

COMPARATIVE COGNITION

Humans share acoustic preferences with other animals

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Many animals produce courtship sounds, and receivers prefer some sounds over others. Shared ancestry and convergent evolution may generate similarities in preference across species and underlie Darwin's conjecture that some animals "have nearly the same taste for the beautiful as we have." In this study, we show that humans share acoustic preferences with a range of animals, that the strength of human preferences correlates with that in other animals, and that humans respond faster when in agreement with animals. Furthermore, we found greatest agreement in preference for adorned, ancestral, and lower-frequency sounds. Humans' music listening experience was associated with preferences. These results are consistent with theories arguing that biases in processing sculpt acoustic preferences, and they confirm Darwin's century-old hunch about the conservation of aesthetics in nature.

Many animals produce signals to attract mates. These signals span sensory modalities from visual color patterns and movements to acoustic songs and calls to olfactory plumes—and are produced throughout the animal kingdom, including in arthropods, mollusks, and all vertebrate classes (1).

The receivers of mating signals generally exhibit preferences for the signals of conspecifics relative to those of other species (1, 2), and mating with conspecifics usually results in more-viable offspring (3, 4). Moreover, mating signals typically vary within a species, and receivers often exhibit preferences for some signal variants over others, which may result from sensory biases (5–15), adaptive pressures (16–20), or both.

Preferences emerge from an interaction between the signal's attributes and the receiver's sensory system. For example, stimuli that evoke greater stimulation of the sensory system are often preferred over stimuli that are less stimulating (14, 21). There is substantial conservation in the organization of sensory systems across species [e.g., (22)], which may explain why the dazzling colors of butterflies, aromas of flowers, and songs of birds are attractive not just to their intended receivers but to humans as well.

Darwin suggested that some animals "have nearly the same taste for the beautiful as we have" (23, 24). Here, we report a citizen-science experiment testing this hypothesis.

Results

We gathered 110 pairs of sounds produced by 16 nonhuman animal species (hereafter, animals), which were recorded in prior research (25–50), and played them to humans recruited globally online ($n = 4196$ participants; geographic distribution shown in fig. S1) in a gamified experiment (51). Participants rated which of the two sounds in a pair they "liked more" (see materials and methods and Fig. 1A; $n = 48,567$ responses).

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For each stimulus pair, the animals from which the sounds originated are known to display a preference for one of the two sounds (hereafter, the more attractive sound). For example, male túngara frogs can produce a simple call or a complex one that includes an acoustic adornment; female frogs choose a complex call over a simple call ~84% of the time, a 5:1 preference (41). The strength of animals' preferences varied (range: 55 to 93%; materials and methods and table S1), enabling tests of the degree to which human preferences were similar to those of other species.

There were three principal findings. First, human preferences for animal sounds correlated with the preferences of the animals themselves. The percent of humans that selected the more attractive sound correlated positively with the animal's strength of preference [linear mixed model (LMM): $F_{1,34.9} = 6.2$, $P = 0.02$; Fig. 1B and table S2], and relatedly, the animal's strength of preference predicted whether participants selected the more attractive sound [generalized linear mixed model (GLMM): $\chi^2_1 = 6.0$, $P = 0.01$; table S2].

Second, agreement between human and animal preferences was higher when the animals' preferences were more robust. When animals exhibited moderately strong preferences (at least 2:1 odds, or 67% preference; materials and methods), humans were significantly more likely than chance to choose the more attractive sound [GLMM: mean 56.4% agreement, 95% confidence interval (CI): 55.8 to 57.0%; $z = 2.3$, $P = 0.02$; Fig. 1C and table S2]. This effect was slightly weaker when including all stimuli (i.e., including those with subtle animal preferences; 54.0% agreement: $z = 1.9$, $P = 0.05$) and stronger with a more stringent cutoff (at least 3:1 odds: 59.5% agreement; $z = 3.4$, $P < 0.01$). All subsequent analyses use the 2:1 animal preference dataset by default. Moreover, we found no significant differences in agreement across the large clades of animals present in the study (birds, mammals, frogs, or insects; $\chi^2_3 = 3.3$, $P = 0.35$; table S2).

Third, shared preferences across humans and animals were supported by two additional measures. Humans answered 51 ms faster, on average, when choosing the more attractive sound than the less attractive one (GLMM: $\chi^2_1 = 32.0$, $P < 0.01$; Fig. 1D and table S2). Their responses were also internally reliable: In a subset of trials, we played participants the same stimulus pair twice and found that their preference was maintained across both presentations at a rate higher than chance (63% were the same choice, on average; $t_{69} = 5.0$, $P < 0.01$; Fig. 1E and table S2).

We next tested the degree to which specific properties of animal sounds are predictive of human preferences. The stimuli studied here derived from three classes of experiments, each originally designed to test whether a specific characteristic was predictive of preferences in animals. In planned analyses, we asked whether humans similarly expressed such preferences.

In the first class of experiments, researchers experimentally manipulated the sounds of animals (table S1). For example, in three pairs of frog calls (38, 44), researchers measured frogs' preferences for frequency-manipulated calls. Our human participants agreed with the frogs (preferring lower frequency calls; GLMM: $z = 3.9$, $P < 0.01$). Similarly, both humans and animals preferred sounds with acoustic adornments, such as "trills," "clicks," and "chucks" ($z = 4.0$, $P < 0.01$). There was no significant agreement for stimuli distinguished primarily by rate or amplitude modulation (Fig. 2A and table S3).

In the second class of experiments, researchers studied animals across experimental conditions (e.g., varied social contexts) and tested preferences for the sounds they produced. Notably, humans disagreed with animals for stimuli that varied in the developmental experience of the signaler ($z = -2.5$, $P = 0.01$). Specifically, humans prefer zebra finch songs from males reared without a tutor ("isolate songs") over songs from birds that learned their song. We found no agreement for songs produced in different social contexts or songs produced with or without a nerve cut (Fig. 2A and table S3).

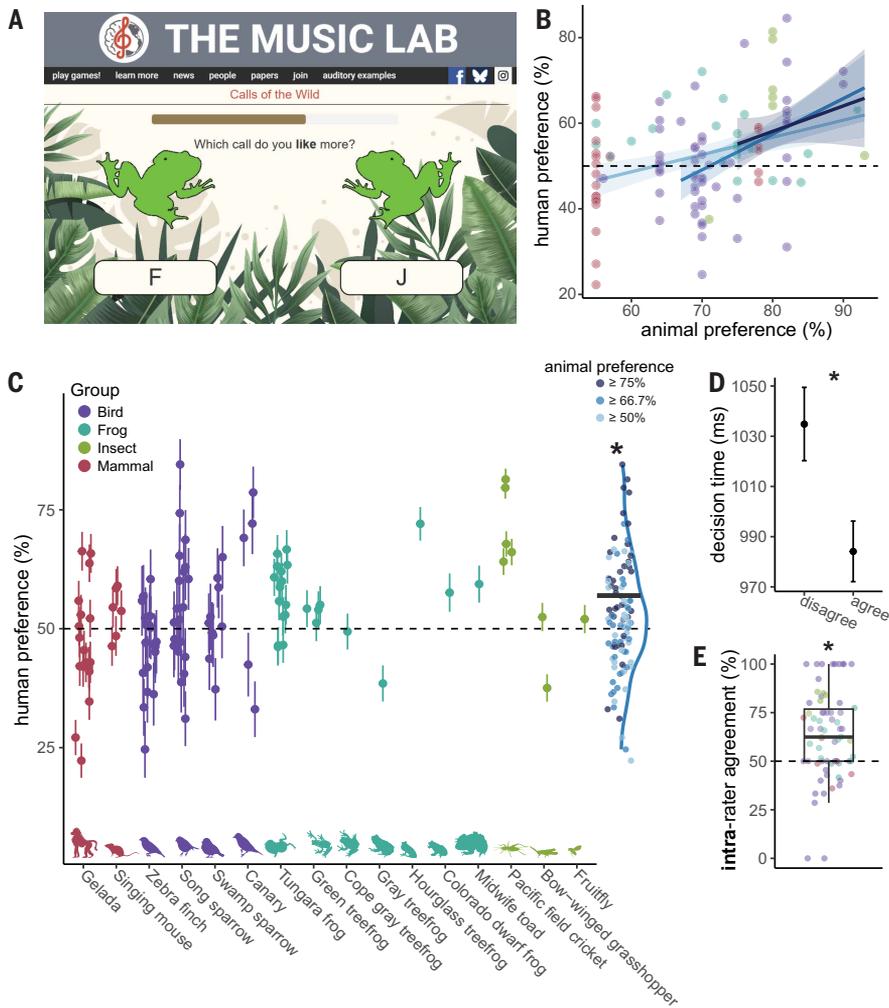


Fig. 1. Humans share acoustic preferences with other animals. (A) The screenshot shows the user interface, as appearing for participants who used a desktop or laptop computer. This screen appears after both sounds on a given trial have played, and the participant responds by pressing the F or J key on their keyboard (or clicking or tapping one of the two animal silhouettes). (B) The scatterplot shows the correlation between the strength of the animal's preference for the more attractive sound in a stimulus pair (x axis) and the percent of humans who preferred the more attractive sound (y axis). Each dot represents a stimulus pair. Trendlines show simple linear correlations (shading for standard error) when analyzing all stimuli (light blue); stimuli with at least a 2:1 animal preference (medium blue); or stimuli with at least a 3:1 animal preference (dark blue). (C) Humans chose the more attractive sound above chance. In the main plot, the dots each depict the percent of humans who preferred the more attractive sound from a given species; the vertical lines represent 95% CIs, and the horizontal dotted line represents chance (50%). To the right, each dot represents the mean level of human preferences for a stimulus pair, with color indicating the strength of preference in animals. The solid blue line represents a kernel density estimation, and the horizontal bar denotes the mean across stimulus pairs with at least a 2:1 preference in animals. (D) Decision-making time was significantly shorter for trials when the participant selected the more attractive stimulus; the dots depict the mean, and the error bars depict 95% CIs, collapsing across all trials (back-transformed from z-scores for visualization). (E) When participants heard the same stimulus pair more than once, their preferences were maintained, on average. Each dot depicts the mean intrarater agreement for a stimulus pair, and the box plot depicts the median, interquartile range (IQR), and $1.5 \times$ IQR. Across all panels, the colors correspond to a large phylogenetic group. * $P < 0.05$.

In the third class of experiments, researchers recorded the natural variation in sounds across individuals and tested animals' preferences for them. Humans shared a preference for sounds that had less evolutionary novelty; both humans and crickets preferred ancestral "chirps" over recently evolved "purrs" ($z = 7.3$, $P < 0.01$; Fig. 2A). In some cases, receivers prefer the sounds produced by certain individuals over

others, but the exact cause of the preference is unknown. We observed a nonsignificant trend toward agreement on these general individual differences ($z = 1.7$, $P = 0.08$; Fig. 2A and table S3).

In exploratory analyses, we also asked whether any single acoustic feature could predict which stimulus was more attractive to humans and/or other animals across all stimuli. Consistent with the idea that preferences arise from complex interactions of multiple cues (52), we did not find that a single acoustic feature predicted the behavior of both humans and animals. In this dataset, our analysis indicated that animals were more likely to prefer the stimulus with greater brightness, higher spectral centroid, or shorter duration (Fig. 2B and table S4), whereas humans were more likely to prefer the stimulus with lower pitch (Fig. 2B, fig. S2, and table S4).

Lastly, we tested whether characteristics of the participants were predictive of their agreement with animals. We predicted that prior experience with animal sounds and musical expertise would predict human preferences given that experience can shape auditory perception and preferences (53–56).

Neither prediction was supported. Humans with experience identifying animals by their sounds, such as birders ("animal experts"; $n = 373$, ~9% of participants) and expert musicians ($n = 730$, ~19% of participants), exhibited similar degrees of agreement as nonexperts (GLMMs: animal experts: $\chi^2_1 = 1.9$, $P = 0.17$; music experts: $\chi^2_1 = 1.3$, $P = 0.25$; Fig. 2C). The only significant predictor of agreement was time listening to music, with those reporting more time listening to music per day agreeing with animals more ($\chi^2_1 = 8.5$, $P < 0.01$; Fig. 2C, fig. S1, and table S5).

In exploratory analyses, we asked whether demographic variables (e.g., age and gender) predict preference; gender is of particular interest given that preferences can vary by sex in animals (57, 58). Although no demographic variable predicted human preference (Fig. 2C and table S5), one result was intriguing: Analysis of the full dataset (i.e., including the stimuli with weak animal preferences) revealed a small significant effect of participant gender, in which male participants agreed with animals more than female participants. But this result was internally inconsistent (materials and methods) and did not hold when limiting the stimulus set to pairs with clear preferences in animals. We therefore suggest caution with interpretation. Notably, human agreement with animals remained significantly above chance ($z = 2.3$, $P = 0.02$; table S1), even after adjusting the main analysis for demographic variables (gender, education, age, and income) or time spent listening to music.

Discussion

We report shared acoustic preferences between humans and other animals, generalizing across insects, frogs, birds, and nonhuman mammals. The strength of preferences for the sound that animals preferred (the more attractive sound) was correlated across humans and animals; humans were more likely than chance to prefer the more attractive

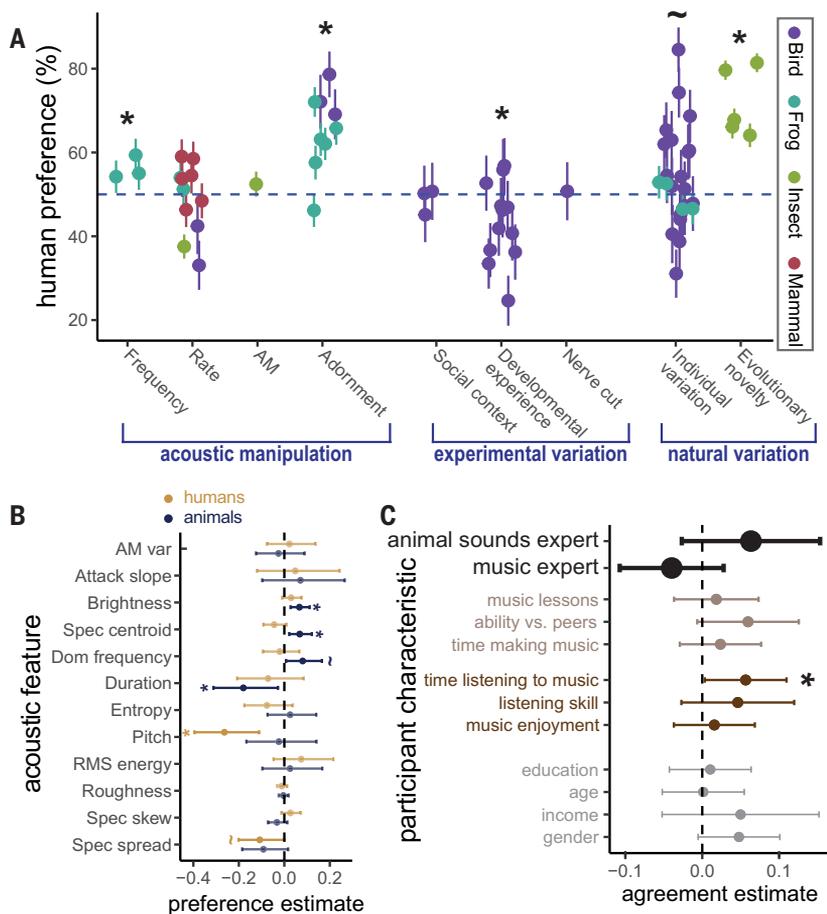


Fig. 2. Influence of acoustic traits and participant characteristics on human-animal agreement.

(A) In some cases, variation within stimulus pairs predicted human preferences. There were three categories of variation: acoustic manipulations; experimental variation, in which the animals producing the sounds differed on the basis of a manipulation; or natural variation, in which the sounds varied without experimental input. Dots denote the mean human preference for the more attractive sound in each stimulus pair, and the vertical lines denote 95% CIs. AM, amplitude modulation. (B) Dots denote model estimates (z-scores), and horizontal lines denote 95% CIs for each acoustic feature on human (tan) or animal (dark blue) preferences. (C) Dots denote estimates from models asking whether a given participant characteristic predicted human agreement with other animals, and the horizontal lines denote 95% CIs (values binarized for visualization). The two large black dots denote planned analyses, and smaller dots indicate exploratory analyses relating to music production (light brown), perception (dark brown), or demographics (gray). * $P < 0.05$, ~ $P < 0.10$. AM var., amplitude modulation variance; Spec centroid, spectral centroid; Dom frequency, dominant frequency; RMS energy; root mean square energy; Spec skew; spectral skewness; Spec spread, spectral spread.

sound; and humans answered more quickly when selecting the more attractive sound.

These results are consistent with general form-function relationships in acoustic signals across species (59–65). For example, sound “roughness” is observed in alarm and distress calls and is perceived as aversive across numerous species (52, 66–72). Humans appear to be sensitive to this and other form-function relationships in other species (73–76). Moreover, some animals are sensitive to distress calls from other species, and many animals respond to heterospecific alarm calls (77, 78). Although most studies have focused on sounds used in aggressive, aversive, or submissive contexts, our results suggest that cross-species form-function relationships may similarly be used for preference. Such relationships may underlie the perception

of attractiveness in our own communicative vocalizations, including speech and music (52, 79–81).

There is little evidence that specific features robustly predict preferred sounds (52, 66, 80), which is consistent with our finding that no single acoustic feature predicted both human and animal preferences across all stimuli. Relatively unstandardized measures of sound (such as “complexity”) are often proposed to explain preferences (82–86). For example, flycatchers and starlings prefer individuals with more complex (larger) repertoires, but this measure cannot be directly applied to all species (83, 84). Humans similarly prefer more complex birdsongs based on acoustic variation within song (87); but again, this measure is difficult to generalize across species (88, 89).

We did find that humans (but not other animals) generally preferred the stimulus with lower pitch (90), which may relate to human-specific pitch perception (91). Overall, there were few similarities across animals and humans in the specific acoustic characteristics that served as cues to attractiveness—despite their shared overall preferences. Future comparative studies could benefit from stimuli with specific acoustic manipulations. Humans’ and animals’ acoustic preferences likely result from multiple, interacting cues, perhaps reflecting cross-species differences in auditory processing (22, 91, 92), as well as shared biases in acoustic processing for complex and nonlinear interactions rather than linear-preference functions for single acoustic features.

Whereas we did not find that experience with animal sounds [compare with (55, 93)] or music production expertise aligned with animal preferences, we did find that higher levels of music listening predicted whether humans agreed with animals. Music training is known to be associated with advantages in auditory processing ability [reviewed in (94)], and at least one study shows an association between auditory discrimination abilities and music listening time (95). Perhaps sustained music listening leads to increased attention or better auditory discrimination ability, which translated to higher concordance with animals—whose vocalizations can share features with music [e.g., (96, 97)].

We note that preferences in animals are often subtle, are context-dependent, and can vary across individuals and populations (98). This may account for the high degree of variation in the strength and direction of human preferences observed across stimuli and the relatively subtle main effect of agreement between humans and other animals. The overall pattern of convergent evidence from multiple analysis approaches, combined with the increasing robustness when limiting the sample to stimulus pairs for which animals themselves show

stronger preferences, suggests a robust main effect.

Taken together, these results confirm that a single species can harbor similar preferences to a taxonomically broad range of species. Whereas Darwin’s original idea of shared preferences alluded to the visual coloration of birds, our findings suggest a more expansive shared “taste for the beautiful” (23, 24), motivating work across many species and in other modalities (99). Lastly, these results remind us that much of the beauty we find in nature was intended for receivers other than ourselves.

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Supplementary Text; Figs. S1 and S2; Tables S1 to S5; References (100–106); MDAR Reproducibility Checklist

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