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Abstract:	<p>Some theories posit that the perception of consonance is based on neural periodicity detection, which is dependent on accurate phase locking of auditory nerve fibers to features of the stimulus waveform. In the current study, 15 listeners were asked to rate the pleasantness of complex tone dyads (two note chords) forming various harmonic intervals, and bandpass filtered in a high frequency region (all components > 5.8 kHz), where phase locking to the rapid stimulus fine structure is thought to be severely degraded or absent. The two notes were presented to opposite ears. Consonant intervals (minor third, and perfect fifth) received higher ratings than dissonant intervals (minor second, and tritone). The results could not be explained in terms of phase locking to the slower waveform envelope, because the preference for consonant intervals was higher when the stimuli were harmonic, compared to a condition in which they were made inharmonic by shifting their component frequencies by a constant offset, so as to preserve their envelope periodicity. Overall the results indicate that, if phase locking is indeed absent at frequencies greater than ~5 kHz, neural periodicity detection is not necessary for the perception of consonance.</p>

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Consonance perception beyond the traditional existence region of pitch

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16 I. INTRODUCTION

17 In Western music certain harmonic intervals such as the perfect fifth and the perfect
18 fourth are regarded as consonant, and are described as producing a pleasant and stable sound
19 sensation; other harmonic intervals, such as the minor second and the tritone, are regarded
20 as dissonant, and are described as producing an unpleasant and tense sound sensation. The
21 origins of this distinction between consonant and dissonant intervals have been debated for
22 centuries. The earliest theory of consonance is often attributed to the Greek mathematician
23 Pythagoras ([Bowling and Purves, 2015](#)), who considered as consonant those musical intervals
24 whose frequencies formed “simple” ratios between small integers (e.g. 2:1, 3:2, 4:3).

25 In the last two centuries the debate has focused on the possible physiological mecha-
26 nisms leading to the sensation of consonance. One of the major psychoacoustical theories
27 of consonance posits that the sensation of dissonance is directly related to the sensation of
28 “roughness” caused by the amplitude fluctuations, also known as “beats”, produced when
29 the frequencies of two tones are close enough as to interact within the same cochlear fil-
30 ter ([Helmholtz, 1954](#); [Kameoka and Kuriyagawa, 1969a](#); [Plomp and Levelt, 1965](#)). There
31 are several pieces of evidence against this theory. Cochlear interactions cannot explain the
32 fact that the sensation of dissonance persists when tones are presented dichotically to pre-
33 vent cochlear interactions ([Bidelman and Krishnan, 2009](#); [Terhardt, 1974b](#)). However, beats
34 could also occur centrally, within a binaural critical band ([Feeney, 1997](#)), rather than being
35 based on cochlear interactions. Additionally, it could be that the negative affect of disso-
36 nance is transferred by associative learning from naturally occurring conditions in which

37 cochlear interactions are present, to artificial conditions in which these are eliminated by
38 dichotic presentation.

39 Additional evidence against the idea that dissonance is caused by amplitude beats comes
40 from the fact that a) intervals such as the perfect fifth are still considered consonant even
41 when presented at low fundamental frequencies (F0s), where the notes produce considerable
42 roughness (Terhardt, 1974b); b) dissonance does not grow with increasing number of har-
43 monics in chords, which increases the sources of amplitude beats (McLachlan *et al.*, 2013);
44 c) interindividual differences in preference for consonant over dissonant musical intervals
45 correlate with preference for harmonic stimuli, rather than with preference for stimuli lack-
46 ing beats (McDermott *et al.*, 2010); d) people with amusia show an aversion to amplitude
47 beats similar to that of controls, but do not show a preference for consonant over dissonant
48 intervals (Cousineau *et al.*, 2012).

49 Another major psychoacoustical theory of consonance holds that consonance is based
50 on harmonicity: Simultaneously presented tones are perceived as more or less consonant
51 depending on how well their frequency components match a single harmonic series (Terhardt,
52 1974b). For example, the frequency components of tones forming musical intervals such as
53 the perfect fifth and the perfect fourth, that are generally perceived as highly consonant,
54 fall closely into a single harmonic series, while the frequency components of tones such as
55 the minor second and the tritone, which are generally perceived as dissonant, do not.

56 Harmonicity plays a key role in the perception of pitch (Plack and Oxenham, 2005), as
57 well as in the segregation of concurrent sounds (Darwin, 2005), but the way harmonicity
58 is encoded in the auditory system is unclear. One major theory holds that harmonicity

59 is encoded by the detection of neural periodicities arising as a result of the phase locking
60 of auditory nerve fibers to periodicities present in the stimuli (Meddis and O’Mard, 2006).
61 Mathematical (Ebeling, 2008), functional (Patterson, 1986) and physiological (Bidelman and
62 Heinz, 2011) models of consonance have been proposed on the basis of this theory. These
63 models are supported by single-fiber recordings in non-human animals showing that temporal
64 information for the perception of consonance is available at the level of the auditory nerve
65 (Tramo *et al.*, 2001). Additionally, several studies in humans have shown that consonance
66 ratings are related to measures of harmonicity derived from the scalp-recorded frequency
67 following response (FFR) (Bidelman and Krishnan, 2009; Bones *et al.*, 2014; Bones and
68 Plack, 2015a·b), a response that reflects neural phase locking in the brainstem.

69 Phase locking in the auditory nerve, which is the basis of the “temporal” models of con-
70 sonance mentioned above, declines progressively with increasing frequency, and for most
71 species studied becomes undetectable above about 5 kHz (Johnson, 1980; Palmer and Rus-
72 sell, 1986; Winter, 2005). The upper limit of phase locking in humans has been estimated
73 from recordings of the auditory nerve compound action potentials to be at best similar
74 to, and likely worse than, this 5 kHz limit (Verschooten *et al.*, 2018). Therefore, “tempo-
75 ral” models of consonance predict that the perception of consonance should break down for
76 stimuli presented above 5 kHz. This frequency was long held to be the upper limit for the
77 perception of pitch, another sensory attribute which is crucial for music and which has also
78 been explained on the basis of neural temporal models. The evidence for such an upper
79 limit came from several pieces of data, including the fact that a) the ability to perceive
80 pure-tone melodies (Attneave and Olson, 1971), or melodic intervals (Semal and Demany,

81 1990) breaks down above 5 kHz, b) pure-tone frequency discrimination declines dramatically
82 above 5 kHz (Moore, 1973), and c) the upper note of most musical instruments lies below 5
83 kHz. However, Oxenham *et al.* (2011), while confirming that the ability to perceive melodies
84 is severely degraded for pure tones above 6 kHz, found that for complex tones whose har-
85 monics all fell above 6 kHz performance in a melody discrimination task was comparable to
86 that obtained with low-frequency pure tones. A follow-up study found that F0 difference
87 limens (F0DLs) for complex tones with all harmonics falling above 8 kHz, although worse
88 than F0DLs for complex tones presented in a low-frequency region, were considerably bet-
89 ter than frequency difference limens (FDLs) for pure tones above 8 kHz (Lau *et al.*, 2017).
90 F0DLs for the high-frequency complex tones were also considerably lower than predicted by
91 the optimal integration of information based on FDL performance, suggesting that the poor
92 FDLs for high-frequency pure tones are not due to peripheral coding constraints related to
93 decreased phase locking at high frequencies.

94 It has also been argued that consonance does not directly depend on low-level physiolog-
95 ical or psychoacoustical invariants such as cochlear beats or regularity of neural firing, but
96 is instead the result of learned cultural conventions. Some support for this “cultural” theory
97 of consonance comes from the observation that in music theory categorizations of consonant
98 and dissonant intervals have changed over the centuries (Tenney, 1988). Further evidence for
99 the cultural theory of consonance comes from the finding of McDermott *et al.* (2016) that an
100 isolated Amazonian tribe with limited exposure to Western music did not show preference
101 for consonant over dissonant musical intervals. There are, however, arguments against a
102 purely cultural origin of consonance preference (reviewed in Bowling *et al.*, 2017), such as

103 the striking similarity of tonal structures across musical cultures from different geographical
104 regions, and different epochs, which suggests that these structures are partly shaped by
105 biological constraints. The debate on the relative role of biological vs cultural factors in the
106 determination of consonance preference remains open.

107 Models of consonance based on harmonicity are closely linked to models of pitch per-
108 ception (Terhardt, 1974b) because both are often based on the concept of an F0 to explain
109 the relations between the frequency components present in a stimulus. Cultural theories of
110 consonance are also linked to pitch perception because they posit that consonance is a cul-
111 turally learned preference for certain pitch combinations. If pitch perception is possible for
112 stimuli with harmonics above 5 kHz, as suggested by the results of Oxenham *et al.* (2011),
113 and Lau *et al.* (2017), it is reasonable to hypothesize that the perception of consonance may
114 also be possible above this frequency limit. The present study sought to test this hypothesis
115 by measuring the pleasantness ratings of 15 listeners for dyads (two note chords) with fre-
116 quency components falling entirely above 5 kHz, and forming musical intervals traditionally
117 considered consonant, or dissonant. To ensure that pleasantness ratings were not based on
118 low-frequency envelope periodicities we used a manipulation similar to the one employed by
119 Oxenham *et al.* (2011): Ratings for harmonic dyads were compared to those for dyads whose
120 components had been shifted by a fixed frequency offset, so as to preserve their envelope pe-
121 riodicity while disrupting their harmonicity. The results were also compared to pleasantness
122 ratings for stimuli with the same root note, but with frequency components below 5 kHz.

123 An additional experiment measured the ability of the same listeners to discriminate musi-
124 cal melodies composed of complex tones with frequency components above 5 kHz. The main

125 purpose of this experiment was to rule out the possibility that, if consonance perception were
126 to be found poor or absent in the high frequency region, this was due to an inability of our
127 listeners to perceive melodic pitch above 5 kHz.

128 It seems reasonable to hypothesize that if melodic pitch perception is present at high fre-
129 quencies, consonance perception should be present too. However, the results of a study by
130 [Gockel and Carlyon \(2018\)](#) suggest that different aspects of pitch processing may show unex-
131 pected dissociations at high frequencies. In a series of experiments they found that while F0
132 discrimination performance at high frequencies was good, and could not be accounted for by
133 residual envelope cues, in line with previous results ([Lau et al., 2017](#); [Oxenham et al., 2011](#)),
134 mistuning detection at high frequencies was unexpectedly poor. Detecting a mistuning of
135 the 8th harmonic of a 1400 Hz F0 complex tone was only slightly above chance level even
136 for a mistuning of $\sim 6\%$, and listeners did not report hearing the mistuned component as
137 perceptually segregated from the complex. [Gockel and Carlyon \(2018\)](#) concluded that either
138 harmonic templates at high frequencies have wider tolerances than those at low frequencies,
139 or even though they have comparable tolerances the mechanism that leads to the perceptual
140 segregation of a mistuned component is absent at high frequencies. In either case, these
141 results suggest that it cannot be assumed that consonance perception at high frequencies
142 will be present simply because melodic pitch perception for complex tones is present at these
143 frequencies.

144 II. METHODS

145 A. Audiometric screening

146 Participants were screened for hearing loss by measuring their thresholds for the detection
147 of a 200-ms pure tone in quiet at octave frequencies ranging from 0.25 to 8 kHz. Only
148 participants with thresholds below 20 dB HL for both ears were included in the study.
149 Additionally, participants were screened for their ability to hear a 300-ms (including 10-ms
150 onset and offset raised-cosine ramps) 12-kHz pure tone in a background of 45 dB SPL/ERB
151 threshold-equalizing noise (TEN) (Moore *et al.*, 2000) bandpass filtered between 0.02 and 16
152 kHz. Only participants with thresholds ≤ 50 dB SPL for both ears in this task were included
153 in the study. Both the audiometric thresholds in quiet and the tone-in-noise detection at
154 12 kHz were measured using a two-interval two-alternative forced-choice task with a two-
155 down one-up adaptive rule tracking the 70.7% correct point on the psychometric function
156 (Levitt, 1971). The step size was 4 dB for the first four reversals, and 2 dB thereafter.
157 For the audiometric thresholds in quiet the adaptive track terminated after eight reversals,
158 and thresholds were estimated by averaging the values of the adaptive track at the last four
159 reversals. For the tone-in-noise detection at 12 kHz the adaptive track was stopped after
160 14 reversals, and thresholds were estimated by averaging the values of the adaptive track at
161 the last 10 reversals.

162 B. Participants

163 Twenty-five listeners in their 20s took part in the study. Fifteen listeners (eight males)
164 passed the audiometric screening and proceeded to run the main experiments, while the 10
165 listeners who failed the audiometric screening were excluded from the study. Nine out of
166 the 15 listeners who passed the audiometric screening were musicians with more than five
167 years of practice with a musical instrument. All participants gave written informed consent
168 for participation in the study, and the study protocols were approved by the Lancaster
169 University Psychology Department Ethics Committee.

170 C. Pleasantness ratings

171 In the rating experiment, listeners were asked to rate the pleasantness of dyads consisting
172 of a low (“root”) note, and a high (“interval”) note. Participants rated each dyad on
173 a scale ranging from -3 to +3 in 0.1 steps by moving, through a computer mouse, a slider
174 presented on a computer monitor (Bones *et al.*, 2014; Bones and Plack, 2015a,b; McDermott
175 *et al.*, 2010). The notes composing the dyads were equal-amplitude complex tones and were
176 presented each to a different ear to eliminate the possibility of cochlear interactions between
177 components of the root and interval notes, which can lead to amplitude fluctuations and
178 perceived “roughness” (Terhardt, 1984). The dyads were bandpass filtered so that their
179 components would fall either in a “low” frequency region, or in a “high” frequency region
180 above the traditional existence region of pitch. The complex tones composing the dyads
181 were either harmonic, or were made inharmonic by shifting all their components by a fixed

182 frequency offset in hertz. In the “harmonic” conditions the root note of each dyad had an
183 F0 of 1174.659 Hz (D6 note in the equal temperament scale). The F0s of the interval notes
184 were 100 cents (minor second), 300 cents (minor third), 600 cents (tritone), or 700 cents
185 (perfect fifth) above the root note (100 cents = 1 semitone), so as to form musical intervals
186 of the equal-tempered scale. The F0s of the interval notes are shown in Table I.

187 Two dyads formed musical intervals which are traditionally considered consonant: the
188 minor third, and the perfect fifth. The other two dyads formed musical intervals which
189 are traditionally considered dissonant: the minor second, and the tritone. Music theory
190 classifications of intervals in terms of consonance and dissonance have evolved and changed
191 in the course of the centuries (Tenney, 1988), and often distinctions are made in terms of
192 their degree of consonance for intervals within each category. The perfect fifth is typically
193 considered a “perfect consonance”, while the minor third is often classified as an “imperfect
194 consonance”.

195 The stimuli for the inharmonic conditions were obtained by shifting each component of
196 the complex tones forming the dyads in the harmonic conditions by 234.9318 Hz (20% of
197 the root note F0). The spectra for the harmonic stimuli are shown in Fig. 1, those of the
198 inharmonic stimuli are shown in Fig. S1 of the supplementary materials¹. The frequency
199 components of the dyads in the harmonic conditions are listed in Table S1, and those of the
200 dyads in the inharmonic conditions in Table S2 of the supplementary materials.

201 In all experimental conditions the dyads had a 2-sec duration, including 10-ms raised-
202 cosine onset and offset ramps. The complex tones forming the dyads had a level of 55 dB
203 SPL per component; each component had a random starting phase. In the low-frequency

204 conditions the dyads were bandpass filtered between 1 and 6 kHz, while in the high-frequency
205 conditions they were bandpass filtered between 7 and 12 kHz, using a 256-taps finite-impulse-
206 response filter (90 dB/octave slope). Keeping the F0 of the root note constant while filtering
207 the stimuli within two different frequency regions with the same bandwidth leads to differ-
208 ences both in the harmonic rank and in the total number of harmonics present in each
209 dyad. These differences are particularly marked between dyads presented in the low and
210 in the high frequency region (harmonic ranks, and total number of harmonics are higher in
211 the high-frequency region). Although these differences could presumably affect pleasantness
212 ratings, they are unlikely to affect greatly the difference in pleasantness ratings between the
213 consonant and dissonant dyads *within* each frequency region, which was the main variable
214 of interest in the experiment.

215 All the dyads were presented in a background TEN bandpass filtered between 0.02 and 16
216 kHz, with a level of 45 dB SPL/ERB. An additional band of 55-dB SPL/ERB TEN bandpass
217 filtered between 0.02 and 5 kHz was added to the dyads in the high-frequency conditions
218 to ensure that low-frequency distortion products would be masked (Oxenham *et al.*, 2011).
219 These noises were gated on and off simultaneously with the dyads with 10-ms raised-cosine
220 onset and offset ramps. On each trial a 2-sec, 45-dB SPL/ERB TEN bandpass filtered
221 between 0.02 and 16 kHz was presented before the presentation of the dyad to “weaken”
222 the sensory memory trace of the dyad presented in the previous trial, so as to minimize any
223 effect it might have on the judgment of the dyad in the current trial (Bones *et al.*, 2014;
224 McDermott *et al.*, 2010). There was a 500-ms silent interval between the presentation of
225 this noise and the onset of the dyad. All noise samples, including those presented together

226 with the dyad and those presented before the dyad, were independent between the left and
227 right ear.

228 There were 16 experimental conditions overall, resulting from the combination of four mu-
229 sical intervals (minor second, minor third, tritone, and perfect fifth), two frequency regions
230 (low, and high), and two harmonicity conditions (harmonic, and inharmonic). Participants
231 first rated two dyads for each condition. These practice trials were discarded from subse-
232 quent analyses. After the practice trials participants rated eight dyads for each experimental
233 condition. For both the practice phase and the main phase the trials were organized in four
234 blocks, corresponding to the four combinations of frequency region and harmonicity: only
235 stimuli of a given frequency region and harmonicity were presented in a block of trials, and
236 all of the different intervals were presented within each block. The presentation order of the
237 blocks was randomized. Within each block the presentation order of the intervals was also
238 randomized. For each interval, the root note was presented to the right ear on half the trials
239 in each block, and to the left ear on the other half, in random order. The interval note was
240 always presented to the opposite ear.

241 **D. Melody discrimination task**

242 This task was similar to the melody discrimination task of [Oxenham *et al.* \(2011\)](#). On each
243 trial participants were presented with two four-note melodies. The first melody consisted of
244 45 dB SPL pure tones drawn from a set of notes from the diatonic scale (C6=1046.502 Hz,
245 D6, E6, F6, G6, A6, B6, C7). On each trial the notes were drawn sequentially at random,
246 with the constraint that if the first and second note, or if the second and third note were

247 the same, that note could not be drawn again for that trial. This constraint implied that
248 no three consecutive notes could be the same. The second melody consisted of harmonic
249 complex tones bandpass filtered between 7 and 12 kHz. The harmonics of the complex tones
250 were added in sine phase² and had a level of 55 dB SPL. Two bands of TEN were added
251 to each note of the second melody to mask low-frequency combination tones and promote
252 harmonic fusion. The first noise was bandpass filtered between 0.02 and 5 kHz, and had a
253 level of 55 dB SPL/ERB. The second noise was bandpass filtered between 0.02 and 16 kHz,
254 and had a level of 45 dB SPL/ERB. On “same” trials the notes of the second melody had
255 the same F0s as the notes of the first melody. On “different” trials the F0 of the third note
256 of the second melody was changed by a step up, or a step down in the diatonic scale with
257 respect to the third note of the first melody, while the F0s of the other three notes were
258 the same in the two melodies. Each note had a duration of 300 ms, including 10-ms raised-
259 cosine ramps. The noise bands for the second melody were gated on and off simultaneously
260 with each note with 10-ms raised-cosine onset and offset ramps. Within each melody the
261 notes were separated by 200-ms silent intervals. A 500-ms silent interval separated the two
262 melodies. Each melody was marked by a flashing light on a computer screen. Listeners had
263 to indicate by means of a key press on a computer keyboard whether the two melodies were
264 the same or different. Feedback was provided by means of a colored light at the end of each
265 trial. Listeners first completed a block of 10 practice trials in which both the first and the
266 second melody consisted of pure tones. They then completed two 100-trial blocks in which
267 the first melody consisted of pure tones, and the second melody consisted of complex tones
268 filtered in the 7–12 kHz frequency region.

269 E. Equipment

270 Testing took place in a double-walled, sound-insulated booth (IAC Acoustics, UK). The
271 stimuli were generated digitally with a 32-bit resolution and a 48-kHz sampling rate in
272 Python, on a GNU/Linux workstation housed outside the booth. The stimuli were sent to
273 a 24-bit digital-to analog converter (E-MU 0204 USB), and played via Sennheiser HDA300
274 headphones. These headphones were chosen both because of their extended high-frequency
275 response, and because being closed-cup headphones they minimize acoustic cross-talk which
276 may have otherwise re-introduced cochlear interactions effects in spite of the dichotic pre-
277 sentation of the root and interval notes in the pleasantness rating task.

278 F. Statistical analyses

279 Analyses were performed using Bayesian models implemented by Markov Chain Monte
280 Carlo (MCMC) simulations using JAGS (Plummer, 2003) and R (R Core Team, 2019).
281 Bayesian analysis methods have several strengths, including the ability to seamlessly fit
282 complex models without having to rely on assumptions of normally distributed residuals,
283 the ability to quantify the uncertainty over parameters of interest without relying on sam-
284 pling distributions (Kruschke, 2014), and the ability to keep false alarms at bay in multiple
285 comparison settings without sapping statistical power, by means of hierarchical modeling
286 (Gelman *et al.*, 2012). For all MCMC simulations the chains were monitored for convergence
287 using trace plots. All chains were also monitored for autocorrelation to ensure an effective
288 sample size of at least around 10,000 samples for the main parameters of interest.

289 The pleasantness ratings of each listener were converted to z scores by subtracting the
290 mean and scaling by the standard deviation of the scores given by that listener across
291 all stimulus conditions (McDermott *et al.*, 2010). These standardized pleasantness ratings
292 were then modeled using a hierarchical Bayesian linear model that estimated the effect of
293 interval, frequency region, harmonicity, and the two- and three-way interactions between
294 these factors, at the level of individual listeners, as well as at the group level. The model
295 is based on a model proposed by Kruschke (2010, chap. 19, p. 532) for the analysis of
296 within-subject designs in which subjects provide more than one datum per condition.

297 The hit and false alarm rates obtained by each listener in the melody-discrimination task
298 were modeled using a Bayesian hierarchical model based on the equations of Macmillan
299 and Creelman (2004) to calculate d' in the same-different task for an observer using the
300 differencing strategy. The model estimated d' both at the individual and at the group
301 level. The model has the advantage of taking into account the uncertainty around the d'
302 estimate for each listener when computing across-listener statistics, rather than relying on
303 point estimates of d' . Another advantage of the model is that it does not require corrections
304 for extreme sampled proportions (i.e. hits or false alarm rates of 0, or 1) that can bias d'
305 estimates (Hautus and Lee, 1998).

306 Details of the models are given in the supplementary material. Effects were summarized
307 by 95% credibility intervals (CIs) of the posterior distribution of the parameter of interest.
308 These indicate that, according to the model, the parameter has a 95% probability of being
309 enclosed between the bounds of the interval. For inferential purposes parameters were

310 deemed as credibly different from zero when the bounds of their 95% CIs did not enclose
311 zero.

312 III. RESULTS

313 A. Pleasantness ratings

314 The mean standardized pleasantness ratings are shown in Fig. 2. The ratings for the
315 harmonic dyads in the low frequency region follow the pattern expected from the literature
316 (Bones and Plack, 2015a; Kameoka and Kuriyagawa, 1969b; Malmberg, 1918; McDermott
317 *et al.*, 2010; Schwartz *et al.*, 2003) with higher average ratings for the consonant over the
318 dissonant intervals. In the inharmonic condition, while the average ratings of the minor
319 third, tritone, and perfect fifth, appear relatively well matched, those of the minor second
320 are lower than those of the other intervals. The dyads in the high-frequency region received
321 generally lower ratings than in the low frequency region, but the pattern with respect to
322 interval type and harmonicity is similar to that observed in the low frequency region.

323 Figure 3 shows the mean consonance preference scores, which were calculated by sub-
324 tracting the standardized scores given to the two dissonant intervals (minor second and
325 tritone) from the standardized scores given to the consonant ones (minor third and perfect
326 fifth). Posterior distributions and 95% CIs for consonance preference scores estimated by
327 the Bayesian model are shown in Fig. 4. The 95% CIs indicate that for harmonic stimuli,
328 consonant intervals are rated higher than dissonant intervals in both the low (CI: 0.53 –
329 1.17), and the high (CI: 0.22–0.8) frequency region. There was a tendency for consonant

330 intervals to be rated higher than dissonant ones also in the inharmonic condition for both
331 the low (CI: -0.03–0.589), and the high (CI: -0.1–0.44) frequency region. This largely re-
332 flects the fact that the minor second was rated lower than consonant intervals also in the
333 inharmonic condition, as shown in Fig. 5 which displays 95% CIs for contrasts between each
334 consonant and dissonant interval by frequency region and harmonicity. Importantly, the
335 posterior distributions for consonance preference shown in Fig. 4 indicate that consonance
336 preference was higher for the harmonic than for the inharmonic conditions not only in the
337 low frequency region (CI: 0.23–0.91), but also in the high frequency region (CI: 0.02–0.66).
338 Therefore, the consonance preference scores obtained in the high frequency region cannot be
339 explained solely on the basis of envelope periodicity cues, which would have been the same
340 for the harmonic as for the inharmonic stimuli.

341 **B. Same-different melody task**

342 The results of the melody discrimination experiment are shown in Fig. 6. Performance
343 in this task was very good, with an average d' close to 3. The 95% CIs of d' estimates for
344 individual listeners generated by the Bayesian model indicate that performance was well
345 above chance level for every listener. The group-level 95% CI for d' ranged from 2.27 to
346 3.46.

347 **IV. HARMONIC SIEVE**

348 It is unclear why the minor second dyad tended to be given lower ratings than the
349 “consonant” dyads in the inharmonic conditions. One possible reason is that the degree

350 of inharmonicity of the minor second in the inharmonic conditions may have been higher
351 than that of the other intervals. To investigate this possibility we passed the dyads through
352 harmonic sieves.

353 As noted by [McDermott *et al.* \(2010, supplementary materials\)](#) there is no standard
354 method for the measurement of the degree of harmonicity of a sound. While it is trivial
355 to distinguish a perfectly harmonic from an inharmonic sound, quantifying the degree of
356 harmonicity of a sound that is not perfectly harmonic, or consists of both harmonic and
357 inharmonic components is not straightforward. A method often employed involves passing
358 the power spectrum of a sound through a harmonic sieve with meshes centered at harmonic
359 frequencies of a given fundamental frequency (F0). The width of the meshes defines the
360 tolerance for slight degrees of inharmonicity. The ratio of the power of the sound passing
361 through the meshes to the power of the sound rejected by the sieve [Harmonic to noise
362 ratio (HNR)] provides a measure of how well the sound fits the harmonic template of a
363 given F0. The sound can be passed through a range of sieves with different F0s to find the
364 best matching template. The HNR for the best matching template provides a measure of
365 the harmonicity of the sound. This measure is affected by several parameters, which can be
366 partly constrained by perceptual considerations but are otherwise to a large extent arbitrary.
367 These include the width and the shape of the meshes, the range of F0s used for finding the
368 best fitting template, and the number of harmonics used in the template.

369 The lowest F0 for a harmonic sieve has been generally chosen to be 30 Hz, which corre-
370 sponds to the lower limit for pitch perception ([Krumbholz *et al.*, 2000](#)). The width of the
371 meshes of the sieve has been sometimes chosen to have a fixed value of a few Hz ($\sim 2 - 8$),

372 in order to tolerate small deviations from perfect harmonicity expected for intervals defined
373 with the equal temperament scale (Bones *et al.*, 2014; Bones and Plack, 2015a·b). While
374 meshes with widths of a few Hz in this range work well at relatively low frequencies, they
375 cannot accommodate small deviations from harmonicity at high frequencies. The largest
376 difference between intervals of the just intonation and of the equal temperament scale oc-
377 curs for the tritone, and has a value of ± 17.49 cents (corresponding to $\sim 1\%$). At 500 Hz
378 this corresponds to a deviation of ~ 5 Hz, while at 5000 Hz the deviation becomes ~ 51
379 Hz. A possible solution to this issue is to define the width of the meshes proportionally to
380 their center frequencies. Duifhuis *et al.* (1982) for example used meshes with a width of
381 $\sim 5\%$ of their center frequency in a model of pitch estimation in speech. Templates with a
382 low F0, however, will generate sieves with progressively larger meshes relative to the har-
383 monic spacing as the center frequency increases, even with a relatively small tolerance. Thus
384 they will increasingly pass more components of a sound at high center frequencies and will
385 eventually pass all components above a certain frequency when the meshes become so large
386 relative to the harmonic spacing that they start overlapping. For example, a template with
387 an F0 of 30 Hz and a tolerance of ± 17.49 cents will have overlapping meshes above ~ 1500
388 Hz, which will effectively pass through all components above that frequency. This issue is
389 largely avoided by pitch models that use only templates with low-numbered harmonics ($\lesssim 10$
390 Duifhuis *et al.*, 1982; Terhardt *et al.*, 1982), which perceptually are the most important for
391 the determination of the pitch of a sound.

392 Given the considerations above, we passed the spectra of the dyads used in the exper-
393 iment through harmonic sieves with meshes ± 17.5 cent wide, and F0s ranging from 30 to

394 1174.569 Hz in 0.1 Hz steps. Only the portions of the spectra between 0.8–7.2 kHz for the
395 low-frequency dyads, and 5.6–14.4 for the high-frequency dyads, were passed through the
396 harmonic sieves. The HNRs for the best fitting template are shown in Fig. 7 for sieves with
397 harmonic numbers 1–10, 1–12, or 1–15. For the low-frequency harmonic dyads the HNRs
398 follow the rankings of the pleasantness ratings in the experiment, with larger HNRs for the
399 perfect fifth and minor third intervals. For the high-frequency harmonic dyads the HNRs
400 also follow the rankings of the pleasantness ratings in the experiment, except for the fact
401 that the tritone has a higher HNR than the minor third. As expected the HNRs for the
402 inharmonic dyads are generally lower than for the harmonic ones. The HNR profiles across
403 the various intervals are also flatter, and except for a small peak for the tritone in the low-
404 frequency conditions with harmonics sieves consisting of 12 or 15 harmonics, generally follow
405 the pattern of the pleasantness ratings. In particular, the minor second dyad consistently
406 shows the lowest HNRs in the inharmonic conditions.

407 The fact that in the inharmonic conditions the minor second dyad had the lowest HNR
408 in our harmonic sieve modeling could explain why this dyad was rated lower than the other
409 dyads in the inharmonic conditions of the pleasantness rating test. However, given that there
410 is no standard way to measure HNRs these results should be interpreted cautiously. We tried
411 to choose reasonable parameters for the harmonic sieves on the basis of known constraints.
412 However, without more definitive knowledge of the psychophysiological mechanisms used
413 by the auditory system to assess harmonicity, results from harmonic sieve models remain
414 necessarily tentative. In any case, it should be remarked that in the inharmonic conditions
415 the minor second dyad was given lower ratings than the “consonant” dyads both in the

416 low, and in the high frequency region. Therefore this result is unlikely to be due to some
417 idiosyncrasy of the high-frequency dyads. Instead, this result supports the view that the
418 pleasantness ratings were determined by the same mechanisms in the low, and in the high
419 frequency regions.

420 Interestingly in the high-frequency harmonic condition the HNR rankings of the tritone
421 and minor third dyads are reversed compared to the pleasantness ratings. This could be
422 taken as evidence against the idea that pleasantness ratings are determined by harmonicity.
423 However, it is possible that a learned association between pleasantness and a given dyad
424 with all its lower harmonics as they occur naturally is transferred to a dyad with only a
425 subset of those harmonics, as is the case for the dyads filtered in the high-frequency region
426 of our experiment. It is also possible that given that the dyads were presented in noise, the
427 lower harmonics, even if absent in the stimulus, are nonetheless perceived through spectral
428 completion effects (McDermott and Oxenham, 2008). Pleasantness ratings for inharmonic
429 stimuli may be more directly related to HNRs given that both learned associations and
430 spectral completion effects are unlikely for this kind of stimuli.

431 V. DISCUSSION

432 We found that two consonant intervals were rated higher than two dissonant intervals
433 even when they were presented in a high frequency region where neural phase locking to
434 individual harmonics is thought to be severely degraded or absent. Given that the envelope
435 repetition rates for our stimuli were higher than the highest rates at which the ability to
436 perceive pitch on the basis of purely envelope rate cues has been observed (Burns and

437 Viemeister, 1976; Macherey and Carlyon, 2014), it was a priori unlikely that the perception
438 of consonance for our stimuli could be mediated by such cues. The finding that consonance
439 preference in the high frequency region was higher for harmonic stimuli than for stimuli
440 that had the same envelope repetition rate, but were made inharmonic by shifting their
441 component frequencies by a fixed offset, further dispels this possibility. This finding also
442 rules out the possibility that preference ratings could have been dictated by the detection
443 of binaural envelope beats, rather than by the detection of harmonic relations between the
444 components of the stimuli. If ratings reflected the detection of binaural envelope beats, they
445 should have been similar for the harmonic and inharmonic stimuli in the high frequency
446 region, given that these stimuli had the same envelope repetition rates. The possibility
447 that preference ratings were mediated by binaural envelope beats in our study seems, in any
448 case, a priori unlikely given that such beats are difficult to detect for interaural envelope rate
449 differences above about 3–5 Hz, well below the interaural envelope beat rates of our stimuli
450 in the high-frequency region, and the ability to detect such beats declines with increasing
451 monaural envelope rate, and is already very poor at 640 Hz (Bernstein and Trahiotis, 1996;
452 McFadden and Pasanen, 1975). An additional reason why binaural envelope beats are
453 unlikely to explain the results of the current study is that the perception of roughness for
454 monaural envelope beats disappears for envelope rates exceeding ~ 300 Hz (Plomp and
455 Steeneken, 1968; Terhardt, 1978). Neurophysiological studies suggest that this upper limit
456 may be related to the upper limit of phase locking of auditory cortex neurons to envelope
457 beats (Fishman *et al.*, 2000, 2001). The binaural envelope beats for some of our stimuli
458 were completely outside the $\sim 20 - 300$ Hz range over which roughness can be perceived

459 (Terhardt, 1974a·b); for example both the minor second and the perfect fifth dyads in the
460 high frequency harmonic condition, which respectively received the lowest and the highest,
461 pleasantness ratings, did not contain any difference frequencies in this range. Therefore, the
462 differences in pleasantness ratings given to these dyads cannot be attributed to perceived
463 roughness caused by envelope beats.

464 Overall, our results indicate that pleasantness ratings in our experiment were determined
465 by pitch relations between the tones forming the dyads rather than by beats. Our results
466 do not shed light on the debate between the “harmonicity”, and the “cultural” theories of
467 consonance, because both theories predict preferences for certain dyads on the basis of the
468 pitch combinations of their component tones. What our results clearly show, is that these
469 pitch combinations can be readily perceived for dyads presented in a high frequency region,
470 where neural phase locking to individual harmonics is either severely degraded or absent.

471 On the basis of the poor performance observed in the detection of mistuning of a single
472 harmonic of a complex tone presented at high frequencies, Gockel and Carlyon (2018) hy-
473 pothesized that harmonic templates at high frequencies may either have wider tolerances
474 than at low frequencies, or even though they may have similar tolerances, the mechanism
475 that leads to the perceptual segregation of the mistuned harmonic is absent at high fre-
476 quencies. Our results suggest that harmonic templates at high frequencies have sufficiently
477 narrow tolerances to support consonance judgments for the dyads used in the study. Al-
478 though determining how narrow these tolerances are from pleasantness ratings data is not
479 straightforward, as it is dependent on several modeling assumptions of harmonic sieves (see
480 sec. IV) it is quite clear that they should be narrower than 100 cents, which corresponds to

481 a mistuning of $\sim 6\%$ that was very difficult to detect in [Gockel and Carlyon \(2018\)](#)'s study.
482 The reasoning behind this is that given that the distance between the root and interval notes
483 of a minor second dyad is 100 cents, a harmonic template at the F0 of the root note with a
484 tolerance ≥ 100 cents would pass through all components of a minor second dyad, just as it
485 would pass through all components of a unison dyad. Given that the unison, together with
486 the octave typically receive the highest pleasantness ratings amongst all musical intervals,
487 the fact that the minor second received the lowest pleasantness ratings in our study clearly
488 shows that it was treated differently than a unison. Therefore our results, combined with
489 those of [Gockel and Carlyon \(2018\)](#) suggest that harmonic templates at high frequencies
490 may not be larger than at low frequencies, but the mechanism that leads to the perceptual
491 segregation of the mistuned harmonic may be absent at high frequencies.

492 **A. Is neural phase locking necessary for the perception of consonance?**

493 Although phase locking is thought to be severely degraded or absent above ~ 5 kHz,
494 some computational models suggest that, theoretically, some residual temporal information
495 usable for pitch coding may be available up to frequencies as high as 10 kHz ([Heinz *et al.*, 2001](#);
496 [Recio-Spinoso *et al.*, 2005](#)). Additionally, [Moore and Ernst \(2012\)](#) have shown that
497 pure tone FDLs increase as a function of frequency up to 8 kHz, and then show a plateau,
498 suggesting that a transition from a temporal to a place code may occur ~ 8 kHz rather
499 than ~ 5 kHz as once commonly thought. On the basis of this evidence it has been argued
500 that, although phase locking may be too weak to support musical pitch perception for
501 individual pure tones above 5 kHz, the combined temporal information across several > 5

502 kHz harmonics of a complex tone may be sufficient to support musical pitch perception.
503 [Lau et al. \(2017\)](#), however, measuring FDLs for pure tones > 8 kHz and F0DLs for complex
504 tones with harmonics > 8 kHz, found that the F0DLs were better than predicted from an
505 optimal combination of peripheral information from each of their component frequencies.
506 This finding poses two additional difficulties to the theory that pitch perception at high
507 frequencies is supported by temporal coding: 1) it pushes the upper limit at which phase
508 locking information would be viable for pitch perception above 8 kHz, the point at which
509 a putative transition between a temporal to a place code would occur according to the
510 data of [Moore and Ernst \(2012\)](#), 2) if pitch were nonetheless coded temporally at such high
511 frequencies, pure tone FDLs would have to be limited by additional central noise sources
512 rather than by peripheral limitations due to degraded phase locking.

513 Another factor to consider when evaluating the possible role of a temporal code for human
514 pitch perception at high frequencies is how the limits of neural phase locking in humans
515 compare to those of other mammalian species for which direct single neuron recordings
516 are available ([Johnson, 1980](#); [Palmer and Russell, 1986](#); [Winter, 2005](#)). Recordings of the
517 compound action potential using a technique that separates the auditory nerve neurophonic
518 from the cochlear microphonic, indicate that this limit is at best similar, and probably lower
519 than the 5 kHz limit recorded in the cat ([Verschooten et al., 2018](#)).

520 Given the results of our study, the question of whether neural phase locking is necessary
521 for the perception of consonance hinges on the issue of whether a temporal code may be
522 used for frequency coding in the high frequency region where the stimuli in our study were
523 presented. The lowest component of the dyads in the high frequency region was the 5th

524 harmonic of the root note, just above 5.8 kHz. However, in order to differentially rate the
525 pleasantness of the consonant and dissonant dyads listeners needed to also perceive at least
526 the pitch of the first audible component of each interval note. This pushes the minimum
527 frequency needed to differentially rate the consonant and dissonant dyads to at least 7
528 kHz. The evidence reviewed above strongly points to the use of a place code rather than a
529 temporal code for frequency coding at such high frequencies.

530 Assuming that the frequency components of our stimuli could not be coded via phase
531 locking, the results of this study indicate that temporal coding is not necessary for the per-
532 ception of consonance. Hence, models of consonance perception based on neural periodicity
533 detection would be either incorrect, or at best incomplete, because they could not explain
534 the perception of consonance at high frequencies observed in the current study. However,
535 our results are not inconsistent with the notion that temporal coding may play an role in
536 the perception of consonance in low frequency regions, and that inter-individual differences
537 in temporal coding (Bones and Plack, 2015b), which can be partly due to factors such as
538 musical experience (Bones *et al.*, 2014) and aging (Bones and Plack, 2015a) may lead to
539 changes in the perception of consonance. For example, it is possible to envisage a model
540 in which the perception of consonance is based on a central harmonic template matching
541 unit similar to the models proposed by Goldstein (1973) and Srulovicz and Goldstein (1983)
542 for the perception of pitch. This template matching unit could receive input from both
543 temporal and place frequency representations. In the low frequency region, where phase
544 locking is good, temporal frequency representations may be dominant. If these frequency
545 representations are degraded, the input to the central harmonic template matching unit will

546 be degraded as well, and the perception of consonance may be affected even though temporal
547 processing plays no direct role in the neural computations determining consonance.

548 The issue of whether sound frequencies are represented via a temporal code based on
549 neural phase locking, or via a “rate” code based on cochlear tonotopy represents a funda-
550 mental aspect of auditory neurophysiology that remains still partly unsolved (Oxenham,
551 2018). The studies of Oxenham *et al.* (2011) and Lau *et al.* (2017) indicate that musical
552 pitch perception is possible at frequencies that are highly unlikely to be coded via neural
553 phase locking. Overall, the results of these studies, together with those of the current study,
554 strongly suggest that a tonotopic rate code is sufficient to convey pitch and consonance
555 information that is crucial for the perception of melody and harmony in music. However,
556 a recent collection of viewpoints on the topic indicates a lack of consensus on the upper
557 limit of phase locking in humans (Verschooten *et al.*, 2019). This consensus may not be
558 reached until further experimental data is available, including direct recordings from the
559 human auditory nerve. The results of our experiment provide further data that is relevant
560 to this debate. Comprehensive neurophysiological models of consonance should be able to
561 explain consonance perception at high frequencies, whether they are based on rate-place or
562 on temporal frequency coding.

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570 available from
571 https://osf.io/vxzbc/?view_only=967c43c5a1084d3bb2874c2073d7b312.

572 ¹See supplementary material at [please insert URL] for additional methods details, additional figures, and
573 additional tables.

574 ²Due to an error during the setup of the experiment the stimuli were presented in sine phase rather than
575 in random phase as in the pleasantness rating test. Presenting the stimuli in random phase reduces the
576 crest factor, or “peakiness” of their envelope, thus reducing (but not eliminating) the usefulness of potential
577 envelope cues (Bernstein and Oxenham, 2005). Performance in the melody discrimination experiment of
578 Oxenham *et al.* (2011) was high with random-phase harmonic complex tones filtered in a high frequency
579 region, but approached chance level when only envelope cues were available. Even though potential envelope
580 cues could have been more salient in the current experiment, envelope-based pitch perception declines
581 dramatically at high frequencies (Burns and Viemeister, 1976; Macherey and Carlyon, 2014). Therefore it
582 is unlikely that envelope cues could account for the high performance levels observed in the current study.

583

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757 **TABLES**

Name	Cents	F0 (Hz)
Minor Second (m2)	100	1244.508
Minor Third (m3)	300	1396.913
Tritone (TT)	600	1661.219
Perfect Fifth (P5)	700	1760.000

TABLE I. Harmonic intervals used in the pleasantness rating experiment. The F0 of the root note was always 1174.659 Hz. The first column shows the name of the interval and its abbreviation, in parentheses. The second column shows the size of the interval in cents. The third column shows the F0 of the interval note.

758 **FIGURE LEGENDS**

759 **FIG. 1.** (Color online) Spectra for the harmonic dyads. The solid blue line plots the
 760 spectrum of the root note. The dotted red line plots the spectrum of the interval note. The
 761 root and interval notes were always presented each to a different ear.

762 **FIG. 2.** (Color online) Mean standardized pleasantness ratings ± 1 s.e.m.

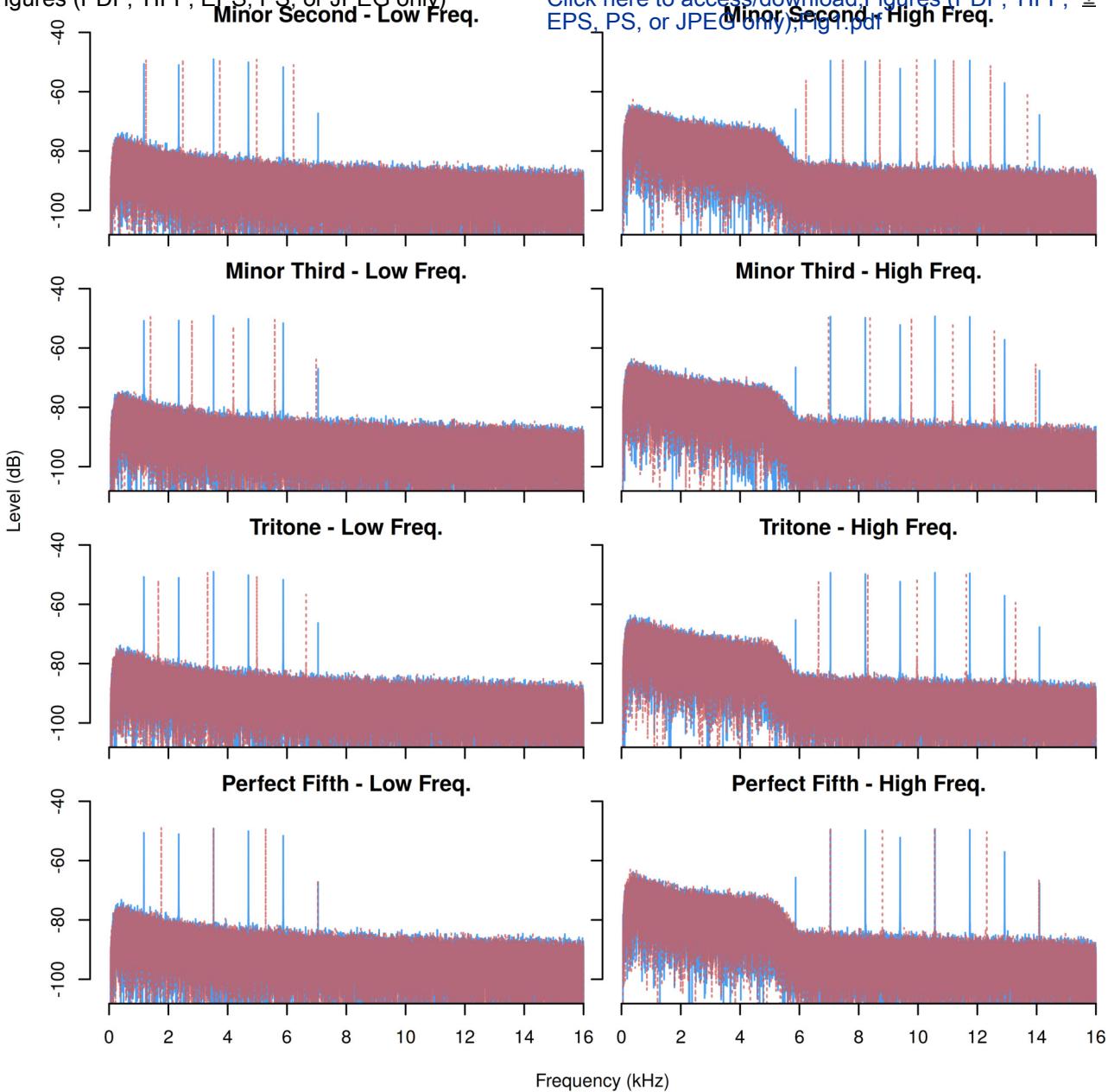
763 **FIG. 3.** Mean consonance preference scores ± 1 s.e.m.

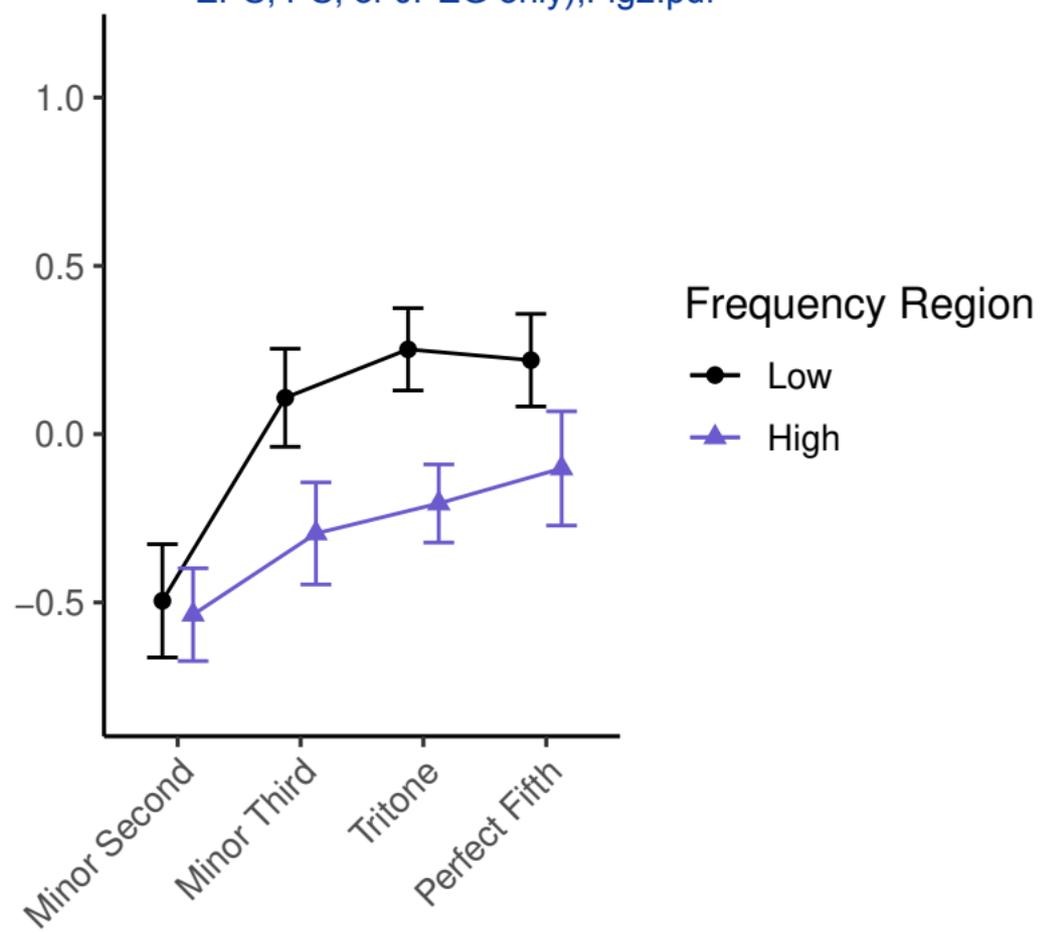
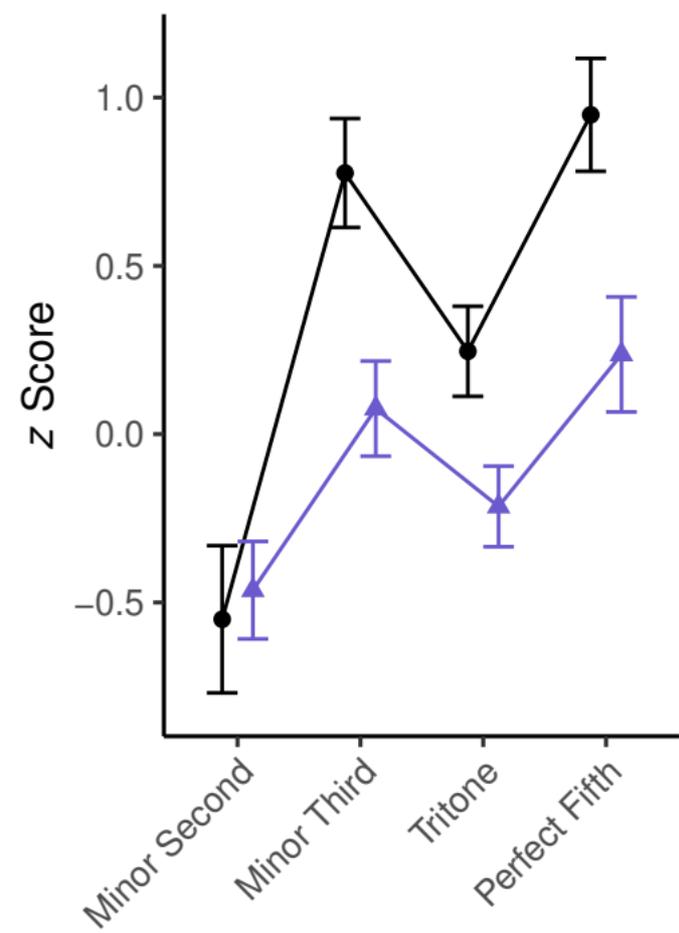
764 **FIG. 4.** (Color online) Posterior distributions estimated by the Bayesian model for con-
 765 sonance preference. The four distributions at the bottom show effects at the low and high
 766 frequency regions, for harmonic and inharmonic stimuli, separately. The two top distri-
 767 butions show the effect difference between the harmonic and inharmonic stimuli for each
 768 frequency region. Circles denote the mode of the distribution. Horizontal segments mark
 769 the 95% CIs.

770 **FIG. 5.** (Color online) Posterior modes and 95% CIs for contrasts between each conso-
 771 nant and dissonant interval, by frequency region and harmonicity.

772 **FIG. 6.** (Color online) Results of the melody discrimination experiment. Points indicate
 773 the d' values estimated by the Bayesian model for each individual listener, and are jittered
 774 for clarity. The vertical segments around these points enclose their 95% CIs. The wide
 775 horizontal bar indicates the group-level d' estimated by the Bayesian model, and the narrow
 776 horizontal bars enclose its 95% CI.

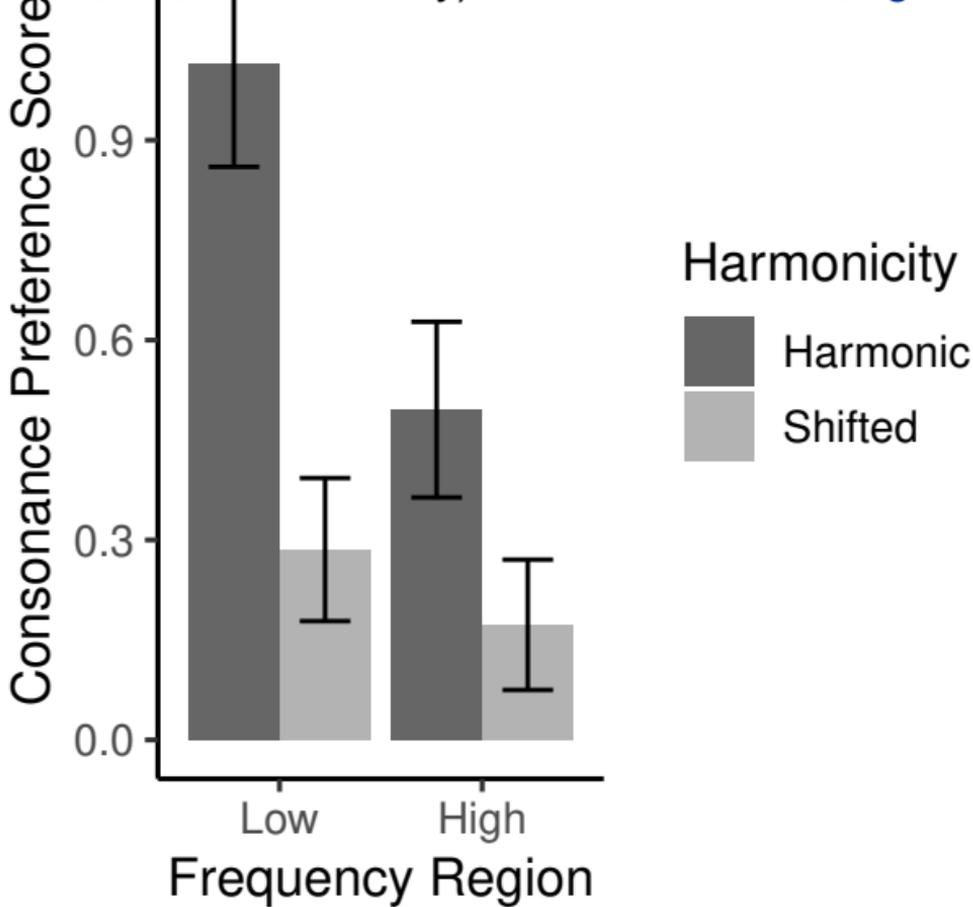
777 **FIG. 7** (color online) Harmonic to noise ratio for the stimuli used in the experiment.
778 The different line colors denote the results for harmonic sieves with harmonic numbers 1–10,
779 1–12, or 1–15.





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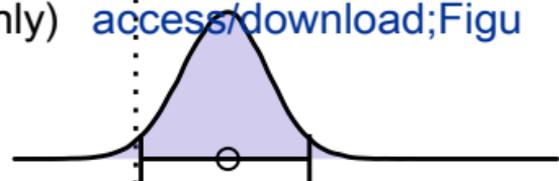


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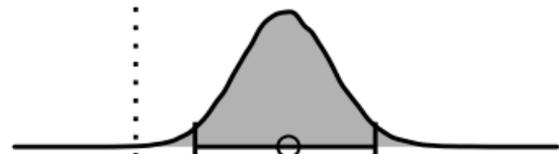
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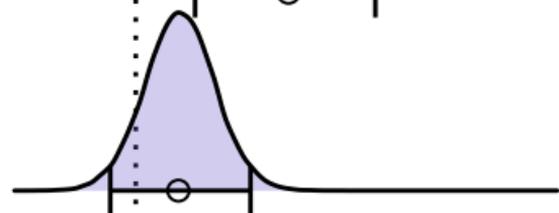
Harm. vs Inharm.
@High Freq.



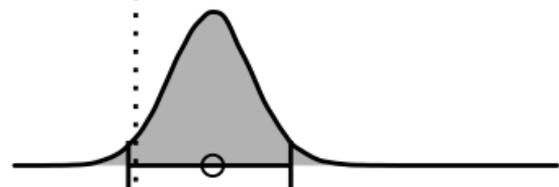
Harm. vs Inharm.
@Low Freq.



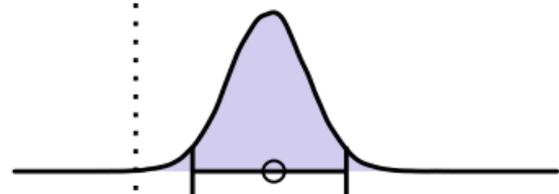
High Freq. Inharm.



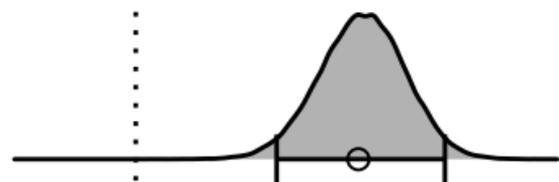
Low Freq. Inharm.



High Freq. Harm.



Low Freq. Harm.

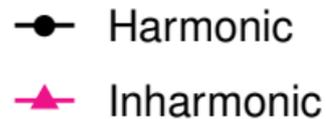
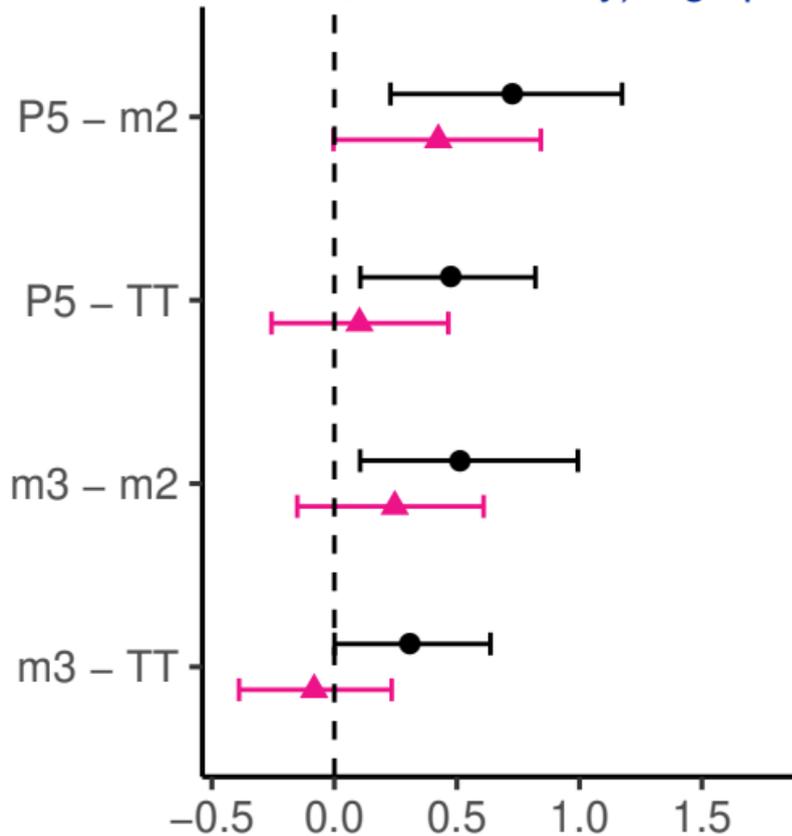
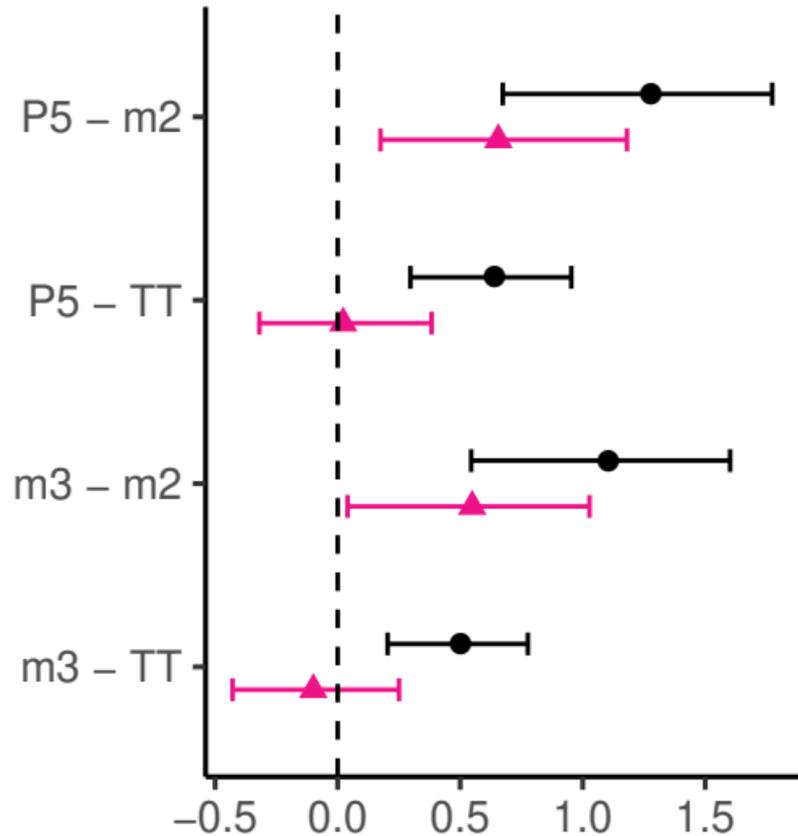


-0.5 0.0 0.5 1.0 1.5
Consonance Preference

Low Freq.

High Freq.

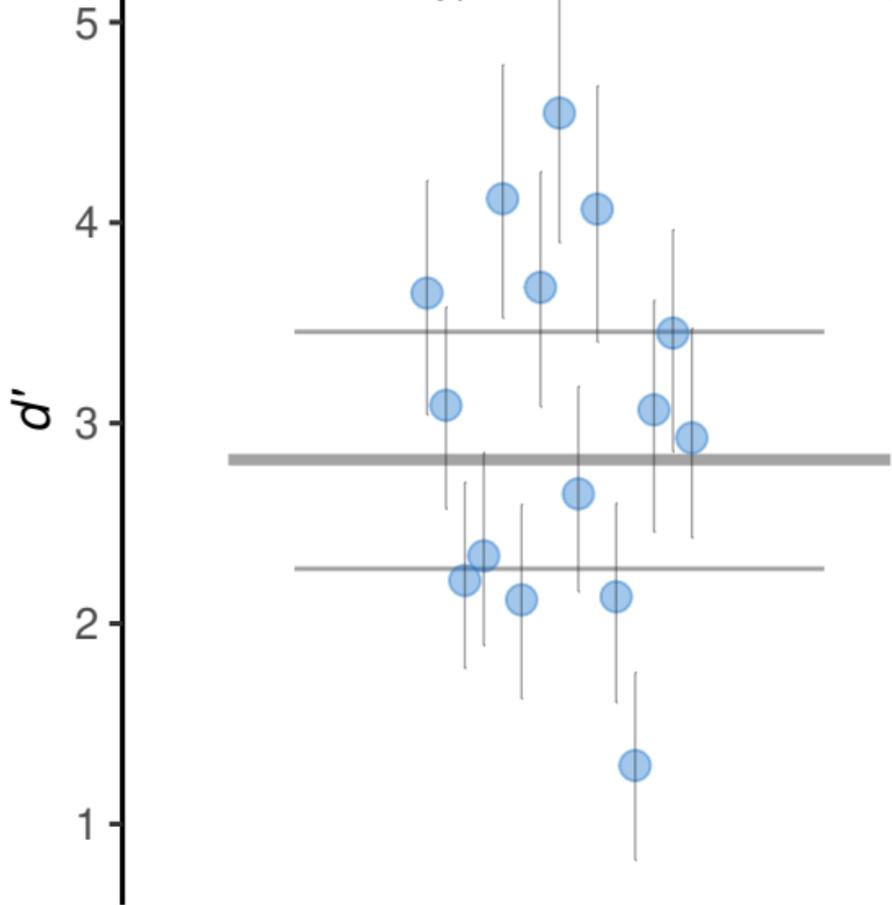
Contrast

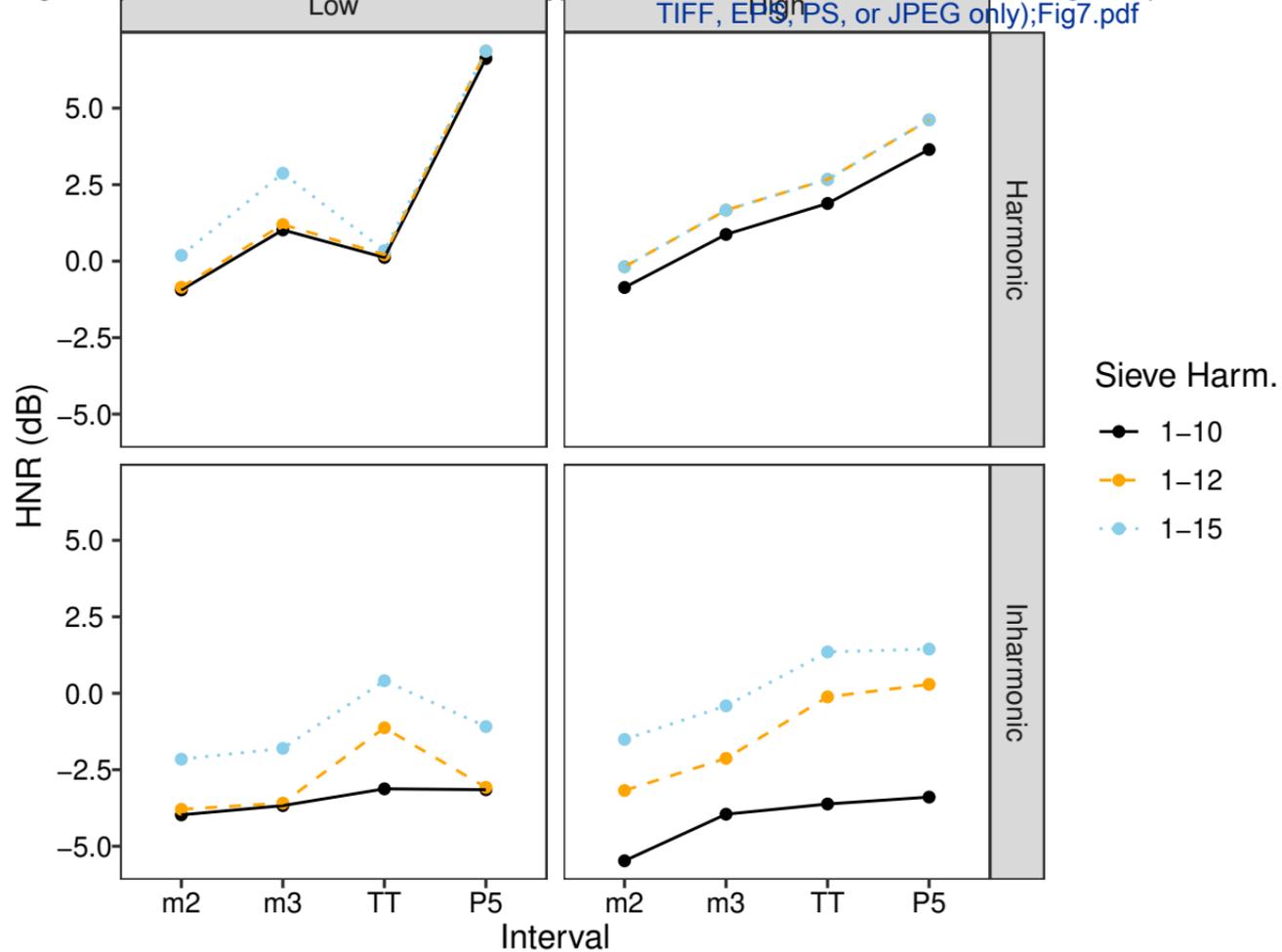


z Score Difference

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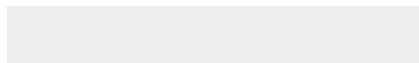






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