

## Auditory temporal resolution in the Zebra Finch (*Taeniopygia guttata*): A model of enhanced temporal acuity

Robert J. DOOLING<sup>#</sup> and Bernard LOHR

University of Maryland, Department of Psychology, College Park, MD, 20742 USA

---

### ORNITHOLOGICAL SCIENCE

© The Ornithological Society  
of Japan 2006

---

**Abstract** We review recent studies that examine the temporal resolution of the avian auditory system as measured behaviorally in a small songbird, the Zebra Finch (*Taeniopygia guttata*). These birds naturally learn and produce complex harmonic vocalizations. Here we created complex harmonic stimuli that simulate the fine temporal properties of these natural calls in order to probe the possible parallels between productive precision and perceptual acuity. The studies we review show that these birds are exquisitely sensitive to changes in temporal fine structure in complex sounds, 3–5 times more sensitive than humans, and probably other mammals. This sensitivity also was obtained with several types of synthetic harmonic stimuli that mimicked particular properties of natural signals, including harmonic sounds with individually altered components, Schroeder-phase complexes that control for envelope cues, and synthetic signals constructed from repeated single periods of natural calls. These last studies confirm that Zebra Finches are capable of discriminating among their species-specific vocalizations using only changes in temporal fine structure—something humans, tested on the same stimuli, cannot do.

**Key words** Fine structure, Hearing, Operant conditioning, Temporal resolution, Zebra Finch

The complexity of birdsong has fascinated us throughout the ages. Students of bird behavior have long suspected that birds are capable of producing, perceiving and learning features of their songs that are beyond the capabilities of human hearing (Pumphrey 1961; Greenwalt 1968; Schwartzkopff 1968; Konishi 1969). One early focus on this issue, that birds might hear better at higher frequencies than humans (Knecht 1940), was quickly dispelled as rigorous psychophysical testing methods demonstrated that birds showed much less sensitivity than humans to frequencies below about 1 kHz or above about 5 kHz (see, for review, Dooling et al. 2000). Birds, in fact, have a much narrower range of auditory sensitivity than do humans and other mammals (for a review, see Fay 1988).

Yet, many birds produce and learn complex tonal or harmonic vocalizations that involve rapid modulations in frequency and amplitude (for reviews, see Kroodma & Miller 1982, 1996; Marler &

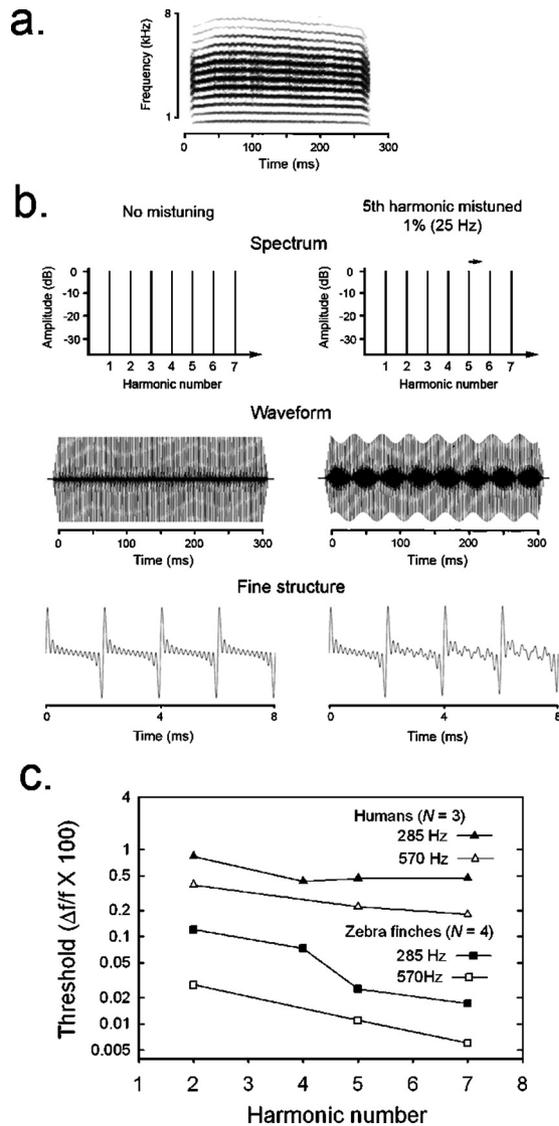
Slabbekoorn 2005). So, while it would perhaps not be too surprising if these complex features were outside the limits of spectral and temporal resolution of humans and other mammals, it would seem impossible for them to also fall outside the perceptual capabilities of the species of birds that learn and use them as communication signals.

An example which illustrates this issue are the harmonic vocalizations of Zebra Finches (*Taeniopygia guttata*), a popular bird used in studies of the neurobiology of song learning. Zebra Finch vocalizations are temporally and spectrally complex (harmonically rich, rapidly modulated; see Fig. 1a and 3a). Small, domesticated birds such as these are easily tested with laboratory physiological and psychophysical procedures. The fact that these birds are easily trained makes Zebra Finch calls and songs an ideal test to examine whether sensitivity to temporal fine structure underlies species-specific perceptual specializations. Zebra Finch contact calls have very short fundamental periods of about 1.5–2.0 ms (Lohr & Dooling 1998), shorter than most estimates of temporal resolution in the human auditory system (Viemeister &

---

(Received 2 April 2006; Accepted 29 May 2006)

<sup>#</sup> Corresponding author, E-mail: dooling@psyc.umd.edu



**Fig. 1.** a) Spectrogram of a female Zebra Finch contact call. These harmonically rich calls typically have fundamentals ranging from 540 to 620 Hz, corresponding to periods of 1.85–1.61 ms (Zann 1984; Simpson & Vicario 1990; Okanoya et al. 1993; Blaich et al. 1995). b) Schematic representation of the mistuning of the 5th harmonic of a standardized harmonic tone (“Spectrum”), and the effects of this mistuning on the overall structure of the waveform (“Waveform”), as well as progressive alterations of the fine temporal structure (“Fine structure”) that result from a mistuning of this type. c) Comparative human and Zebra Finch thresholds for the detection of several mistuned harmonics for standardized harmonic complexes of two different fundamental frequencies (285 Hz—period of 3.51 ms, and 570 Hz—period of 1.75 ms) (adapted from Lohr & Dooling 1998). All components were generated in sine starting phase. Thresholds are plotted as a percentage of harmonic frequency (log scale). Note that thresholds for Zebra Finches are nearly an order of magnitude lower than those for humans.

Plack 1993). It is immediately clear that any acoustic information in the waveform fine structure within these periods is likely lost to humans and at least some other mammals, but one might rightly wonder whether it is available to birds—especially Zebra Finches who produce them.

There is a history of speculation on this topic. The temporal complexity of bird vocalizations along with well-known differences between birds and mammals in the anatomy and physiology of the peripheral and central auditory systems have long been used to argue for extremely fine temporal processing abilities in birds (Pumphrey 1961; Greenewalt 1968; Schwartzkopff 1968; Konishi 1969; Carr & Friedman 1999). Interestingly, by standard measures of temporal resolution, including detection of gaps in noise, temporal integration, duration discrimination, and temporal modulation transfer functions birds have not been shown to be particularly more sensitive to the temporal features of acoustic signals than are other vertebrates (Dooling & Haskell 1978; Dooling & Searcy 1981, 1985; Dooling 1982; Fay 1988; Klump & Maier 1989; Dooling et al. 2000).

One reason why differences in temporal resolving power between birds and mammals do not emerge from such standard tests may be that these conventional measures do not provide an adequate evaluation of the limits of temporal resolution in the avian ear. All of the measures of temporal resolution listed above involve the detection of changes in the relatively slow temporal features of a sound, referred to as the envelope characteristics. However, there are other temporal features of complex sounds that can be very subtle and occur at higher frequencies (Viemeister & Plack 1993). These are referred to as the temporal fine structure of the waveform.

Here we review some of the recent psychophysical research that bears directly on this issue by examining the perception of temporal fine structure of harmonic complexes by Zebra Finches. The Zebra Finch “contact” call is one of the most obvious and most ubiquitous vocalizations given by these birds in captivity (Blaich et al. 1995) or in the wild (Zann 1984). As highly social, colonial songbirds, Zebra Finches must not only learn their own songs and calls (in the case of males), but they must discriminate between the complex harmonic calls and songs of many conspecifics. Signal processing techniques can be used to manipulate these sounds and to create synthetic harmonic models for testing. These models can mimic very closely the natural properties of harmonic bird

sounds, and provide a basis for understanding the relation between production of specific features of natural vocalizations and species-specific perceptual processes. Synthetic stimuli also allow one to pose detailed questions regarding how complex perceptual processes may have become specialized through the course of evolutionary development.

### The Case of the “Mistuned” Harmonic

Fig. 1a shows that the contact call of the female Zebra Finch is a harmonic complex with a fundamental typically around 600 Hz. Fig. 1b shows that it is quite easy to create a synthetic version of this harmonic complex by adding together, in phase, a set of harmonically-related pure tones. It also shows that mistuning one of the harmonics, ever so slightly, creates interesting changes in the time waveform—specifically in the temporal fine structure—in addition to creating alterations to the spectrum. Mistuned harmonics may produce a variety of different auditory cues, and can produce a variety of sensations in human listeners (Moore et al. 1985, 1986; Hartmann et al. 1990). Nevertheless, small changes in the frequency of a single component of a harmonic complex can create perceptible changes that may be tied to temporal phenomena such as neural synchrony (Hartmann 1997).

Using harmonic complexes with either a 285 or a 570 Hz fundamental (modeled after the naturally occurring contact call of Zebra Finches), Lohr and Dooling (1998) measured the threshold for detecting mistuned harmonics in Zebra Finches and humans. These results are shown in Fig. 1c in terms of the log of the Weber fraction for frequency ( $\Delta F/F$ ) for each fundamental. Behavioral thresholds for detecting inharmonicity in Zebra Finches were almost an order of magnitude lower than for humans. A neurophysiological study of single-unit responses in the Zebra Finch auditory forebrain also showed that extremely precise preservation of temporal cues in the auditory forebrain is necessary for a full response to complex, learned, species-specific vocalizations (Theunissen & Doupe 1998). The fact that the mistuning of a harmonic causes a number of changes in a harmonic complex, including changes in the temporal fine structure of the sound, suggested other experiments to measure the sensitivity of Zebra Finches to temporal fine structure.

### Timbre Discrimination

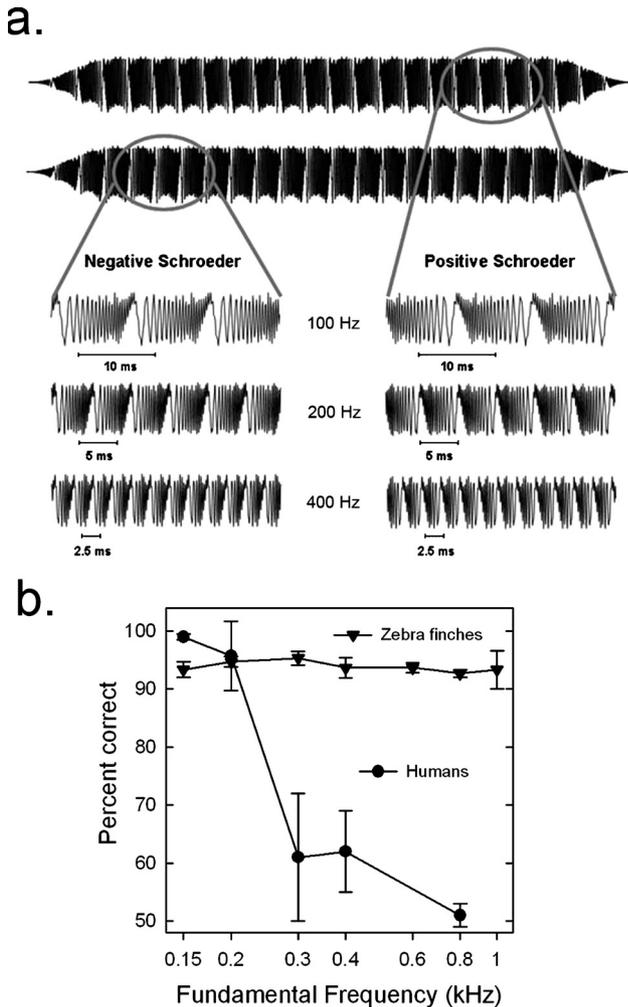
Another kind of manipulation is to change the rela-

tive amplitude of components in a harmonic stimulus. These types of changes result in alterations in the perceptual quality, or “timbre,” of the stimulus and such differences also lead to alterations in the temporal fine structure of the sound. The ability to detect changes in timbre has been tested in birds, both with natural vocalizations, and standard harmonic complexes. Cynx et al. (1990) demonstrated that Zebra Finches were able to detect an amplitude change of 5–10 dB in the second harmonic of a song syllable (fundamental=615 Hz), with some individuals showing a response to changes as small as 2 dB. Lohr and Dooling (1998) tested both Zebra Finches and humans on the ability to detect changes in amplitude of single components of a standard harmonic stimulus. Zebra Finches had thresholds on the order of 1.5–2 dB for detecting changes in amplitude of the 5<sup>th</sup> harmonic in a stimulus with a 570 Hz fundamental. Human thresholds, while quite variable, averaged higher, at 3.8 dB. Zebra Finches are known to produce highly consistent amplitude relationships in their harmonic vocalizations, and the specific relative amplitude relationships may differ in consistent ways among individuals (Williams et al. 1989).

### Discrimination of Schroeder Complexes

Manipulating complex sounds always carries with it the uncertainty that more than one feature of the stimulus is changing. This in turn makes it difficult to define specifically what it is that the auditory system is responding to at a particular threshold. Recent work with harmonic complexes provides a way around this dilemma. Harmonic waveforms constructed with component starting phases selected according to an algorithm developed by Schroeder (1970) have particularly useful characteristics and were used to test Zebra Finches. The stimuli were harmonic complexes consisting of a set of equal-amplitude harmonic components of a given fundamental frequency, with frequencies ranging from 150 (or the fundamental frequency) to 5000 Hz. Seven pairs of these harmonic complexes were produced, with fundamental periods ranging from 6.6 ms (fundamental frequency of 150 Hz) to 1 ms (fundamental frequency of 1000 Hz) in duration. The phases of the components were monotonically increasing (+Schroeder complex) or decreasing (–Schroeder complex) with harmonic number. This results in instantaneous frequencies that fell or rose monotonically across each period but otherwise all the waveforms have a flat envelope and, within a pair defined by the fundamental

frequency, have identical long-term spectra. Fig. 2a shows examples of negative and positive Schroeder-phase waveforms for some of the fundamental frequencies used here. These waveforms were 260 ms in



**Fig. 2.** a) Temporal waveforms of negative and positive Schroeder-phase harmonic complexes. These harmonic sounds were generated using the Schroeder algorithm to minimize envelope cues (Schroeder 1970; see text details). Stimuli were 260 ms in duration. Details are shown for Schroeder-phase waveforms having fundamental frequencies of 100 Hz, 200 Hz, and 400 Hz (period durations of 10 ms, 5 ms, and 2.5 ms, respectively). b) Results for Zebra Finches and humans tested on positive/negative Schroeder waveform discrimination at different fundamental frequencies ranging from 150 Hz–1000 Hz (periods of 6.7–1.0 ms, respectively). Error bars represent standard errors between subjects. Human thresholds begin to fall toward chance levels at fundamental frequencies above about 300 Hz (periods less than 3.3 ms), while Zebra Finch thresholds remain high at fundamental frequencies up to 1000 Hz (periods of 1.0 ms) (Dooling et al. 2002).

duration including 20-ms cosine<sup>2</sup> onset and offset ramps. Even a cursory look at these stimuli shows that the acoustic differences between members of a pair of these complexes are limited to temporal fine structure.

Fig. 2b shows the performance of Zebra Finches and humans tested on the positive/negative Schroeder waveform discriminations at different fundamental frequencies. All finches were able to discriminate between positive and negative Schroeder harmonic complexes at fundamental frequencies up to at least 1000 Hz. Human listeners cannot make these discriminations when the fundamental period becomes shorter than 3–5 ms. Canaries and budgerigars also surpass humans in discrimination of these complexes and electrophysiological measures such as the CAP (compound action potential) from the auditory periphery of birds and gerbils to these same harmonic complexes reveal significant differences between birds and mammals in peripheral processing of these sounds (Dooling et al. 2002). Thus, enhanced temporal processing of complex sounds may be a general characteristic of the avian auditory system.

### Discrimination of Natural Zebra Finch Fine Structure

There are reasons to believe that the sensitivity to temporal fine structure in birds could be related to the mechanisms for producing complex sounds. Studies of the neural responsivity of auditory-motor regions in the songbird brain suggest that they may be particularly sensitive to characteristics of conspecific songs. As an example, the HVC is a central song production nucleus responsible for the motor control of singing behavior (for a description of recent nomenclature, see Jarvis 2005). In Zebra Finches and other species such as white-crowned sparrows and song sparrows, neurons in the HVC are strongly responsive to the auditory stimulus of a bird's own song (BOS) (Margoliash 1983, 1986; Margoliash & Fortune 1992; Volman 1996; Theunissen & Doupe 1998; Nealen & Schmidt 2001). Changes in syllable ordering, or playing the song in reverse, can significantly reduce the response of HVC neurons (Margoliash & Fortune 1992; Lewicki & Konishi 1995; Lewicki & Arthur 1996). Such BOS-selective responses also occur in other portions of the song control motor pathway (Doupe 1997). BOS-selectivity, however, is not generally characteristic of sensory pathways in the anterior forebrain leading up to the HVC (Lewicki & Arthur 1996; Sen et al. 2001). So, it is

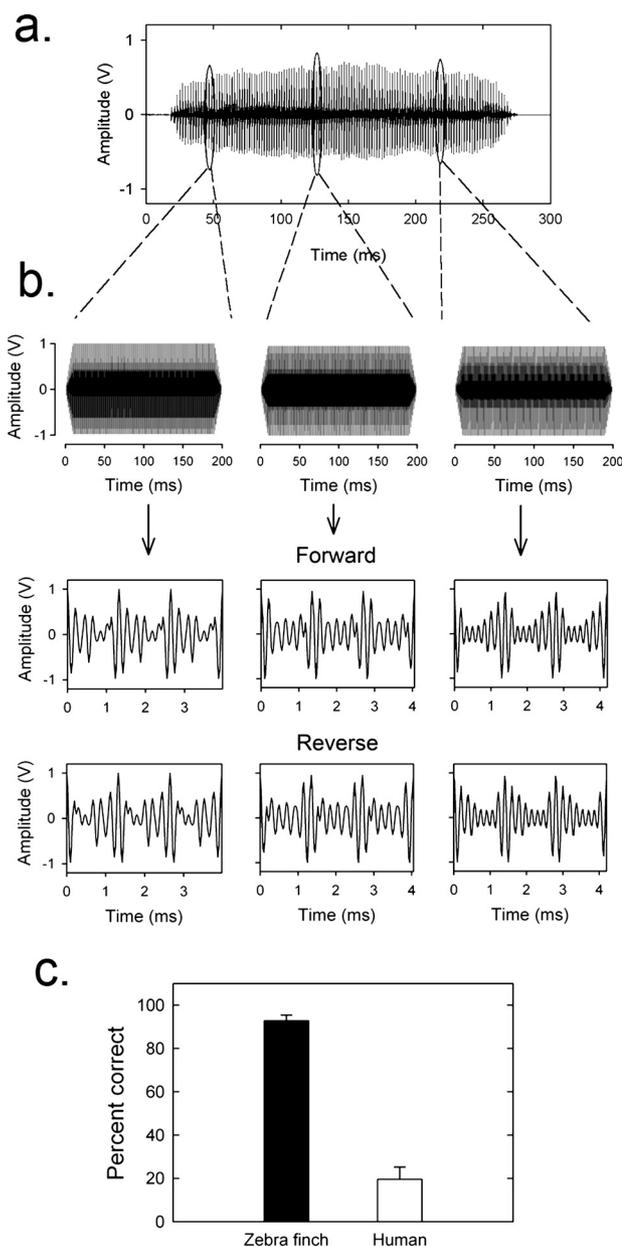
still a mystery how the acute selectivity of vocal motor regions of the songbird brain are associated with the resolution for temporal characteristics of vocal signals that must begin at the auditory periphery.

To address specific questions regarding the temporal acuity for natural calls independent of the continuously varying overall spectral and temporal changes that normally occur in such calls, we designed test stimuli using single periods of a call (Lohr et al. in press). Fig. 3a shows the time waveform of a female Zebra Finch contact call. We randomly selected single periods of contact calls, excised them, and replicated these periods to create stimuli that mimicked natural calls in terms of the waveform within an individual period, but having flat envelopes. Fig. 3 shows examples taken from three locations in a single Zebra Finch contact call. Fig. 3b details the temporal fine structure of the different synthetic calls constructed from these three individual periods. Birds and humans were tested on their ability to discriminate forward versus reversed versions of these calls (Lohr et al. in press). Discriminations between a forward and reversed stimulus—which differed only in the ordering of temporal fine structure—was quite easy for finches and virtually impossible for humans (Fig. 3c).

## DISCUSSION

In summary, the ability of birds to make waveform discriminations at high fundamental frequencies indicates the well-developed precision in temporal resolution that is obtained with natural vocalizations. The basis of this exceptional discrimination of time structure in complex stimuli cannot be explained by performance on other temporal resolution tests involving more standard stimuli. Temporal resolution determined from gap detection in the nerve and forebrain, or from temporal modulation transfer functions in the nerves of starlings is not remarkable (Buchfellner et al. 1989; Klump and Gleich 1991; Gleich and Klump 1995). The exceptional phase locking shown for the owl (Carr and Konishi 1990; Köppl 1997) is probably not representative for the Zebra Finches tested here or for other songbirds (Gleich and Narins 1988).

It is easy to imagine that, aside from sound localization in such species as the barn owl, rapid and precise temporal coding may be important for bird communication and individual identification. With the exception of sound localization studies in the barn owl, these studies are the first to demonstrate exquisite be-



**Fig. 3.** a) Time waveform of a female Zebra Finch contact call showing regions of individual periods that were excised and concatenated to produce 200 ms synthetic calls consisting of repeated single periods of a natural call. Thus, synthetic calls were designed to mimic both the fundamental frequencies and temporal fine structure of natural Zebra Finch calls. b) The fine structure of both forward and reversed versions of these calls is shown below each corresponding synthetic call. c) Results for Zebra Finches and humans tested on forward/reversed synthetic call discrimination. Zebra Finches perform at much higher levels in discriminating between forward and reversed versions of such calls compared with humans. Fundamental frequencies ranged from 690 Hz–816 Hz (periods of 1.45 ms–1.225 ms, respectively) (Fig. modified from Lohr et al. in press).

havioral sensitivity to temporal fine structure as might occur in and underlie the perception of acoustic stimuli with similarities to natural vocal signals. In Zebra Finches, the precise coding of temporal information in the vocal motor circuitry and syringeal mechanisms is currently receiving a great deal of attention (Vicario 1991; Fee et al. 1998; Janata and Margoliash, 1999; Brainard & Doupe 2001; Sen et al. 2001; Tchernichovski et al. 2001). Taken together, these kinds of investigations might offer an important opportunity to understand acoustic communication, song learning, and individual recognition in birds.

The enhanced temporal resolution in Zebra Finches for the processing of acoustic communication signals invites speculation about mechanisms. This enhancement is evident in the auditory periphery since it is reflected, in part, in CAPs recorded to positive and negative Schroeder stimuli (Dooling et al. 2002), just like those used in behavioral tests reported here. CAP differences between birds and mammals, which reflect synchronized activity in the VIIIth nerve, strongly indicate that there are differences in how these stimuli are coded in the earliest stages of avian and mammalian auditory periphery. As of yet, however, it is not clear to what extent these differences are micromechanical, neural, or both.

Finally, it is worthwhile to consider the relevance of these results at the level of acoustic communication. Historically, the analysis of bird vocalizations is usually done in the spectral domain using sonograms or spectrograms, and rarely extends to the level of temporal fine structure. But the results we have reviewed suggests that the avian auditory system may effectively be “stretching” time when perceiving complex sounds such as species-typical vocalizations. Spectrographic analysis would miss such detail—perhaps in a sense confirming the classic refrain of avian ethologists that much of the complexity in bird song cannot be appreciated by human hearing unless the tape is slowed down. The larger implications are that if birds typically perceive detail in their complex vocalizations beyond the range of human discriminatory capabilities, they may have much larger vocabularies than previously thought. Though highly speculative, a super sensitivity to temporal fine structure in vocal signals, might also aid sound localization, ranging, and sound source identification in complex natural environments.

## ACKNOWLEDGMENTS

We thank Beth Brittan-Powell for help with this manuscript. This work was supported by grants from the National Institutes of Health.

## REFERENCES

- Blaich CF, Kovacevik R, Tansinsin SL, Van Hoy B & Syud FA (1995) The distance call of domesticated zebra finches (*Poephila guttata*). *Int J Comp Psychol* 8: 16–30.
- Brainard MS & Doupe AJ (2001) Postlearning consolidation of birdsong: stabilizing effects of age and anterior forebrain lesions. *J Neurosci* 21: 2501–2517.
- Buchfellner E, Leppelsack HJ, Klump GM & Hausler U (1989) Gap-detection in the Starling (*Sturnus vulgaris*): II: coding of gaps by forebrain neurons. *J Comp Physiol A* 164: 539–549.
- Carr CE & Friedman MA (1999) Evolution of time coding systems. *Neural Computation* 11: 1–20.
- Carr CE & Konishi M (1990) A circuit for detection of interaural time differences in the brainstem of the barn owl. *J Neurosci* 10: 3227–3246.
- Cynx J, Williams H & Nottebohm F (1990) Timbre discrimination in zebra finch (*Taeniopygia guttata*) song syllables. *J Comp Psychol* 104: 303–308.
- Dooling RJ (1982) Auditory perception in birds. In: Kroodsma DE & Miller EH (eds) *Acoustic communication in birds*. Vol I. pp. 95–130. Academic Press, London.
- Dooling RJ & Haskell RJ (1978) Auditory duration discrimination in the Parakeet (*Melopsittacus undulatus*). *J Acoust Soc Am* 63: 1640–1642.
- Dooling RJ, Leek MR, Gleich O & Dent ML (2002) Auditory temporal resolution in birds: discrimination of harmonic complexes. *J Acoust Soc Am* 112: 748–759.
- Dooling RJ, Lohr B & Dent ML (2000) Hearing in birds and reptiles. In: Dooling RJ, Popper AN & Fay RR (eds) *Comparative hearing: birds and reptiles*. pp. 308–359. Springer-Verlag, New York.
- Dooling RJ & Searcy MH (1981) Amplitude modulation thresholds for the Parakeet (*Melopsittacus undulatus*). *J Comp Physiol A* 143: 383–388.
- Dooling RJ & Searcy MH (1985) Temporal integration of acoustic signals by the budgerigar (*Melopsittacus undulatus*). *J Acoust Soc Am* 77: 1917–1920.
- Doupe AJ (1997) Song- and order-selective neurons in the songbird anterior forebrain and their emergence during vocal development. *J Neurosci* 17: 1147–1167.
- Fay RR (1988) *Hearing in vertebrates: a psychophysics data book*. Hill-Fay Associates, Winnetka, IL.

- Fee MS, Shraiman B, Pesaran B & Mitra PP (1998) The role of nonlinear dynamics of the syrinx in the vocalizations of a songbird. *Nature* 395: 67–71.
- Gleich O & Klump GM (1995) Temporal modulation transfer functions in the European Starling (*Sturnus vulgaris*): II. responses of auditory nerve fibers. *Hearing Res* 82: 81–92.
- Gleich O & Narins PM (1988) The phase response of primary auditory afferents in a songbird (*Sturnus vulgaris* L.). *Hearing Res* 32: 81–91.
- Greenewalt CH (1968) *Bird song: acoustics and physiology*. Smithsonian Institution Press, Washington DC.
- Hartmann WM (1997) *Signals, sound and sensation*. AIP Press, Woodbury, New York.
- Hartmann WM, McAdams S & Smith BK (1990) Hearing a mistuned harmonic in an otherwise periodic complex tone. *J Acoust Soc Am* 88: 1712–1724.
- Janata P & Margoliash D (1999) Gradual emergence of song selectivity in sensorimotor structures of the male zebra finch song system. *J Neurosci* 19: 5108–5118.
- Jarvis ED (2004) Brains and birdsong. In: Marler P & Slabbekoorn H (eds) *Nature's music: the science of birdsong*. pp. 226–271. Elsevier Academic Press, San Diego.
- Klump GM & Gleich O (1991) Gap detection in the European Starling (*Sturnus vulgaris*). III. processing in the peripheral auditory system. *J Comp Physiol A* 169: 469–476.
- Klump GM & Maier EH (1989) Gap detection in the Starling (*Sturnus vulgaris*). I. Psychophysical thresholds. *J Comp Physiol A* 164: 531–538.
- Knecht S (1940) Über den Gehören und die Musikalität der Vögel. *Zeit Vergleich Physiol* 27: 169–232.
- Konishi M (1969) Time resolution by single auditory neurons in birds. *Nature* 222: 566–567.
- Köpl C (1997) Frequency tuning and spontaneous activity in the auditory nerve and cochlear nucleus magnocellularis of the barn owl *Tyto alba*. *J Neurophysiol* 77: 364–377.
- Lewicki MS & Arthur BJ (1996) Hierarchical organization of auditory context sensitivity. *J Neurosci* 16: 6987–6998.
- Lewicki MS & Konishi M (1995) Mechanisms underlying the sensitivity of songbird forebrain neurons to temporal order. *Proc Nat Acad Sci USA* 92: 5582–5586.
- Lohr B & Dooling RJ (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.
- Lohr B, Dooling RJ & Bartone S (in press) The discrimination of temporal fine structure in call-like harmonic sounds by birds. *J Comp Psychol*.
- Margoliash D (1983) Acoustic parameters underlying the responses of song-specific neurons in the white-crowned sparrow. *J Neurosci* 3: 1039–1057.
- Margoliash D (1986) Preference for autogenous song by auditory neurons in a song system nucleus of the white-crowned sparrow. *J Neurosci* 6: 1643–1661.
- Margoliash D & Fortune ES (1992) Temporal and harmonic combination-sensitive neurons in the zebra finch's HVc. *J Neurosci* 12: 4309–4326.
- Marler P & Slabbekoorn H (2005) *Nature's music, the science of birdsong*. Elsevier Academic Press, San Diego.
- Moore BCJ, Glasberg, BR & Peters RW (1986) Thresholds for hearing mistuned partials as separate tones in harmonic complexes. *J Acoust Soc Am* 80: 479–483.
- Moore BCJ, Peters RW & Glasberg BR (1985) Thresholds for the detection of inharmonicity in complex tones. *J Acoust Soc Am* 77: 1861–1867.
- Nealen PM & Schmidt MF (2002) Comparative approaches to avian song system function: insights into auditory and motor processing. *J Comp Physiol A* 188: 929–941.
- Okanoya K, Yoneda T & Kimura T (1993) Acoustical variations in sexually dimorphic features of distance calls in domesticated zebra finches (*Taeniopygia guttata castanotis*). *J Ethol* 11: 29–36.
- Pumphrey RJ (1961) Sensory organs: hearing. In: Marshall AJ (ed) *Biology and comparative anatomy of birds*. pp. 69–86. Academic Press, New York.
- Schroeder MR (1970) Synthesis of low-peak-factor signals and binary sequences with low autocorrelation. *IEEE Trans Inf Theory* 16: 85–89.
- Schwartzkopff J (1968) Structure and function of the ear and the auditory brain areas in birds. In: De Reuck AVS & Knight J (eds) *Hearing mechanisms in vertebrates*. pp. 41–59. Little, Brown, Boston.
- Sen K, Theunissen FE & Doupe AJ (2001) Feature analysis of natural sounds in the songbird auditory forebrain. *J Neurophysiol* 86: 1445–1459.
- Tchernichovski O, Mitra PP, Lints T & Nottebohm F (2001) Dynamics of the vocal imitation process: how a zebra finch learns its song. *Science* 291: 2564–2569.
- Theunissen FE & Doupe AJ (1998) Temporal and spectral sensitivity of auditory neurons in the nucleus Hvc of male zebra finches. *J Neurosci* 18: 3786–3802.
- Vicario DS (1991) Contributions of syringeal muscles to respiration and vocalization in the zebra finch. *J Neurobiol* 22: 63–73.
- Viemeister NF & Plack CJ (1993) Time analysis. In: Yost WA, Popper AN & Fay RR (eds) *Human psychophysics*. pp. 116–154. Springer-Verlag, New York.

- Volman SF (1996) Quantitative assessment of song-selectivity in the zebra finch "high vocal center." J Comp Physiol A 178: 849–862.
- Williams H, Cynx J & Nottebohm F (1989) Timbre control in zebra finch (*Taeniopygia guttata*) song syllables. J Comp Psychol 103: 366–380.
- Zann R (1984) Structural variation in the zebra finch distance call. Zeit Tierpsychol 66: 328–345.