

1 **On musical interval perception for complex tones at very high**
2 **frequencies**

3

4 Hedwig E. Gockel and Robert P. Carlyon

5 Cambridge Hearing Group

6 MRC Cognition and Brain Sciences Unit, University of Cambridge, 15 Chaucer Rd.,

7 Cambridge CB2 7EF, UK

8

9 Email addresses of all authors:

10 Hedwig.gockel@mrc-cbu.cam.ac.uk, bob.carlyon@mrc-cbu.cam.ac.uk

11

12 Running title: Musical pitch at high frequencies

13

14 Corresponding author:

15 Hedwig E. Gockel

16 MRC Cognition and Brain Sciences Unit, University of Cambridge, 15 Chaucer Road,

17 Cambridge CB2 7EF, UK

18 E-mail : hedwig.gockel@mrc-cbu.cam.ac.uk

19 Tel : +44 1223 769488

20 Fax : +44 1223 300984

21

22

23 **ABSTRACT**

24 Listeners appear able to extract a residue pitch from high-frequency harmonics for
25 which phase locking to the temporal fine structure is weak or absent. The present
26 study investigated musical interval perception for high-frequency harmonic complex
27 tones using the same stimuli as Lau, Mehta, and Oxenham [J. Neurosci. **37**, 9013-
28 9021 (2017)]. Nine young musically trained listeners with especially good high-
29 frequency hearing adjusted various musical intervals using harmonic complex tones
30 containing harmonics 6-10. The reference notes had fundamental frequencies (F0s) of
31 280 or 1400 Hz. Interval matches were possible, albeit markedly worse, even when all
32 harmonic frequencies were above the presumed limit of phase locking. Matches
33 showed significantly larger systematic errors and higher variability and subjects
34 required more trials to finish a match for the high than for the low F0. Additional
35 absolute pitch judgements from one subject with absolute pitch, for complex tones
36 containing harmonics 1-5 or 6-10 with a wide range of F0s, were perfect when the
37 lowest frequency component was below about 7 kHz, but at least 50% of responses
38 were incorrect when it was 8 kHz or higher. The results are discussed in terms of the
39 possible effects of phase-locking information and familiarity with high-frequency
40 stimuli on pitch.

41

42 **Key words:** musical interval adjustment, absolute pitch, phase locking, tonotopic
43 information.

44

45 I. INTRODUCTION

46 It has been widely argued that the perception of tone chroma, and especially of
47 musical intervals, depends at least partly on the use of information derived from the
48 pattern of phase locking in the auditory nerve (Cariani and Delgutte, 1996; Meddis
49 and O'Mard, 1997; de Cheveigné, 1998). If this is the case, then the ability to judge
50 and match musical intervals should be markedly worse for complex tones whose
51 frequency components fall at very high frequencies (≥ 8.4 kHz in the context of the
52 present study), for which phase locking is weak or absent (Johnson, 1980; Palmer and
53 Russell, 1986). The present study tested this prediction by assessing the ability of
54 musically trained listeners to adjust the fundamental frequency (F_0) of complex tones
55 so that there was a specific musical interval between them, using complex tones with
56 harmonics in two frequency regions; a low frequency region where phase locking is
57 robust and a high frequency region where phase locking is usually assumed to be
58 severely reduced or absent. Interval-adjustment tasks provide arguably the most
59 demanding test of musical pitch perception and can provide information both on
60 consistency and biases in pitch perception.

61 The exact upper limit of phase locking in the auditory nerve (AN) in humans is
62 unknown and consensus on this is currently lacking (Verschooten *et al.*, 2019). Phase
63 locking has generally been assumed to be weak or absent for frequencies above about
64 4-5 kHz (Johnson, 1980; Palmer and Russell, 1986; Weiss and Rose, 1988). However,
65 some studies have suggested that weak phase locking to temporal fine structure (TFS)
66 might be available for frequencies up to about 7-8 or possibly even 10 kHz, with the
67 usable limit depending, among other things, on the task used (Heinz *et al.*, 2001;
68 Moore and Sek, 2009; Kale and Heinz, 2012; Moore and Ernst, 2012). Others argue
69 for a limit around 3.5-4.5 kHz in the AN, with a much lower limit of about 1.4 kHz as

70 the highest frequency usable by the central nervous system (Joris and Verschooten,
71 2013; Verschooten *et al.*, 2015; Verschooten *et al.*, 2018).

72 While the predominant view is that perception of musical pitch relies at least
73 partly on the presence of phase locking in the AN, there is some evidence indicating
74 that musical pitch might be perceived in the absence of phase locking. For pure-tone
75 stimuli, Ward (1954) found that while most subjects were unable to adjust the
76 frequency of one tone to be one octave higher than that of a reference tone when the
77 reference frequency was above 2.7 kHz, two of his subjects were able to do so even
78 when the reference frequency was 5 kHz, and thus the octave match was around 10
79 kHz, where phase locking was assumed to be absent. However, subjects needed more
80 time at these high frequencies than at the lower frequencies. Similarly, all three
81 musically trained subjects of Burns and Feth (1983) were able to adjust various
82 musical intervals for reference frequencies of 1 and 10 kHz. However, the within-
83 subject standard deviations (SDEVs) of the adjustments were about 3.5-5.5 times
84 larger for the 10-kHz than for the 1-kHz reference tone. Thus, experiments with pure
85 tones have indicated that, although musical pitch perception may be possible at very
86 high frequencies, performance in pitch-related tasks is usually much worse than at
87 lower frequencies, where phase locking is assumed to be strong.

88 Reasonably good pitch perception has been observed in experiments using
89 complex tones consisting of only high-frequency components but with a “missing
90 fundamental” frequency that is much lower. Oxenham *et al.* (2011) showed that even
91 when all audible harmonics were above 6 kHz, a residue pitch (a pitch corresponding
92 to the missing fundamental) was evoked, and melody discrimination for the high-
93 frequency complex tones was as good as that for low-frequency pure tones. Carcagno
94 *et al.* (2019) also observed good performance in a melody discrimination task for

95 high-frequency complex tones with all audible frequency components above 6 kHz,
96 and reported that the pattern of consonance ratings of various musical intervals for
97 complex-tone dyads was similar to (albeit less distinct than) that observed for the
98 same notes with lower frequency components.

99 Lau *et al.* (2017) used complex tones whose lowest component had an even
100 higher frequency (at or above 8.4 kHz). They measured difference limens for
101 fundamental frequency (F0DLs) and difference limens for frequency (FDLs) for the
102 individual harmonics presented in isolation. They observed surprisingly small F0DLs
103 (around 5%) given that the FDLs were much larger (around 20-30%), and argued that
104 this could be explained by the existence of central harmonic template neurons that
105 receive rate-place information. Gockel and Carlyon (2018) and Gockel *et al.* (2020)
106 reported even smaller F0DLs (around 2%) for the same complex tones as those used
107 by Lau *et al.* (2017). However, neither study assessed whether these tones were able
108 to convey musical pitch.

109 The objective of the current study was to assess musical pitch perception in a
110 stricter sense for complex tones having all components at or above 8.4 kHz. To do this
111 subjects were required to make musical interval adjustments, and, for one subject,
112 absolute pitch judgements. Musical interval adjustments are generally thought of as a
113 stricter test of pitch perception than F0 discrimination or pitch matches to unison,
114 since accurate musical interval judgments require precise frequency-ratio information
115 and not just the ordinal properties of pitch (see e.g. Burns and Feth, 1983).
116 Furthermore, a musical interval adjustment task is likely to be more sensitive to
117 changes in pitch salience than a melody discrimination task, because a change in
118 melody might be detected even if the size of the musical intervals is not precisely
119 perceived. The mean error and the variability of the musical interval adjustments as

120 well as the time (the number of trials) needed to make the adjustments was analyzed.
121 Performance for these high-frequency complex tones was compared with that for
122 lower frequencies, measured for the same subjects. If performance for the high-
123 frequency complex tones was found to be not markedly worse than that for the low-
124 frequency complex tones, this would extend previous results on musical pitch for
125 complex tones to a higher frequency region. Relative performance in the two
126 frequency regions would indicate the relative salience of musical pitch in a low
127 frequency region and in high frequency region where phase locking is presumed to be
128 very weak or absent.

129

130 **II. METHODS**

131 **A. Subjects**

132 Nine young normal-hearing musically trained subjects (5 females and 4 males)
133 between 19 and 28 years of age (mean age of 22.1 years) participated in the
134 experiment proper; many more were initially screened (see below). One of them had
135 absolute pitch, i.e. was able to name notes without a reference (Bachem, 1937). None
136 of them was a professional musician. The average number of years of musical
137 training/practice was 16 (ranging from 13-21 years). Subjects 1, 2, 3, 8 and 9 started
138 playing the violin or cello from age 7 years or earlier, and had played for at least 10
139 years. Subject 9, who had absolute pitch, started violin and piano training at the age of
140 3 years and had played for about 11 years. Subjects 2, 4, 5, and 7 started playing piano
141 from age 7, 5, 8 and 9 years, and had played for at least 12 years. All of them except
142 subject 4 had singing lessons for at least 6 years and most of them were still singing in
143 choirs.

144 To ensure audibility of the high-frequency tones and basic pitch-discrimination
145 ability, subjects had to pass a three-stage screening, as in Lau *et al.* (2017) and Gockel
146 *et al.* (2020), to be eligible for the main part of the study: (1) Pure-tone audiometric
147 thresholds at 0.25, 0.5, 1, 2, 4, 6, and 8 kHz had to be < 20 dB HL. (2) Masked
148 thresholds were measured for 210-ms pure tones at 10, 12, 14 and 16 kHz in a
149 continuous threshold-equalizing noise (TEN; Moore *et al.*, 2000), extending from
150 0.02 - 22 kHz. At 1 kHz, the TEN had a level of 45 dB SPL/ERB_N, the same as used
151 in the experiment (see below), where ERB_N stands for the average value of the
152 equivalent rectangular bandwidth of the auditory filter for young normal-hearing
153 listeners tested at low sound levels (Glasberg and Moore, 1990). Masked thresholds
154 had to be ≤ 45 dB SPL up to 14 kHz, and ≤ 50 dB SPL at 16 kHz. (3) FODLs and
155 FDLs for the same stimuli as in the main experiment but without the TEN and without
156 level randomization had to be < 6% and < 20% in the low and high frequency regions,
157 respectively (see below). The geometric mean DLs for those subjects who passed the
158 screening were 0.29% across frequencies in the low frequency region and 2.5% across
159 frequencies in the high spectral region. These values were smaller than the mean DLs
160 reported for a similar initial pitch-discrimination screening in Lau *et al.* (2017) by
161 factors of 1.9 and 1.8 for the low- and high spectral regions, respectively. Some of the
162 subjects took part in some other experiment(s) involving high-frequency tones, not
163 presented here, before data collection for the present study commenced, and thus had
164 some previous experience with high-frequency tones. All subjects confirmed that they
165 were familiar with musical intervals and that they had learned them as part of their
166 musical training. There was no additional screening for the ability of subjects to
167 perform musical interval adjustments, as the relevant outcome was the within-subject
168 comparison between performance in the high and low frequency regions.

169 Initially 29 musically trained subjects between 19-28 years old were tested,
170 nine of whom passed all screening stages. Three dropped out at the first stage, 13 at
171 the second stage, and four at the last stage of the screening. Informed consent was
172 obtained from all subjects. This study was carried out in accordance with the UK
173 regulations governing biomedical research and was approved by the Cambridge
174 Psychology Research Ethics Committee.

175

176 **B. Screening procedure**

177 Pure-tone audiometric thresholds in quiet were measured at octave frequencies
178 from 0.25 kHz to 8 kHz and at 6 kHz, using a Midimate 602 audiometer (Madsen
179 Electronics, Minneapolis, MN). Masked thresholds for the high-frequency (> 8 kHz)
180 210-ms pure tones (including 10-ms onset and offset hanning-shaped ramps) were
181 measured for each ear using a two-interval two-alternative forced-choice task (2I-
182 2AFC) with a 3-down 1-up adaptive procedure estimating the 79.4% correct point on
183 the psychometric function (Levitt, 1971). The step size was 5 dB until two reversals
184 occurred and 1 dB thereafter. The adaptive track terminated after 10 reversals, and the
185 threshold was determined as the mean of the levels at the last six reversal points. The
186 final threshold was the mean of the thresholds from three adaptive tracks.

187 F0DLs were measured in quiet for diotically presented complex tones
188 containing harmonics 6-10 with an F0 of 280 or 1400 Hz (the same tones as used in
189 the main experiment, i.e. with edge component levels that were 6 dB below that of the
190 other components, but without level randomization; see below), and FDLs were
191 measured for the components of the complex tones presented in isolation. A 2I-2AFC
192 task with a 3-down 1-up adaptive procedure was used. Subjects had to indicate the
193 tone with the higher pitch. For both F0DLs and FDLs, the nominal F0 or frequency

194 was fixed within a given adaptive run, but varied across adaptive runs. The F0s (or
195 frequencies) of the two tones presented within a trial were geometrically centered on
196 the nominal F0 (or frequency). The signal duration was 210 ms (including 10-ms
197 onset and offset hanning-shaped ramps) and the inter-stimulus interval (ISI) was 500
198 ms. Initially, the difference in F0 (or frequency) was 20%. This was reduced (or
199 increased) by a factor of two for the first two reversals, by a factor of $\sqrt{2}$ for the next
200 two reversals and by a factor of 1.2 thereafter. The adaptive track terminated after 12
201 reversals, and the threshold was determined as the geometric mean of the frequency
202 differences at the last eight reversal points. The final threshold was the geometric
203 mean of the thresholds from three adaptive tracks.

204

205 **C. Musical interval adjustments**

206 Subjects had to adjust the F0 of a complex tone so that its pitch was a certain
207 musical interval (target interval) below that of a preceding reference complex tone.
208 Target intervals were a perfect fifth (“Fifth”, 7 semitones down), a major third
209 (“Third”, 4 semitones down) and a major second (“Second”, 2 semitones down). In
210 addition, subjects were asked to match to Unison. The reference tones had an F0 of
211 1400 Hz (“High”) or 280 Hz (“Low”), and all complex tones (reference and
212 adjustable) contained harmonics 6-10 only. The frequency of the lowest component
213 was 8400 Hz for the 1400-Hz F0 reference, so phase locking should have been absent
214 or very weak, while in the Low-F0 condition phase locking should have been strong.
215 The errors and the variability of the musical interval adjustments for the 1400-Hz and
216 the 280-Hz F0 were compared. Also, the number of trials taken to make a match, i.e.
217 the number of times subjects listened to the stimuli, was used as an indicator of the
218 degree of difficulty (Ward, 1954; Cardozo, 1965; Gockel and Carlyon, 2016).

219 The reference tone was presented either diotically (“Dio”) or dichotically
220 (“Dic”). For the latter, odd harmonics were presented to the left and even harmonics
221 to the right ear. At low F0s, this manipulation is not expected to affect pitch
222 discrimination for resolved-harmonic stimuli (Bernstein and Oxenham, 2003). While
223 the temporal envelope rate of 1400 Hz was expected to be too high to lead to a pitch
224 percept (Burns and Viemeister, 1976; Macherey and Carlyon, 2014), dichotic
225 presentation of components would have reduced possible envelope cues to pitch even
226 further due to the doubling of the frequency spacing between components in each ear,
227 which would double the envelope repetition rate. The adjustable tone complex was
228 always presented diotically. For each presentation, the starting phases of all
229 components were randomized and individual component levels were randomized by
230 ± 3 dB about the mean component level, which was 55 dB SPL for harmonics 7-9 and
231 49 dB SPL for the two edge components. This was done to further weaken envelope
232 cues, and to minimize edge pitches (Fastl, 1971; Klein and Hartmann, 1981). The
233 tones were presented in a background of continuous TEN, extending from 0.02 to 22
234 kHz and with a level of 45 dB SPL/ERB_N at 1 kHz, to mask possible distortion
235 products. When the reference tone was diotic, the TEN was presented diotically as
236 well, and when the reference tone was dichotic, an independent TEN was presented to
237 each ear. These stimuli were similar to the ones used by Lau *et al.* (2017), except that
238 they used gated rather than continuous TEN, and were identical to those used by
239 Gockel *et al.* (2020).

240 One match consisted of several trials, and subjects could take as many trials as
241 they wanted to finish a match. A match was finished when the subject indicated by
242 button press that s/he was satisfied with the adjustment. No feedback was provided as
243 to the precision of the adjustment. In each trial, subjects first heard the reference tone,

244 whose F0 was fixed until the match was completed, followed by the adjustable tone.
245 Both tones had a duration of 500 ms (including 10-ms onset and offset hanning-
246 shaped ramps). The ISI was 500 ms. After cessation of the adjustable tone, subjects
247 could adjust its F0 to form the desired musical interval (main task), and adjust its level
248 to produce roughly equal loudness to that of the reference tone (in case of obvious
249 differences in loudness) by button presses, and/or initiate the next trial. In practice, the
250 loudness of the tones was perceived as roughly equal most times, and no level
251 adjustments were made for most matches. Only for the unison adjustments, when the
252 reference complex was presented dichotically, did the level adjustment of the diotic
253 complex, averaged across subjects, reach about -1 dB. In each trial, the subject was
254 allowed an unlimited number of button presses before s/he initiated the next trial. The
255 number of trials taken for a match (“n_listen”) was counted, and was visible to the
256 subject. The starting F0 of the adjustable complex was randomly chosen to be
257 between 0.5 and 1 times the F0 of the reference tone. The F0 could be adjusted
258 upwards or downwards via virtual button presses with mean step sizes of 4, 1, 1/4,
259 and 1/16 semitones. The actual step size associated with each button was randomly
260 varied across matches within the range 0.75-1.25 times the mean step size. This was
261 done to discourage subjects from calculating – after the first sound exposure or after
262 first matching to Unison – a sequence of button presses deemed to give the desired
263 musical interval, rather than actually listening to and comparing the sounds in each
264 trial. Subjects were informed about the random jitter, and it was clear from
265 observation of the matching behaviour of the subjects and from subjects’ reports that
266 subjects did not use this strategy¹.

267 Before data collection proper started, subjects received at least two hours of
268 training in which they got accustomed to the procedure and stimuli and completed on

269 average two matches for each of the 16 conditions (4 musical intervals \times 2 F0s \times 2
270 modes of presentation). The matches from the training were discarded. In the
271 experiment proper, each subject completed at least 20 matches for each of the 16
272 conditions, which took on average 7.4 sessions of two hours each (including breaks).
273 The number of sessions needed varied across subjects, and ranged from 5 to 10. The
274 very slight variation in number of matches was the result of completing full 2-hour
275 sessions. The order of conditions was randomized with the restriction that within a
276 session no condition was repeated before a match was completed for all other
277 conditions.

278

279 **D. Unison adjustments with non-overlapping harmonics**

280 This was a control experiment to verify that the pitch evoked by the 1400-Hz
281 F0 complex tone containing harmonics 6-10 corresponded to its F0, rather than, for
282 example, to the frequency of the lower edge component. Subjects had to adjust the F0
283 of a complex tone containing harmonics 1-5 so that its pitch was the same as that of a
284 reference tone. The reference tone contained harmonics 6-10 only and, for each
285 match, its F0 was drawn randomly from a set of eight F0s, equally spaced on a
286 logarithmic scale, and ranging from 280 to 1400 Hz. For the reference tone, individual
287 component levels were randomized by ± 3 dB about the mean component level, as for
288 the musical interval adjustments. For the adjustable tone, the levels were not
289 randomized. Both tones were presented diotically. Otherwise, the stimuli and methods
290 were the same as for the musical interval adjustment experiment. Subjects needed
291 between three and four two-hour sessions to complete at least 22 matches for each F0.

292

293 **E. Equipment**

294 All stimuli were generated digitally in MATLAB (The Mathworks, Natick,
295 MA) with a sampling rate of 48 kHz. Four separate stimuli were generated: two
296 continuous background noise stimuli (one for each ear) and, for each trial, two
297 complex tone stimuli (one for each ear); in the diotic conditions the stimuli were
298 identical across ears. They were played out through four channels of a Fireface UCX
299 (RME, Haimhausen, Germany) soundcard using 24-bit digital-to-analog conversion,
300 and were attenuated independently with four Tucker-Davis Technologies (Alachua,
301 FL) PA4 attenuators. They were mixed with two Tucker-Davis Technologies SM5
302 signal mixers, and fed into a Tucker-Davis HB 7 headphone driver, which also
303 applied some attenuation. Stimuli were presented via Sennheiser HD 650 headphones
304 (Wedemark, Germany), which have an approximately diffuse-field response. The
305 specified sound levels are approximate equivalent diffuse-field levels. Subjects were
306 seated individually in a double-walled, sound insulated booth (IAC, Winchester, UK).
307

308 **F. Analysis**

309 For statistical analysis, repeated-measures analyses of variance (RM-ANOVA)
310 were calculated using SPSS (Chicago, IL). Throughout the paper, if appropriate, the
311 Huynh-Feldt correction was applied to the degrees of freedom (Howell, 1997). In
312 such cases, the original degrees of freedom and the corrected significance value are
313 reported. The Unison matches were analyzed separately from the musical interval
314 adjustments. Before statistical analysis of the musical interval adjustments, the mean
315 error and the within-subject SDEV of the adjustments were log-transformed to make
316 them more normally distributed. Shapiro-Wilk tests confirmed that the (transformed)
317 data were approximately normally distributed.

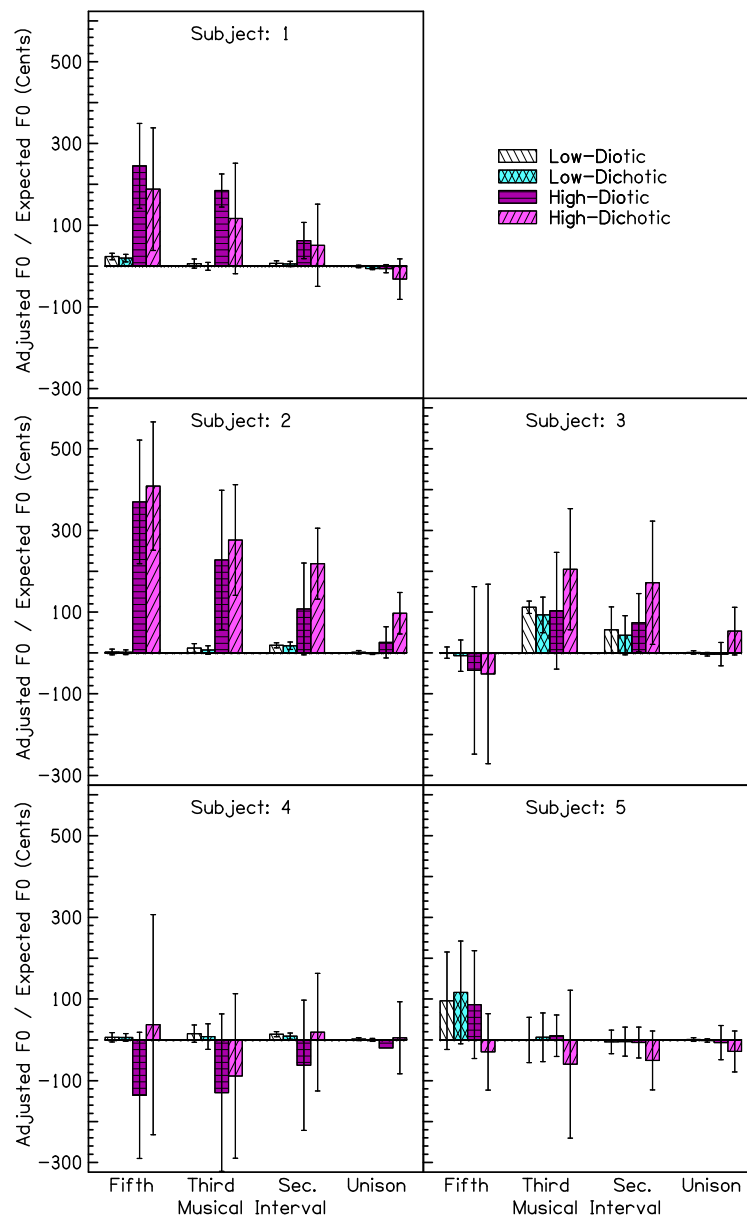
318

319 **III. RESULTS**

320 **A. Musical interval adjustments**

321 The expected F0 for each matched interval was determined on the equal-
322 temperament scale; for the perfect fifth, major third, and major second, the expected
323 F0 was exactly seven semitones (factor of 1/1.498), four semitones (factor of 1/1.26),
324 and two semitones (factor of 1/1.122), respectively, below the F0 of the reference
325 harmonic complex. Figures 1 and 2 show, for all subjects and conditions, the mean
326 (across 20 or more repetitions) deviation of the adjusted F0 from the expected F0 in
327 units of cents, where one cent is equal to 1/100th of a semitone; we refer to this value
328 as the mean error (ME). The error bars show the within-subject SDEVs of the
329 adjustments. Note the scale difference between the two figures; Figs. 1 and 2 show
330 adjustments for a group of five subjects with relatively poor performance and a group
331 of four subjects with relatively good performance, respectively. The group mean (and
332 the corresponding SDEVs across subjects) for the MEs and for the within-subject
333 SDEVs are shown in Fig. 3(a) and Fig. 3(b), respectively. In addition, Fig. 3(c) shows
334 the group mean (and the corresponding SDEVs across subjects) for the absolute
335 values of the MEs (AMEs); the AME gives, for each subject and condition, the size of
336 the mean deviation from the target value regardless of its direction.

337



338

339 **FIG. 1.** (Color online) Mean deviation of adjusted F0 from expected F0 (in cents)

340 for musical interval or unison adjustments for five out of nine subjects with

341 relatively poor performance. Error bars show the within-subject SDEVs. Each

342 group of four bars shows the results for one target musical interval. Within each

343 group of bars, the left-hand two show results for the F0 of 280 Hz and the right-

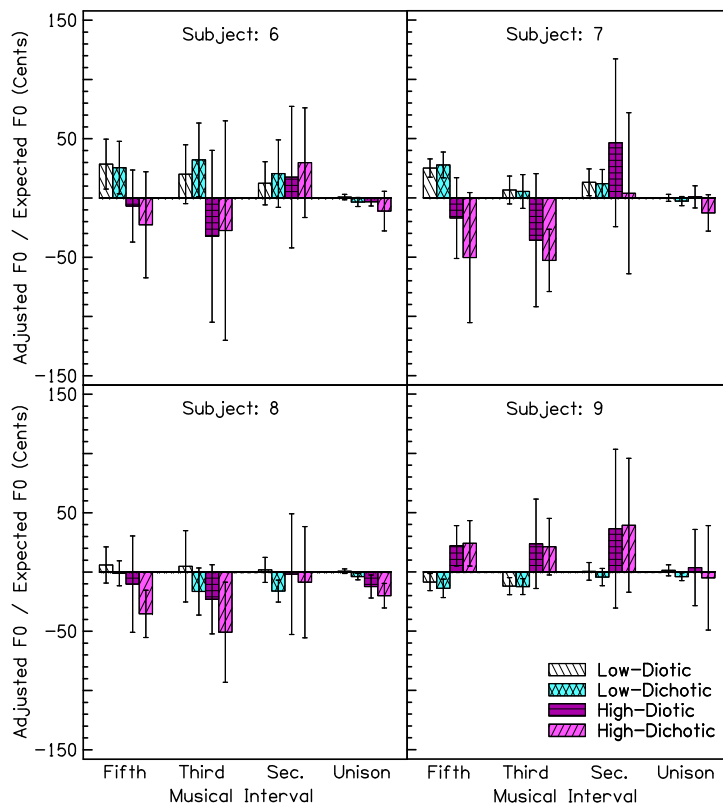
344 hand two show results for the F0 of 1400 Hz. All complex tones contained

345 harmonics 6-10. In condition diotic (1st and 3rd bars in each group) all harmonics346 were presented diotically. In condition dichotic (2nd and 4th bars in each group)

347 even harmonics of the reference tone were presented to the right and odd

348 harmonics to the left ear (see Methods).

349



350

351 **FIG. 2.** (Color online) As Fig. 1, but for the remaining four (out of the nine)

352 subjects, who showed better performance. Note the difference in scales between

353 the two figures.

354

355 Musical-interval adjustments were mostly better, i.e. MEs were closer to zero

356 and within-subject SDEVs were smaller, in the Low-F0 conditions (left two bars

357 within each group of four bars) than in the High-F0 conditions (right two bars within

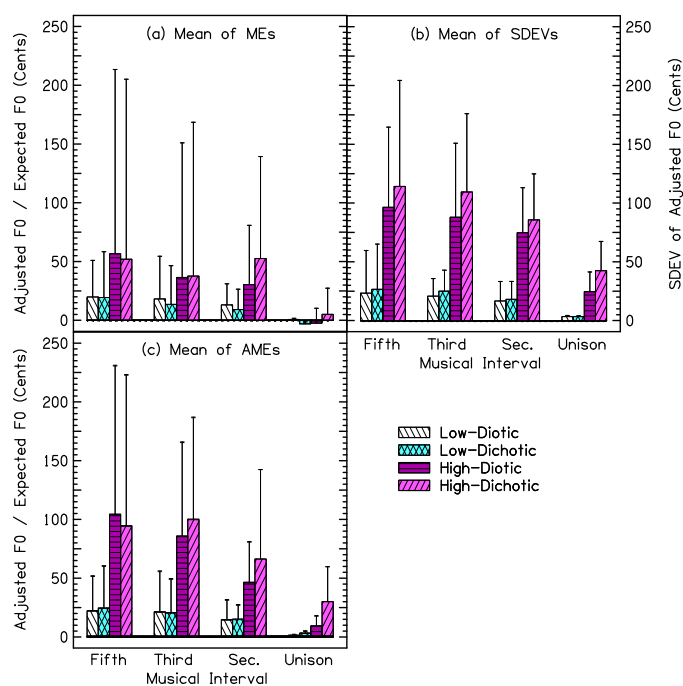
358 each group). For the High-F0 conditions, there were large differences between

359 subjects. For example, for subject 2 the mean adjusted F0 exceeded the expected F0

360 by up to 400 cents for the High-F0 perfect fifth, while in the same condition the

361 deviation between expected and adjusted F0 was around 20 cents for subject 9, even
 362 though both subjects showed excellent performance for the Low-F0 condition. For the
 363 five subjects in Fig. 1, the mean deviation of adjusted from expected F0 often
 364 exceeded ± 100 cents, mostly for the High-F0 conditions, while for subjects 6-9 in Fig.
 365 2 they were mostly below ± 100 cents. It is important to note that, for the Low-F0
 366 conditions, all subjects were able to match all musical intervals well, with two
 367 exceptions (subject 3 for the major third and subject 5 for the fifth). Performance was
 368 often, but not always, worse for the dichotic than for the diotic reference for the High-
 369 F0 conditions.

370



371

372 **FIG. 3.** (Color online) Group means of three measures. Error bars show SDEVs of
 373 each measure across subjects. Panel (a) shows the MEs, i.e. the systematic errors.
 374 Panel (b) shows the within-subject SDEVs. Panel (c) shows the AMEs, i.e. the
 375 absolute values of the systematic errors.

376

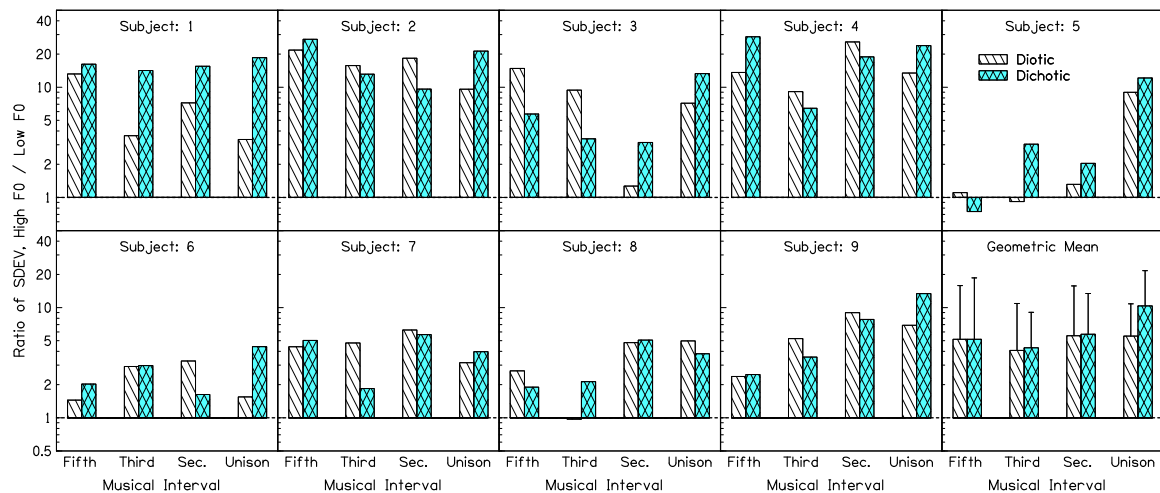
377 If subjects were completely unable to match musical intervals and had
378 responded randomly, then the expected value of the adjusted F0 would be 5.3
379 semitones below the F0 for all conditions². Thus, chance performance would lead to
380 expected MEs of 170, -130, and -330 cents for the perfect fifth, major third, and
381 major second, respectively. The observed MEs did not follow this pattern. In addition,
382 the observed within-subject SDEVs were smaller than expected under the assumption
383 of random button presses. The expected within-subject SDEV depends on the number
384 of button presses: the more random button presses, the larger the expected SDEV.
385 Simulations showed that for 10 and 20 random button presses the expected within-
386 subject SDEV was about 740 and 990 cents, respectively. The observed performance
387 was much better than this, indicating that subjects did not guess randomly in any
388 condition.

389 To compare the accuracy of the musical interval adjustments across F0s, the
390 MEs and the within-subject SDEVs of the adjustments were analyzed separately. The
391 former is a measure of any systematic error (or bias) while the latter is a measure of
392 the precision of the adjustments. To compare the size of the MEs across F0s, their
393 absolute values i.e. the AMEs were used, because the interest was in the size of the
394 mean deviation from the target value regardless of its direction. A three-way RM-
395 ANOVA (with factors: musical interval (excluding Unison), F0 and type of
396 presentation of the reference complex) was calculated on the log-transformed AMEs.
397 The main effect of F0 was highly significant [$F(1,8)=18.34$, $p=0.003$]. There was no
398 other significant main effect or interaction ($p>0.3$ in all cases). For the Unison
399 adjustments, AMEs were also significantly larger for the High- than the Low-F0
400 conditions [RM-ANOVA, $F(1,8)=8.66$, $p=0.019$] and significantly larger for dichotic
401 than diotic reference tones [$F(1,8)=6.54$, $p=0.034$]. The interaction was not significant

402 [F(1,8)=4.39, p=0.069]. There was no significant rank-order correlation between the
403 (signed) MEs across F0s (Spearman's $\rho < 0.55$ and $p > 0.12$ for all intervals).

404 Consider next the variability of the matches. The within-subject SDEVs,
405 shown by the error bars in Figs. 1 and 2, were mostly very small for the Low-F0
406 conditions (mean of 21.8 cents) and substantially larger for the High-F0 conditions
407 (mean of 94.9 cents); see also Fig.3(b) for the group means of the within-subject
408 SDEVs. Figure 4 shows, for each of the nine subjects, the ratio of the SDEV of the
409 adjustments for the High-F0 to the SDEV for the corresponding Low-F0 condition.
410 The geometric mean of this ratio and the standard deviation across subjects are shown
411 in the bottom right panel. The ratios are, with few exceptions, larger than 1 and they
412 range from about 0.75 for subject 5 for the perfect fifth to 29 for subject 4 for the
413 perfect fifth. The few individual cases of small ratios were mostly associated with
414 unusually large SDEVs in the corresponding Low-F0 condition as opposed to
415 unusually small SDEVs in the High-F0 condition. For example, for subject 5 and the
416 perfect fifth, the MEs and variability were unusually large for the low F0 (see error
417 bars for low-F0 conditions in Figs. 1 and 2). On average (geometric mean ratio) the
418 SDEVs were a factor of 5 larger for the High-F0 than for the Low-F0 condition. Note
419 that subject 6, for whom the mean deviation of adjusted from expected F0 was most
420 similar across the two F0s, produced more variable adjustments for the High-F0 than
421 for the Low-F0 condition, like the other subjects. A three-way RM-ANOVA with
422 factors musical interval (excluding Unison), F0 and mode of presentation, with log-
423 transformed within-subject SDEVs as input data gave a significant main effect of F0
424 [F(1,8)=30.64, p=0.001]. There was no other significant main effect or interaction
425 ($p > 0.12$ in all cases). For the Unison adjustments, SDEVs were also significantly
426 larger for the High-F0 than the Low-F0 [significant main effect of F0: F(1,8)=21.49,

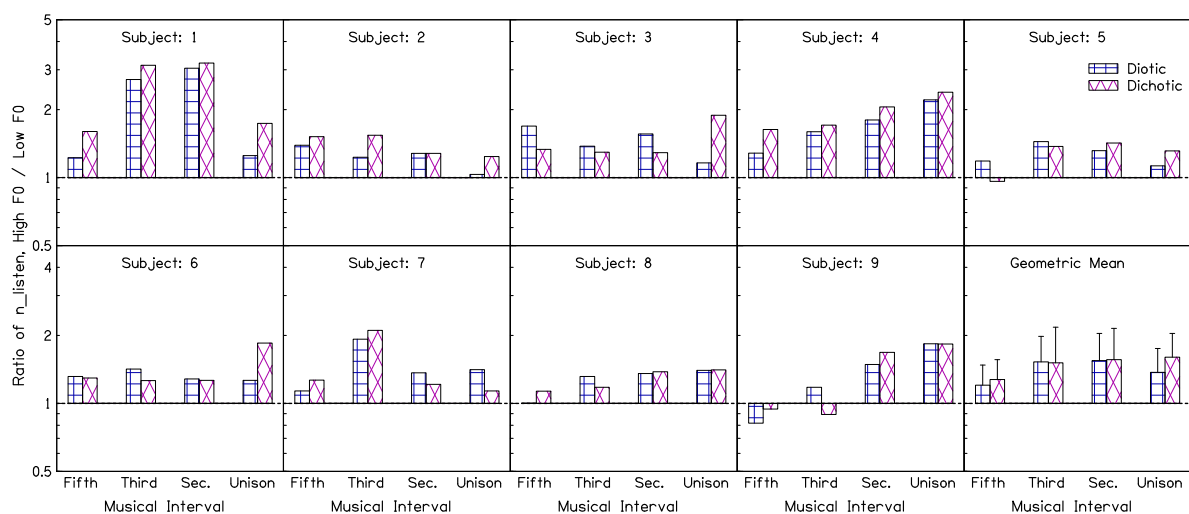
427 $p=0.002$]. In addition, there was a significant main effect of mode of presentation
 428 [$F(1,8)=13.85, p=0.006$], which was driven by larger SDEVs for dichotic than diotic
 429 presentation for the High-F0 but not for the Low-F0, as shown by the significant
 430 interaction between F0 and mode of presentation [$F(1,8)=13.55, p=0.006$].
 431



432
 433 **FIG. 4.** (Color online) Ratio of the within-subject SDEVs (High F0/Low F0) of
 434 musical interval or unison adjustments (across a minimum of 20 matches for each
 435 condition). The bottom right panel shows the geometric mean (and the SDEVs) of
 436 this ratio across subjects.

437
 438 Next, consider the number of trials taken to make a musical interval
 439 adjustment as an indicator of the degree of difficulty. This varied substantially across
 440 subjects, ranging from about 11 trials per adjustment (subjects 2 and 7) to about 30
 441 trials (subject 8). Figure 5 shows the ratios of n_{listen} , High-F0/ Low-F0, for each
 442 condition. The ratios are mostly larger than one, indicating that subjects took longer in
 443 the High-F0 than in the corresponding Low-F0 condition to be satisfied with their
 444 musical interval adjustments. This was reflected in subjective reports; subjects
 445 described the pitch of the high-F0 (reference) tones as unclear and ambiguous. A

446 three-way RM-ANOVA on the values of n_{listen} gave a significant main effect of F0
 447 [$F(1,8)=20.08, p=0.002,$]. There was no other significant main effect or interaction.
 448 For the Unison adjustments, both main effects [F0: $F(1,8)=17.62, p=0.003$; mode of
 449 presentation: $F(1,8)=32.27, p<0.001$] and the interaction [$F(1,8)=10.08, p=0.013$]
 450 were significant; n_{listen} was higher for dichotic than diotic presentation, and
 451 significantly more so for the High-F0 than for the Low-F0.
 452



453

454 **FIG. 5.** (Color online) Ratio of the average number of trials taken to make a
 455 musical interval or unison adjustment for reference complex tones with F0s of
 456 1400 and 280 Hz. The bottom right panel shows the geometric mean (and the
 457 SDEVs) of this ratio across subjects.

458

459 Overall the results showed that musical interval adjustments were not random.
 460 However, they were significantly more biased (had larger AMEs) and were more
 461 variable for the High-F0 than for the Low-F0, despite the fact that n_{listen} was
 462 usually larger for the high-F0.

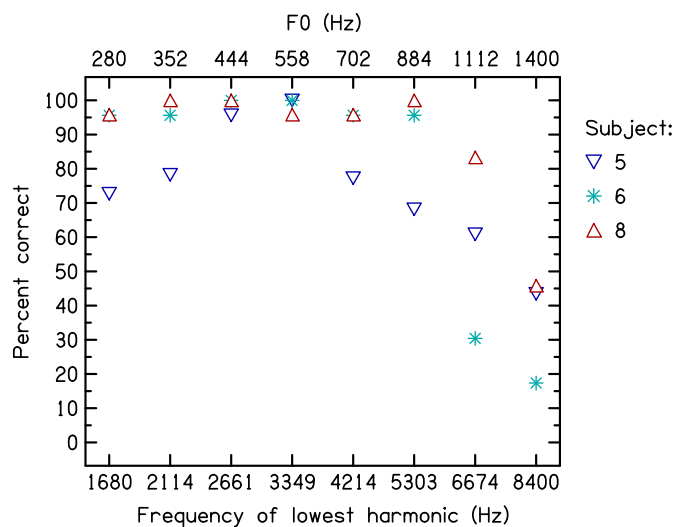
463

464 **B. Unison adjustments with non-overlapping harmonics and**
465 **absolute pitch judgements**

466 It was assumed that subjects perceived a pitch corresponding to the F0 of the
467 reference tones, even for the High-F0 conditions (see Oxenham *et al.*, 2011) and that
468 musical interval adjustments were based on this pitch rather than the pitch of any
469 individual harmonic. A control experiment with three subjects (subjects 5, 6, and 8),
470 who did relatively well in the musical-interval adjustment tasks for the high F0,
471 assessed whether the pitch of the complex tones used here did indeed correspond to its
472 F0. Subjects adjusted the F0 of a complex tone with harmonics 1-5 to have the same
473 pitch as a reference tone containing harmonics 6-10, with F0s ranging from 280-1400
474 Hz. Responses were scored as correct when they fell within ± 25 cents of the reference
475 F0 or of an F0 one or more octaves above or below the reference F0³. Figure 6 shows
476 the percent correct matches as a function of the frequency of the lowest component in
477 the reference tone. Chance performance was at 4.2% correct.

478 Performance ranged from good (70 to 80% correct) to very good (>95%
479 correct) for reference complex tones whose lowest component had a frequency up to
480 5303 Hz. Performance worsened for all subjects when the frequency of the lowest
481 harmonic in the complex was 6674 Hz, and became even worse for a lowest
482 frequency of 8400 Hz, which was the same as that in the High-F0 condition of the
483 musical interval adjustment experiment. Nevertheless, performance was above chance
484 throughout, in agreement with the findings of Oxenham *et al.* (2011). There was no
485 indication in the distribution of the individual matches that subjects perceived a pitch
486 corresponding to the frequency of an individual harmonic. For the two highest F0s
487 employed here, percent-correct values were somewhat lower than those observed by
488 Oxenham *et al.* (2011). This is probably because in that study the individual

489 component levels of the reference complex tone were not randomized and edge
 490 components were not reduced in level by 6 dB.



491

492 **FIG. 6.** (Color online) Average percent of pitch matches to unison, for complex
 493 tones with non-overlapping harmonics, that were within ± 0.25 semitones of the F0
 494 of the reference complex tone or one (or two) octaves below or above, as a
 495 function of the frequency of the lowest component present in the reference
 496 complex. The reference complex always contained harmonics 6-10. The variable
 497 complex contained harmonics 1-5. Chance performance corresponds to 4.2%.

498

499 Overall, these data show that the subjects perceived a pitch corresponding to
 500 the F0 rather than a pitch corresponding to an individual harmonic of the high-F0
 501 complex. However, the pitch of the high-F0 reference note with harmonics 6-10, as
 502 employed in the musical interval adjustment experiment, was less salient than that of
 503 the low-F0 reference note.

504 Subject 9 possessed absolute pitch and was asked to name note chroma and the
 505 register (octave number) of the note for harmonic complex tones with a wide range of
 506 F0s and of the frequency of the lowest harmonic present in the complex (see

507 Appendix). Performance was perfect when the frequency of the lowest harmonic in
508 the complex was below 7000 Hz. When the lowest frequency was at or above 7911
509 Hz, at least 50% of the chroma responses were incorrect. The pattern of responses
510 indicated that the perceived pitch corresponded to the F0 of the complex. It also
511 showed that while absolute pitch judgements were possible and perfect for medium-
512 high component frequencies, performance markedly deteriorated when the frequency
513 of the lowest harmonic was above about 7.5 kHz. This contrasts with the ability of the
514 same subject to adjust musical intervals in the main experiment for a diotic reference
515 tone whose lowest harmonic had a frequency of 8.4 kHz; the AMEs of her musical-
516 interval adjustments were below 37 cents for all target intervals, and had a mean
517 (excluding the unison judgements) of 27.3 cents.

518

519 **IV. GENERAL DISCUSSION**

520 **A. Overview**

521 In the Low-F0 conditions, most subjects were able to match musical intervals
522 with small systematic errors and with small SDEVs for all intervals. The observed
523 mean errors and within-subject SDEVs were similar to those reported previously for
524 musically trained subjects (Burns and Feth, 1983; Rakowski, 1990; Burns, 1999),
525 except for the major third for subject 3 and for the fifth for subject 5. In both cases,
526 the adjustments were one semitone above the expected F0, leading to a smaller
527 interval than expected, i.e. to a minor third and a diminished fifth. Subjective reports
528 indicated that the systematic match to a minor third rather than a major third could be
529 explained by subject 3 wrongly anchoring the reference tone as note C and, going
530 down two notes from there on the major scale, i.e. from note C to note A. Note that
531 the upwards major third interval corresponds to two whole-note steps from note C on

532 the major scale. It is unclear what caused the systematic mismatch of the perfect fifth
533 for subject 5. Musical interval adjustments were not significantly worse in the dichotic
534 than in the diotic condition. This is in agreement with the finding that F0DLs were
535 similar for dichotic and diotic presentation for these types of complex tones (Lau *et*
536 *al.*, 2017; Gockel and Carlyon, 2018), and indicates that the (musical) pitch of these
537 tones does not depend on the temporal envelope rate of the stimulus.

538 The main finding was that musical interval adjustments were possible for both
539 F0s, even though, for the high F0, components with frequencies up to at least 9.8 kHz
540 were required for F0 perception. For frequencies as high as this, phase locking is
541 presumably weak or absent (Verschooten *et al.*, 2019). However, performance was
542 clearly worse for the high than the low F0: The matches showed significantly larger
543 systematic errors and larger within-subject SDEVs for the High-F0 than for the Low-
544 F0 condition, despite the fact that subjects usually took more trials to make the
545 adjustments for the former, probably because High-F0 conditions were perceived as
546 more difficult. Thus, the poorer performance in the High-F0 condition cannot be
547 attributed to subjects putting in less effort for this condition. On the contrary,
548 performance likely would have been even worse in the High-F0 condition if listeners
549 had not taken more trials in the High-F0 than the Low-F0 condition. The high-
550 frequency complex tones clearly had a much less salient pitch than the low-frequency
551 complex tones, and this was also obvious in the unison adjustments with non-
552 overlapping harmonics (control experiment).

553 In the present study, in order to avoid distracting differences in timbre, the
554 number of the lowest harmonic present was not varied across presentations.
555 Conditions were designed to be as easy as possible, whilst still requiring genuine
556 interval adjustments, as it was not *a priori* obvious how well the subjects would be

557 able to perceive musical intervals for the High-F0 condition. Roving of the number of
558 the lowest harmonic is sometimes employed to discourage listeners from using
559 unwanted but useful cues based on the pitches of individual harmonics. Given that
560 FDLs for the individual frequency components used in the High-F0 condition are
561 substantially larger than the F0DL for the complex (Lau *et al.*, 2017; Gockel *et al.*,
562 2020), the pitch of an individual harmonic is unlikely to have provided a useful cue on
563 which to base musical interval adjustments in the High-F0 condition. For the Low-F0
564 condition, FDLs for the individual harmonics are not smaller than the F0DL for the
565 complex, so here too it is unlikely that musical interval adjustments would improve by
566 using the pitch of an individual harmonic rather than that of the complex.

567

568 **B. Comparison to previous results**

569 The present results contrast with those of Oxenham *et al.* (2011) on melody
570 discrimination for high-frequency complex tones (their Experiment 2a). Oxenham *et*
571 *al.* (2011) reported that the ability to discriminate between random melodies was
572 equally good for high-frequency complex tones, where all audible harmonics were
573 above 6 kHz, and for low-frequency pure tones. Several factors might contribute to
574 the different findings. Firstly, in the present study the frequency of the lowest audible
575 component in the complex was higher than in their study and phase locking
576 presumably is weaker at 8.4 than at 6 kHz. Related to this, the level of the edge
577 components was 6 dB lower than that of the inner harmonics in the present study, but
578 not in the study of Oxenham *et al.* (2011), likely reducing the contribution of the 8.4
579 kHz component and shifting upwards the frequency of the most salient harmonic.
580 Secondly, individual component levels were randomized by ± 3 dB about the mean for
581 each presentation in the present study, but not in the study of Oxenham *et al.* (2011).

582 Randomization of component levels might have affected the salience of the pitch of
583 the high-frequency complex tones more than that of the low-frequency complexes, for
584 which phase locking would be available. Thirdly, a melody discrimination task is
585 likely to be less sensitive to changes in pitch salience than a musical interval
586 adjustment task; a change in melody might be perceived even if the size of the
587 musical intervals is not precisely perceived. Oxenham *et al.* (2011) also collected
588 Unison matches between a pure tone and high-frequency complex tones (their
589 Experiment 1) over a range of F0s and frequency regions. Performance deteriorated
590 only when the frequency of the lowest harmonic in the complex was above 10 kHz. In
591 the present study, Unison matches of complex tones with non-overlapping harmonics
592 (control experiment) deteriorated for lower frequencies of the lowest harmonic
593 present (8.4 kHz). Factors contributing to this difference might be the 6-dB decrease
594 in the level of the edge components and the level randomization of the individual
595 components applied in the present study, but not in the study of Oxenham *et al.*
596 (2011).

597 To the best of our knowledge, there are no previous data on musical interval
598 adjustments for high-frequency complex tones. In the following, we compare the
599 present data with previous studies on musical interval adjustments with medium- and
600 high-frequency pure tones. For the present high-frequency complex tones, the within-
601 subject SDEVs of the musical interval adjustments were on average, a factor of 5
602 larger for the High-F0 than for the Low-F0. For the unison adjustments (main
603 experiment), SDEVs increased on average by a factor of 5 in the diotic condition and
604 by a factor of 10 in the dichotic condition. Presumably, unison adjustments were
605 harder in the dichotic than the diotic condition due to the differences in timbre
606 between the dichotic reference tone and the diotic adjusted tone in the former

607 condition, which may have arisen from differences in suppression between
608 components within each ear (Ruggero *et al.*, 1992) and in inhibition across ears
609 (Boudreau and Tsuchitani, 1968).

610 Burns and Feth (1983) obtained musical interval adjustments for pure tones
611 with reference frequencies of 1 and 10 kHz. Matches were less accurate for the high-
612 than for the low-frequency tone, and the within-subject SDEVs increased on average
613 by a factor of about 4-5, which is similar to the increase observed here. In the study of
614 Burns and Feth (1983), musical intervals were adjusted upwards, so for the high-
615 frequency condition both the reference tone and the adjusted tone were above 10 kHz,
616 and thus phase locking would have been very weak or absent for both. In the present
617 study, musical intervals were adjusted downwards to ensure audibility of the
618 harmonics with higher ranks. Therefore, the F0 of the adjusted tone was below that of
619 the reference tone by a factor as big as 1/1.498 for the perfect fifth, the largest musical
620 interval used. The frequency of the lowest harmonic present in the adjusted tone
621 complex would have been about 5.6, 6.7, and 7.5 kHz for the fifth, the major third,
622 and the major second, respectively. The pitch of the adjustable complex probably was
623 more salient than that of the reference complex. If we had used an upward-interval
624 task like Burns and Feth (1983), the increase of the SDEVs might have been even
625 larger than the observed factor of about 5. Note however that, in the present study,
626 there was no indication that the increase in the SDEVs for the High-F0 relative to the
627 Low-F0 condition was affected by the frequency of the lowest harmonic in the
628 adjustable complex, as there was no significant interaction between musical interval
629 and F0. This was presumably because performance was limited by the accuracy with
630 which the pitch of the reference complex was encoded.

631 Gockel and Carlyon (2016) asked subjects to adjust pure tones downwards to
632 form various musical intervals with a preceding Zwicker tone (ZT). A ZT is a tonal
633 auditory afterimage that starts when a band-stop noise is turned off and can persist for
634 5-6 s (Zwicker, 1964). It is generally assumed to be a neural phenomenon, involving a
635 release from neural lateral inhibition in the cochlear nucleus or higher levels in the
636 auditory pathway, and phase locking in the AN to the frequency corresponding to the
637 perceived pitch of the afterimage at the time of the percept is assumed to be absent
638 (Wiegrebe *et al.*, 1995; Wiegrebe *et al.*, 1996; Gockel and Carlyon, 2016). In the
639 study of Gockel and Carlyon (2016), the mean error of the musical interval
640 adjustments with a ZT as reference was similar to that observed when the reference
641 tone was a pure tone; in a first stage, the pure tones had been matched in frequency,
642 level, and decay time so that they sounded similar to the ZTs. However, the within-
643 subject SDEVs of the musical interval adjustments were a factor of about 1.9 larger
644 for the ZT than for the pure tone reference, and subjects took equal time/trials to make
645 the matches. The increase of the SDEVs relative to that in the reference condition
646 was clearly smaller for the ZTs than for the high-frequency pure tones in the study of
647 Burns and Feth (1983), and smaller than for the high-frequency complex tones in the
648 present study. Note, that in the reference conditions the size of the SDEVs was very
649 similar across the three studies (22 cents or 1.3% for the low-frequency complex tones
650 in the present study, 20 cents or 1.2% for the pure tones ranging from 2.2 to 4.2 kHz
651 in the ZT study, and 20 cents or 1.2% for the 1-kHz tone in the study of Burns and
652 Feth).

653 While phase locking in the AN to the frequency corresponding to the perceived
654 pitch of the ZT at the time of the percept is assumed to be absent, its relevance in the
655 debate about the role of phase locking in pitch perception needs some qualification.

656 This is because for the ZT there would be phase locking to components of the band-
657 stop noise, which might be used in creating a central rate-place representation that in
658 turn leads to the ZT percept. This is a different situation from tones with very high
659 frequencies, for which it is mostly assumed that phase locking is absent or very weak,
660 and for which therefore phase locking to the stimulus at a peripheral level does not
661 play a role either in the formation of templates or in the subsequent generation of the
662 pitch.

663 Overall the present data show that while at least some of the subjects seemed to
664 be able to adjust musical intervals for the high-frequency complex tones with
665 “reasonable” accuracy (AMEs smaller than 53 cents and within-subject SDEVs
666 smaller than 93 cents were observed for four of the nine subjects), performance was
667 worse for all subjects for the High-F0 than for the Low-F0. Furthermore, the increase
668 in SDEVs for the High-F0 relative to the Low-F0 was as large as that observed by
669 Burns and Feth (1983) for musical interval adjustments for high frequency pure tones
670 relative to that for low-frequency pure tones.

671 One of our subjects possessed absolute pitch, and additional absolute pitch
672 judgements were collected for complex tones with a wide range of F0s and of the
673 frequency of the lowest harmonic present. When making absolute pitch judgements,
674 the subject listened to the stimulus only once before her response was recorded, while
675 in the musical interval adjustment task she could listen many times before recording
676 her response. This might have increased the difficulty of the former task, explaining
677 why her performance for absolute pitch judgements declined more than for musical
678 interval adjustments when the frequency of the lowest harmonic was at or above 8.4
679 kHz. Overall, the results of the absolute pitch judgements were very much in
680 agreement with those of the musical interval adjustments, showing that musical pitch

681 was much weaker for complex tones with a lowest harmonic frequency around 8.4
682 kHz than for complex tones with components at lower frequencies.

683 We are not aware of any previous data on chroma identification for high-
684 frequency complex tones. Ohgushi and Hatoh (1992) investigated the ability of 93
685 music students to identify the pitch name of 1-s pure tones with frequencies
686 corresponding to notes in the standard tempered scale ranging from C6 (1047 Hz) to
687 C10 (16774 Hz). Up to C8 (4186 Hz), the highest note on the piano, more than 50%
688 of all responses were correct for each tone. Above that, performance decreased
689 markedly and so results were broadly consistent with previous reports suggesting that
690 musical pitch has an upper frequency limit near 5 kHz (Bachem, 1948; Ward, 1954;
691 Attneave and Olson, 1971). However, some subjects performed above chance level
692 beyond 5 kHz, not unlike in the study of Ward (1954), who measured octave
693 adjustments for pure tones. Ohgushi and Hatoh (1992) showed confusion matrices for
694 two exceptionally good subjects who could perform the task for frequencies up to
695 about 7-8 kHz. Thus, performance for the two best subjects in Ohgushi and Hato
696 (1992) was only slightly worse than for the present subject who named complex tones
697 with high component frequencies, and was one of the better ones in the high-
698 frequency musical interval task.

699

700 **C. Explanations for the deterioration in pitch perception at** 701 **high frequencies**

702 Next we consider possible explanations for our observations. The first is that the
703 reduction (or absence) of phase locking information underlies the deterioration of
704 performance in the high frequency region. It has been suggested that the perception of
705 the residue pitch of complex tones containing resolved components involves some

706 type of central harmonic template mechanism (Goldstein, 1973; Terhardt, 1974;
707 Cohen *et al.*, 1995; Shamma and Klein, 2000). This does not mean that phase-locking
708 information is not necessary or discarded. For example, Goldstein (1973) explicitly
709 did not rule out the use of phase-locking information as the measure of the constituent
710 frequencies of complex-tone stimuli in his optimum processor theory, while the model
711 of Shamma and Klein (2000) requires exposure to sounds within the phase-locking
712 range for the harmonic templates to initially form; frequencies for which there is no
713 phase-locking do not contribute to the formation of a template and thus would not
714 activate it at a later time.

715 The present stimuli were similar to the ones used by Lau *et al.* (2017). They
716 observed surprisingly small FODLs (around 5%), given that the FDLs were much
717 larger (around 20-30%). They argued that these results could be explained by the
718 existence of central harmonic template neurons that receive rate-place information. A
719 single high-frequency component will not (or only weakly) activate this central
720 template neuron, but a series of harmonics will, and so can lead to a pitch percept.
721 There is some physiological evidence for the existence of neurons that might serve
722 this role. Feng and Wang (2017) reported single-unit sensitivity in the auditory cortex
723 of marmosets to harmonic structure, i.e. higher firing rates to a combination of
724 harmonically related components than to an individual component, across the entire
725 range of hearing, beyond the limits of peripheral phase locking. If one assumes that
726 the pitch of complex tones is mediated by a central harmonic template mechanism,
727 then the present results together with the findings of Lau *et al.* could be explained
728 either by assuming that central harmonic templates get less activated by stimuli with
729 components above the limits of phase locking because temporal fine structure
730 information, when it is available, provides a “better” input than purely spectral

731 information, and/or by assuming a relative paucity of central harmonic templates
732 receiving input from stimuli above the limits of phase locking because these high
733 frequency input pathways have never been formed due to weak or absent phase
734 locking in this high frequency region (Shamma and Klein, 2000).

735 Overall, the present results are consistent with a role of phase locking
736 information in the production of a salient musical pitch percept that supports precise
737 musical-interval perception. However, while phase locking information might be
738 beneficial, it seems not to be strictly necessary to evoke a musical pitch of complex
739 tones since all subjects performed above chance and some subjects achieved
740 reasonable levels of performance. The latter conclusion is based on the assumption
741 that there is no usable phase-locking information for frequencies above about 8.4 kHz
742 (if phase locking information about all harmonics is supposed to be absent) or above
743 about 9.8 kHz (if phase locking information for all but the lowest harmonic is
744 supposed to be absent). As described in the introduction, whether or not this is the
745 case is still under debate (Verschooten *et al.*, 2019). For their pure tone data, Burns
746 and Feth (1983) concluded that their “results were not incompatible with a temporal
747 basis” and noted that Goldstein and Sruлович (1977) “have recently demonstrated that
748 there is sufficient temporal information in eighth-nerve firing patterns to explain
749 psychophysical frequency DLs at high frequencies. It is not necessary, therefore, to
750 postulate that a separate (tonotopic) mechanism mediates discrimination above 5
751 kHz”. Heinz, in Verschooten *et al.* (2019) noted “the degradation in frequency-
752 discrimination performance as frequency increases is consistent with the ability of
753 human listeners to use phase-locking information at high frequencies (up to ~10000
754 Hz)”. In contrast, Joris and Verschooten in Verschooten *et al.* (2019) argued for an
755 upper limit of phase locking in the AN of humans of about 3.5-4.5 kHz, with a much

756 lower limit of about 1.4 kHz as the highest frequency usable by the central nervous
757 system. Either way, the present results contribute to the growing evidence that
758 musical interval perception is possible with either very weak or absent phase locking,
759 but they also show that performance is worse for these very high frequencies.

760 Another possible explanation for the deterioration of performance at very high
761 frequencies is lack of familiarity with high-frequency tones. Studies of the pitch of
762 pure tones have often used this reasoning (Ward, 1954; Attneave and Olson, 1971).
763 Gockel and Carlyon (2016) mentioned that this might have contributed to the finding
764 that musical interval adjustments were more precise for the ZTs, which had a lower
765 pitch (matched frequencies between 2.2-4.2 kHz) than for the high-frequency pure
766 tones of Burns and Feth (1983). However, for the high-frequency complex tones used
767 here, the F0 was relatively low at 1.4 kHz, and so the pitch itself would not be
768 unfamiliar. Furthermore, there is at least one study that casts doubt on an explanation
769 in terms of lack of familiarity and lack of exposure to tones with very high F0s.
770 Jacoby *et al.* (2019) investigated musical pitch perception for members of a remote
771 tribe, the Tsimane', who live in relative isolation from Western culture. The F0s of
772 their musical instruments all fall below 2000 Hz, much lower than in the Western
773 culture where F0s reach just above 4000 Hz. Moreover, Tsimane' songs typically have
774 notes at the lower end of the F0 range of their instruments. Jacoby *et al.* (2019)
775 assessed the accuracy of the sung reproduction of musical intervals defined by two
776 pure tones that were presented in a wide range of registers. Despite lack of experience
777 of the Tsimane' with high-frequency tones, their accuracy of interval reproduction
778 started to deteriorate above about 4 kHz, the same frequency as for subjects from a
779 Western culture. As argued by Jacoby *et al.* (2019), these results are consistent with
780 biological constraints on the upper limit of musical pitch, for example the breakdown

781 in phase locking for higher frequencies, rather than with constraints imposed by
782 culture and exposure. However, it cannot be ruled out that a lack of exposure to (and
783 familiarity with) resolved components in the very high frequency region, rather than a
784 lack of exposure to high F0s, contributes to the deterioration in performance observed
785 in the present study. In addition, there may be other (yet undiscovered) factors that co-
786 vary with frequency region and that may underlie the observed effects.

787

788 **V. SUMMARY AND CONCLUSIONS**

789 The ability of musically trained subjects to adjust musical intervals for
790 reference complex tones with an F0 of 1.4 kHz and harmonic frequencies ≥ 8.4 kHz
791 was compared to that for reference complex tones with an F0 of 280 Hz and harmonic
792 frequencies from 1680 Hz to 2800 Hz. There were large individual differences in
793 performance for the high-frequency complex. Musical interval adjustments were
794 possible for both F0s, even though for the high F0 all harmonic frequencies were
795 above the presumed limit of phase locking. However, performance was markedly
796 worse for the high F0. The mean error and the within-subject SDEV of the
797 adjustments were significantly larger for the high-frequency than for the low-
798 frequency complex even though subjects took more trials for the former to make the
799 adjustments. Absolute pitch judgements from one of the subjects were perfect for
800 harmonic complex tones with lower component frequencies, but deteriorated once the
801 frequency of the lowest component exceeded 7-8 kHz. The results are consistent with
802 the idea that the salience of musical pitch is greater for tones for which phase-locking
803 information is available, but pitch perception at high frequencies may alternatively or
804 additionally be degraded by a lack of exposure to the upper harmonics (the sixth and
805 above) of complex tones with high F0s.

806

807 **ACKNOWLEDGEMENTS**

808 This research was supported by the Medical Research Council UK
809 (SUAG/042/G101400). We thank Brian Moore for helpful discussions and
810 comments. In compliance with our open access requirements, data from this study are
811 available at <https://www.mrc-cbu.cam.ac.uk/publications/pendata/>.

812

813 **APPENDIX**814 **A.1. Methods for absolute pitch judgements**

815 Subject 9, who possessed absolute pitch, was asked to name the note chroma
816 and the register (octave number) of the note for a wide range of stimuli. This was
817 done by choosing one of 12 virtual chroma buttons labelled C, C#, D, D#, E, F, F#, G,
818 G#, A, A#, or B, and one of 8 virtual register buttons labelled from 1 to 8 on the
819 computer screen. No feedback was provided.

820 In the first two experiments of this type, complex tones with F0s
821 corresponding to piano keys 39-71 (33 F0s ranging from B3=246.94 Hz to
822 G6=1567.98 Hz in one-semitone steps) were used. Piano key 69 (F6) with an F0 of
823 1396.91 Hz corresponds most closely to the 1400-Hz F0 used in the musical interval
824 adjustment tasks. The complex tones contained either harmonics 1-5 or harmonics 6-
825 10. This allowed assessment of the effect of the lowest frequency present in the
826 complex on absolute pitch judgements. In each trial, one of the 66 stimuli was chosen
827 at random for presentation. Tones were presented at the same level and in the same
828 TEN as for the musical interval adjustments. In the first experiment, the stimulus
829 duration was 1 s and there were 20 repetitions for each condition. In the second

830 experiment, the stimulus duration was 210 ms and there were 22 repetitions per
831 condition.

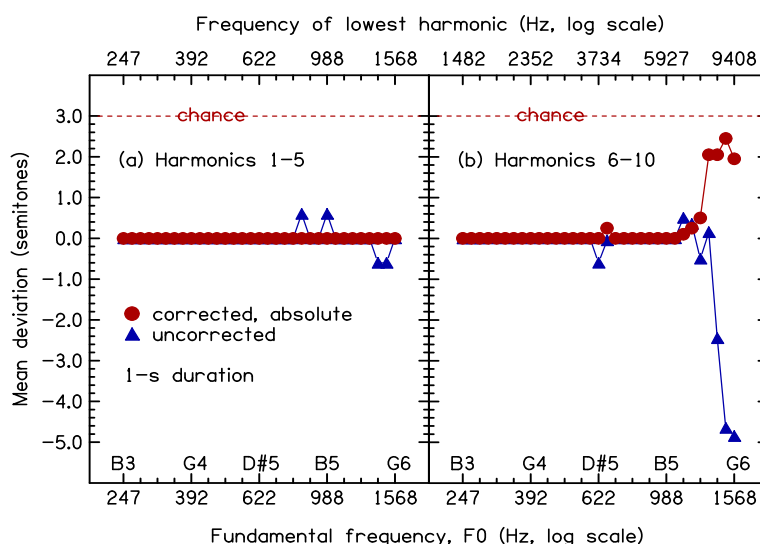
832 In a third experiment, the stimulus range was extended to higher F0s and
833 various lower harmonic ranks, to assess whether, in this extended high-F0 range, the
834 rank of the lowest harmonic in a tone complex influences performance independently
835 from its frequency. F0s corresponding to piano keys 72-85 (14 F0s ranging from
836 G#6=1661.22 Hz to A7=3520 Hz in one-semitone steps) were used. The complex
837 tones always contained five consecutive harmonics. The rank of the lowest harmonic
838 present in a complex tone with fixed F0 was varied from 1 to 6, with the restriction
839 that the frequency of the highest harmonic was always below 18 kHz, to ensure that at
840 least 4 components would have been audible. This resulted in 45 complex tones, for
841 which the frequencies of the lowest-rank harmonics ranged from 1661.22 Hz (1st
842 harmonic of G#6) to 10560 Hz (6th harmonic of A6). The stimulus duration was 210
843 ms and there were 22 repetitions per condition. Nine 2-hour sessions were needed to
844 complete all three experiments.

845

846 **A.2. Results of absolute pitch judgements**

847 Figure 7 shows the mean deviation of the responses from the true note (in
848 semitones) across the 20 trials completed for each condition as a function of the F0 of
849 the 1-s stimulus (x-axis, bottom) and as a function of the frequency of the lowest
850 harmonic present in the stimulus (x-axis, top). The left and right panels show results
851 for the complexes containing harmonics 1-5 and 6-10, respectively. The upward-
852 pointing blue triangles (“uncorrected”) are based on the raw response values, and give
853 an indication of overall biases; the large negative values observed for high F0s when
854 harmonics 6-10 were present indicate a response bias towards lower registers. The

855 circles (“corrected, absolute”) are based on responses after correcting for possible
 856 octave confusions; all responses that differed by more than six semitones from the
 857 true note were adjusted by $\pm n$ octaves, where n was the smallest integer number that
 858 would give an absolute difference between adjusted response and true note smaller
 859 than or equal to six semitones. The mean deviations were calculated from the absolute
 860 values of the deviations between true note and octave-corrected responses. For
 861 random responses, the expected mean deviation based on these octave-corrected
 862 absolute deviations is three semitones. More systematic mistakes can produce larger
 863 or smaller mean deviations. The results show that, after correcting for possible octave
 864 confusions, performance was perfect for all F0s tested when the lower harmonics
 865 were present and for F0s up to about 1100 Hz when the higher harmonics were
 866 present. For F0s above 1100 Hz, i.e. when the lowest frequency present was above
 867 6600 Hz, the mean deviations increased first gradually and then more steeply when
 868 the lowest frequency component fell above 7900 Hz (four right-most circles in panel
 869 b).



870

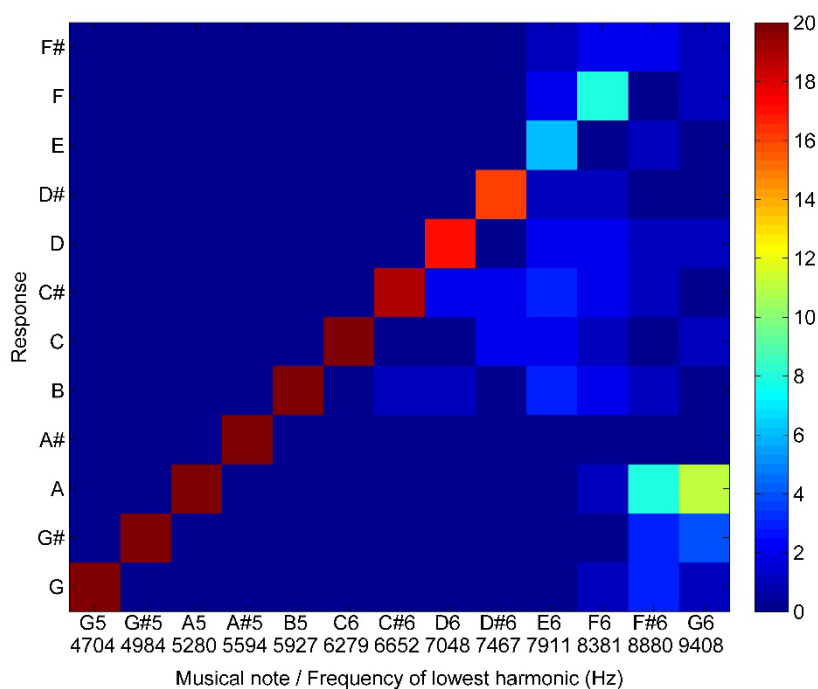
871 **FIG. 7.** (Color online) Results of absolute pitch judgments by subject 9 for a

872 stimulus duration of 1 second. The mean deviation of the responses from the

873 “correct” note is plotted as a function of the F0 of the complex tone stimulus (the
 874 note chroma and register) on the bottom axis and as a function of the frequency of
 875 the lowest harmonic present on the top axis. The complex tone contained
 876 harmonics 1-5 (Panel a) or harmonics 6-10 (Panel b). The (red) circles are based
 877 on octave-corrected responses, while the (blue) triangles are based on uncorrected
 878 responses.

879

880 Figure 8 shows a “confusion matrix” (based on octave-corrected responses)
 881 for complex tones with harmonic ranks 6-10 for the 13 highest notes used. The color
 882 codes the number of times (out of 20) each chroma response (y-axis) occurred for a
 883 given stimulus (x-axis). Responses were 100% correct for all notes up to and
 884 including C6, for which the frequency of the lowest component fell at 6279 Hz. Once
 885 the frequency of the lowest component was at or above 7911 Hz, at least 50% of the
 886 chroma responses were incorrect. In addition, there was a bias towards responding
 887 “A”.

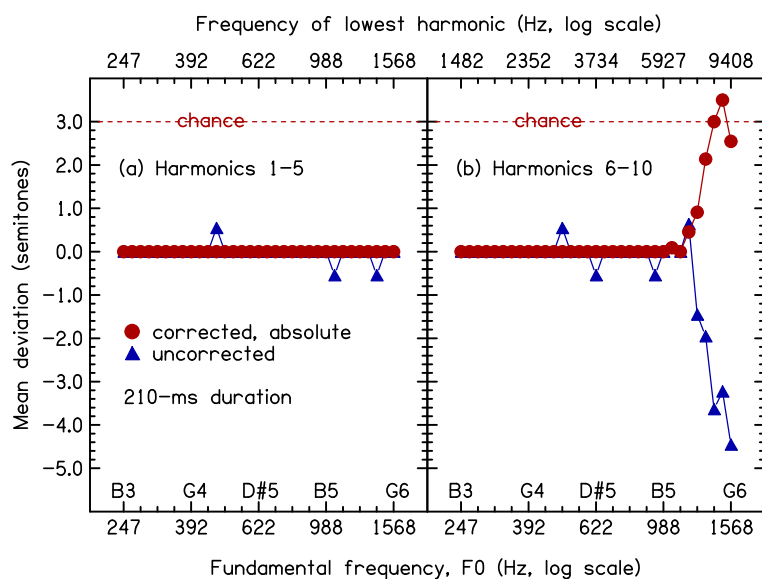


888

889 **FIG. 8.** (Color online) Confusion matrix (based on octave-corrected responses) for
 890 absolute pitch judgements of 1-s complex tones with harmonic ranks 6-10 for the
 891 13 highest F0s shown in Fig. 7. The color codes the number of times (out of 20)
 892 each chroma response (y-axis) occurred for a given stimulus (x-axis).

893

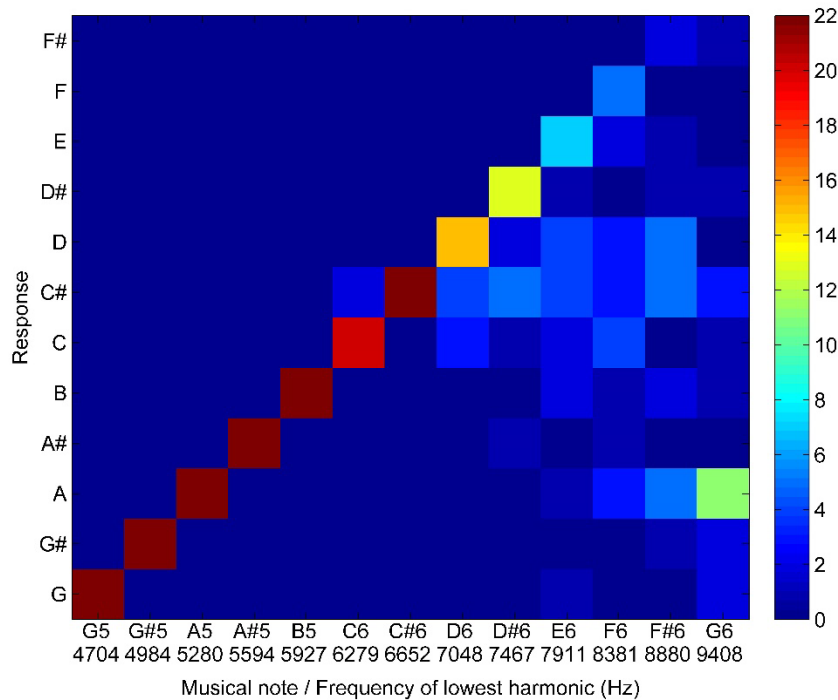
894 The experiment was repeated with a shorter stimulus duration of 210 ms.
 895 Figures 9 and 10 show a very similar pattern of results for this duration; performance
 896 was only slightly worse. Performance deteriorated once the frequency of the lowest
 897 harmonic was above 7000 Hz and chroma identification ability appeared to have been
 898 lost for frequencies above about 8400 Hz.



899

900 **FIG. 9.** (Color online) Results of absolute pitch judgments by subject 9 for a
 901 stimulus duration of 210 ms. Otherwise as Fig. 7.

902



903

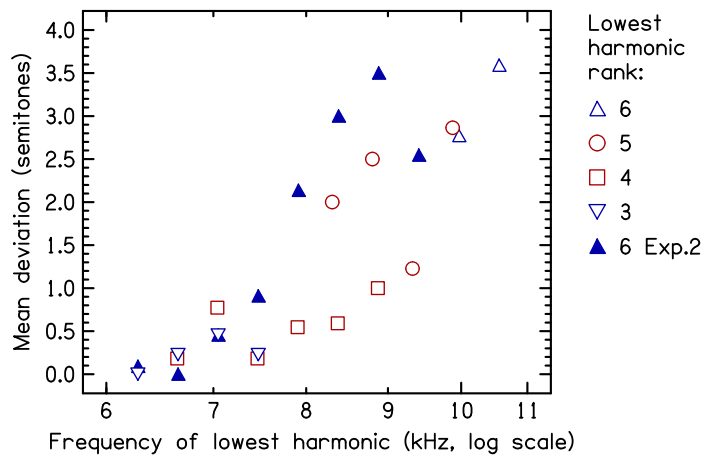
904 **FIG. 10.** (Color online) Confusion matrix (based on octave-corrected responses)

905 for absolute pitch judgments of 210-ms complex tones with harmonic ranks 6-10

906 for the 13 highest F0s shown in Fig. 9. Otherwise as Fig. 8.

907

908 In a third experiment, a higher F0 range (14 notes from G#6=1661.22 Hz to
 909 A7=3520 Hz in one semitone steps) was used and the lowest harmonic rank was
 910 varied. Figure 11 shows the mean absolute deviation of the octave-corrected
 911 responses (across 22 trials for each condition) from the correct chroma as a function
 912 of the frequency of the lowest harmonic. Note, data points are shown only for stimuli
 913 whose lowest component had a frequency above 6 kHz; performance was perfect for
 914 complex tones with lowest-component frequencies below 6 kHz. The results of the
 915 second absolute-pitch experiment, with lowest harmonic rank equal to six, are
 916 replotted for comparison. The rank of the lowest harmonic present in the stimulus is
 917 indicated by the different symbols (see legend).



918

919 **FIG. 11.** (Color online) Results of absolute pitch judgements for the extended
 920 high-frequency range with 210-ms stimulus duration. The mean deviation of the
 921 responses from the “correct” note is plotted as a function of the frequency of the
 922 lowest harmonic present. The complex tones (the notes) always contained five
 923 consecutive harmonics, and the rank of the lowest harmonic present (see legend)
 924 and the F0 were varied.

925

926 In addition to the clear increase in deviation with increasing frequency, there
 927 was a tendency towards larger deviations with increasing harmonic rank.

928 Unfortunately, the possible stimulus space was restricted, as frequencies above 16
 929 kHz were unlikely to be audible, and there are not many informative comparisons
 930 between data points with different lowest harmonic rank, i.e. data points above floor
 931 and below ceiling performance levels. In addition, comparison of data points across
 932 experiments conceivably might be affected by the different context of notes tested
 933 within each experiment. Therefore, unfortunately, no clear conclusion can be drawn
 934 about the role of harmonic rank.

935 The main conclusion to be drawn from these absolute pitch judgements is that
 936 performance deteriorated markedly as the frequency of the lowest harmonic increased

937 above about 7000 Hz. When that frequency was 8381 Hz (Figs. 7b and 9b, 3rd data
938 point from the end), errors were extremely large, despite the ability of this subject to
939 make relatively accurate musical-interval adjustments with this stimulus, with mean
940 errors less than 30 cents, in the main part of the study (Fig. 2).

941

942

943 **Footnotes**

944 1. Several additional analyses indicated that the strategy used by subjects to make
945 musical interval adjustments was not one to first match to unison and then to
946 adjust the F0 to a “mathematically known” ratio using a calculated sequence of
947 button presses. This will be referred to hereafter as the “alternative strategy”.
948 Firstly, if subjects had used the alternative strategy instead of directly matching to
949 their “internal template” of the expected musical interval, n_{listen} for musical
950 interval adjustments would be expected to be higher than n_{listen} for the unison
951 matches. This was not the case. The number of trials taken for the musical interval
952 adjustments was similar to that taken for the unison matches; the geometric mean
953 ratio [± 1 standard deviation] across subjects (n_{listen} for musical interval
954 adjustments divided by n_{listen} for unison matches in the corresponding
955 condition) was 1.01 [0.79, 1.29] and 0.98 [0.85, 1.13] for the low F0 and the high
956 F0, respectively. Secondly, if subjects had used the alternative strategy, n_{listen}
957 should be higher for matches where the starting F0 was further away from unison
958 than for matches where the starting F0 was close to unison (the starting F0 was
959 randomly chosen between F0 and 0.5 F0): Spearman’s rank correlation, ρ ,
960 between the starting F0 and n_{listen} should be negative. This also was not the
961 case. For the four conditions that involved adjusting to a perfect fifth, ρ was
962 negative in 11 out of the 36 cases (9 subjects X 4 conditions), and was significant
963 in only 1 case, i.e. in 3% of the cases. In contrast, for the four conditions where
964 subjects had to match to unison, ρ was negative in 29 out of the 36 cases, and
965 was significant in 22% of the cases. Thirdly, if subjects did not use the alternative
966 strategy, but matched directly to their “template” for the target musical interval,

967 n_listen should be smaller for matches where the randomly chosen starting F0 was
968 closer to the final matched F0 than for matches where the starting F0 was further
969 away from the matched F0. To assess this, *rho* was calculated between n_listen
970 and the absolute difference between the random starting F0 and the final matched
971 F0. If subjects had directly matched to the target F0, this correlation should be
972 positive. This was the case to a similar extent for all musical intervals and for
973 unison: For conditions that involved matching a perfect fifth, a major third, a
974 major second and unison, *rho* was positive (significant) in 72% (22%), 69%
975 (25%), 64% (25%) and 81% (19%) of the cases, respectively. Note that for the
976 latter two analyses, correlations between n_listen and frequency differences were
977 not expected to be very high as subjects probably used bigger step sizes when the
978 perceived difference between the starting F0 and the target F0 was large than
979 when it was small.

980

981 2. If subjects make random adjustments for each match, then the expected adjusted
982 value corresponds to the starting F0 itself. For all conditions, the starting F0 of the
983 adjustable complex was randomly chosen to be between 0.5 and 1 times the F0 of
984 the reference tone (uniformly distributed on a linear frequency scale). The mean of
985 the logarithms of all possible starting F0s is 5.3 semitones below the F0 of the
986 reference tone.

987

988 3. Octave confusions are quite common in pitch-matching experiments (Davis *et al.*,
989 1951). Correcting for octave confusions by dividing or multiplying the adjusted
990 F0 by a factor of 2, so that the adjusted F0 never differs by more than six

- 991 semitones from the true F0, allows correct chroma responses to be counted as
992 correct while ignoring tone height (register) errors.
993
994
- 995 Attneave, F., and Olson, R. K. (1971). "Pitch as a medium: A new approach to
996 psychophysical scaling," *Am. J. Psychol.* **84**, 147-166.
- 997 Bachem, A. (1937). "Various types of absolute pitch," *J. Acoust. Soc. Am.* **9**, 146-
998 151.
- 999 Bachem, A. (1948). "Chroma fixation at the ends of the musical frequency scale," *J.*
1000 *Acoust. Soc. Am.* **20**, 704-705.
- 1001 Bernstein, J. G., and Oxenham, A. J. (2003). "Pitch discrimination of diotic and
1002 dichotic tone complexes: Harmonic resolvability or harmonic number?," *J.*
1003 *Acoust. Soc. Am.* **113**, 3323-3334.
- 1004 Boudreau, J. C., and Tsuchitani, C. (1968). "Binaural interaction in the cat superior
1005 olive S segment," *J. Neurophysiol.* **31**, 442-454.
- 1006 Burns, E. M. (1999). "Intervals, scales, and tuning," in *The Psychology of Music*,
1007 edited by D. Deutsch (Academic Press, Amsterdam), pp. 215-264.
- 1008 Burns, E. M., and Feth, L. L. (1983). "Pitch of sinusoids and complex tones above 10
1009 kHz," in *Hearing - Physiological Bases and Psychophysics*, edited by R. Klinke
1010 and R. Hartmann (Springer, Berlin), pp. 327-333.
- 1011 Burns, E. M., and Viemeister, N. F. (1976). "Nonspectral pitch," *J. Acoust. Soc. Am.*
1012 **60**, 863-869.
- 1013 Carcagno, S., Lakhani, S., and Plack, C. J. (2019). "Consonance perception beyond
1014 the traditional existence region of pitch," *J. Acoust. Soc. Am.* **146**, 2279-2290.
- 1015 Cardozo, B. L. (1965). "Adjusting the method of adjustment: SD vs DL," *J. Acoust.*
1016 *Soc. Am.* **37**, 786-792.
- 1017 Cariani, P. A., and Delgutte, B. (1996). "Neural correlates of the pitch of complex
1018 tones. II. Pitch shift, pitch ambiguity, phase invariance, pitch circularity, rate
1019 pitch, and the dominance region for pitch," *J. Neurophysiol.* **76**, 1717-1734.
- 1020 Cohen, M. A., Grossberg, S., and Wyse, L. L. (1995). "A spectral network model of
1021 pitch perception," *J. Acoust. Soc. Am.* **98**, 862-879.

- 1022 Davis, H., Silverman, S. R., and McAuliffe, D. R. (1951). "Some observations on pitch
1023 and frequency," *J. Acoust. Soc. Am.* **23**, 40-42.
- 1024 de Cheveigné, A. (1998). "Cancellation model of pitch perception," *J. Acoust. Soc.*
1025 *Am.* **103**, 1261-1271.
- 1026 Fastl, H. (1971). "Über Tonhöhenempfindungen bei Rauschen ("On sensations of
1027 pitch evoked by noise")," *Acustica* **25**, 350-354.
- 1028 Feng, L., and Wang, X. Q. (2017). "Harmonic template neurons in primate auditory
1029 cortex underlying complex sound processing," *Proc. Natl. Acad. Sci. USA* **114**,
1030 E840-E848.
- 1031 Glasberg, B. R., and Moore, B. C. J. (1990). "Derivation of auditory filter shapes from
1032 notched-noise data," *Hear. Res.* **47**, 103-138.
- 1033 Gockel, H. E., and Carlyon, R. P. (2016). "On Zwicker tones and musical pitch in the
1034 likely absence of phase locking corresponding to the pitch," *J. Acoust. Soc. Am.*
1035 **140**, 2257-2273.
- 1036 Gockel, H. E., and Carlyon, R. P. (2018). "Detection of mistuning in harmonic
1037 complex tones at high frequencies," *Acta Acust. united Ac.* **104**, 766-769.
- 1038 Gockel, H. E., Moore, B. C. J., and Carlyon, R. P. (2020). "Pitch perception at very
1039 high frequencies: On psychometric functions and integration of frequency
1040 information," *J. Acoust. Soc. Am.* **148**, 3322-3333.
- 1041 Goldstein, J. L. (1973). "An optimum processor theory for the central formation of the
1042 pitch of complex tones," *J. Acoust. Soc. Am.* **54**, 1496-1516.
- 1043 Goldstein, J. L., and Sruлович, P. (1977). "Auditory-nerve spike intervals as an
1044 adequate basis for aural frequency measurement," in *Psychophysics and*
1045 *Physiology of Hearing*, edited by E. F. Evans and J. P. Wilson (Academic Press,
1046 London), pp. 337-346.
- 1047 Heinz, M. G., Colburn, H. S., and Carney, L. H. (2001). "Evaluating auditory
1048 performance limits: I. One-parameter discrimination using a computational model
1049 for the auditory nerve," *Neural Computation* **13**, 2273-2316.
- 1050 Howell, D. C. (1997). *Statistical Methods for Psychology* (Duxbury, Belmont, CA),
1051 pp. 464-466.
- 1052 Jacoby, N., Undurraga, E. A., McPherson, M. J., Valdes, J., Ossandon, T., and
1053 McDermott, J. H. (2019). "Universal and non-universal features of musical pitch
1054 perception revealed by singing," *Curr. Biol.* **29**, 3229-3243 e3212.

- 1055 Johnson, D. H. (1980). "The relationship between spike rate and synchrony in
1056 responses of auditory-nerve fibers to single tones," *J. Acoust. Soc. Am.* **68**, 1115-
1057 1122.
- 1058 Joris, P. X., and Verschooten, E. (2013). "On the limit of neural phase locking to fine
1059 structure in humans," *Adv Exp Med Biol* **787**, 101-108.
- 1060 Kale, S., and Heinz, M. G. (2012). "Temporal fine structure coding at high
1061 frequencies following noise-induced hearing loss," *Assoc. Res. Otolaryngol. Abs.*
1062 **35**, 364.
- 1063 Klein, M. A., and Hartmann, W. M. (1981). "Binaural edge pitch," *J. Acoust. Soc.*
1064 *Am.* **70**, 51-61.
- 1065 Lau, B. K., Mehta, A. H., and Oxenham, A. J. (2017). "Superoptimal perceptual
1066 integration suggests a place-based representation of pitch at high frequencies," *J.*
1067 *Neurosci.* **37**, 9013-9021.
- 1068 Levitt, H. (1971). "Transformed up-down methods in psychoacoustics," *J. Acoust.*
1069 *Soc. Am.* **49**, 467-477.
- 1070 Macherey, O., and Carlyon, R. P. (2014). "Re-examining the upper limit of temporal
1071 pitch," *J. Acoust. Soc. Am.* **136**, 3186-3199.
- 1072 Meddis, R., and O'Mard, L. (1997). "A unitary model of pitch perception," *J. Acoust.*
1073 *Soc. Am.* **102**, 1811-1820.
- 1074 Moore, B. C. J., and Ernst, S. M. A. (2012). "Frequency difference limens at high
1075 frequencies: Evidence for a transition from a temporal to a place code," *J. Acoust.*
1076 *Soc. Am.* **132**, 1542-1547.
- 1077 Moore, B. C. J., Huss, M., Vickers, D. A., Glasberg, B. R., and Alcántara, J. I. (2000).
1078 "A test for the diagnosis of dead regions in the cochlea," *Brit. J. Audiol.* **34**, 205-
1079 224.
- 1080 Moore, B. C. J., and Sek, A. (2009). "Sensitivity of the human auditory system to
1081 temporal fine structure at high frequencies," *J. Acoust. Soc. Am.* **125**, 3186-3193.
- 1082 Ohgushi, K., and Hatoh, T. (1992). "The musical pitch of high-frequency tones," in
1083 *Adv Biosci*, edited by Y. Cazals, L. Demany and K. Horner (Pergamon, Oxford),
1084 pp. 207-213.
- 1085 Oxenham, A. J., Micheyl, C., Keebler, M. V., Loper, A., and Santurette, S. (2011).
1086 "Pitch perception beyond the traditional existence region of pitch," *Proc. Natl.*
1087 *Acad. Sci. USA* **108**, 7629-7634.

- 1088 Palmer, A. R., and Russell, I. J. (1986). "Phase-locking in the cochlear nerve of the
1089 guinea-pig and its relation to the receptor potential of inner hair-cells," *Hear. Res.*
1090 **24**, 1-15.
- 1091 Rakowski, A. (1990). "Intonation variants of musical intervals in isolation and in
1092 musical contexts," *Psychology of Music* **18**, 60-72.
- 1093 Ruggero, M. A., Robles, L., Rich, N. C., and Recio, A. (1992). "Basilar membrane
1094 responses to two-tone and broadband stimuli," *Phil. Trans. R. Soc. Lond. B.* **336**,
1095 307-315.
- 1096 Shamma, S., and Klein, D. (2000). "The case of the missing pitch templates: how
1097 harmonic templates emerge in the early auditory system," *J. Acoust. Soc. Am.*
1098 **107**, 2631-2644.
- 1099 Terhardt, E. (1974). "Pitch, consonance, and harmony," *J. Acoust. Soc. Am.* **55**, 1061-
1100 1069.
- 1101 Verschooten, E., Desloovere, C., and Joris, P. X. (2018). "High-resolution frequency
1102 tuning but not temporal coding in the human cochlea," *Plos Biol* **16**, doi:
1103 10.1371/journal.pbio.2005164.
- 1104 Verschooten, E., Robles, L., and Joris, P. X. (2015). "Assessment of the Limits of
1105 Neural Phase-Locking Using Mass Potentials," *J. Neurosci.* **35**, 2255-2268.
- 1106 Verschooten, E., Shamma, S., Oxenham, A. J., Moore, B. C. J., Joris, P. X., Heinz, M.
1107 G., and Plack, C. J. (2019). "The upper frequency limit for the use of phase
1108 locking to code temporal fine structure in humans: A compilation of viewpoints,"
1109 *Hear. Res.* **377**, 109-121.
- 1110 Ward, W. D. (1954). "Subjective musical pitch," *J. Acoust. Soc. Am.* **26**, 369-380.
- 1111 Weiss, T. F., and Rose, C. (1988). "A comparison of synchronization filters in
1112 different auditory receptor organs," *Hear. Res.* **33**, 175-179.
- 1113 Wiegrebe, L., Kössl, M., and Schmidt, S. (1995). "Auditory sensitization during the
1114 perception of acoustical negative afterimages - Analogies to visual processing,"
1115 *Naturwissenschaften* **82**, 387-389.
- 1116 Wiegrebe, L., Kössl, M., and Schmidt, S. (1996). "Auditory enhancement at the
1117 absolute threshold of hearing and its relationship to the Zwicker tone," *Hear. Res.*
1118 **100**, 171-180.
- 1119 Zwicker, E. (1964). "'Negative afterimage' in hearing," *J. Acoust. Soc. Am.* **36**, 2413-
1120 2415.
- 1121