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Observations on Submergence Reflexes of *Caiman sclerops*

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ABSTRACT—In crocodilians, reflexes of the eye, external auditory meatus and external nares are activated at submergence. Observations of the reflexes of the eyelids and external auditory meatus of immobilized *Caiman sclerops* to rising and lowering water levels and squirts of water into the eye and external auditory meatus demonstrated a dependence of external auditory meatus opening and closure on eyelid opening and closure. Analysis of filmed observations of changing water levels showed that tension developed in the lower eyelid was paralleled by movement in the inferior ear flap; e.g. closure of the lower eyelid resulted in movement of the inferior ear flap to close the external auditory meatus. These results support the notion of a mechanical dependence of external auditory meatus width change solely upon the movement of the lower eyelid.

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INTRODUCTION

Submergence of crocodilians stimulates protective reflexes which may guard the sensory organs of the head from incoming water or damage. For example, the external nares close (Bellairs and Shute, 1953) and the eyes adjust by blinking and movement of the nictitating membrane. Moreover, Wever (1971) suggested that the movable crocodilian ear flaps (a superior and inferior flap surround the external auditory meatus and cover the tympanic membrane) close the meatus during submergence, thereby keeping the tympanum dry. However, Shute and Bellairs (1955) reported that the tympanic membrane may not remain dry after submergence.

Based on dissected material, Shute and Bellairs (1955) proposed that movement of the inferior ear flap effected opening of the anterior region of the auditory meatus. They found a Y-shaped structure of connective tissue, the ypsilon, attached to the inferior ear flap by a lateral arm, and to the postorbital bone by a medial arm; the stem projected into the floor of the orbit to the depressor auriculae inferior muscle. Shute and Bellairs observed that contraction of the *M. depressor auriculae inferior* pulled the stem of the ypsilon causing the medial arm to rotate through its point of attachment at the postorbital bone. In this way the lateral arm and the inferior ear flap are pulled rostrad, ventrad and mediad, thereby causing the external auditory meatus to open. Shute and Bellairs did not discuss the circumstances under which this muscle contracted. The auditory meatus closed when the inferior ear flap rose as a result of contraction of smooth muscle fibers which extend from the lateral aspect of the postorbital bone to the lateral arm and fork of the ypsilon.

Our initial laboratory observations of submergence and ascent behavior of *Caiman sclerops* suggested that a relationship exists between eye closing and external auditory meatus width. This

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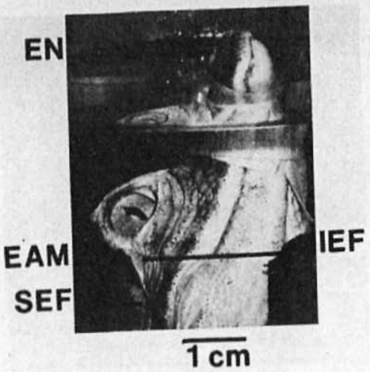

FIGURE 1. Photograph of the anterior portion of a *Caiman* taped to a weighted board in the vertical tube. The water level is just below the external nares. Abbreviations: E.A.M.-external auditory meatus, S.E.F.-superior ear flap, I.E.F.-inferior ear flap, E.N.-external nares.

report presents the results of observations and experiments seeking to elucidate the mechanisms which govern the changing of the width of the external auditory meatus upon submergence.

METHODS

Four young *Caiman sclerops*, two of which were obtained commercially and two through the generosity of Carl F. Kauffeld of the Staten Island Zoo, New York, were housed in a large tank filled with water to a height of 20 cm and containing several large rocks. A heat lamp was turned on daily 9:00 AM-7:00 PM and the animals basked often. Ambient night water temperature was approximately 23 C. They fed on live mice which were presented weekly. All animals were healthy.

The design for studying ear flap closure was similar in all experiments. The subject was taped to a weighted wooden board at the tail, limb girdles, and neck. The mouth was closed by a narrow piece of tape around the jaws behind the external nares. After immobilization, the subject was placed in either a normal horizontal position in an aquarium, or in a large vertical glass cylinder open at the top with the head in the up position (Fig. 1). The water level (temperature was 28 ± 1 C) was raised slowly until a change in the width of the external auditory meatus was perceived. The water level was raised even further to a midsnout position. Then the water level was lowered below the neck and all changes in external auditory meatus width noted. Observations specifically concerned the temporal relationship of eyelid movements and external auditory meatus contraction and dilation.

To isolate the ipsilateral reflex responses in non-submerged *Caiman* a squirt of water was delivered, by a hypodermic syringe, into the external auditory meatus or eye surface of immobilized animals. Water was also squirted onto the external nares of restrained and unrestrained animals.

Some vertical tube experiments, and external auditory meatus and eye squirt sequences were filmed at 18 frames/sec to analyze further the eyelid movement and external auditory meatus width change and their timing sequence.

RESULTS

Submergence and Surfacing.—Upon voluntary submergence in an aquarium, a *Caiman's* eyes blinked and the nictitating membrane swept across the eye and then the eye opened under water. Simulataneous with the eye blink, the external auditory meatus closes and then reopens even while the *Caiman* is submerged. Within the meatus a bubble usually forms. When the animal surfaces, the eye again blinks followed by the closing of the auditory meatus and then its opening again.

Raising water level (Caiman in horizontal or vertical position).—When the water level is raised slowly a response is not observed until the water comes in contact with the posterior margin of the eye. At this stage the auditory meatus is open even though it is submerged. Then, as the water reaches the eye it blinks, and the external auditory meatusshuts and immediately thereafter

opens. This response occurred in every instance (n = 19); the auditory meatus always closed immediately following an eye blink.

Frame by frame analysis of the photographic record of the eye blink response to rising water reveals that the slightest upward movement of the lower eyelid is reflected in a narrowing of the external auditory meatus width. This upward eyelid movement and narrowing both develop within about 100 msec. When the lower eyelid completes its upward movement the auditory meatus is tightly closed. Auditory meatus closure results solely from the movement of the inferior ear flap relative to the fixed superior ear flap.

When the lower eyelid moves downward (the eye opens) the external auditory meatus width expands. A complete sequence starting from both eye and meatus open through closing and then opening lasts about 0.5 sec (0.25 sec to close and 0.25 sec to open). However, in some instances the eye and meatus remain closed up to 5.0 sec before opening.

Lowering water level (Caiman in horizontal or vertical position).—Lowering the water from mid-snout to below eye level gave various results depending upon whether the eye was initially open or closed. When both the eye and external auditory meatus are closed and the water level is lowered, the lower eyelid opens and then immediately the external meatus opens (n = 6); the meatus never remains closed when the eye opens. When both the eye and external auditory meatus were open and the water level is lowered from mid-snout, the eye blinks and then the meatus closes and subsequently reopens (n = 13); the meatus never remains open upon eye blink. A typical sequence of the latter instance taken from the film is illustrated in Fig. 2.

Analysis of the filmed record revealed that most lowering sequences, which proceeded from both eye and auditory meatus open through eye blink and meatus closure to eye and meatus open, last about 0.5 sec. In some instances, however, the eye and meatus remain closed up to 6 sec before opening.

Squirt of water into eye, external auditory meatus and external nares.—When water was squirted into the exposed eye, the eye blinked and the external auditory meatus closed and then opened (n = 15). Film analysis revealed that the above sequence can occur within 0.5 sec but was more variable than the response to rising water level. The mean sequence duration was 1.05 sec (n = 13).

When water was squirted directly into the external auditory meatus for 1, 5, or 10 seconds duration, no response occurred from the eye or inferior ear flap. This was similar to the results when the water level was raised. However, in one instance some local "pumping" movement of the external auditory meatus was observed when water was squirted into the meatus, but simultaneous observation of the lower eyelid was not made. In two cases water was squirted onto the external nares, for at least 10 sec, whereupon the narial musculature closed. No response was elicited from the eye or ear flaps during this procedure.

DISCUSSION

All 3 methods of investigating the submergence reflexes in *Caiman* suggest a dependence of external auditory meatus width upon the movements of the lower eyelid. That is, partial closure of

FIGURE 2. Lowering of water level when *Caiman* is in vertical position. The sequence, A through E, lasts 0.8 seconds.

the lower eyelid yielded partial contraction of the auditory meatus width; complete closure of the eyelid resulted in a tightly shut auditory meatus; and opening of the eyelid resulted in a broadening of the meatus width. Thus, the movement of the inferior ear flap may be graded or complete depending on the tension developed on the lower lid.

These findings also demonstrate that the receptors for the eye blink reflex to water contact, and hence closure of the meatus, are located around the margin of the eyelids. Raising the water level when a *Caiman* was in the vertical position did not evoke either an eye blink or exterior meatus closure until the water had reached the posterior margin of the eye. Moreover, when the water level was lowered such reflexes were not evoked until the water reached about ¼ of the way down the eye. Squirting water into the external auditory meatus did not result in any change in its width nor did squirting water onto the external nares.

It was observed particularly after raising the water level, that in some complete sequences (i.e., eye and external auditory meatus open followed by a reflex blink and meatus closure, then reopening of the meatus), that the eyelid and external meatus remained closed for several seconds. Lowering the water level resulted in the most rapid complete sequences (mean = 0.5 sec), followed next in time by the eye squirt results (mean = 1.05 sec). Thus, the context in which the reflex is elicited appears important for the total sequence duration. For example, the lowering sequence can be interpreted as a water-air transition where there is a rapid blink and nictitating membrane wipe across the eye ball. However, the eye squirt is an unexpected stimulus not associated with submergence. The animal is not preparing for submergence, and therefore, the observed sequence duration may be modified by a startle or fear reaction. Furthermore, raising the water level is an air-water transition in an unnatural situation. Perhaps in this case sustained eye and auditory meatus closure reflect observer presence because voluntary submergence reflex sequences are very rapid.

Suggested Mechanism.–Shute and Bellairs (1955) suggested that the exterior auditory meatus width narrowed when the inferior ear flap was pulled dorsally by a band of smooth muscle acting on the ypsilon, and that the meatus width expanded when the ypsilon was pulled forward and ventrally. Presumably, the muscle responsible for the latter action was the *M. depressor auriculae inferior* (DAI) located within the orbit. Our results, which show a dependence of external auditory meatus opening and closing on eyelid movement, may bring their proposed mechanism into question.

The observation that the slightest tension developed on the lower eyelid was reflected in narrowing of the auditory meatus width suggests that closure is regulated by a mechanism related to the eye. That this could result from mechanical action is supported by the graded response of eyelid closure and resultant narrowing of external auditory width. Therefore, it seems reasonable to question the necessity for a separate (smooth) muscle for closing the external auditory meatus.

Such a mechanical system, wherein the eyelid musculature might work on the ypsilon, necessitates reinterpretation of the *M. depressor auriculae inferior* described by Shute and Bellairs (1955). This orbital muscle supposedly acts on the ypsilon to open the external auditory meatus. That the auditory meatus opens when the lower eyelid opens suggests that the DAI acts in concert with the *M. depressor palpebrae inferioris* (DPI) which pulls down the lower eyelid (Edgeworth, 1935; Jollie, 1962). Moreover, Shute and Bellairs (1955) suggested that the DAI belongs to the same muscle group as the *M. levator bulbi* and the *M. depressor palpebrae inferioris*. All 3 are innervated by nerve V and are derived from the dorsal constrictor musculature (Edgeworth, 1935). Therefore, it appears that the DAI and DPI have a common origin and share a common innervation. Thus it is possible that a portion of the DPI and the DAI could act on the ypsilon to move the inferior ear flap. Disassociation of the action(s) of these muscles would be facilitated by more accurate anatomical information, electrophysiological measurements, and additional functional analysis derived from nerve transection studies. These are now underway.

Finally, it must be mentioned that we have only superficially tested changes in external auditory meatus width to airborne sounds. In several cursory observations, vibrations from a tuning fork (frequency 100 Hz) presented at the auditory meatus did not evoke an alteration in external auditory meatus width.

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