log_2 p(x_i)$  (MacKay, 2003), while the  
176 maximum entropy is reached when all potential events  $x_i$  are equally probable, with  $p(x_i) = 1/n$ , where  
177  $n$  equals the number of stimuli. In psychological terms, information content represents how surprising  
178 each subsequent note is based on its fit to the prior context (Pearce & Wiggins, 2006). In contrast,  
179 entropy refers to the anticipatory difficulty in precisely predicting a subsequent note. Mean entropy  
180 values, obtained by taking the mean entropy of all notes, were used to characterise the predictability  
181 of each melody. Given our manipulation, mean entropy was largely, but not entirely, explained by the  
182 mean interval size of melodies ( $\rho = .474$ ,  $p < .001$ ). These values were then used to predict subjective  
183 inferred uncertainty (measured as unexpectedness of last note) about each melody, and to categorise  
184 melodies into low and high entropy groups. By controlling that the interval preceding the deviant note  
185 was identical across high and low entropy condition, we predicted that a greater PDR to deviant notes  
186 in low than high entropy melodies should be attributable to the difference in the context.

### 187 *Procedure*

188 The experiment was presented using the Experiment Builder Software and pupil diameter was  
189 recorded using EyeLink 1000 eye-tracker at a 250Hz sampling rate (SR Research, [www.sr-research.com/experiment-builder](http://www.sr-research.com/experiment-builder)). Prior to the data acquisition, a three-dot calibration was  
190 conducted to ensure adequate gaze measurements. Participants were further allowed to adjust the  
191 sound volume to a comfortable level and were asked to reduce head movements to a minimum  
192 throughout the recording session. As no differences were anticipated between the left and right pupil,  
193 the left pupil was recorded in ten and the right pupil in 32 participants depending on the participants'  
194 dominant eye. To reduce motion artefacts, the head was stabilized using the SR Research Head Support  
195 chinrest placed 50 cm from the presentation screen.

197 During the experiment, the 120 melodies were presented binaurally through headphones in a  
198 randomized order. Each trial was triggered by the experimenter on the control computer when the  
199 fixation was stable at less than two arbitrary gaze units away from the fixation point. When recording  
200 was enabled, a white fixation dot on the grey screen turned black to prepare participants for the onset  
201 of the melody. The fixation cross was displayed for 7 seconds after stimulus onset. Each trial was  
202 preceded by a 400 ms baseline period and followed by a 2000 ms post stimulus offset. The melody was  
203 5000 ms long and participants were instructed not to blink or move but to fixate during that whole  
204 period. Participants were allowed to take breaks to avoid fatigue effects at their convenience. A re-  
205 calibration procedure using the 3-dot-calibration was applied after each break.

206 Participants were instructed to carefully listen to the melody while fixating on the fixation point in the  
207 centre of the screen throughout the recording period. They were not informed about the deviant  
208 manipulation. After each trial, participants rated the final note on a Likert-scale ranging from 1 (not at  
209 all unpredictable) to 7 (extremely unpredictable) in a forced-choice task on the presentation screen.  
210 Data on the subjects' musical expertise and sociodemographic background was collected at the end of  
211 each experiment using the GoldMSI (Müllensiefen et al., 2014). The whole study lasted approximately  
212 one hour.

### 213 *Data pre-processing*

214 Blinks were identified and removed from the signal using MATLAB R2017b. These were characterized  
215 by a rapid decline towards zero from blink onset, and a rapid rise back to the regular value at blink  
216 offset. 100ms of the signal was removed before and after the missing data points (Troncoso, Macknik,  
217 & Martinez-Conde, 2008) and missing data were interpolated: four equally spaced time points were  
218 used to generate a cubic spline fit to the missing time points between blink onset ( $t_2$ ) and blink offset  
219 ( $t_3$ ) of the unsmoothed signal, with  $t_1 = t_2 - t_3 + t_2$  and  $t_4 = t_3 - t_2 + t_3$  (Mathôt, Fabius, Van Heusden, & Van  
220 der Stigchel, 2018). Trials containing more than 15% missing data were excluded from the analysis ( $M =$   
221  $.3$ ,  $SD = .9$  trials across subjects). Data were cleaned of artefacts using Hampel filtering (median filtered  
222 data; Pearson, Neuvo, Astola, & Gabbouj, 2016), and smoothed using a Savitzky-Golay filter of  
223 polynomial order 1 over the entire trial epoch. Finally, data were z-scored, and then baseline-corrected  
224 by subtracting the median pupil size of 400 ms baseline before melody onset. To analyse the time-  
225 window after deviant onset, data were baselined from 400 ms before deviant onset. The normalized  
226 pupil diameter was time-domain-averaged across trials of each condition.

### 227 *Experimental design and statistical analysis*

228 We estimated a single time series for each sequence type: low or high entropy with either standard or  
229 deviant note type (*S-Low/D-Low/S-High/D-high*) by averaging across trials and participants. Statistical  
230 analysis was performed using Fieldtrip's cluster-based permutation test (Maris & Oostenveld, 2007),  
231 with a significance threshold at 5% to control family-wise error-rate (FWER). This analysis revealed the  
232 time windows showing significant difference between the compared time series.

233 We first compared responses to deviant notes in the low and high entropy contexts with the  
234 corresponding standard notes using signals recorded across the entire melody duration (baselined 400  
235 ms before melody onset). This ensured that differences between deviant and corresponding standards  
236 were not due to differences in the immediately preceding note. Then, to determine how the deviant  
237 PDR is affected by the entropy of the melodic context, we focussed on the time window from deviant  
238 onset to the end of the melody (3000 to 5000 ms epochs). We thus baselined to 400 ms before deviant  
239 onset, and we tested for an interaction of the deviant and context manipulation: (*D-Low – S-low*) vs.  
240 (*D-High – S-High*). Further, we compared the responses to standard tones in the two contexts (*S-Low*  
241 *– S-High*) to ensure that any differences were not driven simply by the standard notes (the control  
242 conditions).

243 To assess a potential influence of expertise on the PDR to deviants (data between 3000 and 5000 ms  
244 baselined to 400 ms before deviant onset), we computed the mean PDR to deviant trials as *D-Low – S-*  
245 *Low* for deviants in low entropy context, and *D-High – S-High* for deviants in high entropy context.  
246 Participants were split into two groups of musical experts and non-experts based on GoldMSI scores  
247 ( $Mdn = 96$ ). An ANOVA with within-subject factor context (low/ high entropy) and expertise as between-  
248 subject factor (expert/non-expert) was computed.

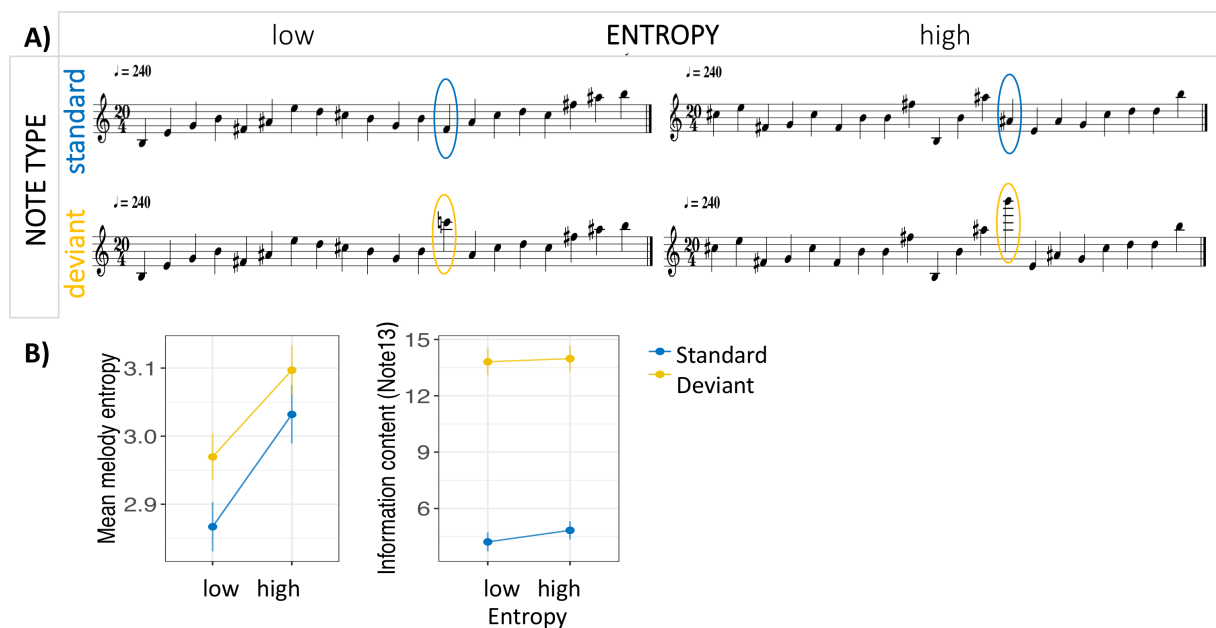
### 249 **Results**

250 *Stimuli characterization.* Analyses were carried out to clarify the nature of all differences in information  
251 theoretic properties of the different stimuli. Figure 1B (left panel) shows the mean entropy values for  
252 all conditions (*D-Low*:  $M = 2.96$ ,  $SD = .18$ ; *D-High*:  $M = 3.09$ ,  $SD = .19$ ; *S-Low*:  $M = 2.86$ ,  $SD = .19$ ; *S-High*:  
253  $M = 3.03$ ,  $SD = .23$ ). An ANOVA with context (low/ high entropy) and note type (deviant / standard) as  
254 between-group factors yielded a main effect of context [ $F(1,116) = 15.20$ ,  $p < .001$ ,  $np2 = .12$ ],  
255 indicating higher entropy in *High* than *Low entropy* melodies [ $t(58) = 2.85$ ,  $p = .006$ ]. A significant main  
256 effect of note type [ $F(1,116) = 5$ ,  $p = .027$ ,  $np2 = .04$ ], was not supported by a further post hoc

257 comparison [ $t(58) = -1.641, p = .11$ ]. No interaction was found between the two factors [ $F(1,116) = .25,$   
 258  $p = .617, np2 < .01$ ].

259 Figure 1B (right panel) shows that the unexpectedness of deviant notes, as reflected by information  
 260 content values, was comparable between low and high entropy melodies. An ANOVA with between  
 261 group factors context (low / high entropy) and note type (deviant / standard) yielded a main effect of  
 262 note type [ $F(1,116) = 239.02, p < .001, np2 = .67$ ], a non-significant main effect of context [ $F(1,116) =$   
 263  $.42, p = .517, np2 = .01$ ], and no interaction between the two factors [ $F(1,116) = .00, p = .714, np2 <$   
 264  $.01$ ] – thus indicating higher information content in deviant than standard notes regardless of the  
 265 context in which they were embedded [ $t(58) = -12.321, p < .001$ ]. The similar IC levels of deviant for  
 266 the two entropy conditions may be due to fact that in both low and high entropy contexts, deviants  
 267 were similar in being characterised by very large interval departures away from the melodic contour  
 268 (as opposed to the relatively naturalistic events that occurred in real melodies (Dean & Pearce, 2016).  
 269 Critically, that deviant IC levels are similar for the two entropy conditions, supports our suggestion that  
 270 stimulus context (and not just the IC level an incoming event) has the ability to modulate the PDR.

271 IC was positively predicted by interval size between the 12th and 13th note ( $rho = .862, p < .001$ ), in  
 272 line with research showing that amongst multiple psychological representations of pitch (e.g., height,  
 273 contour, etc.), interval exerts a major contribution to perception of surprise (Levitin & Tirovolas, 2009;  
 274 Pearce, 2018; Quiroga-martinez et al., 2019).



275

276

277 **Fig. 1. Experimental design.** Participants listened to the melodies of 20 notes and had to rate how  
 278 unexpected they found the last note on a seven-step Likert scale (– 1 equal ‘not at all unpredictable’  
 279 and 7 ‘extremely unpredictable’). The design included two factors: Contextual entropy (low/high) and  
 280 Note type (standard/deviant). Melodies containing deviant notes were 50% of the trials and the  
 281 deviant notes occurred always at the 13<sup>th</sup> position. **B) Characterization of the stimuli.** A model of  
 282 musical expectations was used to characterise the stimuli: Mean entropy was larger for high than low  
 283 entropy melodies regardless of the presence of deviant (yellow) or standard (blue) tones. Mean  
 284 information content of deviants (yellow) was larger than standard (blue) tones regardless of the  
 285 entropy of the context.

286 *PDR characterization.* Figure 2A shows the time course of the PDR across conditions (*S-Low* = standard  
287 low entropy, *S-High* = standard high entropy, *D-Low* = deviant low entropy, *D-High* = deviant high  
288 entropy) baselined 400 ms before melody onset. A comparison between *S-Low* and *S-High* showed no  
289 difference in the PDR as a function of entropy levels of the melody, whilst the PDR to deviants (*D-Low*  
290 vs. *D-High*) was greater in predictable than unpredictable contexts (diverging at .56 s from deviant  
291 onset). The response to deviants in the predictable contexts was greater than the relative standard  
292 condition (*D-Low* vs. *S-Low*:  $p = .029$ ), significantly diverging from *S-Low* between 3.57 and 5.64 s after  
293 melody onset. Conversely, the response to deviants in unpredictable contexts did not differ from the  
294 relative standard condition (*D-High* vs. *S-High*), despite their high information content (see Figure 1B,  
295 middle panel).

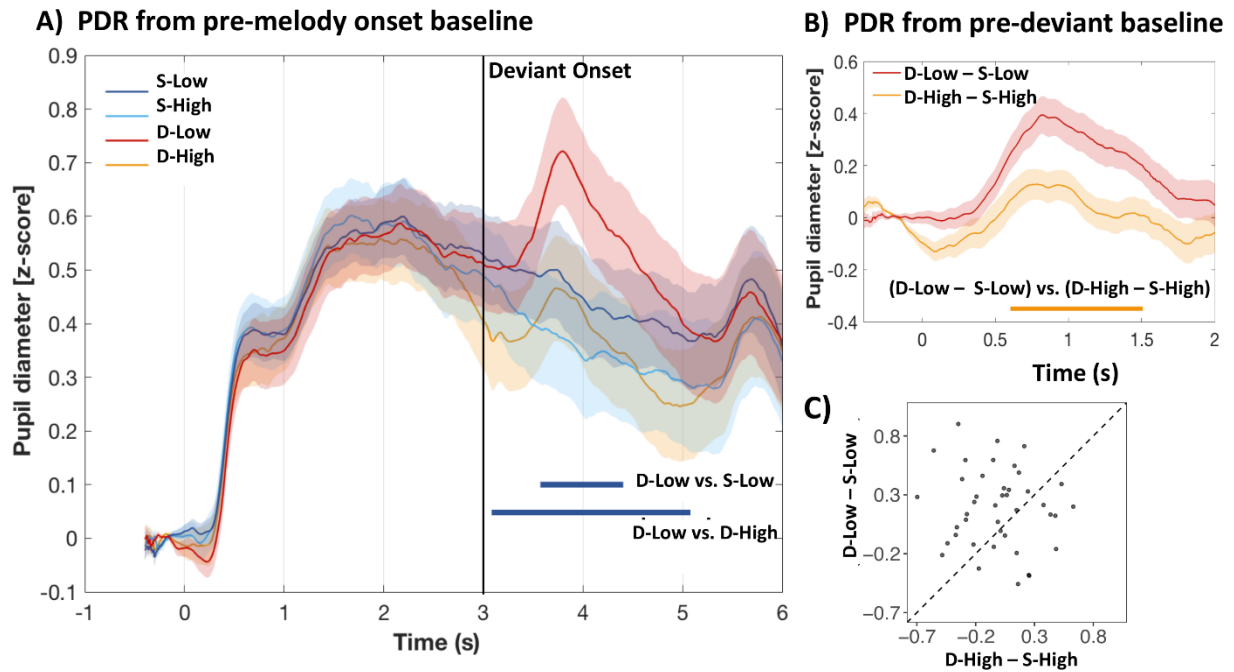
296 Figure 2B shows the PDR to deviants baselined 400 ms before deviant onset. We show the conditions  
297 *D-Low* and *D-High* following subtraction of the relative standard conditions. The comparison between  
298 the two time-courses confirmed that *D-Low* evoked a larger response than *D-High* starting at .59 s from  
299 deviant onset ( $p = .007$ ) and ending at 1.5 s. Intrinsic noise in the baseline may explain the very early  
300 divergence between the curves, which however was not significant. Importantly, this pattern was  
301 observed in 67% of the participants (Figure 2C).

302 We run a post hoc analysis (Figure 3A) to investigate the relationship between the PDR related to the  
303 13<sup>th</sup> note (including both standard and deviant notes) and associated information content for low and  
304 high entropy melodies. For each subject and for each melody, the average PDR to the 13<sup>th</sup> note was  
305 computed from the pre-deviant baseline (as in Figure 2B). A linear model with the factor context (Low  
306 /High) and information content as continuous variable was run to predict the PDR. This analysis yielded  
307 no main effect of context [ $F(1,116) = .005$ ,  $p = .941$ ,  $np2 < .001$ ] and a main effect of information  
308 content [ $F(1,116) = 4.911$ ,  $p = .029$ ,  $np2 = .041$ ] and a no significant interaction [ $F(1,116) = 3.274$ ,  $p =$   
309  $.073$ ,  $np2 = .027$ ]. This suggests that the PDR is sensitive to a large range of unexpectedness levels.

310 We further investigated potential influences of expertise on the mean PDR to deviants (computed as  
311 *D-Low* – *S-Low* for deviants in low entropy contexts, and *D-High* – *S-High* for deviants in high entropy  
312 contexts on the data between 3000 and 5000 ms baselined to 400 ms before deviant onset as in Figure  
313 2B). The ANOVA examining the effect of musical expertise on the mean PDR to deviants yielded a main  
314 effect of context [ $F(1,40) = 5.09$ ,  $p = .03$ ,  $np2 = .11$ ]. The main effect of expertise was not significant  
315 [ $F(1,40) = 3.72$ ,  $p = .061$ ,  $np2 = .09$ ], and no interaction between the two factors was seen [ $F(1,40) =$   
316  $2.18$ ,  $p = .147$ ,  $np2 = .05$ ]. This confirmed that the mean PDR to deviants was greater in low than high  
317 entropy contexts although no considerable difference between experts and non-experts was observed.

318 Finally, we showed that the model reliably predicted subjective uncertainty levels (inferred entropy)  
319 of the melody progressions (Hansen & Pearce, 2014) (Figure 3B). The measure of the unexpectedness  
320 of the last note was collected after participants listened to each melody. We found that the mean  
321 ratings for each melody strongly correlated with the information content of the last note of the melody  
322 ( $\rho = .355$ ,  $p < .001$ ), and with the mean IDyOM entropy values for that melody ( $\rho = .400$ ,  $p < .001$ ).  
323 This analysis validated our categorization of melodies based on the IDyOM output.

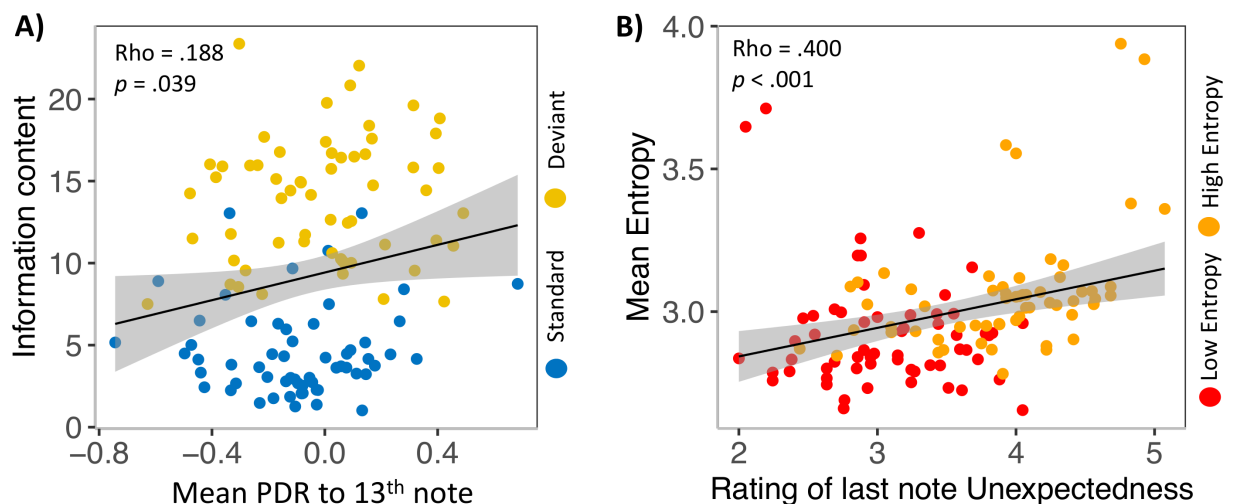




324

325 **Fig. 2. A)** The PDR for all conditions from melody onset (*S-Low* = standard low entropy, *S-High* =  
 326 standard high entropy, *D-Low* = deviant low entropy, *D-High* = deviant high entropy). The PDR to  
 327 deviants compared to standard tones (*D-Low* vs. *S-Low*) in low entropy contexts diverged between  
 328 3.57 and 5.64 s from melody onset (.57 s from deviant onset), but did not differ in high entropy  
 329 contexts. Also, the PDR to deviants was greater in low than in high entropy contexts (*D-Low* vs. *D-High*)  
 330 (diverging at 3.056 s from melody onset), but there was no significant context-dependent difference  
 331 between the standard tones (*S-Low* and *S-High*). Shaded regions around the curves represent standard  
 332 error in the mean estimated with bootstrap resampling (1000 iterations; with replacement). **B)**  
 333 Interaction effect of deviant and context entropy on the PDR after deviant onset. The difference  
 334 between the PDR to deviant and standard tones was greater in low than in high entropy contexts. This  
 335 effect emerged .59 after deviant onset and ended at 1.5 s. **C)** The relationship between the PDR for *D-*  
 336 *High* – *S-High* and *D-Low* – *S-Low* conditions. Each data point represents an individual participant. Dots  
 337 above the diagonal reveal that 67% of participants showed a greater PDR to deviants in low compared  
 338 with high entropy contexts.

339



340

341

342 **Fig. 3. A)** The unexpectedness of the 13<sup>th</sup> notes (deviants and standards) was estimated by the IDyOM  
343 model and showed a positive correlation (Spearman) with the mean evoked PDR. Blue and yellow dots  
344 represent each of the standard and deviant notes. Shading represents s.e.m. **B)** The stimulus entropy  
345 was computed by the IDyOM model, and validated by participants' self-reports about the overall  
346 unexpectedness of each melody. Each dot represents one of the 120 melodies. Red and orange dots  
347 represent each of the low and high entropy melodies, respectively ( $N = 120$ ). Shading represents s.e.m.

### 348 **Discussion**

349 We report that pupil dilation response (PDR) to behaviourally irrelevant deviants occurs when deviants  
350 are embedded in predictable rather than unpredictable melodies. We showed that the amplitude of  
351 the response is predicted by the information content (or unexpectedness) of the musical deviants. We  
352 also replicate the previous finding that listeners' experience of uncertainty is predicted by the entropy  
353 of the music (Hansen & Pearce, 2014). These results show that the same sudden environmental change  
354 leads to differing levels of arousal depending on whether it occurs in low or high states of uncertainty.  
355 Our results suggest that the more stable predictions formed in predictable rather than unpredictable  
356 contexts may be more abruptly violated by surprising events, possibly leading to greater changes in  
357 the listeners' arousal state.

358 The observed modulatory effect of context predictability on the PDR to deviants is consistent with a  
359 body of electrophysiological work showing context effects on mismatch like responses at the cortical  
360 level (Garrido et al., 2013; Quiroga-Martinez et al., 2019; Southwell & Chait, 2018). Here we show a  
361 similar pattern but in autonomic markers of arousal, as reflected by the PDR. Pupil response is thought  
362 to be driven by norepinephrine activity in the locus coeruleus (LC) (Joshi, Li, Kalwani, & Gold, 2016).  
363 This is a key subcortical nucleus which widely connects to the brain (Sara, 2009) to signal unexpected  
364 and abrupt contextual changes (Alamia et al., 2019; Damsma & van Rijn, 2017; Zhao et al., 2019). It has  
365 been hypothesised (Zhao et al., 2019) that MMN-related brain systems (Garrido et al., 2009; Hsu et al.,  
366 2015; Southwell & Chait, 2018) may trigger norepinephrine-mediated updating or interruption of  
367 ongoing top-down expectations. In line with this hypothesis, Alamia et al. (2019) have shown a  
368 correlation between pupillary response and MMN-like response evoked by violations of expectations,  
369 providing evidence of a link between the sources of these two responses. Top-down expectations  
370 about unfolding sensory signals have been associated with the temporo-frontal network in music-  
371 violation paradigms, which is thought to link present and past information to generate predictions  
372 about forthcoming events (Bianco, Novembre, Keller, Seung-Goo, et al., 2016; Koelsch, Gunter, et al.,  
373 2002; Tillmann, Janata, & Bharucha, 2003). Based on this existing evidence and in line with a model  
374 resetting hypothesis, our results suggest that listeners generate stronger predictive models (in the  
375 predictable melodies). These may be supported by temporo-frontal cortical regions, and require a  
376 greater signal (greater PDR) to be interrupted.

377 Albeit indirectly, our results also establish a link between subcortical and cortical activity in response  
378 to unexpected events under different states of uncertainty. Increased MMN response under low states  
379 of uncertainty (Quiroga-Martinez et al., 2019; Southwell & Chait, 2018) are replicated in the pupil  
380 response, reflecting a general increase in arousal. A possible interpretation, in line with the predictive  
381 coding theory (Friston, 2005), is that more stable expectations, representative of a strong predictive  
382 model, are reflected in precision-weighting of the prediction error, and hence a stronger response when  
383 the input mismatches the current predictions. Conversely, in high entropic contexts predictive models  
384 are weak, and the prediction error attenuated. This mirroring pattern between cortical (MMN) and  
385 subcortical (as reflected by the PDR) responses may have important behavioural advantages.

386 Specifically, strong predictive models can suddenly be abandoned when they are revealed to be  
387 erroneous, thus allowing speedy reorienting behaviours and quicker engagement with new potentially  
388 relevant stimuli. One limitation with regard to this possible interpretation is the nature of the deviant  
389 events used here, whereby the deviating event was a single note that did not lead to any long-lasting  
390 changes in the statistics of the unfolding sequence. Further studies combining cortical and pupil  
391 response measurements in continuously changing stimuli are necessary to corroborate our working  
392 hypothesis.

393 The absence of difference between high and low entropic contexts in the sustained pupil response (in  
394 the first half of the melodies) suggests that the pupil is relatively unresponsive to slowly unfolding  
395 stimulus structures, at least when listeners are not required to actively track them (Alamia et al., 2019;  
396 Zhao et al., 2019). Whilst cortical responses have been shown to be sensitive to the statistics of the  
397 unfolding stimulus structure (Barascud, Pearce, Griffiths, Friston, & Chait, 2016; Sohoglu & Chait, 2016;  
398 Southwell et al., 2017), subcortical responses may be less sensitive. This suggests they may be more  
399 vulnerable to stimulus properties and tasks demands (Zhao et al., 2019).

400 We also found that the PDR mismatch response is positively predicted by unexpectedness of incoming  
401 notes (in line with electrophysiological studies (Omigie et al., 2013; Quiroga-martinez et al., 2019), but  
402 it seems not to be modulated by degree of musical expertise. Larger MMN responses have been shown  
403 for musicians in a range of studies examining electrophysiological correlates of expectancy violation in  
404 music (Koelsch, Schmidt, & Kansok, 2002b; Oechslin, Van De Ville, Lazeyras, Hauert, & James, 2013;  
405 Tervaniemi, Tupala, & Brattico, 2012). One possibility is that this reflects a ceiling effect whereby the  
406 rather salient deviants used here were relatively easy to detect (given their large interval departures  
407 away from the melodic contour). Future studies examining the PDR to more subtle differences in  
408 musical structure may be expected to show similar expertise effects to those reported in previous  
409 studies.

410 Finally, our results provide evidence of music's usefulness in investigating the neural mechanisms  
411 underlying processing of stimuli statistical properties in a common, highly structured, and ecologically  
412 valid type of auditory stimulus, as music. While our work here focused on pitch expectations, previous  
413 studies have shown that music-induced temporal expectations are also tracked by the PDR (Damsma  
414 & van Rijn, 2017). Future experiments could address, for example, how introducing rhythm to  
415 concurrent melodic lines may affect the PDR to unexpected events. Similarly, that music induced chills  
416 – high arousal physiological responses associated with subjective pleasure – are associated with  
417 increased PDR (Laeng et al., 2016) suggest a usefulness of music in examining the relationship between  
418 stimulus information theoretic properties and reward processing. Whilst the IDyOM model used here  
419 is only able to deal with monophonic MIDI music, the development of the model for polyphonic music  
420 is underway (<https://psyarxiv.com/wgijyv/>) and it is expected that the approach we take here will be  
421 beneficial in a wider range of contexts in future years. By showing that predictive uncertainty can be  
422 used to modulate prediction-error related arousal, our findings have implications for understanding  
423 the variety of forms listeners' aesthetic appreciation of music may take. However, considering, more  
424 generally, the tight coupling between the error-related norepinephrine system and the reward-seeking  
425 dopaminergic pathway (Laeng et al., 2016; Xing, Li, & Gao, 2016; Zatorre & Salimpoor, 2013), our  
426 results emphasize that measuring the PDR may be useful for investigating the reward value of  
427 information across a range of modalities and domains.

428 In sum, we show that pupillometry in the auditory domain can reliably track the effect of context  
429 uncertainty on responses to sudden environmental change and independently from overt behavioural

430 responses. Given the hypothesised interplay between cortical and subcortical mechanisms in precision  
431 weighted anticipatory processing and prediction resetting, a first milestone is set towards the non-  
432 invasive quantification of the subcortical components.

433

#### 434 **Competing Interests Statement**

435 The author(s) declares no competing interests.

#### 436 **Author Contributions**

437 **RB** conceived the experiments; analysed the bulk of the data; wrote the manuscript.

438 **EP** conceived and performed the experiments; contributed to analysis; wrote the manuscript; secured  
439 the funding.

440 **DO** conceived the experiments; contributed to analysis; wrote the manuscript; secured the funding.

#### 441 **Funding**

442 This study was funded by a grant from the psychology department at Goldsmiths, University of London.

#### 443 **Acknowledgments**

444 We are grateful to Prof. Maria Chait and Sijia Zhao for inspiring discussions.

#### 445 **Data Availability Statement**

446 The datasets for this study can be found in the OSF repository (link:  
447 [https://osf.io/u2qdr/?view\\_only=7a9fa6bacbb249b090282377c1542d29](https://osf.io/u2qdr/?view_only=7a9fa6bacbb249b090282377c1542d29)).

#### 448 **Informed Consent Statement**

449 All participants provided written informed consent. The study was approved by the Ethics Committee  
450 at Goldsmiths, University of London.

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