Redistribution of Air Within The Lungs May Potentiate "Fright" Bradycardia In Submerged Crocodiles *(Crocodylus porosus)*

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Abstract

1. Voluntary undisturbed dives by *Crocodylus porosus* were short in duration (3.08 ± 1.87 min, mean $\pm$ SD) and accompanied by a small but significant bradycardia ($14.3 \pm 5.9\%$ drop).
2. When crocodiles were disturbed underwater there was a rapid onset of "fright" bradycardia, to $65 \pm 6.0\%$ of surface heart rates and dive durations were prolonged to 19.6 ± 1.8 min.
3. The development of "fright" bradycardia was not accompanied by any increase in intratracheal pressure or expulsion of lung gas. However, sustained contraction of,the abdomen and expansion of the thorax revealed a redistribution of air anteriorly within the lungs.
4. We propose that the redistribution of air within the lungs may generate an afferent signal which potentiates the initiation of a severe, dive-prolonging bradycardia.

Introduction

The concept that severe bradycardia is a routine correlate of diving in vertebrates originated from early studies in which dives were forced by the investigators, rather than allowed to occur voluntarily. Subsequently, investigations of a wide variety of unrestrained species have shown that diving vertebrates normally dive within their aerobic limit and usually make only small reductions in heart rate during a dive (Butler and Jones, 1982; Seymour, 1982). The significance of diving bradycardia in crocodilians was reinterpreted when Gaunt and Gans (1969) found that diving bradycardia in *Caiman crocodilus* is slight to negligible during voluntary undisturbed dives but increased dramatically following disturbance. Similar changes in cardiac activity following disturbance have been recorded in a free ranging alligator, *Alligator mississippiensis* (Smith *et al.,* 1974). The phenomenon of fright or disturbance bradycardia has now been documented in several species of diving vertebrates (Belkin, 1968; Gaunt and Gans, 1969; Smith *et al.,* 1974; Butler and Woakes, 1979; Kanwisher *et al.,* 1981; Smith and Tobey, 1983; Smith and DeCarvalho Jr, 1985).

A possible mechanism for the rapid onset of pro-found bradycardia in crocodilians was proposed by White (1970). He noted that *A. mississippiensis* did not develop a full diving bradycardia until air had been expelled from the lungs, suggesting that the state of stretch of the lungs or thorax may influence the degree of diving bradycardia. Despite these findings, no study has yet determined whether disturbance significantly prolongs submergence in a crocodilian or whether expulsion of lung gas is necessary for the development of profound bradycardia during voluntary submergence. The purpose of this study was to determine the effects of disturbance on cardiac activity and diving behaviour of freely diving *Crocodylus porosus* and to establish whether changes in thoracic or lung volume are associated with the onset of "fright" bradycardia during submergence.

Materials and Methods

Experimental animals

Juvenile *Crocodylus porosus* (body mass = 2.25 ± 0.74 kg, mean ± SEM, N = 5) were obtained from the Edward River Crocodile Farm in North Queensland and housed in pens in a controlled temperature room (air temperature 29-33°C, water temperature 25°C) with a 12L: 12D photoperiod. The crocodiles were fed 2-3 times a week.

Protocol

Electrocardiograms (ECG), thoracic and abdominal movements and, in some cases, intratracheal pressures were recorded continuously from C. *porosus* left undisturbed for up to 5 hr in a tank with water to a depth of 35 cm. During this period they were free to surface or dive at will. The crocodiles were then disturbed abruptly by the experimenters entering the room and banging loudly on the side of the tank. Then they were again left alone. Recording of all parameters continued until the animals had recovered from the disturbance.

Instrumentation

The ECG was monitored by suturing fine polyethylene coated wire (SWG 38) to ventral scutes adjacent to the heart. Signals were preamplified (Grass 7P6C) and the ECG displayed on a four channel polygraph (Grass 79D). Thoracic and abdominal movements were monitored with mercury-filled strain gauge transducers secured around the thorax and abdomen, each connected to a plethymograph (Model 270, Parks Electronics). Outputs from the plethymographs were displayed on the polygraph. To ensure comparability of abdominal and thoracic movements recorded from different animals, strain gauges were secured at set positions. Intratracheal pressure was measured by inserting a polyethylene cannulae (o.d. 1.27 mm) down the trachea to the bronchial bifurcation and connecting it to a calibrated pressure transducer (Statham P23 BC) whose signal was preamplified and displayed on the fourth channel of the polygraph.

Statistical analysis

Values are expressed as means ± SD. Student's *t*-tests or Wilcoxon's signed rank tests were used to determine statistical significance ($P < 0.05$).

Results

The crocodiles were generally inactive throughout the experiments and, between breathing episodes at the surface, lay quietly at the bottom of the tank. Voluntary undisturbed dives were short in duration (3.08 ± 1.87 min, Table 1). During dives there was a small but significant decline in heart rate to an average of 14% lower than predive levels (Table 1, Fig. 1). Once a crocodile was at the bottom of the tank, intratracheal pressures remained constant throughout each dive.

Dive durations following disturbance (19.6 ± 1.8 min, $N = 14$) were significantly longer than voluntary undisturbed dives ($P < 0.05$). Disturbance during submergence resulted in a rapid and significant drop in heart rate below voluntary undisturbed dive rates (Figs 1 and 2). Heart rates fell by an average of 65 ± 6.0% ($N = 5$) below predive rates. Immediately following disturbance underwater there was, in each case, a sustained contraction of the abdomen and an expansion

of the thorax without either an increase in tracheal pressure or an expulsion of lung gas. Heart rate declined immediately following these adjustments (Fig. 2). Intratracheal pressure was not affected by disturbance underwater. If a crocodile was at the surface when disturbed, it dived immediately and heart rate declined to levels observed following disturbance underwater. Disturbance of crocodiles out of water did not result in either a bradycardia or any adjustment in thoracic or abdominal volume.
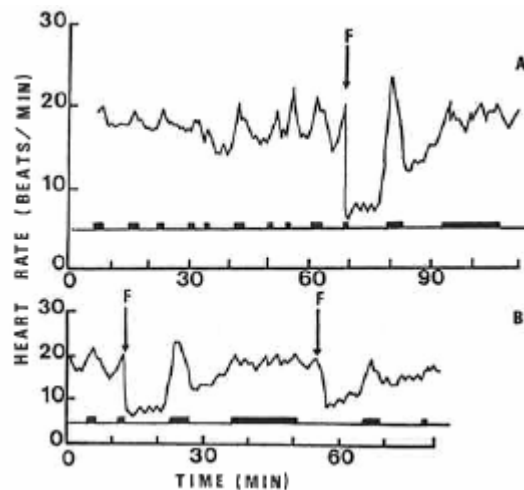

Fig. 1. Changes in cardiac activity during voluntary submergence prior to and following disturbance (F) in C. *porosus.* (A) In response to disturbance at the surface, crocodiles dived immediately and heart rates declined to a few beats per min. (B) Disturbance underwater resulted in an immediate decline in heart rate below voluntary undisturbed rates. Raised, thick line—animal at surface. Thin line—animal submerged.

Discussion

Grigg et al. (1985) recorded natural dives by a 9.75 kg *C. porosus* ranging freely in the Tomkinson River in northern Australia. All but eight of the 127 dives made over a 3.5 day period were of 1-5 min duration, as found in the present study on crocodiles under laboratory conditions, giving rise to confidence that the results from the laboratory study are relevant to behaviour in the wild. Dives of this short duration are known to be endured aerobically (Wright, 1985, 1987). The finding that diving bradycardia was slight during voluntary undisturbed dives but increased dramatically when crocodiles were disturbed prior to or during submergence is consistent with observations on *Caiman crocodilus* (Gaunt and Gans, 1969) and *A. mississippiensis* (Smith et al., 1974), and is likely to be a correlate of all crocodilian diving. Like *A. mississippiensis* (Smith et al., 1974), *C. porosus* did not develop a bradycardia in response to disturbance on land, suggesting that submergence is a necessary pre-condition for the development of "fright" bradycardia.

Table 1. Dive durations, percentage of time spent diving and heart rates (H.R.) during voluntary diving activity in five juvenile *Crocodylus porosus* at 25°C.

Crocodile no.	Dive time (min)	% Dive time	Surface H.R. (BPM)	Diving H.R. (bpm)	% Drop in H.R.
1	2.9 ± 0.2 (70)	73.9	29.1 ± 0.6	25.6 ± 0.4*	12.0
2	4.1 ± 0.4 (58)	29.3	24.1 ± 0.3	20.4 ± 0.4*	15.2
3	1.3 ± 0.2 (39)	11.8	15.1 ± 0.6	11.5 ± 0.5*	23.8
4	5.7 ± 1.3 (27)	46.3	28.9 ± 0.9	26.4 ± 0.4*	8.2
5	1.4 ± 0.2 (54)	62.0	20.4 ± 0.7	17.9 ± 0.4*	12.2

Values are means ± SEM (*N*). *Indicates a significant decrease in heart rate ($P < 0.05$).

What may be the functional significance, if any, of this striking response to fright seen in crocodilians when they are in the water? Gaunt and Gans (1969) and Smith et al. (1974) suggested that a drop in heart rate may signal a redistribution of blood flow, con-serving oxygen for the heart and brain, and prolonging the time that a crocodile may stay underwater, which may be significant for a crocodile trying to avoid predation. The first of these predictions is supported by work on alligators which showed that the blood flow in skeletal muscle is markedly reduced or ceases following disturbance underwater (Weinheimer et al., 1982). The second prediction, of prolonged dive times, is borne by the results of our study in which the provision of a "fright" stimulus extended dive times from a mean of 3.8 min to a mean of 19.6 min.

Concerning the mechanism by which the profound bradycardia is initiated, White (1970), working on a *A. mississippiensis*, found as we did that changes in intra-tracheal pressures remained constant, but that expulsion of lung gas was a correlate of the onset of the drop in heart rate and he proposed that the mechanical state of the lungs, mediated through stretch receptors in the lung parenchyma or thorax wall, influences the degree of bradycardia which develops during submergence. We found, however, that the onset of severe bradycardia following a fright given underwater was not associated with the expulsion of any gas from the lungs. We do agree that stretch receptors are probably involved, however, because, although there was no expulsion of gas and lung volume remained constant, stretch receptors would be stimulated by the abdominal contraction and thoracic expansion accompanying the development of fright bradycardia. In White's study the animals were dived forcibly, so the observations of gas expulsion could have been an artefact of that unnatural situation. If the functional significance of bradycardia and associated physiological events following a fright underwater is to prolong sub-mergence time, as discussed above, it would be counter-productive to have a mechanism which depended upon an expulsion of lung gas to trigger a stretch receptor, for that would reduce the oxygen store which is being conserved. The lungs of crocodiles are multicameral and extend well back into the abdominal cavity (Perry, 1983; Kirshner, 1985), so the anatomical basis of the observed redis-tribution of air from posterior to anterior atria is straightforward. We propose that the redistribution stimulates stretch receptors whose afferent signals potentiate the rapid development of a profound bradycardia.
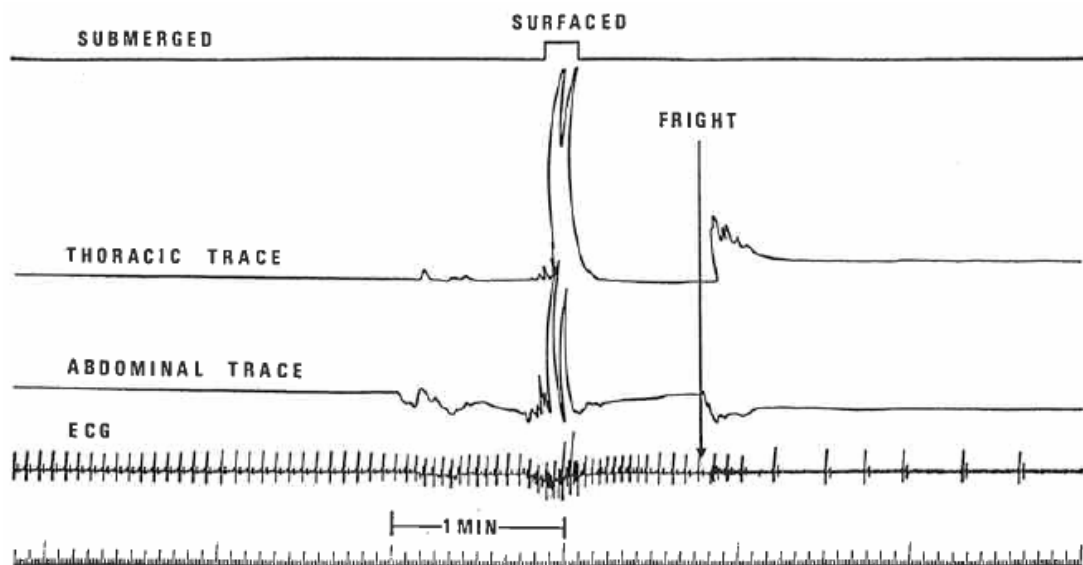
Fig. 2. Changes in the ECG, thoracic and abdominal movements following disturbance during a voluntary dive in *C. porosus*. Immediately following disturbance there was a sustained contraction of the abdomen followed by an expansion of the thorax. Heart rates declined immediately following these adjustments.

White (1970) suggested that a relationship between heart rate and the mechanical state of the lungs may reflect a basic mechanism which enables efficient coupling between pulmonary ventilation and per-fusion in intermittent breathers. It seems likely that a redistribution of blood flow in a "fright" dive is part of the same relationship, reducing both peripheral and pulmonary perfusion and so conserving oxygen supplies. Grigg and Johansen (1987) and Grigg (1989, 1991) have drawn attention to cardiovascular adjustments which accompany voluntary aerobic dives in *C. porosus*. These include the initiation of a pulmonary by-pass shunt via the left systemic arch, apparently enabling the matching of pulmonary perfusion to oxygen requirements. In a "fright" dive, the implication is that the shunt develops more fully, reducing oxygen uptake from the lungs. At such times, metabolism in some tissues will be supported anaerobically, pending the return of an oxygenated blood supply in due course. Grigg (1989) has pointed out that the cardiovascular anatomy of crocodilians is such that a complete cessation of pulmonary perfusion must be recognised as at least a possibility. In such a (theoretical) model, reverse flow of blood through the foramen of Panizza would allow the (presumably anaerobic) animal to be supported by a right ventricle to right aorta to right atrium single circulation, enabling oxygen supplies in the lung to be kept intact until being tapped in small quantities from time to time to support the most sensitive tissues, presumably the brain. This would enable a crocodilian to extend its time submerged very significantly.

Acknowledgements

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