suggest that the preservation of this older age may indicate that whole-rock systems remain closed to U-Pb during amphibolite facies metamorphism. That is, Lewisian zircons that have only undergone amphibolite facies metamorphism may retain ages older than the date from the Scourian peak of granulite facies metamorphism.

The well-rounded shape of many of the purple grains and their frosted, pitted surfaces may imply a more distant source. The Nûk gneisses from the Godthaabsfjord area, western Greenland, for instance, produce primary ages of 2,890-3,065 Myr (ref. 18), and hyacinth zircons from the Amitsôq gneisses in the same region have been dated at 3,650 ± 50 Myr (ref. 19). What the exact sources may be, however, is impossible to tell without, at least, further knowledge of the extent of recycling.

The brown and colourless zircon fractions (mostly euhedral) have $^{207}Pb/^{206}Pb$ ages between 610 and 2,430 Myr. If a 'best-fit' line is fitted to the colourless-brown zircon fractions from the Rough Rock (Fig. 2*b*), the upper intercept age produced is 3,010 ± 70 Myr and the lower intercept 500 Myr. Ages of 2,730 ± 170 Myr and 420 ± 5 Myr respectively are obtained for the Earl Crag Grit zircons (Fig. 2*a*) although these are not very reliable because R1/25 and R1/29 plot so close together that the chord is essentially of two points only. The data could be a result of a failure to separate younger Caledonian zircons and older Archaean zircons, although a greater spread of data might be expected in this case. Alternatively, it is more likely they represent a reverse discordia pattern similar to those described by Pidgeon and Aftalion[12] for zircons from Caledonian granites in northern Britain. That is, the zircons are of Caledonian age but with an older, inherited Precambrian component. The 420-Myr age of the Earl Crag Grit zircons is (within error) consistent with the age of the voluminous suite of late-Silurian to early-Devonian granites exposed in the Highlands and Southern Uplands. The 500-Myr zircons from the Rough Rock are older, corresponding to a phase of Ordovician magmatism. These earlier granites were also exposed, however, as evidenced by clasts from Ordovician and early-Devonian conglomerates dated by Longman *et al.*[20] and by van Breemen and Bluck[21]. Zircon fraction G/35 (Fig. 2*b*) is very nearly concordant at 500 Myr indicating a minimal Pb-loss since formation. Fractions G/43 and G/44, however, appear to have a much larger component of Precambrian age (whether this is in the form of 'composite' grains or a mixture of grains of different ages).

Unpublished work on zircon fractions from other Carboniferous sandstones ranging in age from Dinantian to Westphalian has yielded similar results with 'old' purple zircons occurring throughout the Carboniferous. An earlier study, based on Sm-Nd whole-rock isotope data[22], suggested that the sediments of southern Britain were formed by recycling of pre-existing sediments. This idea is contradicted by the new data presented here, as well as by subsequent Sm-Nd analyses[23].

The simplicity of these results, considering the continental-scale of the river system, is surprising. Mid-Proterozoic ages, for instance, do not seem to be represented in the detritus. This excludes areas such as the Ketilidian and Nagssugtoqidian of Greenland; van Breemen *et al.*[24] dated zircons from granitic belts from the Ketilidian of S. Greenland and found no evidence to support the theory of derivation from older basement. The Nagssugtoqidian of western Greenland is unsuitable because it has new mid-Proterozoic zircons in addition to those inherited from Archaean rocks. Similarly, the Laxfordian of north-west Scotland contains some new zircons[25]. The proportion of detritus that has been recycled through pre-existing sedimentary rocks is not as great as anticipated; only ~10% of the zircon grains overall are well-rounded.

This evidence for sustained, active erosion of Precambrian basement in the late Palaeozoic presents a major sedimentary problem in that hypotheses for the development of the extensional suite of Carboniferous sedimentary basins[26] must also be accompanied by a theory to explain the establishment of a huge continental-scale drainage system. The progradation of this depositional system into northern and central Britain reached its climax in Namurian times, with thick sequences of coarse feldspathic detritus being deposited. The persistence of first-cycle Archaean zircons throughout the Carboniferous implies that the drainage system was not altered substantially in areal extent in the Namurian, rather that a major increase of fluvial discharge and a reduction in hinterland chemical weathering occurred. The disappearance of semi-arid indicators in depositional facies in Namurian times, together with palaeomagnetic indicators of latitudinal shift may favour a climatic change (from semi-arid to monsoonal?) over a tectonic cause, but both variables may have been involved.

We thank members of the Department of Earth Sciences at Leeds for useful discussion. S.D. acknowledges receipt of a NERC studentship. Isotope work at Leeds is supported by NERC.

Received 21 July; accepted 22 October 1986.

1. Sorby, H. C. *Proc. Yorks. Geol. Polytech. Soc.* **3**, 669-675 (1859).
2. Gilligan, A. *Q. Jl geol. Soc. Lond.* **75**, 251-293 (1920).
3. Walker, C. T. thesis, Univ. Leeds (1952).
4. Muir, R. O. *Trans. Edinb. geol. Soc.* **19**, 439-485 (1963).
5. McCabe, P. J. *Sedimentology* **24**, 271-290 (1977).
6. Gaudette, H. E., Vitrac-Michard, A. & Allégre, C. J. *Earth planet. Sci. Lett.* **54**, 248-260 (1981).
7. Gebauer, D. & Grunenfelder, M. *Contr. Miner. Petrol.* **65**, 29-37 (1977).
8. Grauert, B. *Contr. Miner. Petrol.* **40**, 105-130 (1973).
9. Allen, P. *Proc. geol. Ass.* **86**, 389-437 (1975).
10. Gastil, R. G., DeLisle, M. & Morgan, J. R. *Bull. geol. Soc. Am.* **78**, 879-906 (1967).
11. Pupin, J. P. *Contr. Miner. Petrol.* **73**, 207-220 (1980).
12. Pidgeon, R. T. & Aftalion, M. in *Crustal Evolution in Northwestern Britain and Adjacent Regions* (eds Bowes, D. R. & Leake, B. E.) 183-220 (Seel House Press, Liverpool, 1978).
13. Boswell, P. G. H. *Miner. Mag.* **21**, 310-317 (1927).
14. Pidgeon, R. T. & Aftalion, M. *Earth planet. Sci. Lett.* **17**, 269-274 (1972).
15. Pidgeon, R. T. & Bowes, D. R. *Geol. Mag.* **109**, 247-258 (1972).
16. Bowes, D. R., Hopgood, A. M. & Pidgeon, R. T. *Geol. Mag.* **113**, 545-552 (1976).
17. Whitehouse, M. J. & Moorbath, S. *Nature* **319**, 488-489 (1986).
18. Baadsgaard, H. & McGregor, V. R. *Geochim. cosmochim. Acta* **45**, 1099-1109 (1981).
19. Baadsgaard, H. *Earth planet. Sci. Lett.* **19**, 22-28 (1973).
20. Longman, C. D., Bluck, B. J. & van Breemen, O. *Nature* **280**, 578-581 (1979).
21. van Breemen, O. & Bluck, B. J. *Nature* **291**, 113-117 (1981).
22. Miller, R. G. & O'Nions, R. K. *Earth planet. Sci. Lett.* **68**, 459-470 (1984).
23. Davies, G., Gledhill, A. & Hawkesworth, C. *Earth planet. Sci. Lett.* **75**, 1-12 (1985).
24. van Breemen, O., Aftalion, M. & Allaart, J. H. *Bull. geol. Soc. Am.* **85**, 403-412 (1974).
25. van Breemen, O., Aftalion, M. & Pidgeon, R. T. *Scott. J. Geol.* **7**, 139-152 (1971).
26. Leeder, M. R. *Q. Jl geol. Soc. Lond.* **139**, 479-491 (1982).
27. Krogh, T. E. *Geochim. cosmochim. Acta* **37**, 485-494 (1973).

Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere

Stephen Nowicki

The Rockefeller University, Field Research Center, Millbrook,
New York 12545, USA

The complexity and dependence on learning of many bird sounds have suggested parallels between birdsong and human speech[1–4], but the mechanisms by which each is produced have been supposed to differ markedly. In human speech, resonances of the vocal tract are thought to modulate in complex ways the sound produced by vibration of the vocal folds[5–7]. The current theory of birdsong production holds that all variation in sound quality arises from the primary sound-producing organ, the syrinx, and that resonances of the vocal tract play no part[8,9]. Here I present evidence, obtained from acoustic analyses of birdsongs recorded in a helium atmosphere, which contradicts this hypothesis. Not only does the songbird's vocal tract act as an acoustic filter, but its filter characteristics are actively coordinated with the output of the syrinx. Songbird and human phonation are thus more analogous than previously thought, in that both require coordination of an array of diverse motor systems.

One factor determining the acoustic resonances of a tube such as the vocal tract is sound velocity[10]. When atmospheric nitrogen

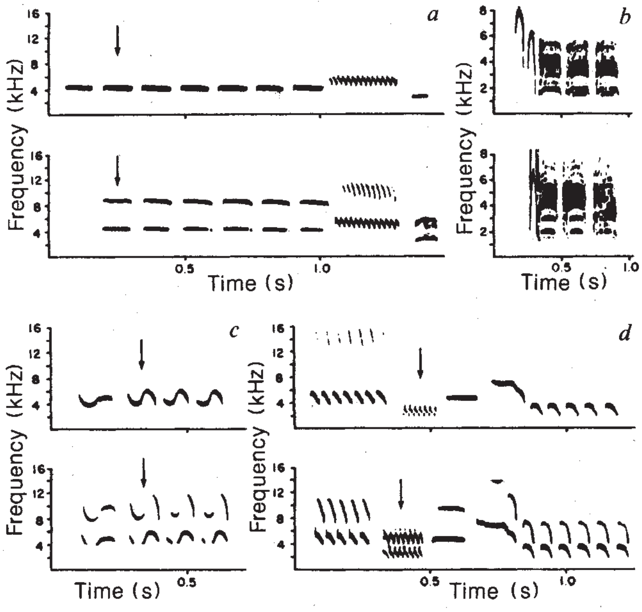

Fig. 1 Sonagrams of bird vocalizations produced in normal air (upper traces) and in the helium atmosphere (lower traces). *a*, *c*, *d*, Three different song sparrow (*Melospiza melodia*) songs (an entire song is depicted in *a*; selected song segments are shown in *c* and *d*). In helium there is a harmonic for every acoustic element normally appearing as a pure tone. *b*, Black-capped chickadee (*Parus atricapillus*) call. The higher frequency components of the terminal syllables are emphasized more in helium than in normal air. Arrows in *a* and *c* indicate syllables represented as amplitude spectra in Figs 2*a* and 2*b*, respectively. Arrow in *d* indicates a syllable for which the second harmonic, apparent in helium, occurs in the same frequency range as the fundamentals of adjacent syllables (Fig. 3). All birds were recorded in a 90×45×45 cm gas-sealed acoustic chamber, using a B&K 4145 calibrated microphone, a B&K 2604 microphone amplifier (flat weighting), and a Nagra 4.2L tape recorder (19 cm s^{-1}). After control vocalizations were recorded in normal atmosphere (upper traces), the chamber was flushed with 80% helium and 20% oxygen, and the bird recorded again (lower traces). Changes in tube resonances were monitored with a toy organ pipe inside the chamber, which showed a 67% increase in its resonance frequencies in heliox, corresponding to an increase in sound velocity from 331.5 m s^{-1} to 554.9 m s^{-1}. Slight variations in timing and syllable composition in all vocalizations pictured are not a consequence of the helium atmosphere. Sonagrams were produced on a Kay Elemetric Digital Sona-graph (Model 7800); *a*, *c* and *d*, 16 kHz analysis range, 300 Hz filter bandwidth; *b*, 8 kHz analysis range, 300 Hz filter bandwidth. Other species so tested, but not pictured, are: swamp sparrow (*Melospiza georgiana*), starling (*Sturnus vulgaris*), chestnut-sided warbler (*Dendroica pensylvanica*), rufous-sided towhee (*Pipilo erythropthalmus*), zebra finch (*Poephila guttata*), society finch (*Lonchura striata*), and brown-headed cowbird (*Molothrus ater*).

(comprising 80% of ordinary air) is replaced with the less dense gas helium, the velocity of sound increases from 331 m sec^{-1} to 578 m sec^{-1}, and the resonance frequencies of a simple tube should increase by 74%[11,12]. The effect of such an atmosphere on the singing of a bird depends on the manner in which resonances interact with the acoustic source. This point is best illustrated by two divergent examples. When a human speaks in helium, the fundamental frequency of vocal fold vibration does not change appreciably[7,13,14]. The increase in pitch which is perceived is due to an upward shifting of the vocal tract resonances, or formants, with resulting emphasis on higher frequency overtones. In contrast, if a wind instrument like a trombone is played in helium, the fundamental frequency of the tone played does increase, in the same proportion as that calculated for resonances of the corresponding tube[15,16]. Acoustic resonances modify the sound output in each case; the difference is due to the degree to which the sound source is acoustically coupled to the resonator. In the trombone, the resonator is strongly coupled to the source, largely determining its mode of vibration, whereas the resonator acts predominantly as a filter in the human voice.

The fact that the two sides of an oscine bird's syrinx seem able to operate independently originally led to the hypothesis that vocal tract resonances play no role in bird phonation[8]. Two harmonically unrelated tones often occur simultaneously in birdsong, which was thought to be impossible if the trachea acted as a coupled resonator. Nor was the vocal tract presumed to act as an uncoupled acoustic filter, since no relationship could be found between the amplitude and frequency of song syllables and predicted tracheal resonances[8]. This second argument is less compelling since it is assumed that filter properties must be static (in contrast to humans where resonances actively change during speech).

I recorded the songs and calls of nine species of oscine birds both in normal air and in a helium atmosphere. The results are equivalent for all species, and are typified by several song types of the song sparrow (*Melospiza melodia*) (Fig. 1*a*, *c*, *d*) and the call of the black-capped chickadee (*Parus atricapillus*) (Fig. 1*b*). The most striking effect of helium is that, to each song element appearing as a pure tone in normal atmosphere, a harmonic overtone is added (Figs 1*a*, 2*a*). The fundamental frequency of these tones increases in helium by 3-5% (Fig. 2*a*), an order of magnitude less than the 67% shift that is observed in the toy organ pipe used for calibration. These notes also decrease in amplitude, often by over 10 decibels (dB). Sounds with a broad band of frequencies, such as the terminal syllables of the chick-

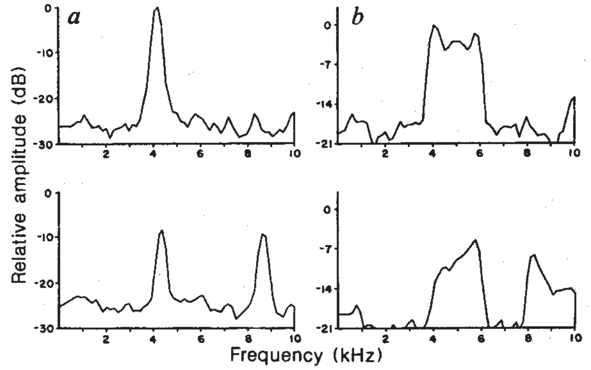

Fig. 2 Amplitude spectra of syllables produced in normal air (upper traces) and in the helium atmosphere (lower traces). Each spectrum is an average calculated over the entire duration of a single syllable (*a* corresponds to arrows in Fig. 1*a*; *b* corresponds to arrows in Fig. 1*c*). The amplitudes of signals in helium have been increased in gain by 10 dB compared to their counterparts in normal air to illustrate optimally the emergent frequency components. Note that if a vocal filter is centred at 4,200 Hz, the frequency of the syllable illustrated in *a* (and a realistic resonance value given the dimensions of the bird's vocal tract), then its centre frequency would shift to 7,000 Hz in the helium atmosphere, a value intermediate between the fundamental frequency and its harmonic. The small shift observed in the fundamental frequencies is similar to that observed in human speech[13,14], and may be caused by differential loading on the vibrating structure in the less dense atmosphere. Spectra were generated digitally, using a 128 point DFT, 10 kHz analysis range, and 156 Hz frequency resolution.

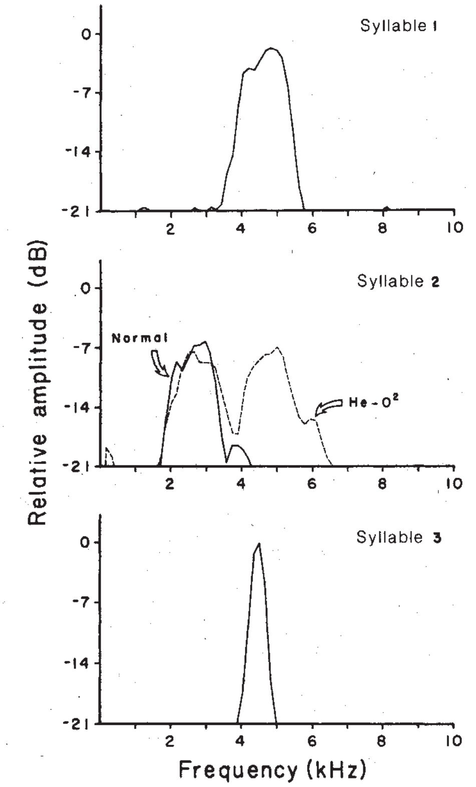

Fig. 3 Amplitude spectra of three consecutive syllables in normal atmosphere (solid lines), illustrating the overlap in frequency ranges of the second harmonic component of syllable 2, apparent only in helium (dashed line), and the normal fundamental frequency components of syllables 1 and 3. A change in the frequency response characteristics of the vocal filter must occur from syllable to syllable in order to account for the lack of energy in the second harmonic component of syllable 2 in normal atmosphere. Each average spectrum is calculated digitally, as in Fig. 2, over the entire duration of a syllable. Syllable 2 corresponds to the rapidly modulated syllable marked with arrows in Fig. 1*d*, while syllables 1 and 3 correspond to the trilled syllable immediately preceding and the tonal syllable immediately following, respectively. The amplitude spectrum in helium (dashed line) is shown for syllable 2 only.

adee's call, display a shift in the amplitudes of frequency components, with higher frequencies emphasized in helium (see Fig. 1*b*).

The changes observed in both pure tone and broad-band sounds are explained if the bird's vocal tract is acting as an acoustic band-pass filter that is not significantly coupled to the vibration source. Thus, the shifted emphasis to higher frequencies in the chickadee's broad-band syllable (Fig. 1*b*) is analogous to the change observed for a human voice in helium. The pure tone case (Figs 1*a*, 2*a*) indicates that the 'whistles' common in birdsong are not pure tones, but rather harmonic sounds with relatively high frequency fundamentals. Normally the energy in their second harmonics is strongly attenuated by a filter centred around the fundamental frequency. In helium, this filter is shifted upward, revealing the harmonic content. Since neither the fundamental frequency nor the second harmonic is now squarely centred on the filter's best frequency, both have reduced amplitudes compared to the fundamental in ordinary atmosphere. In a widely cited earlier study, Hersh[17] recorded two species in helium-air, both of which sang 'whistled' songs with fundamental frequencies above 4 kHz. Because he could only analyse sounds up to 8 kHz (a typical upper frequency limit on older spectrographs), Hersh failed to detect the emergence of harmonics and mistakenly concluded that no change occurred.

Further evidence for a vocal filter comes from frequency modulated whistles, the averaged spectra of which have broad frequency distributions with two distinct amplitude peaks (Figs 1*c*, 2*b*). In helium, the lower peak of the fundamental component is significantly more attenuated than the higher one. The reverse is true of the second harmonic component. These amplitudes can only be accounted for by shifting the centre frequency of a band-pass filter between the two harmonic components; the sloping shoulders of the filter function result in greater attenuation of the peaks further from the centre frequency.

As a bird utters a complex song, the centre frequency of its vocal filter must track actively the fundamental frequency of each syllable. Evidence of tracking comes from cases in which the second harmonic of a syllable falls in the same frequency range as the fundamental of an adjacent syllable (Fig. 1*d*). This harmonic would appear in normal atmosphere if the frequency response of the filter were invariant from syllable to syllable (Fig. 3). Filtering out of the harmonic, which clearly occurs, requires rapid shifting of the centre frequency of the filter before production. A bird could adjust its vocal filter in several ways: for example by varying tracheal length, by constriction of the larynx, or by flaring its throat and beak. Such configurational changes could well correspond to the head movements commonly observed in singing birds.

The parallels drawn between birdsong and human speech[1-4] can now be extended to the level of production. Like human speech, and in contrast to previous theories, birdsong must be viewed as the coordinated output of several motor systems acting in concert. There are contrasts as well, perhaps the greatest being that the oscine bird possesses two potentially independent sound sources. If these sources separately produce sounds, both must fall within the band-pass frequency range of the vocal filter. Further, oscine sounds have fundamentals on the order of several thousand Hz as opposed to human speech fundamentals usually less than 200 Hz. The bird's vocal filter tends to concentrate energy at a single frequency because of the wide separation of harmonic components, whereas the human vocal filter varies the distribution of energy within a wide band of frequencies. Lastly, the bird's filter probably simply tracks the output of the syrinx, whereas the more complex human vocal tract both modulates laryngeal output and generates its own phonemic gestures.

I thank R. R. Capranica, C. W. Clark, A. S. Gaunt, D. R. Griffin, S. Peters, K. N. Stevens, and especially P. Marler for discussion and comments on the manuscript. Supported by Biomedical Research Support Grant S07 RR07065 to The Rockefeller University and USPHS Post-doctoral Fellowship 5 F32 NS07520-02.

Received 7 May; accepted 20 October 1986.

1. Marler, P. *Am. Scient.* **58**, 669-673 (1970).
2. Marler, P. & Peters, S. in *Perspectives on the Study of Speech* (eds Eimas, P. D. & Miller, J. L.) 75-112 (Lawrence Erlbaum Ass., Hillsdale, New Jersey, 1981).
3. Nottebohm, F. *Prog. Psychobiol. & physiol. Psychol.* **9**, 85-124 (1980).
4. Konishi, M. *A. Rev. Neurosci.* **8**, 125-170 (1985).
5. Fant, G. *Acoustic Theory of Speech Production* (Mouton, The Hague, 1960).
6. Flanagan, J. L. *Speech Analysis, Synthesis, and Perception*, 2nd edn (Springer-Verlag, Berlin, 1972).
7. Lieberman, P. *Speech Physiology and Acoustic Phonetics* (Macmillan, New York, 1977).
8. Greenewalt, C. H. *Bird Song: Acoustics and Physiology*, 55-61 & 79-87 (Smithsonian, Washington, D.C., 1968).
9. Gaunt, A. S. & Gaunt, S. L. L. in *Current Ornithology*, Vol. 2 (ed. Johnston, R. F.) 213-246 (Plenum, New York, 1985).
10. Lord Rayleigh *The Theory of Sound* 2nd edn (Dover, New York, 1945).
11. Hardy, H. C., Telfair, D. & Pielemeier, W. H. *J. acoust. Soc. Am.* **13**, 226-233 (1942).
12. Beranek, L. L. *Acoustic Measurements*, 37-49 (Wiley, New York, 1949).
13. Beil, R. G. *J. acoust. Soc. Am.* **34**, 347-349 (1962).
14. Holywell, K. & Harvey, G. *J. acoust. Soc. Am.* **36**, 210-211 (1964).
15. Martin, D. W. *J. acoust. Soc. Am.* **13**, 305-308 (1942).
16. Benade, A. H. *Fundamentals of Musical Acoustics*, 391-429 (Oxford University Press, London, 1976).
17. Hersh, G. L. Thesis, Univ. California, Berkeley (1966).