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Author accepted manuscript

## Harmonicity aids hearing in noise

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**Abstract**

Hearing in noise is a core problem in audition, and a challenge for hearing-impaired listeners, yet the underlying mechanisms are poorly understood. We explored whether harmonic frequency relations, a signature property of many communication sounds, aid hearing in noise for normal hearing listeners. We measured detection thresholds in noise for tones and speech synthesized to have harmonic or inharmonic spectra. Harmonic signals were consistently easier to detect than otherwise identical inharmonic signals. Harmonicity also improved discrimination of sounds in noise. The largest benefits were observed for two-note up-down “pitch” discrimination and melodic contour discrimination, both of which could be performed equally well with harmonic and inharmonic tones in quiet, but which showed large harmonic advantages in noise. The results show that harmonicity facilitates hearing in noise, plausibly by providing a noise-robust pitch cue that aids detection and discrimination.

**Keywords:** auditory scene analysis, pitch discrimination, harmonicity, speech in noise, auditory grouping

**Significance statement**

Noise is ubiquitous, and being able to hear in noise is critical to real-world behavior. We report that hearing in noise is aided by sensitivity to the harmonic frequency relations that occur in vocal communication signals and music: harmonic sounds are easier to hear in noise than inharmonic sounds. This effect was present in both musicians and non-musicians and for synthetic as well as natural sounds, suggesting a role in everyday hearing.

## 31 Introduction

32 Noise is an unavoidable part of our auditory experience. We must pick out sounds of interest amid  
33 background noise on a daily basis – a speaker in a restaurant, a bird song in a windy forest, or a  
34 siren on a city street. Noise distorts the peripheral representation of sounds, but humans with  
35 normal hearing are relatively robust to its presence (Sarampalis et al., 2009). However, hearing  
36 in noise becomes more difficult with age (Ruggles et al., 2012; Tremblay et al., 2003) and for  
37 those with even moderate hearing loss (Bacon et al., 1998; Oxenham, 2008; Plack et al., 2014;  
38 Rossi-Katz & Arehart, 2005; Smoorenburg, 1992; Tremblay et al., 2003). Consequently,  
39 understanding the basis of hearing in noise, and its malfunction in hearing impairment, has  
40 become a major focus of auditory research (Kell & McDermott, 2019; Khalighinejad et al., 2019;  
41 Mesgarani et al., 2014; Moore et al., 2013; Rabinowitz et al., 2013; Town et al., 2019).

42 Hearing in noise can be viewed as a particular case of auditory scene analysis, the problem  
43 listeners solve when segregating individual sources from the mixture of sounds entering the ears  
44 (Bregman, 1990; Carlyon, 2004; Darwin, 1997; McDermott, 2009). In general, segregating  
45 sources from a mixture is possible only because of the regularities in natural sounds (Młynarski  
46 & McDermott, 2019). Most research on the signal properties that help listeners segregate sounds  
47 has focused on situations where people discern concurrent sources of the same type, for  
48 example, multiple speakers (the classic ‘cocktail party problem’ (Assman & Summerfield, 1990;  
49 Culling & Summerfield, 1995a; de Cheveigne, Kawahara, et al., 1997; de Cheveigne et al., 1995;  
50 de Cheveigne, McAdams, et al., 1997)), or multiple concurrent tones (as in music (Micheyl &  
51 Oxenham, 2010; Rasch, 1978)). Concurrent onsets or offsets (Darwin, 1981; Darwin & Ciocca,  
52 1992), co-location in space (Cusack et al., 2004; Freyman et al., 2001; Hawley et al., 2004;  
53 Ihlefeld & Shinn-Cunningham, 2008), and frequency proximity (Chalikia & Bregman, 1993; Darwin  
54 & Hukin, 1997; Młynarski & McDermott, 2019) can all help to group sound elements and segregate  
55 them from other similar sounds in the background. Harmonicity – the property of frequencies that  
56 are multiples of a common ‘fundamental’, or  $f_0$  (Fig. 1a-b) – likewise aids auditory grouping. For  
57 example, harmonic structure can help a listener select a single talker from a mixture of talkers  
58 (Darwin et al., 2003; Josupeit & Hohmann, 2017; Josupeit et al., 2020; Popham et al., 2018;  
59 Woods & McDermott, 2015). And when one harmonic in a complex tone or speech utterance is  
60 mistuned so that it is no longer an integer multiple of the fundamental, it can be heard as a  
61 separate sound (Hartmann et al., 1990; Moore et al., 1986; Popham et al., 2018; Roberts &  
62 Brunstrom, 1998).

63 Less is known about the factors and mechanisms that enable hearing in noise (operationally  
64 defined for the purposes of this paper as a background sound that does not contain audibly  
65 discrete frequency components, for example, white or pink Gaussian noise, and some sound  
66 textures). Previous research on hearing in noise has mainly focused on features of noise, such  
67 as stationarity, that aid its suppression (Kell & McDermott, 2019; Khalighinejad et al., 2019;  
68 Mesgarani et al., 2014; Moore et al., 2013; Rabinowitz et al., 2013) or separation (McWalter &  
69 McDermott, 2019; McWalter & McDermott, 2018) from signals such as speech. Here we instead  
70 study the aspects of a signal that enable it to be heard more readily in noise.

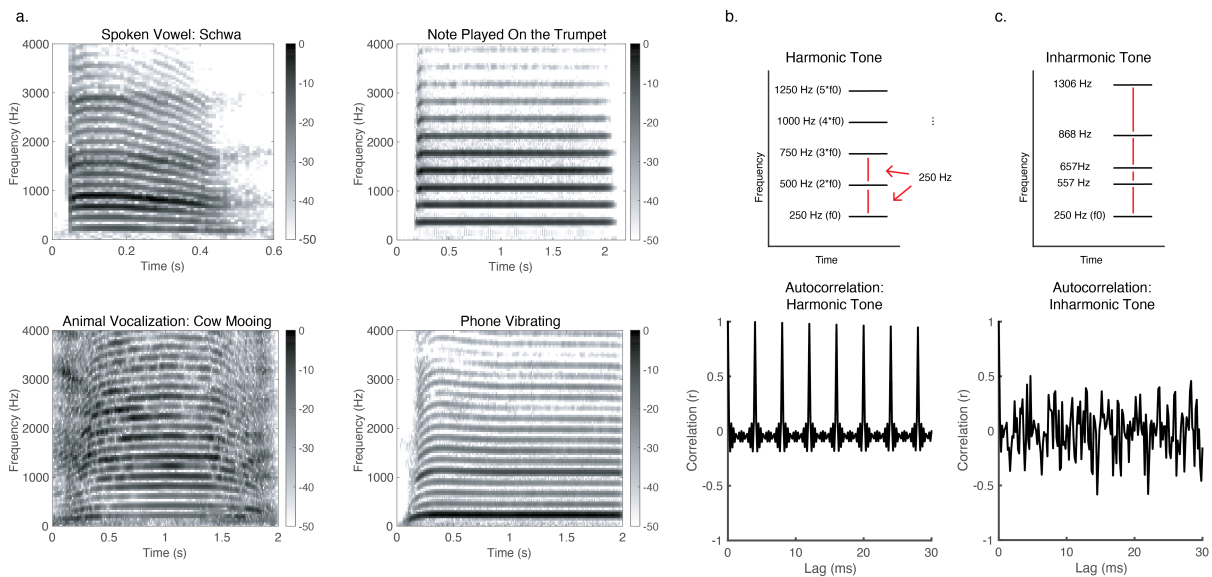
71 Harmonicity is one sound property that differentiates communication signals such as speech and  
72 music from noise (Fig 1a). Although harmonicity is known to aid the segregation of multiple  
73 harmonically structured sounds, its role in hearing in noise is unclear. To explore whether  
74 harmonic frequency relations aid hearing of sounds in noise, we compared detection and  
75 discrimination of harmonic and inharmonic tones and speech embedded in noise. Inharmonic

76 sounds were generated by jittering frequency components so that they were not integer multiples  
77 of the fundamental frequency (McPherson & McDermott, 2018; Roberts & Holmes, 2006). These  
78 inharmonic sounds are inconsistent with any single  $f_0$  in the range of audible pitch (Pressnitzer et  
79 al., 2001) (Fig. 1b&c). Harmonic and inharmonic tones have previously been used to probe the  
80 basis of pitch perception, where under some conditions, but not others, they reveal  
81 representations of  $f_0$  underlying pitch judgments (McPherson & McDermott, 2020).  
82

83 Our first question was whether harmonicity would make sounds easier to detect in noise across  
84 a range of sounds and tasks. The one related prior study we know of found that ‘chords’ composed  
85 of three harmonically related pure tones were somewhat easier to detect in noise than non-  
86 harmonically related tones, but did not pursue the basis of this effect (Hafter & Saberi, 2001).  
87 Classical views of tone-in-noise detection based on energetic masking account for differences  
88 between pure and complex tones (Buus et al., 1997; Dubois et al., 2011; Green, 1958, 1960), but  
89 do not predict effects of harmonicity. To further test their predictions with our stimuli, we  
90 instantiated a simple model of energetic masking and ran it in a simulated detection experiment  
91 using the same stimuli presented to our participants.  
92

93 The second question was whether harmonicity would make sounds easier to discriminate in noise.  
94 We first measured the discrimination of single tones as well as extended melodies in noise,  
95 comparing performance for harmonic and inharmonic tones, asking whether harmonicity would  
96 aid discrimination in noise at supra-threshold SNRs. Pitch discrimination thresholds are known to  
97 be comparable for harmonic and inharmonic tones without noise, suggesting that listeners use a  
98 representation of the spectrum to make up/down discrimination judgments (Faulkner, 1985;  
99 McPherson & McDermott, 2018; McPherson & McDermott, 2020; Micheyl et al., 2012; Moore &  
100 Glasberg, 1990). But in noisy conditions it could be difficult to accurately encode the spectrum,  
101 making it advantageous to rely on harmonic structure. Previous studies have found that it is easier  
102 to hear the  $f_0$  of harmonic sounds when there is background noise (Hall & Peters, 1981; Houtgast,  
103 1976), but it was unclear whether such effects would translate to improved discrimination of tones  
104 and melodies in noise. One other study found harmonicity to aid the discrimination of frequency  
105 modulation in noise (Carlyon & Stubbs, 1989), but did not explore whether this effect could relate  
106 to detection advantages. We also assessed speech discrimination, resynthesizing speech with  
107 harmonic or inharmonic voicing, and measuring the discrimination of English vowels and  
108 Mandarin Chinese tones at a range of SNRs. One previous study had failed to see a benefit of  
109 harmonicity on speech intelligibility of English words in noise (Popham et al., 2018), but it seemed  
110 plausible that effects might be evident in contexts where pitch is linguistically important.  
111

112 We found that harmonic sounds were consistently easier to detect in noise than inharmonic  
113 sounds. This result held for speech as well as synthetic tones. While we observed modest effects  
114 of harmonicity on speech discrimination in noise, tone and melody discrimination thresholds were  
115 considerably better for harmonic than inharmonic tones when presented in noise despite being  
116 indistinguishable in quiet. The results are consistent with the idea that harmonicity improves  
117 hearing in noise by providing a noise-robust pitch signal that can be used to detect and  
118 discriminate sounds.  
119



**Figure 1. Harmonicity**

a. Spectrograms of example natural harmonic sounds: a spoken vowel, a cow mooing, a note played on a trumpet, and a phone vibrating. The frequency components of such sounds are multiples of a fundamental frequency, and are thus regularly spaced across the spectrum. b. Schematic spectrogram of a harmonic tone with an  $f_0$  of 250 Hz, along with its autocorrelation. The autocorrelation has a peak at the lag equal to the period of the  $f_0$  (and at multiples of this lag). c. Schematic spectrogram of an inharmonic tone along with an example autocorrelation. In this example, the inharmonic tone was generated by jittering the frequencies of a 250 Hz harmonic tone. Jittering was accomplished by sampling a jitter value from the distribution  $U(-0.5, 0.5)$ , multiplying by the  $f_0$ , then adding the resulting value to the frequency of the respective harmonic, constraining adjacent components to be separated by at least 30 Hz (via rejection sampling) in order to avoid salient beating. The autocorrelation functions of inharmonic tones do not exhibit strong peaks, indicating that they lack a fundamental frequency in the range of audible pitch.

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### Experiment 1. Detecting harmonic and inharmonic tones in noise.

The purpose of Experiment 1 was to examine the effect of harmonicity on the detection of sounds in noise. We conducted three sub-experiments. Experiment 1a was run online due to the COVID-19 pandemic. We validated this online experiment using data collected in lab (before the pandemic shutdown, Experiment 1b, and during the shutdown, using two of the authors as participants in order to obtain data from highly practiced participants, Experiment 1c). In all three versions of the experiment, participants heard two noise bursts on each trial (Fig. 2a). A complex tone or a pure tone was embedded in one of the noise bursts, and participants were asked to choose which noise burst contained the tone. The complex tones could be harmonic or inharmonic, with constituent frequencies added in sine or random phase (example trials for this and other experiments are available at <http://mcdermottlab.mit.edu/DetectionInNoise.html>). Participants in Experiments 1a and 1b completed four adaptive measurements of the detection threshold for tones in each condition. Participants in Experiment 1c completed 12 adaptive measurements per condition.

135 In addition to our online and in-lab experiments, we created a formal model of this task to  
136 compare our findings with previous theoretical predictions regarding detecting tones in noise  
137 (Buus et al., 1997; Dubois et al., 2011; Green, 1958, 1960). We compared model performance to  
138 the results of the highly practiced participants in Experiment 1c.

## 139 **Method**

140 All experiments (both online and in-lab) were approved by the Committee on the use of  
141 Humans as Experimental Subjects at the Massachusetts Institute of Technology and were  
142 conducted with the informed consent of the participants.

143 **Participants: Online, Experiment 1a.** This experiment was run online because of a lab  
144 closure due to the COVID-19 pandemic. 110 participants completed Experiment 1a on an online  
145 data collection platform (Amazon Mechanical Turk). Here and in all other online experiments in  
146 this paper, we limited participation to individuals with US-based IP addresses. All online  
147 experiments began with a set of screening questions that included a question asking the  
148 participant if they had any hearing loss. Anyone who indicated any known hearing loss was  
149 excluded from the study (across all the online experiments in this paper, 9.5% of participants who  
150 initially enrolled self-reported hearing loss; 89% of these individuals also failed the headphone  
151 screening). All participants in this and other experiments in this paper thus reported normal  
152 hearing. Given the age distribution of participants, and use of self-report, it is possible that some  
153 participants in the study had mild hearing impairment. We include results from an analogous in-  
154 lab experiment with younger participants (Experiment 1b, see below) to assess whether this and  
155 other factors specific to the online format might have influenced the results.

156 12 participants were removed from analysis because their average threshold across  
157 conditions (using the first adaptive run of each condition) was over three standard deviations  
158 worse than the group mean across all conditions. This exclusion criterion is neutral with respect  
159 to the hypotheses being tested, and independent of the data we analyzed (only the subsequent  
160 3 runs were included for analysis in the remaining participants, to avoid double-dipping).  
161 Therefore, our exclusion procedure allowed unbiased threshold estimates from those final three  
162 runs. In previous studies we have found that online results replicate in-lab results when such steps  
163 are taken to exclude the worst-performing participants (McPherson & McDermott, 2020; Woods  
164 & McDermott, 2018). Of the remaining 98 participants, 38 self-identified as female, 60 as male  
165 (binary choice), mean age = 39.2 years, S.D. = 10.6 years. 45 had four or more years of musical  
166 training, with an average of 11.0 years, S.D. = 8.7 years.

167 In this and other experiments, we determined sample sizes a priori based on pilot studies,  
168 and using G\*Power (Faul et al., 2007). We ran a pilot experiment online that was similar to  
169 Experiment 1a. The only difference between this pilot experiment and Experiment 1a was that the  
170 frequencies of each Inharmonic note were jittered independently on each trial (in contrast to  
171 Experiment 1a, and the other experiments reported in this paper, in which each Inharmonic tone  
172 for a participant was made inharmonic in the same way across the entire experiment, as described  
173 below). We ran this pilot experiment in 43 participants, and observed a strong main effect of  
174 harmonicity ( $\eta_p^2 = .37$  for an ANOVA comparing Harmonic vs. Inharmonic conditions). Because we  
175 considered it plausible that the effects of interest might depend on musicianship, we chose our  
176 sample size to be able to detect a potential musicianship effect that might be substantially weaker  
177 than the main effect of harmonicity (see *Effects of Musicianship* section below). Therefore, we  
178 sought to be well-powered to detect an interaction between musicianship and harmonicity 1/8 the  
179 size of the main effect of harmonicity at a significance level of  $p < .01$ , 95% of the time. This yielded  
180 a target sample size of 62 participants (31 musicians and 31 non-musicians). In practice, here  
181 and in all other online experiments we ran participants in batches, and then excluded them based  
182

183 on whether they passed the headphone check and our performance criteria, so the final sample  
184 was somewhat larger than this target.

185 **Participants: In Lab, Experiments 1b&c.** Experiment 1b was run in the lab before the  
186 COVID-19 lab closure. The Harmonic and Pure Tone stimuli and procedures in Experiment 1b  
187 matched those in Experiment 1a. 21 participants completed the experiment (13 self-identified as  
188 female, 7 as male, 1 as nonbinary, mean age = 28.8 years, S.D. = 8.8 years. 12 reported over  
189 four years of musical training, with an average of 17.2 years, S.D. = 5.6 years. All participants  
190 reported normal hearing. No participants performed over three standard deviations away from the  
191 mean on their first run, so none were excluded. Only the final three runs were used for analysis.

192 Experiment 1c was completed in the lab by the first two authors (female, 29 years old, 23  
193 years of musical training, and male, 21 years old, 11 years of musical training).

194 **Procedure: Online, Experiment 1a.** Online experiments were conducted using  
195 Amazon's Mechanical Turk platform. In-person data collection was not possible due to the  
196 COVID-19 virus. Prior to starting the experiment, potential participants were consented, instructed  
197 to wear headphones and ensure they were in a quiet location, and then used a calibration sound  
198 (1.5 seconds of Threshold Equalizing noise (Moore et al., 2000)) to set their audio presentation  
199 volume to a comfortable level. The experimental stimuli were normalized to 6 dB below the level  
200 of the calibration sound to ensure that they were never uncomfortably loud (but likely to be  
201 consistently audible). Participants were then screened with a brief experiment designed to help  
202 ensure they were wearing earphones or headphones, as instructed (Woods et al., 2017), which  
203 should help to attenuate background noise and produce better sound presentation conditions. If  
204 they passed this screening, participants proceeded to the main experiment. For all experiments  
205 in the paper, participants received feedback after each trial, and to incentivize good performance,  
206 they received a compensation bonus proportional to the number of correct trials.

207 We used adaptive procedures to measure detection thresholds. Participants completed 3-  
208 down-1-up two-alternative-forced-choice ('does the first or second noise burst contain a tone?')  
209 adaptive threshold measurements. Adaptive tracks were stopped after 10 reversals. The signal-  
210 to-noise ratio (SNR) per component was changed by 8 dB for the first two reversals, 2 dB for the  
211 subsequent two reversals, and .5 dB for the final six reversals. The threshold estimate from a  
212 track was the average of the SNRs at the final six reversals. Participants completed four adaptive  
213 threshold measurements for each condition. Complex tone conditions (random vs. sine phase  
214 tones, and harmonic vs. inharmonic tones) were randomly intermixed, and the four runs of the  
215 Pure Tone condition were grouped together, run either before or after all of the complex tone  
216 adaptive runs, chosen equiprobably for each participant.

217 **Procedure: In Lab, Experiments 1b-c.** Experiment structure and adaptive procedure  
218 were the same for in-lab and online participants. In-lab participants sat in a soundproof booth  
219 (Industrial Acoustics) and heard sounds played out by a MacMini computer, presented via  
220 Sennheiser HD280 circumaural headphones. The audio presentation system was calibrated  
221 ahead of time with a GRAS 43AG Ear & Cheek Simulator connected to a Svantek SVAN 977  
222 audiometer. The setup is intended to replicate the acoustic effects of the ear, measuring the sound  
223 level expected to be produced at the eardrum of a human listener, enabling sound presentation  
224 at a desired sound pressure level, which in these experiments was 70 dB SNL. All experimental  
225 stimuli in-lab were presented using The Psychtoolbox for MATLAB (Kleiner et al., 2007).

226 The experimental interface also differed somewhat between online and in-lab experiments  
227 – online participants logged responses using a mouse or track-pad click, whereas in-lab  
228 participants used a keyboard. Participants received feedback (correct/incorrect) after each trial.  
229 Like online participants, participants in the in-lab experiment completed four adaptive runs per  
230 condition. In Experiment 1c, the two participants each completed two sessions of two hours, and  
231 during each session completed 12 runs of each condition (3 conditions: harmonic and inharmonic

232 tones added in random phase, and pure tones). The two sessions were completed on separate  
233 days within the same week.

234 **Stimuli.** Trials consisted of two noise bursts, one of which contained a tone. First, two  
235 900ms samples of noise were generated, and one of these noise samples was randomly chosen  
236 to contain the tone. The tone was scaled to have the appropriate power relative to that noise  
237 sample; both stimulus intervals were then normalized to 70 dB SPL. Tones were 500ms in  
238 duration; the noise began and ended 200ms before and after the tone (Fig. 2a). The tones started  
239 200ms after the noise to avoid an ‘overshoot’ effect, whereby tones are harder to detect when  
240 they start near the onset of noise (Zwicker, 1965). The two noise bursts were separated by 200ms  
241 of silence.

242 The noise used in this and all other experiments was Threshold Equalizing (TE) noise  
243 (Moore et al., 2000). Noise was generated in the spectral domain to have the specified duration  
244 and cutoff frequency. Pilot experiments with both white and pink noise suggested that the  
245 harmonic detection advantage is present regardless of the specific shape of the noise spectrum  
246 provided the noise is broadband. In Experiment 1, noise was low-pass filtered with a 6<sup>th</sup> order  
247 Butterworth filter to make it more pleasant for participants. The cutoff frequency was 6000 Hz,  
248 chosen to be well above the highest possible harmonic in the complex tones. Noise in all  
249 experiments was windowed in time with 10ms half-Hanning windows.

250 Complex tones contained ten equal-amplitude harmonics. Depending on the condition,  
251 harmonics were added in sine phase or random phase (Fig. 2c). The two phase conditions were  
252 intended to test whether any harmonic detection advantage might be due to amplitude  
253 modulation; tones whose components are added in sine phase have deeper amplitude  
254 modulations than tones whose components are added in random phase. F0s of the tones (both  
255 complex and pure – pure tones were generated identically to the f0 frequency component of the  
256 harmonic tones) were randomly selected to be between 200-267 Hz (log uniform distribution).  
257 Tones were windowed with 10ms half-Hanning windows, and were 500ms in duration. Each  
258 interval was rms normalized to 70 dB SPL. Tones and noise were sampled at 44.1 kHz.

259 To make tones inharmonic, the frequency of each frequency component (other than the  
260 f0 component) was ‘jittered’ by up to 50% of the f0 value. Jittering was accomplished by sampling  
261 a jitter value from the distribution  $U(-0.5, 0.5)$ , multiplying by the f0, then adding the resulting value  
262 to the frequency of the respective harmonic. Jitter values were selected via rejection sampling,  
263 successively moving up the harmonic series rejecting or accepting sampled jitter values, to ensure  
264 that adjacent harmonics were always separated by at least 30 Hz (to avoid salient beating). Jitter  
265 values varied across participants (described below), but for a given participant were fixed across  
266 the experiment (i.e., each inharmonic tone heard by a given participant had the same jitter  
267 pattern). These inharmonic tones do not have a clear pitch in the traditional sense that listeners  
268 would be able to match through singing, for example, and have a bell-like timbre comparable to  
269 some pitched percussion instruments with inharmonic spectra (McLachlan et al., 2013). Previous  
270 experiments with such sounds have shown that this jitter is sufficient to yield substantial  
271 differences in performance on some tasks compared to that for harmonic sounds (McPherson &  
272 McDermott, 2018; McPherson & McDermott, 2020; Popham et al., 2018).

273 Stimuli for in-lab participants were generated in real time. For technical reasons all stimuli  
274 for online experiments were generated ahead of time and were stored as .wav file on a university  
275 server, from which they could be loaded during the experiments. 20 stimuli were pre-generated  
276 for every possible difficulty level (SNR) within the adaptive procedure. The SNR was capped at  
277 +6 dB SNR per component. If participants in the experiment reached this cap the stimuli remained  
278 at this SNR until participants got three trials in a row correct. In practice, participants who  
279 performed poorly enough to reach this cap were removed post hoc by our exclusion procedure.  
280 Adaptive tracks were initialized at -8 dB SNR per component. For each trial within an adaptive

281 track, one of the 20 stimuli for the current difficulty level within the adaptive track was selected at  
 282 random.

283 To vary the jitters across participants, we generated 20 independent sets of possible  
 284 stimuli, each with a different set of randomly selected jitter values for the Inharmonic trials. Each  
 285 participant only heard trials from one of these sets (i.e., all the inharmonic stimuli they heard were  
 286 'jittered' in the same way throughout the experiment). This was intended to make the inharmonic  
 287 conditions comparable in their uncertainty to the harmonic conditions (which always used the  
 288 same spectral pattern, i.e. that of the harmonic series). As some randomly selected jitter patterns  
 289 can by chance be close to Harmonic, we randomly generated 100,000 possible jitter patterns,  
 290 then selected the 20 patterns that minimized peaks in the autocorrelation function. The resulting  
 291 20 jitters were evaluated by eye to ensure that they were distinct. For Experiment 1c (in which the  
 292 first two authors were the participants), two of these 20 jitters were randomly chosen (one for  
 293 each author).

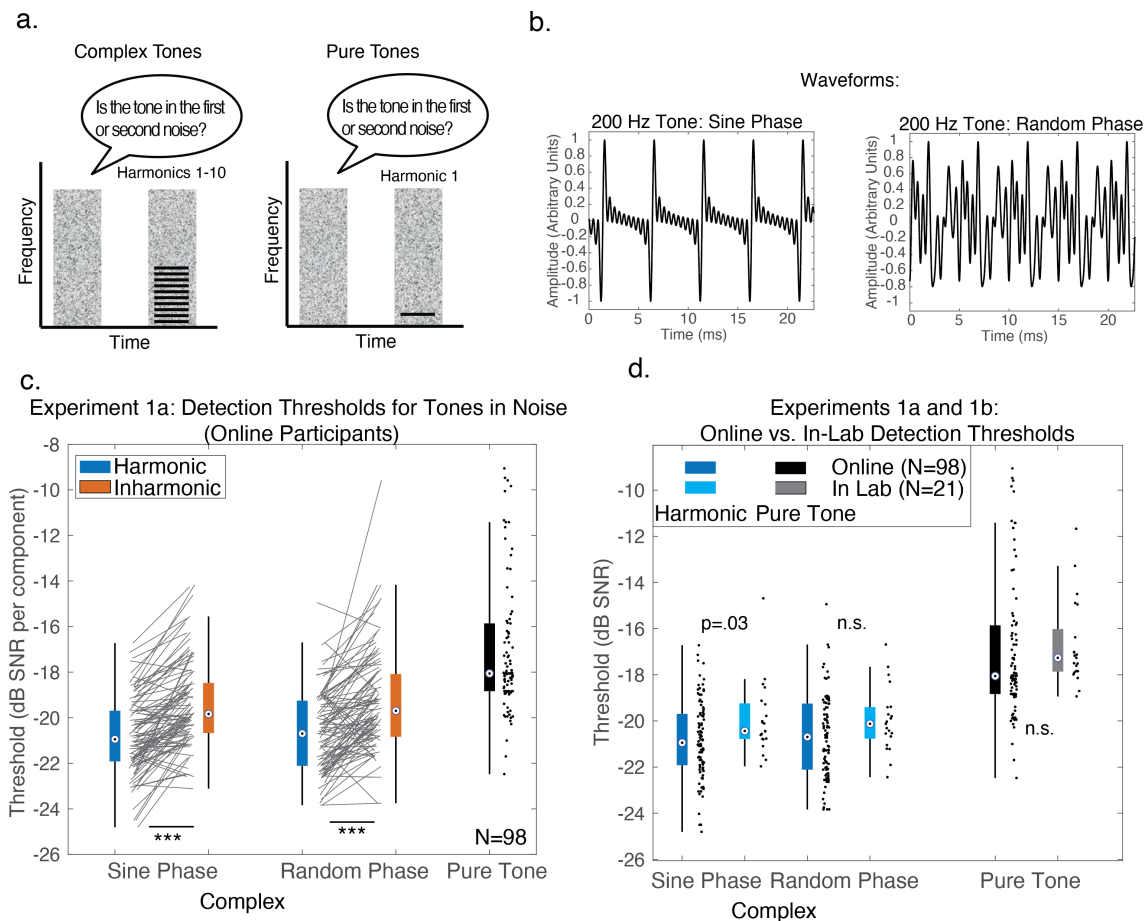


Figure 2: Harmonic advantage for detecting tones in noise (Experiments 1a and 1b)

a. Trial structure for Experiment 1. During each trial, participants heard two noise bursts, one of which contained a complex tone (left) or pure tone (right), and were asked to decide whether the tone was in the first or second noise burst. b. Example waveforms of harmonic tones added in sine phase (left) and random phase (right). The waveform is 'peakier' when the harmonics are added in sine phase. c. Results of Experiment 1a, shown as box-and-whisker-plots, with black lines for individual participant results. For this and other plots, the central mark in the box

indicates the median, and the bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. Whiskers extend 1.5 times the interquartile range away from the 25<sup>th</sup> and 75<sup>th</sup> percentiles. Asterisks denote significance of a Wilcoxon signed-rank test: \*\*\*= $p < 0.001$ . d. Harmonic and Pure Tone detection thresholds collected online (Experiment 1a) and in lab (Experiment 1b). The distributions were similar, suggesting that the online experimental conditions are sufficient to obtain results similar to those that would be obtained in-lab for this experiment.

294  
295 **Statistical Analysis.** Thresholds were calculated by averaging the SNR values of the  
296 final six reversals of the adaptive track. Data distributions were non-normal (skewed), so non-  
297 parametric tests, which are more conservative than parametric tests, were used in all cases. To  
298 compare performance across multiple conditions we used a non-parametric version of a repeated-  
299 measures ANOVA, computing the F statistic but evaluating its significance with approximate  
300 permutation tests. To do this, we randomized the assignment of the data points across the  
301 conditions being tested 10,000 times, re-calculated the F statistic on each permuted sample to  
302 build a null distribution, and then compared the original F statistic to this distribution. For ANOVAs  
303 that did not show significant main effects, we ran additional Bayesian ANOVAs to establish  
304 support for or against the null hypothesis.

305 For post-hoc pairwise comparisons between dependent samples we used Wilcoxon  
306 signed-rank tests. For comparisons of independent samples (online vs. in-lab data) we used  
307 Wilcoxon rank-sum tests. These pair-wise comparisons were not corrected for multiple  
308 comparisons both due to the low number of planned comparisons (only harmonic vs. inharmonic  
309 conditions and pure vs. complex tones), and because they were preceded by ANOVAs that  
310 revealed significant main effects of harmonicity.

311 **Model of energetic masking:** The model performed the experiment task on the stimulus  
312 waveforms, instantiating the assumptions of the standard power spectrum model of masking.  
313 Although there is evidence that listeners do not rely exclusively on power per se when detecting  
314 tones in noise (Lentz et al., 1999; Leong et al., 2020; Maxwell et al., 2020), power is plausibly  
315 correlated in many conditions with the cue(s) that listeners may be using. For each trial, we  
316 generated the two stimulus intervals (one with a tone, one without), using the exact parameters  
317 of the stimuli used with human participants, but without independently rms-normalizing each  
318 interval (noise was generated to be -20 dB rms re. 1 in a one-ERB wide band centered at 1000  
319 Hz). Each interval was passed through a gammatone filter bank (Slaney, 1998) approximating  
320 the frequency selectivity of the cochlea. The resulting subbands were raised to a power of 0.3 to  
321 simulate basilar membrane compression, then half-wave rectified, then averaged over the  
322 duration of the stimulus to yield a measure of the average “energy” in each channel. To simulate  
323 internal noise, we added random noise to each channel’s average energy. This internal noise was  
324 drawn from a Gaussian distribution with a mean of 0 and a standard deviation of .0002 (this  
325 translated to internal noise that was, on average, 18.5 dB below the signal energy). This standard  
326 deviation was selected using a grid search of possible values, in steps of .00005, and chosen to  
327 minimize the mean-squared-error between the average performance on the pure tone condition  
328 for the model and for the human listeners from Experiment 1c. Based on previous results  
329 suggesting that listeners use an unweighted sum across an optimally selected set of frequency  
330 channels (Buus et al., 1986), we summed the energy over each of either the 28 filters that covered  
331 the entire range of frequencies that could occur in the complex tone signals (for conditions with  
332 complex tones), or the 2 filters that covered the frequency range of the pure tones (for trials with  
333 pure tones). The interval with the greater summed power was chosen as that containing the  
334 signal.

335 We ran 10,000 trials at each stimulus SNR ranging from -30 dB SNR to 0 dB SNR in .5  
 336 dB steps, then estimated the threshold by fitting logistic functions to the model results. The model  
 337 threshold was defined as the point at which the fitted logistic function yielded 79.4% correct,  
 338 corresponding to the performance target of the two-down-one-up thresholds measured in human  
 339 listeners. We estimated confidence intervals by bootstrapping samples of the model data with  
 340 replacement, fitting curves to each bootstrapped sample.

341  
 342 **Results & Discussion: Experiment 1a**  
 343 As shown in Fig. 2d, detection in noise was better for the complex tone conditions than the Pure  
 344 Tone conditions ( $Z=6.90$ ,  $p<.0001$ , mean performance for Inharmonic conditions vs. that for Pure  
 345 Tones, Wilcoxon signed-rank test) as expected from signal detection theory given the ten-fold  
 346 increase in harmonics in the complex tones compared to the pure tones (Buus et al., 1997; Dubois  
 347 et al., 2011; Florentine et al., 1978; Green, 1958, 1960). However, detection thresholds were  
 348 substantially better for harmonic than inharmonic complex tones even though they each had 10  
 349 frequency components (main effect of harmonicity,  $F(1,97)=101.00$ ,  $p<.0001$ ,  $\eta_p^2=.51$ , significant  
 350 differences in both sine and random phase conditions: sine phase,  $Z=7.44$ ,  $p<.0001$ ; random  
 351 phase,  $Z=6.31$ ,  $p<.0001$ , Wilcoxon signed-rank test). We observed a 2.65 dB SNR advantage for  
 352 Inharmonic tones compared to Pure Tones, and an additional 1.38 dB SNR advantage for  
 353 Harmonic tones over Inharmonic tones (averaged across phase conditions).

354 These differences are large enough to have some real-life significance. For instance, if a  
 355 harmonic tone could be just detected 10 meters away from its source in free field conditions, an  
 356 otherwise identical inharmonic tone would only be audible 8.53 meters away from the source  
 357 (using the inverse square law; for comparison, a pure tone at the same level as one of the  
 358 frequency components from the complex tone would be audible 6.29 meters away).

359 A priori it seemed plausible that a detection advantage for harmonic tones could be  
 360 explained by the regular amplitude modulation of harmonic sounds, compared to inharmonic  
 361 sounds. However, performance was similar for the sine and random phase conditions (the latter  
 362 of which produces substantially less modulation, Fig. 2c). We observed no significant differences  
 363 between phase conditions or interaction with harmonicity (no significant main effect of phase,  
 364  $F(1,97)=1.12$ ,  $p=.29$ ,  $\eta_p^2=.01$ , and no interaction between harmonicity and phase,  $F(1,97)=0.26$   
 365  $p=.61$ ,  $\eta_p^2=.003$ ). The Bayes factors, ( $BF_{10}$ , specifying a multivariate Cauchy prior on the effects  
 366 (Rouder et al., 2012)), were .13 for the effect of phase, and .10 for the interaction between phase  
 367 and harmonicity, providing moderate support for the null hypotheses in both cases. This result  
 368 indicates that the observed harmonic advantage does not derive from amplitude modulation.

369 The results are also unlikely to be explained by distortion products. Although harmonic  
 370 tones would be expected to produce stronger distortion products than inharmonic tones, these  
 371 should be undetectable for stimuli that include all the lower harmonics (as were used here)  
 372 (Norman-Haignere & McDermott, 2016; Pressnitzer & Patterson, 2001).

373  
 374 **Results & Discussion: Experiment 1b**  
 375 Although online data collection has some advantages relative to in-lab experiments and  
 376 enabled this study to be completed despite the pandemic conditions, sound presentation is less  
 377 controlled compared to in-lab conditions due to the variability of headphones and/or listening  
 378 environments for home listeners. To validate the online results, we compared them to data  
 379 collected under controlled conditions in the lab (Experiment 1b; using calibrated headphones and  
 380 sound-attenuating booths).

381 As shown in Figure 2d, in-lab results from Experiment 1b were qualitatively and  
 382 quantitatively similar to those obtained online in Experiment 1a. We observed no significant

383 differences between online and in-lab data across two of the three conditions (Harmonic, Random  
384 Phase,  $Z=1.77$ ,  $p=.076$ , Pure Tone,  $Z=1.86$ ,  $p=.063$ , using Wilcoxon rank sum tests), and a  
385 marginally significant difference in one condition (Harmonic, Sine Phase,  $Z=2.14$ ,  $p=.033$ ).  
386 However, this latter difference was modest (threshold of  $-20.82$  dB SNR online compared to  $-$   
387  $19.95$  dB SNR in-lab), and not significant after Bonferroni correction for three comparisons  
388 (corrected  $\alpha$  value of  $.017$ ). These results, combined with previous studies that have quantitatively  
389 replicated in-lab results with online experiments (Kell et al., 2018; McPherson et al., 2020;  
390 McPherson & McDermott, 2020; McWalter & McDermott, 2019; Traer et al., 2021; Woods &  
391 McDermott, 2018) suggest that the measures taken here to improve sound presentation quality,  
392 such as requiring participants complete a brief headphone screening (Woods et al., 2017) and  
393 requesting that they situate themselves in a quiet room, and to eliminate non-compliant or  
394 inattentive participants, are sufficient to obtain results comparable to what would be observed in  
395 a traditional laboratory setting. While there are undoubtedly some differences from participant to  
396 participant in the stimulus spectrum with online experiments, these are evidently not sufficient to  
397 substantially alter detection in noise. Moreover, the relatively tight correspondence between in-  
398 lab and online findings suggests that factors such as headphone quality, distractions in at-home  
399 experiment settings, etc., did not greatly influence our overall results.

400

#### 401 **Results & Discussion: Experiment 1c**

402 Previous models of detection in noise predict a 5 dB improvement for detecting a complex  
403 tone with 10 harmonics compared to a pure tone (Buus et al., 1997; Dubois et al., 2011; Green,  
404 1958, 1960). Previous results with human listeners closely match this theoretical prediction for  
405 harmonic complex tones and pure tones. The 5 dB detection advantage predicted by such  
406 energetic masking models should in principle hold for both harmonic and inharmonic tones. Yet  
407 in our main experiment, we observed only a 4.03 dB advantage for harmonic tones over pure  
408 tones, and just a 2.65 dB advantage for Inharmonic tones over pure tones.

409 One possible explanation for this discrepancy is that listeners in our experiments were not  
410 highly practiced and therefore may not have used optimal strategies to perform the task. To test  
411 this possibility, the first and second authors completed two two-hour experimental sessions  
412 (Experiment 1c), each with 12 adaptive runs per condition (six times the number of runs completed  
413 by each participant in Experiments 1a-b) for three conditions: Harmonic (random phase),  
414 Inharmonic (random phase), and Pure Tone. During the first four runs of the first session the  
415 advantage for detecting Harmonic tones over Pure Tones was 3.21 dB for one author and 4.46  
416 for the other. However, in the final four runs of the second session (after extensive practice), the  
417 advantage for detecting Harmonic tones over Pure Tones increased to 4.67 dB for one author  
418 and 4.92 for the other (plotted in Fig. 3a). These results roughly match previous findings  
419 comparing 10-component harmonic complex tones and pure tones. There was a similar practice  
420 effect for the Inharmonic conditions compared to Pure Tones (first four runs: 1.00 dB and 2.60 dB  
421 for MJM and RCG respectively; final four runs: 2.57 and 3.65 dB); the difference between  
422 Harmonic and Inharmonic conditions replicated the harmonic detection advantage of 1.33 dB  
423 observed for random phase tones in Experiment 1a (2.10 dB and 1.27 dB, for each of the authors).

424

#### 425 **Results & Discussion: Model of Energetic Masking**

426 To test whether these results could be explained by a simple model of energetic masking,  
427 we ran a model on a simulated version of the experiment. The model measured the power in each  
428 stimulus interval using an auditory filterbank, and chose the interval with the greatest power (Fig  
429 3b). As with earlier models, our model approximately replicated the difference in thresholds  
430 between harmonic complex tones and pure tones observed in humans (a 5.74 dB advantage for  
431 Harmonic tones over Pure Tones, Fig. 3c). However, the model did not reproduce the empirically

432 observed effect of inharmonicity: the model's thresholds were similar for harmonic and inharmonic  
 433 tones (a 5.73 dB advantage for Inharmonic tones over Pure Tones). The model results confirm  
 434 that the harmonic advantage exhibited by human listeners is not predicted by classical models of  
 435 masking.

436 Taken together, the results suggest that 1) harmonic sounds are more readily detected  
 437 than inharmonic sounds when presented in noise, 2) detection thresholds are similar online and  
 438 in-lab, 3) our effects are quantitatively consistent with prior experiments provided that listeners  
 439 are sufficiently practiced, and 4) classical models of masking are not sufficient to explain our  
 440 results. The results are consistent with the idea that detection is performed using a cue (something  
 441 other than power) that summates differently for harmonic and inharmonic tones.

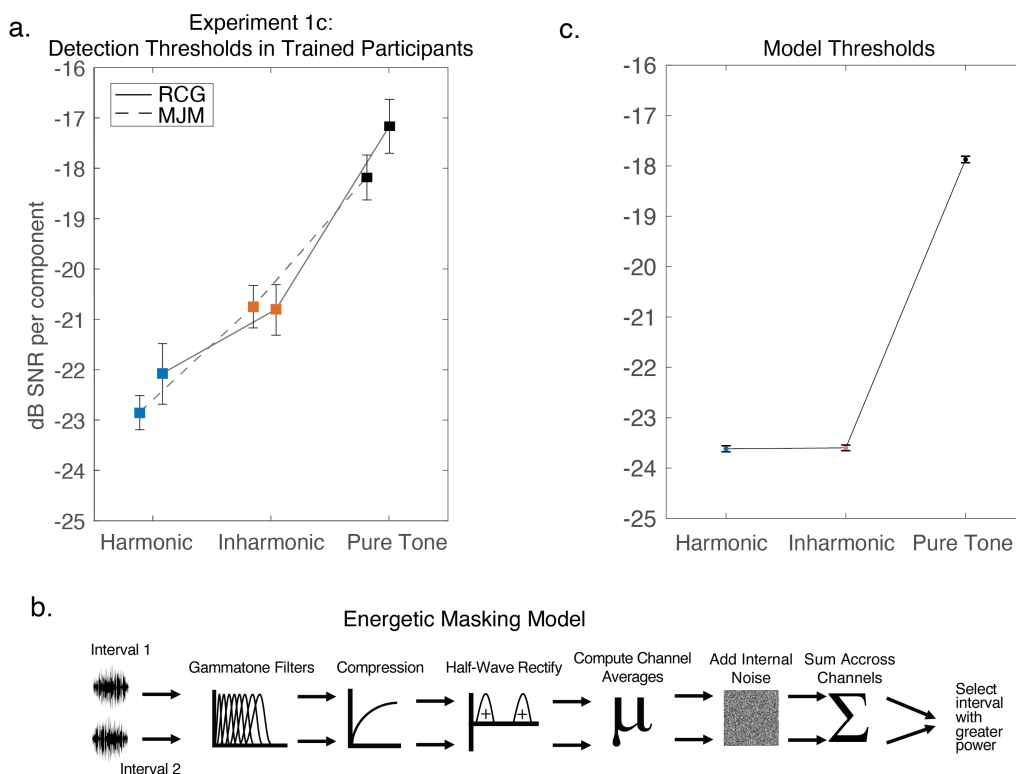


Figure 3: Harmonic advantage for tone-in-noise detection is present in practiced human listeners (Experiment 1c) but not in a model of energetic masking

a. Detection results in trained participants (the first and second authors, indicated by initials). Error bars show standard error of the mean of the last four adaptive tracks of the experiment sessions. b. Schematic of the energetic masking model. c) Model results. Error bars show 95% confidence intervals, calculated via bootstrap.

442  
 443 **Experiment 2. Detecting harmonic and inharmonic tones in noise, with cueing**  
 444 One potential explanation for the observed harmonic detection advantage is that people are  
 445 accustomed to hearing harmonic spectra based on their lifetime of exposure to harmonic sounds,  
 446 and that this familiarity could help listeners know what to listen for in a detection task. Experiment  
 447 2 tested this idea by assessing whether the harmonic advantage persists even when listeners are  
 448 cued beforehand to the target tone. Participants heard two stimulus intervals, each containing a  
 449 “cue” tone followed by a noise burst. One of the noise bursts contained an additional occurrence

450 of the cue tone (Fig. 4a), and participants were asked whether the first or second noise burst  
 451 contained the cued tone.

452  
 453

## Method

454 **Participants.** 66 participants completed Experiment 2 online. 2 participants were removed  
 455 because their average performance across the first run of both conditions was over three standard  
 456 deviations lower than the group mean. As in other experiments in this paper, only the subsequent  
 457 3 runs were used for analysis. 64 participants were included in the final analysis, 21 self-identified  
 458 as female, 45 as male (binary choice), mean age=41.0, S.D.=11.9 years. 25 participants had four  
 459 or more years of musical training, with an average of 11.5 years, S.D.=7.0 years.

460 We used data from a pilot experiment to determine sample size. The pilot experiment  
 461 differed from Experiment in 2 ways: it was run in the lab, and each Inharmonic note contained  
 462 harmonics that were jittered independently from the other trials. The pilot experiment was run on  
 463 17 participants. Since Experiment 2 only had two conditions, we intended to use a single Wilcoxon  
 464 signed-rank test to assess the difference between Harmonic and Inharmonic conditions. The  
 465 effect size for this comparison in the pilot experiment was  $d_z = .76$ . A power analysis indicated  
 466 that a sample size of 32 participants would enable us to see an effect of harmonicity of the size  
 467 observed in the pilot data with a .01 significance threshold, 95% of the time, using a Wilcoxon  
 468 signed-rank test. We exceeded this target by 32 participants at the request of a reviewer who felt  
 469 it would be appropriate to have a sample size on par with that of Experiment 1.

470 **Procedure.** The instructions and adaptive procedure were identical to those used in  
 471 Experiment 1a.

472 **Stimuli.** Participants heard a tone before each of the two noise bursts. This “cue” tone  
 473 was identical to the tone embedded in one of the noise bursts (that participants had to detect).  
 474 Each trial had the following structure: a 500ms tone, followed by 200ms of silence, the first 900ms  
 475 noise burst, 400ms of silence, a 500ms tone, 200ms of silence, and finally, the second 900ms  
 476 noise burst. The target tone was present in either the first or the second noise burst, starting  
 477 200ms into the noise burst and lasting for 500ms. Only tones with harmonics added in random  
 478 phase were used. In all other respects, stimuli were identical to those of Experiment 1a.

479 **Statistical Analysis.** Thresholds were calculated by averaging the SNR values of the final  
 480 six reversals of the adaptive track. A Wilcoxon signed-rank test was used to compare the  
 481 Harmonic and Inharmonic conditions. A Wilcoxon rank-sum test was used to compare between  
 482 Experiment 2 and Experiment 1a, followed by a Bayesian version of the same test to probe  
 483 evidence for the null hypothesis.

484

## Results & Discussion

486 As shown in Fig. 4b, the harmonic advantage persisted with the cue ( $Z=3.78$ ,  $p<.001$ , mean  
 487 Harmonic threshold = -18.60 dB SNR, median = 20.01, mean inharmonic threshold = -17.20 dB  
 488 SNR, median = -18.50 dB SNR, with an average advantage of 1.40 dB for Harmonic tones over  
 489 Inharmonic tones). Even when participants knew exactly what to listen for in the noise, there was  
 490 still an added benefit when detecting harmonic tones. Wilcoxon rank-sum tests showed that the  
 491 harmonic advantage with a cue tone was indistinguishable from that without a cue tone  
 492 (comparison of the difference between Harmonic-random-phase and Inharmonic-random-phase  
 493 thresholds in Experiments 1a and 2),  $Z=.25$ ,  $p=.81$ . The Bayes Factor ( $BF_{10}$ ), using a Cauchy prior  
 494 centered at zero with a scale of .707, was .17, providing moderate support for the null hypothesis  
 495 that there was no difference in the effect size between the two experiments. This result suggests  
 496 that the observed detection advantage for Harmonic over Inharmonic tones does not simply reflect  
 497 knowledge of what to listen for in the noise.

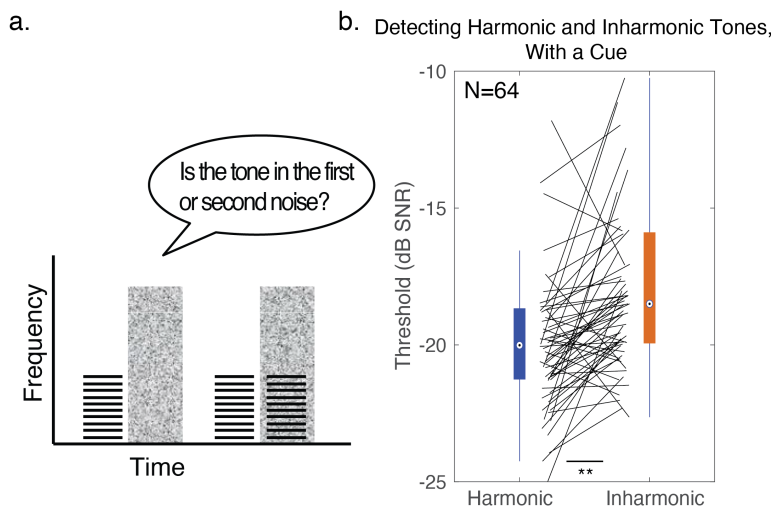


Figure 4: Harmonic advantage persists when listeners know what to listen for (Experiment 2)

a. Schematic of the trial structure for Experiment 2. During each trial, participants heard two noise bursts, both of which were preceded by a 'cue' tone, and one of which contained a tone that was identical to the cue. Participants were asked to decide whether the first or second noise burst contained the cued tone. B. Results from Experiment 2, shown as box-and-whisker-plots, with black lines plotting individual participant results. Asterisks denote significance, Wilcoxon signed-rank test: \*\*= $p < 0.01$ .

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### Experiment 3. Detecting tones without resolved harmonics

Due to the increase in cochlear filtering bandwidth with frequency, only harmonics below about the 10<sup>th</sup> are believed to be individually discernible by the auditory system, and these harmonics dominate the perception of pitch, and aid the segregation of concurrent sounds (Grimault et al., 2000; Shackleton & Carlyon, 1994). To determine whether the harmonic detection advantage observed in Experiments 1 and 2 was driven by low-numbered harmonics that are individually "resolved" by the cochlea, we ran a follow-up experiment with the same task as Experiment 1a, but with tones filtered to only contain harmonics 12-21 ("unresolved" harmonics, Fig. 5a). Tones were again presented in either sine phase or random phase.

#### Method

**Participants.** 62 participants were recruited online for Experiment 3. 7 participants performed over three standard deviations worse than the group mean on the first adaptive run and were excluded from analysis. Only the subsequent 3 runs were analyzed. 55 participants were included in the final analysis, 23 self-identified as female, 32 as male (binary choice), with a mean age of 41.3 years, S.D.=10.1 years. 20 participants had four or more years of musical training, with an average of 11.0 years, S.D.=9.6 years.

We used the data from Experiment 1b to determine sample size. Based on prior work measuring other aspects of harmonicity-related grouping, we hypothesized that the effect of harmonicity might be reduced with unresolved harmonics (Hartmann et al., 1990; Moore et al., 1985). We planned to test for main effects of harmonicity and phase (using ANOVAs). We initially aimed to be able to detect an effect half the size of the main effect of harmonicity seen with resolved harmonics in Experiment 1b ( $\eta_p^2 = .37$ ). This yielded a target sample size of 15 participants (to have a 95% chance of seeing the hypothesized effect with a .01 significance threshold). However, because we obtained a null result after collecting data from the first 15

523

524 participants, we continued data collection (in sets of approximately 8-12 participants) until  
 525 Bayesian statistics converged on support for or against the null hypothesis. Unlike frequentist  
 526 statistics, Bayesian statistics will converge on evidence for the null hypothesis with enough data  
 527 (Rouder et al., 2009).

528 **Procedure.** The instructions and adaptive procedure were identical to those used in  
 529 Experiment 1a.

530 **Stimuli.** Tones contained harmonics 12 to 21 at full amplitude, with a trapezoid-shaped  
 531 filter applied in the frequency domain in order to reduce the sharp spectral edge that might  
 532 otherwise be used to perform the task. On the lower edge of the tone, the 10<sup>th</sup> harmonic was  
 533 attenuated to be 30 dB below the 12<sup>th</sup> harmonic, and the 11<sup>th</sup> harmonic to be 15 dB below. On the  
 534 upper edge of the tone, the same pattern of attenuation was applied in reverse between the 21<sup>st</sup>  
 535 and 23<sup>rd</sup> harmonics. All other harmonics were removed. Additionally, the cutoff frequency for the  
 536 noise (TE-noise) was increased to 10,000 Hz (rather than 6,000 Hz used in Experiment 1), in  
 537 order to cover the stimulus frequencies. Noise was filtered with a 6<sup>th</sup> order Butterworth filter. Other  
 538 aspects of the stimuli (duration of tones, timing of tones in noise, etc.) were matched to  
 539 parameters used in Experiment 1a.

540 **Statistical Analysis.** Statistical analysis was identical to that used in Experiment 1a.

## 541 542 Results and Discussion

543 As shown in Fig. 5b, there was no difference in detectability between harmonic and  
 544 inharmonic stimuli ( $F(1,54)=0.39$ ,  $p=.53$ ,  $\eta_p^2=.007$ ). There was also no main effect of phase  
 545 ( $F(1,54)=0.48$ ,  $p=0.49$ ,  $\eta_p^2=.009$ ). The Bayes factor ( $BF_{10}$ , specifying a multivariate Cauchy prior  
 546 on the effects (Rouder et al., 2012)) was .18, providing moderately strong support for the null  
 547 hypothesis that there was no difference between the detectability of harmonic and inharmonic  
 548 tones without resolved harmonics (*JASP, Version 0.13.1, 2020*). These results suggest that the  
 549 harmonic detection advantage is specific to resolved harmonics.

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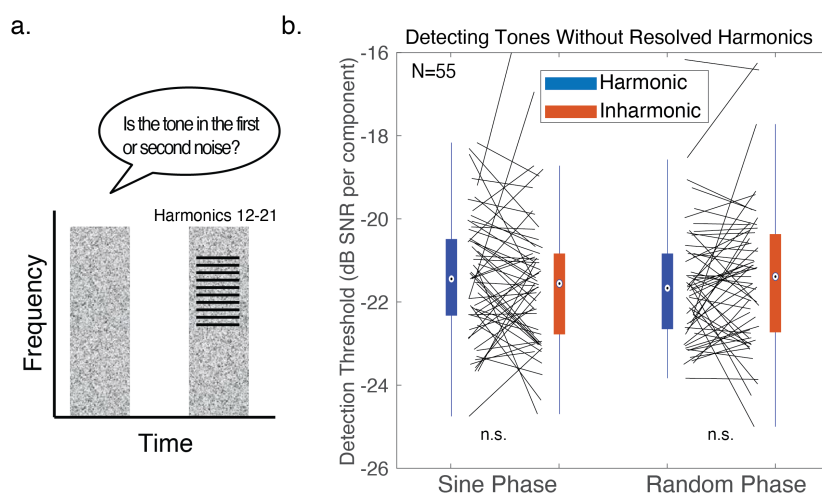


Figure 5: Harmonic detection advantage is specific to resolved harmonics (Experiment 3)

a. Schematic of the trial structure for Experiment 3. During each trial, participants heard two noise bursts, one of which contained a complex tone with unresolved harmonics, and were asked to decide whether the first or second noise burst contained a tones. b. Results from Experiment 3, shown as box-and-whisker-plots, with black lines plotting individual participant

results. The central mark in the box plots the median, and the bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. Whiskers extend to the most extreme data points not considered outliers.

551 **Experiment 4. Discrimination thresholds in noise**  
 552 In Experiments 4 and 5, we investigated whether harmonicity would facilitate other types of  
 553 judgments about sounds in noise. We first examined the discrimination of tones. The  
 554 discrimination of the “pitch” of two successive tones in quiet is comparable for harmonic and  
 555 inharmonic tones (Faulkner, 1985; McPherson & McDermott, 2018; McPherson & McDermott,  
 556 2020; Micheyl et al., 2012; Moore & Glasberg, 1990), and appears to be mediated by comparisons  
 557 of their spectra (McPherson & McDermott, 2020). However, it seemed plausible that  
 558 discrimination in noise might be better for harmonic tones. For instance, being better able to  
 559 separate tones from noise might help listeners discriminate the tones at low SNRs. Alternatively,  
 560 the pitch cue provided by the  $f_0$  (which is available for harmonic but not inharmonic tones) might  
 561 be more noise-robust than that of the spectrum. Using an adaptive procedure, we measured up-  
 562 down discrimination thresholds for Harmonic, Inharmonic, and Pure Tone conditions (Fig. 6a) at  
 563 a range of SNRs.

#### 564 **Method**

565 **Participants.** 81 participants were recruited online for Experiment 3. We excluded  
 566 participants who performed worse than 14.35% across all conditions (averaged across both runs  
 567 of the experiment). This cutoff was based on a pilot experiment run in the lab – it was the average  
 568 performance across all conditions for 10 non-musician participants. We used this cutoff to obtain  
 569 mean performance levels on par with those of compliant and attentive participants run in the lab.  
 570 We used a set exclusion criterion from in-lab data, rather than excluding participants based on  
 571 whether they were 3 standard deviations away from the mean (as in other studies), because  
 572 adaptive tracks were capped at a 4-semitone pitch difference. If participants completed three trials  
 573 incorrectly at this 4-semitone pitch difference, the adaptive track was ended early, and  
 574 subsequently the mean threshold for that adaptive track was conservatively recorded as 4  
 575 semitones (25.99%) for analysis. Measures of variance in the obtained threshold estimates were  
 576 thus under-representative of actual variance in the sample. 29 participants were excluded from  
 577 analysis using this in-lab criterion. This resulted in 52 participants (20 self-identified as female, 32  
 578 as male (binary choice), mean age=39.81 years, S.D.=11.66 years. 25 participants had four or  
 579 more years of musical training, with an average of 10.3 years, S.D.=11.3).

581 We chose our sample size using the same pilot data used to determine the exclusion  
 582 criteria. The pilot experiment, run in 19 participants, differed from the current experiment in a few  
 583 respects. In addition to being run in the lab, the pilot experiment did not include a Pure Tone  
 584 condition, the SNR values were shifted half a semitone higher, and in Inharmonic conditions, a  
 585 different jitter pattern was used for each trial (rather than the same jitter pattern being used across  
 586 trials). We performed ANOVAs testing for effects of harmonicity and musicianship; the pilot data  
 587 showed fairly large main effects of both harmonicity ( $\eta_p^2=.77$ ) and musicianship ( $\eta_p^2=.45$ ),  
 588 suggesting that both these analyses would be well-powered with modest sample sizes. To ensure  
 589 the reliability of planned analyses examining the inflection points and slopes of sigmoid functions  
 590 fitted to the discrimination curves, we also estimated the sample size needed to obtain reliable  
 591 mean thresholds. We extrapolated from our pilot data (via bootstrap) that an N of at least 36 would  
 592 be necessary to have a split-half reliability of the mean measured threshold in each condition

593 (assessed between the first and second adaptive runs of the experiment) greater than  $r=.95$ . This  
 594 sample size was also sufficient for the ANOVA analyses (for example, to see an effect of  
 595 musicianship 1/2 the size of that observed in our pilot experiment 95% of the time at a  $p<.01$   
 596 significance level, one would need a sample size of 28). We thus aimed to recruit at least 36  
 597 participants.

598 **Procedure.** In Experiment 4 we measured classic two-tone up-down “pitch”  
 599 discrimination, but with the tones presented in noise. As in Experiments 1-3, on each trial  
 600 participants heard two noise bursts. However, in this experiment, a tone was presented in each  
 601 of the two noise bursts, and participants judged whether the second tone was higher or lower than  
 602 the first tone. The difference in the  $f_0$ s used to generate the tones was initialized at 1 semitone  
 603 and was changed by a factor of 2 through the first four reversals, and then by a factor of  $\sqrt{2}$   
 604 through the final six reversals. We tested pitch discrimination at 6 SNRs for pure tones, 7 SNRs  
 605 for inharmonic tones, and 8 SNRs for harmonic tones. This choice was motivated by pilot data  
 606 showing that at the lowest SNR tested for harmonic tones, inharmonic tones were undetectable.  
 607 The same logic applied to the lowest two SNRs and pure tones. Because we expected that  
 608 discrimination would be difficult (if not impossible) at the lowest SNR conditions tested in each  
 609 condition, we capped the possible  $f_0$  difference of adaptive tracks at 4 semitones. As discussed  
 610 in the *Participants* section, if participants completed three trials incorrectly at this  $f_0$  difference,  
 611 the adaptive track was ended early. For these trials, the threshold was conservatively recorded  
 612 as 4 semitones for analysis (25.99%). Participants performed 2 adaptive runs per condition.

613 **Stimuli:** The stimuli for Experiment 4 were identical to the random-phase complex tones  
 614 used in Experiment 1, except that each of the two noise bursts contained a tone. Eight SNRs  
 615 were used: -22 (only Harmonic melodies were tested at this SNR), -20.5 (only Harmonic and  
 616 Inharmonic stimuli were tested), -19, -17.5, -16, -14.5, -13 dB, and Infinite (no noise). The  $f_0$  of  
 617 the first note in each trial was randomly selected between 200 and 267 Hz (log uniform  
 618 distribution), and the  $f_0$  for the second note was randomly selected to be higher or lower than the  
 619 first note by the amount specified by the adaptive procedure. For inharmonic trials, the same  
 620 vector of jitter values was applied to each of the two notes (McPherson & McDermott, 2018) used  
 621 in a trial. As in previous experiments, we generated 20 sets of stimuli, each with a different jitter  
 622 pattern, selected from 100,000 randomly generated jitter patterns as those with the smallest  
 623 autocorrelation peaks. Each participant was randomly assigned one of these sets of stimuli, and  
 624 for the inharmonic condition only heard one inharmonic ‘jitter’ pattern throughout the experiment.

625 **Statistical Analysis.** Thresholds were estimated by taking the geometric mean of the  $f_0$   
 626 differences (in semitones) from the final six reversals of the adaptive track. As in Experiment 1a,  
 627 data distributions were non-normal (skewed), so we used non-parametric tests. To compare  
 628 performance across multiple conditions or across musicianship we used non-parametric versions  
 629 of repeated-measures ANOVAs (for within group effects) and mixed-model ANOVAs (to compare  
 630 within and between group effects). We computed the F statistic and evaluated its significance with  
 631 approximate permutation tests, randomizing the assignment of the data points across the  
 632 conditions being tested 10,000 times, and comparing the F statistic to this null distribution.  
 633 Wilcoxon signed-rank tests were used for post-hoc pairwise comparisons between Harmonic and  
 634 Inharmonic conditions that were matched in SNR. These seven comparisons were not corrected  
 635 for multiple comparisons because they were preceded by an ANOVA that revealed a significant  
 636 main effect of harmonicity.

637 We completed a secondary analysis to compare the results for the three stimulus  
 638 conditions (Harmonic, Inharmonic, and Pure Tone) after accounting for differences in detectability  
 639 between conditions. We replotted the pitch discrimination curves relative to the detection  
 640 thresholds measured in Experiment 1a (-20.67 dB SNR, -19.34 dB SNR, -16.72 dB SNR, for

641 Harmonic-Random-Phase, Inharmonic-Random-Phase and Pure Tone conditions, respectively,  
642 Fig. 5b, inset). To evaluate the statistical significance of the differences between conditions that  
643 remained once adjusted for detectability, we bootstrapped over participants. We selected random  
644 subsets of participants with replacement and re-calculated averages of the detection-adjusted  
645 curves. For each bootstrap sample we fit a sigmoid (logistic) function to the averages for each  
646 condition (Harmonic/Inharmonic/Pure). Sigmoid functions can be defined by the slope and x-  
647 coordinate at their inflection point; we compiled distributions of these parameters of the bootstrap  
648 samples. To facilitate the curve fitting we padded the data on either end of the SNR range: with -  
649 25.99 on the low end (the highest possible threshold that could be measured in the experiment,  
650 as if we had added one additional, lower SNR), and with zeros at the high end. We compared the  
651 distributions of the slopes for different conditions, and separately, the distributions of midpoints  
652 (inflection x-coordinates), in order to determine the significance of differences between conditions.  
653

## 654 **Results & Discussion**

655 Replicating prior results (McPherson & McDermott, 2018; McPherson & McDermott,  
656 2020), discrimination thresholds in quiet were similar for Harmonic and Inharmonic tones (around  
657 1.5% in both cases; rightmost conditions of Fig. 5b), with thresholds that were statistically  
658 indistinguishable (Inf dB SNR;  $Z=1.57$ ,  $p=.12$ ). However, at lower SNRs inharmonic discrimination  
659 thresholds were substantially higher than harmonic thresholds (significant differences at all SNRs  
660 between -20.5 and -13 dB;  $Z>2.71$ ,  $p<.01$ , in all cases, largest p value = 0.012). This difference  
661 produced a significant interaction between Harmonicity and SNR ( $F(6,306)=20.98$ ,  $p<.0001$ ,  
662  $\eta_p^2=.29$ ; excluding the -22 dB SNR condition for which only Harmonic thresholds were measured).  
663 There was also a main effect of harmonicity (between Harmonic and Inharmonic tones, again  
664 excluding the -22 dB SNR condition,  $F(1,51)=208.00$ ,  $p<.0001$ ,  $\eta_p^2=.80$ ).

665 When we accounted for differences in the detection thresholds for the three tone types  
666 (as measured in Experiment 1), we found that the inflection points of the sigmoid functions  
667 remained significantly different for Harmonic and Inharmonic conditions ( $p=.017$ ). The adjusted  
668 inflection point for the Pure Tone condition was not significantly different from that of either the  
669 Harmonic ( $p=.99$ ) or Inharmonic conditions ( $p=.32$ ), and the slopes of the three conditions were  
670 not significantly different from each other. The difference between Harmonic and Inharmonic  
671 discrimination after accounting for the detectability of the tones suggests that harmonic  
672 discrimination advantage is better than what would be expected based on detectability, or  
673 conversely, that inharmonic discrimination is worse than what would be expected based on  
674 detectability. Moreover, even at SNRs where people can detect both harmonic and inharmonic  
675 tones reliably, harmonicity aids discrimination in noise, perhaps because representations of the  
676  $f_0$  can be used for discrimination.

677

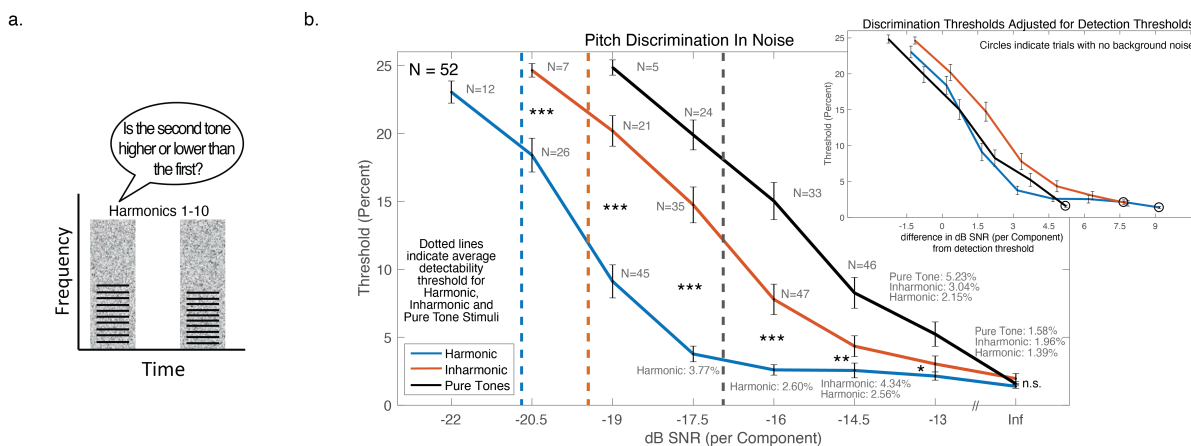


Figure 6: Harmonic advantage for discriminating tones in noise (Experiment 4)

a. Schematic of the trial structure for Experiment 4. During each trial, participants heard two noise bursts, each of which contained a complex tone (both tones were either harmonic or inharmonic), and were asked to decide whether the second tone was higher or lower than the first tone. B. Results from Experiment 4. Error bars denote standard error of the mean. For conditions where we were unable to measure thresholds from all participants, the number of participants with measurable thresholds is indicated next to the data point. Exact threshold values are provided for thresholds under 10%. Asterisks denote statistical significance of a Wilcoxon signed-rank test between Harmonic and Inharmonic conditions: \*\*\*= $p < 0.001$ , \*\*= $p < 0.01$ , \*= $p < 0.05$ . Inset: discrimination thresholds adjusted based on the detection thresholds measured in Experiment 1. The x-axis plots SNR relative to the detection threshold for the three different types of tone.

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### Experiment 5. Discriminating pitch contours in noise

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#### Method:

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**Participants:** 75 participants passed the initial screening and completed Experiment 5. All participants had mean performance within three standard deviations of the mean, so all participants were included in the final analysis. 35 participants self-identified as female, 38 as male, and 2 as nonbinary, mean age=37.1 years, S.D.=12.1 years.

We conducted a power analysis based on a pilot experiment with 74 participants. The pilot experiment differed from the current experiment in that the starting F0s for the first note were chosen from a set of 3, rather than from a uniform distribution over a small range, and in that melodies only contained 1 semitone steps, instead of 1 and 2 semitone steps. We observed

699 a significant main effect of harmonicity in this pilot experiment, with a large effect size ( $\eta_p^2=.29$ ).  
 700 A power analysis indicated that sample size of 15 would enable us to detect an effect this size  
 701 95% of the time at a significance of  $p<.01$ . However, we also sought to achieve a stable results  
 702 graph; using the same pilot data we determined that 60 participants yielded split-half reliability of  
 703 the performance in each condition greater than  $r=.95$ , so we chose this number as our target.

704 **Procedure:** The design of Experiment 5 was inspired by the classic melodic contour  
 705 task of Dowling and Fujitani (Dowling & Fujitani, 1971). Participants were told they would hear  
 706 two melodies in each trial, sometimes with background noise, and were asked to judge whether  
 707 the melodies were the same or different (Fig. 7a). On half of the trials the two melodies were the  
 708 same and on the other half they were different. There were four possible responses “Sure  
 709 Different”, ‘Maybe Different’, ‘Maybe Same’, ‘Sure Same’, and participants were asked to use all  
 710 four responses throughout the experiment. For trials where the melodies were different, we  
 711 counted both ‘Maybe Different’ and ‘Sure Different’ responses as correct (for the purposes of  
 712 both trial-by-trial performance feedback and bonuses, and for analysis); for trials where the two  
 713 melodies were the same, we counted both “Maybe Same” and “Sure Same” responses as  
 714 correct. Participants completed 20 trials for each SNR and Harmonic/Inharmonic combination,  
 715 for a total of 300 trials. The trials were presented in a random order for each participant.

716 **Stimuli:** Each trial contained two extended noise bursts lasting 2.4 seconds, each  
 717 containing a 5-note melody. Each note was a tone like those used for the random phase complex  
 718 tones in Experiment 1. The notes were 400ms in duration and were presented back-to-back, with  
 719 the first note of the melody beginning 200ms after the start of the noise burst (leaving 200 ms of  
 720 noise after the end of the last note). There was a 1-second silent gap between the two noise  
 721 bursts. Eight SNRs were used: -22 (only Harmonic melodies were tested at this SNR), -20.5, -19,  
 722 -17.5, -16, -14.5, -13 dB, and Infinite (no noise). The  $f_0$  for the first note of the first melody in each  
 723 trial was randomly selected from a log-uniform distribution 2 semitones in width, centered on 200  
 724 Hz, and the  $f_0$  of the first note of the second melody was half an octave higher than the  $f_0$  of the  
 725 first note in the first melody. Melodies were generated randomly and could contain step sizes of  
 726 +/- 1 or 2 semitones, chosen from a uniform distribution with replacement. On ‘same’ trials, the  
 727 second melody was identical to the first apart from the half-octave transposition. On ‘different’  
 728 trials, the sign of one of the pitch changes in the second melody was reversed (for example, a  
 729 melody could contain step sizes +1, +1, +2, -1, and a ‘different melody’ could then be +1, +1, -2,  
 730 +1, Fig. 7a). For Inharmonic trials, the same vector of jitter values was applied to all of the notes  
 731 on all of the trials (McPherson & McDermott, 2018). As in previous experiments, 20 different sets  
 732 of stimuli were generated, each with a distinct jitter pattern for inharmonic stimuli. Participants  
 733 were randomly assigned to one of the 20 stimuli sets.

734 **Statistical Analysis:** We used d-prime as the measure of performance on the task. Data  
 735 passed the Lilliefors test at a 5% significance level, so parametric statistics were used to analyze  
 736 the results. A repeated-measures ANOVA was used to test for a main effect of harmonicity, and  
 737 post-hoc paired t-tests were used to compare Harmonic and Inharmonic conditions at matched  
 738 SNRs. These seven comparisons were not corrected for multiple comparisons because they were  
 739 preceded by an ANOVA that revealed a significant main effect of harmonicity.

## 740 **Results & Discussion**

742 Replicating previous results (McPherson & McDermott, 2018), contour discrimination  
 743 without noise was indistinguishable for Harmonic and Inharmonic conditions ( $t=1.12$ ,  $p=.27$ ). But  
 744 in noise, performance with inharmonic stimuli was worse than that for harmonic stimuli (Fig 7b).  
 745 This difference produced a significant interaction between harmonicity and SNR ( $F(6,444)=3.27$ ,  
 746  $p=0.0037$ ,  $\eta_p^2=.04$ ). There was also a significant main effect of harmonicity ( $F(1,74)=58.10$ ,

747  $p < .0001$ ,  $\eta_p^2 = .44$ ). Post-hoc pairwise comparisons showed significant differences between  
 748 Harmonic and Inharmonic conditions for SNRs ranging from -20.5 dB SNR to -14.5 dB SNR  
 749  $t > 2.24$ ,  $p < .05$  in all cases, maximum  $p$  value = 0.028, effect sizes ranged from Cohen's  $D$  of  $d = .37$   
 750 to  $d = .74$ ). These results suggest that even when note-to-note pitch changes are well above  
 751 threshold (with musically relevant intervals such as 1 and 2 semitones) there is a considerable  
 752 advantage for discriminating harmonic tones in noise, compared to inharmonic tones. Additionally,  
 753 as with Experiment 4, inharmonic tones in noise remained more difficult to discriminate than  
 754 harmonic tones even when well above their detection thresholds. This effect is large enough to  
 755 have significant real-world relevance. For instance, harmonic performance at a -17.5 dB SNR  
 756 roughly matched Inharmonic performance at -14.5 dB SNR ( $Z = 1.38$ ,  $p = .17$ ), such that an  
 757 inharmonic melody just discriminable from 5.96 meters away would remain discriminable 10  
 758 meters away if it were harmonic. Harmonicity makes it possible to hear musical structure when  
 759 background noise would otherwise render it inaudible.

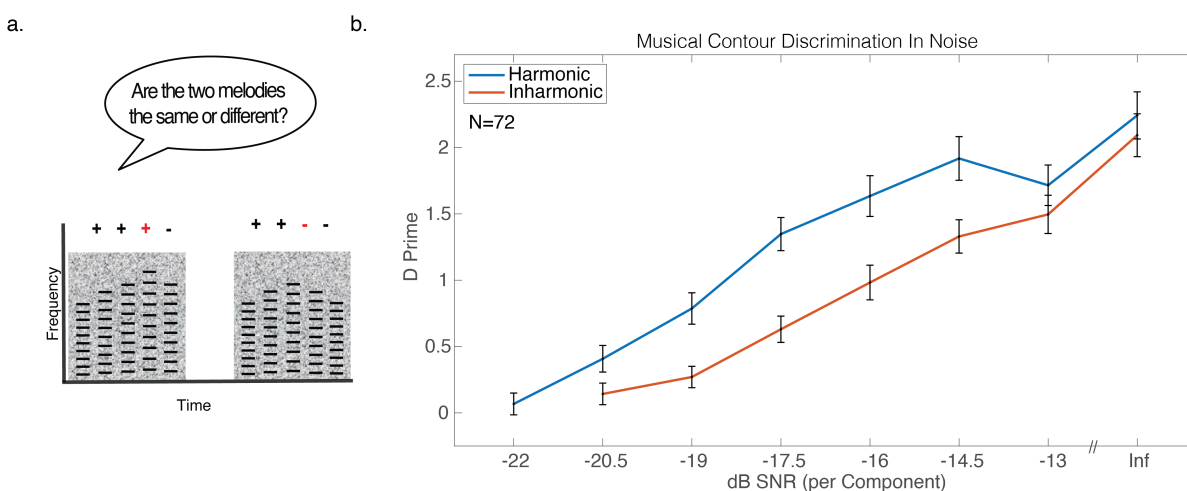


Figure 7: Harmonic advantage for discriminating musical contours in noise (Experiment 5)

a. Schematic of the trial structure for Experiment 5. During each trial, participants heard two five-note melodies made of note-to-note steps of +/- 1 or 2 semitones, and were asked whether the two melodies were the same or different. In this example, the melodies are different (indicated by the red + and - signs). The second melody was always transposed up in pitch relative to the first by half an octave. Melodies were embedded in varying levels of masking noise. b. Results from Experiment 5. Error bars denote standard error of the mean.

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### Experiment 6. Detecting speech in noise

762 The results of Experiments 1-5 with synthetic tones raise the question of whether the detection  
 763 and discrimination advantages for harmonic sounds would extend to natural sounds such as  
 764 speech. In Experiment 6, we addressed this question by measuring detection thresholds for  
 765 spoken syllables embedded in noise (Fig. 8a).

766

#### Method

768 **Participants:** 78 participants completed Experiment 6 online. 2 were removed because their  
 769 average performance across the first run of all conditions was over three standard deviation away  
 770 from the group mean across the first run. As in other detection experiments in this paper, only the  
 771 subsequent 3 runs were used for analysis. 76 participants were included in the final analysis, 33  
 772 self-identified as female, 43 as male, (binary choice), mean age=37.9 years, S.D.=12.5 years).

773 24 participants had four or more years of musical training, with an average of 10.9 years, S.D.=9.1  
774 years.

775 Experiment 6 only had two conditions, and we intended to use a single Wilcoxon signed-  
776 rank test to assess the difference between them. The effect size of harmonicity measured in a  
777 pilot version of Experiment 6 was moderate ( $d_z = 0.39$ , with an average difference between  
778 Harmonic and Inharmonic conditions of 0.89 dB SNR), plausibly because we used natural stimuli,  
779 which are more variable than the synthetic tones used in other experiments (in which we observed  
780 larger effects). The pilot experiment (run with 125 participants) was identical to Experiment 6  
781 except that each Inharmonic trial contained harmonics that were jittered independently from the  
782 other trials. A power analysis indicated that we would need to run 76 participants to be 95% sure  
783 of detecting an effect size like that in the pilot data with a .05 significance threshold. We did not  
784 attempt to recruit equal numbers of musicians and non-musicians because Experiment 1a  
785 showed no obvious difference between musicians and non-musicians (see *Effects of*  
786 *Musicianship* below).

787 **Procedure.** We measured detection thresholds for single spoken vowels embedded in  
788 noise, resynthesized to be inharmonic or harmonic (Fig. 8a). Participants judged whether the first  
789 or second noise burst contained a word. Thresholds were estimated using the same adaptive  
790 procedure as Experiments 1a-c.

791 **Stimuli:** Speech was resynthesized using the STRAIGHT analysis and synthesis method  
792 (Kawahara & Morise, 2011; McDermott et al., 2012). STRAIGHT decomposes a recording of  
793 speech into voiced and unvoiced vocal excitation and vocal tract filtering. If the voiced excitation  
794 is modelled sinusoidally, one can alter the frequencies of individual harmonics and then  
795 recombine them with the unaltered unvoiced excitation and vocal tract filtering to generate  
796 inharmonic speech. This manipulation leaves the spectrotemporal envelope of the speech largely  
797 intact, and intelligibility of inharmonic speech in quiet is comparable to that of harmonic speech  
798 (Popham et al., 2018). The frequency jitters for inharmonic speech were chosen in the same way  
799 as those for the inharmonic complex tones of Experiments 1-5. Speech and noise were sampled  
800 at 16kHz. Code implementing the harmonic/inharmonic resynthesis is available on the senior  
801 author's lab web page. We used the vowels /i/, /u/, /a/ and /ɔ/, spoken by adult male and female  
802 speakers, from the Hillenbrand vowel set (Hillenbrand et al., 1995) (h-V-d syllables). These four  
803 vowels were selected because they bound the English vowel space.

804 Participants heard syllables embedded in threshold-equalizing noise. Noise bursts were  
805 650ms in duration. Vowels were truncated to be 250ms in duration. Vowels were centered on the  
806 noise burst, such that there was 200ms of noise before the onset of the syllable and 200ms of  
807 noise after the syllable ended.

808 Stimuli were pre-generated, and 20 trials were generated in advance for each possible  
809 SNR level. The adaptive procedure was initialized at an SNR of 2 dB SNR and capped at 16 dB  
810 SNR. The same pattern of jitter was used throughout the entire speech syllable, and as in the  
811 other experiments in this paper, 20 different sets of stimuli were generated, each of which used a  
812 distinct jitter pattern for inharmonic stimuli. Participants were randomly assigned to one of the 20  
813 stimuli sets.

814 **Statistical Analysis.** Thresholds were calculated by averaging the SNR values of the final  
815 six reversals of the adaptive track. Data distributions were non-normal (skewed), so a single  
816 Wilcoxon signed-rank test was used to compare the Harmonic and Inharmonic conditions.

## 817 818 **Results & Discussion**

819 As shown in Fig. 8b, harmonic vowels were easier to detect in noise than inharmonic  
820 vowels (difference of .54 dB SNR, Wilcoxon signed-rank test:  $Z=3.45$ ,  $p<.001$ ). This result  
821 demonstrates that the effect observed with complex tones generalizes somewhat to real-world

822 sounds such as speech. However, the effect was smaller than with tones (.88 dB here vs. 1.38  
 823 dB for tones in Experiment 1a; Cohen's  $d=0.35$  vs.  $d=.96$  in Experiment 1a, averaged across Sine  
 824 and Random phase conditions). In addition, the harmonic advantage varied more across  
 825 participants with speech than with tones; the standard deviation of the difference between  
 826 harmonic and inharmonic thresholds was 1.35 dB SNR in Experiment 1a, but 2.40 dB SNR here.  
 827 This variability may reflect the additional cues available in some speech exemplars, including  
 828 concurrent modulation across frequency components (Culling & Summerfield, 1995b; McAdams,  
 829 1989), and onsets and offsets of consonants (Darwin, 1981), that may be used to different extents  
 830 by different listeners. The persistence of the harmonic advantage despite these factors suggests  
 831 that it could affect real-world listening; but the effect may be more modest than with musical  
 832 sounds.

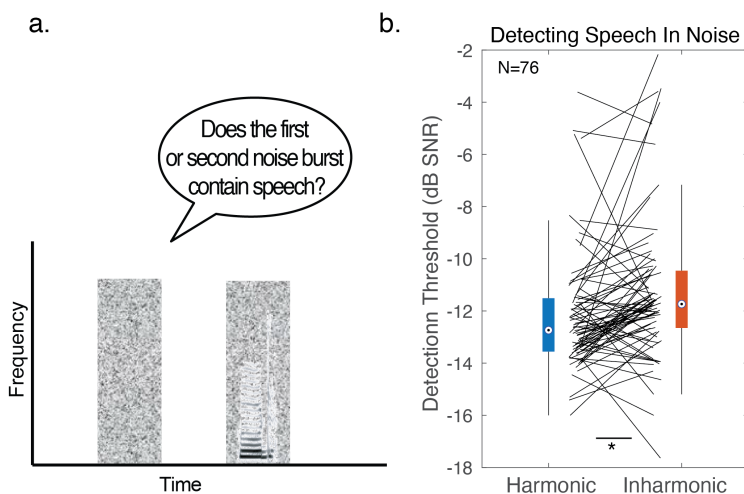


Figure 8: Harmonic advantage for detecting speech in noise (Experiment 6)

a. Schematic of the trial structure for Experiment 6. During each trial, online participants heard two noise bursts, one of which contained a spoken syllable, and were asked to decide whether the first or second noise burst contained speech. Speech was resynthesized to be either harmonic or inharmonic. b. Results of Experiment 6. Results are shown as box-and-whisker-plots, with black lines plotting individual participant results. The central mark in the box plots the median, and the bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. Whiskers extend to the most extreme data points not considered outliers. Asterisks denote significance, Wilcoxon signed-rank test:  $*=p<0.05$ .

833

### 834 Experiments 7 and 8: Discriminating English Vowels & Mandarin Tones in Noise

835 In Experiment 7 and 8, we investigated whether the observed harmonic advantage for detecting  
 836 vowels in noise might translate to speech discrimination. Experiment 7 assessed the  
 837 discrimination of English vowels. Experiment 8 assessed discrimination of Mandarin tones.

838

#### 839 Method

840 **Participants: Experiment 7.** 142 participants (55 self-identified as female, 87 as male, 0  
 841 as non-binary, mean age=38.2 years, S.D.=11.1 years) completed Experiment 7 online. All  
 842 performed within 3 standard deviations of the mean across participants, thus we did not remove  
 843 any participants before analysis.

844 We chose our sample size using data from a pilot experiment run in 276 participants. This  
 845 pilot differed from the current experiment in a few respects. In addition to a slightly different set of  
 846 SNRs, a different jitter pattern was used for each trial (rather than the same jitter pattern being  
 847 used across trials). An ANOVA showed a modest effect of harmonicity ( $\eta_p^2=.03$ ). We aimed to run  
 848 enough participants to have a 95% chance of seeing an effect this size with a .01 significance  
 849 threshold. This yielded a target sample size of 134 participants.

850 **Participants: Experiment 8.** 71 participants completed the experiment online. The data  
 851 had a bimodal distribution, with modes at 24% (chance performance was 25%) and 70%,  
 852 suggesting there was a group of participants who either were not Mandarin Chinese speakers  
 853 (having ignored the initial instructions in which we indicated that fluency in Mandarin was a  
 854 requirement), or were performing at chance for other reasons. To restrict participants to those  
 855 who were able to perform the task, we set an exclusion criterion of 35% accuracy. This left 46  
 856 participants (28 self-identified as female, 18 as male, 0 as non-binary, mean age = 33.3 years,  
 857 S.D. = 9.3 years).

858 We chose our sample size using pilot data. The pilot experiment, run in 13 participants,  
 859 was similar to Experiment 8 apart from using different SNRs. An ANOVA showed an effect of  
 860 harmonicity ( $\eta_p^2=.10$ ). We aimed to run enough participants to have a 95% chance of seeing an  
 861 effect this size with a .01 significance threshold. This yielded a target sample size of 44  
 862 participants.

863 **Procedure: Experiment 7.** Participants identified the vowel they heard, presented with  
 864 varying levels of background noise, via a 4-way forced choice task (Fig. 9a). Participants heard  
 865 both harmonic and inharmonic examples of each vowel (without background noise, and with  
 866 genders of the speakers randomized) before beginning. Participants were provided with feedback  
 867 after each response.

868 **Procedure: Experiment 8.** Participants heard single words in Mandarin Chinese  
 869 presented with varying levels of background noise (Fig. 9c). Words were either harmonic or  
 870 inharmonic. The task was to identify the tone spoken in each word, from 4 options given by the  
 871 four primary tones in Mandarin Chinese: 1 – flat, 2 – rising, 3 – falling then rising, 4 – falling (there  
 872 is a fifth ‘neutral’ tone that we did not include). Participants were provided with feedback after  
 873 each response.

874 **Stimuli: Experiment 7.** As in Experiment 6, participants heard syllables embedded in  
 875 threshold-equalizing noise, but noise bursts were 1500ms in duration and vowels were not  
 876 truncated. Syllables began 200ms after the onset of the noise. Participants heard one syllable per  
 877 condition. The vowels and resynthesis methods were otherwise identical to those of Experiment  
 878 6. Eight SNRs were used: -15, -12.5, -10, -7.5, -5, -2.5, 0 dB, and Infinite (no noise).

879 To avoid the possibility that participants might learn specific exemplars of the vowel set,  
 880 participants completed only eight trials per condition, for a total of 128 trials.

881 **Stimuli: Experiment 8.** On each trial participants heard one of 32 single-syllable words  
 882 spoken by a single female talker, chosen from the ‘Projet SHTOOKA’ database  
 883 (<http://shtookka.net/>). The full list of words is available in Supplementary Table 1. As in Experiments  
 884 6 and 7, words were resynthesized to be harmonic or inharmonic using STRAIGHT (Kawahara &  
 885 Morise, 2011; McDermott et al., 2012), and embedded in threshold-equalizing noise. Noise bursts  
 886 were 2000ms in duration. Words began 200ms after the onset of the noise. Four SNRs were  
 887 used: -17, 13, -9 dB, and Infinite (no noise). Participants completed 12 trials for each SNR and  
 888 harmonicity condition, for a total of 96 trials. Participants heard each word in the set 3 times over  
 889 the course of the experiment, with conditions randomized across words. The same pattern of jitter  
 890 was used for inharmonic conditions throughout the entire experiment for a participant. As with

891 previous experiments in this paper, 20 different sets of stimuli were generated, each with a distinct  
 892 jitter pattern for inharmonic stimuli.

893 **Statistical Analysis: Experiments 7-8.** Across both experiments, data did not  
 894 consistently pass the Lilliefors test at a 5% significance level, so we opted to use non-parametric  
 895 statistics. We used non-parametric versions of repeated-measures ANOVAs identical to those  
 896 used in Experiment 1a.

## 897 Results and Discussion

898 Both experiments showed a slight but significant harmonic advantage for discriminating  
 899 speech in noise. There were statistically significant main effects of harmonicity both for identifying  
 900 English vowels (Fig. 9b,  $F(1,141)=14.54$ ,  $p=.0002$ ,  $\eta_p^2=.09$ ), as well as discriminating Mandarin  
 901 Chinese tones (Fig. 9d, main effect of harmonicity,  $F(1,45)=13.49$ ,  $p=.0006$ ,  $\eta_p^2=.23$ ), though the  
 902 effect size was larger for Mandarin than English. One explanation is that the harmonic advantage  
 903 is largely driven by a pitch cue provided by the  $f_0$ . This cue may be more useful for recognizing  
 904 Mandarin tones in noise than for recognizing English vowels in noise.  
 905

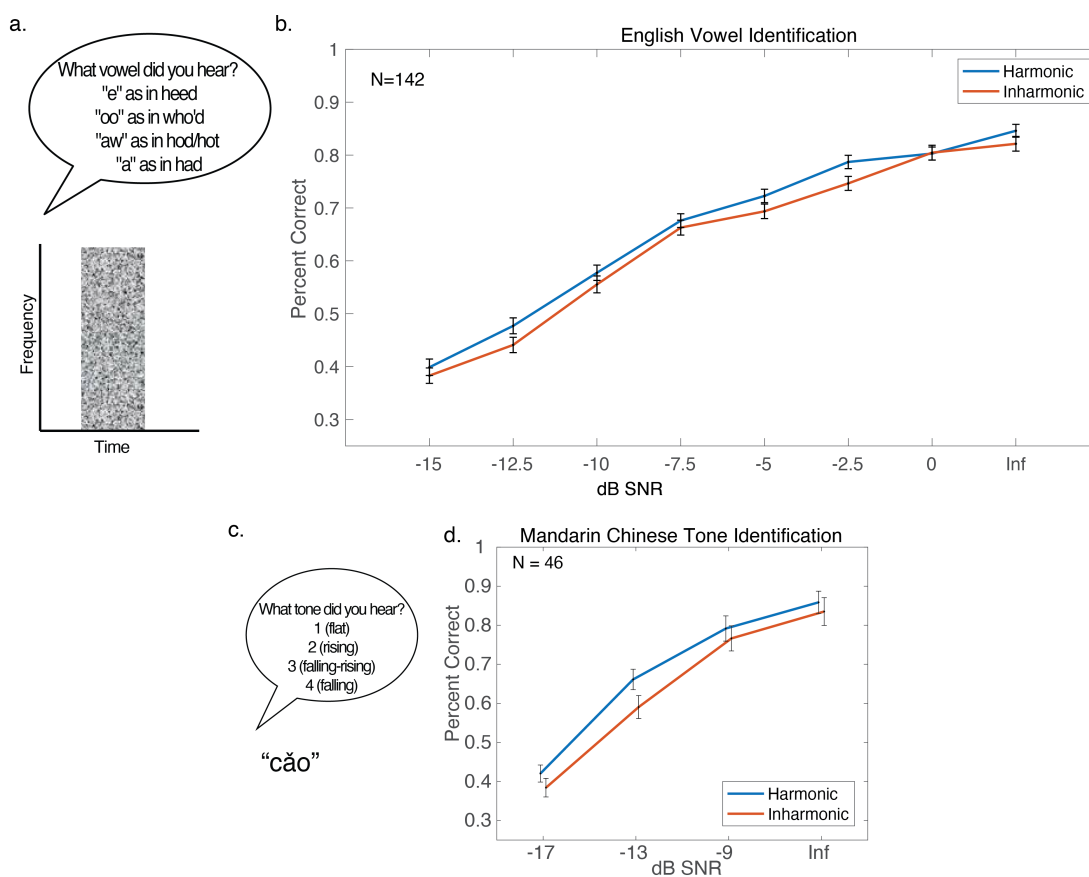


Figure 9: Harmonic advantage for identifying words in noise (Experiments 7 and 8)

a. Schematic of the trial structure for Experiment 7. During each trial, participants heard a noise burst which contained an English syllable and identified the vowel. b. Results from Experiment 7. Error bars denote standard error of the mean. c. Task for Experiment 8. During each trial, participants heard a noise burst which contained a single Mandarin Chinese word and were identified which of four tones they heard. d. Results from Experiment 7. Error bars denote standard error of the mean.

906

907

### Effects of Musicianship

908 Is the benefit of harmonicity influenced by musical experience? Musical training has been  
 909 proposed as beneficial for hearing speech in noise (Clayton et al., 2016; Coffey et al., 2017;  
 910 Parbery-Clark et al., 2011; Swaminathan et al., 2015), but evidence for such musicianship  
 911 advantages has been inconsistent (Boebinger et al., 2015; Madsen et al., 2019). It seemed  
 912 plausible that musicianship effects might relate to harmonicity. Harmonic structure is critical to  
 913 music – most musical instruments have harmonic frequency spectra, and the frequency ratios  
 914 between common intervals in standard Western scales (and other scales around the world) are  
 915 shared with the harmonic series. Musical training has been associated with the enhancement of  
 916 perceptual judgments related to harmonicity, with lower pitch discrimination thresholds (Bianchi  
 917 et al., 2016; Kishon-Rabin et al., 2001; McDermott, Keebler, et al., 2010; Micheyl et al., 2006;  
 918 Spiegel & Watson, 1984), and larger preferences for harmonic over inharmonic sounds in  
 919 musicians (Dellacherie et al., 2010; McDermott, Lehr, et al., 2010; Weiss et al., 2019), or in  
 920 individuals with lifelong exposure to Western music (McDermott et al., 2016; McPherson et al.,  
 921 2020). Consequently, musical training might enhance sensitivity to harmonic structure.

922 To assess effects of musicianship on our harmonicity effect, we tested approximately  
 923 equal numbers of musicians (individuals with four or more years of formal musical training) and  
 924 non-musicians (people with less than four years of formal musical instruction) in Experiments 1a  
 925 and 4 to have sufficient power to analyze the groups separately.

926 For Experiment 1a, we averaged across phase conditions and compared the harmonic  
 927 detection advantage for the two groups ([Inharmonic thresholds - Harmonic thresholds]). The  
 928 distributions of harmonic advantages were approximately normal, evaluated using the Lilliefors  
 929 test at a 5% significance level, so we used parametric tests. We observed no significant  
 930 differences between groups (Supplementary Fig 1a; musician mean advantage = 1.29 dB,  
 931 S.D.=0.92, non-musician mean advantage = 1.27 dB, S.D.1.32,  $t(96)=-0.15$ ,  $p=.88$ ). The Bayes  
 932 factor  $BF_{10}$ , specifying a multivariate Cauchy prior on the effects (Rouder et al., 2012)) was .24,  
 933 providing moderate support for the null hypothesis (*JASP, Version 0.13.1, 2020*).

934 We also examined the effects of musicianship in Experiment 4 (measuring pitch  
 935 discrimination). Consistent with many previous studies (Bianchi et al., 2016; Kishon-Rabin et al.,  
 936 2001; McDermott, Keebler, et al., 2010; Micheyl et al., 2006; Spiegel & Watson, 1984), pitch  
 937 discrimination was better in musicians than non-musicians (Supplementary Fig. 1b). While these  
 938 differences between musicians and non-musicians were significant by a sign test (mean  
 939 thresholds were higher in non-musicians for 16 of 21 conditions,  $p=.03$ ), they were modest, and  
 940 did not reach significance in an ANOVA (excluding the -22 and -20.5 dB SNR conditions, for which  
 941 we didn't measure Pure Tone thresholds,  $F(1,42)=1.66$ ,  $p=.20$ ,  $\eta_p^2=.04$ ). We also did not observe  
 942 a significant interaction between musicianship and harmonicity (only examining the Harmonic and  
 943 Inharmonic conditions, -20.5 dB SNR and greater,  $F(1,50)=0.04$ ,  $p=.84$ ,  $\eta_p^2<.001$ ). Moreover, the  
 944 Harmonic advantage for pitch discrimination was pronounced in both musicians and non-  
 945 musicians (significant main effect in each group, musicians:  $F(1,24)=124.33$ ,  $p<.0001$ ,  $\eta_p^2=.83$ ,  
 946 non-musicians  $F(1,26)=83.11$ ,  $p<.0001$ ,  $\eta_p^2=.76$ ). Given the lack of a musicianship effect in these

947 two experiments, we did not attempt to recruit equal numbers of musicians and non-musicians for  
 948 any other experiment. Overall, the results suggest that the effects of harmonicity are not strongly  
 949 dependent on musical experience.

950  
 951 **General Discussion**  
 952 We examined the effects of harmonicity on the discrimination and detection of sounds in noise.  
 953 Both detection and discrimination in noise were better for harmonic sounds, but the size of the  
 954 harmonic advantage varied across tasks. The largest benefits were evident for tasks involving up-  
 955 down discrimination with synthetic tones: both classic two-tone “pitch” discrimination and melodic  
 956 contour discrimination showed marked advantages for harmonic compared to inharmonic tones  
 957 when presented in noise, despite indistinguishable performance in quiet. We also found detection  
 958 benefits for harmonic tones in noise, as well as modest benefits for detecting and discriminating  
 959 harmonic speech. A model of energetic masking did not replicate the observed harmonic  
 960 detection benefits. Rather than being accounted for by energy or other cues traditionally  
 961 associated with detection in noise, our effects seem plausibly due to a noise-robust pitch signal.

962 Although effect sizes varied across tasks, they were large enough in several settings to  
 963 have relevance for real-world hearing. The harmonic advantage can be quantified in terms of  
 964 distance from a sound source in an environment with spatially uniform background noise. Our  
 965 results indicate that if a listener can just detect a harmonic tone 10 meters away from its source  
 966 in such a scene, they would have to move approximately 1.4 meters closer to the source to detect  
 967 a similar inharmonic sound. Similarly, if discriminating melodies, they would have to move  
 968 approximately 4 meters closer to the source to achieve comparable performance with inharmonic  
 969 notes. The consistency of the effects across musicians and non-musicians further suggests their  
 970 importance for everyday hearing. All together, these results represent a neglected aspect of  
 971 auditory scene analysis.

972  
 973 *A noise-robust pitch representation*

974  
 975 Our experiments build on a body of previous studies examining the basis of pitch discrimination.  
 976 We replicate previous findings that discrimination of tones in quiet is comparable for harmonic  
 977 and inharmonic tones (Faulkner, 1985; McPherson & McDermott, 2018; Micheyl et al., 2012;  
 978 Moore & Glasberg, 1990), likely driven by frequency shifts between notes (Demany & Ramos,  
 979 2005). However, when tones were presented in noise, we found pronounced discrimination  
 980 advantages for harmonic sounds compared to inharmonic sounds. These discrimination benefits  
 981 were not obviously explainable by the detection advantage we saw for harmonic tones – they  
 982 were present well above detection thresholds and remained evident even after the presentation  
 983 SNR was expressed relative to the detection threshold (thus accounting for the harmonic  
 984 advantage in detection). The results suggest that a pitch representation based on the  $f_0$  is more  
 985 noise-robust than that based on spectral features.

986 A noise-robust  $f_0$ -based pitch signal from harmonic sounds may help music and speech  
 987 sounds stand out in noisy backgrounds by contributing to their salience (Patterson, 1990). The  
 988 increased salience of harmonic sounds resulting from such an  $f_0$ -based pitch signal could account  
 989 for the harmonic detection advantage we observed. A role for an  $f_0$ -based pitch signal is also  
 990 consistent with the effects we observed on speech intelligibility – a pitch cue might be more  
 991 important for recognizing Mandarin tones than English vowels, consistent with the larger effect  
 992 for Mandarin compared to English (Experiment 8 vs. 7).

993 The noise-robustness of  $f_0$ -based pitch has been hinted at in several previous lines of  
 994 work. Several studies found that noise can help listeners hear out the  $f_0$  of tones with differing  
 995 spectral compositions, or non-simultaneous frequency components, compared to when such

996 tones are presented in quiet (Hall & Peters, 1981; Houtgast, 1976; Moore & Moore, 2003). The  
 997 current study complements these findings by contrasting judgments of harmonic and inharmonic  
 998 tones, and by using this contrast to show that representations of  $f_0$  facilitate the performance of  
 999 tasks in noisy conditions. We know of one study that compared discrimination of harmonic and  
 1000 inharmonic tones in noise, using an FM detection task (Carlyon & Stubbs, 1989), but they did not  
 1001 explore whether the effect of harmonicity could be explained by its effect on the detectability of  
 1002 the tones. Others have noted the robustness of complex tone discrimination to noise (Gockel et  
 1003 al., 2006; Moore & Glasberg, 1991), but did not compare harmonic with inharmonic tones to  
 1004 isolate representations of  $f_0$ .

1005 The observed harmonic discrimination advantages complement evidence for the  
 1006 importance of  $f_0$  in memory. A recent study found comparable harmonic and inharmonic pitch  
 1007 discrimination when tones were presented back-to-back, but better performance for harmonic  
 1008 tones if a short delay was inserted between tones, suggestive of a memory representation specific  
 1009 to harmonic sounds (McPherson & McDermott, 2020). Correlations between participants'  
 1010 thresholds for different delay and harmonicity conditions indicated that listeners rely on a  
 1011 representation of the spectrum when comparing sounds presented back-to-back, but switch to  
 1012 using a representation of the  $f_0$  when sounds have to be stored over time, perhaps because the  
 1013  $f_0$  provides an efficient representation. The current results suggest that hearing in noise is another  
 1014 domain in which a representation of a sound's  $f_0$  helps to discriminate pitch.

1015  
 1016 *(Non)-effects of phase and cueing*

1017  
 1018 We designed several stimulus manipulations to examine features other than  $f_0$ -based pitch that  
 1019 could possibly drive the observed harmonic advantage. Amplitude fluctuations seem unlikely to  
 1020 account for the results because detection thresholds were similar for sine and random phase  
 1021 tones (Experiment 1a). Moreover, the harmonic advantage appears to be absent for tones  
 1022 containing only unresolved harmonics, in which amplitude fluctuations should be maximally  
 1023 prominent (Experiment 3). It also appears that the results do not reflect listeners having a better  
 1024 sense of what to listen for on trials with harmonic sounds – the harmonic detection advantage  
 1025 persisted even when listeners were cued to the tone in noise (Experiment 2). The results of  
 1026 Experiments 1, 2, and 3 place constraints on the mechanisms underlying the harmonic detection  
 1027 advantage, and when combined with the observed advantage for tone and melody discrimination  
 1028 (Experiments 4 and 5), suggest that the harmonic advantage for detection may be driven by a  
 1029 pitch signal that enables harmonic tones to 'pop out' from noise.

1030  
 1031 *Comparisons to previous studies of harmonicity and speech*

1032  
 1033 One previous paradigm for examining the effects of harmonicity on auditory scene analysis  
 1034 measured recognition of pairs of synthetic vowels synthesized to be either harmonic or  
 1035 inharmonic. These studies found that when one vowel (the 'masker') was higher in level than  
 1036 another vowel (the 'target'), recognition of the target was better when the masker was harmonic  
 1037 rather than inharmonic. By contrast, recognition of the target (lower-amplitude) vowel did not  
 1038 depend on whether it was harmonic or not. This finding has been taken as support for the idea  
 1039 that the auditory system 'cancels' harmonic masking sounds in order to identify concurrent target  
 1040 sounds, rather than 'enhancing' harmonic targets themselves (de Cheveigne, Kawahara, et al.,  
 1041 1997; de Cheveigne et al., 1995; de Cheveigne, McAdams, et al., 1997). It is not obvious how to  
 1042 reconcile these findings with our effects showing benefits of harmonicity on the detection of target  
 1043 sounds, though we note that the setting is quite different (two concurrent tones rather than a tone  
 1044 in noise), such that there is no explicit inconsistency. We also note that we failed to observe

1045 comparable masker/target asymmetries in pilot experiments with natural speech resynthesized to  
1046 be harmonic or inharmonic. We found that participants presented with mixtures of harmonic and  
1047 inharmonic talkers more readily recognized harmonic speech than inharmonic speech regardless  
1048 of the harmonicity of the masker (i.e., the opposite of the result found in the original double vowel  
1049 experiments). It thus appears that harmonicity aids hearing in different ways depending on the  
1050 setting. In some cases it appears to allow distractor sounds to be more easily ignored or  
1051 suppressed, whereas in others it aids target sound detection. Future work involving models  
1052 optimized for natural auditory scene analysis may help to understand the basis of these disparate  
1053 effects.

1054 The modest effects of harmonicity on the recognition of speech in noise observed here  
1055 are consistent with two previous studies (Popham et al., 2018; Steinmetzger & Rosen, 2015). The  
1056 first study measured the intelligibility of speech with either harmonic or noise excitation presented  
1057 with various types of masking sounds (Steinmetzger & Rosen, 2015). They found benefits of  
1058 masker harmonicity, akin to the double vowel experiments discussed above, but little effect of the  
1059 harmonicity of the target speech. The second study found benefits of speech harmonicity when  
1060 speech was presented in babble but not when it was presented in noise (Popham et al., 2018).  
1061 This latter study used the same synthesis methods used here, and the results are consistent with  
1062 the small benefit of harmonicity on English vowel recognition in noise observed here.

1063

#### 1064 *Models of detection in noise*

1065

1066 We compared our measurements of human detection thresholds with those for a simple energetic  
1067 masking model of tone detection. Although our model replicated the difference between harmonic  
1068 complex tone and pure tone detection thresholds observed in practiced participants (Experiment  
1069 1c), and evident in previous work on masking (Buus et al., 1997; Dubois et al., 2011; Green, 1958,  
1070 1960), it did not replicate the effects of inharmonicity. Specifically, the model overestimated the  
1071 detectability of inharmonic tones. This finding provides additional evidence that tone-in-noise  
1072 detection is not entirely mediated by the energy cues formalized in this and previous models. It is  
1073 well established that pure tone detection thresholds are relatively unaffected by level differences  
1074 between the two stimulus intervals in a 2AFC paradigm, suggesting that listeners use some other  
1075 cue (Kidd Jr et al., 1989; Lentz et al., 1999; Leong et al., 2020; Maxwell et al., 2020) that happens  
1076 to be correlated with the signal-to-noise energy ratio. Our results suggest a cue that is aggregated  
1077 differently across frequency channels for harmonic vs. inharmonic tones, plausibly related to f0-  
1078 based pitch. Future modeling work should help distinguish these alternatives.

1079

#### 1080 *Validity of online data collection*

1081

1082 Due to the COVID-19 shutdown that occurred while we were completing this study, we relied  
1083 heavily on online data collection. Online experiments facilitate the recruitment of large numbers  
1084 of participants, but sacrifice control over experimental conditions. Compared with data collected  
1085 in person in a laboratory setting, there are fewer safeguards to ensure that participants are not  
1086 distracted and are complying with task instructions. Additional points of concern for  
1087 psychoacoustics in particular include lack of control over the participant's sound presentation  
1088 hardware and listening environment, lack of control over absolute sound levels, and the inability  
1089 to measure audiograms to confirm normal hearing. Here and in our previously published online  
1090 experiments we took several steps to mitigate the impact of these issues. First, we included a  
1091 headphone check pre-test to help ensure headphone or earphones are worn during the  
1092 experiment (Woods et al., 2017). Use of headphones/earphones should improve sound  
1093 presentation quality and attenuate noise. The headphone check also serves as a basic test of

1094 task compliance. Participants who fail this check do not proceed to the main experiment (typically  
1095 this is about a third of participants). Second, we ask participants to situate themselves in a quiet  
1096 environment to avoid distraction. Third, the experiment begins with a level calibration step in which  
1097 participants adjust the level of a calibration sound to a comfortable level. This helps ensure that  
1098 stimuli are audible. Fourth, participants are asked if they have hearing loss, and are excluded  
1099 from the main experiment if they self-report as such (in this study, about 9% of participants were  
1100 excluded on this basis, though most of them also failed the headphone check and would have  
1101 been excluded regardless). Fifth, we excluded participants whose performance was so poor as  
1102 to suggest that they had misunderstood the instructions or were otherwise non-compliant. Here  
1103 and in our previously published online experiments, the exclusion criterion was neutral with  
1104 respect to the hypotheses being tested, and independent of the data we analyzed, allowing  
1105 unbiased threshold estimates for the participants who were not excluded.

1106  
1107 Are these steps sufficient to reproduce results that one would obtain in the lab? Clearly there are  
1108 experiments that would not make sense to run online even with these precautions, such as those  
1109 that require precise control over absolute sound levels (Florentine, 1986; Hellman & Zwislocki,  
1110 1961; Traer et al., 2021). But in many cases, online experiments produce results that are  
1111 indistinguishable from those obtained in more controlled conditions. Our lab has made regular  
1112 use of online experiments since well before the pandemic, and has documented numerous  
1113 examples of experiments that have been run both online and in the lab. In all cases we have  
1114 found that online results replicate those obtained in the lab provided the precautions described  
1115 above are taken to help ensure sound presentation quality and participant compliance. These  
1116 paradigms include attentive tracking (Woods & McDermott, 2018), speech recognition in noise  
1117 (Kell et al., 2018), ratings of subjective continuity (McWalter & McDermott, 2019), judgments of  
1118 tonal fusion (McPherson et al., 2020), adaptive pitch discrimination thresholds (McPherson &  
1119 McDermott, 2020), and environmental sound recognition (Traer et al., 2021), among others.

1120  
1121 Detection-in-noise thresholds might be expected to be vulnerable to variation in sound  
1122 presentation given that they depend on the spectral content of the target and masker. To validate  
1123 our online threshold measurements, we compared them to those obtained in the lab prior to the  
1124 COVID-19 shutdown. In-lab measurements for matched experimental conditions produced similar  
1125 results to those obtained online (Fig. 2d). It appears that the inevitable participant-to-participant  
1126 variation in stimulus spectrum and levels that one faces with an online experiment do not have a  
1127 large effect on detection thresholds in noise, as with many other aspects of auditory perception  
1128 that we have measured in previous studies. We regard this general finding as indicative of a  
1129 strength of our field – perceptual science often involves robust effects. Careful control of stimuli  
1130 is desirable and important, but when one is forced to work through a pandemic, or when in need  
1131 of a particularly large sample, online experiments appear to be an adequate substitute in many  
1132 cases.

1133  
1134 *Future Directions*

1135  
1136 Our findings suggest that harmonic structure improves detection and discrimination of sounds in  
1137 noisy auditory scenes by providing a noise-robust pitch signal. The behavioral effects of  
1138 harmonicity evident in noisy conditions may be useful for studying representations of harmonicity.  
1139 For instance, detection tasks might be easily adapted to non-human animal models of hearing,  
1140 and could be used to further explore and understand cross-species similarities and differences in  
1141 the representations of harmonic sounds (Feng & Wang, 2017; Kalluri et al., 2008; Norman-  
1142 Haignere et al., 2019; Shofner & Chaney, 2013; Song et al., 2016; Walker et al., 2019). Another

1143 promising future direction may be to use the tasks developed here to search for neural signatures  
1144 of harmonicity tuning (by searching for differences in response to harmonic and inharmonic tones  
1145 in noise). It could also be informative to measure the harmonic detection advantage in individuals  
1146 with listening disorders, as its presence or absence might help pin down the origins of commonly  
1147 observed hearing-in-noise deficits (Boets et al., 2007; Cameron et al., 2006; Dole et al., 2012;  
1148 Lagace et al., 2010; Ziegler et al., 2009).  
1149

1150 **Data Availability and Open Practices Statement**

1151 All data are provided in the supplementary information files. None of the experiments were  
1152 preregistered.

1153

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