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Phonology and Geographic Song Discrimination in Song Sparrows

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Abstract

We investigated whether song sparrows discriminate foreign from local songs using specific phonologic markers, a mechanism of geographic discrimination previously described for some other songbirds. Song sparrows from Linesville, Pennsylvania (PA) respond more strongly to local songs than to songs from Millbrook, New York (NY). We identify 61 note categories in PA and NY songs, of which 13 are unique to PA, 17 are unique to NY, and 31 are shared. The most common note category in PA song, 'buzz BO5', is present in 89% of PA songs and only in 8% of NY songs; this difference in percentage representation is the largest we found for any note category. Substituting this potential PA marker into NY songs, however, did not make those songs more salient to PA sparrows; instead, PA males tested with territorial playback responded significantly less aggressively to NY/PA hybrid songs than to NY songs. A series of control experiments showed that song sparrows do not detect substitution of PA notes into PA songs or of NY notes into NY songs. The results weigh against the hypothesis that geographic discrimination in song sparrows is accomplished simply by recognition of a small number of phonologic markers.

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Introduction

In many taxa, animals have been shown to respond differently to signals typical of their own population as compared with functionally identical signals produced by individuals of a foreign population (Milligan and Verner 1971; Ritchie 1991, Wright and Dorin 2001). In fewer cases, however, is it known what signal features provide the perceptual basis of this discrimination. Identifying the physical cues that animals use to discriminate among categories of signals has long been of interest to ethologists and comparative psychologists studying the mechanisms that underlie communication systems (Marler and Hamilton 1966).

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Recent analyses have used knowledge of the salience of signal features as a starting point for understanding the role of production mechanisms, perception mechanisms and the environment in shaping signal evolution (Bradbury and Vehrencamp 1998). Thus, analysis of the features used by animals to discriminate local from foreign signals may be a useful step toward understanding the functional consequences of geographic variation in signal structure.

Song sparrows (*Melospiza melodia*) discriminate local songs from songs produced by song sparrows at distant sites (Harris & Lemon 1974; Searcy et al. 1997, 2002). An ability to discriminate geographic variants of vocal signals is common among songbirds (King et al. 1980; Tomback et al. 1983; Balaban 1988). Many of the species showing geographic discrimination exhibit low within-population variation in song structure, making it relatively easy for us, and presumably for the birds, to discern differences between populations. Song sparrows, by contrast, show extremely high within-population variation in song, and against this background between-population differences are difficult to detect. How, then, are song sparrows able to discriminate local from foreign songs? Here we address this question through experiments in which we measure the response of male song sparrows to foreign songs into which we have inserted local notes.

Geographic variants might be discriminated based on either element composition (phonology) or element order (syntax). In white-crowned sparrows (*Zonotrichia leucophrys*), females respond more strongly to local than to foreign dialects (Baker 1983; Baker et al. 1987). In most cases, male white-crowned sparrows also respond more strongly to local than to foreign dialects (Tomback et al. 1983), but sometimes male response is strongest to an adjacent foreign dialect (Baker et al. 1981). Possible cues for dialect discrimination are easy to identify, as all the males within a dialect population sing the same, single song type (Marler and Tamura 1962), making differences between dialects obvious. Baker et al. (1987) and Thompson & Baker (1993) studied two adjacent dialects from Northern California that differ in three of the four phrase types making up white-crowned sparrow song. For each phrase type, substitution of a foreign for a local phrase lowers both courtship response in females and aggressive response in males. In this case, then, birds of both sexes discriminate between geographic dialects based on a series of phonologic markers.

Two subspecies of brown-headed cowbirds, *Molothrus ater ater* and *M. a. obscurus*, also show consistent differences in song structure despite the existence of within-subspecies variation. King et al. (1980) found that 87% of *obscurus* songs included a particular element type, the 'mid-song element' or MSE. Only 3% of *ater* songs contained this element. Females of both subspecies give more courtship display in response to their own subspecies songs (King et al. 1980). When the MSE is reduced in amplitude, *obscurus* females respond less to the altered songs, whereas *ater* response is unchanged (King & West 1983). Female *obscurus* thus recognize their own subspecies at least in part by the presence of this single, phonologic marker.

In swamp sparrows (*Melospiza georgiana*), Marler & Pickert (1984) found that all notes from NY and Minnesota populations could be sorted into the same six categories based on multivariate analysis of frequency and time measurements of sonagrams. Clark et al. (1987) supported this finding using spectrographic crosscorrelation to sort notes into categories. On a gross level, then, no phonologic differences exist between these populations. By contrast, the two populations differ significantly in the relative order in which notes occurred in songs, a syntactic difference. In playback experiments with these two populations, Balaban (1988) found both sexes to be responsive to note syntax. Females in particular prefer their own population's syntax, but they also show some preference for their own population's notes. Swamp sparrows thus must make finer phonologic discriminations than suggested by Marler & Pickert's (1984) categories.

In song sparrows, identification of geographic song variants seems more difficult than in these other species. Each song sparrow song is complex, containing two to five phrases and large numbers of note types (Mulligan 1966; Podos et al. 1992), and each male sings a repertoire of five to 16 markedly different song types (Borror 1965: Podos et al. 1992). In western populations of song sparrows, neighboring males share a substantial proportion of their song types (Hill et al. 1999; Wilson et al. 2000), but in eastern populations, such as the ones we study, sharing is uncommon (Borror 1965; Hughes et al. 1998). With each male singing a substantial number of song types, and most of these apparently unique, the total number of distinct song types sung in a given area can be very large. Against this background of high within-population variation, consistent differences between populations are difficult to discern. Nevertheless, song sparrows clearly do have the capacity to discriminate geographic variants of song. Searcy et al. (1997) found that both male and female song sparrows from Linesville, PA responded more strongly to local songs than to songs recorded from song sparrows in Millbrook, NY, 540 km distant. Later work showed that PA females are able to discriminate local songs from foreign songs recorded from as close as 34 km (Searcy et al. 2002).

Here we report on our attempts to identify a cue used by male song sparrows from Linesville, PA to discriminate local songs from Millbrook, NY songs. We concentrate on phonology rather than syntax, because syntax is so complex and variable in song sparrow song that we are doubtful that syntactical differences could provide consistent cues to distinguish songs from different populations. In testing for an effect of phonology on geographic discrimination, our first step was to survey the note composition of PA and NY songs. Here our goal was not to describe a full catalog of phonologic elements, but instead to identify one or more phonologic elements that are substantially more common in PA than NY, and which thus may serve as potential markers of PA song. Next, we digitally substituted a potential PA marker into a series of NY songs, producing hybrid NY/PA songs. Finally, we tested the response of PA males to PA, NY, and NY/PA songs using territorial playback. If the potential marker is used as a cue to identify local song, then response to NY/PA songs should be stronger than response to unmodified NY songs, i.e. addition of a local marker to foreign song should make the foreign song more acceptable. As there is every reason to think that multiple markers are needed to identify local songs in song sparrows, and because we altered only one of these markers in NY/PA songs, we predicted that response would be weaker to NY/PA than to PA songs.

Methods

Phonologic Survey

We recorded the complete repertoires of eight male song sparrows from each of two populations: Linesville, Crawford County, PA (41°40'N, 80°30'W) and Millbrook, Dutchess County, NY (41°50'N, 73°40'W). In PA, we recorded territorial males with either a Sony TCM5000EV or a Marantz PMD 221 cassette recorder and a Realistic Omnidirectional microphone (RadioShack, Fort Worth, USA) in a Sony PBR-330 parabola. New York birds were captured on their territories and recorded in captivity. Four of the NY males sang spontaneously, and the other four were induced to sing by testosterone treatment. New York males were recorded with a Marantz PMD 221 cassette recorder and a Tandy 1070A microphone (RadioShack, Fort Worth, USA). Searcy (1984) suggests that 300 songs are necessary to find the complete repertoire of eastern song sparrows; we exceeded that criteria for all 16 males.

We identified song types for each male using minimal unit of production (MUP) analysis (Podos et al. 1992; Peters et al. 2000). The eight PA males sang a mean of 8.4 (± 0.5 SE) and a total of 67 song types. The eight NY males sang a mean of 10.9 (\pm 1.4) and a total of 87 song types. We produced representative sonograms of each song type in each male's repertoire using a Kay Elemetrics DSP Sona-Graph Model 5500 (Key Electronics, Lincoln Park, USA; 0-8 kHz and 300 Hz filter bandwidth). We identified all the unique notes (referred to as note types) sung by each male, and chose one note spectrogram to represent the type. The note types were then grouped into categories based on acoustic properties and shape, without reference to the individual or population source. We took a 'splitter's' approach (Marler & Pickert 1984) to forming note categories to insure that we had a high degree of similarity within each category, with the restriction that each category had to contain more than one note type. We first divided note types into buzzes, tones, and buzz/tone combinations. 'Buzzes', as defined by Marler (1969), are notes with rapid amplitude and frequency modulation. Buzzes were further divided based on the shape of the pulse (i.e. a wideband upsweep, narrow band downsweep, etc.), the general rate of the pulse, and/or the overall shape of the buzz. We divided tones into those with a single trace and those with simultaneous traces and then made further subdivisions based on the shapes of the traces. Buzz/tone combinations were categorized based on a mix of the criteria for buzzes and tones. Again, we did not intend this classification to be a definitive taxonomy of song sparrow note phonology; instead, we simply grouped note exemplars into types in order to identify classes of notes that occurred frequently in one population and not the other.

Playback Design

We measured response to songs in males using territorial playback. The experiments contrasted response to either three (expt 1) or two (expts 2–5) categories of stimuli. All song categories were represented by 12 stimulus tapes, each containing a different natural or modified song. The stimulus tapes were matched across categories to form stimulus sets; for example, in experiment 1, each set contained one PA song, one NY song, and one NY/PA song. Each subject in each experiment was presented with all the stimulus tapes in one set. Order of presentation of the tapes was randomized for each subject.

Playback methods were those of Searcy et al. (1997), with slight modifications. Playback tapes were 6 min long and contained a single song repeated once per 10 s. We played the tapes using a Sony TCM 5000EV cassette recorder and a Nagra DSM speaker (Kudelski, Cheseaux, Switzerland). The speaker was placed face up on the ground, well within the boundaries of the subject's territory. Songs were played at an amplitude of 82–86 dB (measured at 1 m). We marked the position of the speaker with flagging, so that the same position could be used during each trial with that subject, and waited at least 2 d between successive trials with any subject.

We used as our sole response measure the distance of the subject to the speaker (averaged over the 6 min of playback), as past work with song sparrows indicated that this was the most reliable measure of response to territorial playback (Peters et al. 1980; Searcy et al. 1981). Before a trial commenced, we set out flagging at measured distances from the speaker, to aid in estimating distances. During trials, one observer reported the subject's distance to the speaker, while a second recorded these distances on flow sheets broken into 5-s intervals. In experiments 2–5, the primary observer was blind to the playback category being presented during each trial. Distance categories used were 0-2, 2-4, 4-8, 8-16, and > 16 m. Mean distances were calculated using the method of Peters et al. (1980).

Test Stimuli

The test stimuli in each experiment were some combination of songs recorded earlier near Linesville, PA (PA songs), songs recorded near Millbrook, NY (NY songs), and songs from either the PA or NY population modified with buzz substitutions. Although the PA songs and the male subjects were drawn from the same population, it is unlikely that our subjects were familiar with any of the individual birds from whom the songs were recorded because the recordings were made 3–6 yr before the playback tests were performed.

All playback songs were digitized at 25 kpts/s using 'SIGNAL' v 3.0 or v 3.1 software (Engineering Design, Belmont, MA, USA). Normal stimuli songs were recorded for playback directly from these digitized files. We constructed modified songs by digitally cutting out selected buzzes and pasting in buzzes from other source songs; 2–4 buzzes were substituted in this way for each modified song (e.g. Fig. 1), as described further below for each experiment. Care was taken during



Fig. 1: Sonagrams of one example of each of the song categories used in the playback experiments. (a) An unmodified PA song, with brackets indicating the buzzes that were taken from this song and substituted into the matching NY/PA song. (b) An NY/PA song, with brackets showing the buzzes obtained from the matching PA song. (c) An unmodified NY song, with brackets indicating the buzzes that were replaced in the matching NY/PA song. (d) A PA/PA(self) song, with brackets indicating the buzzes obtained from another song type belonging to the same PA individual. (e) A PA/PA(other) song, with brackets indicating the buzzes obtained from a song of another PA individual. (f) An NY/NY(other) song, with brackets indicating buzzes obtained from a song of another NY individual

cutting and pasting to maintain the same durations of silent gaps preceding and following the pasted notes.

The rationale for the choice of stimuli for each experiment will be explained more fully in the Results. In brief, in experiment 1 we made a three-way comparison of individuals' responses to unmodified PA songs, unmodified NY songs, and those same NY songs with buzzes from the PA songs substituted into them (e.g. Fig. 1a vs. 1c vs. 1b). Choice of the category of PA buzzes (B05) used for substitutions is explained in the Results.

In experiment 2, we measured responses to unmodified NY songs and NY songs modified with PA buzzes, using the same stimuli as in experiment 1, but in a two-way comparison with new subjects.

In experiment 3, we contrasted response to unmodified PA songs and response to the same PA songs modified by substituting in buzzes taken from other song types produced by the same individual (e.g. Fig. 1d). Substituted

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buzzes were taken from buzz categories other than B05, but were chosen based on visual inspection of sonograms so as to approximate the same center frequency, bandwidth, and duration of the notes they replaced; of these three characteristics, center frequency was most easily and thus most closely matched, followed by duration and bandwidth. Special care was taken so that the range of deviation in the substituted buzzes of modified songs was the same as in the original buzzes they replaced.

In experiment 4, we contrasted response to unmodified PA songs and response to those same PA songs modified by substituting in buzzes from songs produced by other individuals in the same PA population (e.g. Fig. 1e). In this case, substituted buzzes were all B05 buzzes, and thus very closely matched the buzzes they replaced.

In experiment 5, we contrasted response to unmodified NY songs and response to those same NY songs modified by substituting in buzzes produced by other individuals in the same NY population (e.g. Fig. 1f). Here, the degree to which substituted buzzes matched the buzzes they replaced was similar to experiment 3, i.e. the buzzes were not taken from the same category but were generally matched for center frequency, duration and bandwidth. Unlike experiment 3, these buzzes were taken from other individuals' repertoires.

Statistical Analysis

Each stimulus set was played to two subjects in experiments 1, 2, 4, and 5 and to three subjects in experiment 3. As the number of stimulus sets was 12 in each experiment, the number of subjects was 24 in experiments 1, 2, 4, and 5 and 36 in experiment 3. In all experiments, results were averaged across the two or three subjects played a particular stimulus set. Statistical tests were then performed using these per-stimulus averages. The sample size in all tests is thus the number of stimulus sets (12) rather than the number of subjects, as recommended by Kroodsma (1989). We used non-parametric statistical analyses that took advantage of the matching of stimulus tapes in stimulus sets; these analyses were the Wilcoxon matched pairs signed rank test and Friedman non-parametric ANOVA.

Results

Phonologic Survey

We identified a total of 1393 note types in the combined sample of 67 PA and 87 NY song types. We were unable to categorize six note types sung by NY birds and 10 note types sung by PA birds, i.e. these note types each appeared only once in our entire sample of songs. The remaining 1377 note types were classified into 61 categories, of which 13 (21%) were unique to PA birds, 17 (28%) were unique to NY birds, and 31 (51%) were shared by both populations.

We calculated the frequency of occurrence of each note type in a bird's repertoire as the proportion of his song types in which the note occurred. We then calculated the overall frequency of the note type in the population as the mean of these per bird frequencies, averaged over the eight males in each population. The note category with the highest frequency of use by PA birds was a particular buzz (B05), consisting of 4–14 broad band (2 kHz) 'upswept' pulses delivered at a rate of approx. 60 kHz. This note type was sung by all eight PA birds and occurred on average in 89 (\pm 5% SE) of each PA male's song types. B05 was sung by only one NY bird, and on average occurred in only 8 (\pm 8%) of each NY male's song types. The difference between the frequency of this note category in the PA and NY samples (89 – 8% = 81%) was substantially greater than the corresponding difference for any other note category; the next largest difference was only 47%. We therefore focussed on this note category as potentially the most useful phonologic marker for discriminating PA from NY songs.

Playback Experiments

In experiment 1 we compared response of territorial male song sparrows unmodified PA songs, unmodified NY songs, and NY songs into which the PA note type B05 had been substituted (NY/PA songs). PA males showed significant variation in response to these three stimulus categories ($\chi^2 = 11.6$, df = 2, p < 0.01 by a Friedman non-parametric ANOVA). The ranking of responses was not as predicted, however (Fig. 2). Rather than being intermediate, response to



Fig. 2: Mean distance $(\pm SE)$ to speakers playing unmodified PA songs, NY/PA songs, and unmodified NY songs. Variation in response was significant across the three playback categories (p < 0.01)

NY/PA songs was weaker than response to either PA or NY songs. Response to NY/PA was significantly weaker than response to PA (Wilcoxon T = 1, z = 2.98, p < 0.01). Response to NY was also significantly weaker than response to PA (Wilcoxon T = 9, z = 2.13, p < 0.05). The difference in response to NY and NY/PA songs was not significant (T = 24, z = 1.18, p > 0.10).

Experiment 2 was designed to determine whether the trend toward weaker response to NY/PA than to NY songs was real. The same NY and NY/PA songs were used as in experiment 1, but the tests were performed with a new group of subjects. The PA song sparrows averaged 2.6 m (± 0.3 SE) from the speaker during NY song playback and 3.7 (± 0.5) m during NY/PA playback. This difference in response was significant (Wilcoxon T = 13, z = 2.04, p < 0.05). Substitution of the putative PA marker into NY songs thus made those songs less acceptable to PA males, rather than more acceptable.

One possible explanation for the surprising result that response is lower to NY/PA than to NY songs is that the subjects could discern the digital alterations that had been made to NY/PA songs. In other words, it is conceivable that the cutting out and pasting in of buzzes produced acoustic artifacts that the birds could hear, although we could not, and that these artifacts lowered response to playback. In experiment 3 we tested this possibility by digitally removing buzzes from PA songs and replacing them with buzzes obtained from another song type of the same PA male, producing what we term PA/PA(self) songs. During territorial playback, PA males maintained a mean distance of 2.5 (\pm 0.3) m to PA song and 3.3 (\pm 0.6) m to PA/PA(self) song. The difference in response was not significant (Wilcoxon T = 22, z = 1.33, p > 0.10).

A second possible explanation for the low response to NY/PA songs is that song sparrows can discern individual differences in the production of notes, so that an NY/PA song mixing notes of two individuals sounds somehow wrong to them. To test this possibility, in experiment 4 we modified PA songs by cutting out buzzes and digitally replacing them with buzzes obtained from the songs of another PA individual. We then contrasted response to these PA/PA(other) songs and the original, unmodified PA songs. In the playback trials, PA males maintained a mean distance of 5.4 (\pm 1.0) m from PA songs compared with a mean of 5.4 (\pm 1.0) m from PA/PA(other) songs. Response to PA/PA(other) songs thus was no different than response to PA songs (Wilcoxon T = 38, z = 0.08, p > 0.10).

As a final control, in experiment 5 we tested PA males for response to NY songs that had been modified by the substitution of buzzes from a second NY individual. We refer to these modified NY songs as NY/NY(other). This experiment tests the remote possibility that PA song sparrows are more sensitive to digital alteration of NY songs than they are to digital alteration of PA songs, and the equally remote possibility that they are more attuned to individual differences in NY songs than in PA songs. During playback PA males maintained a mean distance of 3.4 (± 0.5) to NY/NY(other) song compared with a mean distance of 3.8 (± 0.6) m to NY songs. This difference was not significant (Wilcoxon T = 33, z = 0.47, p > 0.10).

Discussion

Using sonagraphic analysis, we identified a phonologic marker that seemingly ought to facilitate the discrimination of PA and NY songs, namely the buzz category B05. This buzz category was found in 89% of PA song types compared with only 8% of NY song types. This difference closely parallels that found by King & West (1983) for the MSE of brown-headed cowbirds; the MSE occurred in 87% of the songs of the *obscurus* subspecies and 3% of the songs of the *ater* subspecies. For *obscurus* females, adding the MSE to manipulated songs made those songs more acceptable, whereas attenuating MSE made the songs less acceptable (King and West 1983). In our results with PA song sparrows, however, substituting the B05 buzz into foreign songs made those songs less, rather than more, acceptable. This result weighs against our original hypothesis, that song sparrows discriminate local songs from foreign ones using simple phonologic markers.

A possible problem with this conclusion is that song sparrows might be sensitive to the kind of digital manipulations necessary to substitute local buzzes into foreign songs. If digital manipulation alone lowers the acceptability of songs, this might be enough to counter any increase in acceptability caused by the introduction of local buzzes. To evaluate this possibility, we performed a control experiment that tested whether response to playback was affected by the substitution of different buzzes from the same individual into local songs. The results were negative, showing that digital substitutions alone do not affect responses of song sparrows.

A second alternative is that substituting elements from one individual into another individual's songs might make those songs less acceptable. Humans are able to discriminate among unfamiliar speakers by individual voice characteristics alone (van Lancker & Kreiman 1987). If song sparrows have a parallel ability, then they would be able to recognize when we combine elements from two individuals in the same song, and they might react unfavorably to such mixing. Song sparrows can recognize familiar individuals by song alone (Stoddard et al. 1991; O'Loghlen & Beecher 1997), but this might be done by memorizing each of the relevant song types, and does not necessarily imply an ability to discriminate unfamiliar individuals. Discriminating unfamiliar individuals requires recognition of some 'signature' or 'voice quality' (Beecher 1989; Weary et al. 1990) that would carry over from one song type to another in the same individual's repertoire. Beecher et al. (1994) tested for voice recognition in song sparrows using operant techniques. After having been taught to classify several song types to each of two singers, subjects showed no ability to classify an unfamiliar test song to the correct singer. Our results also weigh against the possibility of voice recognition in song sparrows, in that our subjects showed no evidence of recognizing when buzzes of one PA individual had been substituted into the song of another PA individual (exp 4), nor of recognizing when buzzes of one NY individual had been substituted into the song of another NY individual (exp 5). These experiments also serve as further controls against the possibility of sensitivity to digital manipulation.

If song sparrows cannot discern when we have digitally manipulated songs, and cannot tell (or do not care) when we have substituted the buzz of one individual for another, why then was response to NY/PA songs actually lower than to NY songs? If buzz category B05, the putative PA marker, was simply irrelevant to geographic discrimination, then response to NY/PA songs should be indistinguishable from response to NY songs. Instead, response to NY/PA songs was significantly lower than to NY songs. One explanation is that in substituting PA buzzes into NY songs we violated some unknown syntactical rule about what note goes where, causing the hybrid song to seem unnatural. The problem with this explanation is that, if such elaborate syntactical rules exist, we ought also to have broken them in substituting PA buzzes into PA songs and NY buzzes into NY songs, whereas in fact such substitutions did not alter response.

Instead, we suggest as a working hypothesis that song sparrows make much finer phonologic distinctions than we expected based on our spectrographic analysis. Under this hypothesis, NY and PA notes that we consider to be in the same category are perceptually distinct to song sparrows and considered by them to be different categories, as Balaban's (1988) data suggest is the case for swamp sparrows. By our classification, NY songs have 31 familiar (shared) notes and 17 foreign ones as compared with PA songs, and most or all NY songs should seem to PA birds to be composed of a mixture of familiar local notes and unfamiliar foreign ones. Under these assumptions, both the NY and the NY/PA songs would appear as mixtures, and we would expect a stronger response to the mixture with the higher proportion of local notes (i.e. NY/PA songs). If, instead, song sparrows are making much finer phonologic distinctions, NY songs may seem to them to contain no familiar notes at all. Of all our manipulations, only the NY/PA songs would appear as mixtures, and our results would be explained if phonologic mixing is perceived as unnatural by the birds.

Our results are consistent with the hypothesis that song sparrows use very fine phonologic distinctions to discriminate foreign from local songs. Although further work is required to test this hypothesis more thoroughly, our findings to date raise additional questions about the functional significance, if any, of such finely tuned discrimination abilities. We used male subjects in the tests we report here because territorial playbacks provide a relatively convenient and accurate way to determine differences in the perceptual salience of songs. We have shown in other work (Searcy et al. 2002) that female song sparrows are even more attuned to geographic differences than are males. Whereas males in our tests do not discriminate against foreign songs unless they are recorded more than 270 km away from their local population, females discriminate against songs recorded as little as 34 km away. Questions about how experience and perceptual mechanisms interact in the development of such preferences, and about the functional consequences of having such preferences, become more tractable as we begin to understand what features do and do not provide the basis of discrimination.

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