

Age effects and size effects in the ears of gekkonomorph lizards: inner ear

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Abstract

Audiograms have indicated greater auditory sensitivity in larger than in smaller geckos; part of this difference, interspecifically and intraspecifically, is explained by middle-ear proportions. To investigate the contribution of the inner ear to the variation in sensitivity, we examined it in museum specimens representing 11 species and three subfamilies. We measured papilla basilaris length, and, when intact, the saccular otoconial mass. Papilla length approximated 1% of rostrum-anus length in large geckos but 2% in small geckos; in some species some inter-aural difference was indicated. Over the lumped material, relative papilla length varied as a function of body length, with highly significant correlation. Similar relations prevailed within each subfamily. However, intraspecifically the correlation of papilla basilaris length with animal size was usually nonsignificant. Hair cell populations assessed from SEM photographs were larger in the larger species but intraspecifically did not relate to an individual's size. Hence interspecifically, the dependence of auditory sensitivity on animal size seems supported by inner-ear differences but intraspecifically this relation derives only from the middle ear. Otoconial mass, as measured by its volume, was correlated with animal length both interspecifically and intraspecifically.

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1. Introduction

Recent reviews of the medically crucial question whether new auditory hair cells can arise in the post-natal

life of man and of other vertebrates have emphasized the dichotomy between fish and amphibians on the one hand, in which auditory hair cells proliferate throughout post-natal ontogeny, and birds and mammals on the other hand, in which this does not normally happen (Popper and Hoxter, 1984; Katayama and Corwin, 1989; Corwin and Warchol, 1991; Corwin, 1992; Corwin and Oberholzer, 1997). The latter generalization notwithstanding, the cochlear duct grows in length during the early post-natal development of the chick, *Gallus domesticus*, and duckling, *Anas platyrhynchos* (Schwartzkopff, 1957; Ryals et al., 1984). Auditory hair cell production, despite its absence in normal post-natal avian development, does occur in the post-natal and even adult avian cochlea as damage repair (Corwin and Cotanche, 1988; Cotanche and Corwin, 1991; Saunders et al., 1992; Roberson

Abbreviations: RA, Rostrum-anus length (Werner, 1971); PER-CRA, Percents of rostrum-anus length (Werner, 1971); *Ema*, *Eublepharis macularius* adults; *Emj*, *Eublepharis macularius* juveniles; *Cm*, *Coleonyx mitratus*; *Oma*, *Oedura marmorata* adults; *Omj*, *Oedura marmorata* juveniles; *Or*, *Oedura reticulata*; *Um*, *Underwoodisaurus milii*; *Chm*, *Christinus marmoratus*; *Gg*, *Gekko gekko*; *Gpa*, *Gehyra punctata* adults; *Gpj*, *Gehyra punctata* juveniles; *Gv*, *Gehyra variegata*; *Pga*, *Ptyodactylus guttatus* adults; *Tn*, *Tropicolotes nattereri*

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et al., 2002). In adult mammals, so far, only utricular hair cells have been reported to regenerate (Forge et al., 1993). Experimentally, new cochlear hair cells were induced in adult *Cavia* by *Math1* gene transfer (Kavamoto et al., 2003).

In contrast with the knowledge of auditory development in both lower and higher vertebrates, and of post-traumatic hair cell regeneration in the latter, there is little comparable information on the situation in the intermediate vertebrate group, reptiles. Only Miller (1966) examined an age series of one lizard species, *Leiolopisma assatum* (Scincidae), and concluded that neither papilla length nor hair cell number increased with body size. Later, Miller (1985) quantitatively described the cochlear ducts of many lizard species and concluded that intraspecifically, papilla length and hair cell number never varied with body size (since body size increases with age, this meant that papilla length and hair cell number were independent of age). However, he provided no quantitative evidence. In view of all that is now known of other vertebrates (as above), and the recent discovery of hair cell regeneration in the crista ampullaris of a lizard (Avallone et al., 2003), we believe that it would be prudent to reexamine Miller's conclusions.

Therefore, we report here on the variation, among species and within species, of several parameters of the saurian inner ear. We do so within a broader project striving to distinguish the effects of age from those of size in the ears of reptiles, wishing to explain why the electrophysiological audiograms of small gecko lizards indicate lesser sensitivity than those of large geckos (Werner et al., 1998; Johnstone and Werner, 2001; Werner and Igić, 2002). Geckos, lizards of the family-cluster Gekkonomorpha, are used as examples, because interest in their audition is enhanced by their frequent use of vocal communication (Frankenberg and Werner, 1992; Manley, 2000; Werner et al., 2001c). Evans (1936) had already expounded the relation of the vocalicity of geckos to the structure of their inner ear, in which the "cochlea" is large relative to the lagena.

Our overall experimental design has been to compare the ear's structure and function among samples making up a number of triads (each derived from another subfamily): Each triad comprises adults of a relatively large species of gecko; adults of a closely related but much smaller species; and juveniles of the former, of the same size as the latter. Hopefully, the results from a number of such triads comprising different species would give parallel results that would thus indicate any differences between interspecific and intraspecific size effects. We applied four methodologies to the same ears, in sequence: (1) For assessing the function of the tympanic membrane, its vibration in response to sounds of constant intensity and varied frequency was measured by laser interferometry (Werner et al., 1998, 2001a,b, 2002). (2) Thereafter, for assessing the reception of sound, elec-

trophysiological threshold CAP responses to a series of tone bursts were recorded from the round window membrane (Montgomery et al., 1995; Werner et al., 1998, in preparation). (3) After killing the subject, we quantified the morphology of the middle-ear components (Safford et al., 1995; Werner et al., 1998, in press). In this we wished both to formulate middle-ear data that may help to explain size-related variations in auditory sensitivity, and to compare the allometry of presumably relevant structures as observed within species (mainly post-natal ontogenetic allometry) with that among adults of species of varying body size (interspecific, evolutionary, allometry). This would indicate whether the middle ears of differently sized species vary merely as a function of the interspecific variation of adult body size, or have evolved through modifications of their own growth trajectories (Cheverud, 1982; Reiss, 1989). (4) Finally for the present study we retrieved the inner ear from the carcasses.

In the present study, we examined the variation of several parameters of inner-ear size (explained below) as related to body size and also endeavored to assess hair cell numbers. Additionally, when available, we measured also the saccular otoconial mass, the reptilian counterpart of fish otoliths, and its constituent otoconia (Lewis et al., 1985; statoconial mass of Carlstrom, 1963). In each case, we first tested for inter-aural and sexual differences. Both occur regularly in the auditory physiology of man (Kannan and Lipscomb, 1974; Bilger et al., 1990; Newmark et al., 1997; Ismail and Thornton, 2003) and occasionally in the morphology of the external and middle ears of gekkonomorph lizards (Werner et al., 1991, 1997, in press). Thereafter we examined both the intraspecific (ontogenetic) and interspecific (evolutionary) variation of organ size and relative organ size (Cheverud, 1982; Reiss, 1989).

2. Morphological background

The morphology of the membranous labyrinth of geckos, including its development and its peculiarities relative to other lizards, has been amply described and depicted in the literature (Retzius, 1884; Fleissig, 1908; Evans, 1936; Shute and Bellairs, 1953; Hamilton, 1964). The narrow and elongate auditory papilla, papilla basilaris, is situated on the somewhat wider basilar membrane (separating the otic and periotic spaces), that is suspended in a surrounding bulging frame of ear-specific connective tissue, the limbus. The shape of the limbus is thus similar to that of the papilla. Along one side of the papilla the limbus bulges into the otic space, a bulge that in geckos rises to form an overhanging lip "above" the papilla. This bulge, or limbic lip in geckos, supports the tectorial membrane, which from there extends and overlies the papilla.

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