Improvisation: A novel tool to study musicality

Michael W. Weiss & Isabelle Peretz

International Laboratory for Brain, Music, and Sound Research (BRAMS), University of
Montreal

Author Note

Michael W. Weiss and Isabelle Peretz, Department of Psychology, University of Montreal, QC, Canada. Funded by the Fonds de Recherche du Québec: Nature et Technologies (MWW), the Natural Sciences and Engineering Research Council of Canada (IP), and the Canada Research Chairs program (IP). We thank Mihaela Felezeu for recruiting and testing participants, Dawn Merrett for assistance in recording stimuli, Emanuele Blasioli and Nicola Teolis for assistance in analysis, E. Glenn Schellenberg for feedback on an earlier draft, and Nori Jacoby and Peter Pfordresher for insightful discussions. Address correspondence to Michael W. Weiss, Department of Psychology, University of Montreal, QC, Canada. E-mail: michael.weiss@umontreal.ca

Abstract

Humans spontaneously invent songs from an early age. Here, we exploit this natural inclination to probe implicit musical knowledge in 33 untrained and poor singers (amusia). Each sang 28 long improvisations as a response to a verbal prompt or a continuation of a melodic stem. To assess the extent to which each improvisation reflects tonality, a core organizational principle of musicality, we developed a new algorithm that compares a sung excerpt to a probability density function representing the tonal hierarchy of Western music. The results show signatures of tonality in both nonmusicians and individuals with congenital amusia, who have notorious difficulty performing musical tasks that require explicit responses and memory. The findings are a proof of concept that improvisation can serve as a novel, even enjoyable method for systematically measuring hidden aspects of musicality across the spectrum of musical ability.

Keywords: Implicit Knowledge, Musicality, Improvisation, Tonality, Amusia

Music invented in the moment of performance, termed *improvisation*, is regarded as a honed skill reserved for expert musicians. Yet there are indications that improvisation is a natural, widespread behavior. Improvisation is common in many of the world's musical traditions (Nettl & Russell, 1998), young children sing novel songs or rework familiar songs spontaneously (Kartomi, 1991), and the vast majority of adults report improvisational singing in the absence of other people and music (74%; see Figure S1). Thus, improvisation represents a unique chance to uncover the rules acquired by the general population in everyday music, just as speech does for language.

Here, we examine whether sung improvisations demonstrate one of the fundamental components of musicality: tonal organization of pitch (Honing et al., 2015). Most music uses 4–7 focal pitches, forming a scale. Scale tones are organized around a central tone, called the tonic, which usually starts and ends a musical piece. Among the other scale tones, there is a hierarchy of importance or stability (Krumhansl, 1990). Nonscale tones are the least stable and often sound “sour”. These tonal principles allow, for example, any individual to detect an out-of-scale note in the musical surface. The organizational principle of tonality is largely absent in speech (Kuroyanagi et al., 2019; Patel, 2010) yet universal across musical systems (Savage et al., 2015), even as scales differ across societies (Burns, 1999). Tonal hierarchical organization of pitch is central because it facilitates perception, memory, and performance by creating expectancies (Pearce, 2018; Tillmann et al., 2000).

Prior behavioral studies of inner tonal knowledge have used paradigms that induce a sense of tonality (Auhagen & Vos, 2000). For example, the classic probe tone technique consists of presenting a tonal sequence of pitches ending on a variable probe tone. Listeners rate whether the final tone fits the preceding context (e.g., Krumhansl & Kessler, 1982). In Western listeners,

the ratings typically follow a profile where the tonic and closely related tones (the fifth and third degrees) are preferred over other scale and out-of-scale tones. Another widely used method consists of presenting a priming context of notes or chords that generate tonal expectancies for the final target event. An irrelevant change on the target event, such as a change of timbre, will be more rapidly detected if the chord conforms to tonal expectations (e.g., Marmel & Tillmann, 2009). Variations of these methods reveal implicit tonal knowledge among children as young as 4–5 years old, nonmusicians, and even amusic individuals who have little or no awareness of music rules or theory (Bigand & Poulin-Charronnat, 2006; Corrigan & Trainor, 2014; Tillmann, 2005; Tillmann et al., 2012; Trainor & Hannon, 2013). Production paradigms (*‘sing the next note’*) are less common and tend to be restricted to musically experienced participants (e.g., Cohen, 1991). In all cases, however, a musical context guides the behavioral response.

Tonal induction created by the presentation of a musical context is akin to presenting an incomplete sentence and asking the participant to choose or produce only the final word, whereas one could ask the participant to invent the sentence themselves. The advantage of freeform production, as in sung improvisation, is that participants may directly express an abstracted rule (e.g., scale) whereas tonal knowledge measured by tonal induction may simply reflect an accumulation of pitch frequencies. Indeed, there is a debate over the representation of implicit knowledge of music and whether it truly involves abstract rules or is simply the accumulation of knowledge fragments (Rohrmeier & Rebuschat, 2012). Differentiating between these possibilities requires testing individuals who lack metacognitive awareness of musical rules, and who are not guided by the paradigm.

Individuals with congenital amusia are an ideal population to test for the presence of tonal knowledge without awareness. These rare cases demonstrate a lifelong inability to detect

out-of-scale notes in melodies that typically elicit strong tonal expectations (Ayotte et al., 2002), yet indirect measures indicate that some tonal knowledge is spared (Peretz et al., 2009; Tillmann et al., 2012). Early-right anterior negativities in electroencephalography indicate normal tracking of tonality in the amusic brain, whereas later indicators that signify awareness (e.g., P600) are diminished or absent (Peretz et al., 2009; Zendel et al., 2015). In short, the amusic brain is ‘in tune but unaware’ (Peretz, 2016). Yet, this notion rests on the method of tonal induction and may not reflect the ability to follow the rules of tonality without musical context, as in spontaneous singing.

The possibility of observing implicit knowledge without awareness in singing comes from an early case study of amusia acquired through brain damage. Peretz (1993) observed that the case GL spontaneously sang a “totally unrelated and unrecognizable tune” (p. 31) when he could not recall the familiar songs asked of him. The individual tones in these improvisations were judged by two experts to be more consistent with a single key (more tonal) than were the tones produced in the remembered songs. Yet, GL was unable to use tonal knowledge in perceptual tasks that involved interpreting melodic closure, discriminating melodies, or aesthetic preference for notes conforming to a scale. These findings suggest that implicit tonal knowledge shapes production in the absence of explicit knowledge. Whether similar results are observed in individuals who exhibit a lifelong deficit in explicit processing of tonal material will be assessed in the present study.

The current research focuses on two core aspects of tonality: the tendency to produce or expect notes that conform to a scale, and the tendency to end melodies on the tonic. Participants who represent the lower end of the spectrum of musical ability and have limited access or awareness of tonal knowledge—nonmusicians and individuals with congenital amusia—are

asked to invent melodies based on a series of verbal and musical prompts. We expect nonmusicians to produce improvisations that conform to the familiar hierarchy of the Western tonal system. Similarly, individuals with congenital amusia should produce songs that are more tonally consistent than expected by chance. However, amusic performance may be less stable than controls. Indeed, amusic individuals have no concept of what a deviant note is and hence cannot monitor and correct their performance via auditory feedback (Peretz, 2016).

Method

Participants

Eighteen adults with congenital amusia ($M = 57.0$, $SD = 20.8$ years; 12 female), and 15 nonmusician controls ($M = 58.6$, $SD = 21.3$ years; 10 female) were recruited from a database of individuals who participated in previous research. Status as *amusic* or *control* was established prior to the study using the Montreal Protocol for Identification of Amusia (Vuvar et al., 2018). In the course of those evaluations, participants completed both the Brief Assessment of Music Perception (Peretz & Vuvar, 2017; www.peretzlab.ca/online-test/) and the Montreal Battery for Evaluation of Amusia (MBEA; Peretz et al., 2003). Both batteries involve listening to short melodies and noticing musical deviations or deciding whether two melodies are the same or different by a single note shift of 3–7 semitones that changes the scale (or key), intervals, or contour of the melody. Typical listeners detect these changes readily, and the batteries elicit high performance, but performance is markedly reduced for individuals with amusia. As a measure of individual differences, we calculated a composite score of *melodic pitch perception* (Weiss & Peretz, 2019) by averaging the percentage of correct responses across the five melodic subtests (MBEA: scale, contour, interval; Online Test: scale, off-key; the two scale tests are identical in the two batteries). As a group, participants with amusia were above chance, corresponding to

50% ($M = 61.8$, $SD = 8.2$, range = 44.8–71.8%, $t(17) = 6.11$, $p < .001$, Cohen's $d = 1.44$, 95% CI [57.7, 65.9]), but importantly, all individuals with amusia were more than 3 SD below the control group mean in our sample ($M = 88.4$, $SD = 5.1$, range = 79.0–97.3%, see Figure S2).

Participants also completed an acoustical pitch-change detection task. On each trial they heard five identical tones, of which the fourth tone was the same or changed in pitch by some amount (± 25 , 50, 100, 200, or 300 cents; Hyde & Peretz, 2004). Whether individuals with amusia can perceive subtle pitch changes is relevant to the acquisition of implicit tonality, so here we report their performance across all changing relative to non-changing trials. In terms of hits minus false alarms (chance = 0%, perfect = 100%), the group with amusia ($M = 68.8$, $SD = 20.8$, range = 35.4–95.6%) performed more poorly than controls ($M = 94.5$, $SD = 4.7\%$, range = 86.0–100%), $t(31) = 4.68$, $p < .001$, $d = 1.63$, 95% CI [14.47, 36.86]. These results indicate that pitch-change detection thresholds in amusia are higher than in controls (less sensitive), although it should be emphasized that pitch-change detection in invariant sequences is considerably simpler than detecting pitch violations in varying musical sequences.

All participants had 5 or fewer years of music lessons and there was no group difference between those with amusia (median = 0, $M = 0.4$, $SD = 1.2$, range = 0–5 years) and controls (median = 0, $M = 0.5$, $SD = 1.1$, range = 0–4 years), $p > .7$. There were no differences in hearing threshold reduction (dB, 0.5–8 kHz) between groups, $t(29) = 0.80$, $p > .4$, 95% CI [-6.1, 14.0] (two participants did not complete audiometry). All provided informed consent and received payment for participation. Procedures were approved by the Comité d'éthique de la recherche en éducation et en psychologie (CEREP), University of Montreal. The datasets generated and analyzed in the current study are available from the corresponding author on reasonable request.

Improvisation task

The task was to sing improvisations in response to different verbal prompts or as extensions of short melodic stems. Figure 1A displays an overview of the task. Improvisations were explained to be “making up a new melody,” which was (1) different from any melody the participant already knew, and (2) different from any previous attempts. For every trial, the experimenter checked whether the participant had inadvertently violated those instructions (self-report) and repeated the trial if they did. If the experimenter noticed a familiar or repeated melody, the trial was discarded and repeated. Participants were instructed to sing without lyrics, using the syllable ‘*da*’ to distinguish each note (i.e., without gliding between notes). Participants were encouraged to sing for a length of time that felt appropriate to them, but instructed not to pause or restart in the middle of an improvisation. The experimenter was available throughout the session to answer questions and monitor compliance.

Figure 1. Overview of the task and key-finding algorithm. **Panel A** visualizes the general progression of the study. **Panel B** visualizes the waveform of an actual improvisation (Audio S1). **Panel C** visualizes the semi-automated annotation of note boundaries (blue boxes) and pitch (black line) in the program Tony. **Panel D** visualizes the Krumhansl tone-probe ratings (here, minor mode). **Panel E** visualizes ratings for the in-scale intervals that determine the height of Gaussians in a normalized probability density function. **Panel F** visualizes a histogram of notes from the performance as pitch class in cents (i.e., 0–1200). All notes are transposed together in steps of one cent, covering the entire octave. **Panel G** visualizes the mean negative log likelihood across notes, weighted by note duration, at each transposition. The minimum value indicates the transposition or index with the best fit (vertical red line). The algorithm is visualized dynamically in Supplementary Materials (Movie S1).

As described in Figure 1A, participants performed vocal warm-ups by gliding across their vocal range. The task began with a free improvisation (i.e., no prompt). Next, participants sang a familiar song (*Happy Birthday* or *Gens du Pays*, Figure S3) with lyrics in English or French, and again without lyrics (*da da*). The familiar songs were not included in the improvisation analyses, and were included to evaluate singing ability, as in prior research (Dalla Bella et al., 2007, 2009; Tremblay-Champoux et al., 2010). Participants then improvised four melodies based on song forms common across cultures (Mehr et al., 2018): a lullaby, a dance song, a love song, and a healing song. Next, participants improvised 16 melodies as completion of short melodic stems (3 or 4 notes), as well as two melodies based on longer stems (10 notes). For these 18 trials, participants were asked to repeat the stem (shorter stems) or the final notes (longer stems) in their vocal range and continue it. A short example, recorded by the vocalist who recorded the stimuli, preceded the trials. For trials with longer stems, participants were asked to improvise an extension of the last few notes, although some participants attempted to repeat more of the melody.

The 18 melodic stems (Figure S4) were composed in pairs. One version was composed to elicit a greater sense of tonality, the other a lesser sense, while keeping the same contour, although the short stems were unlikely to impose a strong sense or absence of tonality. Due to an error, the eighth short tonal stem was presented twice in place of the less tonal version. In total, there were 10 trials with more tonal stems, and 8 trials with less tonal stems. The stems were recorded by an amateur female singer using the syllable *da* and pitch-corrected in Melodyne (Celemony, Inc.). The stems were normalized (RMS) and saved as high-quality digital audio files (48 kHz, 16-bit). They included notes A3 to A4 (i.e., 220–440 Hz). Most intervals were small (< 4 semitones), and all were 7 semitones or less, requiring no particular effort.

Following the 18 musical prompt trials, participants were asked to improvise two happy and two sad songs, in alternating order. Finally, the session concluded with a second free improvisation. In total there were 30 recordings per participant: 28 improvisations and 2 familiar songs. The recording session lasted approximately 30–40 minutes.

Participants were tested individually in a sound-attenuating booth, while seated in front of a computer running Audition software (Adobe, Inc.), which controlled presentation of melodic prompts via headphones (DT-770 Pro, Beyerdynamic, Inc.) and recorded improvisations via microphone (Neumann TLM-103) as high-quality digital sound files. An experimenter controlled the program from outside the booth and communicated through the participant's headphones. Volume was adjusted to a comfortable level for each participant.

Analyses

Pre-processing. Continuous pitch (Hz) and note boundaries were generated automatically for each recording using the program Tony (Mauch et al., 2015), and checked manually for transcription errors (Figure 1B–C). Impossibly short notes (< 50 ms) were excluded automatically. In some instances (33 of 924 improvisations, or 3.6% of total trials), the recording was truncated because participants began singing before the record button was pressed, or they sang indefinitely, forcing the experimenter to end the trial. Trials ended early by the experimenter were excluded from analyses of final note.

A central pitch value for each note was calculated as the median of the continuous frequency values within the middle 50% of the note. The pitch value was transformed from frequency (logarithmic) to semitone (linear) using A440 as reference (i.e., standard MIDI values, where 60 = C4). Each value was calculated to the nearest cent (i.e., two decimals, 100 cents per semitone). In rare instances, the pitch-tracking algorithm in Tony (pYIN) was indeterminate for

more than half of a note due to recording or voicing quality, and that note alone was excluded (0.12% of total notes). From the remaining notes, intervals in pitch were calculated for each pair of adjacent notes to the nearest cent.

Determining the nearest key. In contrast to tones produced by instruments with stable, discrete pitches (e.g., piano), sung tones are rarely aligned perfectly with equal-temperament tuning (i.e., 440 Hz reference pitch), even among professional vocalists. We developed an algorithm to determine the nearest tonic/key using continuous pitch values (i.e., to nearest cent). Pitch values were compared to the in-scale intervals of the major and minor ratings of Krumhansl (1990) using a probability density distribution (PDF; see Figure 1D–E) to reveal tonal relations among sung pitches. The PDF was built by summing a series of Gaussian curves with means centred on intervals in the scale. The spread of all Gaussians (i.e., *SD*) was determined by calculating the pitch stability (i.e., *SD*) within notes, averaged across all notes sung in the study (40,032 notes, $M = 26.1$ cents). Gaussians were evaluated at steps of 1 cent across the octave, resulting in 1200 values which were then normalized to sum to 1. Together, they represent a probability for pitches in-scale. MIDI values were converted to pitch class using modulo arithmetic (e.g., mod 12 of MIDI note 65.45 becomes 5.45), then converted to cents (e.g., $5.45 * 100 = 545$), and the negative log likelihood of the distribution at that index (e.g., index 545 of 1200) served as a measure of fit for that tone. In turn, the *mean* of negative log likelihoods for all tones in an improvisation, weighted by relative duration, measured the fit of the improvisation as a whole. The entire melody was then transposed in steps of 1 cent (1200 times) to find the best fit across the octave, and the index at that transposition was used to determine the tonic (see Figure 1F–G). For every improvisation, this procedure was completed

for both the major and minor scale profile (best fit of $2 * 1200 = 2400$ comparisons total) to determine the tonic and mode to the nearest cent.

Proportion of tonal notes. The proportion of notes in the rendition that were tonal was calculated using the determined key. For example, in the key of C-major, notes in the list [C, D, E, F, G, A, B] would be marked as in-scale and notes in the list [C#, D#, F#, G#, A#] would be marked as out-of-scale. Individual notes were marked as tonal if they were less than 50 cents from an interval that was in-scale.

Because chance performance depends on the number of notes (see Figure S5), a null distribution was calculated for every improvisation: (1) the pitch of each sung tone was reassigned at random (i.e., preserving durations), (2) the key-finding algorithm located the nearest key and mode given the random pitch values, (3) the proportion of randomized notes that were in-key relative to that key and mode was logged, and (4) the process was repeated for a total of 1000 iterations. The M and SD from the null distribution were used to calculate a z-score of the proportion of tonal notes in the actual improvisation ($z = [\text{actual} - M] / \text{SD}$), such that a score of 0 approximates chance regardless of number of notes.

Excerpts of improvisations which received high and low scores and the code for the nearest key algorithm are available in Supplementary Materials (Audio S1–S4). All statistical tests are two-sided unless otherwise noted.

Results

Characteristics of improvisations are summarized in Table 1. Both groups produced on average more than 30 notes in each improvisation. There were no differences between groups in median number of notes, $t(31) = 0.12$, $p > .9$, $d = 0.04$, 95% CI [-12.50, 14.04], nor median duration in seconds, $t(31) = 0.90$, $p > .3$, $d = 0.31$, 95% CI [-4.5, 11.6], suggesting that both

groups approached the task with a similar degree of enthusiasm. Both groups also favored small intervals, with 56.5% being smaller than $|250|$ cents (see also Figure 2A), as is typical in most music (Vos & Troost, 1989), and controls used small intervals more than did participants with amusia, $t(31) = 2.65$, $p = .013$, $d = 0.93$, 95% CI [.028, .215]. There was no difference between groups in the number of unique pitch values sung per improvisation, $t(31) = 0.92$, $p > .3$, $d = 0.32$, 95% CI [-0.51, 1.34]. The proportion of improvisations determined to be in the major mode differed by group, $t(31) = 3.97$, $p < .001$, $d = 1.39$, 95% CI [.088, .273]. Analysis of the algorithm revealed that the group with amusia did not differ from chance (proportion major = .458), $t(17) = 1.19$, $p > .2$, $d = 0.28$, 95% CI [.438, .531]. Rather, the control group sang more in major-key than expected by chance, $t(14) = 4.88$, $p < .001$, $d = 1.26$, 95% CI [.573, .755], in line with historically greater prevalence of major mode in popular music (Schellenberg & von Scheve, 2012).

Characteristics of Improvisations		
Median or Proportion $\pm$ IQR (Min – Max)		
	Amusic	Control
N	18	15
Median number of notes	34.2 $\pm$ 14.0 (15.0–77.0)	31.5 $\pm$ 18.2 (15.5–97.0)
Median duration (s)	22.9 $\pm$ 6.5 (12.0–62.1)	19.7 $\pm$ 8.1 (11.3–42.3)
Median pitch range (semitones)	11.9 $\pm$ 2.8 (8.3–20.7)	11.7 $\pm$ 3.5 (7.7–17.2)
Median number of pitch classes	10.0 $\pm$ 2.0 (8.0–12.0)	10.0 $\pm$ 1.0 (7.0–12.0)
Median prop. small intervals (< 250 cents)	0.49 $\pm$ 0.23 (0.33–0.76)	0.68 $\pm$ 0.19 (0.44–0.81)
Proportion major mode	0.46 $\pm$ 0.10 (0.36–0.68)	0.68 $\pm$ 0.16 (0.39–0.96)
Proportion of tonal notes	0.72 $\pm$ 0.09 (0.69–0.85)	0.83 $\pm$ 0.08 (0.74–0.96)
Note: Scores were summarized by individual (28 trials) prior to group-level summary statistics displayed here.		

Table 1. Improvisation characteristics by group.

Figure 2. Panel A shows the distribution of sung intervals (comprising both ascending and descending intervals) in improvisations by group. Intervals beyond 12 semitones were infrequent and are omitted for clarity. *Panels B and C* show the density plot of all notes sung during improvisations relative to the tonic. Vertical dashed lines represent intervals in-scale by mode. KDE = Kernel density estimate, an estimate of the probability density function; kernel bandwidth = 1/10.

The distribution of pitches relative to the tonic (tonic interval) is a signature of the tonal hierarchy. Figure 2B visualizes the global distribution of tonic intervals for individual notes ($n = 38,131$), separately by group and whether the algorithm labeled the rendition as ‘major’ or ‘minor’ but pooled across participants and trials ($n = 9,979$ amusic/major; $n = 10,951$ amusic/minor; $n = 11,265$ control/major; $n = 5,936$ control/minor). The difference in density distributions by mode (upper versus lower panel) confirms that the algorithm returned results that approximated the a priori distribution of in-scale intervals used in the algorithm (i.e., distance between peaks), and to a lesser degree, the probe-tone ratings used to build those distributions (i.e., relative peak heights; see Figure S6 for direct comparison in controls). The vast majority of both major and minor distributions overlapped across groups (purple shading). For several in-scale intervals, controls show clearer ‘peaks’ (e.g., blue shading at major mode intervals of 0, 2, or 4 semitones) and ‘valleys’, collectively indicating greater adherence to the scale in controls.

Additional analyses on repetition in improvisations (Figure S7) and singing accuracy (Figure S8) are included in Supplementary Information.

Tonality

In order to measure the tonality of each improvisation, a z-score was computed for the proportion of tonal notes relative to chance in each improvisation, as detailed above. The z-scores obtained from all 28 improvisations were averaged into a single score for each participant. As visible in the individual data points in Figure 3A, each group showed a wide range of performance, including individuals near chance in the control group, and individuals in the group with amusia near or above the control group median. Despite the large variability, an independent-samples *t*-test revealed a significant difference between groups, $t(31) = 2.90$, p

= .007, $d = 1.01$, 95% CI [0.37, 2.14]. Both the group with amusia, $M = 0.77$, $SD = 1.08$, $t(17) = 3.02$, $p = .008$, $d = 0.71$, 95% CI [0.23, 1.31], and the control group, $M = 2.03$, $SD = 1.41$, $t(14) = 5.58$, $p < .001$, $d = 1.44$, 95% CI [1.25, 2.80], had significantly better performance than chance.

Figure 3. Tonality of improvised songs. **Panel A** shows the z-transformed proportion of tonal notes. Individual data points were calculated as the average of 28 improvisations, which were z-transformed against 1000 randomly-generated melodies. The upper dashed line represents the score of a professional baritone singer with 11 years of formal training and 29 years of total singing experience. His data provide a benchmark of proficient singing since the measures are standardized with a clear baseline but no clear ceiling. The lower dashed line represents chance, i.e., z-score of 0. Both groups were above chance and the control group had higher scores than the group with amusia. **Panel B** shows the proportion of trials in which the participant ended their improvisation within 50 cents of the tonic determined by the key-finding algorithm. Each value was calculated as an average from 28 improvisations, except in a handful of cases with truncated recordings. The upper dashed line represents the score of a professional singer. The lower dashed line represents chance (0.149), as estimated from over one million random permutations generated over the course of the analyses. Both groups were above chance and the control group had higher scores than the group with amusia. **Panel C** shows mean tonality of improvisation as measured by proportion of tonal notes (z-score) according to group and type of stem. An interaction between group and stem was driven by a significant difference between more tonal over less tonal stems in the control group only. All subgroupings of the data (i.e., individual boxplots) were significantly above chance (i.e., z-score of 0). Boxplots display median (line) and 25th and 75th percentiles (box edges). **Panel D** shows individual melodic perception scores (see Participants) as a function of tonality of improvisations. The solid trend line visualizes a significant positive correlation across all participants.

In addition, the proportion of all 28 improvisations that ended on the tonic was calculated for each participant, excluding instances of truncated recordings (Figure 3B). An independent-samples *t*-test revealed a significant difference between groups for proportion of final notes within 50 cents of the tonic, $t(31) = 3.84$, $p < .001$, $d = 1.34$, 95% CI [.103, .339]. We used the null distributions ($n = 1,020,000$) generated for the z-scores to examine the proportion of times that the final note matched the tonic by chance. Melodies composed of random notes ended on a note within 50 cents of the tonic identified by the PDF algorithm .149 proportion of the time. Both the group with amusia, $M = .25$, $SD = .12$, $t(17) = 3.64$, $p = .002$, $d = 0.86$, 95% CI [.191, .306], and controls, $M = .47$, $SD = .21$, $t(14) = 5.92$, $p < .001$, $d = 1.53$, 95% CI [.354, .586], had significantly higher proportions than chance, despite wide inter-participant variability. At the individual level, the proportion of improvisations that ended on the tonic was greater than chance (i.e., proportion $> .149$) for 15 of 18 amusics and 14 of 15 controls.

Next, the tonality of improvisations in response to musical stems was examined with a mixed-model ANOVA with group (amusic, control) as a between-participant factor and stem (more tonal stem, less tonal stem) as a within-participant factor (Figure 3C). There was a significant main effect of group, $F(1, 31) = 6.94$, $p = .013$, $\eta_p^2 = .18$, replicating the previous analyses showing more tonal performance in the control group. There was also a main effect for stem, $F(1, 31) = 4.50$, $p = .042$, $\eta_p^2 = .13$; however these main effects were qualified by an interaction, $F(1, 31) = 5.86$, $p = .021$, $\eta_p^2 = .16$. Follow-up pairwise comparisons (Bonferroni-Holm) showed that the advantage of tonality for only one comparison—more tonal stems versus less tonal stems—reached a statistically significant difference in controls, $t(14) = 4.05$, $p = .002$, $d = .31$, 95% CI [0.223, 0.728], but not in participants with amusia, $t(17) = 0.19$, $p > .8$, $d = 0.03$, 95% CI [-0.314, 0.378]. Whereas controls tended to sing more tonal improvisations when

starting from tonal versus atonal stems, there was no effect of stem tonality in the group with amusia. Nevertheless, for both groups, more tonal and less tonal stems were above chance in tonality (Bonferroni-Holm), $ps < .05$.

The ability to detect pitch changes of 25–300 cents in an acoustic context (see Participants) did not correlate with mean tonality of improvisations across all participants, $r(31) = .06$, $p > .7$, 95% CI [-.29, .39]. In contrast, the relationship between *musical* pitch perception (i.e., mean of tonal subtests of online test and MBEA) and mean tonality of improvisations was positive across all participants, $r(31) = .44$, $p = .010$, 95% CI [.12, .68] (Figure 3D). The latter relationship was not, however, significant for either group when examined separately, $ps > .5$.

Discussion

We show that improvisation can serve as a novel tool to study tonality, which is a core component of musicality. Even the poorest singers invent songs with pitch variations conforming to the tonal hierarchy of Western music. Moreover, the task is surprisingly straightforward and approachable by everyone. The main benefit of using improvisations over perceptual or other production tasks is that measures of implicit knowledge of music can be collected directly and without guiding the behavior of interest.

Tonal organization of pitch is traditionally assessed by induction (Auhagen & Vos, 2000). We provide the first evidence that two core aspects of tonality—tonal hierarchy of pitches and resolution on the tonic—occur in the absence of tonal induction. The observation of tonality in freeform productions suggests that abstract rules guide adult musicality. These rules were assessed over the rendition as a whole, with median length over 20 s and 30 notes, far exceeding the limits of short-term memory. Such stability showcases the robustness of tonal schemas. Moreover, signatures of tonality were observed in both typical nonmusicians and individuals

with amusia, which supports the view that awareness is not required for acquiring and sustaining tonal organization over time. In short, even the least musical among us spontaneously produce the learned tonal regularities of music.

However, expressions of tonality varied. Some individuals in both the amusic and control groups were above both group medians (more tonal), and some were below both group medians (less tonal), with considerable overlap between groups. Nevertheless, those with amusia produced less tonal improvisations than did nonmusicians overall. Groupwise differences in tonality could not be explained by motor limitations (pitch range) or enthusiasm (duration, number of notes), and their distribution of intervals was similar to what has been reported in various corpora of Western music (Vos & Troost, 1989). The findings of groupwise differences and overlap across groups suggest that congenital amusia leads to a difference in tonal knowledge as a matter of degree rather than category.

Uncovering the origins of this difference, especially in populations who cannot readily correct errors, is a key to harnessing optimal learning conditions. Congenital amusia is a model condition for delineating those conditions because musical knowledge is built in isolation from tutoring, awareness, and feedback. Peretz (2016) proposed that deficits in amusia, like other congenital disorders of awareness (prosopagnosia, dyslexia), may indicate sparse knowledge that is functional only at an implicit level. This suggests that awareness is necessary to shape musical knowledge acquired by mere exposure to enjoy a normally functioning system.

The role of awareness is hard to distinguish from feedback in auditory-vocal learning. The auditory feedback system serves a major role in monitoring and adjusting errors. If altered, a poor calibration occurs between the implicitly learned (bottom-up) knowledge in the auditory cortex and the (top-down) control of that knowledge from frontal brain areas, as modeled in

Peretz (2016). As a result, a poor assessment of whether a note fits the preceding context, as in the melodic subtests of the MBEA (Peretz et al., 2003), occurs, as observed here. Across all participants, there was a positive correlation between performance on those subtests and tonality of improvisations. Thus, the results are consistent with a poor feedback loop. As a matter of fact, it is relatively easy to alter the detection of an out-of-scale note by manipulated feedback in typical listeners (Vuvar et al., 2018). In that study, nonmusicians were asked to evaluate whether a melody contained a “wrong” (out-of-scale) note and received audiovisual feedback about whether they were correct. Unbeknownst to participants, the researchers manipulated whether the feedback was random or accurate. In the accurate condition, participants demonstrated typical behavioral and neurophysiological responses to out-of-scale notes, but in the random feedback condition, both types of measures showed responses more typical of amusia. Whether task feedback can, in turn, be used to train individuals to overcome their deficit is a key question for future research.

Fortunately, improvisation can bypass individual limitations in learning and is arguably the most suitable method to capture individual variation in musical knowledge representations. The present study of tonality is a proof of concept that improvisations can serve as a rich source of data for exploring the internal architecture of musicality. Improvisation could reveal many other aspects of musicality. One important building block of tonal music concerns temporal regularities and structures. For example, to what degree do improvisations show the presence of a steady beat (Honing & Bouwer, 2019), or simple integer subdivisions of the beat (Jacoby & McDermott, 2017)? Furthermore, improvised music could be used to train or compare computational models of expectancy that are used widely in psychology and neuroscience of music (Morgan et al., 2019; Pearce, 2018). More generally, we envision that the method of

improvisation, which places few constraints on the participant and uses the ‘universal’ instrument—the voice—could facilitate cross-cultural and cross-species research on regularities in music, such as comparing songs across developmental periods (*when do children acquire the rules of music?*), across cultures (*what rules are universal?*), or even across species (*what rules are unique to humans or shared with other vocal learners?*). The present data forms the basis for a novel corpus that will be a springboard for such analyses.

Finally, we were pleased to discover that participants with amusia improvised enthusiastically. One participant with amusia later communicated that she enrolled in singing lessons because she enjoyed her experience in the study. Other typically shy populations, such as young children, might find improvisation more approachable than other production tasks because it is a natural propensity. Indeed, given its prevalence as an everyday behavior, future research might study the origins of reward and pleasure from spontaneous music making, as well as its physiological effects (Bernardi et al., 2017) and potential as a therapeutic tool (Dubinsky et al., 2019).

References

- Auhagen, W., & Vos, P. G. (2000). Experimental methods in tonality induction research: A review. *Music Perception*, 17(4), 417–436. <https://doi.org/10.2307/40285827>
- Ayotte, J., Peretz, I., & Hyde, K. (2002). Congenital amusia: A group study of adults afflicted with a music-specific disorder. *Brain*, 125(2), 238–251.
- Bernardi, N. F., Snow, S., Peretz, I., Orozco Perez, H. D., Sabet-Kassouf, N., & Lehmann, A. (2017). Cardiorespiratory optimization during improvised singing and toning. *Scientific Reports*, 7(1), 8113. <https://doi.org/10.1038/s41598-017-07171-2>
- Bigand, E., & Poulin-Charronnat, B. (2006). Are we “experienced listeners”? A review of the musical capacities that do not depend on formal musical training. *Cognition*, 100(1), 100–130. <https://doi.org/10.1016/j.cognition.2005.11.007>
- Burns, E. M. (1999). Intervals, scales, and tuning. In D. Deutsch (Ed.), *The psychology of music* (2nd ed., pp. 215–264). Elsevier.
- Cohen, A. J. (1991). Tonality and perception: Musical scales primed by excerpts from The Well-Tempered Clavier of J. S. Bach. *Psychological Research*, 53(4), 305–314. <https://doi.org/10.1007/BF00920484>
- Corrigall, K. A., & Trainor, L. J. (2014). Enculturation to musical pitch structure in young children: Evidence from behavioral and electrophysiological methods. *Developmental Science*, 17(1), 142–158. <https://doi.org/10.1111/desc.12100>
- Dalla Bella, S., Deutsch, D., Giguère, J.-F., Peretz, I., & Deutsch, D. (2007). Singing proficiency in the general population. *Journal of the Acoustical Society of America*, 121, 1182–1189. <https://doi.org/10.1121/1.2427111>
- Dalla Bella, S., Giguère, J.-F., & Peretz, I. (2009). Singing in congenital amusia. *Journal of the*

- Acoustical Society of America*, 126(1), 414–424. <https://doi.org/10.1121/1.3132504>
- Dubinsky, E., Wood, E. A., Nespoli, G., & Russo, F. A. (2019). Short-term choir singing supports speech-in-noise perception and neural pitch strength in older adults with age-related hearing loss. *Frontiers in Neuroscience*, 13. <https://doi.org/10.3389/fnins.2019.01153>
- Honing, H., & Bouwer, F. L. (2019). Rhythm. In P. J. Rentfrow & D. J. Levitin (Eds.), *Foundations in music psychology: Theory and research* (pp. 33–70). MIT Press.
- Honing, H., ten Cate, C., Peretz, I., & Trehub, S. E. (2015). Without it no music: Cognition, biology and evolution of musicality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1664), 20140088. <https://doi.org/10.1098/rstb.2014.0088>
- Hyde, K. L., & Peretz, I. (2004). Brains that are out of tune but in time. *Psychological Science*, 15(5), 356–360. <https://doi.org/10.1111/j.0956-7976.2004.00683.x>
- Jacoby, N., & McDermott, J. H. (2017). Integer ratio priors on musical rhythm revealed cross-culturally by iterated reproduction. *Current Biology*, 27(3), 359–370. <https://doi.org/10.1016/j.cub.2016.12.031>
- Kartomi, M. J. (1991). Musical improvisations by children at play. *The World of Music*, 33, 53–65. JSTOR.
- Krumhansl, C. L. (1990). *Cognitive foundations of musical pitch*. Oxford University Press.
- Krumhansl, C. L., & Kessler, E. J. (1982). Tracing the dynamic changes in perceived tonal organization in a spatial representation of musical keys. *Psychological Review*, 89(4), 334–368. <https://doi.org/10.1037/0033-295X.89.4.334>
- Kuroyanagi, J., Sato, S., Ho, M.-J., Chiba, G., Six, J., Pfordresher, P., Tierney, A., Fujii, S., & Savage, P. E. (2019). *Automatic comparison of human music, speech, and bird song*

- suggests uniqueness of human scales* [Preprint]. PsyArXiv.
<https://doi.org/10.31234/osf.io/zpv5w>
- Marmel, F., & Tillmann, B. (2009). Tonal priming beyond tonics. *Music Perception*, 26(3), 211–221. <https://doi.org/10.1525/mp.2009.26.3.211>
- Mauch, M., Cannam, C., Bittner, R., Fazekas, G., Salamon, J., Dai, J., Bello, J., & Dixon, S. (2015). Computer-aided melody note transcription using the tony software: Accuracy and efficiency. *Proceedings of the First International Conference on Technologies for Music Notation and Representation*.
- Mehr, S. A., Singh, M., York, H., Glowacki, L., & Krasnow, M. M. (2018). Form and function in human song. *Current Biology*, 28(3), 356-368.e5.
<https://doi.org/10.1016/j.cub.2017.12.042>
- Morgan, E., Fogel, A., Nair, A., & Patel, A. D. (2019). Statistical learning and Gestalt-like principles predict melodic expectations. *Cognition*, 189, 23–34.
<https://doi.org/10.1016/j.cognition.2018.12.015>
- Nettl, B., & Russell, M. (1998). *In the course of performance: Studies in the world of musical improvisation*. University of Chicago Press.
<https://archive.org/details/incourseofperfor0000unse>
- Patel, A. D. (2010). *Music, Language, and the Brain*. Oxford University Press, USA.
- Pearce, M. T. (2018). Statistical learning and probabilistic prediction in music cognition: Mechanisms of stylistic enculturation. *Annals of the New York Academy of Sciences*, 1423(1), 378–395. <https://doi.org/10.1111/nyas.13654>
- Peretz, I. (1993). Auditory atonalia for melodies. *Cognitive Neuropsychology*, 10(1), 21–56.
<https://doi.org/10.1080/02643299308253455>

- Peretz, I. (2016). Neurobiology of congenital amusia. *Trends in Cognitive Sciences*, 20(11), 857–867. <https://doi.org/10.1016/j.tics.2016.09.002>
- Peretz, I., Brattico, E., Järvenpää, M., & Tervaniemi, M. (2009). The amusic brain: In tune, out of key, and unaware. *Brain*, 132(5), 1277–1286. <https://doi.org/10.1093/brain/awp055>
- Peretz, I., Champod, A. S., & Hyde, K. (2003). Varieties of musical disorders. *Annals of the New York Academy of Sciences*, 999(1), 58–75. <https://doi.org/10.1196/annals.1284.006>
- Peretz, I., & Vuvan, D. T. (2017). Prevalence of congenital amusia. *European Journal of Human Genetics*, 25(5), 625–630. <https://doi.org/10.1038/ejhg.2017.15>
- Rohrmeier, M., & Rebuschat, P. (2012). Implicit learning and acquisition of music. *Topics in Cognitive Science*, 4(4), 525–553. <https://doi.org/10.1111/j.1756-8765.2012.01223.x>
- Savage, P. E., Brown, S., Sakai, E., & Currie, T. E. (2015). Statistical universals reveal the structures and functions of human music. *Proceedings of the National Academy of Sciences*, 112(29), 8987–8992. <https://doi.org/10.1073/pnas.1414495112>
- Schellenberg, E. G., & von Scheve, C. (2012). Emotional cues in American popular music: Five decades of the Top 40. *Psychology of Aesthetics, Creativity, and the Arts*, 6, 196–203. <https://doi.org/10.1037/a0028024>
- Tillmann, B. (2005). Implicit investigations of tonal knowledge in nonmusician listeners. *Annals of the New York Academy of Sciences*, 1060(1), 100–110. <https://doi.org/10.1196/annals.1360.007>
- Tillmann, B., Bharucha, J. J., & Bigand, E. (2000). Implicit learning of tonality: A self-organizing approach. *Psychological Review*, 107(4), 885.
- Tillmann, B., Gosselin, N., Bigand, E., & Peretz, I. (2012). Priming paradigm reveals harmonic structure processing in congenital amusia. *Cortex*, 48(8), 1073–1078.

- Trainor, L. J., & Hannon, E. E. (2013). Musical development. In D. Deutsch (Ed.), *The psychology of music*, 3rd ed (pp. 423–497). Elsevier Academic Press.
<https://doi.org/10.1016/B978-0-12-381460-9.00011-0>
- Tremblay-Champoux, A., Dalla Bella, S., Phillips-Silver, J., Lebrun, M.-A., & Peretz, I. (2010). Singing proficiency in congenital amusia: Imitation helps. *Cognitive Neuropsychology*, 27(6), 463–476. <https://doi.org/10.1080/02643294.2011.567258>
- Vos, P. G., & Troost, J. M. (1989). Ascending and descending melodic intervals: Statistical findings and their perceptual relevance. *Music Perception*, 6(4), 383–396.
<https://doi.org/10.2307/40285439>
- Vuvan, D. T., Paquette, S., Mignault Goulet, G., Royal, I., Felezeu, M., & Peretz, I. (2018). The Montreal Protocol for Identification of Amusia. *Behavior Research Methods*, 50(2), 662–672. <https://doi.org/10.3758/s13428-017-0892-8>
- Vuvan, D. T., Zendel, B. R., & Peretz, I. (2018). Random feedback makes listeners tone-deaf. *Scientific Reports*, 8(1), 7283. <https://doi.org/10.1038/s41598-018-25518-1>
- Weiss, M. W., & Peretz, I. (2019). Ability to process musical pitch is unrelated to the memory advantage for vocal music. *Brain and Cognition*, 129, 35–39.
<https://doi.org/10.1016/j.bandc.2018.11.011>
- Zendel, B. R., Lagrois, M.-É., Robitaille, N., & Peretz, I. (2015). Attending to pitch information inhibits processing of pitch information: The curious case of amusia. *Journal of Neuroscience*, 35(9), 3815–3824.

Fig. S1. Prevalence of spontaneous improvisation in adults. We surveyed 65 undergraduates who were not majoring in a music-related field and had never taken singing lessons. Among the sample, 39 individuals could be considered nonmusicians (0–2 years of lessons) and 26 could be considered more musical or musicians (3+ years of lessons). Respondents were excluded if they majored in a musical field or had taken singing lessons. The prompts asked how often they (1) sang while improvising or (2) danced, in the absence of other people and music, on a scale from 1 (never) to 5 (always). For singing, 74.4% of nonmusician respondents answered “sometimes” ($n = 9$), “often” ($n = 15$), or “always” ($n = 5$), and only 25.6% responded “rarely” ($n = 3$) or “never” ($n = 7$). In contrast, the majority of those same nonmusicians (69.2%) reported that they “never” ($n = 12$) or “rarely” ($n = 15$) danced in the same conditions. Those with more musical training were more likely to report both behaviors, as might be expected.

Fig. S2. Melody perception. Individual mean scores obtained on five tests requiring detection of a pitch change in melodies from the Online Test and Montreal Battery for Evaluation of Amusia (MBEA) are plotted according to age and gender of participant. Chance performance is 50% correct. Both tests are designed to elicit high scores in the general population, and performance below 72.2% (dashed line) is rare and indicative of amusia (Peretz et al., 2003).

Fig. S4. Musical notation for the melodic stems used in the study. Eight short melodic stems were more tonal (left column) or less tonal (right column) versions of the same three- or four-note melodic contour, with the exception of the eighth less-tonal stem, which was repeated due to an error. There were also two long melodic stems, one more tonal (upper) and one less tonal (lower) version of the same melodic contour.

Fig. S5. Visualization of key-finding performance with melody length. The plot visualizes the change in mean (points) and standard deviation (error bars) of the null distribution of “best fit” returned by the PDF algorithm (major scale), where lower values indicate better fit. Plotted values here are based on 1,000 random-note permutations per melody length. Because the mean and standard deviation of random sequences changes with melody length, each improvisation must be z-scored against a large set of random-pitch sequences that match the number of notes and duration of each note.

Fig. S6. Proportion of notes as intervals relative to the tonic. Tonal profiles generated from improvisations are visualized as grey bars. Only data from control participants and from trials without musical stems ($n = 10$ verbal prompts) are included here, to remove the possibility that observed deviations are due to perceptual deficits (amusia) or tonal induction (e.g., tonal or atonal stems). For comparison, Krumhansl's (1990) ratings for the major (top) and minor scale (bottom) profiles are visualized (horizontal red lines). Asterisks represent a significant one-sample t-test for the proportion of notes (Bonferroni-Holm). Error bars are S.E.M. Music theory and the Krumhansl ratings predict a hierarchy of tonic (I) > fifth scale degree (V) > third scale degree (III) > out-of-scale notes. Here we observe some deviations from that pattern. In the major profile, scale degrees II and III were more prevalent than predicted by ratings, and higher scale degrees (V and VI) were less prevalent. Moreover, while the tonic (I) was more prevalent than predicted by ratings, it was not clearly more prevalent than scale degrees II or III. Improvisations in the minor mode generally followed the profile of ratings, except that the second scale degree (II) was again more prevalent than predicted by ratings.

Fig. S7. Analysis of repetition in improvisations. An overreliance on repetition could boost scores of tonality artificially (e.g., singing the same note or pattern repeatedly). To rule out the possibility that participants with amusia were simply more reliant on repetition, we analyzed improvisations using “m-gram” analyses (Müllensiefen, 2009). Following the convention of Müllensiefen (2009) we collapsed all possible intervals into 19 categories (-13 or less, -12, -11 or -10, -9 or -8, -7, -6, -5, -4 or -3, -2 or -1, 0, +1 or +2, +3 or +4, +5, +6, +7, +8 or +9, +10 or +11, +12, +13 or more semitones). In order to maximize detection of repeating patterns of pitch, relative note duration was not considered. Pitch intervals of a melody were considered in windows of size n (i.e., number of intervals), sliding across the melody interval-by-interval. At each step, the intervals in that window, termed an m -token, were logged. Then, across all logged m -tokens, unique values were tallied, such that m -tokens occurring repeatedly were summed. If an observed m -token never repeats, that particular m -type sequence has a frequency of 1. The analysis was repeated by changing the size of the sliding window, n , for which we used values of 1–3 intervals (2–4 notes) to capture patterns of different lengths. For each window size n , the frequency of the m -type with the most repeats was divided by the total number of m -tokens at that window size. A summary score was calculated by averaging across window sizes. In other words, the more that an improviser repeats a single pattern, the closer the score will approach 1, and if they never repeat themselves, the score will be 0. The dashed line represents the scores of a professional singer.

The results suggest slightly more repetition in the improvisations of controls ($M = .21$, $SD = .03$) compared to those with amusia ($M = .18$, $SD = .04$), $t(31) = 2.45$, $p = .020$, but the group distributions overlapped considerably. The measure of repetition did not correlate with either measure of tonality: z -transformed proportion of tonal notes, $r(31) = .19$, $p = .292$; proportion of final note ending on the tonic, $r(31) = .24$, $p = .177$.

Fig. S8. Singing accuracy for highly familiar tunes. To provide an estimate of singing proficiency in each group and in the amusic group in particular, we measured the proportion of incorrect intervals in the rendition of one highly familiar tune relative to the musical notation (Fig. S4). An interval was incorrect if it was not within 50 cents of the notated interval. Panel A shows the individual proportion of incorrect intervals. Controls (blue squares) show more accuracy than individuals with amusia (red triangles). The horizontal dashed line marks the score of a professional singer. As expected, amusic participants performed more poorly than controls, $F(1, 31) = 11.94$, $p = .002$, $\eta_p^2 = .23$. Note that 6 of 17 participants with amusia (~35%) in the present sample sang in tune or within 1 SD from the control group mean. Several individuals with amusia failed to generate a recognizable rendition of the melody without lyrics and improvised instead (gray circles), which could indicate inability to access the melody in memory or extremely poor singing. Altogether, the results replicate previous research showing that individuals with amusia sing familiar songs less accurately than controls (Dalla Bella et al., 2007, 2009; Tremblay-Champoux et al., 2010). We note that the proportion of incorrect intervals appears higher in the current data than in other research (e.g., Dalla Bella et al., 2007, 2009), but we used stricter criteria, incorporating both direction and magnitude (i.e., less than 50 cents error rather than 100 cents). Even accurate untrained singers tend to produce a median interval deviation in the range of 50–100 cents (Pfordresher and Brown, 2017). Thus, the accuracy of the controls can be considered typical of untrained singers.

Panel B examines tonality of renditions of familiar tunes (z-transformed proportion of tonal notes) plotted against singing accuracy (proportion of incorrect intervals, averaged across lyric or no lyric attempts) by individual. If the errors are tonally consistent with the melody (e.g., substituting one in-scale note for another), then the proportion of tonal notes should be high regardless of the number of errors. Alternatively, if singing errors deviate from the scale, then the tonality of the performance should decrease when the amount of singing error increases. Separate one-sample t -tests showed that the tonality of familiar renditions was above chance (z-score of 0) for the controls as a group, $M = 1.40$, $SD = 0.69$, $t(14) = 7.83$, $p < .001$, $d = 2.02$, 95% CI [1.02, 1.79], as well as for the group with amusia, $M = 0.71$, $SD = 1.27$, $t(17) = 2.37$, $p = .030$, $d = .56$, 95% CI [0.08, 1.34]. The tonality was greater than chance in absolute terms (i.e., z-score of 0) for 13 of 18 amusics and 15 of 15 controls. However, there was a negative correlation between the proportion of incorrect intervals and the z-

transformed proportion of tonal notes in familiar tune performances, $r(31) = -.56$, $p < .001$, 95% CI $[-.76, -.27]$ (solid trend line), indicating that more errors in accuracy coincide with more deviations from tonality. The dashed vertical and horizontal lines mark the scores of a professional singer.

Singing inaccuracy on familiar tunes also correlated negatively with both measures of tonality for improvisations: z-transformed proportion of tonal notes, $r(31) = -.56$, $p < .001$, 95% CI $[-.76, -.27]$ (i.e., identical to the result from familiar tunes); proportion of final note ending on the tonic, $r(31) = -.53$, $p = .001$, 95% CI $[-.74, -.23]$. In short, inaccurate singers tended to be less tonal improvisers.

Movie S1 (separate file). Movie file visualizing key-finding algorithm. The upper plot visualizes the continuous probability density function (PDF) of the Krumhansl ratings for the minor mode. Size and position of the red dots represent the position and height of the histogram bars in the middle plot, respectively. The histogram bars in the middle plot represent the distribution of pitches across the octave, with height corresponding to pitch duration. The rightward shift represents transposition of the distribution in small steps. Note that bins/steps of 10 cents are used here for visualization, whereas the algorithm uses bins/steps of 1 cent. The lower plot represents the weighted mean of the negative log likelihood at each step, i.e., mean of NLL at each red dot index in the upper panel weighted by dot size. Lower values represent better fit, and a minimum value is reached at index 729 (i.e., transposition of 729 cents), which can be used to derive the tonic. The static red bars that appear when the minimum is reached represent the “best fit” between the PDF in the upper panel and the histogram in the middle panel.

Audio S1 (separate file). Audio file of a more tonal improvisation. The song was recorded by a participant with amusia to the verbal prompt, ‘love song’. This item received a z-score of 1.80, corresponding to 22 of 26 notes (84.6%) being in the determined scale, and ending on the tonic. The key-finding analysis of this file is visualized in Figure 1.

Audio S2 (separate file). Audio file of a less tonal improvisation. The song was recorded by a participant with amusia to a short musical stem (not provided). This item received a z-score of -2.06, corresponding to 14 of 24 notes (58.3%) being in the determined scale, and with the final note *not* matching the determined tonic.

Audio S3 (separate file). Audio file of a more tonal improvisation. The song was recorded by a nonmusician control participant to a short musical stem (not provided). This item received a z-score of 2.46, corresponding to 19 of 20 notes (95.0%) being in the determined scale, and with the final note matching the determined tonic.

Audio S4 (separate file). Audio file of a less tonal improvisation. The song was recorded by a nonmusician control participant to the prompt “sad song”. This item received a z-score of -1.76, corresponding to 15 of 25 notes (60.0%) being in the determined scale, and with the final note *not* matching the determined tonic.

SI References

- Dalla Bella, S., Deutsch, D., Giguère, J.-F., Peretz, I., & Deutsch, D. (2007). Singing proficiency in the general population. *Journal of the Acoustical Society of America*, 121, 1182–1189. <https://doi.org/10.1121/1.2427111>
- Dalla Bella, S., Giguère, J.-F., & Peretz, I. (2009). Singing in congenital amusia. *Journal of the Acoustical Society of America*, 126, 414–424. <https://doi.org/10.1121/1.3132504>
- Krumhansl, C. L. (1990). *Cognitive foundations of musical pitch*. Oxford University Press.
- Müllensiefen, D. (2009). Fantastic: Feature ANalysis Technology Accessing STatistics (In a Corpus): Technical Report v1.5. 37.
- Pfordresher, P. Q., & Brown, S. (2017). Vocal mistuning reveals the origin of musical scales. *Journal of Cognitive Psychology*, 29, 35–52. <https://doi.org/10.1080/20445911.2015.1132024>
- Tremblay-Champoux, A., Dalla Bella, S., Phillips-Silver, J., Lebrun, M.-A., & Peretz, I. (2010). Singing proficiency in congenital amusia: Imitation helps. *Cognitive Neuropsychology*, 27, 463–476. <https://doi.org/10.1080/02643294.2011.567258>