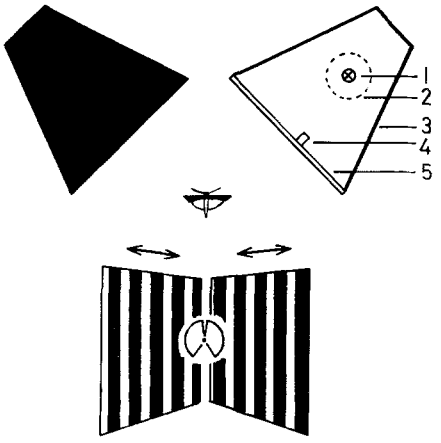


Fig. 1. Experimental setup as seen from above (top) and from the front (bottom). A slit cylinder (*2*) inside a black wooden box (*3*) revolves round a tungsten light source (*1*) and generates a pattern of shadow stripes on a screen (*5*). The pattern movement is recorded by a photocell (*4*). Two of these screens are directed each toward one compound eye of the moth so that angular widths of the stripes on the screens are constant as seen from the positions of the eyes. By adjusting the directions of rotation of the slit cylinders (in opposite directions or in the same direction) the optical equivalents of straight flight or turning flight are simulated. The moths are fixed to a torsion wire. A light beam is reflected from a small mirror on the lower end of the wire onto a screen. The angle of deflection is used as a relative measure of the turning tendency of the animal

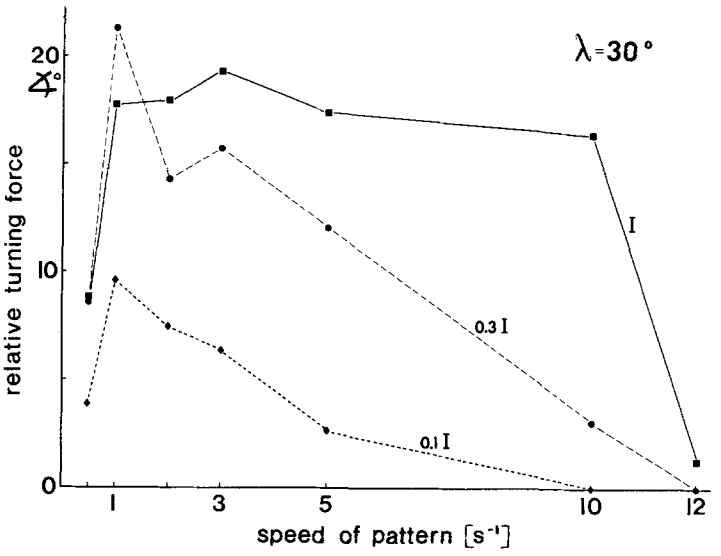


Fig. 2. Turning force of moths flying on a torsion wire (setup s. Fig. 1), measured at three light intensities (*I*). λ: angular width of one black and one white stripe as seen from the position of the moth. The moths are active only within a narrow range of light intensities

antennae, heads, wings, or body. It is by far the longer phase and lasts for nearly the total flight time.

(2) A short "reactive" phase directly before the end of the flight, when they react in the classical way, i.e., by trying to follow the pattern movement, whether they are able to turn or not. This phase lasts usually for some seconds only, and in no case longer than 2 min. Flight phase (1) was not observed in moths which had been reared solitarily and may therefore be identified with the migratory flight phase *sensu strictu* (cf. [6]). During migratory flights, moths may often be tossed about in turbulent air. As there is no danger of collision, the moths should simply try to remain airborne. When descending to land, however, they have to react in the usual way in order to stabilize their position relative to their surroundings.

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# Length of Hair Cells as a Measure of Frequency Representation in the Mammalian Inner Ear?

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In the cochlea, the coiled auditory segment of the inner ear of mammals, two types of receptor cells exist: the bottle-shaped inner hair cells (IHC) and the cylindrical outer hair cells (OHC). In general, the IHC are arranged in one row and the OHC in three rows (Fig. 1). Differences concerning the ultrastructure, the innervation, and the cellular movements (found only in OHC) lead to the assumption of dissimilar functions of the two types of hair cells. The IHC are thought to have sensory and the OHC to have motor functions (for review [1]).

In a former study one of the authors worked out figures of the cellular organization of the cochlea which allow direct morphological comparison between a number of mammalian species [2]. These figures revealed that the IHC are relatively constant in size while the length of the OHC varies. The knowledge of the frequency dispersion along the cochlear duct (base = high fre-

 

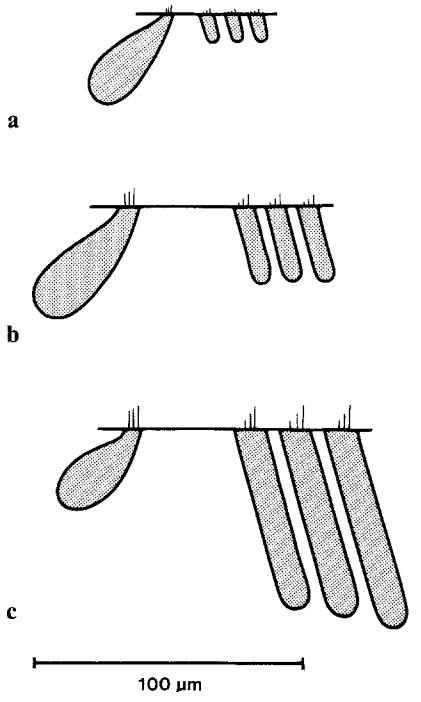


Fig. 1. The inner hair cells (left) and three outer hair cells (right) from the basal cochlear region in the bat *Hipposideros bicolor* (a), the middle region in the rat *Rattus norvegicus* (b), and the apical region in the guinea pig *Cavia porcellus* (c). The represented frequencies are 150 kHz in the bat, 15 kHz in the rat, and 1.8 kHz in the guinea pig

quency, apex = low frequency) enables a preliminary correlation of structure and function: OHC are short at that high-frequency region and long at the low-frequency region of the cochlea while the length of the IHC seems to be almost constant. Recent quantitative investigations [3] confirmed these results, but some important questions are still open: Can the putative correlation of the OHC length and the represented frequency be verified? Is there really no correlation at all between the length of IHC and the represented frequency? Can these correlations (if they exist) be generalized for all mammals? If a general relationship exists, the frequency place in the cochlea could be determined by the length of the hair cells. To clarify these questions one has to determine precisely the following data in different mammalian species: the length of hair cells, the position along the cochlear duct where the length of hair cells is measured, and the frequency represented at this cochlear position.

For the selection of the species phylogenetic aspects as well as adaptive ones were taken into consideration. The investigated representatives of Marsupialia and Placentalia are: gray short-tailed opossum, *Monodelphis domestica* (Didelphidae, Marsupialia); rat, *Rattus norvegicus* (Muridae, Rodentia); gerbil, *Pachyuromys duprasi* (Gerbillidae, Rodentia); mole rat, *Cryptomys hottentotus* (Bathyergidae, Rodentia); guinea pig, *Cavia porcellus* (Caviidae, Rodentia); bat, *Hipposideros bicolor* (Hipposideridae, Chiroptera). Frequency place maps of the rat, gerbil, of *Monodelphis* and *Cryptomys* were established in our laboratory [4–7]. For *Hipposideros* we assume a frequency representation along the cochlear duct corresponding to that in *Rhinolophus rouxi* [8], a closely related bat within the same superfamily, Rhinolophoidae (for details [9]). For the guinea pig we applied the frequency map established in [10]. The species investigated cover the complete hearing range of mammals. The rat and *Monodelphis* are species with an unspecialized auditory system and a hearing range common for mammals. The bat *Hipposideros bicolor* ist the mammalian species with the highest upper limit of hearing (up to 200 kHz, [11]) in which the cochlea has been studied. The gerbil, the guinea pig, and *Cryptomys* are adapted to low frequencies. *Cryptomys hottentotus* is known as the mammalian species with the lowest best frequency region so far studied (0.5 – 1 kHz, [12]).

In total, cochleae of four rats, two gerbils, four gray short-tailed opossums, three bats, one mole rat, and three guinea pigs were investigated. Additional data of rats and opossums originate from [13]. After dissection, the cochleae were fixed by immersion in 2.5% glutaraldehyde in phosphate buffer (pH 7.4, 305 mOsm). The specimens were postfixed in 2% $OsO_4$ (phosphate-buffered), dehydrated, and embedded in epoxy resin (Epon). The cochleae were dissected following the block surface technique used in our laboratory [14, 15]. This method allows one to determine the baso-apical position along the cochlear duct (error of measurement < 0.1 mm). Radial semithin sections (1 – 2 µm) were taken at approximately ten equidistant positions along the cochlear duct. In *Cryptomys* only two positions along the cochlear duct were investigated. Semithin sectioning is necessary for the exact delimitation of the cell borders, especially of the IHC. One to 2 µm semithin sections require a reconstruction of each hair cell (diameter 5 – 10 µm) out of several sections. At each position the length of approximately ten hair cells was measured. At all examined positions the length of all three rows of OHC and IHC was measured. For simplification only the data of the second

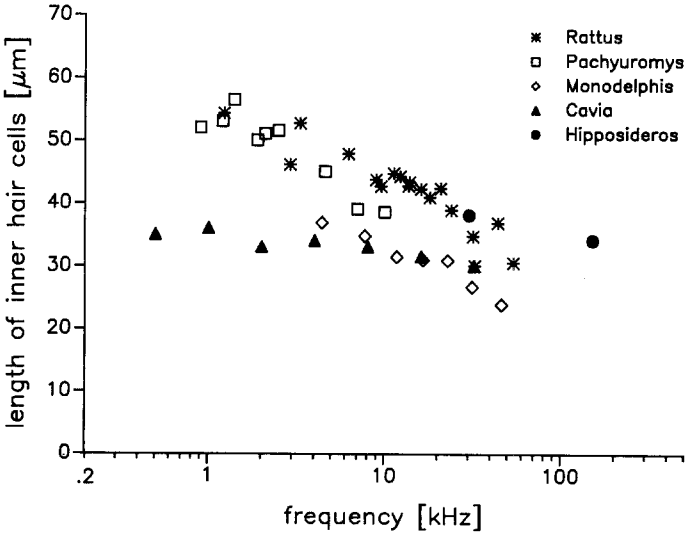


Fig. 2. Length of inner hair cells as a function of frequency in the gray short-tailed opossum, *Monodelphis domestica*, the rat, *Rattus norvegicus*, the gerbil, *Pachyuromys duprasi*, the guinea pig, *Cavia porcellus*, and the bat, *Hipposideros bicolor*

row of OHC were taken into consideration.

In the basal part of the cochlea in all species the IHC are longer than the OHC (Fig. 1, above). In the middle part this difference is less pronounced (Fig. 1, middle). In the apical part in most species the IHC and OHC are about the same length with one exception: in the guinea pig the OHC are clearly longer than the IHC (Fig. 1, below).

The shortest IHC (23 μm) were found in the basal (high-frequency) region in *Monodelphis* where 45 kHz is represented (Fig. 2). The longest IHC (56 μm) were found in the apical (low-frequency) region of the gerbil where 1.5 kHz is represented. The length of IHC increases from the basal region to the apical region 1.1 times in the bat and in the guinea pig, 1.4 times in the gerbil, 1.6 times in the opossum, and 1.8 times in the rat.

The shortest OHC (11 μm) were found in the basal (high-frequency) region in *Hipposideros* where 150 kHz is represented (Fig. 3). The longest OHC (65 μm) were found in the apical (low-frequency) region of the guinea pig where 0.5 kHz is represented. The length of OHC increases from the basal region to the apical region 1.1 times in the bat, 1.5 times in *Cryptomys*, 1.6 times in the gerbil, 2.1 times in the opossum, 2.9 times in the guinea pig, and 3.9 times in the rat. All measurements form a curve which can be described by the function $Y = 74.1644 \cdot X^{-0.2015} - 19.7950$ ($r = 0.97$). In Table 1 we calculated the length increase of the OHC per octave at different frequency regions. The length increase of the OHC is frequency-dependent and not linear. The length change per octave decreases from high to low frequencies.

Table 1. Length inrease of OHC

| Frequency | OHC length | Difference of OHC length | |
|---|---|---|---|
| | | [μm] | [%] |
| 0.5 | 65.5 | | |
| | | 11.1 | 17.0 |
| 1 | 54.4 | | |
| | | 9.7 | 17.8 |
| 2 | 44.7 | | |
| | | 8.4 | 18.8 |
| 4 | 36.3 | | |
| | | 7.3 | 20.1 |
| 8 | 29.0 | | |
| | | 6.4 | 21.9 |
| 16 | 22.6 | | |
| | | 5.5 | 24.4 |
| 32 | 17.1 | | |
| | | 4.8 | 28.1 |
| 64 | 12.3 | | |
| | | 4.2 | 34.0 |
| 128 | 8.1 | | |

The conclusions of the above results are: The length of both IHC and OHC shows a graded decrease from low- to high-frequency cochlear regions. With the exception of the bat the length gradient of OHC is steeper than that of IHC. The length of the IHC at a given frequency position is species-specific; in IHC one distinct frequency is represented in different species by different lengths. The length of the OHC is species-independent; in OHC one distinct frequency is represented by the same length of OHC in all species. This indicates a general relationship between frequency and OHC length.

Concerning the OHC, one of the most striking results of the last years was the discovery that the OHC show contractions and elongations along their length axis (= motility, [16, 17]). This motility can be induced by electrical and chemical stimulation [16, 17]. At least two types of motility can be distinguished: slow and fast motility. Slow motility is characterized by "slow" contractions of the hair cells over 30–60 s [16]. Fast motility is characterized by "fast" contractions of the OHC. In dependence on the frequency of the given stimulus (so far shown for frequencies up to 30 kHz, [18]) the OHC respond with lengthwise oscillations of their cell bodies. Brundin et al. [19] demonstrated on isolated OHC of the guinea pig that the motile response to acoustic stimuli is sharply tuned. The frequency to which the motile response is tuned correlates with the length of the isolated OHC. Long OHC are tuned to lower frequencies and short OHC are tuned to higher frequencies. Therefore the investigation of Brundin et al. [19] supports one of the major results of or study.

Finally, is the length of the hair cells a measure of frequency representation in the mammalian cochlea? The length of the OHC, but not that one of the IHC, is indeed a measure of frequency representation. The measurements of OHC length fit into a general relationship among mammals. That means that the complicated method of physiological frequency mappings could be substituted by morphological measurements of OHC length.

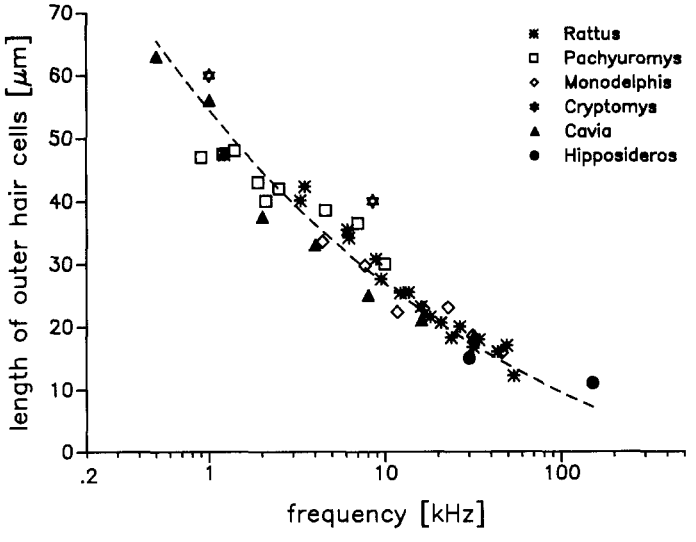


Fig. 3. Length of outer hair cells as a function of frequency in the gray short-tailed opossum, *Monodelphis domestica*, the rat, *Rattus norvegicus*, the gerbil, *Pachyuromys duprasi*, the mole rat, *Cryptomys hottentotus*, the guinea pig, *Cavia porcellus*, and the bat, *Hipposideros bicolor*. The *dashed line* shows the function calculated by nonlinear regression analysis

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# Naturwissenschaften Buchbesprechungen

**Wissenschaft ohne Grenzen?** Geistes- und Naturwissenschaften stellen sich der Verantwortungsfrage. Hrsg. von R. Schmitt, H. Altner und D. Burkhardt. Regensburg: Buchverlag der Mittelbayerischen Zeitung 1991. 170 S. DM 20,–.

Die Vorträge dieser Ringvorlesung entstanden auf Anregung eines Arbeitskreises für studentische Angelegenheiten, an dem auch Dozenten und wissenschaftliche Mitarbeiter beteiligt waren. Alle Vorträge behandeln die drängenden Fragen der Verantwortung, der methodologischen Grundlagen und der ethischen Grenzen der Wissenschaften. Die Beiträge im einzelnen: E. L. Wienacker (Biochemie, Genetik): „Die Neue Biologie und die Öffentlichkeit – eine Perspektive". Hier werden die „neue" Biologie, d.h. Molekularbiologie und moderne Genetik, ihre Möglichkeiten und Grenzen, die Utopien in der Öffentlichkeit sehr anschaulich dargestellt. Die Frage der Mitwirkung der Öffentlichkeit bei der Entscheidung über gentechnische Versuche wird eingehend diskutiert. – R. Schwarz (Evangelische Theologie): „Braucht wissenschaftliche Forschung einen ethischen Rahmen?" behandelt die Geschichte der *curiositas*, die „zum Menschsein wesentlich dazu gehört, heute aber oft als *superbia* zur Diskussion steht". Die Mathematisierung der modernen Wissenschaften klammert menschliche Qualitäten aus. Die Konsequenzen aus seinen Darlegungen faßt der Verf. in 4 Leitsätzen zusammen. Das Fazit: Ein ethischer Rahmen für die „Neugier" ist Notwendigkeit. – B. Müller-Hill (Genetik): „Humangenetik im Dritten Reich – was ist daraus zu lernen?" Der Vortrag will die Frage beantworten: Worin bestand die herausragende Schuld *der* Humangenetiker an den Greueln und Untaten im Dritten Reich? Nun ist nach Ansicht des Autors der Referent 1. ein „Täter", weil er als Großvater das Dritte Reich erlebt und überlebt hat; 2. haben alle „Täter" die Aufarbeitung der Nazizeit blockiert, zumindest bis in die 60er Jahre, wo dann die Enkel (der Autor ist Jahrgang 1933) endlich unbelastet die Bewältigung der Vergangenheit in Angriff nehmen konnten. Müller-Hill versucht also, vorsorglich den Referenten als Kritiker auszuschalten. So sei zunächst der Autor selbst zitiert: „Wir selber sind aus dem Dritten Reich hervorgegangen." „Wir sind ein Land von Tätern." „Die Regensburger Universität ist zu jung, um direkt aus dem Dritten Reich zu kommen." Alsdann sei ein einwandfreier Nicht-Täter zu Müller-Hill zitiert (R. L. Berg, University of Missouri – St. Louis, USA. In: Q. Rev. Biol. *65,* 472, 1990): „Müller-Hill's charge that everyone knew that Jews and mentally ill persons were killed, simply does not correspond with the facts." Dies nur eine von anderen Unwahrheiten in den Schriften von Müller-Hill, angeführt in dem Artikel von Berg. – Der Beitrag verallgemeinert unzulässig, ist unausgewogen und läßt das notwendige Ethos gegenüber der Wissenschaft vermissen. Sicher ist, daß *einige* Humangenetiker der Ideologie Hitlers zugestimmt haben. Aber historische Wahrheit ist auch, daß öffentlicher Widerspruch schwere Folgen hatte [z.B. R. Hesse (Berlin) wurde vorzeitig emeritiert, weil er sich weigerte, Güntersche Rassenlehre im Staatsexamen zu prüfen; Walther Arndt (Berlin) wurde wegen einer *privaten* Äußerung hingerichtet]. Mit leichtfertigen Einseitigkeiten à la Müller-Hill können wir die Vergangenheit nicht bewältigen. – Franz Böckle (Katholische Moraltheologie): „Biotechnik und Menschenwürde. Zur Verantwortung der Naturwissenschaft". Wendet sich zunächst gegen die Ansicht, es gehe nicht um die Maximierung des Guten, sondern um die Minimierung des Übels (Jonas 1986). Wir sollten vielmehr im Umgang mit neuen Techniken step-by-step vorgehen und dabei verantwortungsvoll die Risiken abwägen. Im Umgang mit der uns umgebenden Natur vermittelt der religiöse Glaube keine unmittelbaren Regeln für unser Handeln. Die Wahrnehmung konkreter Verantwortung ist Sache praktischer Vernunft. Das wird an den Problemen der Analyse des menschlichen Genoms, der pränatalen Diagnose, der Gentherapie und des Gentransfers sehr ausgewogen dargestellt. – R. Hettlage (Soziologie): „Kritischer Rationalismus als Wissenschaftsethik?" Der Vortrag behandelt ausführlich den kritischen Rationalismus (Popper), ergänzt und erweitert ihn dann durch die wissenschaftstheoretischen Grundlagen, die aus den Gedankengängen von Thomas Kuhn folgen. Es gibt auch eine Ethik des Verhaltens von Wissenschaftlern. – Christian Vogel (Anthropologie): „Ethische Probleme im Bereich der Evolutionsbiologie, der Verhaltensforschung und der Soziobiologie". Auch das ein ausgezeichneter Beitrag. Er enthält eine klare Kritik des Sozialdarwinismus, lehnt für die Verhaltensforschung den Begriff „moral-analoges Verhalten" (Konrad Lorenz) ab und