

Individual voice recognition in a territorial frog (*Rana catesbeiana*)

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Some territorial animals display low levels of aggression towards a familiar territorial neighbour in its usual territory, but exhibit high levels of aggression towards neighbours in novel locations and unfamiliar individuals. Here, we report results from a field playback study that investigated whether territorial males of the North American bullfrog (*Rana catesbeiana*) could discriminate between the acoustic signals of simulated neighbours and strangers in the absence of contextual cues associated with a specific location. Following repeated exposures to synthetic bullfrog calls from a particular location, subjects responded significantly less aggressively to a familiar call, compared with an unfamiliar one, when both calls were broadcast from familiar and novel locations, indicating that bullfrogs could recognize a neighbour's calls independently of the contextual cues provided by the direction of the neighbour's territory. Subjects responded equally aggressively to unfamiliar calls broadcast from either a familiar or a novel location, which indicates that they could perceive unfamiliar calls as those of a stranger, regardless of where the stranger was encountered. Together, these two results provide evidence that a frog possesses a capacity for individual voice recognition.

Keywords: individual recognition; neighbour recognition; voice recognition; territoriality; acoustic communication; *Rana catesbeiana*

1. INTRODUCTION

Individuals of some territorial species exhibit lower levels of aggression towards familiar neighbours compared with unfamiliar individuals based on the recognition of the neighbour's individually distinct voice characteristics (reviewed in Temeles (1994)). Most previous playback studies of vocally mediated neighbour recognition have compared a resident's responses with only two signals—that of a neighbour and that of a single unfamiliar animal—from locations associated with the neighbour's territory (reviews in Falls 1982; Lambrechts & Dhondt 1995; Stoddard 1996). Falls & Brooks (1975), studying white-throated sparrows (*Zonotrichia albicollis*), first demonstrated that territorial residents also respond with increased aggression to a neighbour's signals broadcast from outside the neighbour's usual territory. This general result has been reported in other songbirds (Falls 1982; Lambrechts & Dhondt 1995; Stoddard 1996) and in two kinds of lower vertebrates (Myrberg & Riggio 1985; Davis 1987). Following Beer (1970), Falls & Brooks (1975) argued that aggressive responses to a familiar sound in a novel location indicated not only that residents discriminated between familiar and unfamiliar conspecifics but also that residents recognized neighbours by voice as particular individuals associated with a particular territory. Associations between a neighbour's vocalizations and its territory location are now widely accepted as evidence of individual voice recognition in territorial animals (Lambrechts & Dhondt 1995; Stoddard 1996).

We think that the use of location dependence as a criterion for individual voice recognition is problematic for

two reasons. First, in studies that have compared responses to neighbours and strangers from the territory boundary opposite with that of the neighbour, residents responded as aggressively towards the neighbour's signal as they did towards the unfamiliar signal (Falls & Brooks 1975; Elfström 1990; Stoddard *et al.* 1991). At face value, these results are consistent with the hypothesis that a neighbour's signals in a novel location are perceived as those of an unfamiliar individual and thus fail to demonstrate recognition of a familiar voice. The interpretation is equivocal because aggressive responses in field playbacks are unconditioned responses (Shettleworth 1998). Second, the criterion of location dependence contradicts Falls's (1982) own operational definition of individual voice recognition in birds as discrimination 'among similar sounds of different individuals in the absence of other identifying cues'. Logically, the fact that the songbirds respond differently to the same signal in different locations indicates that location could be another identifying cue that facilitates neighbour recognition. Such cues are usually classified as contextual cues in studies of animal learning and memory (Bouton 1993). We therefore assert that location-independent discrimination of the signals of neighbours and strangers is convincing evidence of individual voice recognition that also corresponds to everyday human experience: recognition of individual voices is not limited to a single location. In fact, this criterion was fulfilled in one study of white-throated sparrows (Falls & Brooks 1975) in which discrimination occurred at the centre of the territory as well as at the neighbour's territorial boundary, albeit not at the opposite side of the territory.

Our goal in this study was to investigate location-independent voice recognition in a lower vertebrate. Despite the importance of vocal signals in territorial behaviour of many species of frogs, few studies have investigated neighbour recognition by voice. Such studies have the potential

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to identify perceptual and cognitive processes that might be common to species that communicate acoustically during territorial encounters. Davis (1987) demonstrated that territorial males of the North American bullfrog (*Rana catesbeiana*) respond less aggressively to broadcasts of a neighbour's advertisement calls from the direction of the neighbour's usual territory compared with broadcasts of the neighbour's calls from a novel location and to broadcasts of the calls of strangers. In a previous study (Bee & Gerhardt 2001*b*), we demonstrated that several acoustic properties of bullfrog advertisement calls are individually distinctive, and that properties related to the perceived pitch of the calls (e.g. fundamental frequency) are the most individually distinctive properties of bullfrog vocalizations. Using the habituation/discrimination paradigm, we also showed that male bullfrogs learn about fundamental frequency (or correlated spectral properties) and the signal's location of origin as a result of repeated exposures to the sound from a particular location (Bee & Gerhardt 2001*a,c*). Here we use the same procedure to show that territorial bullfrogs discriminate between familiar and unfamiliar signals based on differences in pitch in both familiar and novel locations. Pitch is by far the most reliable acoustic indicator of individual identity in bullfrogs (Bee & Gerhardt 2001*b*).

2. METHODS

Between 15 May and 18 July 2000, we conducted a playback experiment in ponds at the Little Dixie Lake Conservation Area (Callaway County, MO, USA) under ambient light between 21.30 and 06.00, Central Daylight Time (CDT). We had previously captured each male, measured its snout-to-vent length (SVL) and individually marked it by waistbands and tags with identifying numbers.

(a) Playback equipment

The sound output of notebook computers (Dell Inspiron 3500 or 5000) was amplified (Rockford Fosgate 2.6 \times) and broadcast through one of four 25 cm diameter Optimus speakers mounted in wooden boxes and floated on styrofoam platforms. The frequency response of each speaker was flat (± 4 dB) between 60–3000 Hz; all spectral components of our stimuli fell within this range. We broadcast stimuli at a sound pressure level of 87 dB (re 20 μ Pa, fast RMS, C-weighted, measured in the field at a distance of 1 m).

(b) Playback stimuli

Bullfrogs respond with encounter calls and stereotyped aggressive movements towards, around and away from speakers broadcasting natural and synthetic models of advertisement calls (Davis 1987; Bee & Gerhardt 2001*a,c*). We used synthetic advertisement calls (16-bit, output sampling rate 20 kHz). Each stimulus consisted of five consecutive advertisement calls separated by 30 s inter-call intervals (figure 1). Each call consisted of five identical notes comprised of 10 harmonics (f_2 – f_4 and f_{10} – f_{16}) of a missing fundamental frequency (f_1) with the same starting phase relationship (0°). The spectral envelope was shaped to reflect a typical advertisement call by attenuating harmonics by 5–20 dB relative to a dominant second harmonic. The final call of the stimulus was followed by a silent 5 min inter-stimulus interval. The combination of the stimulus and the inter-stimulus interval was repeated as a continuous loop and,

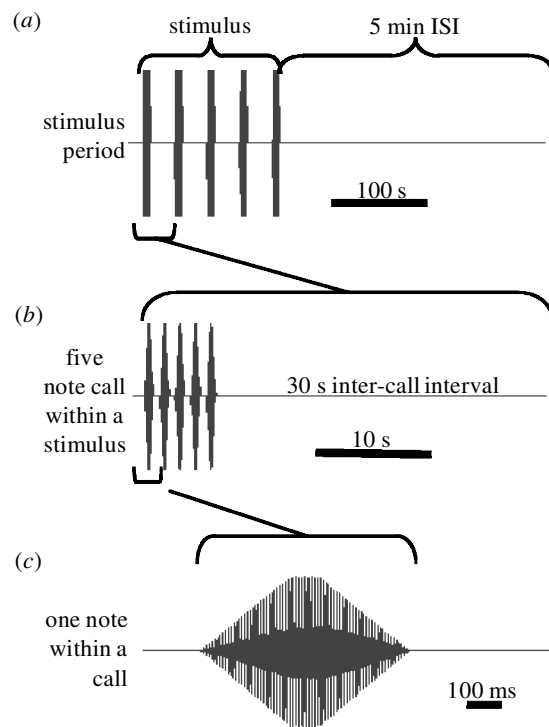


Figure 1. Synthetic bullfrog advertisement calls used as stimuli in this study. (a) One 'stimulus period' comprising one 'stimulus' with five consecutive five note calls followed by a 5 min 'interstimulus interval' (ISI). (b) One five note call followed by the 30 s inter-call interval. (c) A single note from the stimulus. Horizontal bars indicate time-scales.

together, they constitute a 'stimulus period' (figure 1; additional details in Bee & Gerhardt (2001*a*)).

(c) Experimental design

Our experiment consisted of a 'habituation phase' (HP) followed immediately by a 'discrimination phase' (DP). During the HP, we simulated the arrival of a new territorial neighbour by broadcasting one of two training stimuli differing only in fundamental frequency (and correlated spectral differences) from an unoccupied position adjacent to the subject's territory. One training stimulus simulated a 'large' male ($f_1 = 95$ Hz), and the other simulated a 'small' male ($f_1 = 125$ Hz). Male bullfrogs can perceptually discriminate between these two stimuli, which span the range of natural variation in fundamental frequency (Bee & Gerhardt 2001*a,b,c*), but the intensity of aggressive responses does not differ in response to these two stimuli (Bee 2002). We repeatedly broadcast the training stimulus for 30 stimulus periods, which was equivalent to approximately 3.75 h of continuous playbacks. The aggressive response usually habituates to asymptotic levels in fewer than 30 repetitions using this protocol (Bee 2002).

During the DP, which lasted for three consecutive stimulus periods, we manipulated the location of the stimulus (same/different) and the 'identity' of the stimulus (same/different) in a 2×2 fully factorial design. We manipulated location by presenting stimuli from a second speaker located in a novel position. Identity was manipulated by broadcasting the stimulus that was not used as the training stimulus during the HP. The four treatment groups in the DP are denoted as follows: same frog/same location (SFSL) ($n = 12$, control), same frog/different location (SFDL) ($n = 12$), different frog/same

location (DFSL) ($n = 12$), and different frog/different location (DFDL) ($n = 12$). Forty-eight male bullfrogs were used as subjects in this study. Playbacks occurred in six temporal blocks of eight randomly ordered tests. Both stimuli were used as the training stimulus four times in each block, once for each of the four experimental treatments in the DP.

(d) *Playback protocol*

Prior to beginning a test, we placed speakers at a distance of 6 m from the subject along the pond bank. Typical distances between adjacent territorial males range between 3–16 m (Emlen 1976). We preferentially tested males that did not have nearest neighbours within 10 m in any direction to avoid interference from other territorial males. For control tests (SFSL) and tests involving only a change in frog identity (DFSL), a single speaker was placed in the direction of the subject's most distant neighbour. If there were no nearby neighbours (less than 15–20 m away), speaker position (left or right relative to the frog) was randomly determined. For tests involving changes in location (SFDL and DFDL), two speakers were placed on opposite sides of the frog (12 m and 180° apart), and the speaker used during the HP was placed in the direction of the subject's closest neighbour. Once subjects resumed normal calling, we waited 10–20 min before beginning the HP. During each stimulus period of the HP and DP, one or two observers seated near the pond bank (usually less than 5 m from the subject at all times) counted the number of encounter calls and aggressive movements towards, around and away from the playback speaker, and estimated the subject's closest approach towards the speaker to the nearest metre from its original calling site.

(e) *Data analysis*

Subjects included in the dataset gave at least one encounter call during the first stimulus period of the HP. One subject in the SFSL group was excluded from statistical analyses because it did not meet this criterion. For the remaining 47 subjects, we calculated the mean number of encounter calls, movements and maximum approach distance in temporal blocks averaged over three consecutive stimulus periods. The first 10 blocks comprised the HP. The eleventh block comprised the DP. Because our response variables were correlated within subjects (r -values > 0.74), and are therefore redundant measures of aggression, we used principal components analysis to extract the first principal component as a single measure of aggressive response magnitude. Principal component scores were correlated with all three aggressive response variables (r -values > 0.91). We computed an 'aggressive index' (AI) by adjusting the principal component scores upwards to an arbitrary minimum of zero, and expressing the score for each block as a percentage of the score on the first block (block 1, 100%). AI scores were log-transformed ($Y' = \log_{10}(Y + 1)$) to improve normality and homoscedasticity and to eliminate a positive correlation between the means and variances across treatment groups.

Analysis of variance revealed significant differences in the body sizes of the subjects in the four treatment groups ($F_{3,44} = 8.30$, $p = 0.0002$). Because aggressive responses of male frogs can depend on body size (Bee *et al.* 2000), we used SVL as a covariate in all between-subjects comparisons. Changes in AI scores during the HP were assessed using repeated measures analysis of covariance (ANCOVA), with identity and location included as between-subjects factors. The methods of Greenhouse & Geisser (1959) were used to adjust the degrees of free-

dom and p -values of omnibus within-subjects effects for violations of assumptions of repeated measures ANOVAs. Recovery during the DP was assessed using paired-sample t -tests to compare the average AI scores from blocks 10 and 11. We also compared the magnitude of the raw AI scores in the DP with those from the first block of the HP in order to contrast the degree of recovery with initial responses. We used Wilcoxon's matched-pairs signed-ranks (WMPSR) tests on the raw AI scores, instead of a parametric equivalent, because there was no variance in the initial block of the habituation phase. We compared the magnitude of response recovery in the four treatment groups of the DP in a 2 (identity) \times 2 (location) factorial ANCOVA. We used focused contrasts (Rosenthal & Rosnow 1985) to compare each main effect at each level of the other main effect. Statistical significance was set at $\alpha = 0.05$. Principal component scores were calculated using SAS v. 8.0; ANOVAs, t -tests and non-parametric tests were computed using STATISTICA v. 5.5.

3. RESULTS

(a) *Habituation of the aggressive response*

The magnitude of the AI varied significantly over the 10 blocks of the HP ($F_{9,387} = 28.45$, $p < 0.0001$), declining from 100% in the first block to a mean (\pm s.e.) of $21.1 \pm 4.8\%$ in the final block of habituation training (figure 2). There were no significant differences in the habituation of the aggressive response among subjects in the four treatment groups of the DP.

(b) *Recovery during the discrimination phase*

No recovery occurred in the control treatment (SFSL: $t_{10} = 1.17$, $p = 0.2700$; figure 2). The average raw AI scores of this group in the DP were $18.9 \pm 12.2\%$ and were significantly less than the initial block of habituation training (WMPSR: $T = 1.0$, $p = 0.0044$, $n = 11$). Significant recovery of aggression occurred when we changed identity (DFSL: $t_{11} = 4.47$, $p = 0.0009$) and both identity and location (DFDL: $t_{11} = 2.82$, $p = 0.0166$) (figure 2). In response to a change in identity alone (DFSL), raw AI scores recovered to an average of $109.2 \pm 22.7\%$ of the response on the initial block of the HP and did not differ significantly from responses during the first block of habituation training (WMPSR: $T = 37$, $p = 0.8753$, $n = 12$). The average raw AI score of the response to changes in both location and identity (DFDL) was $144.2 \pm 39.9\%$ after excluding one subject whose raw AI score in block 11 was nearly 600% and far exceeded the values of other subjects (mean = 182.0% including this subject). Responses during the DP in group DFDL also did not differ significantly from responses during the first block of habituation training (WMPSR: $T = 26$, $p = 0.3078$, $n = 12$). Recovery in response to changes in location alone (SFDL) was intermediate between controls and changes in frog identity and approached statistical significance in a parametric test ($t_{11} = 2.07$, $p = 0.0626$; figure 2). A non-parametric comparison of the raw AI scores in blocks 10 and 11 revealed significant recovery in the SFDL treatment (WMPSR: $T = 7.0$, $p = 0.0367$, $n = 12$). During the DP, raw AI scores in the SFDL group were significantly less than initial responses (WMPSR: $T = 11.0$, $p = 0.0281$, $n = 12$) and recovered to an average of $54.2 \pm 17.0\%$. The average log₁₀-transformed AI scores

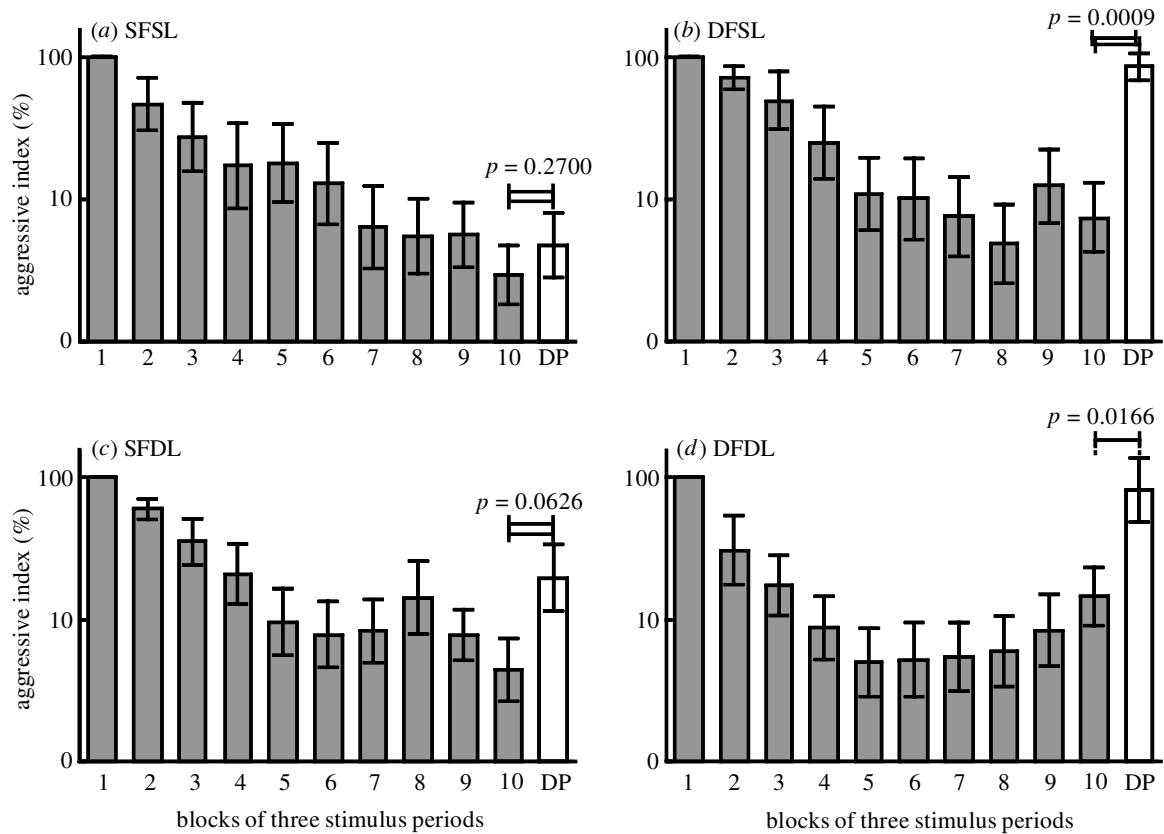


Figure 2. Mean (\pm s.e.) AI scores during the HP (shaded blocks 1–10) and the DP (open block 11–‘DP’). Values represent the log-transformed means depicted on a log scale and expressed as the percentage of the response during the first block of the HP. The p -values are results of paired-sample t -tests comparing blocks 10 and 11.

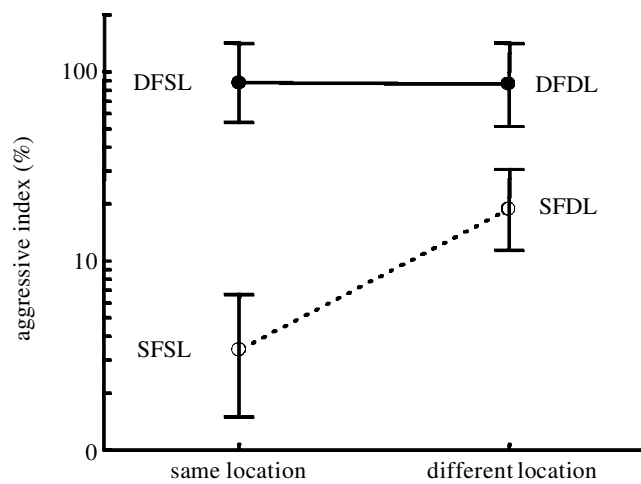


Figure 3. Mean (\pm s.e.) AI scores depicting the recovery of the aggressive response in the four treatment groups of the DP. Values represent the covariate-adjusted, log-transformed means depicted on a log scale and expressed as a percentage of the initial response during the HP. The filled circles and solid line depict responses to an unfamiliar stimulus; the open circles and dashed line depict responses to the familiar stimulus.

of all subjects in the SFSL, SFDL, DFSL and DFDL groups were 5%, 20%, 85% and 81%, respectively, following an inverse \log_{10} -transformation.

(c) Context-independence of responses

Figure 3 depicts the AI scores for the four treatment groups during the DP. A 2×2 ANCOVA revealed a sig-

nificant main effect of identity ($F_{1,42} = 17.07$, $p = 0.0002$). Responses were significantly greater when stimulus identity was changed. There was no significant main effect of location ($F_{1,42} = 2.17$, $p = 0.1479$) or an identity \times location interaction ($F_{1,42} = 2.50$, $p = 0.1210$).

With identity constant, changing location resulted in significantly greater response recovery (SFSL versus SFDL, $F_{1,42} = 15.34$, $p = 0.0448$). However, when identity was also changed, there was no effect of changing location (DFSL versus DFDL: $F_{1,42} < 0.01$, $p = 0.9746$). In the familiar location, significantly greater recovery occurred to the sounds of an unfamiliar animal, compared with a familiar sound (SFSL versus DFSL: $F_{1,42} = 15.34$, $p = 0.0003$). Habituated aggressive responses also recovered significantly more in response to the unfamiliar stimulus, compared with the familiar one, when both stimuli were heard from the novel location (SFDL versus DFDL: $F_{1,42} = 4.69$, $p = 0.0361$).

4. CONCLUSIONS

From this study, we conclude that bullfrogs can learn to discriminate between two signals that differ in an individually distinctive voice property (fundamental frequency) in the absence of other sensory and spatial cues. Fundamental frequency or correlated spectral properties are the most important acoustic properties for discriminating among the voices of different individuals. Therefore, our results indicate that bullfrogs possess some capacity to recognize a familiar voice as that of a particular individual. Subjects responded equally strongly to unfam-

iliar calls in familiar and novel locations. Most importantly, even though subjects responded more aggressively to the familiar stimulus in the novel location, they also responded more strongly to the novel stimulus in a novel location. Thus male bullfrogs can discriminate between the familiar and unfamiliar vocalizations of conspecifics independently of spatial context. According to Falls's operational definition of individual voice recognition in songbirds (Falls 1982), our result indicates that bullfrogs possess a capacity for individual voice recognition.

Four caveats are worth considering. First, in this study we have manipulated only a single voice characteristic (pitch). The vocalizations of bullfrogs exhibit reliable individual variation along multiple acoustic dimensions that could function as voice recognition cues (Bee & Gerhardt 2001*b*). However, in a multivariate statistical analysis of call properties, the first canonical root was only correlated with fundamental frequency ($r = 0.79$) and explained nearly 80% of the among-individual variation in vocalizations (Bee & Gerhardt 2001*b*). Hence, we have manipulated the voice characteristic that best discriminates among individual voices. Second, subjects were presented with two invariant synthetic stimuli with fundamental frequencies from opposite ends of the population range (Bee & Gerhardt 2001*b*). Male bullfrogs can discriminate much smaller differences in fundamental frequency (Bee & Gerhardt 2001*a,c*). Whether location-independent discrimination could occur, based on smaller differences in fundamental frequency after exposure to stimuli incorporating natural variation, remains to be determined. We emphasize again, however, that the signals of our simulated individuals differed in a single acoustic property, while natural signals from real frogs would differ along multiple acoustic dimensions (Bee & Gerhardt 2001*b*), which could facilitate recognition by voice. Third, a 180° change in speaker location represents a realistic but limited change in the context of stimulus presentation. Because individual male bullfrogs can occupy several different, spatially separated territories each breeding season (Emlen 1976), future studies could examine larger changes in context. Fourth, bullfrogs can have up to three or four territorial neighbours simultaneously. Additional experiments will be required to determine whether bullfrogs can simultaneously recognize the different voices of multiple individual neighbours (e.g. Myrberg & Riggio 1985).

We adopt Falls's (1982) operational definition of individual voice recognition in birds and we consider the neighbour's usual location to be a potentially useful identifying cue. We are thus puzzled by the widespread acceptance of the criterion of location-dependent discrimination. The lack of behavioural discrimination at a novel location could logically be attributable to a partial reliance on spatial cues to solve voice recognition tasks, to a perceptual inability to discriminate (perhaps in part influenced by habitat acoustics or background sounds), to the equivalence of the threat represented by neighbours and strangers in that location (Stoddard 1996), or to some combination of these factors. At the same time, we doubt that songbird discrimination is limited to the usual territorial boundary, and other qualitative criteria provide strong evidence for individual voice recognition. For example, Beecher *et al.*

(1996) demonstrated that song sparrows respond to a specific neighbour's song with another song shared with that neighbour's repertoire instead of merely matching the specific song. This result and the long-term memory of a neighbour's song from season to season (McGregor & Avery 1986; Godard 1991) indicate that songbirds have sophisticated cognitive abilities to recognize voices.

What factors might be responsible for the differences between songbird studies and this one in the patterns of responsiveness to familiar and unfamiliar vocalizations in novel locations? First, studies of songbirds used natural signals, one of which the birds had presumably become familiar with through normal interactions. The birds were not previously habituated by the experimenter as were the bullfrogs. Moreover, there was a single salient acoustic difference between the training and novel stimuli used in this study, which could have facilitated the discrimination task. Second, songbird neighbours encountered in unfamiliar locations may represent serious threats to territory stability, hence differences in aggressive responses to the songs of neighbours and strangers are likely to be subtle (Stoddard 1996). Perhaps the design used here would also be sensitive enough to detect such differences in songbirds (e.g. Petrinovich 1984). Of course, bullfrogs and songbirds might also differ in the perceived threat represented by the detection of a neighbour in an unexpected location.

In conclusion, our results indicate some degree of convergence in the evolution of cognitive abilities in birds and frogs in the context of vocally mediated recognition in a territorial social system. Mechanisms that allow for reduced displays of aggression between neighbours are expected to evolve in taxa that defend long-term, multi-purpose breeding territories (Temeles 1994). The mating systems of bullfrogs and songbirds share this feature in common, and vocalizations are of paramount importance in mediating social interactions between territorial neighbours in both groups. Hence, a capability to recognize individual voices has apparently evolved independently in both groups in response to similar selection pressures associated with the defence of long-term territories. Future comparative studies should investigate the similarities and differences in the perceptual and cognitive mechanisms of voice recognition in birds and frogs.

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