Heishijiao, Shahekou, Dalian, China
†Department of Earth Sciences, Montana State University, Bozeman, Montana 59717, USA
e-mail: djv@montana.edu
‡PaleoWorld Research Foundation, Asian Operation B-1 22-2, Lane 256, RuiAn Street, Taipei, Taiwan 106, Republic of China

1. Magnusson, W. E., Vliet, K. A., Pooley, A. C. & Whitaker, R. in *Reproduction in Crocodiles and Alligators* (ed. Ross, C. A.) 118–135 (Facts on File, New York, 1989).
2. Gill, F. B. *Ornithology* (Freeman, New York, 1990).
3. Horner, J. R. *Annu. Rev. Earth Planet. Sci.* **28,** 19–45 (2000).
4. Zhou, Z., Barrett, P. M. & Hilton, J. *Nature* **421,** 807–814 (2003).
5. Voorhies, M. R. *Natl Geogr. Soc. Res. Rep.* **19,** 671–688 (1985).
6. Groenewald, G. H., Welman, J. & MacEachern, J. A. *Palaios* **16,** 148–160 (2001).
7. Erickson, G. M. & Tumanova, T. A. *Zool. J. Linn. Soc.* **130,** 551–566 (2000).
8. Bakker, R. T. & Bir, G. in *Feathered Dragons* (eds Currie, P. J., Koppelhus, E. B., Shugar, M. A. & Wright, J. L.) 301–342 (Indiana University, Bloomington, 2004).
9. Geist, N. R. & Jones, T. D. *Science* **272,** 712–714 (2003).
10. Carpenter, K. *Eggs, Nests, and Baby Dinosaurs* (Indiana University, Bloomington, 1999).
11. Tullberg, B. S., Ah-King, M. & Temrin, H. *Phil. Trans. R. Soc. Lond. B* **357,** 251–257 (2002).
12. Wesolowski, T. *Am. Nat.* **143,** 39–53 (1994).
13. Kavanau, J. L. *Lovebirds, Cockatiels, Budgerigars: Behavior and Evolution* (Science Software Systems, Los Angeles, 1987).

Competing financial interests: declared none.

Bird song

Superfast muscles control dove's trill

Bird songs frequently contain trilling sounds that demand extremely fast vocalization control[1,2]. Here we show that doves control their syrinx, a vocal organ that is unique to birds, by using superfast muscles. These muscles, which are similar to those that operate highly specialist acoustic organs such as the rattle of the rattlesnake, are among the fastest vertebrate muscles known and could be much more widespread than previously thought if they are the principal muscle type used to control bird songs.

The syrinx of ring doves (*Streptopelia risoria*) generates a relatively simple, highly stereotyped song — the familiar cooing sound. The coo contains a trill, whose elements are generated at repetition rates of up to 30 Hz (Fig. 1a). When doves coo, respiratory airflow excites membranes in the syrinx[3], causing them to vibrate[4,5]. The vibrations depend on the tension in the membranes[3,6], which is modified by activating two pairs of syringeal muscles[5,7]. These muscle pairs act as antagonists[5]: the tracheolateralis muscles cause the membranes to move out of the tracheal lumen (abduct), whereas the sternotrachealis muscles cause the membranes to slacken and to adduct.

We made simultaneous *in vivo* recordings of muscle activity and sound in cooing doves and found that the electromyographic (EMG) activity of the tracheolateralis muscles correlated significantly more strongly with voiced, rather than silent, periods: activating these muscles switches the sound on, and not off as previously thought[5], by positioning the membrane in the airflow. We also found that modulation of the tracheolateralis muscles' EMG correlated strongly with changes in sound frequency: the muscles change the tension in the membranes, which changes the frequency of the sound. (For methods, see supplementary information.)

A dove's trill cannot be achieved using typical vertebrate muscles, because they do not switch on and off fast enough to control the trill's brief sound elements ($\geqslant$9 ms). The syringeal muscles must also contract aerobically to power cooing sessions that can last for many minutes. These extreme requirements can be met only by aerobic superfast muscles[8]. This muscle type is the fastest known in vertebrates: its twitch half-time is less than 10 ms, which is one to two orders of magnitude faster than that of typical locomotory muscles[8].

Our measurements show that dove syringeal muscles attain superfast kinetics. The twitch half-times of the tracheolateralis and sternotrachealis muscles are 9.2 ± 0.8 ms and 10.3 ± 1.7 ms, respectively, and the stimulus repetition rates necessary to obtain tetanic contraction are 200–275 Hz for tracheolateralis and 200–400 Hz for sternotrachealis muscles. But, like all superfast muscles, the syringeal muscles trade force for speed[9]: they exert low twitch stresses (tracheolateralis: 8.0 ± 4.8 kilonewtons per m^2; sternotrachealis: $20.6 \pm 15.7\,kN\,m^{-2}$).

We also subjected the syringeal muscles to a playback signal based on the *in vivo* EMG pattern. During the simulated trill, both types of muscle modulate force (Fig. 1b). As the silent intervals in the playback signal shorten from 12 to 3.5 ms, neither is able to relax completely between trill elements.

Our results indicate that both muscles exert control directly at the syringeal membranes by altering the membrane position, which in turn alters membrane tension. The tracheolateralis muscles pull the syringeal membranes apart, thereby allowing them to vibrate in the airflow, which supports indirect evidence that the syrinx is closed between trills[10]. This control mode implies that gating is determined by the membrane position and that membrane tension determines pitch.

Our *in vitro* experiments show that both syringeal muscles have the superfast properties necessary to control individual sound elements during the dove's trill. Co-activation of the antagonistic muscles affords the bird very fast and accurate position control of the syringeal membranes, akin to saccadic eye and rapid arm movements[11].

Birds modulate their songs extremely rapidly, with frequencies exceeding 100 Hz (ref. 2). Although the intrinsic nonlinear properties of the syrinx[6] add complexity to the level of motor control, only muscle control can explain the fast but gradual modulations that underlie the extraordinary intraspecific variability and flexibility of phonation[1]. The stereotyped coos of doves are considered to be simple vocalizations among birds, but even doves use superfast muscles to control their song. Given their added vocal complexity[12], songbirds have probably evolved muscles that outperform the syringeal muscles of doves. Superfast muscle can no longer be considered a rare adaptation, found for example in the highly derived acoustic organs of the toadfish and rattlesnake[8]. We suspect that superfast vocal muscles are widespread among birds.

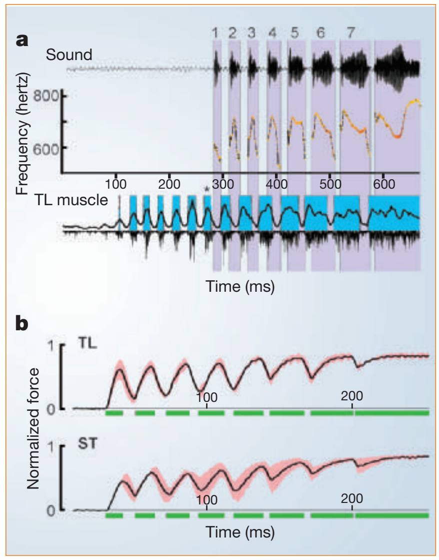

Figure 1 Superfast muscles control song sound in ring doves. **a,** Sound oscillogram, spectrogram and electromyographic activity of tracheolateralis (TL) muscles (upward, integrated; downward, rectified) during the trill. TL activation (blue boxes) precedes the corresponding trill elements (purple boxes). Asterisk indicates TL burst associated with the first trill pulse (trill 1). **b,** Normalized traces of *in vitro* force modulation of TL and sternotrachealis (ST) muscles during a stimulation pattern (green bars) based on an averaged trill (mean (black trace) ± s.d. (pink trace); $n = 4$).

Coen P. H. Elemans*, Igor L. Y. Spierts*, Ulrike K. Müller*, Johan L. van Leeuwen*, Franz Goller†
**Experimental Zoology Group, Wageningen University, 6709 PG Wageningen, The Netherlands*
e-mail: coen.elemans@wur.nl
†Department of Biology, University of Utah, Utah 84112, USA

1. Greenewalt, C. H. *Bird Song: Acoustics and Physiology* (Smithsonian Institute, Washington DC, 1968).
2. Goller, F. & Suthers, R. A. *J. Neurophysiol.* **75,** 867–876 (1996).
3. Fletcher, N. H. *J. Theor. Biol.* **135,** 455–481 (1988).
4. Larsen, O. N. & Goller, F. *Proc. R. Soc. Lond. B* **266,** 1609–1615 (1999).
5. Goller, F. & Larsen, O. N. *J. Exp. Biol.* **200,** 2165–2176 (1997).
6. Fee, M. S., Shraiman, B., Pesaran, B. & Mitra, P. P. *Nature* **395,** 67–71 (1998).
7. Gardner, T., Cecchi, G., Magnasco, M., Laje, R. & Mindlin, G. B. *Phys. Rev. Lett.* **87,** 208101 (2001).
8. Young, I. S. & Rome, L. C. *Proc. R. Soc. Lond. B* **268,** 1965–1070 (2001).
9. Rome, L. C., Syme, D. A., Hollingworth, S., Lindstedt, S. L. & Baylor, S. M. *Proc. Natl Acad. Sci. USA* **96,** 5826–5831 (1999).
10. Beckers, G. B. L., Suthers, R. A. & ten Cate, C. *J. Exp. Biol.* **206,** 1833–1843 (2003).
11. Harris, C. M. & Wolpert, D. M. *Nature* **384,** 780–784 (1998).
12. Goller, F. *Nature* **395,** 11–12 (1998).

Supplementary information accompanies this communication on *Nature*'s website.
Competing financial interests: declared none.