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# Harmonic calls and indifferent females: no preference for human consonance in an anuran

Karin L. Akre[1,2], Ximena Bernal[3,4], A. Stanley Rand[4,†] and Michael J. Ryan[4,5]

[1]Biology Department, Duke University, Durham, NC 27708, USA
[2]Department of Psychology, Hunter College, New York, NY 10065, USA
[3]Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA
[4]Smithsonian Tropical Research Institute, Balboa, Panama
[5]Department of Integrative Biology, University of Texas at Austin, Austin, TX 78712, USA

The human music faculty might have evolved from rudimentary components that occur in non-human animals. The evolutionary history of these rudimentary perceptual features is not well understood and rarely extends beyond a consideration of vertebrates that possess a cochlea. One such antecedent is a preferential response to what humans perceive as consonant harmonic sounds, which are common in many animal vocal repertoires. We tested the phonotactic response of female túngara frogs (*Physalaemus pustulosus*) to variations in the frequency ratios of their harmonically structured mating call to determine whether frequency ratio influences attraction to acoustic stimuli in this vertebrate that lacks a cochlea. We found that the ratio of frequencies present in acoustic stimuli did not influence female response. Instead, the amount of inner ear stimulation predicted female preference behaviour. We conclude that the harmonic relationships that characterize the vocalizations of these frogs did not evolve in response to a preference for frequency intervals with low-integer ratios. Instead, the presence of harmonics in their mating call, and perhaps in the vocalizations of many other animals, is more likely due to the biomechanics of sound production rather than any preference for 'more musical' sounds.

## 1. Introduction

The evolution of the human music faculty, our neural system for processing music, is mysterious from both functional and phylogenetic perspectives. We might begin to understand the evolution of this complex trait by considering the evolutionary history of the rudimentary cognitive components that make up this system [1–4]. Several vertebrate species exhibit simple cognitive features that are a part of our music faculty, such as octave generalization in rhesus macaques [5], chord discrimination in pigeons [6], tone-sequence recognition in chickadees and starlings [7,8], relative pitch recognition in ferrets [9] and motor entrainment to rhythm in cockatoos and parrots [10,11]. Such antecedents of musicality are not universally held: fish cannot generalize octaves [12], and pigeons cannot learn rhythmic structure [13]. Understanding which animals possess which antecedents might help illuminate the path by which a music faculty evolved.

Preferential response to consonance is a component of the music faculty that occurs in human infants [14] and in some non-human primates [15] but not in others [16]. In human research, consonance is a psychophysical phenomenon and defines how the receiver perceives a stimulus—consonant listening experiences are pleasant and dissonant ones are unpleasant [17]. Pythagoras, however, defined consonance according to the physical characteristics of the sound. He proposed that simultaneous tones are more consonant when the mathematical ratio of their frequencies has lower integer values [18]. Human consonance rankings match Pythagoras' predictions for many intervals [17–19] but average consonance rankings compiled from several psychophysical studies demonstrate that the integer numbers do not accurately

predict all rankings [17], and a clear mathematical predictor of human consonance is not known. This could be related to the influence of human language on the evolution of consonance perception [17,20].

Listening experience cannot be reported in animals, but we can quantify their reactions to sounds that we find consonant or dissonant. Differential reactions to these sounds might derive from a simple biophysical interaction between sound and the auditory system, which would vary with sound properties such as frequency ratios. Such interactions might be a precursor to human consonance perception. Helmholtz proposed that the properties of our auditory system dictate consonance perception [21]. Research with domestic cats illustrates this principle. Spike patterns recorded in the auditory nerve fibres are temporally regular in response to what we perceive as consonant intervals and irregular in response to dissonant intervals [19]. In addition to spike rate, 'place' or location of excitation also contributes to frequency perception due to the tonotopic nature of the basilar membrane. Membrane vibrations caused by closely located frequencies might physically interact, contributing to a dissonant experience [22]. Given some of the shared properties of vertebrate auditory systems, it is expected that some antecedents to the music faculty appear in non-human vertebrates. Attraction to sounds that cause temporally regular spike rates or avoid close membrane interactions might be an antecedent to human consonance perception.

Many animal signals are consonant to humans, and one might expect this acoustic structure evolved in response to receiver preference for low-integer frequency intervals that humans find to be consonant [23,24]. On the other hand, when membranes such as vocal folds are excited, they vibrate in multiple modes, producing a fundamental frequency and higher harmonics determined by the resonance of the vibrating material [25,26]. Thus, the perceptual properties of the receiver, the biophysical properties of the sender or both could be responsible for widespread production of consonant low-integer frequency ratios in the animal kingdom. To demonstrate a preference for these simple ratios, it is necessary to study the preference directly and not assume it exists because of signal structure.

This study explores whether an anuran preferentially approaches dyadic frequency intervals with low-integer ratios. The anuran inner ear has two separate organs, the amphibian papilla (AP) and the basilar papilla (BP) [27]. The AP is structured tonotopically, in a similar manner as the basilar membrane. The BP is not structured in this way, so harmonic frequencies cannot elicit a place-dependent response in the BP. In the túngara frog (*Physalaemus pustulosus*), stimulation of primarily the AP by the call's main component is necessary and sufficient for mate recognition. Stimulation of primarily the BP by an additional element further enhances the call's attractiveness [24]. Both call components are harmonically structured.

We added artificial frequencies to attractive stimuli and measured female preference between stimuli with variable frequency intervals. We also considered whether BP stimulation explained female preference. Our results bring insight into two broad questions. First, does a preference for consonant sounds relate to tonotopic inner ear organization? If tonotopy contributes to preference for low-integer ratio sounds, females should preferentially approach lower integer frequency ratios only when they stimulate the AP alone. Second, did the harmonic structure of frog vocalizations evolve in response to a receiver bias for musicality? If females do not preferentially approach harmonic sounds, the production of harmonic vocalizations likely results from physical features of the vocal apparatus.

## 2. Methods and results
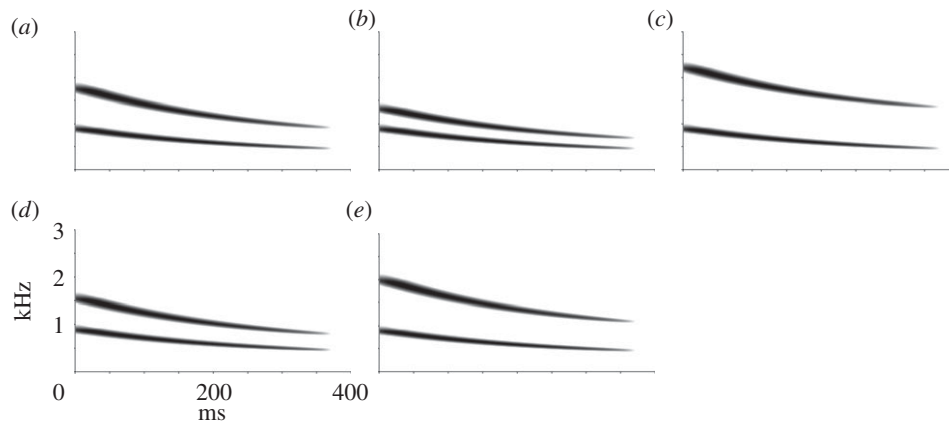
### (a) General experimental methods

The túngara frog's AP is most sensitive to sounds below 1500 Hz, with a best excitatory frequency (BEF) of 500 Hz. The BP is sensitive to sounds above 1500 Hz, with a BEF of 2100 Hz [28,29]. Males produce advertisement calls with an initial whine followed by 0–7 terminal chucks [24,30]. The whine is a downward frequency sweep from about 900 to 400 Hz and has substantial energy in harmonics 2–6 [29]. Females do not discriminate between the fundamental frequency sweep and the fundamental plus harmonics 2 and 3 [29]. It is not known, however, whether in other cases adding harmonics increases attractiveness, or conversely whether inharmonic upper frequencies decrease a signal's attractiveness. Although some anurans are sensitive to the harmonicity of frequency intervals [31,32], phonotaxis studies show either no influence on attraction [33] or an influence that depends on frequency modulation in stimuli with multiple frequency bands [34]. This study uses simple frequency dyads, considers ordinal variation in frequency ratios that might relate to biophysical origins of consonance and controls for BP stimulation by presenting frequencies that stimulate only the AP.

Frogs were collected between May and August of 2003 and 2004 in Gamboa, Panama. We performed phonotaxis tests, offering females a choice between two speakers broadcasting different stimuli. Collection, testing and stimulus construction procedures followed methods published previously [35].
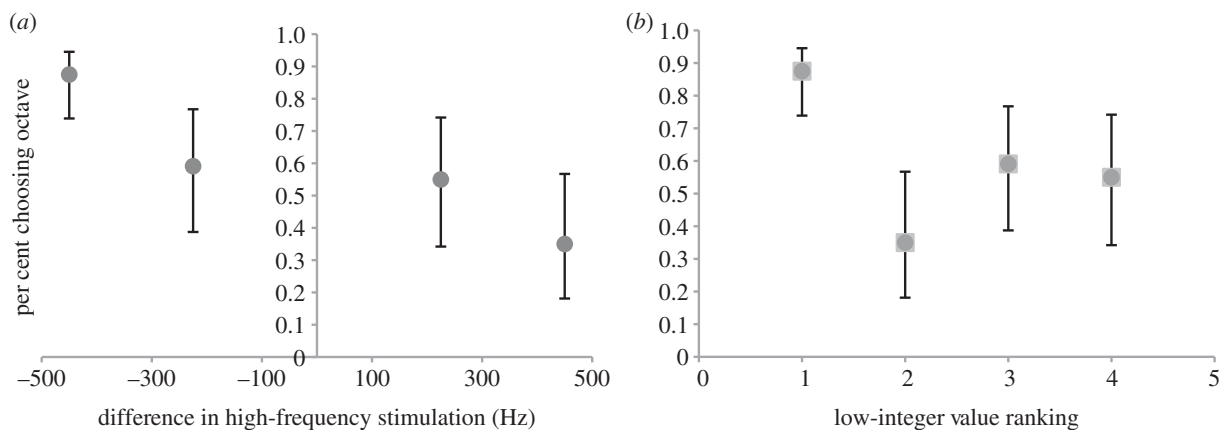
### (b) Do frequency ratios influence the attractiveness of a stimulus?

If frequency ratio integer values predict a female's attraction to a stimulus, dyads with lower integer ratios would be more attractive. This theory has informed research on cats [19] and on human consonance [18]. However, the biophysical interaction between sound, auditory organs and behavioural attraction is not clearly understood. Thus, we also tested whether the simple distinction between harmonic and inharmonic intervals explains female preference.

We created stimuli with two pure tones that swept downward. We tested whether females preferred a harmonic 2 : 1 relationship to four other stimuli with the same lower frequency, but variable inharmonic upper frequencies in ratios of 3 : 2, 5 : 2, 7 : 4 and 9 : 4 (figure 1). If frogs prefer lower integer ratios, they will always choose 2 : 1. We ranked each stimulus according to the ratio integer values. The octave (2 : 1) has the lowest integers, followed by the 3 : 2, 5 : 2, 7 : 4 and 9 : 4 stimuli, ranked 1, 2, 3 and 4, respectively. If ratio integers explain preference, then the proportion of females that prefer the octave should increase along with the integer values of the alternative stimulus. If females choose based on a general preference for harmonic over inharmonic sounds, then the proportion of females that prefer the octave should be significant and consistent for each test.

**Figure 1.** Sonograms for 900–450 Hz sweeps with variable higher frequencies: (*a*) 1800–900 Hz, 2 : 1; (*b*) 1350–675 Hz, 3 : 2; (*c*) 2250–1250 Hz, 5 : 2; (*d*) 1575–787.5 Hz, 7 : 4 and (*e*) 2025–1075 Hz, 9 : 4.



**Figure 2.** The percentage of females choosing the octave over the inharmonic call (*a*) decreased as the difference between the maximum frequencies of the inharmonic and octave stimuli increased and (*b*) was not influenced by the low-integer value ranking of the inharmonic stimulus. Bars show 95% CIs.

Alternatively, the amount of BP stimulation might determine preference. Decades of work show that sound stimulating both inner ear organs is most attractive to anuran females [36,37], including túngara frogs [38]. Frequency sweeps that cover a greater range of frequencies above 1500 Hz will stimulate the BP more. If this determines female preference, we predict a preference for 2 : 1 (maximum frequency 1800 Hz) over 3 : 2 (1350 Hz), and over 7 : 4 (1575 Hz). But the other stimuli (9 : 4, 2025 Hz; 5 : 2, 2250 Hz) would be preferred to 2 : 1, with the strongest preference for 5 : 2. We calculated the difference in BP stimulation for each pair of sounds as the maximum frequency of the test stimulus minus that of the octave.

Females could respond to multiple tests, but each female was presented with a given test only once. Females completing some but not all tests were included in the dataset, and the generalized estimating equation (GEE) in SPSS 21 accounted for one individual completing multiple tests as repeated measures with missing data. Experiment 1 used 80 females to complete 102 choices (2 : 1 versus 3 : 2 $N = 40$; versus 7 : 4 $N = 22$; versus 9 : 4 $N = 20$; versus 5 : 2 $N = 20$).
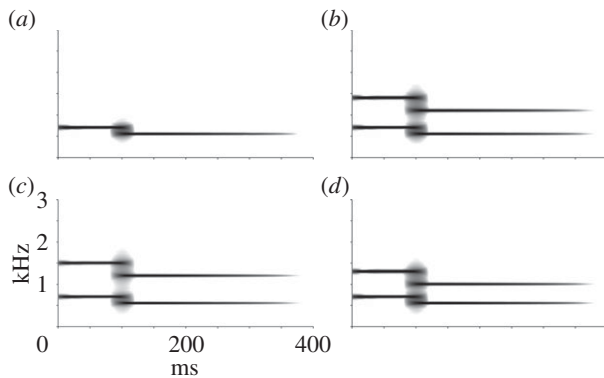
Females preferred 2 : 1 over 3 : 2 (87.5% preference, two-tailed exact binomial test $p = 0.0000014$) and showed no preference in the other tests (59% preference for 2 : 1 over 7 : 4, $p = 0.5235$; 55% preference for 2 : 1 over 9 : 4, $p = 0.8238$; 65% preference for 5 : 2 over 2 : 1, $p = 0.2632$). Females preferred

the octave only when the BP is not stimulated by the alternative, thus there is no evidence that túngara frogs prefer harmonic over inharmonic intervals.

A GEE test with choice (octave or inharmonic stimulus) as the dependent variable, and integer value ranking, difference in maximum frequency and their interaction as independent variables reveals that maximum frequency difference was the only significant factor explaining female response (Wald $\chi^2 = 7.286$, d.f. $= 1$, $p = 0.007$). Removing the interaction and integer value ranking variables improved the corrected quasi-likelihood under independence model criterion (QICC), a goodness-of-fit statistic, and in this model maximum frequency difference was significant at $p < 0.0001$ (Wald $\chi^2 = 16.371$, d.f. $= 1$). Thus, preference increased with BP stimulation (figure 2*a*), but the ratio integer values did not influence preference (figure 2*b*).

## (c) Within the amphibian papilla, does low ratio integer value increase attractiveness?

We tested whether frequency ratios within the response range of the tonotopic AP influence call attractiveness. Here, we tested preference between stimuli each consisting of two sequential tones. Sequential pure tones, resembling a frequency sweep, elicit phonotaxis. First, we tested whether a pure tone stimulus with no upper frequencies is equally

**4**



**Figure 3.** Sonograms for a 700 Hz tone followed by a 550 Hz tone, with variable higher frequencies: (*a*) none; (*b*) 1400 Hz followed by 1100 Hz, 2 : 1; (*c*) 1500 Hz followed by 1200 Hz, 15 : 7 and 24 : 11 (100 Hz above 2 : 1) and (*d*) 1300 Hz followed by 1000 Hz, 13 : 7 and 20 : 11 (100 Hz below 2 : 1).

preferred to a one with the first harmonic added (figure 3). Then we asked how the integer values for ratios of two frequencies within the AP influences preference. To test this, we presented the 2 : 1 stimulus versus a stimulus with identical lower frequency but with an inharmonic upper frequency distorting the ratio relationship by 100 Hz above or below the 2 : 1 ratio, creating high-integer ratios (15 : 7 followed by 24 : 11, and 13 : 7 followed by 20 : 11). If frogs prefer harmonic stimuli, they should choose the octave in both tests. We also considered whether frogs prefer sounds with frequencies closer to the AP's BEF (500 Hz) [28,29]. If so, females should prefer the lower frequency call in each test. No female responded more than once in a given test.

Within the AP, harmonics influence the attractiveness of artificial stimuli. Females prefer a two tone series when the 2 : 1 harmonic is added (75% preference, $N = 20$, two-tailed exact binomial test, $p = 0.0414$). Neither ratio integer values nor coincidence with the AP's BEF influenced phonotaxis. Females showed no preference between a 2 : 1 ratio series of two tones and a stimulus distorting the relationship by 100 Hz above (50% preference, $N = 20$, two-tailed exact binomial test, $p = 1.0$) or below (50% preference, $N = 20$, two-tailed exact binomial test, $p = 1.0$) the 2 : 1 ratio.

## 3. Discussion

Attraction to harmonically structured sounds is a basic feature of human consonance perception. Harmonic vocalizations abound in the animal kingdom, including the mating calls of túngara frogs. Harmonicity, however, does not influence female túngara frog attraction to acoustic stimuli, even when controlling for BP stimulation by restricting frequencies to those detected by the AP. Although females do attend to harmonic components of mating calls, they do not discriminate based on frequency ratio, and they do not avoid intervals that would be dissonant to humans. Instead, their preference behaviour matches the prediction that increased BP stimulation increases attraction.

Although some melodic animal vocalizations are not strictly musical [39], consonant harmonics are common in animal vocalizations. Yet, it is not clear whether such signal structures evolved in response to selection generated by

receivers, or even whether harmonics *per se* matter to receivers. Removing the harmonics completely from conspecific calls does not inhibit recognition, and calls with only upper harmonics are not attractive [29]. Disrupting the harmonic relationships as we have done in this study demonstrates that these intervals are not important to receivers even though they are present. This finding suggests that vocalizations are bound by the laws of physics, and when membranes such as vocal folds are set to vibrate certain frequencies resonate according to the properties of the tissues in the vocal apparatus, and these by their nature produce sounds defined consonant by both Pythagoras and listening experience. Thus the consonance of animal sounds cannot be taken as an indication that animals possess antecedents to human consonance perception.

In túngara frogs and anurans in general, stimulation of the BP is important in eliciting female choice [36,37,38]. Thus, it is not surprising that we found that the maximum frequency present was a significant factor in female response to variable frequency intervals. It is possible that controlling for amount of BP stimulation while still stimulating both the AP and BP would reveal more sensitivity to harmonicity, but this would require changing the lower frequency, which would compromise species recognition by females.

The tonotopic nature of the cochlea might influence consonance perception in humans [22,40], although this possibility is debated [41–43]. Even when stimulation of the BP was eliminated, we found no evidence that the tonotopic nature of the AP causes females to prefer consonant sounds. Thus, our data do not support the idea that tonotopic auditory organs result in attraction to frequency combinations in low-integer ratios. Also, previous studies found anuran sensitivity to harmonicity using sounds stimulating both the AP and BP [31–32,34], which further suggest that tonotopic organization does not play a role in harmonicity detection.

Although our results do not support an evolutionary origin to human consonance perception in a common ancestor with anurans, it is possible that other rudimentary components to the music faculty are present in anurans. Some anurans do respond differently to harmonic and inharmonic sounds [31,32], which might be a relevant antecedent to consonance perception even without behavioural attraction. Also, music is an emergent process drawing from several aspects of sound perception, including both tonality and rhythmicity. Anurans might have some sensitivity to rhythm, since males that call with alternating or synchronous patterns in a chorus must respond to perceiving other males' call timing [44,45]. Extending an understanding of the types of cognitive processing abilities that make up the music faculty and the diversity of animals that express these abilities will improve our understanding of how such a complex trait could evolve in humans.

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