Hearing in the Crocodilia

(cochlear potentials/*Caiman crocodilus*/*Alligator mississippiensis*)

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ABSTRACT Measurements of auditory sensitivity in terms of the cochlear potentials were made in young specimens of three species of crocodilians, *Caiman crocodilus* and *Alligator mississippiensis* of the subfamily Alligatorinae and *Crocodylus acutus* of the subfamily Crocodylinae. These species show considerable similarity in their capabilities for sound reception. All have the best sensitivity in a fairly broad middle range, and fall off for lower tones and particularly rapidly for the high tones. The level of sensitivity in the middle range is of high degree in comparison with other reptiles and with many birds and mammals.

The auditory capabilities of one species of crocodiles, the spectacled caiman, were investigated by the cochlear potential method by Vernon and me in 1957 (1). At that time we reviewed what was known about hearing in general among members of the order Crocodilia, which came mainly from observations by Berger (2) and Beach (3) of responses to sudden sounds and the recording of cochlear and nerve potentials by Adrian, Craik, and Sturdy (4). These observations, though limited in scope, demonstrated clearly that crocodilians are sensitive to sounds over a wide range of frequencies.

Our study of the spectacled caiman (then called *Caiman sclerops* but now designated as *Caiman crocodilus*) showed a good level of auditory capability over the range 20-6000 Hz, with the best sensitivity in the region 150-3000 Hz. These observations also included measurements of the effects of closing the earlids, which serve to protect the tympanic membrane and prevent the entrance of water when the animal submerges. Also noted was the practically equal stimulation of both ears by sounds introduced into one auditory meatus, which is the result of a connection of the two tympanic cavities by a passage running transversely across the head.

The cochlear potential measurements in *Caiman crocodilus* have now been repeated in three additional specimens, and similar observations have been made in three each of two other crocodilian species, *Alligator mississippiensis* and *Crocodylus acutus*. The last-named species belongs to the subfamily Crocodylinae and the others are in the subfamily Alligatorinae (5). All the experiments were carried out on young animals.

METHOD

The animals were anesthetized with ethyl carbamate (Urethane) in a 20% solution in Ringer's fluid, at a dosage of 0.01 ml/g body weight. The middle ear cavity was entered by drilling a small hole at the edge of the transverse passage, at a point indicated in Fig. 1. The location is critical, and must be

far enough medially to avoid damage to the tympanic membrane and its suspension, and yet afford a view into the middle ear cavity to disclose the round window membrane on its lateral wall. The tympanic membrane lies in a shallow meatal cavity beneath the upper earlid, and faces dorsally and a little laterally. In Fig. 1 the right earlids have been removed to show the tympanic membrane on this side. The drilled opening on the left is represented, and the small arrow indicates the direction of view into the interior that discloses the round window membrane. The active electrode was inserted through this opening and guided past the shaft of the columella, which served as a useful landmark.

The active electrode was a fine silver wire with a beaded tip about 0.2 mm in diameter, and this tip made a light contact with the membrane surface. Two other electrodes, one of which was grounded, were located in inactive tissues in the region of the exposure. The upper earlid on the left side was held open, or sometimes a small portion was removed, because in the anesthetized animal the lids were usually closed.

A sound tube leading from a loudspeaker was sealed tightly over the ear opening for the application of sound stimuli, and a probe tube concentric with this sound tube led to a calibrated condenser microphone to indicate sound pressure levels at the entrance to the ear. Stimulation was carried out ordinarily

FIG. 1. Dorsal view of the head of *Caiman crocodilus* showing the closed earlids on the left and a drilled opening for access to the middle ear cavity and the round window membrane. The location of the tympanic membrane is shown by removal of the earlid on the right side. One-half natural size.

FIG. 2. A sensitivity function for a specimen of *Caiman crocodilus*. The curve shows the sound pressure in decibels relative to 1 dyn/cm² required to produce a response of 0.1 μ V.

with 24 tones over the range 30–10,000 Hz, and the resulting cochlear potentials were measured with a wave analyzer serving as a selective voltmeter.

RESULTS

A sensitivity curve for a specimen of *Caiman crocodilus* for the range 30–5000 Hz is given in Fig. 2. This curve shows the sound pressures in decibels, relative to a zero level of 1 dyn/cm², required at the various frequencies to produce a standard response of 0.1 μ V. As may be seen, the best sensitivity is in a broad region 300–2000 Hz, and falls off progressively for lower tones and especially for higher tones. The tests were not extended to higher frequencies in this animal because of the risk of damage to the ear from the intensities required.

In two other animals, as shown in Fig. 3, it was safe to work with higher tones, and in one animal the range was extended to 15,000 Hz. The rapid loss of sensitivity in the uppermost frequencies, which reaches a rate of 45 dB per octave, is a striking feature. In these ears the region of best sensitivity is a little broader than in the preceding one, and extends 200–2500 Hz.

Fig. 4 shows sensitivity curves for two specimens of *Alligator mississippiensis*. For these ears the best sensitivity is in the region of 100–1000 Hz, and again there is a decline in sensitivity for lower tones and especially for tones above 3000 Hz. These curves are less regular than the ones obtained for

FIG. 3. Sensitivity curves for two specimens of *Caiman crocodilus*, plotted as in the preceding figure.

FIG. 4. Sensitivity curves for two specimens of *Alligator mississippiensis*.

Caiman, but the rate of decline in the upper frequencies is similar.

Results for two specimens of *Crocodylus acutus* are given in Fig. 5. There is a fair degree of agreement between these two curves, and both indicate a slight upward shift of the region of best sensitivity as compared with the preceding species. One curve has its best region at 700 Hz and a favorable point at 2000 Hz, whereas the other reaches its best point at 3000 Hz. The responses to the low tones hold up fairly well, much as in *Alligator*, and the extreme high tones suffer a rapid loss as in the other animals.

CONCLUSIONS

The results for the *Caiman* specimen shown in Fig. 2 are in close agreement with the ones reported earlier for this species, but the other two animals show significantly greater sensitivity. The differences probably represent individual variations.

In general, the sensitivity functions for the three crocodilian species are much alike. All show the best performance of the ear in a middle range, with a moderate rate of decline for the low tones and a very rapid loss for the high tones. The level of best sensitivity for all three species is around -60 dB for the standard response of 0.1 μ V, which in comparison with other

FIG. 5. Sensitivity curves for two specimens of *Crocodylus acutus*.

reptile ears studied in a similar manner represents a high grade of auditory effectiveness. The performance is also to be rated as excellent in comparison with most birds and with many of the mammals.

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