

Within-individual variation in bullfrog vocalizations: Implications for a vocally mediated social recognition system

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Acoustic signals provide a basis for social recognition in a wide range of animals. Few studies, however, have attempted to relate the patterns of individual variation in signals to behavioral discrimination thresholds used by receivers to discriminate among individuals. North American bullfrogs (*Rana catesbeiana*) discriminate among familiar and unfamiliar individuals based on individual variation in advertisement calls. The sources, patterns, and magnitudes of variation in eight acoustic properties of multiple-note advertisement calls were examined to understand how patterns of within-individual variation might either constrain, or provide additional cues for, vocal recognition. Six of eight acoustic properties exhibited significant note-to-note variation within multiple-note calls. Despite this source of within-individual variation, all call properties varied significantly among individuals, and multivariate analyses indicated that call notes were individually distinct. Fine-temporal and spectral call properties exhibited less within-individual variation compared to gross-temporal properties and contributed most toward statistically distinguishing among individuals. Among-individual differences in the patterns of within-individual variation in some properties suggest that within-individual variation could also function as a recognition cue. The distributions of among-individual and within-individual differences were used to generate hypotheses about the expected behavioral discrimination thresholds of receivers. © 2004 Acoustical Society of America. [DOI: 10.1121/1.1784445]

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I. INTRODUCTION

Vocal communication plays important roles in social recognition by allowing animals to direct appropriate behaviors toward other individuals after learning to recognize individually distinct properties of their acoustic signals. Patterns of individual variation in acoustic signals contribute toward identifying individuals in a number of taxa, including fish (Myrberg *et al.*, 1993; Crawford *et al.*, 1997), frogs (Bee and Gerhardt, 2001a; Bee *et al.*, 2001), reptiles (Polakow, 1997); birds (Weary *et al.*, 1990; Robertson, 1996; Lengagne *et al.*, 1997), and mammals (Gelfand and McCracken, 1986; Hauser, 1991; Insley, 1992; Fischer *et al.*, 2002). Field and laboratory playback studies in a wide range of taxa have confirmed that animals behaviorally discriminate among individuals based on the learned recognition of individually distinct acoustic signals in a number of different behavioral contexts, such as kin recognition (Beecher, 1991; Balcombe, 1990; Aubin and Jouventin, 2002), mate recognition (Robertson, 1996; Lengagne *et al.*, 2000), territorial neighbor recognition (Brooks and Falls, 1975a; Myrberg and Riggio, 1985; Bee and Gerhardt, 2001b, c, 2002), and individual recognition (Beecher *et al.*, 1996; Cheney and Seyfarth, 1999; Gentner and Hulse, 1998, 2000).

Relatively few studies, however, have sought to understand the mechanisms and evolution of vocally mediated social recognition by systematically investigating the acoustic and perceptual bases of recognition either within or across

taxa (e.g., Beecher, 1991; Gentner and Hulse, 1998, 2000; Bee and Gerhardt, 2001a, b, 2002; Bee, 2001, 2003). Clearly an important aspect of acoustically mediated recognition systems involves the patterns of variation in acoustic signals that identify individuals (Beecher, 1989, 1991; Sherman *et al.*, 1997). Only after characterizing the potential for specific acoustic properties to identify individuals can researchers investigate in an informed way the perceptual basis of recognition using playback experiments.

Here I report results from a study of a vocally mediated social recognition system in a frog. Davis (1987) demonstrated that territorial males of the North American bullfrog (*Rana catesbeiana*) exhibit relatively lower levels of aggression in response to playbacks of their adjacent neighbor's advertisement calls from the neighbor's territory in comparison to responses to the calls of strangers. Hence, as in territorial songbirds (reviewed in Stoddard, 1996), territorial male bullfrogs learn to recognize their neighbor's vocalizations and rely on individual variation in vocalizations to discriminate among neighbors and strangers. Bee and Gerhardt (2001a) investigated the acoustic basis of neighbor-stranger discrimination in bullfrogs by analyzing the patterns of individual variation present in the first note of advertisement calls, which are more commonly produced as multiple-note calls (Fig. 1). The fundamental frequency (and correlated spectral properties) exhibited the greatest among-individual variation relative to within-individual variation, and contributed most toward statistically discriminating among individuals in multivariate statistical analyses.

Using the habituation-discrimination paradigm, Bee and

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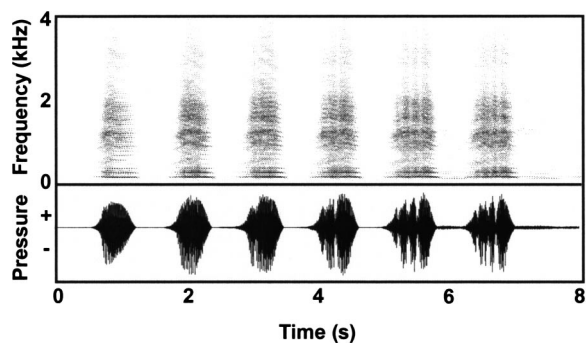


FIG. 1. Sonogram (top) and oscillogram (bottom) of a six-note advertisement call.

Gerhardt (2001b, c, 2002; Bee, 2003) tested the hypothesis that repeated exposure to a territorial neighbor's advertisement calls would allow males to learn to recognize acoustic properties related to the pitch of a neighbor's advertisement calls. In a discrimination phase following habituation trials, changes in the fundamental frequency of the synthetic stimulus elicited a recovery of habituated territorial aggressive responses, as predicted if territory residents use features related to call pitch to identify neighbors as familiar.

Based on the results of their acoustic analyses and field playback experiments, Bee and Gerhardt (2001a, b, c) estimated that the "just-meaningful difference" (JMD) (Nelson and Marler, 1990; Gerhardt, 1992) in fundamental frequency required to elicit renewed territorial aggression following habituation training was between 5% and 10%. Bee and Gerhardt (2001b, c, 2002) stressed, however, that this conclusion was provisional for two important reasons. First, Bee and Gerhardt (2001a) reported, but did not describe, variation in several acoustic properties, including fundamental frequency, that occurred *among* the separate notes *within* the multiple note advertisement calls produced by an individual (Fig. 1). This note-to-note variation in advertisement calls could make discriminating among individuals more difficult due to increased overlap of the signal properties of different individuals' calls. Second, the synthetic stimuli used in the habituation-discrimination tasks were invariant, meaning that the note-to-note within-individual variation present in multiple-note advertisement calls was not incorporated in the perceptual learning and discrimination task. Thus, an important and unanswered question concerns the implications of the patterns and magnitudes of within-individual variation in multiple-note advertisement calls for the behavioral discrimination thresholds that receivers should use to discriminate among familiar and unfamiliar signals. As a first step toward addressing this issue, I describe here the sources, magnitudes, and patterns of variation in multiple-note advertisement calls. The main objective of this study was to determine the ways in which note-to-note within-individual variation in multiple-note calls can either constrain or provide additional cues for acoustically mediated neighbor recognition.

II. METHOD

A. Study organism

During their breeding season, male bullfrogs establish and defend territories in permanent bodies of water from

which they emit advertisement calls to attract gravid females and to repel rival males (Howard, 1978). During periods of active calling, which typically occur between 2300 and 0400 hours, most advertisement calls consist of four to seven notes (Fig. 1; Bee unpublished data). The individual notes comprising multiple-note advertisement calls are about 700 ms in duration, are separated by intervals of about 500 ms, and have a quasiperiodic fine-temporal waveform with a periodicity that varies inversely with body size and corresponds to the fundamental frequency of the call (Capranica, 1965; Bee and Gerhardt, 2001a). The frequency spectrum of a call note consists of a series of harmonics with a bimodal distribution of sound energy. The lower frequency peak is centered between 200 and 400 Hz; a broader, higher frequency band occurs between 1000 and 2000 Hz (Fig. 2). The fundamental frequency (90–130 Hz) is usually absent from the frequency spectrum or contains relatively little sound energy compared to other spectral components (Capranica, 1965).

B. Recording of vocalizations

Between May and August 1998, the advertisement calls of 25 territorial male bullfrogs were recorded in ponds located in the Little Dixie Lake Conservation Area (Callaway Co., Missouri, USA). Recordings were made during active choruses under ambient light conditions, usually between 2300 and 0400 hours, central daylight time. At least five multiple-note advertisement calls were recorded from each of the 25 males using an HHb PDR-1000 DAT recorder (sampling rate=32 kHz) and a Sennheiser MKH 70 shotgun microphone (with a Windtech SG-3 windscreens) that was mounted on a tripod placed 1–2 m from a subject and angled downward between 25° and 45° from parallel with the surface of the pond. Immediately after each recording, the air and water temperatures at the frog's position were determined to the nearest 0.1 °C. Each subject had been captured and individually marked, and had its snout-to-vent length (SVL) measured, on a night prior to that of recording [following Bee and Gerhardt (2001a)].

C. Acoustical analysis of vocalizations

Most of the calls analyzed in this study consisted of between three and seven notes. To examine the patterns of within-individual variation among separate notes in multiple-note advertisement calls, I analyzed eight acoustic properties for the first, middle, and last notes of five multiple-note calls from each individual (5 calls×3 notes×25 individuals=375 total call notes) using a Kay DSP Sona-Graph Model 5500.¹ In calls having an even number of notes, one of the two middle notes was chosen randomly. I analyzed call notes in the relative positions of the first, middle, and last notes of calls, instead of notes in fixed positions within a call (e.g., the second, third, and fourth notes), because preliminary analyses of sonograms indicated that this would be the most effective method for capturing the range of within-individual variation in multiple-note calls, as adjacent call notes are often more similar to one another than are call notes spaced further apart (Fig. 1). The person performing the acoustical analyses was different from the person who made the record-

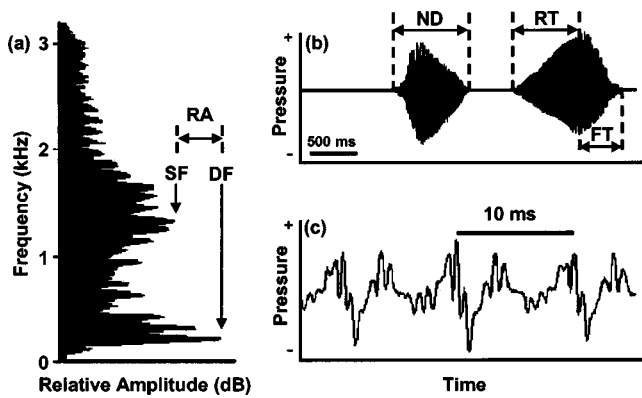


FIG. 2. (a) Power spectrum of an advertisement call note averaged over a 100-ms section from the middle of the note, beginning at the peak of the amplitude envelope. (b) Oscillogram depicting two call notes. (c) Oscillogram of the middle of the first call note in (b) illustrating the fine-temporal waveform. Dominant frequency (DF), secondary frequency (SF), and the relative amplitude (RA) were measured from power spectra as in (a). Dominant frequency is the harmonic of single greatest amplitude and corresponds to the second harmonic. Secondary frequency is defined as the harmonic of greatest relative amplitude in the higher frequency band of the bimodal spectrum. The amplitude (in dB) of the dominant frequency, relative to that of the secondary frequency, was expressed as the ratio of the sound pressure of the dominant frequency relative to that of the secondary frequency [$\text{dB} = 20 \times \log_{10}(\text{pressure ratio})$; 0 dB=1, +6 dB=2, +12 dB=4, etc.]. Note duration (ND), rise time (RT), and fall time (FT) were measured from oscillograms as in (b). Note duration was defined as the time between the onset and offset of an advertisement call note. Rise time was defined as the time from note onset to the time of maximum amplitude; fall time was defined as the time from maximum amplitude to note offset. Fundamental frequency (FF) was determined as the reciprocal of the average period of five repetitions of the fine-temporal waveform as shown in (c). Horizontal bars indicate time scales in (b) and (c).

ings and, although aware of each bullfrog's individual number (e.g., BF9-98), had no *a priori* expectations about the values to be determined in the analyses. The calls analyzed in this study are the same as those analyzed by Bee and Gerhardt (2001a) for the purpose of comparing among-individual variability in analyses of one call note versus multiple call notes; however, that study did not describe the patterns and magnitudes of individual variation in multiple-note calls.

Three spectral properties of advertisement calls were measured from power spectra generated by fast Fourier transformation (FFT) over a 100-ms interval from the middle of a call note, beginning at the point of peak signal amplitude (transform size=1024 points, filter bandwidth=14.5 Hz, 0–4 kHz setting). The spectral properties that were measured included dominant frequency and secondary frequency (to the nearest 10 Hz), and the amplitude of the dominant frequency relative to the secondary frequency (to the nearest dB) [Fig. 2]. I also determined the ratio of secondary frequency to dominant frequency (hereafter “frequency ratio”) as a measure of the distribution of sound energy in the bimodal frequency spectrum. The fundamental frequency is equal to the reciprocal of the waveform periodicity and is related to the “periodicity pitch” of the signal (Simmons and Ferragamo, 1993). Using an oscillogram with an expanded time base, fundamental frequency was determined (to the nearest 1 Hz) as the reciprocal of the average period of five repetitions of the fine-temporal waveform measured from the middle of a call note [Fig. 2]. Three gross-temporal properties were mea-

sured (to the nearest 1 ms) from oscillograms, including note duration, rise time, and fall time [Fig. 2]. The recordings had sufficiently high signal-to-noise ratios to readily distinguish the onsets and offsets of individual notes from the background noise.

D. Statistical analysis of vocalizations

The statistical analyses described below were performed on call properties that were corrected for variation in water temperature at the times different individuals were recorded using the procedures outlined in Bee and Gerhardt (2001a).

1. Sources and patterns of variation

Two goals of the present study were to test for the presence of systematic *within-individual* variation in multiple-note advertisement calls that occurs among the separate notes within a call, and to compare this variation to the magnitude of among-individual variation present in the population. I used model II ANOVAs (Sokal and Rohlf, 1994) to examine the variation in call properties that was due to among-individual differences (*individual*) and among-note differences (*note*) by treating *individual* and *note* as main effects in a factorial design.² These analyses were designed to address three questions. First, the effect of *individual* tested whether the among-individual variation in call properties was significantly greater than the within-individual variation, which included variation due to among-note differences and among-call differences in the 15 call notes recorded from each individual. Second, the effect of *note* tested whether any systematic variation among separate notes within multiple-note calls was significantly greater than the within-note variation that was due to among-individual and among-call differences in each of the 125 exemplars (25 individuals \times 5 calls) of notes in the first, middle, and last positions of a call. Bonferroni *posthoc* comparisons were used to examine differences among first, middle, and last notes if the main effect of *note* was significant. Finally, the *individual* \times *note* interaction term tested for any among-individual differences in the patterns of systematic variation among notes within an individual's calls. Because calls with different numbers of notes were included in these analyses, any variation due to the *individual* \times *note* interaction must be interpreted with caution, as some of this variation could be due to differences in the number of call notes that different bullfrogs produced in their multiple note calls. For these and all subsequent statistical analyses, a criterion of $\alpha=0.05$ was used to determine significance.

2. Relative variation among acoustic properties

A third goal of this study was to compare the magnitude of within-individual variation among different call properties. Within-individual variability in each call property was estimated in two standardized ways. First, within-individual coefficients of variation ($=\text{SD}/\text{mean} \cdot 100\%$) for each call property were calculated separately for each individual using the mean and standard deviation from the sample of 15 call notes (5 calls \times 3 notes) recorded from the individual. Second, the within-individual range of variation for each call property was calculated separately for each individual as a

percentage of the within-individual mean from the sample of 15 call notes recorded from the individual. These estimates of within-individual variation were log-transformed to improve normality and compared among call properties using a MANOVA approach to test for within-subjects effects. Subsequent Bonferroni *posthoc* tests were used to compare individual call properties.

3. Individual distinctiveness

The fourth goal of this study was to assess the extent to which advertisement calls can be considered individually distinct given the within-individual variation that occurs among separate notes within a call. Discriminant function analysis (DFA) is a commonly used multivariate statistical approach for examining the individual distinctiveness of acoustic signals (Nelson and Marler, 1990; Weary *et al.*, 1990; Hauser, 1991; Insley, 1992; Bee *et al.*, 2001; Fischer *et al.*, 2002). Instead of performing a DFA on the values for all eight call properties, which were highly intercorrelated (see the Appendix), I subjected the data to a principal components analysis (PCA) to extract orthogonal principal components and performed a DFA using the factor scores from the PCA as input variables. The discriminant functions were used to classify each of the 375 call notes as belonging to a particular individual based on a cross validation procedure.

4. Generating hypotheses about JMDs

The final goal of the present study was to generate testable hypotheses about a receiver's behavioral discrimination thresholds, or JMDs (Nelson and Marler, 1990; Gerhardt, 1992), based on the patterns of among-individual and within-individual variation present in multiple-note advertisement calls. Signal detection theory provides an appropriate framework for understanding the relationships between individual variation in signals and behavioral discrimination thresholds (Wiley, 1994; Sherman *et al.*, 1997; Bradbury and Vehrencamp, 1998; Gerhardt and Huber, 2002). In a social recognition system, receivers are faced with the general problem of discriminating between familiar and unfamiliar signals, or between multiple familiar signals. From the receiver's perspective, there are four basic associations between the perceived signal and the behavioral response: correct detection, correct rejection, false alarm, and missed detection. As Wiley (1994) and others (Sherman *et al.*, 1997; Bradbury and Vehrencamp, 1998; Gerhardt and Huber, 2002) have pointed out, natural selection should favor behavioral discrimination thresholds that optimize the sum of the net advantages of each of these four behavioral outcomes weighted by its probability. The probability of each outcome depends on the overlap in the distributions of the signal properties of the individuals to be discriminated, which in turn depends on the magnitudes of differences among individuals in the population and on the variance in the signal distributions within individuals. Comparisons of the distribution of within-individual differences to that of among-individual differences provide a way to generate hypotheses about a receiver's

TABLE I. Results of model II ANOVAs for each call property comparing the variation due to among-individual differences (*individual*), among-note differences (*note*), and among-note differences that varied among individuals (*individual*×*note*).

Call property	Source ^a	F	P
Fundamental frequency	individual	145.0	<0.01
	note	67.6	<0.01
	individual×note	1.9	<0.01
Dominant frequency	individual	113.2	<0.01
	note	51.3	<0.01
	individual×note	2.6	<0.01
Secondary frequency	individual	8.2	<0.01
	note	5.2	0.01
	individual×note	5.9	<0.01
Frequency ratio	individual	11.3	<0.01
	note	1.5	0.24
	individual×note	5.4	<0.01
Relative amplitude	individual	9.8	<0.01
	note	5.9	<0.01
	individual×note	3.0	<0.01
Note duration	individual	8.4	<0.01
	note	0.0	0.97
	individual×note	5.5	<0.01
Rise time	individual	10.7	<0.01
	note	41.1	<0.01
	individual×note	2.3	<0.01
Fall time	individual	3.8	<0.01
	note	32.5	<0.01
	individual×note	3.0	<0.01

^aDegrees of freedom: *individual* (24,48), *note* (2,48), *individual*×*note* (48,300).

er's behavioral threshold differences in the acoustic properties of familiar and unfamiliar signals that should lead to a discriminative behavioral response.

I used the following procedure to estimate JMDs. First, a distribution of among-individual differences was created by computing the absolute value of the difference between each of an individual's 15 call notes and each of the other 360 call notes from the remaining 24 individuals. This was repeated for each of the 25 individuals to create a distribution of among-individual differences based on a total of 67 500 pairwise among-individual comparisons. Second, a distribution of within-individual differences was created by computing the absolute value of the difference between each call note from an individual and the other 14 call notes recorded from that individual. This was repeated for each of the 25 individuals to create a distribution of within-individual differences based on 2625 pairwise within-individual comparisons. The among-individual and within-individual differences were standardized as percentages of the grand mean determined from all 375 call notes. Finally, as an estimate of a discrimination threshold, I computed the percentage difference in each signal property at which the cumulative proportion of among-individual differences falling below the threshold first exceeded the cumulative proportion of within-individual differences falling above this threshold. The JMD estimated in this way corresponds to the level of difference between two signals at which the difference is more likely attributable to an among-individual difference than to a within-individual difference.

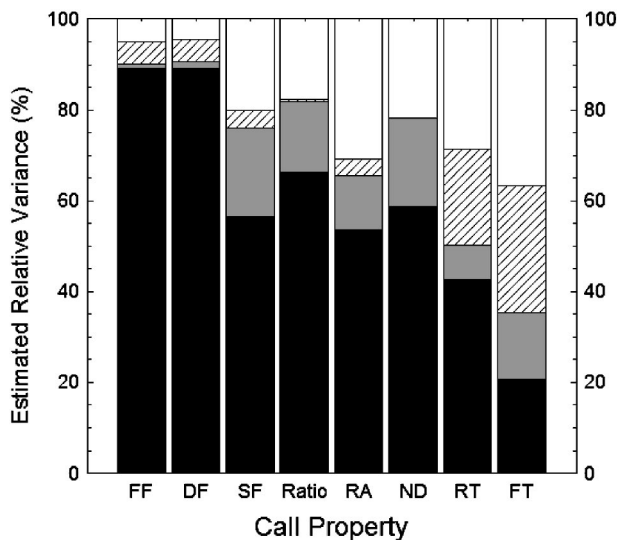


FIG. 3. Estimated relative variance accounted for by the main effects of *individual* (solid black) and *note* (diagonal lines), and the *individual*×*note* interaction (gray) in model II ANOVAs in which *individual* and *note* were tested as main effects in a factorial design. The white bars indicate the relative unexplained error variance. (FF=fundamental frequency; DF=dominant frequency; SF=secondary frequency; Ratio=ratio of SF:DF; RA=sound pressure of DF relative to that of SF; ND=note duration; RT=rise time; FT=fall time).

III. RESULTS

A. Sources and patterns of variation

Overall, the effects included in the model II ANOVAs explained substantial amounts of variation in each call property, as indicated by R^2 values that ranged from 0.59 for fall time to 0.95 for fundamental frequency and dominant frequency. Variation among individuals was significantly greater than that within individuals, even after including variation that occurred among three separate notes within each of five exemplars of an individual's multiple-note calls (Table 1). The proportions of variation that were due to among-individual differences (Fig. 3, black bars) were highest for fundamental frequency and dominant frequency (89%), intermediate for secondary frequency, frequency ratio, relative amplitude, and note duration (54%–66%), and lowest for rise time (43%) and fall time (21%).

There was also significant systematic variation that depended on the position of a note within a multiple-note call (*note*) for several call properties (Table I). The proportions of variation explained by systematic among-note differences (Fig. 3, diagonally patterned bars) were highest for rise time (21%) and fall time (28%). Fundamental frequency, dominant frequency, secondary frequency, and relative amplitude exhibited relatively less variation among notes (4%–5%). The variance components attributable to systematic among-note differences were negligible for frequency ratio and note duration (<0.5%).

For fine-temporal and spectral properties, *posthoc* comparisons revealed that fundamental frequency [Fig. 4(a)] and dominant frequency [Fig. 4(b)] were significantly lower in the first note of a call compared to the middle and last notes, which did not differ significantly. Secondary frequency [Fig. 4(c)] was significantly lower at the beginning and end of a

call compared to notes from the middle of the call, and notes at the beginning of a call had significantly lower secondary frequencies than notes at the end of a call. The amplitude of the dominant frequency relative to that of the secondary frequency [Fig. 4(e)] was significantly lower in the first note of a call compared to the middle and last notes, which did not differ significantly.

The general similarities among the patterns of variation in fundamental frequency, dominant frequency, and secondary frequency reflect the fact that dominant frequency and secondary frequency are harmonically related to the fundamental. Slight differences among these patterns of variation can arise, however, because the secondary frequency can correspond to different harmonic components among different notes within a call, while the dominant frequency of each call note was always the second harmonic. Although there were no significant differences in the ratio of secondary frequency to dominant frequency [Fig. 4(d)], there was a slight trend for frequency ratio to be higher in notes from the middle of a call. Together, the results for secondary frequency and frequency ratio suggest that the peak of the spectral energy in the upper mode of the frequency spectrum shifted to slightly higher harmonics in the middle of the calls given by some individuals (see below).

Average note duration [Fig. 4(f)] was constant within a call, while there were significant differences in rise times [Fig. 4(g)] and fall times [Fig. 4(h)] that depended on the position of notes within a call. *Posthoc* comparisons indicated that rise times increased, and fall times decreased, between notes within a call [Figs. 4(g) and (h); see also Fig. 1].

Patterns of within-individual variation among first, middle, and last notes similar to those depicted in Fig. 4 were also observed after separately standardizing the values for each call note from each individual as a percentage deviation from the within-individual mean for that individual (Fig. 5). On average, fine-temporal and spectral call properties tended to vary little around the individual mean: fundamental frequency (3%), dominant frequency (3%), secondary frequency (7%), and frequency ratio (4%). The exception was relative amplitude, which varied about 18% around the individual mean. Among gross temporal properties of the amplitude envelope, the average note duration was constant across multiple notes, varying less than 1% around the individual mean, although the variability in note duration, as depicted by the size of the error bars in Fig. 5, was greater than that for fundamental frequency and dominant frequency. Compared to note duration, considerably more variation was observed for rise time (25%) and fall time (24%).

The *individual*×*note* interactions were significant for all call properties (Table I). The variance that could be attributed to the *individual*×*note* interaction (Fig. 3, gray bars) was greatest for secondary frequency, frequency ratio, relative amplitude, note duration, and fall time (15%–20%). The variance components for fundamental frequency and dominant frequency were the smallest (1%–2%), and that for rise time was intermediate (8%). Notice, in Fig. 3, that the proportion of variation in several call properties that could be attributed to the *individual*×*note* interaction was greater than that explained by systematic differences due to note position

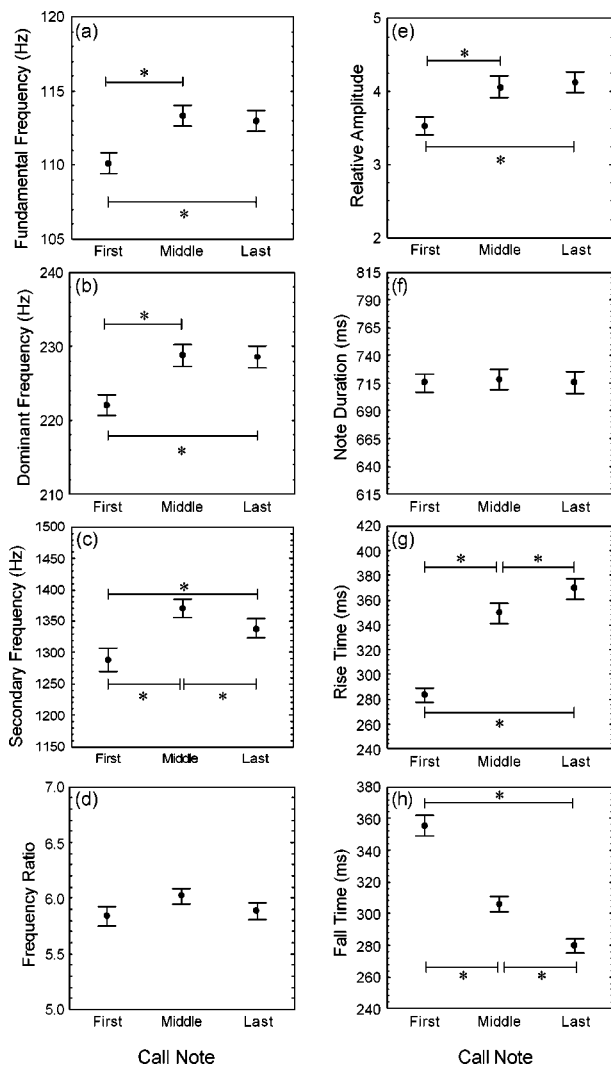


FIG. 4. Mean (\pm SE) values of the first, middle, and last notes for (a) fundamental frequency, (b) dominant frequency, (c) secondary frequency, (d) frequency ratio, (e) relative amplitude, (f) note duration, (g) rise time, and (h) fall time. These mean values are based on 125 exemplars of each call note (5 calls \times 25 individuals). The range of values depicted on each y axis approximately extends from one standard deviation below to one standard deviation above the sample means for each property, averaged over 3 notes, 5 calls, and 25 individuals. Asterisks indicate significant differences ($P < 0.05$) in Bonferroni *posthoc* tests for model II ANOVAs in which the main effect of *note* was significant ($P < 0.05$).

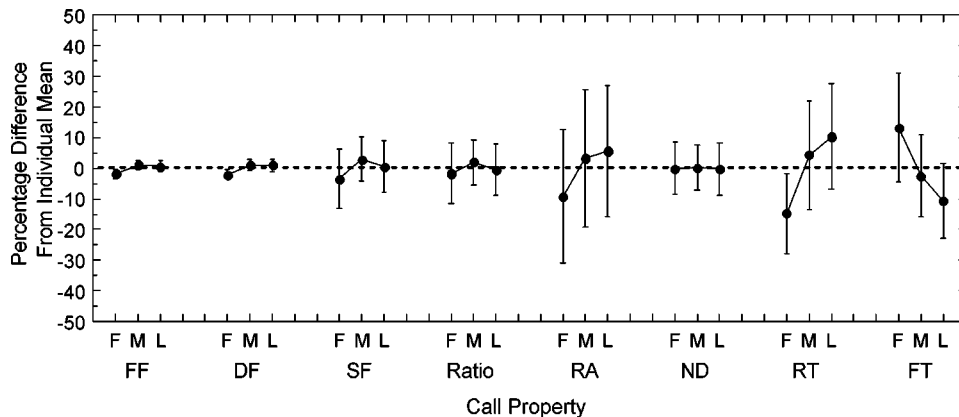


FIG. 5. Magnitudes of variation in the eight call properties among the first (F), middle (M), and last (L) notes within a call standardized as deviations from the within-individual means. Points and error bars depict the mean and ± 1 SD, respectively. Percentage deviation scores were calculated separately for each individual ($N = 25$) based on the deviation of values for each single note from the within-individual mean averaged over all 15 call notes (5 calls \times 3 notes) recorded from the individual. (FF=fundamental frequency; DF=dominant frequency; SF=secondary frequency; Ratio=ratio of SF:DF; RA=sound pressure of DF relative to that of SF; ND=note duration; RT=rise time; FT=fall time).

alone. This point is illustrated in Fig. 6 for the call properties of secondary frequency and note duration. As Fig. 6(a) illustrates, most individuals had secondary frequencies that were either relatively constant or increased slightly during multiple-note calls. However, at least a few individuals had average secondary frequencies that were considerably more variable among notes within calls [Fig. 6(b)]. Because male bullfrogs generally do not change position during the production of a single call, it is unlikely that differences in secondary frequency among notes within calls could arise due to changes in the positions of some individuals relative to the microphone, which could affect the relative amplitudes of harmonic components, and thus determination of secondary frequency. Hence, the patterns of changes in the frequency of peak sound energy in the upper mode of the bimodal frequency spectrum that occurred among notes within multiple note calls differed reliably (i.e., statistically) among individuals. The reliable individual differences in note-to-note variation were even more pronounced for the gross temporal property of note duration [Figs. 6(c)–(f)], for which less than 0.5% of the variation was explained by note position alone. The duration of notes within multiple-note calls was nearly constant within the calls of some individuals while for other individuals note duration changed by 100–200 ms during a call and exhibited either systematic decreases or increases. It seems unlikely that these distinct individual differences in the patterns of among-note variation exhibited in the calls of some individuals could result only from the fact that calls with different numbers of notes were included in the analysis, although additional work may be needed to clarify this point.

B. Relative variation among acoustic properties

There were significant differences in the variability among call properties both for the within-individual coefficients of variation [Wilks' $\lambda < 0.01$, $F_{7,18} = 423.1$, $P < 0.0001$ and for within-individual ranges [Wilks' $\lambda = 0.01$, $F_{7,18} = 223.7$, $P < 0.0001$]. *Posthoc* tests revealed the same pattern of significant differences for both estimates of within-individual variation (Fig. 7). Fundamental frequency and

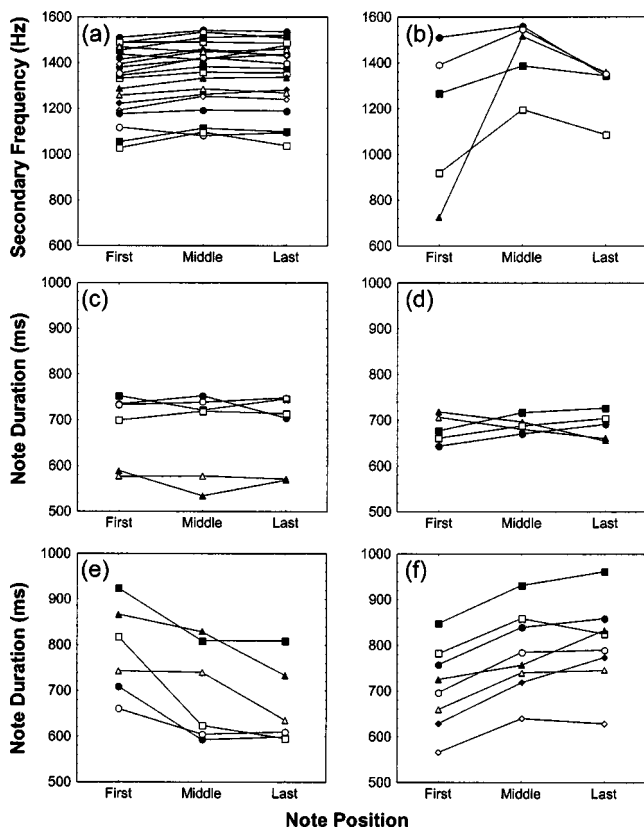


FIG. 6. *Individual* × *note* interactions from model II ANOVAs showing individual differences in the patterns of among-note variation in multiple-note advertisement calls for the call properties of (a,b) secondary frequency and (c–f) note duration. The value for each call note from each individual represents the average value of five calls.

dominant frequency exhibited significantly lower variability within individuals compared to the other six call properties. Secondary frequency, frequency ratio, and note duration exhibited significantly greater variability within individuals compared to fundamental frequency and dominant frequency. Note duration was also significantly more variable than secondary frequency and frequency ratio. The relative amplitude of the dominant and secondary frequencies, and the gross temporal properties of rise time and fall time, exhibited significantly more variability within individuals than the other call properties.

C. Individual distinctiveness

A PCA of the values for each of the eight acoustic properties generated four factors with eigenvalues greater than 1.0. However, because the fifth factor had an eigenvalue of 0.75 and explained an additional 10% of the variance, I included the factor scores from the first five factors as input variables to the DFA (Table II). Together, the first five factors from the PCA explained 98.4% of the variance in the acoustic properties. The DFA generated five significant discriminant functions (P 's < 0.01). Three discriminant functions had eigenvalues greater than 1.0 and, together, they accounted for 96% of the variation (Table III). The first discriminant function accounted for 80% of the variation and was highly correlated with scores from the first PCA factor, which loaded heavily on fundamental frequency and domi-

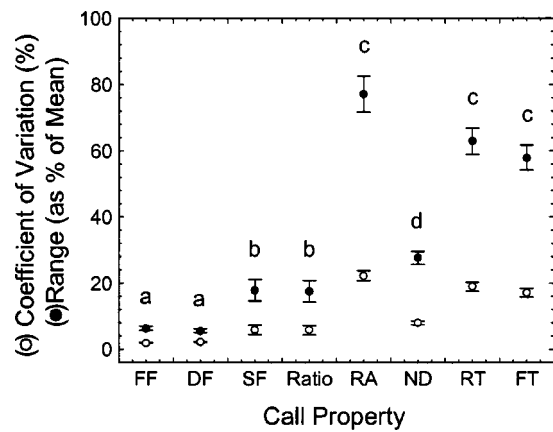


FIG. 7. Comparisons of the relative variability in different call properties. Points and error bars depict the mean and ± 1 SE, respectively. Different letters above the error bars indicate significant differences ($P < 0.05$) between call properties in *posthoc* tests following MANOVAs of the log-transformed data. (FF=fundamental frequency; DF=dominant frequency; SF=secondary frequency; Ratio=ratio of SF:DF; RA=sound pressure of DF relative to that of SF; ND=note duration; RT=rise time; FT=fall time).

nant frequency (Table III). The second discriminant function, which accounted for an additional 10% of the variance, was correlated with PCA factor 3, which loaded most heavily on secondary frequency and frequency ratio (Table III). The third discriminant function explained an additional 6% of the variance and was highly correlated with PCA factor 2, which loaded heavily on note duration and rise time (Table III). The DFA successfully assigned 283 of the 375 recorded call notes (75.5%) to the correct individual, which is significantly higher than the classification success of 4% expected by randomly assigning notes to individuals (Fisher's exact test, $P < 0.01$). Therefore, individuals can be statistically distinguished by their multiple-note advertisement calls.

D. Estimated JMDs

Figure 8 depicts histograms showing the distributions of among-individual differences (black bars) and within-individual differences (white bars) in acoustic properties of bullfrog advertisement calls. Table IV shows the estimated JMDs for each call property computed from similar histograms having 1%-wide bins. These estimated JMDs are also compared to the within-individual coefficients of variation and the mean-standardized within-individual ranges of variation that were depicted in Fig. 7. Table IV also shows the proportions of among-individual differences and within-individual differences that fall above and below the estimated JMDs. The estimated JMD of most call properties generally falls between the within-individual coefficient of variation and the mean-standardized range, with the exception of fall time, which has an estimated JMD that is slightly less than the coefficient of variation (Table IV). With the exception of relative amplitude, the estimated JMDs for fine-temporal and spectral call properties are generally lower (4%–6%) than those for gross temporal call properties (10%–21%).

In the context of territorial neighbor recognition, in which individuals respond more aggressively toward unfamiliar individuals, a correct detection is the equivalent of

TABLE II. Normalized factor loadings (varimax rotation) from a principal components analysis of the eight acoustic properties. Bold type indicates the heaviest factor loadings.

Call property	Factor				
	1	2	3	4	5
Fundamental frequency	0.98	0.02	0.11	0.02	0.10
Dominant frequency	0.98	0.03	0.05	0.06	0.12
Secondary frequency	0.12	-0.01	-0.99	0.00	0.08
Frequency ratio	-0.40	-0.02	-0.92	-0.02	0.00
Relative amplitude	-0.16	0.10	0.07	-0.06	-0.98
Note duration	0.02	0.92	-0.01	0.33	-0.04
Rise time	0.04	0.93	0.04	-0.29	-0.09
Fall time	0.06	0.01	0.01	0.99	0.06

responding aggressively to the signals of stranger, while a false alarm is the equivalent of aggressively responding to a familiar neighbor that already shares an established territorial boundary. A correct rejection involves withholding an aggressive response to the signals of a familiar neighbor, while a missed detection is the equivalent of failing to respond aggressively toward an unfamiliar individual. Because a territory holder is much more likely to hear its nearby neighbors than the occasional stranger, at least after stable boundaries have been established, and because aggressive interactions are probably costly, we should assume that there would be a selective advantage to having a behavioral discrimination threshold that leads to high correct rejection rates and low false alarm rates. As shown in Table IV, the likelihood that individuals would respond appropriately to the calls of a familiar neighbor (correct rejection) are considerably higher than the likelihood of mistakenly responding to the neighbor's calls (false alarm). Notice, also, that *differences* in the estimated rates of correct rejections and false alarms are highest for fundamental frequency and dominant frequency. However, as the results in Table IV also make clear, if discrimination were based on the estimated JMD for a single call property, there could be a relatively high rate of missed detections (26%–47%), in which the individual could fail to respond aggressively toward an unfamiliar individual. This result, of course, stems from the overlap in the distributions of among-individual and within-individual differences, and the fact that it is impossible to simultaneously maximize both correct rejections and missed detections.

TABLE III. Factor structure from a discriminant function analysis showing the correlations between principal component scores and the canonical roots. For each factor from the principal components analysis (PCA), the acoustic properties with the heaviest factor loadings, as depicted in Table II, are shown in parentheses. Bold type indicates correlations greater than $r=0.50$.

PCA factor	Canonical Root				
	1	2	3	4	5
Factor 1 (fundamental and dominant frequencies)	-0.61	-0.07	-0.11	-0.25	0.74
Factor 2 (note duration and rise time)	0.05	-0.39	-0.79	0.19	0.43
Factor 3 (secondary frequency and frequency ratio)	-0.04	-0.61	0.45	0.59	-0.28
Factor 4 (fall time)	-0.04	-0.12	-0.22	-0.31	-0.92
Factor 5 (relative amplitude)	-0.06	0.36	-0.24	0.81	-0.40
Eigenvalue	22.0	2.8	1.6	1.0	0.2
Cumulative proportion of variance explained	0.80	0.90	0.96	0.99	1.00

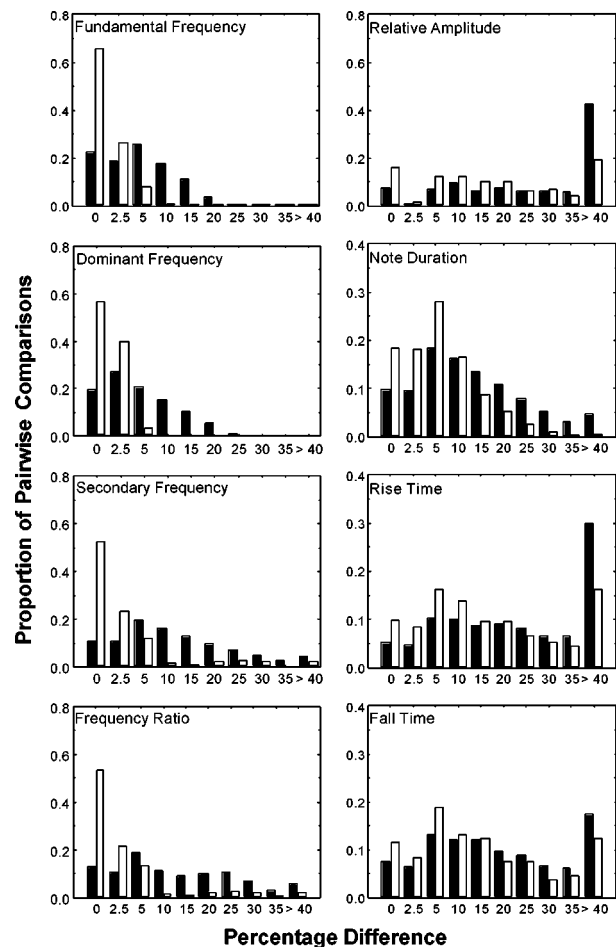


FIG. 8. Histograms showing the distributions of percentage differences in each acoustic property that occurred among individuals (black bars) and within-individuals (white bars). Numbers along the x axis depict the lower bounds of the histogram bins.

IV. DISCUSSION

A. Implications of within-individual variation for vocally mediated recognition in bullfrogs

Bee and Gerhardt (2001a) reported that several acoustic properties of bullfrog advertisement calls exhibited significant variation both among individuals and among separate notes within individuals. The results reported above extend this previous work in several important ways. First, the re-

TABLE IV. Estimated “just-meaningful differences” (JMDs) for each call property in relation to within-individual coefficients of variation and mean-standardized ranges, and the proportion of among-individual and within-individual differences that fall above and below the estimated JMD.

Call property	Within-individual coefficient of variation (%)	Within-individual range (%)	Estimated JMD (%) ^a	Among-individual differences (%)		Within-individual differences (%)	
				Above estimated JMD (correct detections)	Below estimated JMD (missed detections)	Below estimated JMD (correct rejections)	Above estimated JMD (false alarms)
Fundamental frequency	1.9	6.3	4	66	34	84	16
Dominant frequency	2.1	5.6	5	53	47	96	4
Secondary frequency	5.9	17.8	6	74	26	82	18
Frequency ratio	5.8	17.5	6	72	28	80	20
Relative amplitude	22.3	77.2	25	61	39	63	37
Note duration	8.0	27.6	10	62	38	65	35
Rise time	18.9	62.9	21	58	42	60	40
Fall time	17.8	58.0	17	56	44	57	43

^aJMDs were estimated from histograms of the among-individual and within-individual differences in bins of 1%. See Sec. II D 4. for additional details.

sults describe the systematic patterns of variation in call properties present among notes within an individual’s calls. These findings can be used to improve the design of future playback experiments that investigate the perceptual basis of discrimination by providing the data necessary to incorporate natural levels of within-individual variation into perceptual learning and discrimination tasks. Second, the results from the present study suggest that there may be significant among-individual differences in the patterns of within-individual variation in some call properties, as indicated by the significant *individual* × *note* interactions in the model II ANOVAs (Table I). This finding suggests that within-individual variation need not function solely as a constraint on recognition, and suggests the hypothesis that among-individual differences in the patterns of within-individual (i.e., among-note) variation in the calls of some individuals might function as an additional source of acoustic recognition cues. Third, the results show that, with the exception of relative amplitude, fine-temporal and spectral call properties exhibited significantly lower magnitudes of variation within individuals than did gross temporal properties. Finally, the present study demonstrates that fundamental frequency and the correlated property of dominant frequency exhibited the most reliable among-individual differences, contributed most toward statistically discriminating among individuals based on variation in multiple-note calls, and had the lowest estimated JMDs, even though these two correlated call properties also vary significantly among the notes within multiple-note calls. One general conclusion that may be drawn from this study and that by Bee and Gerhardt (2001a) is that fine-temporal and spectral call properties are potentially better vocal recognition cues than gross temporal call properties, despite the fact that fine-temporal and spectral call properties also exhibit significant within-individual variation among the notes in an individual’s multiple-note calls.

B. Individual discrimination based on “pitch”

As in some songbirds (Brooks and Falls, 1975b; Nelson, 1989), male bullfrogs appear to use acoustic properties related to pitch to discriminate among familiar and unfamiliar vocalizations. In habituation-discrimination experiments,

Bee and Gerhardt (2001b,c) demonstrated that a 5–10% change in fundamental frequency was sufficient to elicit significant levels of recovery of the habituated aggressive response. Hence, the JMDs for fundamental frequency and correlated spectral properties of 4%–6% that were estimated above (Table IV) appear to be in line with the presently available data from field playback tests. Psychophysical estimates of frequency discrimination are available for only one frog, the South African clawed frog, *Xenopus leavis* (Elpefandt *et al.*, 2000). Frequency difference limens for pure tones measured using a GO/NO-GO conditioning paradigm were approximately 5% in the hearing range of the amphibian papilla, and 2.4%–6% in the hearing range of the basilar papilla. The current estimates of JMDs for fine-temporal or spectral properties of bullfrog advertisement calls may, therefore, approach the absolute limits of the anuran auditory system.

C. Individual discrimination based on other acoustic properties

At present, there have been only limited efforts to investigate the use of other call properties as recognition cues in bullfrogs. As pointed out by Bee and Gerhardt (2001a), and as illustrated in Table IV, discrimination based only on call properties related to the pitch of the call would likely be far from perfect because of the non-negligible proportion of relatively small among-male differences in these properties present in the population (Fig. 8, Table IV). Other properties of advertisement calls also have some potential to statistically distinguish among male bullfrogs (Table I, Bee and Gerhardt, 2001a; Simmons, 2004), and therefore we might expect behavioral discrimination to be based on multiple dimensions of signal variability. Although the sample sizes were small, Bee and Gerhardt (2001c) found no evidence in their habituation-discrimination experiments that 10% decreases in note duration and internote interval or 10% increases in rise and fall times elicit recovery of habituated aggressive responses. Novel stimuli having differences in the harmonic fine-structure (presence/absence and relative amplitudes of harmonic components), but a constant fundamen-

tal frequency, also failed to elicit recovery of habituated aggressive responses (Bee and Gerhardt, 2001c). On the one hand, these previous findings are consistent with the relatively higher estimated JMDs for rise time, fall time, and relative amplitude (Table IV) in comparison to those for fine-temporal and spectral call properties. On the other hand, however, if note duration is used as a recognition cue, then these results suggest that the JMD for note duration used by receivers is higher than that estimated here. Estimating JMDs for note duration is complicated by the relatively large among-individual differences in the patterns of note-to-note variation. Clearly, more work is needed to determine whether receivers use gross temporal call properties as recognition cues.

Three properties of bullfrog advertisement calls, for which the patterns of among-individual and within-individual variation have not been investigated thoroughly, are internote interval, note duty cycle, and phase spectrum. At a constant note duty cycle, a 10% decrease in internote interval (and note duration) failed to elicit response recovery (Bee and Gerhardt, 2001c). When note duration was held constant and the duty cycle was increased 20% (from 0.5 to 0.7) by decreasing internote interval by 57% (700 to 300 ms), half of the subjects responded aggressively to the novel stimulus [only 25% responded to the control stimulus (Bee and Gerhardt, 2001c)]. None of the subjects responded to a novel stimulus having a 10% increase in duty cycle (from 0.5 to 0.6) effected by a 33% decrease in internote interval (700 to 467 ms). In a field playback test examining habituation and recovery of evoked advertisement calling, Hainfeld *et al.* (1996) found some evidence to suggest that territorial male bullfrogs might behaviorally discriminate among advertisement calls differing in phase spectrum based on differences in waveform periodicity. If there were reliable individual differences in the phase spectra of advertisement calls that were reliably transmitted through the environment across distances that separate individuals, then the phase spectrum of a neighbor's calls might also function as an additional acoustic cue for recognition. This seems unlikely, however, as Hainfeld *et al.* (1996) argued that phase spectrum was not a particularly salient cue for discriminating among advertisement calls in the natural environment.

D. Relevance of estimating JMDs from patterns of individual variation in signals

Acoustical and statistical analyses of signals cannot determine a receiver's discrimination thresholds, which instead requires experimentation. Therefore, it is important for readers to keep in mind that estimating JMDs from the degree of overlap in the distributions of among-individual and within-individual differences in multiple note calls represents one way to generate hypotheses about a receiver's behavioral discrimination threshold that can be tested in future studies. The value of deriving estimated JMDs in this way is that it provides a reasonable starting point from which to assess actual JMDs in field playback experiments.

The actual discrimination thresholds of receivers could differ from those estimated above for numerous reasons. For

example, the estimated JMDs may fall below the resolution of the bullfrog auditory system. This possibility is difficult to address because psychophysical estimates of spectral and temporal resolution of the anuran auditory system are still generally lacking. Alternatively, the actual and estimated JMDs might differ because natural selection favors behavioral discrimination thresholds that are flexible within individuals and can be adjusted according to spatial and temporal variation in the level of competition for territories. If suitable territories were limited, or stable territory boundaries were in flux, this could increase the benefits of correct detections (i.e., responding aggressively toward strangers) and increase the costs of missed detections (i.e., failing to respond aggressively toward strangers), which would shift the discrimination threshold toward lower values for threshold differences. One result of such a threshold shift would be an increase in the false alarm rate, so that individuals would also more often respond aggressively toward neighbors. Indeed, Stoddard (1996) describes a situation in song sparrows (*Melospiza melodia*) in which strong neighbor-stranger discrimination occurred in two seasons in which territories were relatively stable, but not in an intervening season in which territory boundaries were in constant flux due to an unusually high predation rate. As argued by Stoddard (1996), an ultimate level explanation for his finding is that neighbors and strangers were equally threatening during the period of high territory turn over, and thus deserved similar responses. A shift in the birds' behavioral discrimination threshold might explain this finding at a more proximate level.

An important limitation of the above discussion of estimated JMDs is that these estimates assume that within-individual variation functions as a constraint on recognition by increasing the overlap in the distributions of signal properties of different individuals. However, this need not be the case. If particular call properties vary substantially within individuals, but there are also reliable among-individual differences in the *patterns* of within-individual variation, then the pattern of within-individual variation itself may be used as an additional cue to identify the individual. This point is best illustrated by the gross temporal property of note duration [Figs. 6(c)–(f)], for which there was a significant *individual* × *note* interaction that accounted for 20% of the variation in the sample of recorded call notes (Table I, Fig. 3). Determining whether receivers take advantage of this additional source of among-individual variation will require testing in future playback studies.

E. Conclusions

Surprisingly little effort has been made to integrate, either within or across species, an understanding of the underlying acoustic and perceptual bases of vocally mediated social recognition. More commonly, studies of vocal recognition examine either (i) the ability of signals to statistically identify individuals without regard for whether or not the animals actually do, or possibly even could, discriminate among individuals based on the patterns of observed signal variation, or (ii) the ability of animals to discriminate between the signals of individuals with little or no regard for understanding the underlying acoustic basis of recognition.

The present study represents the latest effort to better understand both the acoustic and perceptual bases of vocally mediated neighbor recognition in North American bullfrogs (Bee and Gerhardt, 2001a,b,c, 2002, Bee, 2001, 2003). A better understanding of the bioacoustic basis of vocally mediated social recognition systems requires a description of the within-signal variation that individuals experience both when learning to recognize, and when discriminating among, the signals of other individuals. The ultimate goal of acoustical and statistical analyses like those reported here should be to relate patterns of signal variation both to the JMD required to elicit evolutionarily adaptive behavioral responses from receivers, as well as to the “just-noticeable difference” (JND) of the receiver’s auditory system. The habituation-discrimination paradigm represents a powerful experimental tool for providing behavioral estimates of receivers’ JMDs under natural conditions. Psychophysical estimates of the JNDs of acoustic signal properties are generally still lacking for frogs. Future psychophysical experiments with bullfrogs that employ techniques based on conditioning (Elepfandt *et al.*, 2000) or reflex modification (Megela-Simmons *et al.*, 1985; Megela-Simmons, 1988) could provide much needed insights into the mechanisms of vocal recognition in bullfrogs by illuminating the relationships between the spectral and temporal resolution of the

auditory system, on the one hand, and patterns of signal variation and the behavioral threshold for discriminating between familiar and unfamiliar signals on the other.

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APPENDIX: CORRELATIONS AMONG CALL PROPERTIES

Pearson product-moment correlation coefficients (r , below the diagonal) and the associated P -values (above the diagonal) for correlations between call properties calculated over 375 call notes.

Call property	Call Property							
	Fundamental frequency	Dominant frequency	Secondary frequency	Frequency ratio	Relative amplitude	Note duration	Rise time	Fall time
Fundamental frequency		<0.01	0.78	<0.01	<0.01	0.47	0.36	0.08
Dominant frequency	0.95		0.08	<0.01	<0.01	0.25	0.36	0.02
Secondary frequency	0.01	0.09		<0.01	<0.01	0.95	0.36	0.97
Frequency ratio	-0.48	-0.44	0.85		0.93	0.67	0.20	0.30
Relative amplitude	-0.25	-0.27	-0.16	0.00		0.03	<0.01	0.02
Note duration	0.04	0.06	0.00	-0.02	0.11		<0.01	<0.01
Rise time	0.05	0.05	-0.05	-0.07	0.20	0.74		<0.01
Fall time	0.09	0.12	0.00	-0.05	-0.13	0.32	-0.26	

¹The five exemplars of multiple-note calls analyzed from each individual were selected from a longer sequence of 20 consecutive advertisement calls recorded during a single night. Bee and Gerhardt (2001a) have shown that the acoustic properties of the first note of multiple-note calls are highly repeatable across separate nights. Model II ANOVAs that tested the effect of among-call variation in the five exemplars recorded from each individual in an individual×call factorial design confirmed that little of the variation in the sample of recordings was explained by systematic variation among calls (all F 's < 1.2, all P 's > 0.17).

²Separate univariate analyses were performed for each acoustic property because the question of interest addressed how each call property varied among individuals and among notes within calls, and not whether there was overall significant variation. This is not meant to imply that all eight acoustic properties uniquely contribute to the total amount of information in the signal (Beecher, 1989). This is certainly not the case, as there are significant correlations among several call properties (see the Appendix).

Aubin, T., and Jouventin, P. (2002). “How to vocally identify kin in a crowd: The penguin model,” *Adv. Study Behav.* **31**, 243–277.

Balcombe, J. P. (1990). “Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*,” *Anim. Behav.* **39**, 960–966.

Bee, M. A. (2001). “Habituation and sensitization of aggression in bullfrogs (*Rana catesbeiana*): Testing the dual-process theory of habituation,” *J. Comp. Psychol.* **115**, 307–316.

Bee, M. A. (2003). “Experience-based plasticity in acoustically evoked aggression in a territorial frog,” *J. Comp. Physiol., A* **189**, 485–496.

Bee, M. A., and Gerhardt, H. C. (2001a). “Neighbour-stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*): I. Acoustic basis,” *Anim. Behav.* **62**, 1129–1140.

Bee, M. A., and Gerhardt, H. C. (2001b). “Neighbour-stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*): II. Perceptual basis,” *Anim. Behav.* **62**, 1141–1150.

Bee, M. A., and Gerhardt, H. C. (2001c). “Habituation as a mechanism of reduced aggression between neighboring territorial male bullfrogs, *Rana catesbeiana*,” *J. Comp. Psychol.* **115**, 68–82.

Bee, M. A., and Gerhardt, H. C. (2002). “Individual voice recognition in a territorial frog (*Rana catesbeiana*),” *Proc. R. Soc. London, Ser. B* **269**, 1443–1448.

Bee, M. A., Kozich, C. E., Blackwell, K. J., and Gerhardt, H. C. (2001). “Individually distinct advertisement calls of territorial male green frogs, *Rana clamitans*: Implications for individual discrimination,” *Ethology* **107**, 65–84.

Beecher, M. D. (1989). “Signalling systems for individual recognition: an information theory approach,” *Anim. Behav.* **38**, 248–261.

Beecher, M. D. (1991). “Successes and failures of parent-offspring recognition in animals,” in *Kin Recognition*, edited by P. G. Hepper (Cambridge U.P., Cambridge), pp. 94–124.

Beecher, M. D., Stoddard, P. K., Campbell, S. E., and Horning, C. L. (1996).

- “Repertoire matching between neighbouring song sparrows,” *Anim. Behav.* **51**, 917–923.
- Bradbury, J. W., and Vehrencamp, S. L. (1998). *Principles of Animal Communication* (Sinauer, Sunderland, MA).
- Brooks, R. J., and Falls, J. B. (1975a). “Individual recognition by song in white-throated sparrows. I. Discrimination of songs of neighbors and strangers,” *Can. J. Zool.* **53**, 879–888.
- Brooks, R. J., and Falls, J. B. (1975b). “Individual recognition by song in white-throated sparrows. III. Song features used in individual recognition,” *Can. J. Zool.* **53**, 1749–1761.
- Capranica, R. A. (1965). *The Evoked Vocal Response of the Bullfrog* (MIT, Cambridge).
- Cheney, D. L., and Seyfarth, R. M. (1999). “Recognition of other individuals’ social relationships by female baboons,” *Anim. Behav.* **58**, 67–75.
- Crawford, J. D., Cook, A. P., and Heberlein, A. S. (1997). “Bioacoustic behavior of African fishes (Mormyridae): Potential cues for species and individual recognition in *Pollimyrus*,” *J. Acoust. Soc. Am.* **102**, 1200–1212.
- Davis, M. S. (1987). “Acoustically mediated neighbor recognition in the North American bullfrog, *Rana catesbeiana*,” *Behav. Ecol. Sociobiol.* **21**, 185–190.
- Elepfandt, A., Eistetter, I., Fleig, A., Günther, E., Hainich, M., Hepperle, S., and Traub, B. (2000). “Hearing threshold and frequency discrimination in the purely aquatic frog *Xenopus laevis* (Pipidae): Measurement by means of conditioning,” *J. Exp. Biol.* **203**, 3621–3629.
- Fischer, J., Hammerschmidt, K., Cheney, D. L., and Seyfarth, R. M. (2002). “Acoustic features of male baboon loud calls: Influences of context, age, and individuality,” *J. Acoust. Soc. Am.* **1115**, 1465–1474.
- Gelfand, D. L., and McCracken, G. F. (1986). “Individual variation in the isolation calls of Mexican free-tailed bat pups (*Tadarida brasiliensis mexicana*),” *Anim. Behav.* **34**, 1078–1086.
- Gentner, T. Q., and Hulse, S. H. (1998). “Perceptual mechanisms for individual vocal recognition in European starlings, *Sturnus vulgaris*,” *Anim. Behav.* **56**, 579–594.
- Gentner, T. Q., and Hulse, S. H. (2000). “Perceptual classification based on the component structure of song in European starlings,” *J. Acoust. Soc. Am.* **107**, 3369–3381.
- Gerhardt, H. C. (1992). “Multiple messages in acoustic signals,” *Semin. Neurosci.* **4**, 391–400.
- Gerhardt, H. C., and Huber, F. (2002). *Acoustic Communication in Insects and Anurans* (Univ. of Chicago, Chicago).
- Hainfeld, C. A., Boatright-Horowitz, S. L., Boatright-Horowitz, S. S., and Megela Simmons, A. (1996). “Discrimination of phase spectra in complex sounds by the bullfrog (*Rana catesbeiana*),” *J. Comp. Physiol., A* **179**, 75–87.
- Hauser, M. D. (1991). “Sources of acoustic variation in rhesus macaque (*Macaca mulatta*) vocalizations,” *Ethology* **89**, 29–46.
- Howard, R. D. (1978). “The evolution of mating strategies in bullfrogs, *Rana catesbeiana*,” *Evolution* (Lawrence, Kans.) **32**, 850–871.
- Innsley, S. J. (1992). “Mother-offspring separation and acoustic stereotypy: A comparison of call morphology in two species of pinnipeds,” *Behaviour* **120**, 103–122.
- Lengagne, T., Lauga, J., and Jouventin, P. (1997). “A method of independent time and frequency decomposition of bioacoustic signals: inter-individual recognition in four species of penguins,” *C. R. Acad. Sci. Paris, Sci. Vie* **320**, 885–891.
- Megela-Simmons, A. (1988). “Masking patterns in the bullfrog (*Rana catesbeiana*). I. Behavioral effects,” *J. Acoust. Soc. Am.* **83**, 1087–1092.
- Megela-Simmons, A., Moss, C. F., and Daniel, K. M. (1985). “Behavioral audiograms of the bullfrog (*Rana catesbeiana*) and the green tree frog (*Hyla cinerea*),” *J. Acoust. Soc. Am.* **78**, 1236–1244.
- Myrberg, A. A., and Riggio, R. J. (1985). “Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*),” *Anim. Behav.* **33**, 411–416.
- Myrberg, A. A., Ha, S. J., and Shambloot, M. J. (1993). “The sounds of bicolor damselfish (*Pomacentrus partitus*): Predictors of body size and a spectral basis for individual recognition and assessment,” *J. Acoust. Soc. Am.* **94**, 3067–3070.
- Nelson, D. A. (1989). “Song frequency as a cue for recognition of species and individuals in the field sparrow (*Spizella pusilla*),” *J. Comp. Psychol.* **103**, 171–176.
- Nelson, D. A., and Marler, P. (1990). “The perception of birdsong and an ecological concept of signal space,” in *Comparative Perception Vol. 2*, edited by W. C. Stebbins and M. A. Berkley (Wiley, New York), pp. 443–478.
- Polakow, D. A. (1997). “Communication and sexual selection in the barking gecko (*Ptenopus kochi*),” unpublished M.Sc. thesis, University of Capetown, Capetown.
- Robertson, B. C. (1996). “Vocal mate recognition in a monogamous, flock-forming bird, the silvereye, *Zosterops lateralis*,” *Anim. Behav.* **51**, 303–311.
- Sherman, P. W., Reeve, H. K., and Pfennig, D. W. (1997). “Recognition systems,” in *Behavioral Ecology: An Evolutionary Approach*, edited by J. R. Krebs and N. B. Davies (Blackwell, Malden, MA), pp. 69–96.
- Simmons, A. M. (2004). “Call recognition in the bullfrog, *Rana catesbeiana*: Generalization along the duration continuum,” *J. Acoust. Soc. Am.* **115**, 1345–1355.
- Simmons, A. M., and Ferragamo, M. (1993). “Periodicity extraction in the anuran auditory nerve I. Pitch-shift effects,” *J. Comp. Physiol., A* **172**, 57–69.
- Sokal, R. R., and Rohlf, F. J. (1994). *Biometry* (Freeman, New York).
- Stoddard, P. K. (1996). “Vocal recognition of neighbors by territorial passerines,” in *Ecology and Evolution of Acoustic Communication in Birds*, edited by D. E. Kroodsma and E. H. Miller (Cornell U.P., Ithaca, NY), pp. 356–374.
- Weary, D. M., Norris, K. J., and Falls, J. B. (1990). “Song features birds use to identify individuals,” *Auk* **107**, 623–625.
- Wiley, R. H. (1994). “Errors, exaggeration, and deception in animal communication,” in *Behavioral Mechanisms in Evolutionary Ecology*, edited by L. A. Real (Univ. of Chicago, Chicago), pp. 157–189.