# Sympatric speciation by sexual selection

**M. Higashi, G. Takimoto & N. Yamamura**

*Center for Ecological Research, Kyoto University, Kyoto 606-8502, Japan*

**There is increasing evidence[1–6] for the process of sympatric speciation[7,8], in which reproductive isolation of species occurs without physical isolation. Theoretical models[9–14] have focused on disruptive natural selection as the crucial pressure for splitting a species. Here we report the theoretical finding that sympatric speciation may be caused by sexual selection even without disruptive natural selection. Specifically, we show that variation in a male secondary sexual character with two conspicuous extremes and the corresponding variance in female mating preference around no preference may jointly evolve into bimodal distributions with increasing modal divergence of the male and female traits, pulling a population apart into two prezygotically isolated populations. This mode of speciation, driven by two runaway processes[15–17] in different directions, is promoted by an increase in the efficiency of females in discriminating among males or a decrease in the cost of male conspicuousness, indicating that sympatric speciation may occur more readily if barrier-free or predator-free conditions arise. Although even a slight cost of female preference would cancel the runaway process of sexual selection[18], it would not cancel the divergent runaway processes of sympatric speciation.**

Consider a diploid species with polygynous mating (that is, each female chooses one mate and breeds once, but the entire set of males

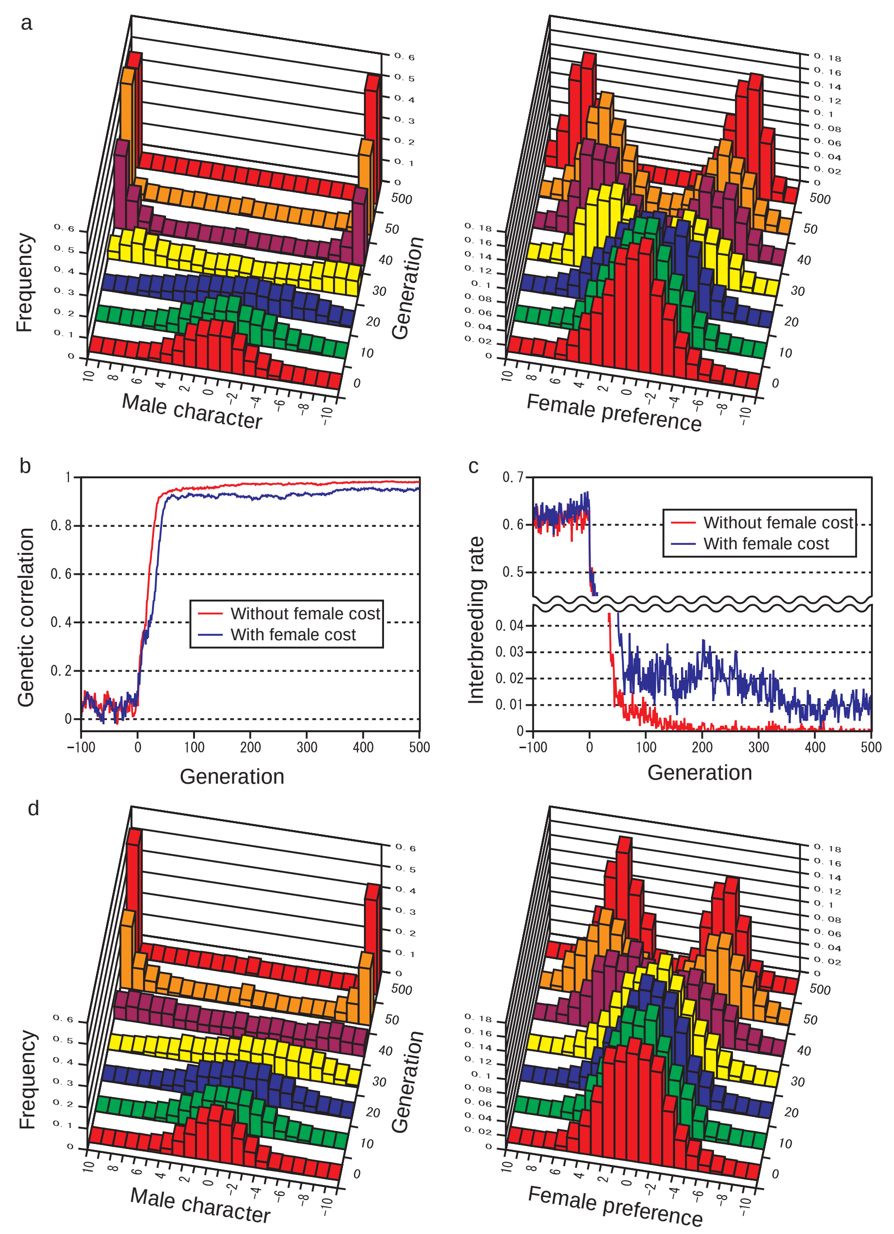

**Figure 1** Examples of sympatric speciation generated by our model. We set $N = 1{,}000$ and $m = n = 5$. The initial distributions of male and female mating traits ($x$ and $y$) were generated as their stationary distributions with $\alpha = 0.02$ and $\omega_M = 10$; the evolutionary dynamics of speciation were generated with $\alpha = 0.2$ and $\omega_M = 10$. **a**, The evolutionary changes in the distributions of male and female mating traits in the case without female cost. **b**, **c**. The genetic correlation between male and female mating trait loci (**b**) and the evolutionary change in the interbreeding rate between the two subpopulations, each of which comprises the males and females of the same sign at the breeding season (**c**), in cases without and with female cost ($\omega_F = 20$). **d**, The evolutionary changes in the distributions of male and female mating traits in a case with female cost ($\omega_F = 20$).

is available to every female). Suppose[19] that males have a secondary sexual character $x$ with two extremes, whose value is additively determined by $m$ loci (each taking three alleles: −1, 0, +1) as $-2m \le x \le 2m$ (where − and + represent alternative directions of the male trait), and that females have the corresponding alternative mating preferences, $y$, additively determined by $n$ loci (each taking three alleles: −1, 0, +1) as $-2n \le y \le 2n$. For example[20], in some fish males range from black to white through different shades of grey; the extremely black and white males, represented by $-2m$ and $+2m$, respectively, in our model, are the most conspicuous and suffer the highest predation. Females have varying degrees of mating preferences for either black or white males; the most choosy females for black and white males are represented in our model by $-2n$ and $+2n$, respectively, and $y = 0$ means no preference.

Assume that for one-time mating a female of mating preference $y$ chooses a male of trait value $x$ out of the entire set of surviving male adults with a probability proportional to $e^{\alpha xy}$ (that is, the probability $e^{\alpha xy}/\Sigma_x p(x)e^{\alpha xy}$, where $p(x)$ denotes the number of males of trait value $x$ at the breeding season, which varies from generation to generation, and $\alpha$ represents the efficiency of male discrimination by females)[16]. She produces a fixed number of offspring, each of which is assigned a sex with a 1 : 1 ratio and receives from each of its parents one genome randomly chosen after free recombination.

We assume a cost to the male of his secondary sexual character $x$, which is reflected in the relative premating survival probability (under predation pressure) of a male of trait value $x$, $\exp[(-x^2/2\omega_M^2)]$, where $\omega_M$ denotes the range of $x$ with high viability[16]. We assume that there is no cost to the female of her mating preferences[18] (although we will later consider such a cost). $N$ male and $N$ female adults are randomly chosen as survivors at the breeding season out of the male and female offspring populations, respectively, weighted by their relative survival probability distributions.

Although we assume here that there are no mutations (mutations from ±1 to 0 and their back mutations), numerical simulations show that the following theoretical results are also true with mutations. Also, the adoption of an alternative mate choice by females according to the 'best of $n$ rule'[17] (that is, a female courts with $n$ males and chooses the one with the greatest $xy$ value) would lead to the same main conclusions, where the male discrimination efficiency of females is reflected in the sample size $n$. (In fact, speciation occurs more readily with the best of $n$ rule as long as $n$ is sufficiently large, because discriminating females avoid males of the opposite sign more strongly when conspicuous males appear.)

Starting with a pair of unimodal distributions around $x = y = 0$ for the male and female mating traits ($x$ and $y$), generated as the stationary distributions for a case in which speciation does not occur, our model simulates the evolutionary process of speciation under certain conditions. In such a case, the initial unimodal distributions are transformed into bimodal ones whose modal distance increases with time (Fig. 1a), where the genetic correlation (linkage disequilibrium) between the loci of male secondary sexual character and those of female mating preference builds up quickly (Fig. 1b). Also, the interbreeding rate between the two subpopulations, each of which comprises the males and females of the same sign at the breeding season (that is, the ratio of the frequency with which females mate with a male of the opposite sign to that of all mating events) rapidly declines almost to zero, indicating that prezygotic isolation is quickly established (Fig. 1c).

The population bifurcation is driven by divergent runaway processes. There is mutual reinforcement of male and female mating traits such that more conspicuous males increase because they are preferred by discriminating females of the same sign (while intermediate males decrease), and then more discriminating females increase by hitchhiking (owing to increasing linkage disequilibrium). This in turn enhances the advantage of more conspicuous males over intermediate males.

With the same initial unimodal distributions around $x = y = 0$, three distinct evolutionary outcomes may occur: no change, trait shift (in a stochastically determined direction) and speciation. Which occurs will depend on the change in the values of parameters involved (Fig. 2). Given the other parameter values, speciation may occur if the efficiency $\alpha$ of male discrimination by females exceeds a threshold. As $\alpha$ increases from 0 to the threshold the frequency of trait shift increases relative to that of no change; after $\alpha$ exceeds the threshold speciation occurs with increasing frequency and then replaces trait shift (Fig. 3a). Speciation may be prevented by too high a cost of male secondary sexual character (that is, too small a value of $\omega_M$), and be promoted by a reduction in male cost (Fig. 3b). (Note that the likelihood of speciation is greater in the case of Fig. 3a than in that of Fig. 3b for the same parameter values $\alpha = 0.2$ and $\omega_M = 10$. This is because the variances of the initial distributions are greater in the former case (in which the initial distributions are generated under $\alpha = 0.02$ and $\omega_M = 10$) than in the latter case (in which the initial distributions are generated under $\alpha = 0.2$ and $\omega_M = 1$), indicating that greater genetic variability in the original population should facilitate speciation.)

These dependencies of the model dynamics on the parameter values suggest the following evolutionary mechanism: a species population with moderate mating traits is sustained as long as the male discrimination efficiency of females is sufficiently low, or the predation pressure on conspicuous males is sufficiently high. If these barriers are weakened (owing to a change in the physical or biological environment) the population may either shift its mating traits, if the change is limited, or undergo speciation. Numerical simulations show that if a trait shift occurs following a change in either of these parameters, a further change in that parameter (in the same direction) will not lead to speciation (although it is possible to return to the original state by reversing the parameter change and then produce speciation by a large change in either of the parameters, noting that the evolutionary processes of trait shift and speciation are reversible, as indicated in Fig. 2). Thus, speciation may occur with rapid, not gradual, changes in these key parameters.

A larger population size, $N$ (more strictly, more males or females participating in reproduction), would facilitate speciation (Fig. 3c) because it would reduce the random drift in the trait distributions. Furthermore, numerical simulations (performed with scaling for comparison) confirm that a change in the remaining parameters $m$ and $n$, the numbers of the loci determining the male and female mating traits, respectively, would not affect the evolutionary outcome.

It might be thought that the mechanism for sympatric speciation

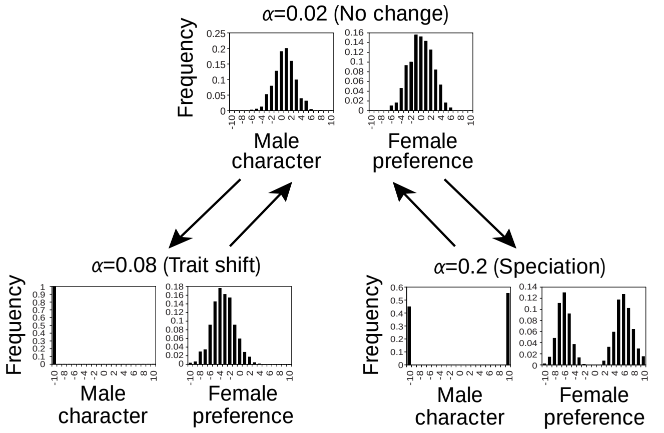

**Figure 2** Three possible evolutionary outcomes: no change, trait shift and speciation. The evolutionary transitions (indicated by arrows) may occur with changes in the parameters $\alpha$ and $\omega_M$. Here we changed $\alpha$ as indicated, while fixing the other parameters as $\omega_M = 10$, $N = 1{,}000$ and $m = n = 5$.

driven by divergent runaway processes hinges on the symmetry of the dipolar female mating preference, which is the ultimate force for pulling the population apart in two directions, or on that of male cost, which in contrast suppresses the growth of divergent runaway processes. Speciation may, however, occur even if the female mating preferences or male costs on the − and + sides of the trait ranges are not exactly balanced: that is, $\alpha^- \neq \alpha^+$ or $\omega_M^- \neq \omega_M^+$, where $\alpha^-$ and $\alpha^+$ ($\omega_M^-$ and $\omega_M^+$) are, respectively, the $\alpha$ ($\omega_M$) values for the negative and positive $y$ ($x$) values (Fig. 3d, e). This indicates that this mechanism for sympatric speciation does not depend on this subtle balance, and that, even if the forces in the opposite directions are off balance, speciation may be achieved as long as prezygotic isolation can be established before either of the two subpopulations (on the negative and positive sides of the mating trait ranges) becomes extinct.

It is known[18] that the incorporation of even a slight cost of female mating preference into a model for sexual selection by a runaway process causes the system to return to its original state, cancelling the runaway process, and that additional factors have to be considered to prevent this cancellation[21,22]. To examine the effect of this cost to the female, we incorporated it into our model for sympatric speciation in a similar way to male cost; that is, in terms of the relative survival probability of a female of value $y$, $\exp[-y^2/(2\omega_F^2)]$, where $\omega_F$ indicates the range of $y$ with high viability. As long as it is sufficiently small (that is, $\omega_F$ is sufficiently large), a female cost would not cancel the divergent runaway processes, but only reduce the modal divergence of the male and female mating traits in the case of sympatric speciation by sexual selection (Fig. 1c, d). The reason for this difference in the effect of female cost between the case of a single runaway process and that of divergent runaway processes is inferred to be as follows: in the former case females can without any loss, avoid the costly mating preference when the male trait of the entire population evolves to its steady state (that is, the balance between sexual selection benefit from, and natural selection cost of the male mating trait). In the latter case they have to pay a greater cost for disadvantageous interbreeding (because of the presence of another peak on the opposite-signed side of the male mating trait range) as they reduce their mating preference intensity.

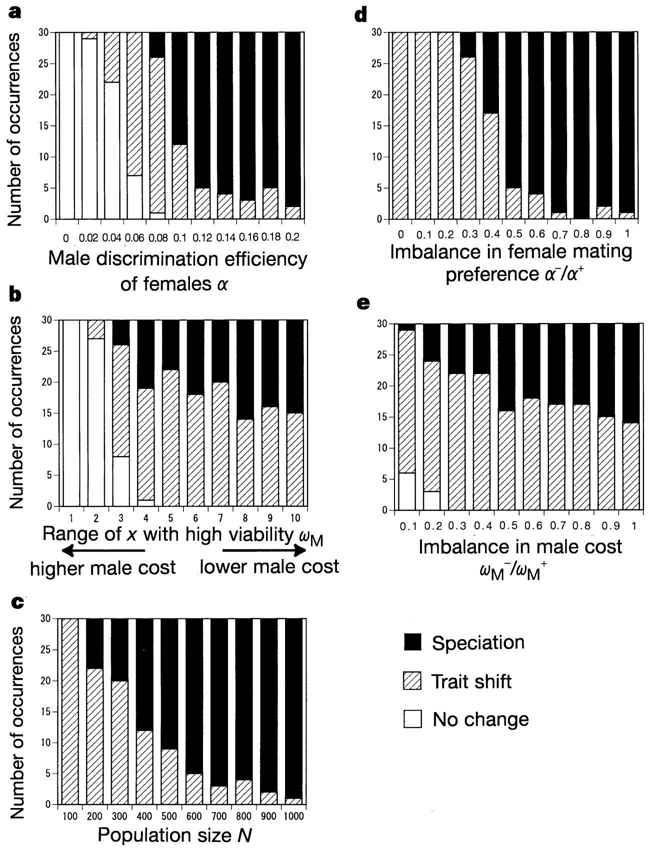

**Figure 3** The likelihood (represented here by the number of occurrences out of 30 simulations runs) of each of the three evolutionary outcomes, speciation (defined here as a case in which the interbreeding rate is less than 0.05), trait shift and no change, when either $\alpha$ or $\omega_M$ is changed from a value for generating initial stationary unimodal distributions to another value. $m = n = 5$. **a**, The results when $\alpha$ is changed from 0.02 (for generating the initial distributions) to the values indicated while fixing $\omega_M = 10$, $N = 1{,}000$. **b**, The results when $\omega_N$ is changed from 1 (for generating the initial distributions) to the values indicated while fixing $\alpha = 0.2$, $N = 1{,}000$. **c**, The results when $\alpha$ is changed from 0.02 (for generating the initial distributions) to 0.2, while fixing $\omega_M = 10$, under the different population sizes indicated. **d**, The results when $\alpha^+$ and $\alpha$ $^-$ are changed from 0.02 (for generating the initial distributions) to 0.2 and the values indicated on the horizontal axis multiplied by 0.2, respectively, while fixing $\omega_M = 10$, $N = 1{,}000$. $\alpha^-$ and $\alpha^+$, respectively, denote the $\alpha$ value for the negative $y$ values and that for the positive $y$ values. **e**, The results when $\omega_M^+$ and $\omega_M^-$ are changed from 1 (for generating the initial distributions) to 10 and the values indicated on the horizontal axis multiplied by 10, respectively, while fixing $\alpha = 0.2$, $N = 1{,}000$, where $\omega_M^-$ and $\omega_M^+$, respectively, denote the $\omega_M$ value for the negative $y$ values and that for the positive $y$ values.

We have derived from a theoretical model a novel mechanism for sympatric speciation driven by divergent runaway processes. Our main conclusions also follow from a simplified deterministic model (G.T., M.H. and N.Y., in preparation), suggesting their robustness.

Wu[23] presented a sexual selection model which assumes that females have an absolute mating preference (that is, a female most prefers males with a male mating trait value uniquely specified by her preference trait value) and showed that sympatric speciation was possible. However, prezygotic isolation could not be sustained in the long term in a small population (in contrast to our model, in which relative mating preference is assumed), indicating that relative mating preference is required for lasting sympatric speciation.

Another model[20], which is similar to, but different in several key features from, our model, showed that sympatric speciation may occur if all females initially possess an extreme mating preference and the corresponding male secondary sexual character has a distribution biased toward the extreme preferred by the females. Assuming such a specific initial condition, this model leads to the conclusion that speciation requires a cost of male secondary sexual character; the authors considered this male cost to be the driving force for speciation (although it is not clear whether their conclusion, that is, their interpretation of the model results, is correct because they did not examine the effect of male cost by comparing cases with different male costs, including the case with no cost). Their conclusion is completely opposite to the prediction derived from our model that male cost is not necessary for, but its reduction promotes, speciation (Fig. 3b). This prediction leads to a hypothesis that sympatric speciation by sexual selection tends to occur as predation pressure is reduced (with other conditions unchanged) by, for example, a population entering into a new enemy-free habitat such as an island or a lake.

Another prediction derived from our model, that sympatric speciation is promoted by the efficiency of male discrimination by females (Fig. 3a), explains high species diversity in a habitat with good visibility (for example, cichlid fish diversity in the African great lakes[2,3,6]), and implies that high species diversity depends critically on the integrity of the environment[3]. ☐

Received 2 September; accepted 14 September 1999.

---

1. Turner, G. F. Speciation mechanism in Lake Malawi cichlids: A critical review. *Arch. Hydrobiol.* **44,** 139–160 (1994).
2. Deutsch, J. C. Colour diversification in Malawi cichlids: evidence for adaptation, reinforcement or sexual selection? *Biol. J. Linn. Soc.* **62,** 1–14 (1997).
3. Seehausen, O., Alphen, J. J. M. & Witte, F. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277,** 1808–1811 (1997).
4. Seehausen, O. & Alphen, J. J. M. The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behav. Ecol. Sociobiol.* **42,** 1–8 (1998).

5. Ritchie, M. G. & Phillips, S. D. F. in *Endless Forms: Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 291–308 (Oxford Univ. Press, New York, 1998).
6. Albertson, R. C., Markert, J. A., Danley, P. D. & Kocher, T. D. Phylogeny of a rapidly evolving clade: The cichlid fishes of Lake Malawi, East Africa. *Proc. Natl Acad. Sci. USA* **96,** 5107–5110 (1999).
7. Tauber, C. A. & Tauber, M. J. in *Speciation and its Consequences* (eds Otte, D. & Endler, J. A.) 307–344 (Sinauer, Sunderland, 1989).
8. Bush, G. L. Sympatric speciation in animals: new wine in old bottles. *Trends Ecol. Evol.* **9,** 285–288 (1994).
9. Maynard Smith, J. Sympatric speciation. *Am. Nat.* **100,** 637–650 (1966).
10. Tauber, G. A. & Tauber, M. J. A genetic model for sympatric speciation through habitat diversification and seasonal isolation. *Nature* **268,** 702–705 (1977).
11. Doebeli, M. A quantitative genetic competition model for sympatric speciation. *J. Evol. Biol.* **9,** 893–909 (1996).
12. Kawecki, T. J. Sympatric speciation via habitat specialization driven by deleterious mutations. *Evolution* **51,** 1751–1763 (1997).
13. Kodrashov, A. S. & Kondrashov, F. A. Interactions among quantitative traits in the course of sympatric speciation. *Nature* **400,** 351–354 (1999).
14. Dieckmann, U. & Doebeli, M. On the origin of species by sympatric speciation. *Nature* **400,** 354–357 (1999).
15. Fisher, R. A. *The Genetical Theory of Natural Selection* (Clarendon, Oxford, 1930).
16. Lande, R. Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78,** 3721–3725 (1981).
17. Seger, J. Unifying genetic models for the evolution of female choice. *Evolution* **39,** 1185–1193 (1985).
18. Pomiankowski, A. The costs of choice in sexual selection. *J. Theor. Biol.* **128,** 195–218 (1987).
19. Liou, L. W. & Price, T. D. Speciation by reinforcement of premating isolation. *Evolution* **48,** 1451–1459 (1994).
20. Turner, G. F. & Burrows, M. T. A model of sympatric speciation by sexual selection. *Proc. R. Soc. Lond. B* **260,** 287–292 (1995).
21. Pomiankowski, A., Iwasa, Y. & Nee, S. The evolution of costly mate preferences I. Fisher and biased mutation. *Evolution* **45,** 1422–1430 (1991).
22. Iwasa, Y., Pomiankowski, A. & Nee, S. The evolution of costly mate preferences II. The 'handicap' principle. *Evolution* **45,** 1431–1442 (1991).
23. Wu, G.-I. A stochastic simulation study on speciation by sexual selection. *Evolution* **39,** 66–82 (1985).

**Acknowledgements**

M.H. thanks J. Lawton and the NERC Centre for Population Biology for their hospitality. This work was supported by a MESSC grant to M.H.

Correspondence and requests for materials should be addressed to M.H. (e-mail: higashi@ecology.kyoto-u.ac.jp).

# Direct measurement of intra-cochlear pressure waves

**Elizabeth S. Olson**

*Physics Department, Princeton University, Princeton, New Jersey 08544, USA*

**The cochlear travelling wave is fundamental to the ability of the mammalian auditory system to resolve frequency. The seashell-shaped outer bone of the cochlea (the auditory inner ear) contains a spiral of cochlear fluid and the sensory tissue known as the cochlear partition. Sound travels down the ear canal to the eardrum, causing its flexible tympanic membrane to vibrate. This vibration is transmitted to the cochlea via the ossicles. Motion of the stapes (the stirrup ossicle) sets the cochlear fluid in motion, which in turn sets the cochlear partition near the stapes in motion. The motion of the cochlear partition ripples down the cochlear spiral as a travelling wave, stimulating the cochlea's sensory hair cells. The wave peaks near the base (the stapes end) of the cochlea for high frequency tones and near the apex for low frequencies[1]. The fundamental elements of the cochlear travelling wave are fluid pressure and motion and partition forces and motion. However, the wave's direct experimental study has to date relied almost solely on measurements of the partition motion. Here I report finely spaced measurements of intracochlear pressure close to the partition, which reveal the fluid component of the cochlear wave. The penetration depth of the wave is very limited, ~15 μm. Over a range of frequencies at least an octave wide, the depth is independent of frequency.**

I recently described pressure measurements made in the extreme base of the cochlea[2]; here a turn-one location, 14% further towards the apex along the cochlear spiral, is emphasized. Strong nonlinearity was detected at the turn-one location, whereas in the extreme base the responses were nearly linear, owing to the extreme fragility of that region. Therefore, the basal results describe the passive cochlea. Nonlinearity in the cochlea's mechanical response to sound is the key to its dynamic range and ability to finely separate frequencies. Outer hair cells appear to be essential to this mechanical enhancement[3,4], whereas the inner hair cells communicate information about the partition's motion to the auditory neurons[5].

Here I demonstrate the frequency and position dependence of the nonlinear fluid pressure. Pressure differences are used to find fluid velocity, and the results are interpreted with respect to the cochlear travelling wave. In particular, the wave's penetration depth is found to be ~15 μm. The penetration depth indicates how much fluid the wave contains, and its size and frequency dependence constrain cochlear models. In models, the fluid component of the cochlea is often simplified to one dimension—along the partition. In two-dimensional models the height of the fluid is included, and in three-

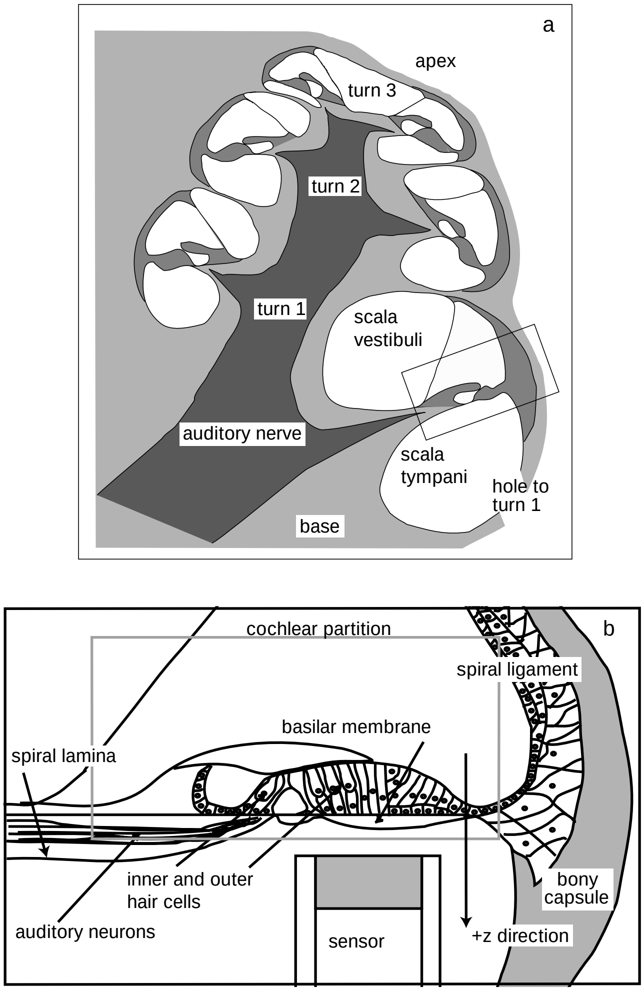

**Figure 1** The cochlea. **a**, Cross-section of the gerbil cochlea; the boxed section is enlarged in **b**. The cochlear partition and the fluid compartments scala tympani and scala vestibuli spiral around the auditory nerve. The mongolian gerbil cochlea is ~2.6 mm in diameter, with a cochlear partition length of ~13 mm (ref. 16). In the extreme base of the cochlea the scala vestibuli is terminated by the stapes, the scala tympani by the round window membrane (not shown). The general location of a hand-drilled hole used to access turn one scala tympani is indicated in **a**. The scala tympani pressure sensor was positioned to approach the basilar membrane approximately perpendicularly. The sensor's outer diameter is 170 μm. (The drawings derive from a 2-mm plastic-embedded section prepared by M. Feldman.)