Efficient codes for memory determine pitch representations

Malinda J. McPherson[1,2] and Josh H. McDermott[1,2,3,4]

1 Department of Brain and Cognitive Sciences, MIT

2 Program in Speech and Hearing Biosciences and Technology, Harvard University

3 McGovern Institute for Brain Research, MIT

4 Center for Brains, Minds and Machines, MIT

Abstract

Perceptual systems have finite memory resources and must store incoming signals in compressed formats. To test whether representations of a sound's pitch might derive from this need for compression, we compared discrimination of harmonic and inharmonic sounds across delays. In contrast to inharmonic spectra, harmonic spectra can be summarized, and thus compressed, using their fundamental frequency (f0). Despite being comparable for sounds presented back-to-back, discrimination was better for harmonic than inharmonic stimuli when sounds were separated in time, implicating memory representations unique to harmonic sounds. Patterns of individual differences indicated that listeners use different representations depending on the time delay between sounds, directly comparing the spectra of temporally adjacent sounds, but transitioning to comparing f0s across delays. The need to compress sound into memory appears to determine reliance on f0-based pitch, and may explain its importance in music, in which listeners must extract relationships between notes separated in time.

Introduction

Our sensory systems transduce information at high bandwidths, but have limited resources to hold this information in memory. In vision, short-term memory is believed to store schematic structure extracted from image intensities, e.g. object shape, or gist, that might be represented with fewer bits than the detailed patterns of intensity represented on the retina (1-4). For instance, at brief delays visual discrimination shows signs of being based on image intensities, believed to be represented in high-capacity but short-lasting sensory representations (5). By contrast, at longer delays more abstract (6, 7) or categorical (8) representations are implicated as the basis of short-term memory.

In other sensory modalities the situation is less clear. Audition, for instance, is argued to also make use of both a sensory trace and a short-term memory store (9), but the representational characteristics of the memory store are not well characterized. There is evidence that memory for speech includes abstracted representations of phonetic features (10, 11) or categorical representations of phonemes themselves (12-14). Beyond speech, the differences between transient and persistent representations of sound remain unclear. This situation plausibly reflects a historical tendency within hearing research to favor simple stimuli, such as single frequencies, for which there is not much to abstract or compress. Such stimuli have been used to characterize the decay characteristics of auditory memory (15-18), its vulnerability to interference (19, 20), and the possibility of distinct memory resources for different sound attributes (21, 22), but otherwise place few constraints on the underlying representations.

Here we explore whether auditory perceptual representations could be explained in part by memory capacity limitations. One widely proposed auditory representation is that of pitch (23, 24). Pitch is the property which enables sounds to be ordered from low to high (25), and is a salient perceptual characteristic of voices, musical instrument notes, and some environmental sounds. Such sounds often contain frequencies that are harmonics – integer multiples of a single fundamental frequency (f0). Pitch is classically thought to be the perceptual correlate of this f0. Despite the prevalence of this idea in textbook accounts of pitch, there is surprisingly little direct evidence that listeners utilize representations of a sound's f0 when making judgments about pitch. For instance, discrimination of two harmonic sounds is normally envisioned to involve a comparison of estimates of the sounds' f0s (23, 26). But if the frequencies of the sounds are altered to make them inharmonic (lacking a single f0), discrimination remains accurate (26-29),

even though there are no f0s to be compared. This result is what would be expected if listeners were using the spectrum rather than the f0, e.g. by tracking shifts in harmonics between sounds (30). Although harmonic advantages are evident in some other tasks plausibly related to pitch perception (such as recognizing familiar melodies, or detecting out-of-key notes (29)), the cause of this task dependence remains unclear.

In this paper we consider whether these characteristics of pitch perception could be explained by memory constraints. One reason to estimate a sound's f0 might be that it provides an efficient summary of the spectrum: a harmonic sound contains many frequencies, but their values can all be predicted as integer multiples of the f0. This summary might not be needed if two sounds are presented back-to-back, as high-fidelity (but quickly-fading) sensory traces of the sounds could be compared. But it might become useful in situations where listeners are more dependent on a longer-lasting memory representation.

We explored this issue by measuring effects of time delay on discrimination. Our hypothesis was that time delays would cause discrimination to be based on auditory memory representations (16, 31). We tested pitch discrimination with harmonic and inharmonic stimuli, varying the length of silent pauses between sounds being compared. We predicted that if listeners summarize harmonic sounds with a representation of their f0, then performance should be better for harmonic compared to inharmonic stimuli. This prediction held across a variety of different types of sounds and task conditions, but only when sounds were separated in time. In addition, individual differences in performance across conditions indicate that listeners switch from representing the spectrum to representing the f0 depending on memory demands. Reliance on f0-based pitch thus appears to be driven in part by the need to compress sound into memory.

Results

Experiment 1: Discriminating instrument notes with intervening silence

We began by measuring pitch discrimination with and without an intervening delay between notes (Figure 1a), using recordings of real instruments that were resynthesized to be either harmonic or inharmonic (Figure 1b). We used real instrument sounds to maximize ecological relevance. Here and in subsequent experiments, sounds were made inharmonic by adding a random frequency 'jitter' to each successive harmonic; each harmonic could be jittered in frequency by up to 50% of the original f0 of the tone. Making sounds inharmonic renders them inconsistent with

any f0, such that the frequencies cannot be summarized by a single f0. The same pattern of random 'jitter' was added to each of the two notes in a trial. There was thus a direct correspondence between the frequencies of the first and second note even though the inharmonic stimuli lacked an f0.

Participants heard two notes played by the same instrument (randomly selected on each trial from the set of cello, baritone saxophone, ukulele, pipe organ, and oboe, with the instruments each appearing an equal number of times within a given condition). The two notes were separated by 0, 5, or 10 seconds of silence. Notes always differed by either a quarter of a semitone (~1.5% difference between the note f0s) or a half semitone (~3% difference between the note f0s). Participants judged whether the second note was higher or lower than the first.

We found modest decreases in performance for harmonic stimuli as the delay period increased (significant main effect of delay for both .25 semitone ($F(2,22)=25.19$, $p<.001$, $\eta_p^2=.70$, Figure 2c), and .5 semitone conditions ($F(2,22)=5.31$, $p<.05$, $\eta_p^2=.33$). This decrease in performance is consistent with previous studies examining memory for complex tones (20, 32). However, we observed a more pronounced decrease in performance for inharmonic stimuli, with worse performance compared to harmonic stimuli at both delays (5 seconds: $t(11)=4.48$, $p<.001$ for .25 semitone trials, $t(11)=2.12$, $p=.057$ for .5 semitone trials; 10 seconds: $t(11)=3.64$, $p<.01$ for .25 semitone trials, $t(11)=4.07$, $p<.01$ for .5 semitone trials) despite indistinguishable performance for harmonic and inharmonic sounds without a delay ($t(11)=0.43$, $p=.67$ for .25 semitone trials, $t(11)=-0.77$, $p=.46$ for .5 semitone trials). These differences produced a significant interaction between the effect of delay and that of harmonicity ($F(2, 22)=7.66$, $p<.01$, $\eta_p^2=.41$ for .25 semitone trials, $F(2, 22)=3.77$, $p<.05$, $\eta_p^2=.26$ for .5 semitone trials). This effect was present in both musicians and non-musicians (Supplementary Figure 1; averaging across the two difficulty conditions we found no main effect of musicianship: $F(1,10)=3.73$, $p=.08$, $\eta_p^2=.27$, and no interaction between musicianship, harmonicity and delay length $F(2,20)=0.58$, $p=.57$, $\eta_p^2=.06$), suggesting that the harmonic advantage is not dependent on extensive musical training. Overall, the results of Experiment 1 are consistent with the idea that a sound's spectrum can mediate pitch discrimination over short time intervals (potentially via a sensory trace of the spectrum), but that the memory of a sound's pitch over longer periods relies on a representation of f0.

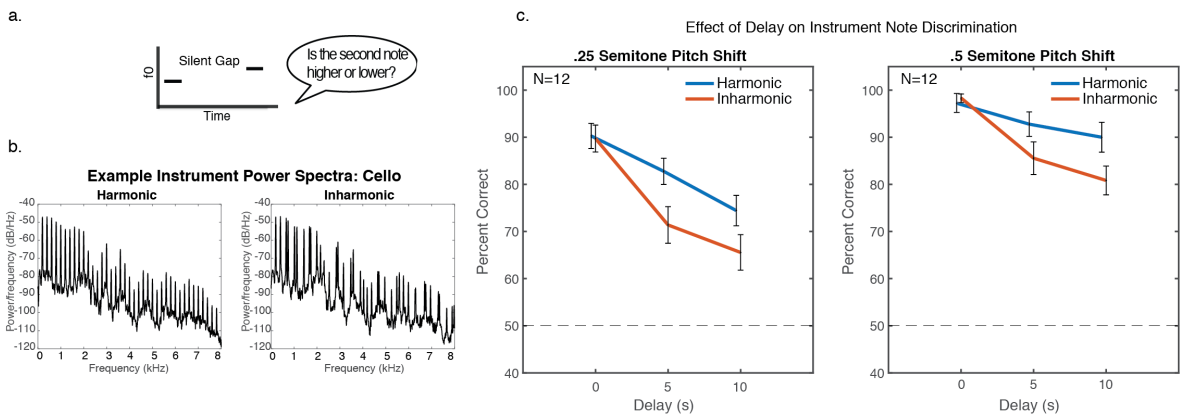


Figure 1. Experiment 1 – Harmonic advantage when discriminating instrument notes across a delay.

a. Schematic of trial structure for Experiment 1. During each trial, participants heard two notes played by the same instrument and judged whether the second note was higher or lower than the first note. Notes were separated by a delay of 0, 5, or 10 seconds. b. Power spectra of example harmonic and inharmonic (with frequencies jittered) notes from a cello. c. Results of Experiment 1 plotted separately for the two difficulty levels that were used. Error bars plot standard error of the mean.

Experiment 2: Discriminating synthetic tones with intervening silence

We replicated and extended the results of Experiment 1 using synthetic tones, the acoustic features of which can be more precisely manipulated. We generated complex tones that were either Harmonic or Inharmonic, applying fixed bandpass filters to all tones in order to remove coarse spectral cues that could otherwise be used to detect pitch changes (Figure 2a). The first audible harmonic of these tones was generally the 4th harmonic (though could be the 3rd or 5th, depending on the f0 or jitter pattern). To gauge the robustness of the effect across difficulty levels, we again used two different f0 differences (.25 and .5 semitones).

To further probe the effect of delay on representations of f0, we included a third condition ('Interleaved Harmonic') where each of the two tones on a trial contained half of the harmonic series (Figure 2a). One tone always contained harmonics [1, 4, 5, 8, 9, etc.], and the other always contained harmonics [2, 3, 6, 7, 10, etc.] (26). The order of the two sets of harmonics was randomized across trials. This selection of harmonics isolates f0-based pitch by eliminating common harmonics between the tones to be compared. While in the Harmonic and Inharmonic conditions listeners could use the correspondence of the individual harmonics to perform a pitch

comparison, in the Interleaved Harmonic condition there is no direct correspondence between harmonics present in the first and second notes, such that the task can only be performed by estimating and comparing the f0s of the tones. By applying the same bandpass filter to each Interleaved Harmonic tone we sought to minimize timbral differences that are known to impair f0 discrimination (33). Masking noise was included in all conditions to prevent distortion products from being audible, which might otherwise be used to perform the task.

As in Experiment 1, Harmonic and Inharmonic tones were similarly discriminable with no delay (Figure 2b; $t(24)=-0.72$, $p=.48$ for .5 semitone trials, $t(24)=0.09$, $p=.93$ for .25 semitone trials). Discrimination thresholds were comparable to previous measurements for stimuli with resolved harmonics (34, 35). However, performance with Inharmonic tones was again significantly worse with a delay (5-second delay: $t(24)=4.61$ $p<.001$ for .25 semitones, $t(24)=4.96$, $p<.0001$ for .5 semitones; 10-second delay: $t(24)=4.92$, $p<.0001$ for .25 semitones, $t(24)=6.11$, $p<.0001$ for .5 semitones), yielding interactions between delay and harmonicity ($F(2,48)=10.71$, $p<.001$, $\eta_p^2=.31$ for .25 semitones, $F(2,48)=26.17$, $p<.0001$, $\eta_p^2=.52$ for .5 semitones).

Performance without a delay was worse for Interleaved Harmonic tones than for the regular Harmonic and Inharmonic tones, but unlike those other two conditions, Interleaved Harmonic performance did not deteriorate significantly over time (Figure 2b). There was no main effect of delay for either .25 semitones ($F(2,48)=1.23$, $p=.30$, $\eta_p^2=.05$) or .5 semitones ($F(2,48)=2.56$, $p=.09$, $\eta_p^2=.10$), in contrast to the significant main effects of delay for Harmonic and Inharmonic conditions at both difficulty levels ($p<.001$ in all cases). This pattern of results is consistent with the idea that there are two representations that listeners could use to discriminate pitch: a sensory trace of the spectrum which decays quickly over time, and a representation of the f0 which is better retained over a delay. The spectrum can be used in the Harmonic and Inharmonic conditions, but not in the Interleaved Harmonic condition.

As in Experiment 1, the effects were qualitatively similar for musicians and non-musicians (Supplementary Figure 2). Although there was a significant main effect of musicianship ($F(1,23)=10.28$, $p<.01$, $\eta_p^2=.99$), there was no interaction between musicianship, stimulus type (Harmonic, Inharmonic, Interleaved Harmonic), and delay length ($F(4,92)=0.19$, $p=.94$, $\eta_p^2=.01$).

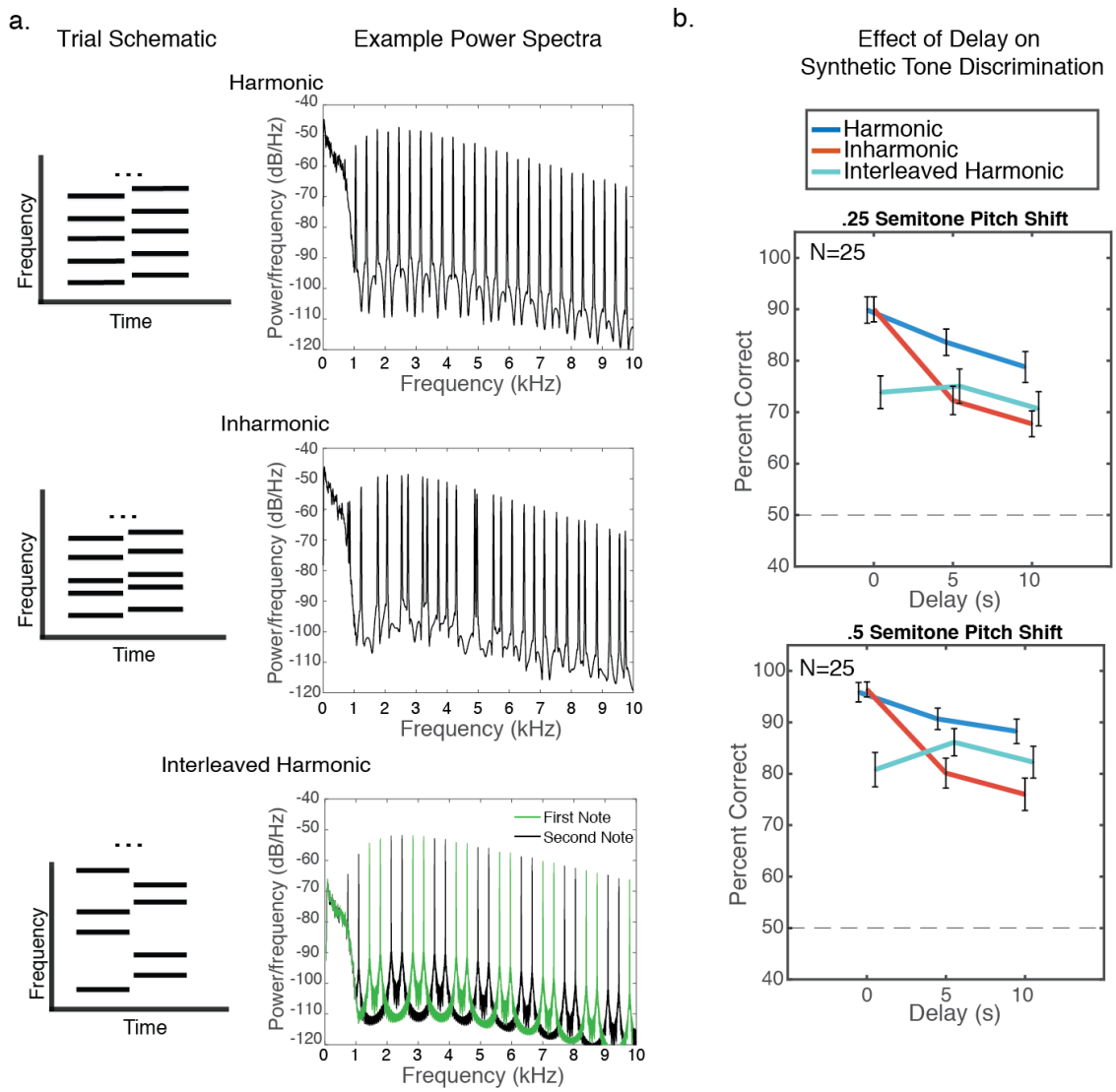


Figure 2. Experiment 2 – Harmonic advantage when discriminating synthetic tones across a delay.

a. Schematic of stimuli and trial structure in Experiment 2. Left: During each trial, participants heard two tones and judged whether the second was higher or lower than the first. Tones were separated by a delay of 0, 5, or 10 seconds. Right: Power spectra of example notes from Harmonic, Inharmonic, and Interleaved Harmonic conditions. d. Results of Experiment 2, plotted separately for the two difficulty levels that were used. Error bars plot standard error of the mean.

Experiment 3: Discriminating synthetic tones with a consistent inharmonic spectrum

The purpose of Experiment 3 was to examine the effects of the specific inharmonicity manipulation used in Experiments 1 and 2. In Experiments 1 and 2, we used a different inharmonic

jitter pattern for each trial. In principle, listeners might be able to learn a spectral pattern if it repeats across trials (36, 37), such that the harmonic advantage found in Experiments 1 and 2 might not have been due to harmonicity per se, but rather to the fact that the harmonic pattern occurred repeatedly whereas the inharmonic pattern did not. In Experiment 3 we compared performance in a condition where the jitter pattern was held constant across trials ('Inharmonic-Fixed') vs. when it was altered every trial (though the same on the two notes of a trial) as in the previous experiments ('Inharmonic').

Unlike the first two experiments we used adaptive procedures to measure discrimination thresholds. The transition to adaptive threshold measurements avoided difficulties associated with choosing pitch differences appropriate for the anticipated range of performance across the conditions. Participants completed 3-down-1-up two-alternative-forced-choice ('is the second tone higher or lower than the first') adaptive threshold measurements. Tones were either separated by no delay, a 1-second delay, or a 3-second delay (Figure 3a). There were three different stimulus conditions: Harmonic tones (as in Experiment 2), Inharmonic tones where the jitter changed for every trial (as in Experiment 2), and Inharmonic-Fixed tones where the jitter pattern was fixed across a block of adaptive runs. Participants completed four adaptive runs for each delay and stimulus pair. Harmonic, Inharmonic and Inharmonic-Fixed conditions were each blocked; the delay conditions were intermixed within a block, resulting in 12 adaptive runs per block (Figure 3b), with approximately 60 trials per run on average. The order of these three blocks was randomized across participants. This design does not preclude the possibility that participants might learn a repeating inharmonic pattern given even more exposure to it, but it puts the inharmonic and harmonic tones on equal footing, testing whether the harmonic advantage might be due to relatively short-term learning of the consistent spectral pattern provided by harmonic tones.

As shown in Figure 3c, thresholds were matched for all conditions with no delay (no significant difference between any of the conditions ($Z<1.61$, $p>.11$ for all pairwise comparisons, Wilcoxon sign rank test, used because the distribution of thresholds was non-normal). However, thresholds were elevated (worse) for both the Inharmonic and Inharmonic-Fixed conditions with even a 1 second delay (Inharmonic: $Z=2.86$, $p<.01$; Inharmonic-Fixed: $Z=2.19$, $p<.05$), and were much worse in both conditions with a 3-second delay (Inharmonic: $Z=3.98$, $p<.0001$; Inharmonic-Fixed: $Z=2.52$, $p<.05$). We again observed no interaction between musicianship, stimulus type

(Harmonic, Inharmonic, Inharmonic-Fixed), and delay length ($F(4,84)=1.05$, $p=.39$, $\eta_p^2=.05$, see Supplementary Figure 3).

There was not a significant effect of the type of inharmonicity ($F(1,22)=.07$, $p=.78$, $\eta_p^2=.003$, comparing Inharmonic vs. Inharmonic-Fixed conditions), providing no evidence that participants learn to use specific jitter patterns over the course of a typical experiment duration. The harmonic advantage cannot be explained by the consistency of the harmonic spectral pattern across trials, as making the inharmonic spectral pattern consistent did not reduce the effect. Given this result, in subsequent experiments we opted to use 'Inharmonic' rather than 'Inharmonic-Fixed' stimuli, to avoid the possibility that the results might otherwise be biased by the choice of a particular jitter pattern.

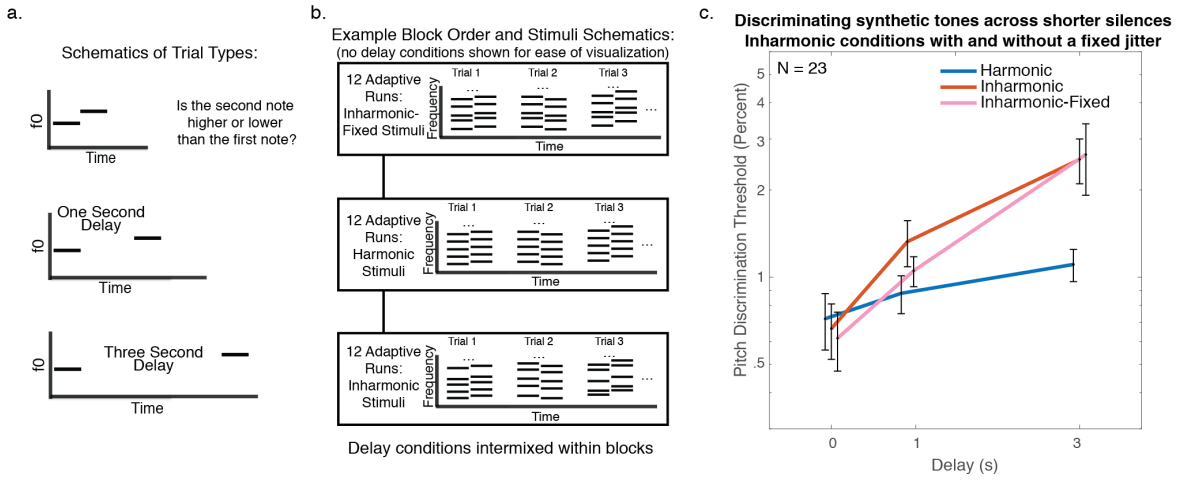


Figure 3. Experiment 3 – Harmonic advantage persists for consistent inharmonic jitter pattern. a. Schematic of trial structure for Experiment 3. Task was identical to that of Experiments 1 and 2, but with delay durations of 0, 1 and 3 seconds, and adaptive threshold measurements rather than method of constant stimuli. b. Example block order for Experiment 3, in which the 12 adaptive runs for each condition were presented within a contiguous block. The beginning of an example run is shown schematically for each type of condition. Stimulus conditions (Harmonic, Inharmonic, Inharmonic-Fixed) were blocked. Note the difference between the Inharmonic-Fixed condition, in which the same jitter pattern is used across all trials within a block, and the Inharmonic condition, in which the jitter pattern is different on every trial. Delay conditions were intermixed within each block. c. Results of Experiment 3. Error bars plot within-subject standard error of the mean.

Experiment 4: Discriminating synthetic tones with a longer inter-trial interval

To assess whether the inharmonic deficit could somehow reflect interference from successive trials (38) rather than the decay of memory during the inter-stimulus delay, we replicated Experiment 3 with a longer inter-trial interval. We included only the Harmonic and Inharmonic conditions, with and without a 3 second delay between notes. For each condition participants completed four adaptive threshold measurements without any enforced delay between trials, and four adaptive thresholds where we imposed a 4 second inter-trial interval (such that the delay between trials would always be at least 1 second longer than the delay between notes of the same trial). This experiment was run online because the lab was temporarily closed due to the COVID-19 virus.

The results were similar irrespective of the inter-trial interval. We found no significant interaction between inter-trial interval, within-trial delay, and Harmonic vs. Inharmonic stimuli ($F(1,25)=0.05$, $p=.82$, $\eta_p^2=.002$, Supplementary Figure 4). This result suggests that the inharmonic deficit is due to difficulties retaining the tones during the delay period, rather than some sort of interference from preceding stimuli.

Experiments 5.1 and 5.2: One-shot discrimination with a longer intervening delay

Experiments 1-4 leave open the possibility that listeners might use active rehearsal of the stimuli (singing to themselves) to perform the task over delays. Although prior results suggest that active rehearsal does not obviously aid pitch discrimination over delays (16, 39), it could in principle explain the harmonic advantage on the assumption that it is more difficult to rehearse an inharmonic stimulus, and so it seemed important to address. To assess whether the harmonic advantage reflects rehearsal, we ran two “one-shot” online experiments with much longer delay times, during which participants filled out a demographic survey. We assumed this unrelated task would prevent them from actively rehearsing the heard tone. These experiments were run online to recruit the large number of participants needed to obtain sufficient power. We have previously found that online participants can perform about as well as in-lab participants (37, 40) provided basic steps are taken to help ensure reasonable sound presentation (41).

Each participant completed only two trials in the main experiment. One trial had no delay between notes, as in the 0s delay conditions of the previous experiments. During the other trial participants heard one tone, then were redirected to a short demographic survey, and then heard the second tone (Figure 4a). The order of the two trials was randomized across participants. For each

participant, both trials contained the same type of tones, randomly assigned. For Experiment 5.1, the tones were either Harmonic, Inharmonic, or Interleaved Harmonic (each identical to the tones used in Experiment 2). The two tones always differed in f0 by a semitone. The discrimination task was described to participants at the start of the experiment, such that participants knew they should try to remember the first tone before the survey and that they would be asked to compare it to a second tone heard after the survey. After participants had finished both trials of the experiment, they completed an additional short task originally intended to screen for poorly performing participants. In this task, participants completed 40 up/down discrimination trials – Harmonic and Inharmonic tones separated by 1 semitone in pitch and no delay in time.

For both experiments we ran a large number of participants to obtain sufficient power given the small number of trials per participant. Participants completed the survey at their own pace. We measured the time interval between the onset of the first note before the survey and the onset of the second note after the survey. Prior to analysis we removed participants who completed the survey in under 20 seconds (proceeding through the survey so rapidly as to suggest that the participant did not read the questions; 1 participant), or participants who took longer than 3 minutes (12 participants). Of the remaining 801 participants across both experiments, the mean time spent on the survey was 61.2 seconds (standard deviation of 25.9, median of 55.1 seconds and median absolute deviation of 19.0 seconds. There was no significant difference between the time taken for each of the conditions ($Z<=1.13$, $p>=.10$ for all pairwise comparisons).

As shown in Figure 4b, Experiment 5.1 qualitatively replicated the results of Experiments 1 and 2 even with the longer delay period and concurrent demographic survey. Performance in the Inharmonic condition was worse with the delay than without a delay ($p<.001$, via bootstrap), whereas performance in the Harmonic and Interleaved Harmonic conditions was similar with and without a delay (Harmonic with vs. without delay: $p=.30$; Interleaved Harmonic with vs. without delay: $p=.36$). Moreover, performance in the Harmonic condition was better than that in the Inharmonic condition only with a delay ($p<.001$), producing an interaction between the type of tone and the delay ($p=.02$).

One surprising aspect of these results is that performance for harmonic tones was no worse with the (long) delay between tones. We suspect this is related to the relatively low overall performance – pitch discrimination with a one-semitone difference is normally easy for typical human listeners.

To get insight into this issue, we analyzed the additional task completed after the two main experimental trials. This additional task was identical to that of the no-delay trial of the main experiment, but with 40 trials (half with Harmonic and half with Inharmonic tones). Performance was 83.9% correct on average (Supplementary Figure 5a) – substantially higher than the average performance on the single no-delay trial with Harmonic and Inharmonic stimuli (71.5%). This difference suggests that the absence of practice trials (intended to avoid putting the delay and no-delay conditions on unequal footing) reduced performance on the two test trials, potentially particularly limiting performance without a delay. Regardless of the explanation, this issue cannot account for the critical interaction between delay and harmonicity that we observed here as in the previous experiments.

Experiment 5.2 was identical to Experiment 5.1 except the stimuli were Harmonic and Inharmonic Shepard tones (42). These tones had only one frequency component per octave, rendered either in perfect octave relations (Harmonic) or with the component frequencies jittered (Inharmonic). In the latter case frequencies were each jittered by a random amount between half an octave up or down (uniformly distributed). This experiment was intended as a replication of Experiment 5.1 with somewhat different stimuli. We saw a similar effect as in Experiment 5.1 (Supplementary Figure 5b) – discrimination of harmonic tones was similar with and without the delay (p=.13), but performance for inharmonic tones was worse with the delay (p=.032).

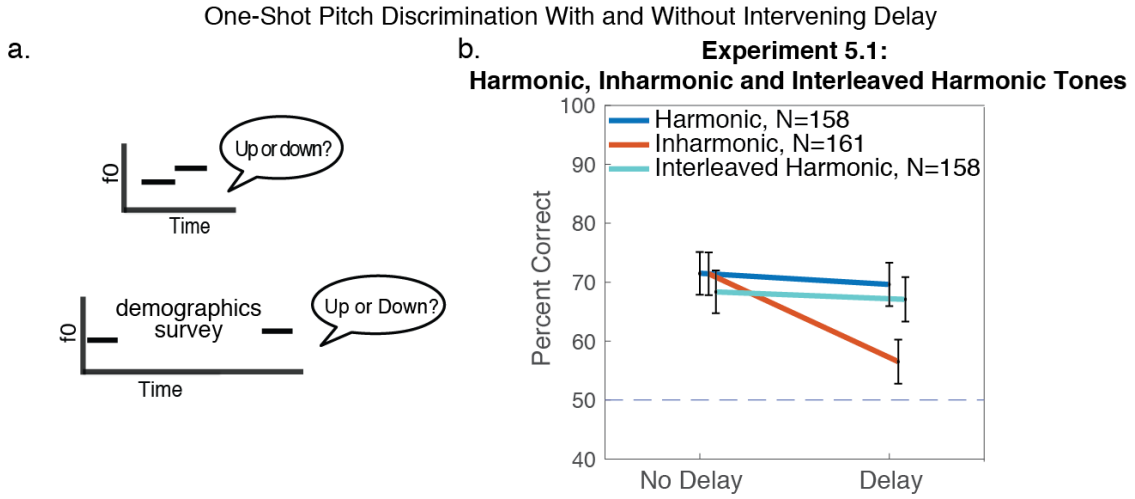


Figure 4. Experiment 5 – Harmonic advantage persists over longer delays with intervening task. a. Schematic of the two trial types in Experiment 5. Task was identical to that of Experiment 2, however for the 'delay' condition participants were redirected to a short demographic survey that they could complete at their own pace. b. Results of Experiment 5.1 (which had the same stimulus conditions as Experiment 2). Error bars plot standard error of the mean, calculated via bootstrap.

Experiment 6: Individual differences in pitch discrimination

The similarity in performance between harmonic and inharmonic tones without a delay provides circumstantial evidence that listeners are computing pitch changes in the same way for both types of stimuli, presumably using a representation of the spectrum in both cases. However, the results leave open the alternative possibility that listeners use a representation of the f0 for the harmonic tones despite having access to a representation of the spectrum (which they must use with the inharmonic tones), with the two strategies happening to support similar accuracy.

To address these possibilities, and to explore whether listeners use different pitch encoding strategies depending on memory constraints, we employed an individual differences approach (43, 44). The underlying logic is that performance on tasks that rely on the same perceptual representations should correlate across participants. Thus, if two discrimination tasks rely on similar representations, a participant with a low threshold on one task should tend to have a low threshold on the other task.

In Experiment 6, we estimated participants' pitch discrimination thresholds either with or without a 3-second delay between stimuli, using a 3-down-1-up adaptive procedure (Figure 5a). Stimuli included Harmonic, Inharmonic, and Interleaved Harmonic complex tones, generated as in Experiments 2-5. We used Inharmonic stimuli for which a different pattern of jitter was chosen for each trial (as opposed to the Inharmonic-Fixed stimuli from Experiment 3, where one pattern was used for all trials), because Experiment 3 showed similar results whether the inharmonic pattern was consistent or not, and because it seemed better to avoid a consistent jitter. Specifically, it seemed possible that fixing the jitter pattern across trials for each participant might create artifactual individual differences given that some jitter patterns are by chance closer to harmonic than others. Having the jitter pattern change from trial to trial produces a similar distribution of stimuli across participants and averages out the effect of idiosyncratic jitter patterns. We also tested Pure tones, and a fifth condition where each note contained two randomly chosen harmonics from each successive set of four (1 to 4, 5 to 8, etc.). By chance, some harmonics could be found in both notes. This condition (Random Harmonic) was intended as an internal

replication of the anticipated results with Interleaved Harmonics.

The main hypothesis we sought to test was that listeners use different representations of sound with and without a delay. The key predictions of this hypothesis are that listeners should use 1) the same representation for Harmonic and Inharmonic discrimination without a delay (indicated by high correlations between these two conditions), 2) different representations for Harmonic and Inharmonic discrimination with a delay (lower correlation), 3) different representations for Interleaved Harmonic discrimination compared to the other two conditions with no delay (because it requires a representation of the f0), but 4) similar representations for Interleaved Harmonic and Harmonic discrimination over a delay.

We ran this study online to recruit sufficient numbers to measure the correlations of interest. This experiment was relatively long and difficult (it took approximately 2 hours to complete), and based on pilot experiments we anticipated that many online participants would perform poorly relative to in-lab participants. To obtain a criterion level of performance with which to determine inclusion for online participants, we ran 10 participants in the lab to establish acceptable performance levels. We calculated the overall mean threshold from the best three of four runs from the in-lab data for all conditions without a delay (five conditions), and excluded online participants whose mean threshold on the first run of those same 5 conditions (without a delay) were above this mean in-lab performance level. To avoid non-independence, we analyzed only the three subsequent threshold measurements from online participants. This inclusion procedure selected 160 of 450 participants for the final analyses shown in Figure 5b-e. See Supplementary Figure 6 for in-lab results and Supplementary Figure 7 for results with a less stringent inclusion criteria (the main effects remain unchanged with this less stringent criteria).

Mean Thresholds

The pattern of mean threshold measurements obtained online qualitatively replicated the results of Experiments 1-5 (Figure 5b). Inharmonic thresholds were indistinguishable from Harmonic thresholds without a delay ($Z=1.28$, $p=.20$), but were higher when there was a delay between sounds ($Z=-8.83$, $p<.0001$). This produced a significant interaction between effects of tone type and delay ($F(1,159)=80.84$, $p<.0001$, $\eta_p^2=.34$). And as in the previous experiments, there was no significant effect of delay for the Interleaved Harmonic condition (Interleaved Harmonic condition with vs. without delay; $Z=-0.06$, $p=.96$).

Individual Differences – Harmonic, Inharmonic and Interleaved Harmonic conditions

As shown in Figure 5c, thresholds were correlated to some extent for all pairs of conditions, presumably reflecting general factors such as attention or motivation that produce variation in performance across participants. However, some correlations were higher than others. Figure 5d plots the correlations for which our hypothesis makes critical predictions. Correlations here and elsewhere were corrected for the reliability of the threshold measurements (45), and thus could in principle be as high as 1 in the limit of large data. Because the threshold reliabilities were calculated from noisy threshold estimates, the corrected correlations could in practice slightly exceed 1.

Across participants, performance on Harmonic and Inharmonic conditions was highly correlated without a delay (rho=.89, p<.001). However, the correlation between Harmonic and Inharmonic conditions decreased with a delay (r=.71, p<.001, significant difference between correlations with and without a delay, p<.05, calculated via bootstrap). We observed the opposite pattern for the Harmonic and the Interleaved Harmonic conditions: the correlation was lower without a delay (r=.70, p<.001), and increased with a delay (r=.90, p<.001, significant difference between correlations, p<.05). This pattern of results yielded a significant interaction between the conditions being compared and the effect of delay (difference of differences between correlations with and without a delay = 0.38, p<.01). Overall, the results of the individual differences analysis indicate that when listening to normal harmonic tones, participants switch between two different pitch mechanisms depending on whether they are reliant on memory.

Results with Pure Tones and Random Harmonic Condition

The results for Pure Tones were similar to those for the Harmonic condition (Figure 5e), with quantitatively indistinguishable mean thresholds (without delay: Z=0.95, p=.34, with delay: Z=-0.85, p=.39). Moreover, the correlations between Harmonic and Pure Tone thresholds were high both without and with a delay, and not significantly different (p=.52). These results suggest that similar representations are used to discriminate pure and harmonic complex tones. In addition the correlations between the Pure Tone condition and the Inharmonic and Interleaved Harmonic conditions showed a similar pattern to that for the Harmonic condition, producing a significant interaction between the conditions being compared and the effect of delay (difference of differences between correlations with and without a delay = 0.32, p<.05).

The Random Harmonic results largely replicated the findings from the Interleaved Harmonic condition (Figure 5c). Evidently the changes that we introduced in the harmonic composition of the tones being compared in this condition were sufficient to preclude the use of

the spectrum, and, as in the Interleaved Harmonic condition, performance was determined by f0-based pitch regardless of the delay between notes.

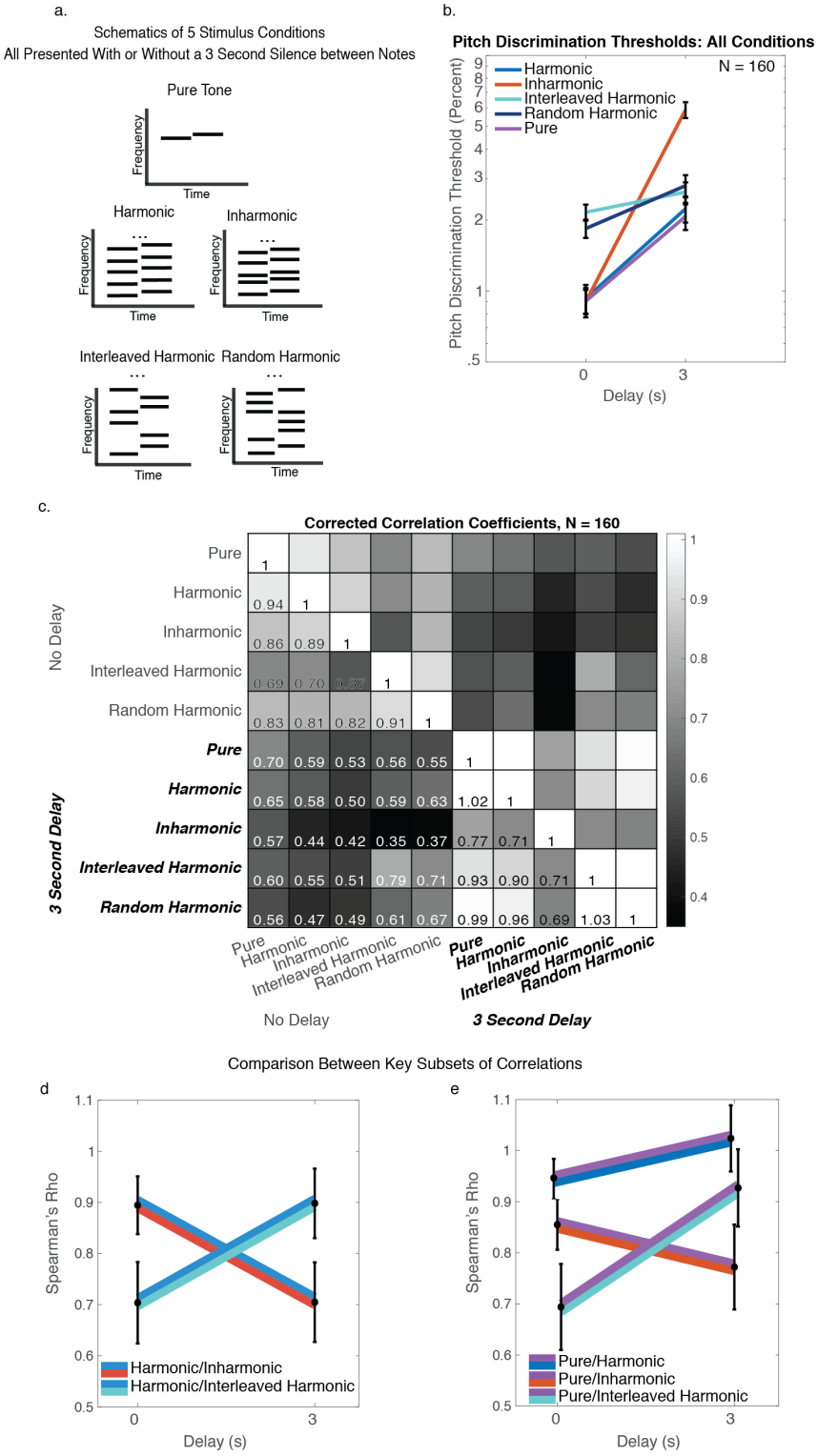


Figure 5. **Experiment 6 – Individual differences suggest different pitch representations depending on memory demands.**

a. Schematic of the five types of stimuli used in Experiment 6. Task and procedure (adaptive threshold measurements) were identical to those of Experiment 4, but with no inter-trial delays. b. Discrimination thresholds for all stimulus conditions, with and without a 3-second delay between tones. Here and in panels d-e, error bars plot standard error of the mean, calculated via bootstrap. c. Matrix of the correlation between thresholds for all pairs of conditions. Correlations are Spearman's rho, corrected for the reliability of the threshold measurements (i.e., corrected for attenuation). Corrected correlations can slightly exceed 1 given that they are corrected with imperfect estimates of the reliabilities. d. Comparison between Harmonic/Inharmonic and Harmonic/Interleaved Harmonic threshold correlations, with and without a delay. e. Comparison between Pure Tone condition correlation with and without a delay.

Discussion

We examined the relationship between pitch perception and memory by measuring pitch discrimination with and without a time delay between stimuli. Across several experiments, we found that discrimination across a delay was better for harmonic sounds than for inharmonic sounds, despite being comparably accurate without a delay. This effect was observed over delays of a few seconds and persisted over longer delays with an intervening distractor task. We also analyzed individual differences in pitch discrimination thresholds across a large number of participants. This analysis showed that harmonic and inharmonic discrimination thresholds were highly correlated without a delay between sounds, but were less so with a delay. By contrast, thresholds for harmonic tones and tones designed to isolate f0-based discrimination showed the opposite pattern, becoming more correlated with a delay between sounds. Together, the results suggest that listeners use different representations depending on memory demands, comparing spectra for sounds nearby in time, and the f0 for sounds separated in time. The results provide evidence for multiple pitch mechanisms, reveal the constraints that determine when they are used, and demonstrate a form of abstraction within the auditory system whereby the representations of memory differ in format from those used for rapid on-line judgments about sounds.

Although the harmonic series imposes mathematical regularity on sound frequencies that is preserved to some extent by the peripheral auditory system (46), it is unclear whether this regularity is essential to the memory benefit we describe here. Harmonic sounds may be more

easily remembered simply because they are prevalent in the environment, such that humans have acquired representational transforms to efficiently represent them (e.g. by projection onto harmonic templates) (47). In an alternate world in which vocalizations or other musical sounds all had a particular inharmonic spectral pattern, we might develop efficient representations of their spectrum instead (48), conferring a memory advantage even in the absence of harmonicity.

Why don't listeners base pitch judgments of harmonic sounds on their f0s when sounds are back-to-back? One possibility is that representations of f0 are in some cases less accurate and produce poorer discrimination than those of the spectrum if memory is not involved. The results with interleaved harmonics (stimuli designed to isolate f0-based pitch) are consistent with this idea, as discrimination without a delay was worse for interleaved harmonics than for either harmonic or inharmonic tones that had similar spectral composition across notes (we note that this deficit could also reflect other stimulus differences, such as the potentially interfering effects of the changes in the spectrum from note to note). The fact that performance with interleaved harmonics was similar with and without modest delays suggests that representations of the f0 are initially available in parallel with representations of the spectrum, with task demands determining which is used in the service of behavior. As time passes the high-fidelity representation of the spectrum appears to degrade, and listeners switch to more exclusively using a representation of the f0.

In hearing research, the word 'pitch' has traditionally referred to the perceptual correlate of the f0 (24). Here we presented evidence that listeners rely on a representation of the spectrum in some cases where scientists have presumed them to use the f0. However, under normal conditions (where sounds are harmonic) the note-to-note changes in the spectrum convey changes in f0, and thus help listeners make judgments about the f0 even though the f0 is apparently not explicitly represented. Consistent with this idea, listeners readily describe what they hear in the Inharmonic conditions of our experiments as a pitch change, as though the consistent shift in the spectrum is interpreted as a change in the f0. We thus propose that these spectral judgments should be considered part of pitch perception, which we construe to be the set of computations that enable judgments about a sound's f0.

Relation to previous studies of pitch and pitch memory

The use of time delays to study memory for frequency and/or pitch has a long tradition (49, 50). Our results here are broadly consistent with this previous work, but to our knowledge provide the

first evidence for differences in how representations of the f0 and the spectrum are retained over time. A number of studies have examined memory for tones separated by various types of interfering stimuli, and collectively provide evidence that the f0 of a sound is retained in memory. For example, intervening sounds interfere most with discrimination if their f0s are similar to the tones being discriminated, irrespective of whether the intervening sounds are speech or synthetic tones (21), and irrespective of the spectral content of the intervening notes or the two comparison tones (20). Our results complement these findings by showing that memory for f0 has different characteristics from that for frequency content (spectra), in showing how these differences impact pitch discrimination, and in suggesting that memory for f0 should be viewed as a form of compression. We also show that introducing a delay between notes forces listeners to use the f0 rather than the spectrum, which may be useful in experimentally isolating f0-based pitch in future studies.

Relevance of f0-based pitch to music

F0-based pitch seems to be particularly important in music perception, evident in prior results documenting the effect of inharmonicity on music-related tasks. Melody recognition, “sour” note detection, and pitch interval discrimination are all worse for inharmonic compared to harmonic tones, in contrast to other tasks such as up/down discrimination which can be performed equally well for both types of tones (29). Our results here provide a potential explanation for these effects. Music often requires notes to be compared across delays or intervening sounds, as when assessing a note’s relation to the tonic (51), and the present results suggest that this should necessitate f0-based pitch. Musical pitch perception may have come to rely on representations of f0 as a result, such that even in musical tasks that do not involve storage across a delay, such as musical interval discrimination, listeners use f0-based pitch rather than the spectrum (29). It is possible that similar effects occur for other patterns that occur frequently in music, such as common chords.

Given its evident role in music perception, it is natural to wonder whether f0-based pitch is honed by musical training. Western-trained musicians are known to have better pitch discrimination than Western non-musicians (52-54). But previous studies examining effects of musicianship on pitch discrimination used either pure tone or harmonic tone stimuli, and thus do not differentiate between representations of the f0 vs. the spectrum. We found consistent overall pitch discrimination advantages for musicians compared to non-musicians (Supplementary Figures 1-

3), but found no evidence that this benefit was specific to f0 representations: musicianship did not interact with the effects of inharmonicity or inter-stimulus delay. It is possible that more extreme variation in musical experience might show f0-specific effects. For instance, indigenous cultures in the Amazon appear to differ from Westerners in basic aspects of pitch (55) and harmony perception (56, 57), raising the possibility that they might also differ in the extent of reliance on f0-based pitch. It is also possible that musicianship effects might be more evident if memory were additionally taxed with intervening distractor tones.

Abstraction in perception and memory

Perception is often posited to involve inferences of parameters that capture how a stimulus was generated (58). Such parameters can also provide compressed representations of sensory signals. Efficient coding has been proposed as a way to estimate generative parameters (59, 60), and aspects of auditory representations (61) and discrimination (62) can be explained as consequences of efficient coding. Our results further link efficient coding to audition via memory. We provide an example of abstract and compressed auditory memory representations that are plausibly domain-general, and in doing so explain some otherwise puzzling results in pitch perception (chiefly, the fact that conventional pitch discrimination tasks often do not tap into f0-based pitch).

Memory could be particularly important in audition given that sound unfolds over time, with the structures that matter in speech, music, and other domains often extending over many seconds. Other examples of auditory representations that discard details in favor of more abstract structures include the pitch “contour” of melodies, that listeners retain in some conditions in favor of the exact pitch intervals between notes (63), or summary statistics of sound textures that average across temporal details (64). These representations may reflect memory constraints involved in comparing two extended stimuli even without a pronounced inter-stimulus delay.

Future directions

Our results leave open how the two representations implicated in pitch judgments are instantiated in the brain. Pitch-related brain responses measured in humans have generally not distinguished representations of the f0 from that of the spectrum (65-69), in part because of the coarse nature of human neuroscience methods. Moreover, we know little about how pitch representations are stored over time in order to mediate discrimination across a delay. In non-human primates there

is evidence for representations of the spectrum of harmonic complex tones (70) as well as of their f0 (71), though there is increasing evidence for heterogeneity in pitch across species (72-76). Neurophysiological and behavioral experiments with delayed discrimination tasks in non-human animals could shed light on these issues.

Our results also indicate that we unconsciously switch between representations depending on the conditions in which we must make pitch judgments (i.e., whether there is a delay between sounds). One possibility is that sensory systems can assess the reliability of their representations and base decisions on the representation that is most reliable for a given context. Evidence weighting according to reliability is a common strategy in perceptual decisions (77), and our results raise the possibility that such frameworks could be applied to understand memory-driven perceptual decisions.

Another open question concerns the role of f0-based encoding in speech and voice perception (78). Previous results suggest that f0 partially underlies recognition of familiar voices (29), potentially indicating another domain where f0-based compression aids memory. However, memory for speech, and for music, is not limited to the f0 (79-81). Our results suggest that examining the effects of memory on tasks in these domains could help to understand the underlying perceptual representations.

Methods

Participants.

All experiments were approved by the Committee on the use of Humans as Experimental Subjects at the Massachusetts Institute of Technology, and were conducted with the informed consent of the participants.

Musicianship: Across all experiments, musicians were defined as individuals with five or more years of self-reported musical training and/or active practice/performance. Non-musicians had four or fewer years of self-reported musical training and/or active practice/performance.

Experiment 1: 16 participants were recruited for Experiment 1. 4 of these scored less than 60% correct across all conditions and their data was removed. The remaining participants (N=12, 5 female, mean age = 42.5 years, S.D. = 19 years) included 6 non-musicians and 6 musicians (24.5 years of training and active performance, S.D. = 16).

Experiment 2:

34 participants were recruited for Experiment 2. 2 of these did not finish the experiment, and their data was not analyzed. Of the remaining 32 participants, 7 scored less than 60% correct across all conditions and were removed. The remaining participants (N=25, 12 female, mean age= 31.4 years, S.D.=14.7 years) included 10 non-musicians and 15 musicians (mean=16 years of musical training and active performance, S.D.=12.2 years).

Experiment 3: 35 participants were recruited for Experiment 3. 3 of these did not complete the experiment or were removed for non-compliance. An additional 9 participants were removed from analysis because their average threshold across the first run of each condition was greater than 3% (approximately half a semitone). The remaining participants (N=23, 9 female, mean age=36.0 years, S.D.=16.6 years) included 11 non-musicians and 12 musicians (mean=17.1 years of musical training and active, S.D.=13.5)

Experiment 4: 50 participants were recruited online for Experiment 4. 24 participants were removed from analysis because their average threshold across the first run of each condition was greater than 3% (approximately half a semitone). The remaining participants (N=26, 13 female,

mean age=38.5 years, S.D.=13.1 years) included 15 non-musicians and 10 musicians (mean=8.9 years of musical training and active, S.D.=3.1).

Experiment 5.1-5.2: Before analysis, we removed the participants who completed the demographic survey (the intervening task that all participants completed between presentations of the first and second notes in the 'delay' condition) in either less than 20 seconds, which we believed made it unlikely that those participants read and paid attention to all the questions, or greater than 3 minutes. 1 and 12 participants were excluded via these criteria, respectively. After these exclusions, 477 people completed experiment 5.1 (186 female, mean age = 36.7 years, S.D. = 12.2 years), and 324 people completed experiment 5.2 (137 female, mean age = 37.9 years, S.D. = 12.3 years). Of the total 801 participants, 383 reported some form of musical training, and 171 of those reported greater than four years of training (mean=13.7 years, S.D.=11.9 years).

Experiment 6: 10 participants were recruited for the in-lab baseline for Experiment 6 (5 female, mean age=34.1, S.D.=13.8, 6 had over 4 years of musical training, mean=18.3 years, S.D.=7.8 years).

450 participants were recruited for the online component of Experiment 6. 290 were removed from analysis because their average threshold (across all 5 conditions) on the first run of the no-delay trials was greater than the in-lab average for those same conditions (2.47%). The remaining set of 160 participants (71 female, mean age=25.3 years, S.D.=9.1 years) included 110 who reported some form of musical training, and 72 participants who reported greater than four years of musical training (mean=10.9 years, S.D.=6.9 years).

Audio Presentation: In-Lab.

In all experiments, a MacMini computer running Psychtoolbox for MATLAB (82) was used to play sound waveforms. Sounds were presented to participants at 70 dB over Sennheiser HD280 headphones (circumaural) in a soundproof booth (Industrial Acoustics). Participants logged their responses via keyboard press.

Audio Presentation: Online.

We used the crowdsourcing platform provided by Amazon Mechanical Turk to run experiments that necessitated large numbers of participants (Experiments 5 and 6), or when in-person data collection was not possible due to the COVID-19 virus (Experiment 4). Each participant in these studies used a calibration sound to set a comfortable level, and then had to pass a "headphone check" experiment that helped ensure they were wearing headphones or earphones as instructed (41) before they could complete the full experiment. The experimental stimuli were set to 15.5 dB below the level of the calibration sound, to ensure that stimuli were never uncomfortably loud. Participants logged their responses by clicking buttons on their computer monitors using their mouse.

Feedback.

Feedback (correct/incorrect) was given after each trial for all tasks except for the two test trials of Experiment 5.1-5.2.

Experiment 1: Discriminating instrument notes with intervening silence

Procedure: Participants heard two instrument notes per trial, separated by varying amounts of silence (0, 5, and 10 seconds) and judged whether the second note was higher or lower than the first note. Participants heard 30 trials per condition, and all conditions were intermixed. The first stimulus for a trial began one second after the response was entered for the previous trial, such that there was at least a 1-second gap between successive trials.

Stimuli: Instrument notes were derived from the RWC Instrument database, which contains recordings of chromatic scales played on different instruments (83). We used recordings of baritone saxophone, cello, ukulele, pipe organ and oboe, chosen to cover a wide range of timbres. Instrument tones were manipulated using the STRAIGHT analysis and synthesis method (84-86). STRAIGHT is normally used to decompose speech into excitation and vocal tract filtering, but can also decompose a recording of an instrument into an excitation signal and a spectrotemporal filter. If the voiced part of the excitation is modeled sinusoidally, one can alter the frequencies of individual harmonics, and then recombine them with the unaltered instrument body filtering to generate inharmonic notes. This manipulation (86) leaves the spectral shape of the instrument largely intact. Previous studies with speech suggest that intelligibility of inharmonic speech is comparable to that of harmonic speech (87). The frequency jitters for inharmonic instruments were chosen in the same way as the jitters for the inharmonic synthetic tones used in Experiments

2-6 (described below). The same pattern of jitter was used for both notes in a trial. STRAIGHT was also used to pitch shift the instrument notes to create pairs of notes that differed in f0 by a specific amount. Audio was sampled at 16,000 Hz. All notes were 400 ms in duration and were windowed by 20 ms half-Hanning windows.

Each trial consisted of two notes. The second note differed from the first by .25 or .5 semitone. To generate individual trials, the f0 of the first note of each trial was randomly selected from a uniform distribution over the notes in a Western classical chromatic scale between 196 and 392 Hz (G3 to G4). A recording of this note, from an instrument selected from the set of 5 that were used (baritone saxophone, cello, ukulele, pipe organ and oboe), was chosen as the source for the first note in the trial (instruments were counterbalanced across conditions). If the second note in the trial was higher, the note 1 semitone above was used to generate the second note (the note 1 semitone lower was used if the second note of the trial was lower). The two notes were analyzed and modified using the STRAIGHT analysis and synthesis method[39,37,38]; the notes were pitch flattened to remove any vibrato, shifted to ensure that the pitch differences would be exactly the intended pitch difference apart, and resynthesized with harmonic or inharmonic excitation. Some instruments, such as the ukulele, have slightly inharmonic spectra. These slight inharmonicities were removed for the 'harmonic' conditions due to the resynthesis.

Stimuli for Experiments 2-6.

Experiments 2, 3, 4, 5.1, and 6 used the same types of tones. The stimuli for Experiment 5.2 are described below. Synthetic complex tones were generated with exponentially decaying temporal envelopes (decay constant of 4 s^{-1}) to which onset and offset ramps were applied (20 ms half-Hanning window). The sampling rate was 16,000 Hz for Experiment 2, and 48,000 for all others. Tones included all harmonics up to the Nyquist limit, in sine phase, and were always 400 ms in duration.

In order to make notes inharmonic, the frequency of each harmonic, excluding the fundamental, was perturbed (jittered) by an amount chosen randomly from a uniform distribution, $U(-.5, .5)$. This jitter value was chosen to maximally perturb f0. Jitter values were multiplied by the f0 of the tone, and added to the frequency of the respective harmonic. For example, if the f0 was 200 Hz and a jitter value of -0.39 was selected for the second harmonic; its frequency would be set to 322 Hz. To minimize salient differences in beating, jitter values were constrained (via rejection sampling)

such that adjacent harmonics were always separated by at least 30 Hz. The same jitter pattern was applied to every note of the stimulus for a given trial, such that the spectral pattern shifted coherently up or down even in the absence of an f0. Except for the Inharmonic-Fixed condition of Experiment 3, where one random jitter pattern was used for entire blocks of the experiment, a new jitter pattern was chosen for each trial.

Each complex tone was band-pass filtered in the frequency domain with a Gaussian transfer function (in log frequency) centered at 2,500 Hz with a standard deviation of half an octave. This filter served to ensure that participants could not perform the tasks using changes in the spectral envelope, and also to minimize timbral differences between notes in the Interleaved Harmonic condition. The filter parameters were chosen to ensure that the f0 was attenuated (to eliminate variation in a spectral edge at the f0) while preserving audibility of resolved harmonics (harmonics below the 10th, approximately).

To ensure that differences in performance for Harmonic and Inharmonic conditions could not be mediated by distortion products, we added masking noise to these bandpass filtered notes. We low pass filtered pink noise using a sigmoidal (logistic) transfer function in the frequency domain. The sigmoid had an inflection point at the third harmonic of the highest of the two notes on a trial, and a maximum slope yielding 40 dB of gain or attenuation per octave. We scaled the noise so that the noise power in a gammatone filter centered at the f0 was 10dB lower than the mean power of the three harmonics of the highest note of the trial that were closest to the 2,500Hz peak (and thus had greatest magnitude) of the Gaussian spectral envelope (29). This noise power is sufficient to mask distortion products at the f0 (88, 89). This filtered and scaled pink noise was added to each note, and did not continue through the silence in 'delay' conditions.

Experiment 2: Discriminating synthetic tones with intervening silence

Procedure: Procedure was identical to Experiment 1, except stimuli were synthetic tones.

Stimuli: Each trial consisted of two notes, described above in **Stimuli for Experiments 2-6**. The second tone differed from the first by .25 or .5 semitones. The first note of each trial was randomly selected from a uniform distribution on a logarithmic scale spanning 200 to 400 Hz. Tones were either Harmonic, Inharmonic, or Interleaved Harmonic. Interleaved Harmonic notes were synthesized by removing harmonics [1,4, 5, 8, 9, etc.] in one note, and harmonics [2, 3, 6, 7, etc.]

in the other note. They were otherwise identical to the Harmonic tones (identical bandpass filter in the frequency domain, as well as noise to mask a distortion product at the fundamental). This manipulation was intended to isolate f0-based pitch, as it removes the note-to-note spectral correspondence between harmonics.

Experiment 3: Discriminating synthetic tones with a consistent inharmonic spectrum

Procedure: Participants heard two notes per trial, separated by varying amounts of silence (0, 1 and 3 seconds) and were asked whether the second note was higher or lower than the first note. Unlike Experiments 1 and 2, which used the method of constant stimuli, participants completed 2-up-1-down adaptive threshold measurements for each condition. Each run was initialized at a 1-semitone pitch difference and ended after 10 reversals. For the first 4 reversals, the f0 changed by a factor of 2, and for subsequent reversals by a factor of sqrt(2). Each adaptive run was initialized at an f0 difference of 1 semitone (approximately 6%), and the maximum f0 difference was limited to 16 semitones. The adaptive procedure proceeded if participants reached this 16 semitone limit; if they continued to get trials incorrect the pitch difference would not increase above the 16 semitone limit, and if they got two in a row right, the pitch difference would decrease from 16 semitones by a factor of 2 or sqrt(2), depending on how many reversals had already occurred. In practice participants who hit this limit repeatedly were removed before analysis due to our exclusion criteria. Thresholds were estimated by taking the average of the final 6 reversals. The first stimulus for a trial began one second after the response was entered for the previous trial, such that there was at least a 1-second gap between successive trials.

Stimuli: Each trial consisted of two notes, described above in **Stimuli for Experiments 2-6**. The first note of each trial was randomly selected from a uniform distribution on a logarithmic scale spanning 200 to 400Hz. Tones were either Harmonic, Inharmonic, or Inharmonic-Fixed, separated into three blocks, the order of which was counterbalanced across participants. Participants completed 12 adaptive thresholds within each block (3 delay conditions x 4 runs per condition). For the Inharmonic-Fixed block, a random jitter pattern was chosen at the beginning of the block and used for every trial within the entire block.

Experiment 4: Discriminating synthetic tones with a longer inter-trial interval

Procedure: The procedure for Experiment 4 was identical to Experiment 3, except that the experiment was run on Amazon Mechanical Turk, with different time intervals between trials.

Participants completed two sets of adaptive threshold measurements. In the first, trials were initiated by the participant, and could begin as soon as they entered the response for the previous trial and clicked a button to start the next trial. Four adaptive threshold measurements per condition were taken in this way (Harmonic and Inharmonic stimuli both with and without a 3-second delay). In the second set, a mandatory 4-second pause inserted between each trial, which could be initiated by the participant once the pause had elapsed. Four threshold measurements for the same conditions were taken in this way. The two sets of measurements were randomly intermixed.

To perform adaptive procedures online, stimuli were pre-generated (instead of being generated in real-time as was done for the in-lab studies). For each condition and possible f0 difference, the stimuli were drawn randomly from a set of 20 pre-generated trials (varying in the f0 of the first note, and in the jitter pattern for the Inharmonic trials).

Stimuli: Stimuli were identical to the Harmonic and Inharmonic conditions in Experiment 3.

Experiment 5.1, 5.2: One-shot discrimination with longer intervening delay

Procedure. Participants were recruited using the Amazon Mechanical Turk crowdsourcing platform. Each participant completed two types of trials. In the first type of trial, they heard two consecutive notes and were asked whether the second note was higher or lower than the first. Notes were always separated in pitch by a semitone. They were allowed to listen to the trial twice before responding. For the second type of trial, participants were allowed to hear one note twice, then were directed to a demographic survey. Before the presentation of the first note participants were told that they would be subsequently asked whether a note heard after the survey was higher or lower in pitch than the note heard before the survey. After the survey, participants were presented with the second note (they could again listen to the note twice), and were asked to respond. Each participant heard the same stimulus type (Harmonic, Inharmonic, etc.) for each of the two trials. The order of the trials (with and without the intervening survey) was randomized across participants. Participants initiated the second trial by clicking a button after they entered their response for the first trial. For the trials with the demographic survey, we collected time stamps of when participants heard the first and second note in order to calculate the delay between notes. After completing the two trials and the survey, participants completed 40 up/down discrimination trials without a delay, half with Harmonic and half with Inharmonic tones. The pitch

difference in all trials was 1 semitone. The purpose of this task was to estimate baseline performance for each participant. We originally planned to use this to exclude poorly performing participants, but ended up using it as a comparison for the two main experimental trials, as described in the Results section.

Stimuli. Stimuli for Experiment 5.1 were identical to those used in Experiments 2-4 (Harmonic, Inharmonic and Interleaved Harmonic conditions). Stimuli for Experiment 5.2 were Shepard tone stimuli generated by adding sine waves separated by octaves, then passing the resulting complex tones through the same fixed filter used in 5.1 (described above in **Stimuli for Experiments 2-6**), and adding the same type of low pass masking noise (calculated as if all the harmonics were present). To make Shepard tones inharmonic, we jittered each frequency by up to half an octave up or down, with jitter values chosen from a uniform distribution on a logarithmic frequency scale.

Experiment 6: Individual differences in pitch discrimination

Procedure: Both in lab and on Mechanical Turk, participants completed 2-up-1-down adaptive threshold measurements. The instructions were to judge whether the second note was higher or lower than the first note. The adaptive procedure was identical to that used in the first set of threshold measurements of Experiment 4 (each trial could be initiated by the participant as soon as they had entered their response for the previous trial). For the in-lab participants, we used the best three runs from each condition to set the inclusion criteria for online studies. For online participants, the first run of each condition was used to determine inclusion, and the final three runs of each condition were used for analysis. The order of the adaptive runs was randomized for each participant. There were 4 runs for each of the 10 conditions, for a total of 40 adaptive runs, randomized in order for each participant. Participants received feedback after each trial.

Stimuli: Participants in lab and online were tested on 5 different types of stimuli, presented either with no delay or a 3-second delay between tones (10 conditions). The five types of stimuli were as follows:

(1) Harmonic, (2) Inharmonic, and (3) Interleaved Harmonic, all identical to the same conditions in Experiment 2. (4) Pure Tones: We used the 4th harmonic of the f0 (f0*4) so that the stimuli would overlap in frequency with the complex tones used in other conditions, which were filtered so that first audible harmonic was generally the 3rd or 4th harmonic. Low pass masking noise was omitted from the Pure condition given that distortion products were not a concern. (5) Random

Harmonic: For each note, two harmonics were randomly chosen from harmonics 1 to 4, 5 to 8, etc. By chance, some harmonics could be present in both notes. This manipulation was intended to be intermediate between the Harmonic and Interleaved Harmonic conditions.

In all conditions, the f0 of the initial tone for each trial was chosen randomly from a from a uniform distribution on a logarithmic scale spanning 200-400 Hz.

As in Experiment 4, stimuli were pre-generated to enable online threshold measurements. For each condition and possible f0 difference, the stimuli were drawn randomly from a set of 20 pre-generated trials (varying in the f0 of the first note, and in the jitter pattern for the inharmonic conditions).

Sample Sizes.

Experiments 1 and 2: A power analysis of pilot data for Experiments 1 and 2 showed an effect size of d=1.25 for the difference between harmonic and inharmonic conditions at 5 seconds. We thus aimed to run at least 6 musicians and 6 non-musicians to be able to analyze the two groups separately and have an 80% chance of detecting the harmonic advantage at a $p<.05$ significance level (using paired t-tests). Power analyses for Experiments 1-4 and Experiment 6 (in lab baseline) used G*Power (90). Experiment 2 was run in combination with other experiments (not described here) that were not as well powered and required more data, hence the additional participants.

Experiment 6 (in-lab baseline): A pilot experiment for the in-lab portion of Experiment 6 showed an effect size of $d=1.32$ for the difference for the best three runs of 17 pilot participants between Harmonic and Inharmonic thresholds with a delay. Thus, for the in-lab portion of Experiment 6 we aimed to run at least 6 participants in order to be 80% sure of seeing an effect this size at a $p<.05$ significance level (using a one-sided Wilcoxon signed-rank test).

Experiments 3 and 4: Experiments 3-4 used the same basic method as Experiment 6, with the addition of a 1-second-delay condition and the Fixed-Jitter condition (Experiment 3) and inter-trial delays (Experiment 4). We used the same pilot data described above for Experiment 6 (in-lab baseline), but with the exclusion criteria to be used for Experiments 3-4, eliminating participants whose average threshold across the first run of each condition was greater than 3%

(approximately half a semitone). This eliminated 6 of 17 pilot participants, and the resulting effect size for the Harmonic-Inharmonic difference at a 3-second delay was d=1.49. Based on the rough intuition that the effect of the Inharmonic-Fixed manipulation or the inter-trial delay might produce an effect approximately half this size, we sought to be 80% likely to detect an effect half as big as that observed in our pilot data, at a $p<.05$ significance (using a two-sided Wilcoxon signed-rank test). This yielded a target sample size of 17 participants. We did not plan to recruit equal numbers of musicians and non-musicians due to the similarity between groups in Experiments 1-2.

Experiment 5: Experiment 5 used stimuli similar to those of Experiment 2 (same tones but a larger pitch difference: 1 semitone in Experiment 5 compared to .25 and .5 semitones in Experiment 2), but had a one-shot design (each participant only had two trials, one without a delay and one with a delay). To approximate the number of participants needed we bootstrapped using data from Experiment 2, treating each trial as an independent participant and estimating data distributions using different numbers of sampled trials. For each possible sample size we computed the bootstrap distribution of the difference in performance between the Harmonic and Inharmonic conditions with a delay, as well as a null distribution obtained with conditions permuted across participants. We sought the sample size yielding an 80% chance of seeing a significant Harmonic-Inharmonic difference (i.e. where 95% of the bootstrap samples showed a difference exceeding the 97.5th percentile of the null distribution), yielding a target sample size of 151 participants in each condition. We made no attempt to recruit equal numbers of musicians and non-musicians, as we did not plan to analyze those groups separately given the similar results across groups observed in the experiments we ran prior to this.

Experiment 6, Online Participants: For the online portion of Experiment 6, we performed a power analysis by bootstrapping pilot data (an earlier version of Experiment 6 with slightly different stimuli). For each of a set of sample sizes we computed bootstrap distributions of the interaction term (difference of differences between the conditions being compared, Harmonic/Inharmonic and Interleaved-Harmonic), as well as null distributions obtained by permuting conditions across participants. We found that a sample size of 154 yielded a 90% chance of seeing the interaction present in our pilot data at a $p<.05$ significance level. We ran more than this number of participants to allow performance-based exclusion. As with Experiments 3-5, we made no attempt to recruit equal numbers of musicians and non-musicians.

Statistics.

For Experiments 1, 2 and 5 we calculated percent correct for each condition. For Experiments 1 and 2, data was evaluated as normal by eye and significance was calculated using paired t-tests and repeated-measures ANOVAs. We used mixed-model ANOVAs to examine the effects of musicianship (to compare within- and between-group effects).

For Experiment 5, the significance of the differences between conditions and the significance of interactions were calculated via bootstrap (10,000 samples). To calculate the significance of the interaction between conditions, we first calculated the interaction (the difference of differences in means with and without a delay). For instance, for the Harmonic and Inharmonic conditions this term is as follow:

$$(\mu_{Harmonic}^{no-delay} - \mu_{Harmonic}^{delay}) - (\mu_{Inharmonic}^{no-delay} - \mu_{Inharmonic}^{delay})$$

Then, we approximated a null distribution for this interaction, permuting conditions across participants and recalculating the difference of differences 10,000 times. To determine statistical significance we compared the actual value of the interaction to this null distribution.

Data distributions were non-normal (skewed) for threshold experiments (Experiments 3,4 and 6), so non-parametric tests were used for all comparisons. Wilcoxon signed-rank tests were used for pairwise comparisons between dependent samples (for example, two conditions for the same participant group). To compare performance across multiple conditions or across musicianship we used F statistics for repeated-measures ANOVAs (for within group effects) and mixed-model ANOVAs (to compare within and between group effects). However, because data were non-normal, we evaluated the significance of the F statistic with approximate permutation tests, randomizing the assignment of the data points across the conditions being tested 10,000 times, and comparing the F statistic to this distribution.

We used Spearman's rank correlations to examine individual differences in Experiment 6. Correlations were corrected for the reliability of the threshold measurements using the Spearman correction for attenuation (45). We used standardized Cronbach's alpha as a measure of reliability (91, 92), calculating the reliability across the 3 analyzed adaptive track runs for each condition. Standard errors for correlations were estimated by bootstrapping the correlations 10,000 times. To calculate the significance of the interaction between conditions, we first calculated the

interaction (the difference of differences). For instance, for the Harmonic and Inharmonic conditions, this term was:

$$(r_{s_{Harmonic}}^{no-delay} - r_{s_{Harmonic}}^{delay}) - (r_{s_{Inharmonic}}^{no-delay} - r_{s_{Inharmonic}}^{delay})$$

Then, we approximated a null distribution for this interaction, permuting conditions across participants and recalculating the difference of differences 10,000 times. To determine statistical significance we compared the actual value of the interaction to this null distribution.

Acknowledgements

The authors thank R. Grace, S. Dolan, and C. Wang for assistance with data collection, and L. Demany, and the entire McDermott Lab for comments on the full manuscript. The work was supported by the McDonnell Foundation Scholar Award and NIH grant No. R01DC014739 to J.H.M. and NIH grant F31DCO18433 and a NSF Graduate Research Fellowship to M.J.M. The funding agencies were not otherwise involved in the research, and any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the McDonnell Foundation, NIH, or NSF.

Author Contributions

M.J.M. designed the experiments, collected and analyzed the results, made the figures, and wrote the paper. J.H.M. designed the experiments and wrote the paper.

Declaration of Interests

The authors declare no competing interests.

References

1. Bartlett FC (1932) *Remembering: A Study in Experimental and Social Psychology* (Cambridge University Press).

2. Phillips WA (1974) On the distinction between sensory storage and short-term visual memory. *Percept. Psychophys.* 16(2):283-290.

3. Jiang Y, Olson IR, & Chun MM (2000) Organization of visual short-term memory. *Journal of Experimental Psychology: Learning, Memory and Cognition* 26(3):683-702.

4. Brady TJ, Konkle T, & Alvarez G (2009) Compression in visual working memory: Using statistical regularities to form more efficient memory representations. *Journal of Experimental Psychology: General* 138(4):487-502.

5. Sperling G (1960) The information available in brief visual presentations. *Psychological Monographs* 74(11):1-29.

6. Posner MI (1969) Abstraction and the process of recognition. *Psychology of learning and motivation: Advances in research and theory*, eds Spence JT & Bower GH (Academic Press, New York), Vol 3.

7. Posner MI & Keele SW (1970) Retention of abstract ideas. *Journal of Experimental Psychology* 83(2):304-308.

8. Panichello MF, DePasquale B, Pillow JW, & Buschman TJ (2019) Error-correcting dynamics in visual working memory. *Nature Communications* 10:3366.

9. Cowan N (1984) On short and long auditory stores. *Psychological Bulletin* 96(2):341-370.

10. Wickelgren WA (1965) Distinctive features and errors in short-term memory for English vowels. *J. Acoust. Soc. Am.* 38:583-588.

11. Wickelgren WA (1966) Distinctive features and errors in short-term memory for English consonants. *J. Acoust. Soc. Am.* 39:388-398.

12. Pisoni DB (1973) Auditory and phonetic memory codes in the discrimination of consonants and vowels. *Percept. Psychophys.* 13:253-260.

13. Pisoni DB (1975) The role of auditory short-term memory in vowel perception. *Memory and Cognition* 3:7-18.

14. Repp BH (1984) Categorical perception: Issues, methods, findings. *Speech and Language* 10:243-335.

15. Wickelgren WA (1969) Associative strength theory of recognition memory for pitch. *Journal of Mathematical Psychology* 6:13-61.

16. Massaro DW (1970) Retroactive interference in short-term recognition memory for pitch. *Journal of Experimental Psychology* 83(1):32-39.

17. Clément S, Demany L, & Semal C (1999) Memory for pitch versus memory for loudness. *The Journal of the Acoustical Society of America* 106(5):2805-2811.

18. Demany L, Trost W, Serman M, & Semal C (2008) Auditory change detection: Simple sounds are not memorized better than complex sounds. *Psychol. Sci.* 19:85-91.

19. Deutsch D (1972) Mapping of interactions in the pitch memory store. *Science* 175:1020-1022.

20. Semal C & Demany L (1991) Dissociation of pitch from timbre in auditory short-term memory. *The Journal of the Acoustical Society of America* 89(5):2404-2410.

21. Semal C, Demany L, Ueda K, & Halle P-A (1996) Speech versus nonspeech in pitch memory. *J. Acoust. Soc. Am.* 100(2):1132-1140.

22. Tillmann B, Leveque Y, Fornoni L, Albouy P, & Caclin A (2016) Impaired short-term memory for pitch in congenital amusia. *Brain Research* 1640:251-263.

23. Plack CJ & Oxenham AJ (2005) The psychophysics of pitch. *Pitch - Neural Coding and Perception*, eds Plack CJ, Oxenham AJ, Fay RR, & Popper AJ (Springer Verlag, New York).

24. de Cheveigne A (2010) Pitch perception. *The Oxford Handbook of Auditory Science: Hearing*, ed Plack CJ (Oxford University Press, New York), Vol 3.

25. ANSI A (1994) American National Standard Acoustical Terminology. *ANSI SI* 11994.

26. Moore BCJ & Glasberg BR (1990) Frequency discrimination of complex tones with overlapping and non-overlapping harmonics. *The Journal of the Acoustical Society of America* 87.

27. Faulkner A (1985) Pitch discrimination of harmonic complex signals: Residue pitch or multiple component discriminations? *The Journal of the Acoustical Society of America* 78.

28. Micheyl C, Divis K, Wrobleski DM, & Oxenham AJ (2010) Does fundamental-frequency discrimination measure virtual pitch discrimination? *The Journal of the Acoustical Society of America* 128(4):1930-1942.

29. McPherson MJ & McDermott JH (2018) Diversity in pitch perception revealed by task dependence. *Nature Hum. Behav.* 2:52-66.

30. Demany L & Ramos C (2005) On the binding of successive sounds: Perceiving shifts in nonperceived pitches. *J. Acoust. Soc. Am.* 117(2):833-841.

31. Crowder RG (1982) Decay of auditory memory in vowel discrimination. *Journal of Experimental Psychology: Learning, Memory and Cognition* 8(2):153-162.

32. Demany L, Semal C, Cazalets J-R, & Pressnitzer D (2010) Fundamental differences in change detection between vision and audition. *Experimental Brain Research* 203(2):261-270.

33. Borchert EMO, Micheyl C, & Oxenham AJ (2011) Perceptual grouping affects pitch judgments across time and frequency. *Journal of Experimental Psychology: Human Perception and Performance* 37(1).

34. Shackleton TM & Carlyon RP (1994) The role of resolved and unresolved harmonics in pitch perception and frequency modulation discrimination. *J. Acoust. Soc. Am.* 95(6):3529-3540.

35. Bernstein JGW & Oxenham AJ (2005) An autocorrelation model with place dependence to account for the effect of harmonic number on fundamental frequency discrimination. *J. Acoust. Soc. Am.* 117(6):3816-3831.

36. Agus TA, Thorpe SJ, & Pressnitzer D (2010) Rapid formation of auditory memories: Insights from noise. *Neuron* 66:610-618.

37. Woods KJP & McDermott J (2018) Schema learning for the cocktail party problem. *Proc. Natl. Acad. Sci. USA* 115:E3313-E3322.

38. Cowan N, Saults JS, & Nugent LD (1997) The role of absolute and relative amounts of time in forgetting within immediate memory: The case of tone-pitch comparisons. *Psychonomic Bulletin & Review* 4(3):393-397.

39. Kaernbach C & Schlemmer K (2008) The decay of pitch memory during rehearsal. *J. Acoust. Soc. Am.* 123(4):1846-1849.

40. McWalter R & McDermott JH (2019) Illusory sound texture reveals multi-second statistical completion in auditory scene analysis. *Nature communications* 10(1):1-18.

41. Woods KJP, Siegel MH, Traer J, & McDermott JH (2017) Headphone screening to facilitate web-based auditory experiments. *Attention, Perception, and Psychophysics* 79:2064-2072.

42. Shepard RN (1964) Circularity in judgments of relative pitch. *J. Acoust. Soc. Am.* 36(12):2346-2353.

43. Wilmer JB (2008) How to use individual differences to isolate functional organization, biology and utility of visual perception; with illustrative proposals for stereopsis. *Spatial Vision* 21:561-579.

44. McDermott JH, Lehr AJ, & Oxenham AJ (2010) Individual differences reveal the basis of consonance. *Curr. Biol.* 20:1035-1041.

45. Spearman C (1904) The proof and measurement of association between two things. *The American Journal of Psychology* 15(1):72-101.

46. Cedolin L & Delgutte B (2005) Pitch of complex tones: Rate-place and interspike interval representations in the auditory nerve. *Journal of Neurophysiology* 94:347-362.

47. Mlynarski W & McDermott JH (2018) Learning mid-level auditory codes from natural sound statistics. *Neural Computation* 30(3):631-669.

48. McLachlan NM, Marco DJT, & Wilson SJ (2013) The musical environment and auditory plasticity: hearing the pitch of percussion. *Frontiers in Psychology* 4(768):1-6.

49. Harris JD (1952) The decline of pitch discrimination with time. *Journal of experimental psychology* 43(2):96.

50. Bachem A (1954) Time factors in relative and absolute pitch discrimination. *J. Acoust. Soc. Am.* 26(5):751-753.

51. Krumhansl CL (1990) *Cognitive foundations of musical pitch* (Oxford University Press, New York) pp x, 307.

52. Kishon-Rabin L, Amir O, Vexler Y, & Zaltz Y (2001) Pitch discrimination: are professional musicians better than non-musicians? *Journal of Basic Clinical Physiology and Pharmacology* 12:125-143.

53. Micheyl C, Delhommeau K, Perrot X, & Oxenham AJ (2006) Influence of musical and psychoacoustical training on pitch discrimination. *Hear. Res.* 219:36-47.

54. Bianchi F, Santurette S, Wendt D, & Dau T (2016) Pitch discrimination in musicians and non-musicians: Effects of harmonic resolvability and processing effort. *Journal of the Association for Research in Otolaryngology* 17(1):69-79.

55. Jacoby N*, et al.* (2019) Universal and non-universal features of musical pitch perception revealed by singing. *Curr. Biol.* 29:3229-3243.

56. McDermott JH, Schultz AF, Undurraga EA, & Godoy RA (2016) Indifference to dissonance in native Amazonians reveals cultural variation in music perception. *Nature* 535:547-550.

57. McPherson MJ*, et al.* (2020) Perceptual fusion of musical notes by native Amazonians suggests universal representations of musical intervals. *Nature Communications* in press.

58. Kersten D, Mamassian P, & Yuille A (2004) Object perception as Bayesian inference. *Annual Review of Psychology* 55:271-304.

59. Barlow HB (1961) Possible principles underlying the transformation of sensory messages. *Sensory communication* 1:217-234.

60. Barlow HB (1989) Unsupervised learning. *Neural computation* 1(3):295-311.

61. Lewicki MS (2002) Efficient coding of natural sounds. *Nature Neuroscience* 5(4):356-363.

62. Stilp CE, Rogers TT, & Kluender KR (2010) Rapid efficient coding of correlated complex acoustic properties. *Proc. Natl. Acad. Sci. USA* 107(50):21914-21919.

63. Dowling WJ & Fujitani DS (1971) Contour, interval, and pitch recognition in memory for melodies. *The Journal of the Acoustical Society of America* 49:524-531.

64. McDermott JH, Schemitsch M, & Simoncelli EP (2013) Summary statistics in auditory perception. *Nature Neuroscience* 16(4):493-498.

65. Patterson RD, Uppenkamp S, Johnsrude IS, & Griffiths TD (2002) The processing of temporal pitch and melody information in auditory cortex. *Neuron* 36(4):767-776.

66. Penagos H, Melcher JR, & Oxenham AJ (2004) A neural representation of pitch salience in nonprimary human auditory cortex revealed with functional magnetic resonance imaging. *Journal of Neuroscience* 24(30):6810-6815.

67. Norman-Haignere S, Kanwisher N, & McDermott JH (2013) Cortical pitch regions in humans respond primarily to resolved harmonics and are located in specific tonotopic regions of anterior auditory cortex. *Journal of Neuroscience* 33(50):19451-19469.

68. Allen EJ, Burton PC, Olman CA, & Oxenham AJ (2017) Representations of pitch and timbre variation in human auditory cortex. *Journal of Neuroscience* 37(5):1284-1293.

69. Tang C, Hamilton LS, & Chang EF (2017) Intonational speech prosody encoding in the human auditory cortex. *Science* 357(6353):797-801.

70. Fishman YI, Micheyl C, & Steinschneider M (2013) Neural representation of harmonic complex tones in primary auditory cortex of the awake monkey. *Journal of Neuroscience* 33(25):10312-10323.

71. Bendor D & Wang X (2005) The neuronal representation of pitch in primate auditory cortex. *Nature* 426:1161-1165.

72. Bizley JK, Walker KMM, King AJ, & Schnupp JW (2010) Neural ensemble codes for stimulus periodicity in auditory cortex. *Journal of Neuroscience* 30(14):5078-5091.

73. Song X, Osmanski MS, Guo Y, & Wang X (2016) Complex pitch perception mechanisms are shared by humans and a New World monkey. *Proc. Natl. Acad. Sci. USA* 113(3):781-786.

74. Bregman MR, Patel AD, & Gentner TQ (2016) Songbirds use spectral shape, not pitch, for sound pattern recognition. *Proc. Natl. Acad. Sci. USA* 113(6):1666-1671.

75. Walker KMM, Gonzalez R, Kang JZ, McDermott JH, & King AJ (2019) Across-species differences in pitch perception are consistent with differences in cochlear filtering. *eLIFE* 8:e41626.

76. Norman-Haignere SV, Kanwisher NG, McDermott JH, & Conway BR (2019) Divergence in the functional organization of human and macaque auditory cortex revealed by fMRI responses to harmonic tones. *Nature Neuroscience* 22:1057-1060.

77. Ernst MO & Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415:429-433.

78. Latinus M & Belin P (2011) Human voice perception. *Curr. Biol.* 21(4):R143-R145.

79. Schellenberg EG, Iverson P, & McKinnon MC (1999) Name that tune: Identifying popular recordings from brief excerpts. *Psychonomic Bulletin & Review* 6(4):641-646.

80. Krumhansl CL (2010) Plink: "Thin slices" of music. *Music Perception* 27(5):337-354.

81. Weiss MW, Trehub SE, & Schellenberg EG (2012) Something in the way she sings: Enhanced memory for vocal melodies. *Psychol. Sci.* 23(10):1074-1078.

82. Kleiner M, Brainard D, & Pelli D (2007) What's new in Psychtoolbox-3?

83. Goto M, Hashiguchi H, Nishimura T, & Oka R (2003) RWC Music Database: Music Genre Database and Musical Instrument Sound Database. *The 4th International Conference on Music Information Retrieval (ISMIR 2003)*, pp 229-230.

84. Kawahara H (2006) STRAIGHT, exploitation of the other aspect of VOCODER: Perceptually isomorphic decomposition of speech sounds. *Acoustical science and technology* 27(6):349-353.

85. Kawahara H & Morise M (2011) TANDEM-STRAIGHT: A temporally stable power spectral representation for periodic signals and applications to interference-free spectrum, F0, and aperiodicity estimation. *SADHANA* 36(5):713-722.

86. McDermott JH, Ellis DPW, & Kawahara H (2012) Inharmonic speech: A tool for the study of speech perception and separation. *Proceedings of SAPA-SCALE*, pp 114-117.

87. Popham S, Boebinger D, Ellis DP, Kawahara H, & McDermott JH (2018) Inharmonic speech reveals the role of harmonicity in the cocktail party problem. *Nature Communications* 9(1):2122.

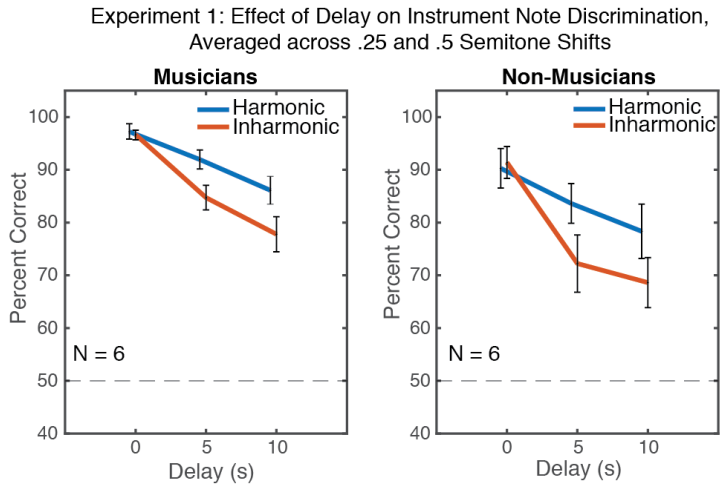
88. Pressnitzer D & Patterson RD (2001) Distortion products and the perceived pitch of harmonic complex tones. *Physiological and Psychophysical Bases of Auditory Function*, (Shaker Publishing), pp 97-104.

89. Norman-Haignere S & McDermott JH (2016) Distortion products in auditory fMRI research: Measurements and solutions. *Neuroimage* 129:401-413.

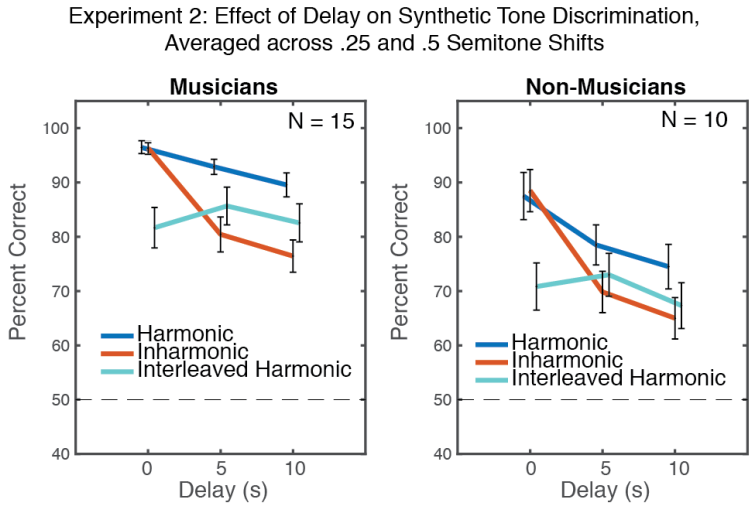
90. Faul F, Erdfelder E, Lang A-G, & Buchner A (2007) G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior research methods* 39(2):175-191.

91. Cronbach LJ (1951) Coefficient alpha and the internal structure of tests. *psychometrika* 16(3):297-334.

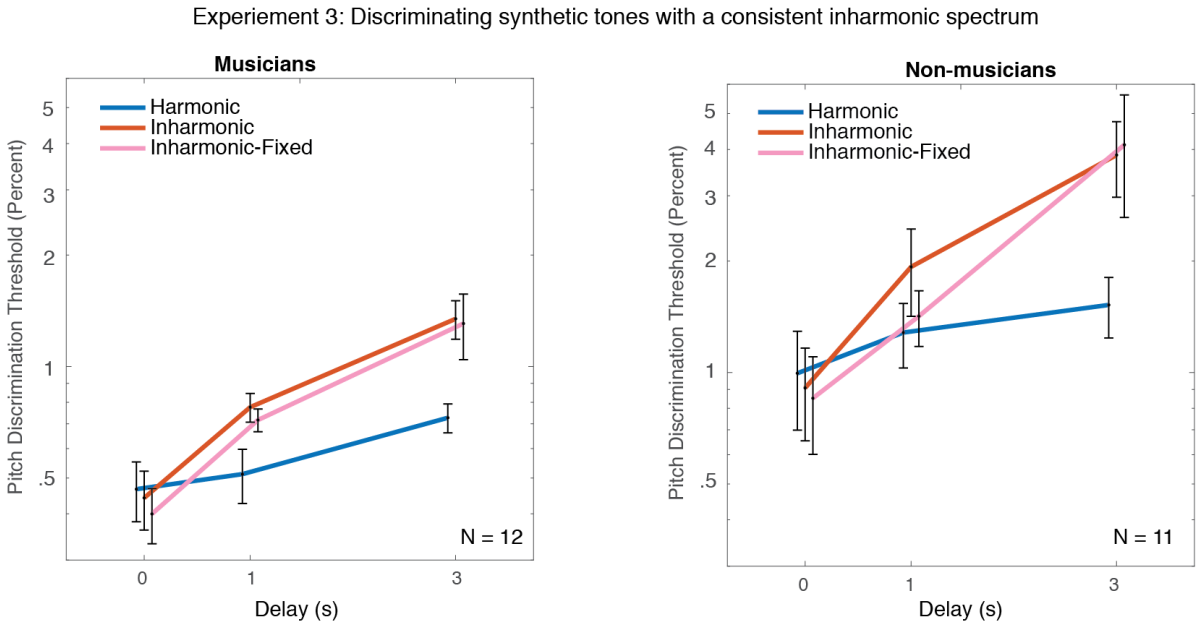
92. Falk CF & Savalei V (2011) The relationship between unstandardized and standardized alpha, true reliability, and the underlying measurement model. *Journal of personality assessment* 93(5):445-453.



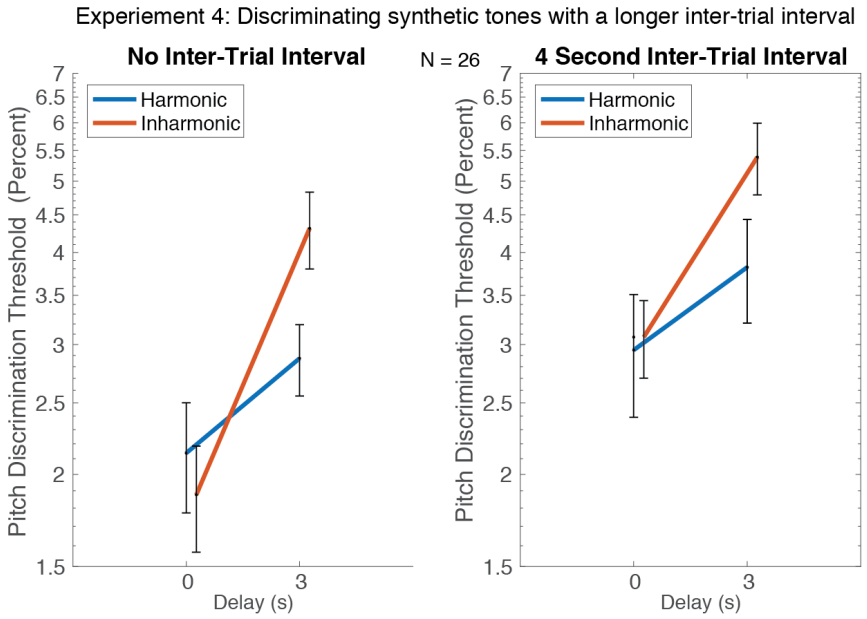
Supplementary Figure 1. Results from Experiment 1, plotted separately for musicians and non-musicians. Results are averaged across the two difficulty levels (.25 and .5 semitones) to maximize power. Error bars plot standard error of the mean.



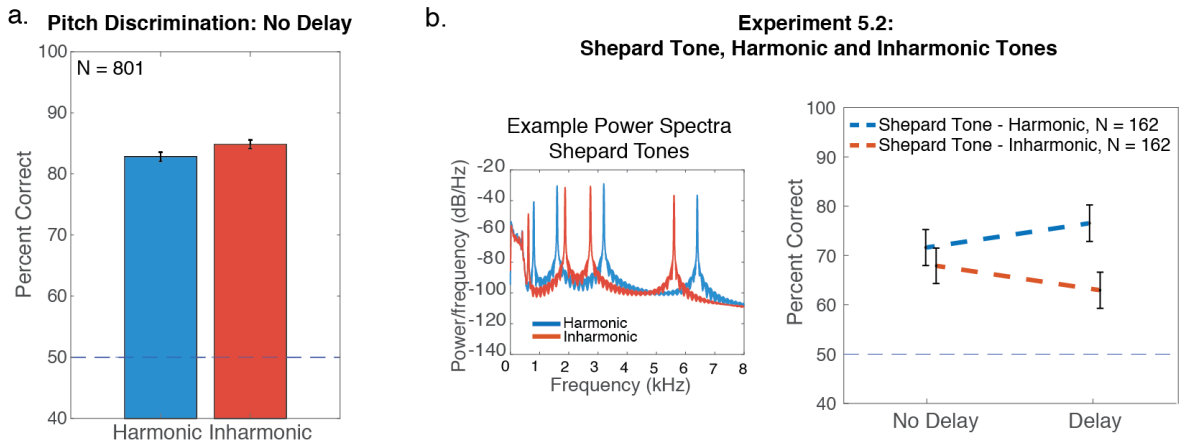
Supplementary Figure 2. Results from Experiment 2, plotted separately for musicians and non-musicians. Results are averaged across the two difficulty levels (.25 and .5 semitones) to maximize power. Error bars plot standard error of the mean.



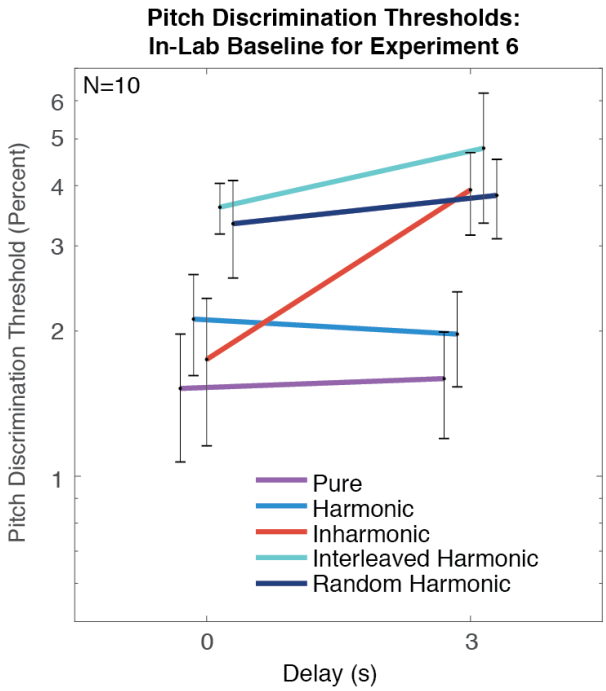
Supplementary Figure 3. Results from Experiment 3, plotted separately for musicians and non-musicians. Error bars plot within-subject standard error of the mean.



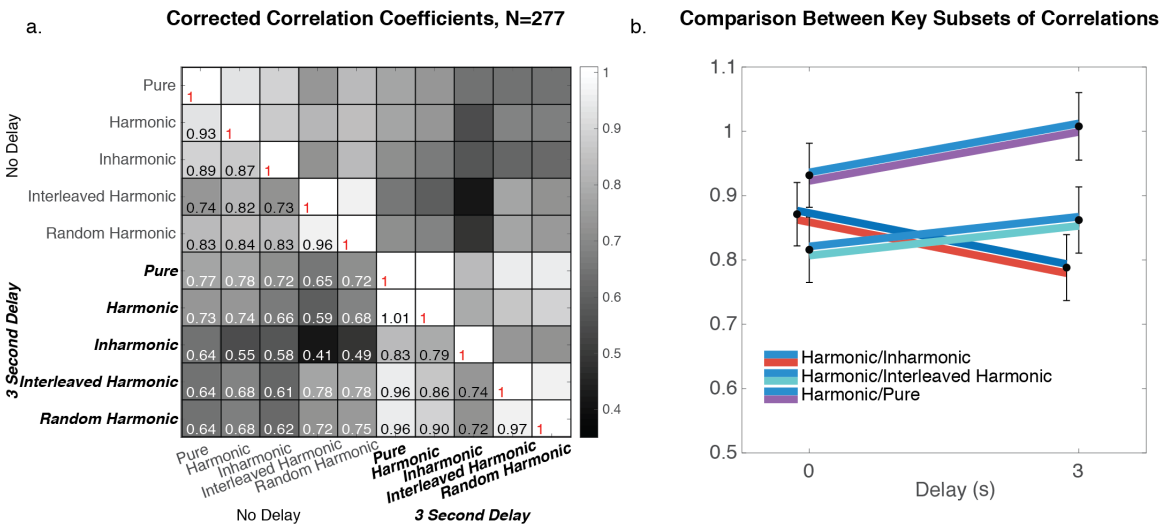
Supplementary Figure 4: Results from Experiment 4. Results from trials with and without an added 4 second delay between trials plotted separately. Error bars plot within-subject standard error of the mean.



Supplementary Figure 5. Results from additional task in Experiment 5.1/5.2 and Results from Experiment 5.2. a. results from the additional task, completed after the two main trials of Experiment 5. Participants each completed 40 trials, 20 with Harmonic stimuli, 20 with Inharmonic stimuli, all with no delay between tones. Error bars show standard error of the mean. b. Results of Experiment 5.2, replication of Experiment 5.1 with Harmonic and Inharmonic Shepard tones. Error bars plot standard error of the mean, calculated via bootstrap.



Supplementary Figure 6. In-lab results, Experiment 6. The mean thresholds shown here provided a performance baseline used to determine inclusion of the online participants. Error bars denote within subject standard error of the mean.



Supplementary Figure 7. Individual Differences Results with Less Stringent Inclusion Criteria. Instead of including only those participants who performed as well as in-lab participants, we excluded participants if their average threshold across all 5 conditions on the first run of the no-delay trials was greater than 6% (approximately 1 semitone). This excluded 173 of 450 participants, leaving 277 (126 female, mean age=35.6 years, S.D.=9.6 years), 170 of who reported some form of musical training, and 93 participants who reported greater than four years of musical training (mean=10.9, S.D.=6.6 years). a. Matrix of the correlation between thresholds for all pairs of conditions. Correlations are Spearman's rho, corrected for the reliability of the threshold measurements (i.e., corrected for attenuation). b. Comparison between Harmonic/Inharmonic and Harmonic/Interleaved Harmonic, and Harmonic/Pure threshold correlations, with and without a delay. The interaction between Harmonic/Inharmonic and Harmonic/Interleaved harmonic remained significant even with this more lenient inclusion policy. (difference of differences between correlations with and without a delay = 0.13, p=.026). Error bars plot standard error of the mean, calculated via bootstrap.