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THE EMETIC REFLEX IN A REPTILE (*CROCODYLUS POROSUS*)

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Summary

The emetic (vomiting) reflex in a crocodilian, *Crocodylus porosus*, was characterised for the first time using the plant alkaloid veratrine (5 mg kg^{-1} i.v. or i.p.) as an emetic stimulus. The latency to the onset of vomiting was 8.0±0.9 min (mean ± S.E.M., *N*=5 animals). Vomiting was preceded by a clearly defined set of prodromal behaviours including, in temporal sequence, rhythmic contraction of the pharynx, sneezing and jaw snapping. Expulsion of vomitus was not particularly forceful and was accompanied by lateral shaking of the head. Physiological studies revealed that vomiting was accompanied by oscillatory (9.1±0.7 oscillations over 29.7±3.6 s, *N*=9 episodes in three animals) increases in intraperitoneal pressure (7.0±0.9 kPa, cf. 0.7±0.1 kPa during respiration). The significance of these results is discussed in the context of the role(s) of vomiting as a protective reflex and as a mechanism for removal of indigestible food residues (e.g. fur, claws) from the gut.

Key words: Estuarine crocodile, *Crocodylus porosus*, reptile, veratrine, emesis.

Introduction

Nausea and vomiting (emesis) are commonly perceived as symptoms of disease or infection (e.g. labyrinthitis, renal failure and food poisoning), or as side effects of various forms of therapy (e.g. anti-cancer chemotherapy; see Andrews and Davis, 1995, for a review). Both are components of a defensive system that is presumed to have evolved to protect the body against toxins accidentally ingested with the food. Nausea serves to generate an aversive response to that food (Grant, 1987) and the vomiting is used to expel gastric contents forcefully via the mouth (Lang et al., 1986). In addition to this protective role, some species also use the emetic mechanism as part of the normal digestive process to void indigestible constituents of the food, which, if they remained in the stomach, could cause obstruction and compromise further food intake. For example, sharks and sperm whales, both of which may ingest considerable quantities of squid periodically, use vomiting to expel the indigestible chitinous squid beaks from their stomach (Clarke, 1972; Clarke and Stevens, 1974; Clarke et al., 1988). This phenomenon is also seen in some birds (e.g. owl *Bubo bubo*, Darolova, 1991) which 'cast up' indigestible residues, including bones.

The emetic reflex is widespread throughout the vertebrates being present in mammals (e.g. sperm whale *Physeter macrocephalus* L., Clarke et al., 1988; monkey *Macaca mulatia*, *M. cynomologus*, Borison and Wang, 1953; ferret *Mustela purorius furo* L., Andrews et al., 1990; dog, Monges et al., 1978; cat, Borison and Wang, 1953; house musk shrew *Suncus murinus*, Ueno et al., 1987), birds (e.g. pigeon *Columbia livia*, Saxena et al., 1977; petrel *Hydrobates pelagicus*, Matthews, 1949), amphibians (e.g. frog *Xenopus laevis*, Wassersug et al., 1993; Naitoh et al., 1989; salamander *Hynobius nebulosus*, Naitoh and Wassersug, 1994) and fish (e.g. dogfish *Sciliorhinus canicula*, Andrews et al., 1998; catfish *Clarias gariepinus*, Sims and Andrews, 1996; tuna *Thunnus thynnus*, Carey et al., 1984; trout *Oncorhynchus mykiss*, Tiersch and Griffith, 1988). In these taxa, it has been relatively well characterised in terms of the mechanics and mechanisms.

Whilst there are anecdotal reports that 'many herpetofauna can vomit' (Marcus, 1981) systematic descriptions of such behaviour are scant. Gans (1952) described the selective regurgitation of eggshells from the oesophagus in snakes of the genus *Dasypeltis*. Recently ingested and partially digested food in the oesophagus and stomach can also be ejected with some force from the mouth, although Gans (1952) comments that this usually occurs in times of danger to facilitate escape and defence. We are aware of reports of emesis in only two crocodilian species. Schapiro (1968, 1978) reported that electrical stimulation of the dorsolateral striatum evoked retching (not defined) in the unrestrained *Caiman sklerops* after a latency of 2–5 min. The response was not quantified and no comment was made about whether the animal vomited. Farmed and wild *Crocodylus porosus* vomit indigestible material (Grigg and Gans, 1993; G. Grigg, personal communication)

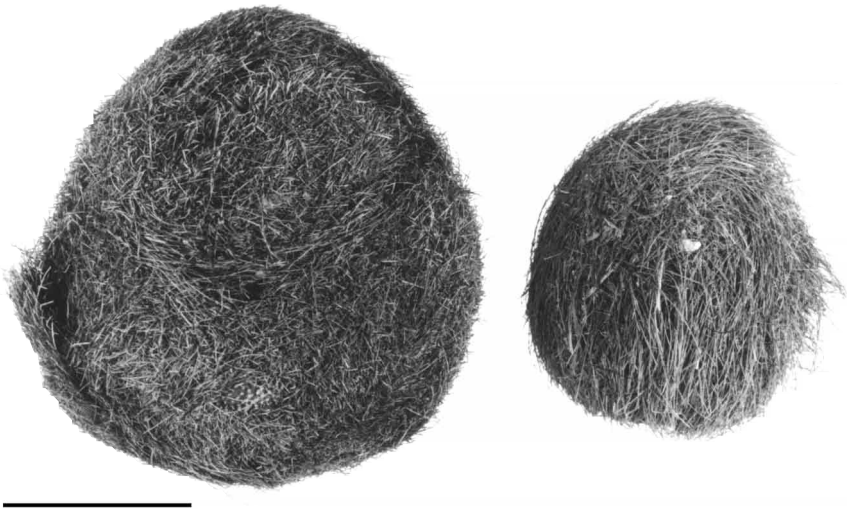

Fig. 1. Photograph of trichobezoars (‘hair-balls’) from *Crocodylus porosus*. Bar, 4 cm. Picture courtesy of G. Grigg.

including trichobezoars (‘hair-balls’, Fig. 1). A crocodile (species not stated) was seen to vomit hair upon arrival at Lincoln Park Zoo in Chicago, USA (Dolowy et al., 1960). However, there are no systematic descriptions of the emesis or the accompanying behaviour. Chitinous and keratinous residues from food are likely to accumulate in the stomach and must be removed to avoid obstruction. The above anecdotal observations suggest that vomiting may play a role in the normal digestive behaviour of the crocodile, as has been suggested for some elasmobranch fish (e.g. dogfish *Scyliorhinus canicula*, Andrews and Young, 1993), birds (e.g. owl *Bubo bubo*, Darolova, 1991) and the sperm whale *Physeter macrocephalus* L. (Clarke et al., 1988).

The aim of the present study was to investigate the vomiting reflex in the Estuarine crocodile *Crocodylus porosus* and to provide a description of this phenomenon using direct observation and recording of physiological variables. The broader goal was to gain insights into the evolution of this important protective reflex.

The plant alkaloid veratrine was selected as the emetic stimulus because it has been shown to induce emesis in a variety of species including fish (e.g. *Scyliorhinus cannicula*, Andrews et al., 1998) and mammals (e.g. *Suncus murinus*, Ueno et al., 1987; cat and dog, Borison and Fairbanks, 1952; Bobkov, 1964). In mammals, its site of action is within the nodose ganglion (the location of the cell bodies of vagal afferents) and the receptor region of vagal afferents (Bobkov, 1964; Borison and Fairbanks, 1952).

Materials and methods

Experimental animals

Estuarine crocodiles *Crocodylus porosus* (Schneider) were purchased from the Edward River Crocodile Farm, Queensland, Australia and flown to Brisbane, where they were housed outdoors in a 4 m diameter fibreglass tank. They were kept in fresh water thermostatically controlled at 28 °C and had access to platforms on which they could bask. They were fed twice a week with chicken pieces but it was not possible to assess the amount eaten (if any) by individual animals. In particular it has been noted that following surgery (C. Franklin and M. Axelsson, unpublished observations) animals do not feed reliably. The animals used in the experiments had a mass of 450–1800 g and body lengths of 30–150 cm. They were not sexually mature. During the experiments, the crocodiles were kept individually at 28 °C in smaller plastic tanks (100 cm × 80 cm) with shallow water (2–3 cm). The studies were approved by the University of Queensland, Animal Experimentation Ethics Committee, approval number ZOO/020/96/URG.

Surgical procedures

Prior to surgery animals were not fed for at least 48 h. The animals were intubated using a 5-6 mm tracheal tube after local application of lignocaine (20 mg ml^{-1} Lignomav, Mavlab, Slacks Creek, Australia) to the glottis. Halothane (Fluothane, Zeneca, UK) anaesthesia from an Ohmeda Fluotec 3 dispenser was used throughout the surgery. A concentration of 4–5 % halothane in pure oxygen was used to induce a suitable level of anaesthesia, which was then maintained using 1–2 % halothane in oxygen. The animals were manually ventilated during surgery. Emesis was not observed during the induction or maintenance of anaesthesia.

ECG electrodes

To record the electrocardiogram (ECG), two resin-coated stainless steel wires (80 cm long, 0.27 mm diameter, Driver Harris SA, insulated by Aismalibar SA) were inserted subdermally on the ventral side (two scales right and left from the midline, respectively) in a caudocephalic direction using an 18-gauge needle. 3 cm of insulation at the tip of each electrode was stripped away in order to achieve a good contact surface to pick up the ECG signal.

The ECG wires were looped and sutured on the skin at the base of the implantation site and then led to the dorsal part of the animal, sutured and passed through a polyethylene cannula

(SP55 0.8 mm i.d., 1.2 mm o.d., Dural, Australia). 2 mm plugs were soldered at the end of each wire and the whole wiring set was looped and tied on the back of the animal with umbilical cotton tape (3 mm, Ethicon).

Intraperitoneal pressure

A thin-walled rubber balloon (approximately 1 cm diameter, uninflated) attached to a PE160 polythene cannula was inserted into the peritoneal cavity through a 1 cm long ventral midline incision two-thirds of the distance between the front and hind limbs. The cannula was externalised and sutured to the back of the animal. The balloon and cannula were filled with 154 mol l^{-1} NaCl for pressure recording.

Blood pressure

The right femoral artery was exposed through a 3–4 cm long ventral incision. It was cleared of connective tissue and cannulated with a polyurethane cannula (PU 90, 0.9 mm i.d.; 1.2 mm o.d.) tipped with 2 cm of a thin-walled polyurethane cannula (0.7 mm i.d.; 1.0 mm o.d.) and filled with heparinised (100 i.u. ml^{-1}) 154 mol l^{-1} NaCl. The femoral vein was also cannulated at the same time with a PU 90 cannula for administration of veratrine and fluid. Both the arterial and venous cannulae were externalised at the base of the leg and connected to two titanium ports (internal volume 0.17 ml), which were sutured to the back of the animal, allowing a needle-tipped polythene catheter to be attached during the experiments. These injection ports provided easy access to both arterial and venous cannulae and minimised the disturbance of the animals without affecting the frequency response of the cannula/transducer system.

The skin incision was closed with sutures and the area treated with antibiotic powder (Cicatrin, Wellcome, containing bacitracin and neomycin). Amoxycillin (Amoxil, Beecham Veterinary Products, Victoria, Australia) was given by intramuscular injection every 48 h.

Postsurgical animal maintenance

Vomiting was not seen during recovery from anaesthesia, which was assessed by the return of locomotor activity and spontaneous ventilation. After recovery from anaesthesia the animals were individually housed in plastic tanks (100 cm × 80 cm) where they were kept for a minimum of 36 h without disturbance.

Data acquisition and presentation

Before the start of the experimental period the ECG cable was connected to an EEG amplifier unit (GRASS Model 7P511K) and the output displayed on a GRASS polygraph (Model 7D). Systemic arterial blood pressure was recorded using a NaCl (154 mmol l^{-1})-filled needle-tipped catheter (PE90) connected to the femoral artery cannula *via* the titanium port and attached to a pressure transducer. The intraperitoneal pressure was recorded by connecting the catheter from the balloon to a second pressure transducer. Both pressures were recorded using Statham Pressure Transducers (Model P23Dc) calibrated against a 100 cm static water column and displayed on the polygraph.

Heart rate (HR) was derived from the ECG signal by direct measurement from the polygraph traces. In addition to the polygraph ECG, intraperitoneal pressure and arterial blood pressure were recorded on a computer (Toshiba T6400DX) using a 12 bit data-acquisition card and LabPC+ and LabView version 3.1.1. software (National Instruments, Austin, Texas, USA). The sampling frequency employed was 250 Hz.

A needle-tipped PE50 catheter filled with NaCl (154 mol l^{-1}) was connected to the femoral vein titanium port for later administration of drugs and fluid.

Values are presented as means ± S.E.M.

Drug

Veratrine hydrochloride (Sigma) was dissolved in sterile 154 mol l^{-1} NaCl, injected intravenously in a bolus and flushed in with 1 ml of 154 mol l^{-1} NaCl. Intravenous 154 mol l^{-1} NaCl was used for control injections. Saline was also used as the vehicle for intraperitoneal injection of veratrine hydrochloride.

Observation and video recording

Animals were observed directly. In addition, colour videotape recordings were made of both surgically manipulated and intact animals using a National NV-M5 VHS camera in combination with a Sony 14 inch black and white monitor. The tapes were later analysed quantitatively frame by frame using a Panasonic AG-7355 videorecorder connected to a Panasonic TX 3370URS television. Selected frames were printed using a Panasonic NV-MP1 colour video printer and were used for the drawings presented in this paper.

Results

The general description of emetic behaviour in *C. porosus* is based upon the larger individuals given veratrine intravenously (i.v.; 5 mg kg^{-1}). Because the larger animals were difficult to videotape in full profile, recordings of the response of one small (400 g) animal given veratrine intraperitoneally (i.p.; 5 mg kg^{-1}) were used for the more detailed quantitative analysis of the emetic response.

General observations

No emetic or other behavioural response was elicited by intravenous injection of saline alone given intravenously prior to the injection of veratrine to flush the intravenous line (N=5) or given intraperitoneally (N=2) in a volume comparable to that used for the injections of veratrine. Veratrine induced emesis in all five animals with the number of episodes ranging from one to five (Fig. 2). The latency to the first vomiting episode was 8.0±0.9 min (N=5 animals).

Analysis of the behaviour showed that within 30 s of injection of veratrine there was an increase in motor activity such as jaw snapping, rapid lateral movement of the head and mouth gaping. The intensity of this reaction differed markedly among the animals. The crocodile is an intermittent ventilator

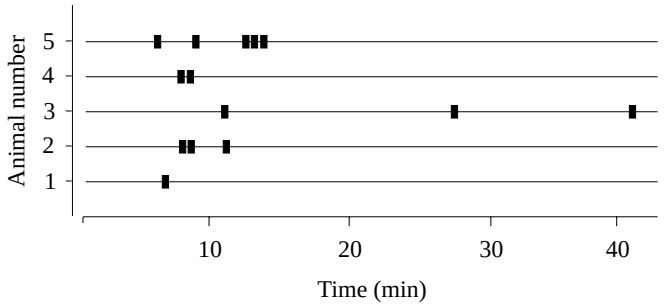

Fig. 2. The timing of episodes of vomiting (indicated by the vertical bars) in five crocodiles injected with veratrine (i.v.; 5 mg kg^{-1}) at time zero.

but ventilation appeared to be stimulated, manifested by contraction of the thorax and abdomen, and this was confirmed by inspection of the intra-abdominal pressure records (see below). Occasional lunging, as if to attack, was observed. Over approximately 5 min the animals returned to their normal quiescent state, occasionally walking around the observation pen.

In all animals immediately prior to the onset of emesis, one or more episodes of jaw snapping occurred with the head elevated and the animal raised on its forelimbs. Each episode lasted approximately 1 s, was usually audible and the abdominal wall was seen to contract. These episodes increased in frequency and intensity and in all the animals studied culminated in an episode of vomiting. Vomiting was accompanied by wide opening of the mouth, extension of the neck and to a lesser extent the abdomen, often a high-pitched sound and lateral shaking of the head. The vomit in four animals was liquid and mucoid in nature and in one animal a small seed was expelled. Following the vomiting, animals returned to their normal relatively quiescent state.

Specific observations

The observations above clearly demonstrate that veratrine can induce vomiting in the crocodile. The size of the animals made it difficult to obtain videotape recordings of sufficient quality for detailed frame by frame analysis of the behavioural responses. We therefore studied the response to veratrine (i.p.; 5 mg kg^{-1}) in a small (400 g) animal that had not been surgically prepared for physiological study. This study also had the additional advantage that the animal was known to have eaten recently.

Fig. 3 presents the temporal sequence of the major behaviours observed. With the exception of infrequent respiration, none of the behaviours plotted in Fig. 3 occurred during a comparable period of observation prior to veratrine injection. As in the larger animals, vomiting occurred after a latency of 6.4 min, when dark mucoid fluid was ejected, followed by another episode at 9.1 min when three pieces of chicken were expelled. Two other episodes were seen at 12.2 min and 13.6 min. In total six pieces of chicken were expelled weighing 18.6 g but, interestingly, post-mortem analysis of the gastric contents of this animal revealed the presence of another 33 g of food still in the stomach.

Analysis of this animal enabled the division of the emetic response into two components, which will be described separately:

Pre-ejection phase

This phase was characterised by relative inactivity during which small, rapid (approximately 0.1 s^{-1}) rhythmic contractions of the pharynx were visible and, most notably, multiple episodes of sneezing-like behaviour were observed. The latter were characterised by a brief but clearly identifiable sound made with the mouth partially open followed by an inspiration. Whilst ventilation occurred in isolation from the sneezing-like behaviour, it was rare. The other notable behaviour was jaw snapping, which was the earliest indication that vomiting was imminent. This behaviour consisted of opening and closing of the jaws approximately once per second, with the animal usually swallowing after each closure.

Vomiting

Jaw snapping appeared to mark the transition between the pre-ejection phase and the initiation of vomiting. Vomiting was

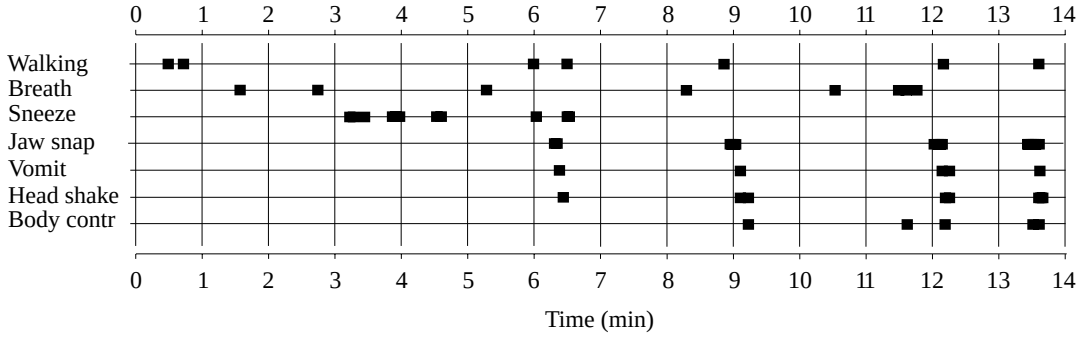

Fig. 3. The temporal pattern of several behaviours (indicated by bars) observed in one crocodile during multiple episodes of vomiting following administration of veratrine (i.p.; 5 mg kg^{-1}). Note the close temporal relationship between jaw snap, vomiting and head shaking. Body contr, body contraction (a brief, intense contraction of the thorax and abdomen associated with a hunched posture; see Fig. 4F–H). Data derived from analysis of video recording.

always preceded by jaw snapping, which appeared to build in intensity and frequency and was often accompanied by a postural change with the animal raising itself on its forelimbs and extending the neck (Fig. 4A–D). After a few jaw snaps it was noted that the pharyngeal region appeared to suddenly become distended (Fig. 4E), and jaw snapping was no longer followed by a swallow. During one emetic episode it was possible to see a piece of food in the pharynx (Fig. 4F), which occurred coincidentally with relaxation of the throat and wide opening of the mouth. Pieces of food or fluid were not expelled from the mouth with any great force but were ejected by powerful lateral shaking movements of the head with the mouth agape (Figs 3, 4G,H). Ejection was sometimes accompanied by a brief high-pitched vocalisation.

Physiological study

Recordings of the electrocardiogram and intra-abdominal pressure were obtained in three of the larger animals. In two of these animals arterial blood pressure was also recorded.

The typical pattern of intraperitoneal pressure and blood pressure changes associated with vomiting is illustrated in Fig. 5B. This shows a progressive increase in the amplitude of the intraperitoneal pressure culminating in two large, longer duration oscillations superimposed upon an overall rise in baseline pressure. As far as was possible to ascertain, the jaw snapping was associated with the initial oscillations in intraperitoneal pressure, whereas the appearance of vomit was associated with the larger contractions at the latter part of this pressure complex. Analysis of nine episodes of vomiting in

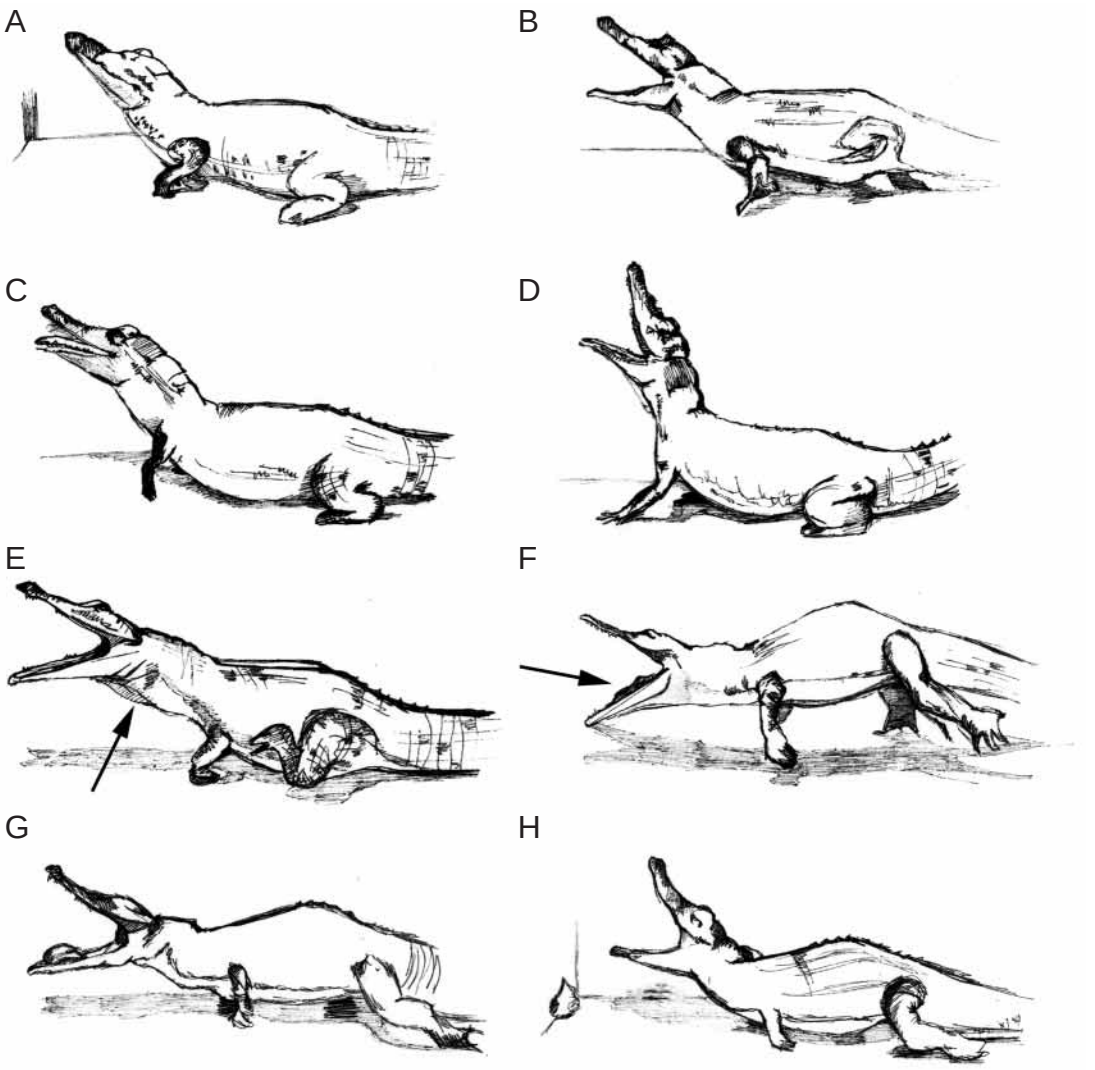

Fig. 4. A sequence of drawings made from frame-captures of video recordings of one vomiting episode from the crocodile, whose behaviours are plotted in Fig. 3, following injection of veratrine (i.p.; 5 mg kg^{-1}). The sequence shown lasted approximately 2 s. (A–D) The preparatory behaviour of jaw snapping accompanied by a postural change with the animal raising itself on its forelimbs and extending the neck (D). This was followed by pharyngeal distension (E, arrow) with gastric contents (a piece of chicken) visible in the mouth shortly after (F, arrow), coincident with relaxation of the throat and wide opening of the mouth. Solid gastric contents or fluid were ejected by powerful lateral shaking movements of the head with the mouth agape (G,H).

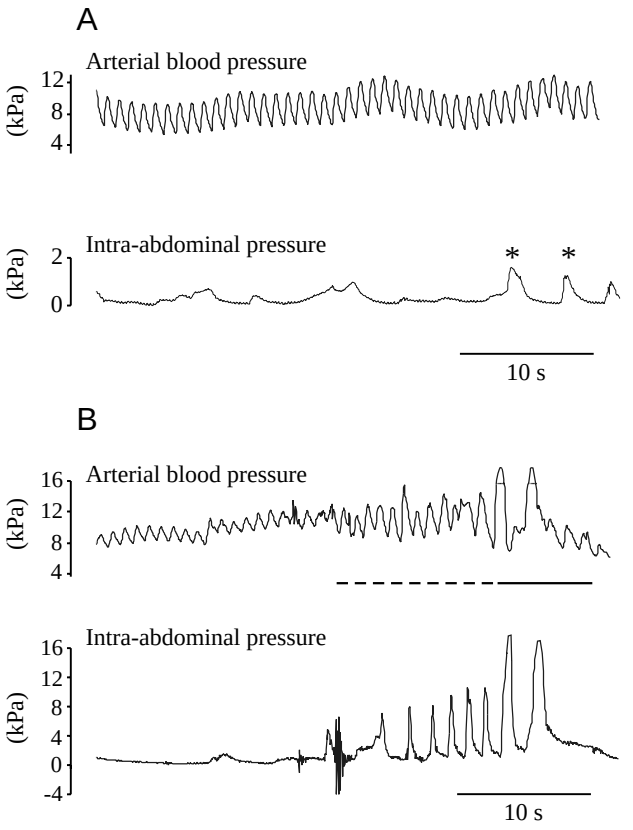

Fig. 5. (A) Recording of arterial blood pressure and intra-abdominal pressure (an index of respiration) in an unrestrained, untreated crocodile. *Spontaneous breaths. (B) Recording of arterial and intra-abdominal pressure during an episode of vomiting induced by veratrine (i.v.; 5 mg kg^{-1}). The dashed line indicates the period when jaw snapping was observed and the solid line when vomiting occurred.

three animals showed that the mean number of oscillations comprising an emetic episode was 9.1±0.7 over a period of 29.7±3.6 s. The increases in intraperitoneal pressure did not occur at regular intervals and the usual pattern was that the last one or two contractions were not only of longer duration but also occurred after a pause, as can be seen in Fig. 5B. The mean amplitude of the largest pressure rise during each emetic episode was 7.0±0.9 kPa, compared with 0.7±0.1 kPa for the rises in intra-abdominal pressure associated with inspiration in the same animals. The largest pressure rise recorded during an emetic episode was 14.2 kPa.

Veratrine did not have any effect on baseline arterial pressure. However, oscillations in arterial pressure were seen to accompany the larger increases in intra-abdominal pressure that accompanied emesis (Fig. 5).

The baseline heart rate in three animals was 35±3 beats min^{-1} and this increased to 48±8 beats min^{-1} in the minute immediately preceding the first emetic episode. In the minute following the emetic episode the heart rate was 58±2 beats min^{-1}. In two animals it was possible to record the ECG following the first emetic episode and this revealed that the heart rate remained elevated for 30 min after the first emetic episode at which time recording stopped.

Discussion

This study has demonstrated for the first time under experimental conditions that the crocodile can vomit in response to an emetic stimulus that induces emesis in other species. Although we have demonstrated that *Crocodyus porosus* can vomit, the strictly limited number of animals which it was possible to study meant that we were unable to investigate the effect of age, size, sex and the volume and nature of the gastric contents on the response. Here, we compare the mechanics of emesis in *Crocodylus porosus* with that observed in other vertebrates. The physiological regulation and functional significance of this emetic response are also considered.

Mechanics of the response

Prior to vomiting all vertebrates studied have a prodromal preparatory phase consisting of a particular set of behaviours (e.g. head shaking and mouth gaping in fish, Andrews et al., 1998; walking backwards and chin rubbing in ferrets, Bermudez et al., 1988). In mammals, vomiting is usually, but not inevitably, preceded by retching. Retching involves activation of the diaphragm and abdominal muscles as in vomiting, but there is no expulsion. The function of retching is unclear but it is proposed to be involved in overcoming the resistance to expulsion at the gastro-esophageal junction. In crocodiles, no direct behavioural parallel to retching was noted. However, the jaw snapping could be considered equivalent, as it occurred immediately prior to vomiting and was clearly a preparatory manoeuvre. In one animal, food appeared in the mouth immediately following the snapping. We propose that the snapping behaviour is linked to the entry of food into the oesophagus from the stomach. The snapping appeared to occur simultaneously with the small elevations in abdominal pressure whereas vomiting was clearly accompanied by larger and more sustained rises in abdominal pressure. These could be distinguished from normal ventilation as they occurred in bursts rather than singly and were approximately 10 times the amplitude of the pressure changes associated with respiration.

Crocodiles lack a muscular diaphragm separating the thoracic and abdominal cavities (Young, 1962; Gans, 1970; Grigg and Gans, 1993) and which provides the major force for expulsion of the vomitus in mammals (Borison and Wang, 1963). This necessitates that the mechanism for vomiting in the crocodile differs from that of mammals.

Based on the behavioural and physiological observations in the present study, we propose that the main force for the expulsion of vomitus in *Crocodylus porosus* is elevation of intra-abdominal pressure compressing the stomach. Intra-abdominal pressure is elevated by rhythmic contractions of increasing intensity of a number of abdominal muscles. Of particular relevance are the following. (1) The ‘diaphragmatic’

muscle, two lateral bands of muscle stretching from the anterior face of the pelvic girdle to the liver, which itself is intimately connected to a radial sheet of connective tissue separating the pleural and peritoneal cavities (Gans, 1970). Contraction of this muscle moves the liver caudally (Gans, 1970), increasing intra-thoracic volume and decreasing intra-abdominal volume with the effect of increasing intra-abdominal pressure (see Fig. 5). (2) Simultaneous contraction of the transversus abdominis, rectus abdominis and possibly the oblique abdominis internus muscles (Chiasson, 1962) will also tense the abdominal wall, contributing to the rise in abdominal pressure, and amplify the effect of the m. diaphragmaticus contraction. It is noteworthy that it is contraction of the transverse musculature of the abdomen that is proposed to move the liver anteriorly during expiration (Gans, 1970). However, in vomiting, to achieve the maximum increase in intra-abdominal pressure it appears likely that there is co-activation of the m. diaphragmaticus and the transverse muscles, suggesting that vomiting may be achieved by a specific motor programme, as is the case in mammals. Recordings from these two muscle groups should be the focus of electromyographic studies.

The above description ascribes an essentially passive role to the stomach; however, this requires direct investigation, particularly as the pylorus is very muscular (Davenport et al., 1990; Skoczylas, 1978). In addition, contraction of the powerful striated muscle of the oesophagus may also be involved in moving material from the stomach to the mouth.

The wide opening of the jaws, extension of the neck and the lateral shaking of the head are all reminiscent of the inertial feeding and shake-feeding behaviours described in crocodilians (Taylor, 1987, Cleuren and De Vree, 1992). Gans (1952) commented that in some snakes, oral expulsion of food was accompanied by a wide gaping of the mouth and a rapid whipping motion of the head and neck. Thus the final motor actions of emesis culminating in the oral expulsion of gastric contents could be considered to be inertial feeding acting in reverse.

Physiological regulation and functional significance

The results from this study have demonstrated that vomiting in the Estuarine crocodile is associated with a number of specific behaviours. Whilst we have not performed studies to identify the site and mechanism by which veratrine induces emesis in crocodiles, it is not unreasonable to assume that it is similar to that in other investigated species. In the cat and the dog, the site of action is the peripheral terminals of the vagal afferents and/or their cell bodies located in the nodose ganglion. Whilst vagal afferents have not been demonstrated formally in the crocodile, neurophysiological studies demonstrating their presence in amphibia (Niijima, 1967), birds (Hodgkiss, 1981) and mammals (Grundy and Scratcherd, 1989) makes it highly likely that they are present in crocodiles. In addition, immunohistochemical studies (Karila et al., 1995) in *Crocodylus porosus* have identified in the nodose ganglion (the location of the cell bodies of vagal afferents) the presence of peptides (substance P, calcitonin gene related peptide CGRP), which in mammals are known to be neurotransmitters at the central terminals of the vagal afferents in the brainstem (Zhuo et al., 1997). Although the vagal afferents and nodose ganglion are the most likely site of action, a central site such as the area postrema, reported to be present in diapsid reptiles, cannot be excluded until more direct studies have been undertaken (Butler and Hodos, 1996).

The emetic reflex in *Crocodylus porosus* probably has two functions, both of which are found in other vertebrates: (1) a protective reflex to eject toxins accidentally ingested with food and (2) to provide a mechanism for the ejection of indigestible food residues (e.g. fur, claws) which, if left to accumulate, could obstruct the gut. Thus periodic vomiting may have a role in the feeding habits of *Crocodylus porosus*.

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