

Length of tail streamers in barn swallows

Both natural and sexual selection affect the expression of secondary sexual characters¹, so any secondary sexual character will be affected by a mixture of selection pressures. Evans² has compared the flight performance of male barn swallows (*Hirundo rustica*) whose tail lengths have been altered with that of controls, and concludes that the outermost tail feathers of these birds are mainly the outcome of natural selection.

If tail length has been determined by natural selection, then both elongation and shortening of tail feathers should lead to reduced flight performance. If sexual selection is involved, it will reduce the flight performance of males with elongated tails, so shortening the tail will improve performance. It is widely accepted that sexual selection cannot on its own be responsible for the elongated tail, but it may have an influence, as males have allometrically longer tails and streamers than females³.

The average difference in tail length between the sexes is about 15 mm in northern European barn swallows⁴. Because the female tail presumably represents the aerodynamic optimum in adult barn swallows^{3,4}, shortening the male tail by less than 15 mm should provide a test for the sexual selection hypothesis (Fig. 1). But Evans shortened male tails by 20 mm, reducing them beyond the aerodynamic optimum. His experiment could therefore demonstrate reduced flight performance only in support of natural selection, and so could not discriminate between the two hypotheses.

Norberg⁵ has proposed an aerodynamic mechanism to account for the elongated tail streamers in barn swallows, but Evans did not test this. According to Norberg, when the tail is lowered, the tail streamer is bent by air flow, causing an aeroelastic twist through the entire feather that is passively rotated. This rotation turns the outer tail into a flap that provides increased lift of the entire tail. For this to work, the tail must be considered as a finely tuned structure in which the entire tail is a coadapted complex of characteristics. If the tail streamers are manipulated beyond their aerodynamic optimum, other characteristics will also be affected, such as planform, curvature of the feather shaft, flexural stiffness, and torsional rigidity of the outermost tail feathers, which supposedly evolved to compensate for increased pitching moments caused by exaggerated streamers⁵. Any experimental shortening is therefore liable to disrupt performance even in male swallows.

The tail of male barn swallows has some functional utility, but it is the difference

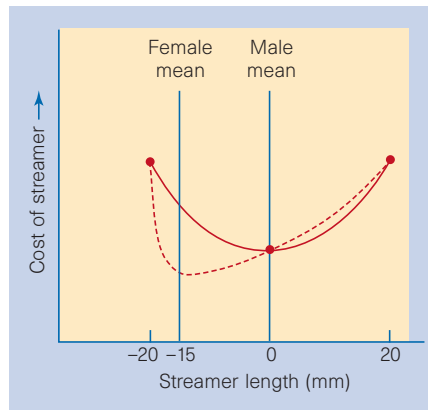


Figure 1 Models for the relation between streamer length and aerodynamic cost in barn swallows, as tested in tail-manipulation experiments. Filled circles, tail-streamer manipulations and effects described by Evans²; the solid curve shows his model. Our alternative model (broken curve) assumes that female streamer length represents the aerodynamic optimum and associated costs away from this optimum. If male streamer length has been modified by sexual selection, this gives an increased cost in relation to female streamer length. We have assumed that the differences between the sexes are controlled for allometric size differences.

between the sexes that is crucial to mate choice. Longer tails in male barn swallows may increase several components of sexual selection (reviewed in refs 4, 6), which has been demonstrated by manipulating apparent tail length without affecting aerodynamic function⁷. All the evidence indicates that the difference in tail length between the sexes is caused by sexual selection.

Anders Hedenström*, **Anders Pape Møller†**

*Department of Animal Ecology,
Ecology Building, S-223 62 Lund, Sweden
e-mail: anders.hedenstrom@zoekol.lu.se

†Laboratoire d'Ecologie, CNRS URA 258,
Université Pierre et Marie Curie,
Case 237, F-75252 Paris, Cedex 05, France

1. Darwin, C. *The Descent of Man, and Selection in Relation to Sex* (Murray, London, 1871).
2. Evans, M. R. *Nature* **394**, 233–234 (1998).
3. Hedenström, A. *Trends Ecol. Evol.* **10**, 140–141 (1995).
4. Møller, A. P. *Sexual Selection and the Barn Swallow* (Oxford Univ. Press, 1994).
5. Norberg, R. Å. *Proc. R. Soc. Lond. B* **257**, 227–233 (1994).
6. Møller, A. P. et al. *Proc. R. Soc. Lond. B* **265**, 409–414 (1998).
7. Møller, A. P. *Behav. Ecol. Sociobiol.* **32**, 371–376 (1993).

Evans replies — I have demonstrated that the tail streamers of male swallows are mainly the product of natural selection, although I suggested that sexual selection may have extended the streamer by less than the length the birds' tails were shortened in my experiments (20 mm)¹. My objective was to test whether tail streamers evolved as a result of sexual selection or of natural selection. Over the past eleven years, Møller and co-workers have shown that males with longer tails have many mating advantages². They conclude that “tail

ornaments in the monogamous swallow have evolved as a result of female choice”³.

In the population of barn swallows I studied, the difference in male and female streamer length is 14 mm, although there is extensive overlap between the sexes, so the manipulation of 20 mm I used is greater than the degree of sexual dimorphism. Hedenström and Møller say this invalidates experiments on sexual dimorphism. I chose 20 mm as this was the ‘standard size’ used by Møller and co-workers in their studies of sexual dimorphism in this species.

Hedenström and Møller claim that female streamer length represents the aerodynamic optimum in swallows. Yet in a previous study⁴, Møller and colleagues examined the function of the tail streamer in female swallows and concluded that female streamer length was longer than the optimum, possibly because of a genetic correlation with male streamer length. They suggested that the short tail streamers of juvenile swallows “must be close to the optimum under natural selection”⁴. It follows that female streamer length is unlikely to be the naturally selected optimum, as Hedenström and Møller have assumed⁵. Møller has also shown that male and female swallows have different morphologies⁶, so female streamer length would not represent the aerodynamic optimum for males even if female streamers were naturally selected.

My previous experiment could be improved by making a series of small removal manipulations, when the line relating flight performance to streamer length should have a turning point at the boundary between the naturally and sexually selected regions⁵. The results of such an experiment^{6–8} indicate that for the independent flight parameters there is a minimum 12 mm below the original streamer length. They also show that female tail streamers have been extended by a similar amount beyond the aerodynamic optimum, and so are in accord with Møller's earlier results⁴. To treat female streamer length as the aerodynamic optimum is therefore misleading.

Finally, my experiments did not attempt to test any particular aerodynamic mechanism². I have tested various functional hypotheses for streamer evolution, but the mechanism underlying this functional relation has not yet been proven. Our results indicate that the streamers of both male and female swallows evolved primarily as a result of natural selection, but that they have been extended by about 12 mm beyond this point by sexual selection.

Matthew R. Evans

Department of Biological Sciences,
University of Stirling, Stirling FK9 4LA, UK
e-mail: mre2@stir.ac.uk

1. Evans, M. R. *Nature* **394**, 233–234 (1998).
2. Møller, A. P. *Sexual Selection and the Barn Swallow* (Oxford Univ. Press, 1994).

3. Møller, A. P. *Nature* **332**, 640–642 (1988)
4. Cuervo, J. J., de Lope, F. & Møller, A. P. *Behav. Ecol.* **7**, 132–136 (1996).
5. Evans, M. R. & Thomas, A. L. R. *Proc. R. Soc. Lond. B* **264**, 211–217 (1997).
6. Buchanan, K. L. & Evans, M. R. *Behav. Ecol.* (submitted).
7. Rowe, L. V., Buchanan, K. L. & Evans, M. R. *Proc. R. Soc. Lond. B* (submitted).
8. Evans, M. R., Buchanan, K. L. & Rowe, L. V. *Proc. Natl Acad. Sci. USA* (submitted).

Sign language ‘heard’ in the auditory cortex

The upper regions of the brain’s temporal lobe are important both for hearing and for comprehending spoken language. We have discovered that these regions can be activated by sign language in congenitally deaf subjects, even though the temporal lobe normally functions as an auditory area. This finding indicates that, in deaf people, the brain region usually reserved for hearing may be activated by other sensory modalities, providing striking evidence of neural plasticity.

The auditory areas consist of the primary auditory cortex and the auditory association area (the supratemporal gyrus). The neural network that projects from the inner ear to the primary auditory cerebral cortex is formed without any auditory input, whereas post-processing neurons develop by learning with proper neural input. The learning period for the mother tongue is thought to be below five to six years of age¹. Reducing the auditory signals during the critical language-learning period can severely limit a child’s potential for developing an effective communication system². ‘Pre-lingual deaf’ patients, who were deafened before acquiring language, communicate using sign language.

In an attempt to understand how these auditory areas function in the congenitally deaf, we used positron emission tomography (PET) to measure cortical activation during a sign-language task. In the main experiment we sought to localize the ‘sign

language’ areas, but a secondary experiment was set up to localize both the auditory areas that had been dormant and the visual areas.

In the main experiment, the subject viewed a video of sign-language words being signed by a native signer; a still frame of the video was viewed in the control task. PET images were seen using statistical parametric mapping software³, and maps were superimposed onto magnetic resonance images of the subject’s brain for spatial localization. We found that sign language activated the supratemporal gyri bilaterally (left, $z = 4.52$; $P = 0.005$, corrected; Fig. 1).

The subject was scheduled to have a cochlear implant in his left ear. The implant is an artificial prosthesis, inserted into the inner ear, that electrically stimulates the cochlear nerve and enables the profoundly deaf to hear sounds. To distinguish the supratemporal gyri from the visual and dormant auditory areas, a secondary experiment was performed after the operation, consisting of an auditory task, a visual task and rest. In the visual task, the subject watched a video showing someone moving both hands up and down in a meaningless manner. In the auditory task, the words of the tape were delivered through the cochlear implant. The visual stimulation was found to activate the visual cortex in the occipital lobe ($P = 0.001$, corrected), and the auditory stimulation activated the right primary auditory cortex, contralateral to the auditory input ($P = 0.002$, uncorrected) (Fig. 1).

Pre-lingual deaf people can hear when a cochlear implant is switched on, but this does not allow them to understand words. Language stimulation through the implant activates only the primary auditory cortex in the pre-lingual deaf, whereas in the post-lingual deaf it activates both the primary and the secondary auditory areas⁴. The result of our secondary experiment was compatible with these findings. Our study of native signers and those who learnt sign language later showed that the nature and timing of sensory and linguistic experience

significantly affect the development of the language systems of the brain⁵.

In bilingual subjects (those with both signed and spoken language), sign language activates the visual areas⁶, whereas our study showed activation of the auditory area in the sign-language task. Because our subject had never received auditory input while the neural network was being formed, it seems that the supratemporal lobe was engaged in processing sign language. Using sign language elicits considerable activation of the left hemisphere in Broca’s area and Wernicke’s area, as well as of the right hemisphere⁷, whereas our results indicated limited activation of Wernicke’s area by sign-language words.

This cross-modal plasticity is also seen in visual areas. Braille-reading blind subjects have activation of the primary and secondary visual cortical areas when they perform tactile tasks⁸, although congenitally blind Braille readers have activation of visual reading areas but not primary visual cortex⁹. Our results indicate that the primary auditory cortex of deaf people is reserved for hearing sounds, whereas the secondary areas are used for processing sign language. This cross-modal non-plasticity of the primary auditory cortex is supported by functional magnetic resonance imaging of a congenitally deaf subject¹⁰, which suggests that the primary projection areas might be rigidly organized.

We observed that sign language activates the ‘language’ areas but not primary auditory cortex. The finding that, after a cochlear implant is in place, spoken words activate primary auditory cortex but not adjacent language areas indicates that primary auditory cortex still functions as an auditory area in this patient. We also identified the ‘sign-language’ area as the supratemporal gyri, which is usually the auditory area.

Hiroshi Nishimura*†, Kazuo Hashikawa‡, Katsumi Doi†, Takako Iwaki†, Yoshiyuki Watanabe§, Hideo Kusuoka*, Tsunehiko Nishimura*, Takeshi Kubo†

*Division of Tracer Kinetics, †Department of Otorhinolaryngology, ‡Department of Nuclear Medicine, and §Department of Radiology, Osaka University Medical School, Yamada-oka, Suita City, Osaka, Japan
e-mail: hiroshi@tracer.med.osaka-u.ac.jp

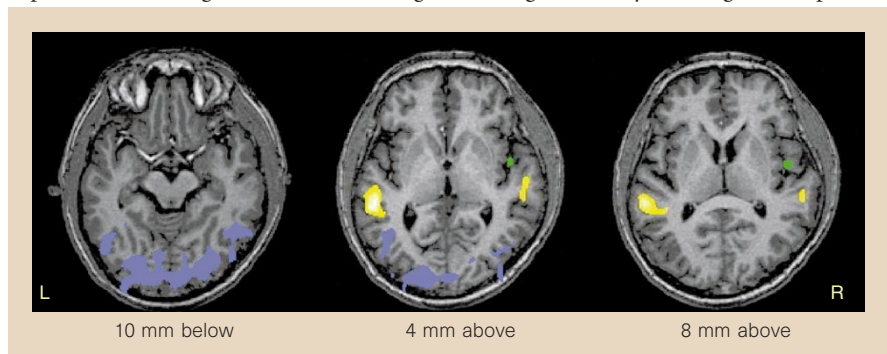


Figure 1 Activation of areas of the brain. The activated areas were superimposed onto the three horizontal sections (10 mm below, and 4 mm and 8 mm above, the intercommissural plane) of the subject’s magnetic resonance image. Yellow areas were activated by sign language in the main experiment; green areas were activated by audition, and blue areas by vision, in the secondary experiment.

1. Osberger, M. J. *et al. Ann. Otol. Rhinol. Laryngol.* **100**, 883–888 (1991).
2. Fitch, J. L., Williams, T. F. & Etienne, J. E. *J. Speech Hear. Disord.* **47**, 373–375 (1982).
3. SPM96 (Wellcome Department of Cognitive Neurology, London, 1996).
4. Naito, Y. *et al. Acta Otolaryngol.* **117**, 490–496 (1997).
5. Neville, H. J. *et al. Brain Lang.* **57**, 285–308 (1997).
6. Soderfeldt, B. *et al. Neurology* **49**, 82–87 (1997).
7. Neville, H. J. *et al. Proc. Natl Acad. Sci. USA* **95**, 922–929 (1998).
8. Sadato, N. *et al. Nature* **380**, 526–528 (1996).
9. Büchel, C., Price, C., Frachowiak, R. S. J. & Friston, K. *Brain* **121**, 409–419 (1998).
10. Hickok, G. *et al. Hum. Brain Mapping* **5**, 437–444 (1997).