

9. Medeiros, N.A., Burnette, D.T., and Forscher, P. (2006). Myosin II functions in actin-bundle turnover in neuronal growth cones. *Nat. Cell Biol.* 8, 215–226.
10. Ponti, A., Machacek, M., Gupton, S.L., Waterman-Storer, C.M., and Danuser, G. (2004). Two distinct actin networks drive the protrusion of migrating cells. *Science* 305, 1782–1786.
11. Waterman-Storer, C.M., and Salmon, E.D. (1997). Actomyosin-based retrograde flow of microtubules in the lamella of migrating epithelial cells influences microtubule dynamic instability and turnover and is associated with microtubule breakage and treadmilling. *J. Cell Biol.* 139, 417–434.
12. Bretscher, A. (2003). Polarized growth and organelle segregation in yeast: the tracks, motors, and receptors. *J. Cell Biol.* 160, 811–816.
13. Evangelista, M., Pruyne, D., Amberg, D.C., Boone, C., and Bretscher, A. (2002). Formins direct Arp2/3-independent actin filament assembly to polarize cell growth in yeast. *Nat. Cell Biol.* 4, 260–269.
14. Sagot, I., Rodal, A.A., Moseley, J., Goode, B.L., and Pellman, D. (2002). An actin nucleation mechanism mediated by Bni1 and profilin. *Nat. Cell Biol.* 4, 626–631.
15. Yang, H.C., and Pon, L.A. (2002). Actin cable dynamics in budding yeast. *Proc. Natl. Acad. Sci. USA* 99, 751–756.
16. Bi, E., Maddox, P., Lew, D.J., Salmon, E.D., McMillan, J.N., Yeh, E., and Pringle, J.R. (1998). Involvement of an actomyosin contractile ring in *Saccharomyces cerevisiae* cytokinesis. *J. Cell Biol.* 142, 1301–1312.
17. Lippincott, J., and Li, R. (1998). Sequential assembly of myosin II, an IQGAP-like protein, and filamentous actin to a ring structure involved in budding yeast cytokinesis. *J. Cell Biol.* 140, 355–366.
18. Lord, M., Laves, E., and Pollard, T.D. (2005). Cytokinesis depends on the motor domains of myosin-II in fission yeast but not in budding yeast. *Mol. Biol. Cell* 16, 5346–5355.
19. Watanabe, N., and Mitchison, T.J. (2002). Single-molecule speckle analysis of actin filament turnover in lamellipodia. *Science* 295, 1083–1086.
20. Waterman-Storer, C.M., Desai, A., Bulinski, J.C., and Salmon, E.D. (1998). Fluorescent speckle microscopy, a method to visualize the dynamics of protein assemblies in living cells. *Curr. Biol.* 8, 1227–1230.

Departments of Molecular Genetics and Cell Biology and of Biochemistry and Molecular Biology, University of Chicago, Chicago, Illinois 60637, USA.
E-mail: drkovar@uchicago.edu

DOI: 10.1016/j.cub.2007.02.004

Animal Communication: Big Talkers and Small Talk

Vocal tract resonances, known as formants, are important perceptual cues for the identification of human speech and animal calls. A recent study shows that monkeys can also use formants to determine the age and size of the monkey producing a call.

K.G. Munhall and S.K. Byrne

On Regina Spektor's album 'Soviet Kitsch' her younger brother whispers her name repeatedly and whispers questions to her. Even from a single listening, it is obvious that this is a child's voice. Yet, it is a whisper with no vocal pitch to act as a cue for age. From anecdotal evidence such as this, and a growing body of research [1], it is clear that the sounds that humans and other species produce carry much information about the speaker beyond the messages they transmit. Like bullets shot from a particular gun, vocal acoustics bear the traces of the acoustic tube they pass through.

The British phonetician, David Abercrombie [2], drawing from C.S. Peirce's philosophy of signs, coined the term indexical properties to refer to the aspects of sound production that convey information about the producer. In Abercrombie's view, indexical properties include a wide range of factors, such as regional accents, physical or mental states and, most important biologically, the size and morphology of the speaker's vocal

tract. For more than 50 years (for example [3,4]) a model of sound production that formalizes the relationship between the area function of the vocal tract and the acoustics has been the dominant framework for understanding human speech production and the vocalization of other species. In this source-filter framework, vocal tract dimensions determine the resonances of the airway above the larynx and thus filter the acoustic energy emanating from the sound source. Generally, the length of the vocal tract is a major determinant of the distribution of resonances or formants. If the vocal tract is modeled as a straight tube open at one end, the first three formants are given by these formulas, where c is the speed of sound and L is the vocal tract length:

$$\begin{aligned}F_1 &= c/4L \\F_2 &= 3c/4L \\F_3 &= 5c/4L\end{aligned}$$

Thus, everything else being equal, the formant frequencies are indexical properties for the size of the vocal tract.

This specification of vocal dimensions by the acoustic

resonance patterns has an added evolutionary significance if two conditions are met. First, some aspect of vocal tract dimension must be correlated with body size or other physical measures that may be related to fitness. Second, listeners must be able to match the acoustics with these body size characteristics. In a paper published recently in *Current Biology*, Ghazanfar *et al.* [1] provide evidence for the first time in monkeys for this latter condition. Specifically, they show that rhesus monkeys can match the faces of two different-aged monkeys with their appropriate call.

Using a method adapted from the infant perception literature, Ghazanfar *et al.* [1] found that rhesus monkeys had a visual preference for videos of monkey faces that were consistent in age and size with the distribution of formants in a call that was played along with the film clips. Like a whispered utterance, the monkey calls used in their experiment had no vocal pitch cues that could be used to distinguish the age or size of the monkey that produced the call. Using a sophisticated formant synthesis technique, STRAIGHT [5], the authors created calls in which the vocal pitch, duration and amplitude contours were similar but the formant distributions were those produced by either a larger or smaller vocal tract (10 cm versus 5.5 cm in length).

While a number of previous studies had shown that nonhuman

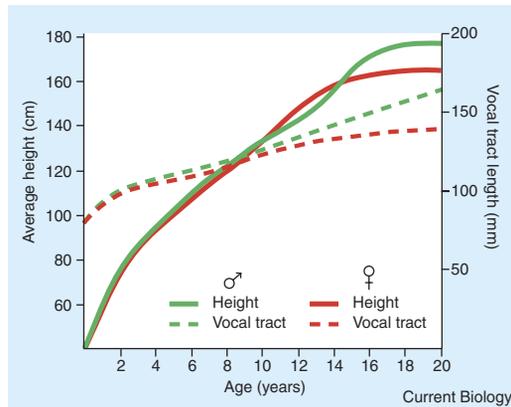


Figure 1. Growth curves for human male and female height and vocal tract length.

(Adapted from [18] and the unpublished doctoral thesis 'An articulatory model for the vocal tracts of growing children' by U.G. Goldstein, MIT, 1980.)

primates could be trained to discriminate vowel stimuli that varied only in formant structure [6] or could even do so spontaneously [7], Ghazanfar *et al.* [1] have shown something far more significant. They demonstrated that untrained monkeys spontaneously associate visual age and size cues with acoustic stimuli that varied in formant patterns. As has been shown in humans [8], the monkeys know that size scales inversely with formant frequency. Bigger and older monkeys produce the same calls as smaller and younger monkeys with lower formant frequencies.

The literature documenting the correlations between body size and formants is not, however, as straightforward as these perceptual results might lead one to believe. It is true that, when the analyses are computed across a broad age range, the correlations are relatively strong between body size and a variety of acoustic parameters [9]. For example, human vocal pitch, formant frequencies and durations of productions systematically change with age [10], as does body size and vocal tract dimensions (documented in an unpublished doctoral thesis 'An articulatory model for the vocal tracts of growing children' by U.G. Goldstein, MIT, 1980). Figure 1 shows the growth curves for height and vocal tract length. As Ghazanfar *et al.* [1] point out, however, the literature on the relationship between adult size and formants is more complex and varied. Fitch [11] reported that formant frequency and formant dispersion correlated well in his

sample of rhesus macaques, but in a study of body size and formant frequencies in adult humans, Gonzalez [12] found only modest correlations with larger correlation coefficients being observed for females. In contrast, Rendall *et al.* [13] found a correlation between height and formants (particularly the fourth formant) only for human males. Collins [14] reported no significant correlations between adult human body size measures and formants.

The reasons for this variability are diverse. The simple relationship between tube length and formant frequencies summarized in the equations above is for unconstricted tubes, but humans and other animals have great ability to deform the vocal tract during articulation and thus modify the formant structure of their utterances. We do so to produce different vowels, as animals do for different calls or even to seem larger (for example, by lowering the larynx [15]). The virtuoso voice actor, Mel Blanc, used a wide range of vocal tract configurations and larynx heights to achieve the many different cartoon voices he produced. Another potential reason for the variability in correlation measures is that the studies are sampling a very large number of potential acoustic cues for size. Formant frequencies, for example, are good descriptions of the sound structure of speech and animal calls but they are far from complete descriptors [16]. Failure to find consistent correlations may simply indicate that the acoustic parameters being tested are not suitable candidates for judging size not that there are no such acoustic

parameters. The perceptual system is computationally sophisticated and may find statistical regularities that involve some initial analysis. Witness the evidence for the use of depth cues in the auditory signal to 'compute' the perception of audiovisual synchrony [17].

In the end, the best evidence that there is auditory information for size may come from perceptual studies. It is clear that there are strong biases in people's judgments of size based on auditory recordings [15]. More studies like that of Ghazanfar *et al.* [1] may help us uncover the possible sources of these perceptual decisions and discover which information is a reliable indexical cue for body size.

References

- Ghazanfar, A.A., Turesson, H.J., Maier, J.X., van Dinther, R., Patterson, R.D., and Logothetis, N.K. (2007). Vocal tract resonances as indexical cues in rhesus monkeys. *Curr. Biol.* 17, 425–430.
- Abercrombie, D. (1967). *Elements of General Phonetics* (Chicago: Aldine Publishing Co).
- Chiba, T., and Kajiyama, M. (1941). *The Vowel: Its Nature and Structure* (Tokyo: Tokyo-Kaiseikan Pub. Co. Ltd.).
- Fant, G. (1960). *Acoustic Theory of Speech Production*, Second Edition, 1970. (The Hague, Netherlands: Mouton).
- Kawahara, H., Masuda-Kasuse, I., and de Cheveigne, A. (1999). Restructuring speech representations using pitch-adaptive time-frequency smoothing and instantaneous-frequency-based F0 extraction: a possible role of repetitive structure in sounds. *Speech Comm.* 27, 187–207.
- Sommers, M.S., Moody, D.B., Prosen, C.A., and Stebbins, W.C. (1992). Formant frequency discrimination by Japanese macaques (*Macaca-Fuscata*). *J. Acoust. Soc. Am.* 91, 3499–3510.
- Fitch, W.T., and Fritz, J.B. (2006). Rhesus macaques spontaneously perceive formants in conspecific vocalizations. *J. Acoust. Soc. Am.* 120, 2132–2141.
- Smith, D.R.R., Patterson, R.D., Turner, R., Kawahara, H., and Irino, T. (2005). The processing and perception of size information in speech sounds. *J. Acoust. Soc. Am.* 117, 305–318.
- Ey, E., Pfefferle, D., and Fischer, J. (2007). Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. *Primates* Jan 17 [Epub ahead of print].
- Lee, S., Potamianos, A., and Narayanan, S. (1999). Acoustics of children's speech: developmental changes of temporal and spectral parameters. *J. Acoust. Soc. Am.* 105, 1455–1468.
- Fitch, W.T. (1997). Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *J. Acoust. Soc. Am.* 102, 1213–1222.
- Gonzalez, J. (2004). Formant frequencies and body size of speaker: a weak relationship in adult humans. *J. Phonetics* 32, 277–287.

13. Rendall, D., Kollias, S., Ney, C., and Lloyd, P. (2005). Pitch (F0) and formant profiles of human vowels and vowel-like baboon grunts: the role of vocalizer body size and voice-acoustic allometry. *J. Acoust. Soc. Am.* 117, 944–955.
14. Collins, S.A. (2000). Men's voices and women's choices. *Anim. Behav.* 60, 773–780.
15. Fitch, W.T., and Reby, D. (2001). The descended larynx is not uniquely human. *Proc. R. Soc. Lond. B.* 268, 1669–1675.
16. Bladon, R.A.W. (1982). Arguments against formants in the auditory representation of speech. In *The Representation of Speech in the Peripheral Auditory System*, R. Carlson and B. Granstrom, eds. (Amsterdam: Elsevier Biomedical Press).
17. Alais, D., and Carlile, S. (2005). Synchronizing to real events: subjective audiovisual alignment scales with perceived auditory depth and speech of sound. *Proc. Natl. Acad. Sci. USA* 102, 2244–2247.
18. Malina, R.M. (1975). *Growth and Development: The First Twenty Years* (Minneapolis: Burgess Publishing).

Department of Psychology, Department of Otolaryngology, Queen's University, Kingston, Ontario, Canada, K7L 3N6.
E-mail: kevin.munhall@queensu.ca

DOI: 10.1016/j.cub.2007.02.007

Microtubule Organization: Cell Shape Is Destiny

A simple self-assembly pathway generates cytoplasmic microtubule bundles that can locate the cell center and guide spindle assembly in fission yeast. The cylindrical cell shape automatically corrects spindle orientation errors, rendering a checkpoint unnecessary.

Steven B. Haase¹
and Daniel J. Lew²

In many animal cells, the mitotic spindle provides spatial cues that position the cleavage plane perpendicular to the spindle axis. But in all fungal and plant cells, and in some animal cells, it is the mitotic spindles that must be positioned so that they lie perpendicular to a pre-ordained cleavage plane set by cell shape or tissue patterning. Studies in budding yeast uncovered an actin-assisted spindle-orienting strategy [1] which, along with back-up pathways and checkpoint surveillance systems [2], ensures that the process succeeds despite the significant challenges posed by the budding cell's shape (Figure 1A). But fission yeast take a simpler approach: a study published recently in *Current Biology* [3] has shown how these cells exploit the opportunities provided by their simpler cylindrical shape to position and orient their spindles without such regulatory bells and whistles (Figure 1B). Recent work has demonstrated that interphase microtubules self-assemble into linear bundles which align along the cell's long axis even in the absence of nuclei [4–6], and then orient the yeast centrosomes, called spindle pole bodies, in a manner that guides spindle assembly in mitosis [3].

Because interphase microtubule organizers are associated with the nucleus in fission yeast, it was assumed that nuclei would play a critical role in organizing the characteristic linear bundles of antiparallel microtubules — with minus ends in the center of the cell and plus ends in the periphery — which help guide cell growth to the ends of the cylinder. To test this idea, two groups [4,5] used tricks involving centrifugation to generate anucleate fission yeast cells. Remarkably, these cylinders were found to generate properly aligned microtubule bundles resembling those in nucleated cells. A primary organizing principle here is that given the shape and dimensions of the cylinder, the rigid microtubules — which have a Young's modulus of approximately 1.2 GPa, similar to that of plexiglas [7] — will rotate to align with the long axis once they grow longer than the 3 μm width of the cylinder and bump into the sides.

A remarkably simple mechanism for bundle self-organization was proposed by Tran and colleagues [6], supported by the results of live-cell imaging, biochemical analysis and mathematical modeling. New microtubules are nucleated at random sites on pre-existing microtubules by a microtubule-bound nucleating complex. Although they can grow

in any direction, a cross-linker that joins microtubules preferentially in an antiparallel orientation favors bundling. A minus-end-directed kinesin motor protein binds to the plus ends of the new microtubules and drags them towards the minus end of the starting microtubule. However, the movement is opposed by the cross-linking protein, and as the length of the apposed cross-linked microtubules grows, this brake eventually stalls the motor, leading to a central crosslinked core with plus ends growing out towards the cell periphery [6]. Strikingly, this simple bundling pathway exploits the cylinder's geometry to locate its center, where the cross-linked microtubule minus ends remain [4–6,8–10].

Unlike the spindle pole bodies of budding yeast, which nucleate microtubules constitutively, those of fission yeast lie dormant in the cytoplasm during interphase, attached to the outside of the nuclear envelope and also to the sides of cytoplasmic microtubules [11,12]. At the G2/M transition, the spindle pole bodies are inserted into the nuclear envelope — which does not break down during the closed mitosis — and their nuclear faces become active as microtubule nucleators [11,12]. An intranuclear spindle then forms, and cytoplasmic microtubules disassemble [13]. In their new work, Tolic-Nørrelykke and colleagues [3] showed that, when duplicated spindle pole bodies separate to form a spindle, they do so in good alignment with the long axis of the cell. This initial spindle alignment depends on the prior presence of well-aligned interphase microtubule bundles, suggesting that the cytoplasmic microtubules facilitate spindle pole