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Postnatal Changes in the Size of the Avian Cochlear Duct*

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The length of the cochlear duct was measured in chicks aged embryonic day 14 to post-hatch day 469. Chicks were anesthetized, decapitated and their cochlear ducts exposed under an operating microscope. Because of the very thin bone and cartilage surrounding the relatively straight tube of the papilla the entire cochlear duct could rapidly be exposed and measured without fixation or removal from the head. The length of the duct was measured using a computer based Zeiss Videoplan Image Analysis System. A total 41% increase in length was seen from embryonic day 14 to post-hatch day 469; 20% of this increase occurred after hatching. It is suggested that this increase in cochlear duct length could influence basilar membrane properties important to frequency coding mechanisms during development.

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It has recently been suggested that the site of maximum stimulation of the basilar membrane caused by an intense sound changes postnatally (Rubel & Ryals, 1983). A corresponding change in the place most sensitive to a given frequency within the central auditory nuclei was suggested by Lippe & Rubel (1983). The mechanisms underlying this ontogenetic shift in frequency coding are unknown, but one possibility is that changes in the dimensional, mass or stiffness characteristics of the basilar membrane are occurring during this time period. Anatomical studies which have investigated the dimensional properties of the cochlear duct have shown a good deal of variation between the measurements taken (Held, 1926; Bekesy, 1944; Jordan et al., 1973; Tanaka, 1978; Bohne, 1979). These variations may have been due to a number of factors: normal variations between animals, fixation differences, variation in reference points for measurements or developmental differences in size. We have noted that, in fixed tissue, the cochlear duct appears to increase in size with age (unpublished observation).

Recent anatomical studies of the avian inner ear have stressed its microstructure and have only briefly mentioned length of the entire cochlear duct (Takasaka, 1971; Tanaka, 1978). We know of none which have provided this measure developmentally. Postnatal changes in cochlear duct length may be relevant to understanding the mechanisms underlying changes in frequency organization within the cochlea. Therefore, the present study was designed to investigate changes in the length of the avian cochlear duct occurring between embryonic day 14 (E14) just after onset of function and post-hatch day 469 (P469) adulthood.

METHODS

Chicks (Hubbard×Hubbard) at embryonic day 14 (E14, N=3), E16 (N=4), E20 (N=3), postnatal day 1 (Pl, N=4), P20 (N=4), P35 (N=4) and P469 (N=3) were anesthetized

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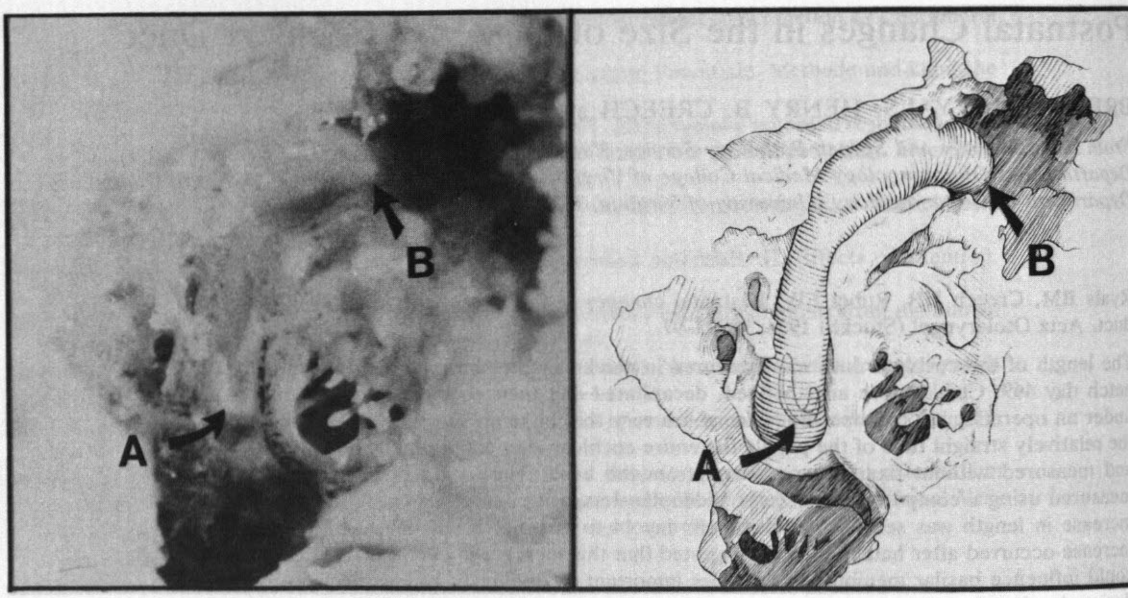

Fig. 1. (a) Photograph of the exposed cochlear duct in situ taken through the operating microscope (20×). Length measurements were made from the lagenar macula (A) at the distal tip to the proximal tip (B). (b) Drawing representing the same cochlear duct for clarification of anatomic landmarks.

(intravenous injection of Nembutal) decapitated, and their cochlear ducts rapidly exposed under a Zeiss Operating microscope. Embryos were staged for chronological age according to the method of Hamburger & Hamilton (1951).

Measurements of the length of the duct were then taken using a computer based Zeiss Videoplan Image Analysis System. Briefly, a videocamera attached to the operating microscope projected the image of the cochlear duct in situ onto a TV monitor. The head was positioned such that the entire duct was in focus. The videoplan stylus was then used in conjunction with its calibrated grid for computer assisted measurement of the distance from the distal tip to the proximal tip of the cochlear duct along its center (see Fig. 2) as

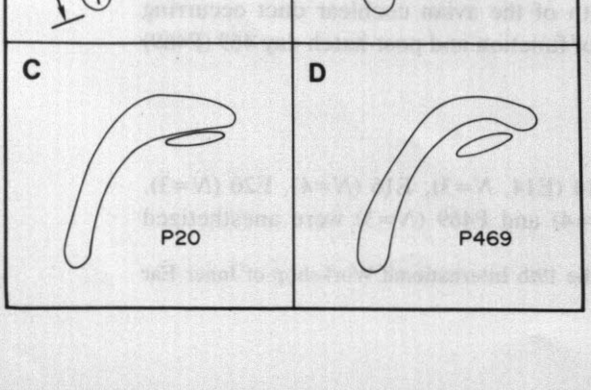

Fig. 2. Mean cochlear duct length (±1 SD) is shown from E14 to P469. Insert shows percent change in length from late embryonic stages through hatching and adulthood.

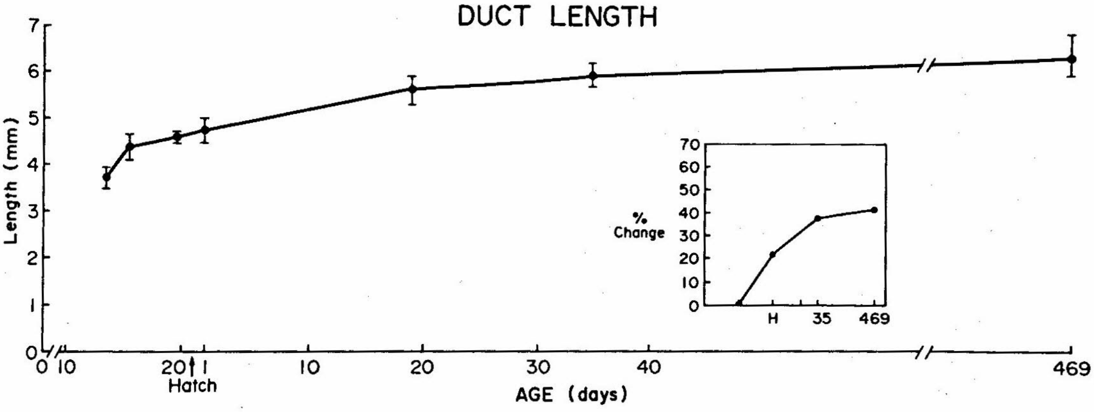

Fig. 3. Diagrammatic illustration of the qualitative changes in overall cochlear duct dimensions during development from E14 (A) to adulthood (D). All drawn at same magnification. Dotted line shows the course of videoplan length measurement taken from distal to proximal tip.

seen on the TV monitor. Magnification of the operating scope was set between 16X and 40X in order to provide the clearest view of the entire cochlear duct. Calibration of the videoplan system was performed each day prior to measurement. The length measurement was made four (4) times and the mean taken as the final measure for that animal. In addition, videotapes of each duct and calibration were made for a permanent record. Fig. 1 shows a typical view of the cochlear duct seen through the operating microscope for measurement.

RESULTS

Fig. 2 is a diagrammatic illustration of the dimensional changes seen in the cochlear duct from E14 to P469. Qualitatively, the entire duct appeared to lengthen and became narrower throughout. The slight curvature just above the round window seen in 14-day-old embryos (E14) was pronounced in 1-year-old chickens (P469). The round window appeared to remain at approximately one-third of length from the proximal tip of the duct from E14 to P469.

Quantitative analysis of the length of the cochlear duct is shown in Fig. 3. At E14 the in situ mean cochlear duct length was 3.72 mm. A significant increase in cochlear duct length to 4.75 mm was seen by 1 day post-hatch ($t_{obs.}=5.42$, df=5). Duct length continued to increase, at a less rapid pace, to 5.99 mm by 35 days post-hatch. This was, again, a significant change in total duct length between P1 and P35 ($t_{obs.}=7.75$, df=6). The length of the cochlear duct did not change significantly between P35 and P469 ($t_{obs.}=0.90$, df=5).

A separate, but related observation concerning the basilar papilla, which divides the cochlear duct and contains the auditory sensory cells, should be noted here. We did not attempt to make direct measurements of the papilla within the duct itself. However, in fixed and Epon embedded tissue, we did observe an increase in basilar papilla length from P10 to P50. Sampling 3 micron sections serially at 100 micron intervals, we found an average of 30 intervals necessary to complete sampling in the 10-day-old chick, while an average of 50 intervals was necessary in 50–60-day-olds. While this result is consistent with the results presented above from in situ measurements, a precise correspondence should not be expected. Measurements from the sectioned material are confounded by developmental changes in shrinkage due to fixation and embedding procedures.

CONCLUSIONS

The purpose of the present study was to determine changes in cochlear duct length during development. We have shown that the cochlear duct systematically increases in length during the last third of embryogenesis and postnatally. A 22% increase in duct length occurs prenatally from E14 to hatching; postnatally, the duct continues to lengthen, increasing another 16% by P35. The basilar papilla, which is within the duct and contains the auditory sensory cells, also continues to lengthen postnatally. During this time period development of auditory function has progressed from onset (approximately embryonic day 11–12) to mature auditory thresholds for frequencies below 3000 Hz (24 hours after hatch) to completely adult-like thresholds for all frequencies (within 10 days after hatch). (Jackson et al., 1982; Saunders et al., 1973; Rebillard & Rubel, 1981). Thus the cochlear duct continues to lengthen even after mature auditory threshold responses have been reached. This postnatal continuation in growth may be a function of continuing growth and ossification of the skull and cranium. Ossification of the otic capsule has begun by embryonic day 12 but is still incomplete at hatching (Romanoff, 1960). During the postnatal period from P1 to P35 the chick is undergoing tremendous overall body growth, increasing its body weight by more than twenty times in the first month.

Morphologically, the ultrastructure of the basilar papilla is adultlike at hatch; we have seen no evidence of the addition of further sensory cells after hatching (Rubel & Ryals, 1982). Since no further sensory cells are being added, we may infer a change in the overall dimensions of the sensory cells themselves and/or an increase in the size or number of supporting cells along the basilar papilla.

The increase in cochlear duct and basilar papilla length could influence basilar membrane properties important to frequency coding mechanisms during development. We have previously shown a shift in the place of maximal response along the basilar papilla caused by intense pure tone frequency stimulation during postnatal development (Rubel & Ryals, 1983). The dimensional changes described in the present study offer one morphological correlate for alterations within the basilar papilla which may be involved in such a shift in place coding for frequency. Evidence is available which indicates this shift in the place coding of frequency may be a generalized phenomenon across species during early development (Pujol, 1968; Ryan et al., 1982; Harris & Dallos, 1983; Rubel, 1983). If this is so, then measurement of cochlear duct length during development in other species is of interest. In humans, the cochlear duct has been reported to reach its maximum size by about mid-term, with the organ of Corti at its mature length at the 4th gestational month (Bast & Anson, 1949; Bredberg, 1968). These measurements were taken, however, in fixed tissue and therefore are subject to the inherent inaccuracies imposed by embedding procedures. In light of our current findings, a re-evaluation of the ontogenesis of cochlear duct and organ of Corti length in mammals may be in order.

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