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HEARING IN THE RED-BILLED FIREFINCH *LAGONOSTICTA SENEGALA* AND THE SPANISH TIMBRADO CANARY *SERINUS CANARIA*: THE INFLUENCE OF NATURAL AND ARTIFICIAL SELECTION ON AUDITORY ABILITIES AND VOCAL STRUCTURE

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ABSTRACT

We tested the auditory sensitivity of red-billed firefinches *Lagonosticta senegala* and Spanish timbrado canaries *Serinus canaria*. Both these species produce songs and calls that are narrowband and relatively high in frequency, with spectral energy falling predominantly in the region of 3-6 kHz. Hearing thresholds were measured in these two species and compared to the auditory sensitivity of closely related species: the well studied zebra finch *Taeniopygia guttata*, and other strains of canary bred for song. Auditory thresholds were similar in both groups of birds, with firefinches having an audiogram typical for that of small birds. Timbrado canaries exhibited an audiogram with its greatest sensitivity in the relatively high region of 4-6 kHz, corresponding to the peak frequency of its calls. Critical ratios measured over a range of several octaves increased in a monotonic fashion at a rate of 2-3 dB per octave for both firefinches and timbrado canaries. Critical ratios in these two species are similar to what has been found in most other small passerine species, suggesting spectral resolving abilities similar to most small birds tested to date.

Keywords: behavioural audiogram, hearing, red-billed firefinch, Spanish timbrado canary, vocalisations.

INTRODUCTION

The red-billed firefinch *Lagonosticta senegala* is a small finch in the family Estrildidae native to sub-Saharan Africa (Payne 1980). Like many songbirds, it produces songs and calls that are narrowband, consisting primarily of single predominant frequency components (Sullivan 1976; Payne 1990) (Figure 1a). Another estrildid, the zebra finch *Taeniopygia guttata*, has become a popular songbird model for

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studies of vocal learning and song production, and is one of the best studied species of birds from the perspective of its auditory perceptual capabilities. The research focus on the latter species is in large part due to its domestication and propensity to breed well in captivity (Zann 1996). Unlike most songbirds studied to date, zebra finches produce calls and songs that are broadband, containing a large number of harmonics with substantial energy (Zann 1984; 1993) (Figure 1b). While the structure of vocalisations in zebra finches may have been influenced by domestication, such effects appear to be limited to the presence, order, or delivery rate of specific song elements and do not involve increases or decreases in overall bandwidth (Slater & Clayton 1991; Okanoya et al. 1993; Blaich et al. 1995; Zann 1996). In addition, a number of other non-domesticated estrildids produce broadband songs and calls (Hall 1962). In contrast to zebra finches, little is known regarding the hearing abilities of most other species of estrildid finches, in particular those whose songs and calls are narrower in bandwidth.

Canaries *Serinus canaria*, like zebra finches, have been bred in captivity for over 100 years (Güttinger 1985; Walker & Avon 1993; Zann 1996). Aviculturalists have selected birds for their song, posture, and plumage. Studies have shown that a particular strain of canary, the Belgian waterslager, has a substantial high-frequency hearing deficit (Okanoya & Dooling 1985, 1987b). While Belgian waterslager canaries were bred to produce loud, low-pitched song, breeders inadvertently may have been selecting birds for poor high-frequency hearing. Prior results from hearing tests in Belgian waterslager canaries inspired us to begin testing the hearing of other canary strains. One of these other strains, the Spanish timbrado canary, produces songs that emphasise high rather than low frequencies. Though it is difficult to trace their heritage, the Spanish timbrado has been recognised as a distinct strain since 1962 (Walker & Avon 1993). This strain may have resulted from crossbreeding of the wild-type canary *Serinus canaria* with a congeneric species, the serin *Serinus serinus*, to produce a songbird with high-pitched vocalisations (Walker & Avon 1993). Anecdotal reports indicate that breeders have continued to cross this strain with wild canaries, suggesting that it is perhaps the most closely related domesticated variety to the wild-type bird.

We were interested in whether the frequency range and bandwidth of vocal signals were predictive of a bird's hearing abilities, among species in which similar high-frequency, narrowband vocalisations evolved in a natural context and in an artificial one. The present study reports on the auditory sensitivity and vocal characteristics of red-billed firefinches and timbrado canaries. We provide a comparison between these two species and related birds whose auditory abilities have been tested previously. In the case of the firefinch, this contrast allows for a comparison of a domesticated species,

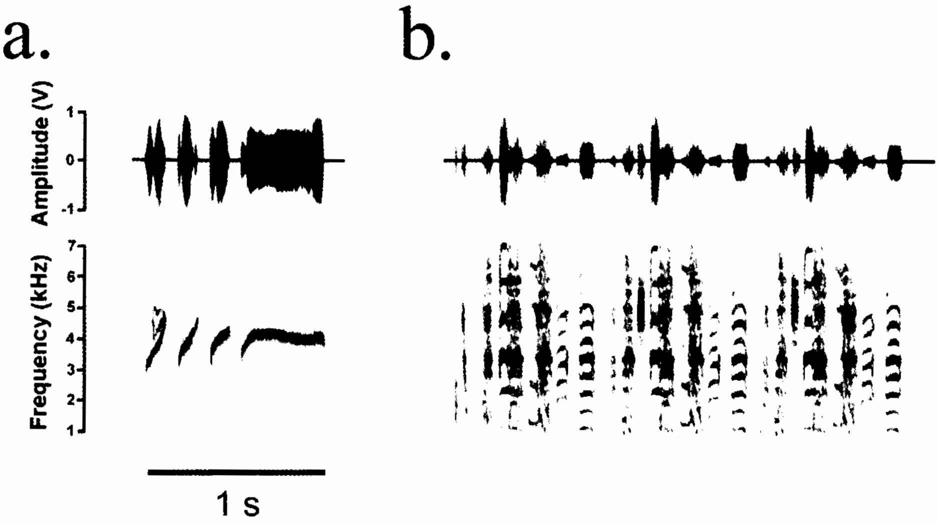

Figure 1. a) Time waveform and sound spectrogram of red-billed firefinch *Lagnosticta senegala* song. b) Time waveform and sound spectrogram of zebra finch *Taeniopygia guttata* song. Spectrogram FFT size = 256 pts. (78 Hz frequency resolution).

the zebra finch, with a wild relative having vocalisations that differ in both bandwidth and frequency of emphasis. In the case of the Spanish timbrado and Belgian waterslager canaries, our comparison is between conspecifics that have been bred for very different types of songs (differing primarily in the frequency, or pitch, of song) (Güttinger 1985; Walker & Avon 1993). Thus, we have a contrast of species in which natural selection has acted to produce different types of vocalisations, and a contrast of strains within a species in which artificial selection has been used to produce divergent vocalisations. The purpose of tests reported here was two-fold: 1) to measure hearing in two species of birds (red-billed firefinches and Spanish timbrado canaries) in which natural and artificial selection resulted in spectrally similar vocalisations, and 2) to examine relatives of two domesticated bird species popular in laboratory vocal studies, each of which produce vocalisations very different from the two laboratory species.

METHODS

Subjects

Four red-billed firefinches (2 male, 2 female), and five Spanish timbrado canaries (2 male, 3 female) served as subjects in these experiments. Red-billed firefinches are small (8-10 g) finches that are predominantly granivorous like zebra finches and canaries. The firefinches used in this study were 1st or 2nd generation captive birds. Two of the firefinches (1 male, 1 female) were cross-fostered by Bengalese finches *Lonchura striata*. Thresholds were similar for all individuals regardless of rearing conditions, however, and in all cases individuals were exposed to songs and calls of adult conspecifics in the same large aviary throughout development. Spanish timbrado canaries used in this study were obtained from a breeder. Young timbrado canaries were reared by parents of the same strain.

All birds ranged in age from 2-5 years. Birds were kept in a vivarium at the University of Maryland on a normal light/dark cycle corresponding to the season. Birds were housed individually in the same room and kept at 90 percent of their free feeding weight. They had free access to water and grit in their home cages, and were food deprived several hours prior to each training and testing session. All birds used in these experiments were naive and were trained to perform the operant procedure prior to the start of the experiment. The care and use of animals reported on in this study was approved by the University of Maryland Animal Care and Use Committee, and conformed to guidelines set forth by the National Institutes of Health.

Vocal recording

Songs and calls of firefinches and timbrado canaries were recorded in custom-built, anechoic chambers using a Realistic 33-3003 omnidirectional condenser microphone and a Marantz PMD 740 analogue tape deck. Vocalisations were analysed using the SIGNAL / RTSD sound analysis software (Beeman 1998).

Operant testing apparatus

Birds were tested in a small animal operant conditioning chamber whose design and set-up has been described previously (Dooling & Okanoya 1995). Briefly, birds were tested in a 25 cm x 25 cm x 25 cm wire cage mounted in an IAC sound-attenuated booth. A custom-built response panel, consisting of two sensitive microswitches with attached light emitting diodes (LEDs), was mounted on one side of the cage. The left microswitch served as an observation key and the right microswitch served as a report key. Small yellow millet served as a positive reinforcer and was delivered via a grain hopper mounted in the front of the cage beneath and between the observation and report keys. All experimental events were controlled with a Pentium microcomputer. The behaviour of the birds was monitored during test sessions by a closed-circuit video camera system.

Stimuli

Tone stimuli were generated digitally and stored on a hard disk. All tones were 400 ms in duration with 10 ms rise/fall, and were played at a rate of 2/s (cycle length of 500 ms). Masking noise used in measuring critical ratios was generated online using a Tucker-Davis Technologies (TDT) System 2 WG1 waveform generator module and was bandlimited with a TDT PF1 programmable filter. During an experiment, tone and noise stimuli were output through a TDT DD1 stereo analogue interface at 40 kHz, low-pass filtered at 8.5 kHz, sent to a Crown D-75 amplifier, and finally to a KEF 60S loudspeaker mounted 40 cm above the bird's head in the operant chamber. Sound calibration was accomplished by placing the half-inch microphone of a Larson-Davis System 824 sound level meter in front of the microswitches in the position normally occupied by the bird's head. The intensities of test tones and noise were measured weekly during the testing phase as a check that they remained constant.

Testing procedures

Birds were trained to peck one LED (observation key) until a tone was presented. Birds were then required to peck the other LED (report key) when they detected a tone. A peck on the report key within 2 s of a tone presentation was defined as a correct response and was rewarded with a 2 s access to food. A failure of the subject to peck at either the observation key or the report key within 2 s of the presentation of a tone was recorded as a miss, and the trial was automatically ended and a new trial begun. Thirty percent of all trials were 'sham' trials during which no tone was presented. A peck to the report key during a sham trial was recorded as a false alarm, and was punished with a 5 s timeout period during which lights in the test chamber were extinguished. Percentage of responses during sham trials provided a measure of false alarm rate.

Thresholds for pure tones were measured in the quiet (absolute thresholds) for both species. In addition, we measured masked thresholds in a background of constant broadband white noise (critical ratios). For absolute thresholds, birds were tested on tones at 0.5, 1.0, 2.0, 2.86, 4.0, 5.7, and 8.0 kHz. Masked thresholds were tested on a subset of these frequencies. Thresholds were determined using the method of constant stimuli (Dooling & Okanoya 1995), and were defined as the level of tone corresponding to a 50 percent correct. Within each 10-trial block, the test tone was presented at seven different predetermined levels using a step size of 5 or 10 dB. Sessions with false alarm rates greater than 20 percent were discarded. In practice, thresholds also were calculated using a d' of 1.5 and a 50 percent correct rate corrected for false alarm rate: Pc* = (Pc - FA)/(1 - FA), where FA = false alarm, Pc = percent correct, and Pc* = corrected percent correct (Dooling & Okanoya 1995). Thresholds were nearly identical as estimated from these three procedures, since false alarm rate was consistently low. Birds were tested repeatedly until threshold values showed no further improvement, defined as two successive 100-trial blocks in which the threshold was within ± $^1/_3$ the step size. This criterion typically resulted in a total of 400-600 trials per bird per test frequency. The final two 100-trial sessions were averaged for our threshold at each frequency.

RESULTS

Vocalisations

Both red-billed firefinches and Spanish timbrado canaries produce songs and calls composed predominantly of single frequency components, with substantial energy at mid to high frequencies for songbirds (3-6 kHz). Firefinches differ from the closely-related zebra finch in the bandwidth of their vocalisations. Figures 1 and 2a illustrate examples from birds used in this study, in the case of firefinches, and from our colony in the case of zebra finches. The difference in bandwidth between the songs of these two species is characteristic and consistent across individuals. While these spectra come from individuals reared in captivity (and in the case of one firefinch, cross-fostered by Bengalese finches), both the firefinch and zebra finch spectral data correspond well to published accounts of the species' vocalisations in the wild (Sullivan 1976; Payne 1990; Zann 1996).

Among canaries, the Spanish timbrado strain is characterised by producing high-frequency song while the Belgian waterslager produces low-frequency song. The consequences of breeding and artificial selection for timbrado canaries and waterslager canaries on the region of peak spectral energy of both calls and songs is obvious from average power spectra of these vocalisations (Figures 2b and c). Calls in the two canary strains are similar in overall acoustic structure, but Spanish timbrado calls have substantially more energy in higher frequency regions (Figure 2c). Songs are repeated sequences of tones, or 'notes', at different frequencies in both strains, but there is a greater emphasis on higher frequency elements in the timbrado. The spectra of calls and songs from Belgian waterslager canaries in our colony shown here correspond well to power spectra and spectrograms of vocalisations published previously (Dooling et al. 1971; Nottebohm & Nottebohm 1978; Güttinger 1985), and were recorded from birds in our colony. Timbrado vocalisations were recorded from subjects used in

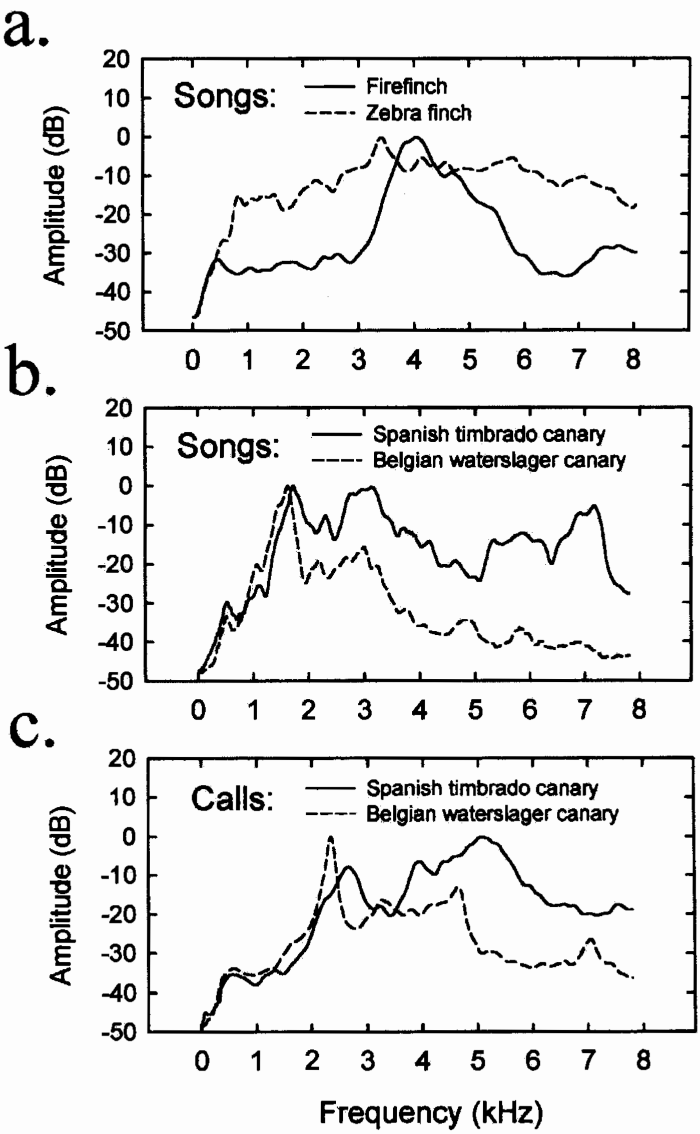

Figure 2. Superimposed power spectra of a) red-billed firefinch and zebra finch songs, b) Spanish timbrado and Belgian waterslager canary *Serinus canaria* songs, and c) Spanish timbrado and Belgian waterslager canary calls. Power spectra were calculated using a 16 K FFT (frequency resolution of 1.5 Hz) and were smoothed using a running average with a 100 Hz window size. Spectra are an average of 7-15 songs per individual across $n = 3$ red-billed firefinches and $n = 3$ zebra finches. For canary songs, spectra are an average of 10 songs from one representative timbrado male and 10 songs from one representative waterslager male. For canary calls, spectra are an average of 8-12 calls per individual averaged across $n = 3$ Spanish timbrado canaries and $n = 3$ Belgian waterslager canaries.

this study, and are more similar in region of spectral emphasis to the vocalisations of wild canaries (Güttinger 1985; Leitner et al. 2001). When considering the spectral structure of vocalisations in canaries, artificial selection has had a clearly divergent effect on peak frequency region in song of this species.

Audiograms

Absolute auditory thresholds for red-billed firefinches and zebra finches are plotted in Figure 3. For comparison, the average threshold for small passerine birds (20 species: Dooling et al. 2000) is also shown. Auditory sensitivity in the red-billed firefinch and the zebra finch is very similar, particularly at frequencies above 2 kHz. At 2 kHz and below, the average hearing ability of the firefinch is somewhat better than that of zebra finches, but is not as sensitive as the hearing of an average passerine (Dooling et al. 2000). In general, however, firefinch auditory sensitivity does not differ substantially from expectations based on thresholds obtained for most species of small birds either in the shape of the audiogram, or in the level of best sensitivity.

Hearing in the Spanish timbrado canary is better than that of typical domesticated strains of canary not bred for song, particularly in higher frequency regions (4-6 kHz), and also at low frequencies (< 2 kHz) (Figure 4). Unlike the audiograms of most small birds, which exhibit their best sensitivity from 2-4 kHz, the greatest sensitivity of the Spanish timbrado canary lies in the region of 4-6 kHz. At intermediate frequencies (2-4 kHz), timbrado hearing is similar to that of domesticated canaries not bred for song. As in most strains of canary tested to date, timbrado hearing is markedly better at high frequencies than the auditory sensitivity of Belgian waterslager canaries (Dooling et al. 1971; Okanoya & Dooling 1985, 1987b; Okanoya et al. 1990). Absolute thresholds in canaries on the whole are not as sensitive as that of most passerines (compare Figures 4 and 3), though timbrado hearing is as good as that of the average passerine at frequencies above 4 kHz. Red-billed firefinches exhibit better absolute thresholds than all the canary strains tested thus far except Spanish timbrados. Interestingly, timbrados are more sensitive than firefinches at frequencies above 3 kHz, while firefinches are more sensitive in the region of 2-3 kHz.

Critical ratios

The critical masking ratio, or signal-to-noise ratio at masked threshold expressed in dB, shows a similar pattern across frequencies for most

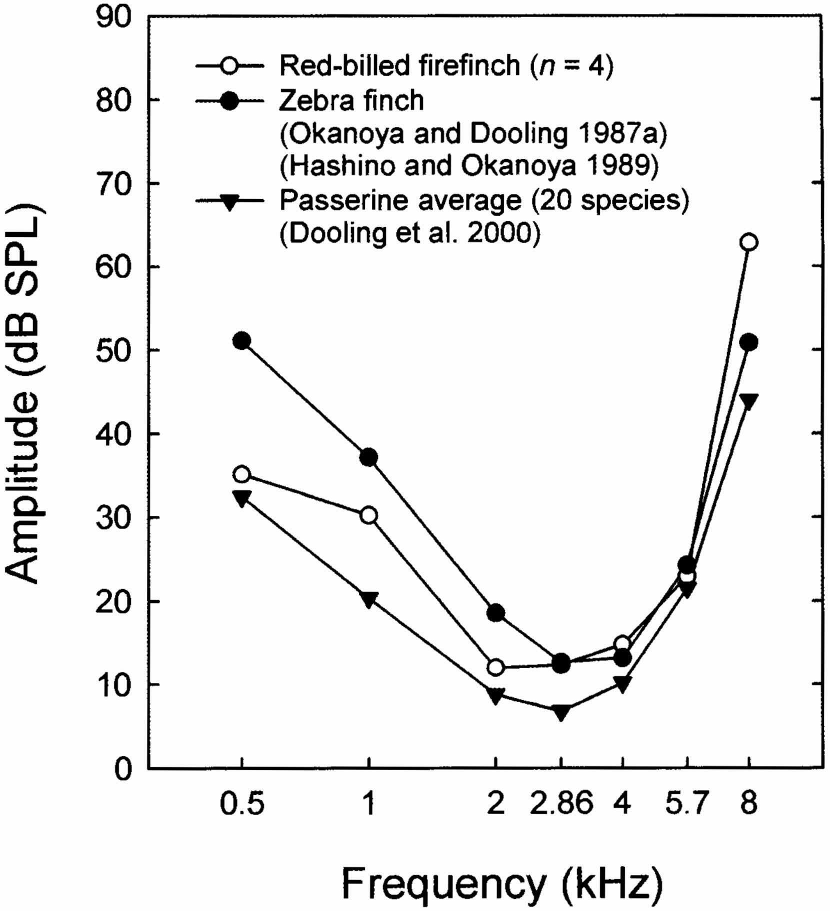

Figure 3. Average audiogram (*n* = 4) for red-billed firefinches, compared with that for zebra finches (Okanoya & Dooling 1987a; Hashino & Okanoya 1989). The procedure for determining thresholds is described in the section on testing procedures. Also included for comparison is an average audiogram for small passerines based on data for 20 species (Dooling et al. 2000).

small passerine birds, increasing at the rate of about 3 dB/octave. We measured masked thresholds for 3 of the red-billed firefinches used in the previous experiment (one bird died before this experiment began) at 1.0 kHz, 2.86 kHz, and 5.7 kHz. We also obtained masked thresholds for 2 timbrado canaries (1 male, 1 female) at 1.0 kHz, 2.0 kHz, 4.0 kHz, and 5.7 kHz. As in most species tested to date, these two species show a general monotonic increase in critical ratio of 2 - 3 dB / octave. Critical ratio functions for the red-billed firefinch and Spanish timbrado canary are compared with an average function for small birds (10 species: Dooling et al. 2000) in Figure 5.

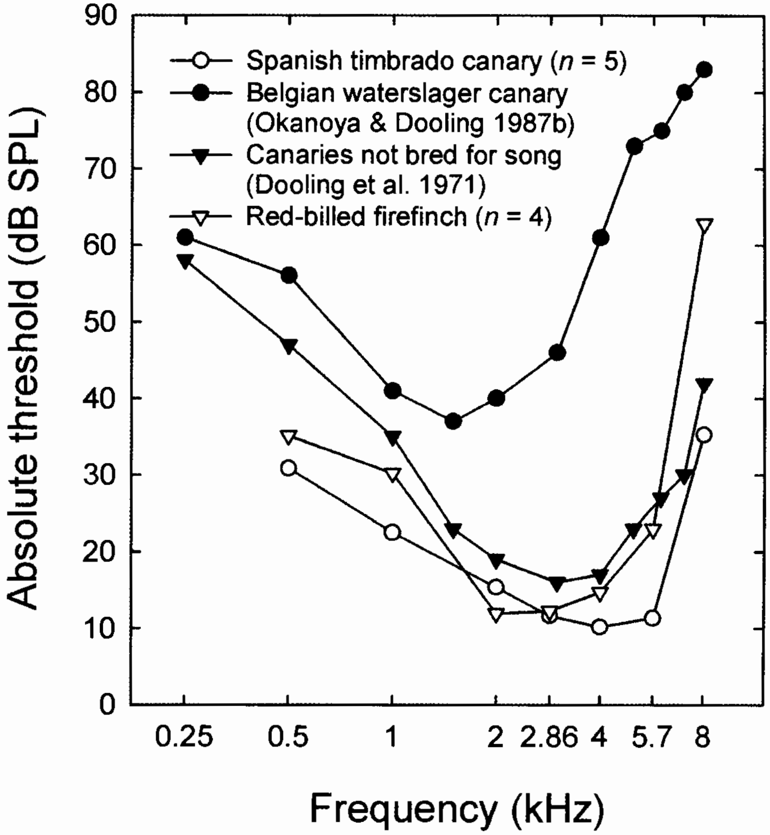

Figure 4. Average audiogram (n = 5) for Spanish timbrado canaries, compared with that for Belgian waterslager canaries, an average audiogram for standard, domestic canaries not bred for song (Okanoya & Dooling 1985, 1987b), and the average audiogram for red-billed firefinches.

DISCUSSION

A number of studies with birds have shown that the vocalisations a species produces may be associated with an improved ability to detect and discriminate changes in acoustically related stimuli. These enhanced abilities may involve, for example, superior discrimination between exemplars of conspecific versus heterospecific vocalisations (Dooling et al. 1992), or the ability to detect changes in call-like harmonic stimuli (Lohr & Dooling 1998). Ecological constraints and phylogenetic relationships also play a role in shaping the auditory sensitivity of birds. Owls (Strigiformes), for instance, are known to possess hearing sensitivities more closely tied to the sounds produced

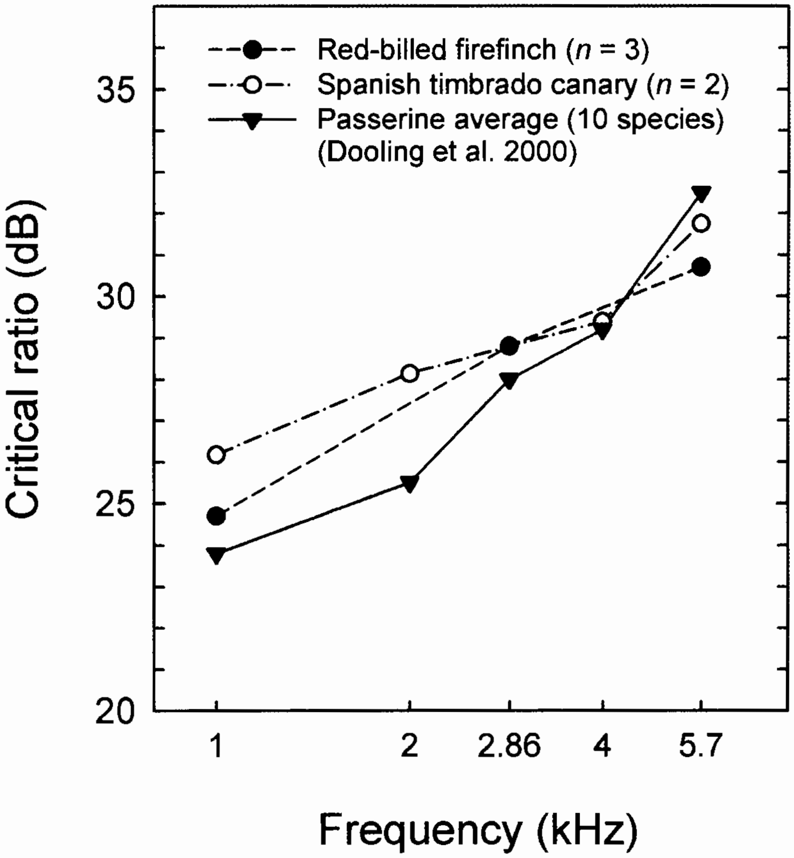

Figure 5. Critical ratio functions for red-billed firefinches (*n* = 3) and Spanish timbrado canaries (*n* = 2) compared with an average critical ratio function for small passerines (Dooling et al. 2000).

by prey than to the spectrum of their own vocalisations (Konishi 1973; Dyson et al. 1998). Undoubtedly the auditory system of owls is influenced to some degree by the auditory characteristics of the shared common ancestor of this group of birds. We wished to examine if closely-related birds producing vocalisations that differ in form exhibit differences in basic hearing ability. Furthermore, we were interested in whether bandwidth and frequency range of vocalisations were predictive of basic hearing abilities, even among birds in which similar narrowband vocalisations evolved in a natural context (firefinches), or an artificial one (timbrado canaries).

We examined two closely-related finches whose natural vocalisations differ dramatically in overall bandwidth, red-billed firefinches and zebra finches, to determine if this vocal difference was associated with a difference in basic hearing measures. Both wild and domesticated zebra finches produce songs and calls having a wide bandwidth, while red-billed firefinches produce songs and calls consisting of single predominant frequency components (Sullivan 1976; Payne 1990; Zann 1996, Figures 1 and 2a). We found no association of these substantial differences in bandwidth with differences in auditory sensitivity in these two species. In this case, despite substantial differences in the structure of vocalisations, these closely-related species showed no major differences in basic hearing abilities. It is possible, of course, that differences exist, but are more subtle and related more specifically to the auditory perception of complex, broadband sounds. Zebra finches, for example, are more sensitive to mistuned components of complex harmonic sounds than budgerigars *Melopsittacus undulatus*, an unrelated species that produces single frequency components like the firefinch (Lohr & Dooling 1998). Firefinches have yet to be tested for their ability to detect changes in complex harmonic stimuli, and it is unknown whether they would show the same sensitivities as zebra finches to alterations in such stimuli.

We tested basic hearing abilities in the Spanish timbrado canary as a counterpart to tests in the Belgian waterslager canary. The former strain has been under selection by breeders to produce high-pitched songs, while the latter strain was bred to produce low-pitched songs. Recently, it has been established that differences in hearing ability between Belgian waterslager canaries and domesticated strains not bred for song are associated with anatomical differences at the auditory periphery. Belgian waterslager canaries exhibit a number of hair cell pathologies in the cochlea (Gleich et al. 1995; Gleich et al. 1997). Missing and damaged hair cells in the basilar papilla contribute to a 20-40 dB increase in threshold at frequencies above about 1.5 kHz (Okanoya & Dooling 1985, 1987b), resulting in a mid and high-frequency hearing deficit in these birds.

Spanish timbrado canary hearing, in contrast to that of waterslagers, is not substantially different from the hearing of domesticated canaries not bred for song. In fact, it is better at both high and low frequencies by about 5-10 dB, with the timbrado best sensitivity in the region of 4-6 kHz (Figure 4); relatively high for songbirds (Dooling et al. 2000). Therefore, like the Belgian waterslager, the Spanish timbrado canary shows a good match between the peak power in the spectrum of its vocalisations and its best hearing sensitivity. It remains to be seen whether the modest differences between Spanish timbrado canaries and those of domesticated canaries not bred for song are the result of hearing pathologies reinforced by artificial selection as may be the case in Belgian waterslager canaries. If so, the degree of difference in threshold between these two strains and canaries not bred for song may be due at least in part to the amount of time each strain has been under selection. The Belgian waterslager canary has been bred for its song for at least twice as long as the Spanish timbrado canary (Walker & Avon 1993).

Red-billed firefinches and Spanish timbrado canaries both produce high-frequency songs. It is therefore interesting to compare the two species since the selective pressures resulting in similar song frequencies were undoubtedly very different; firefinches are not domesticated birds, while timbrado canaries have undergone selective breeding for song for at least 40 years. Both species have similar best sensitivities, in the range of 10-12 dB SPL, and in this respect they are fairly typical for small passerine birds (Fay 1988; Dooling et al. 2000). However, they differ from each other in the frequency region of best sensitivity, with the firefinch emphasizing relatively lower best frequencies (2-3 kHz), and the timbrado audiogram skewed to somewhat higher best frequencies (4-6 kHz). Firefinch song is relatively simple, consisting of a few short notes at similar frequency (Payne 1990) (Figure 1). Timbrado canary song in contrast is a complex series of notes at many different frequencies, some of which can be quite high (5-7 kHz) (summarised in Figure 2b). The number, complexity, and relatively higher frequency of some song elements in this canary may be related to the relatively higher region of best sensitivity in the audiogram. Despite their specific differences, however, both the Spanish timbrado canary and the red-billed firefinch have fairly typical absolute auditory sensitivities when compared with an unusual bird like the Belgian waterslager canary (Fay 1988; Dooling et al. 2000).

The critical ratio functions of these two birds also fit well with the pattern of most small bird species tested to date (summarised in Fay 1988; Dooling et al. 2000). Critical ratios are measured as masked thresholds in a known level of broadband, ‘white’ noise (equal energy at all frequencies), and are defined as the ratio between the power in a pure tone at threshold and the power per Hertz (spectrum level) of the noise. In practice, the critical masking ratio amounts to the difference, in dB, between the tone threshold and the spectrum level (i.e. energy in a single cycle) of background noise.

For example, the critical ratio function of timbrado canaries (Figure 5) indicates that for a tone to be detected, the power in a tone at 2 kHz must be 28.15 dB greater than the spectrum level of background noise in the same frequency region. On the assumption that a tone is masked when the power in the tone equals the power in the noise surrounding the tone, the threshold of a just-masked tone is sometimes taken as an indirect means of evaluating filter bandwidth, and therefore spectral resolving ability, in the auditory system. This approach to estimating auditory filter size has been criticised for a number of reasons (Patterson & Moore 1986), and other techniques may provide different estimates of filter bandwidth in the auditory system. In birds, different techniques for measuring auditory filter bandwidth have yielded similar results in the starling *Sturnus vulgaris*, though not in the budgerigar (see Dooling et al. 2000, for a comparison of measures). Nevertheless, the similarity between firefinch and timbrado canary critical ratio functions suggests that filter bandwidths are similar in these two species, and by extension that frequency resolving power should be similar, despite the differences in frequency regions of best sensitivity in the audiogram.

As a whole, hearing in small songbirds is relatively conservative with respect to the variation in bandwidth and frequency range of vocal signals produced by these birds. There were no major distinctions in general auditory sensitivity between zebra finches and red-billed firefinches, for instance, despite zebra finches having very different vocalisations, and having been bred in captivity for over 100 years. While zebra finches and firefinches come from different subfamilies within the Estrildidae (Kakizawa & Watada 1985; Christidis 1987), a comparison within this family provides an important phylogenetic control for hearing characteristics. Our results suggest that a common ancestor to zebra finches and firefinches also likely showed similar auditory sensitivities, and that domestication in this instance has not had a noticeable effect on basic hearing measures.

The comparison within estrildid finches stands in contrast to the comparison between different strains of the canary, however. In this case selective breeding may have acted to produce alterations in sensitivity that had profound effects on hearing ability (as in the Belgian waterslager), or more minor effects (as in the Spanish timbrado). Clearly, selection may act rapidly to modify both the spectral characteristics of vocalisations and the sensitivity of the auditory system, though auditory sensitivity in the Belgian waterslager canary is quite possibly also affected by artificial selection producing an inner ear pathology. We may be watching a similar process unfold in the case of the timbrado canary, given that it is a more recently domesticated strain than the waterslager (Walker & Avon 1993).

The implications of our results for basic auditory sensitivity in domesticated species such as the zebra finch and different strains of canary suggest some areas of future study. Both anatomical studies and more detailed auditory operant tests are necessary to document more subtle differences, if any, that may exist in the auditory system of these birds. Behavioural tests using complex sounds with timbrado canaries and estrildid finches may point to such subtle differences as well, and to any distinctions there may be between the hearing abilities of zebra finches and firefinches. However, at least in species examined thus far, natural selection does not appear to have had a robust effect on the bandwidth and frequency range of hearing among songbirds.

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REFERENCES

Beeman, K. (1998). *SIGNAL/RTS User's Guide*. Belmont, Massachusetts: Engineering design.

Blaich, C. F., Kovacevik, R., Tansinsin, S. L., Van Hoy, B. & Syud, F. A. (1995). The distance call of domesticated zebra finches (*Poephila guttata*). *Int. J. Comp. Psychol.*, **8**, 16-30.

Christidis, L. (1987). Phylogeny and systematics of estrildine finches and their relationships to other seed-eating passerines. *Emu*, **87**, 119-123.

Dooling, R. J., Brown, S. D., Klump, G. M. & Okanoya, K. (1992). Auditory perception of conspecific and heterospecific vocalisations in birds: evidence for special processes. *J. Comp. Psychol.*, **106**, 20-28.

Dooling, R. J., Lohr, B. & Dent, M. L. (2000). Hearing in birds and reptiles. In *Comparative Hearing: Birds and Reptiles* (Ed. by R. J. Dooling, R. R. Fay & A. N. Popper), pp. 308-359. New York: Springer-Verlag.

Dooling, R. J., Mulligan, J. A. & Miller, J. D. (1971). Auditory sensitivity and song spectrum of the common canary (*Serinus canarius*). *J. Acoust. Soc. Am.*, **50**, 700-709.

Dooling, R. J. & Okanoya, K. (1995). The method of constant stimuli in testing auditory sensitivity in small birds. In *Methods in Comparative Psychoacoustics* (Ed. by G. M. Klump, R. J. Dooling, R. R. Fay & W. C. Stebbins), pp. 161-169. Basel: Birkhäuser Verlag.

Dyson, M. L., Klump, G. M. & Gauger, B. (1998). Absolute hearing thresholds and critical masking ratios in the European barn owl: a comparison with other owls. *J. Comp. Physiol. A*, **182**, 695-702.

Fay, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Data Book*. Winnetka, Illinois: Hill-Fay Associates.

Gleich, O., Dooling, R. J. & Presson, J. C. (1997). Evidence for supporting cell proliferation and hair cell differentiation in the basilar papilla of adult Belgian waterslager canaries (*Serinus canarius*). *J. Comp. Neurol.*, **377**, 5-14.

Gleich, O., Klump, G. M. & Dooling, R. J. (1995). Peripheral basis for the auditory deficit in Belgian waterslager canaries (*Serinus canarius*). *Hearing Res.*, **82**, 100-108.

Güttinger, H. R. (1985). Consequences of domestication on the song structures in the canary. *Behaviour*, **94**, 254-278.

Hall, M. F. (1962). Evolutionary aspects of estrildid song. *Symp. Zool. Soc. Lond.*, **8**, 37-55.

Hashino, E. & Okanoya, K. (1989). Auditory sensitivity in the zebra finch (*Poephila guttata castanotis*). *J. Acoust. Soc. Jpn.*, **10**, 1-2.

Kakizawa, R. & Watada, M. (1985). The evolutionary genetics of the Estrildidae. *J. Yamashina Inst. Ornith.*, **17**, 143-158.

Konishi, M. (1973). Locatable and nonlocatable acoustic signals for barn owls. *Am. Nat.*, **107**, 775-785.

Leitner, S., Voigt, C. & Gahr, M. (2001). Seasonal changes in the song pattern of the non-domesticated island canary (*Serinus canaria*), a field study. *Behaviour*, **138**, 885-904.

Lohr, B. & Dooling, R. J. (1998). Detection of changes in timbre and harmonicity in complex sounds by zebra finches (*Taeniopygia guttata*) and budgerigars (*Melopsittacus undulatus*). *J. Comp. Psychol.*, **112**, 36-47.

Nottebohm, F. & Nottebohm, M. E. (1978). Relationship between song repertoire and age in the canary. *Z. Tierpsychol.*, **46**, 298-305.

Okanoya, K. & Dooling, R. J. (1985). Colony differences in auditory thresholds in the canary (*Serinus canarius*). *J. Acoust. Soc. Am.*, **78**, 1170-1176.

Okanoya, K. & Dooling, R. J. (1987a). Hearing in passerine and psittacine birds: a comparative study of absolute and masked auditory thresholds. *J. Comp. Psychol.*, **101**, 7-15.

Okanoya, K. & Dooling, R. J. (1987b). Strain differences in auditory thresholds in the canary (*Serinus canarius*). *J. Comp. Psychol.*, **101**, 213-215.

Okanoya, K., Dooling, R. J., & Downing, J. D. (1990). Hearing and vocalisations in hybrid waterslager-roller canaries (*Serinus canarius*). *Hearing Res.*, **46**, 271-276.

Okanoya, K., Yoneda, T. & Kimura, T. (1993). Acoustical variations in sexually dimorphic features of distance calls in domesticated zebra finches (*Taeniopygia guttata castanotis*). *J. Jap. Ethol.*, **11**, 29-36.

Patterson, R. D. & Moore, B. C. J. (1986). Auditory filters and excitation patterns as representations of frequency resolution. In *Frequency Selectivity in Hearing* (Ed. by B. C. J. Moore), pp. 123-177. London: Academic Press.

Payne, R. B. (1980). Seasonal incidence of breeding, moult and local dispersal of red-billed firefinches *Lagonosticta senegala* in Zambia. *Ibis*, **122**, 43-56.

Payne, R. B. (1990). Song mimicry by the village indigobird (*Vidua chalybeata*) of the red-billed firefinch (*Lagonosticta senegala*). *Vogelwarte*, **35**, 321-328.

Slater, P. J. B. & Clayton, N. S. (1991). Domestication and song learning in zebra finches *Taeniopygia guttata*. *Emu*, **91**, 126-128.

Sullivan, G. A. (1976). Song of the finch *Lagonosticta senegala*: interspecific mimicry by its brood-parasite *Vidua chalybeata* and the role of song in the host's social context. *Anim. Behav.*, **24**, 880-888.

Walker, G. B. R. & Avon, D. (1993). *Coloured, Type and Song Canaries: A Complete Guide, 2nd edition.* London: Blandford Press.

Zann, R. (1984). Structural variation in the zebra finch distance call. *Z. Tierpsychol.*, **66**, 328-345.

Zann, R. (1993). Structure, sequence, and evolution of song elements in wild Australian zebra finches. *Auk*, **110**, 702-715.

Zann, R. (1996). *The Zebra Finch: A Synthesis of Field and Laboratory Studies.* Oxford: Oxford University Press.

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