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REGULATION OF ARTERIAL BLOOD PRESSURE IN AUSTRALIAN TIGER SNAKES

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SUMMARY

1. Blood pressure was measured in the dorsal aorta of restrained, unanaesthetized tiger snakes (*Notechis scutatus*) at different body temperatures during graded, passive tilt. Aortic blood pressure in horizontal snakes showed no significant change over a range of body temperatures between 18 and 33 °C (mean of measurements on 16 snakes = 42·2 ± 1·98 mmHg), while heart rate increased logarithmically (Q_{10} approximately 2·5). Blood pressure was stable during heating and cooling between body temperatures of 15 and 30 °C, but the pressure was 10–50% higher during heating than during cooling.

2. Head-up tilt usually caused a brief fall in pressure at heart level followed by partial or complete recovery and tachycardia. At the cessation of tilt, there was a characteristic overshoot of the blood pressure followed by readjustment to control (pretilt) levels. Head-down tilt typically increased pressure which then either stabilized or returned toward pretilt levels. Heart rate changes during head-down tilt were not consistent in direction or magnitude. Stabilized pressures at mid-body usually increased following head-up tilt and decreased following head-down tilt, indicating physiological adjustment to posture change. Blood pressure control was evident at body temperatures ranging from 10 to 38 °C, but was most effective at the higher and behaviourally preferred temperatures.

3. Propranolol lowered heart rate but did not influence pressure in horizontal snakes. During head-up tilt propranolol eliminated or reduced tachycardia and sometimes reduced the efficacy of pressure compensation for tilt. Phentolamine increased heart rate, lowered blood pressure, and eliminated pressure regulation during tilt. The results suggest that sympathetically mediated reflexes assist central blood pressure regulation in the tiger snake, with vasomotor adjustments having greater importance than changes in heart rate.

INTRODUCTION

Regulatory aspects of blood circulation in snakes are of interest because of the morphology and behavioural adaptations of this group of reptiles. We recently reported the occurrence in snakes of adaptive trends in arterial blood pressure

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regulation: aquatic species have low arterial pressure and poor regulatory ability while terrestrial species are characterized by high pressure and good homeostasis (Seymour & Lillywhite, 1976). Terrestrial snakes are sensitive to the hydrodynamic effects of gravity and appear to provide ideal subjects for studies of arterial blood-pressure regulation. To date, little insight has been provided on mechanisms that could mediate blood pressure control in reptiles or in other poikilothermic vertebrates.

The present study was undertaken to characterize arterial blood pressure regulation in the terrestrial tiger snake, *Notechis scutatus* (Elapidae), and partially to assess the mechanism(s) by which blood pressure is regulated. The matter of blood pressure regulation in snakes is complicated by body temperature lability (poikilothermy) which has a profound influence on metabolism and circulatory dynamics. We therefore have examined the control of arterial blood pressure over a range of biologically relevant body temperatures. These determinations are desired before more elaborate cardiovascular functions can be properly studied.

MATERIALS AND METHODS

Observations were made on 16 adult tiger snakes, 65–126 cm in length and weighing between 205 and 669 g (mean weight = 359 g). The snakes were collected from southern localities in Victoria, Australia and were maintained in the laboratory for only a few days before use.

Surgical procedures were performed while snakes were anaesthetized in chipped ice and exposed briefly to vapours of halothane (Fluothane). The dorsal aorta was exposed by blunt dissection through a small mid-ventral incision located just cephalad of the vent. A catheter fashioned from polyethylene tubing (Clay Adams PE 50) and filled with heparinized saline (250 i.u./ml) was tied occlusively into the dorsal aorta and externalized by means of a lateral stab wound. The incision was closed with sutures, and the intravascular catheter was secured externally by suture to the body scales. Sutures were covered with cyanoacrylate adhesive.

The intravascular catheters were flushed daily and remained patent for variable periods up to a week or more. Snakes were occasionally allowed to drink water during this period.

For measurement of arterial blood pressure, the unanaesthetized snakes were held in individually fitted Perspex tubes and allowed at least 24 h to become accustomed to the restraint. The tubes straightened the snakes but allowed unimpaired respiratory movements. Blood pressures at heart level were recorded with a Statham P23 transducer coupled to a Grass model 79 polygraph. Heart rates were determined from the pressure trace.

The ability of snakes to compensate for shifts in intravascular pressure was assessed by subjecting them to graded, passive tilt. Snakes were rotated about their body centres to angles of 20, 30, 45, 60, and 90°, up or down, in a vertical plane. Experiments were conducted in a controlled-temperature room, and each snake's responses were measured at stabilized body temperatures of 10, 18, 23, 28, 33 and 38 °C. Colonic temperatures were measured with a thermocouple inserted about 10 cm through the vent. Responses of blood pressure to changing temperature during heating or cooling were determined in snakes transferred between rooms at 33 and 12 °C.

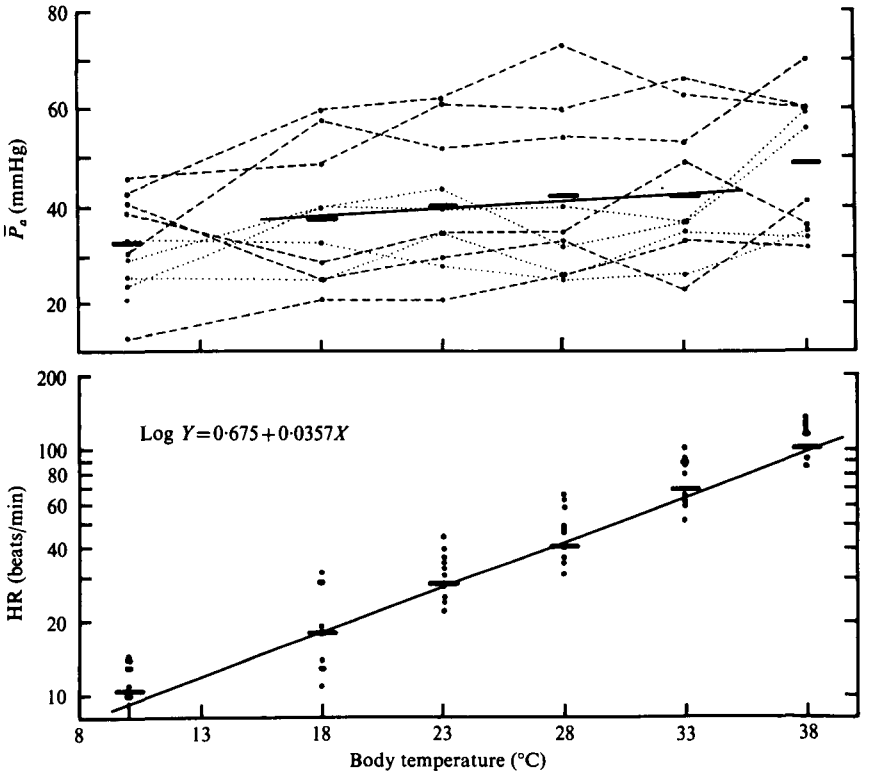

Fig. 1. Steady-state relations of heart rate and mean aortic blood pressure to body temperature in horizontal tiger snakes at rest. In the top graph, data points for male and female snakes are connected by dashed and dotted lines respectively. Heavy horizontal lines denote means. Regression lines were fitted to data by the method of least squares.

In experiments investigating acute responses to nerve-blocking agents, drugs were administered through the aortic catheter.

RESULTS

(A) *Blood pressure and heart rate in horizontal snakes at steady state*

Heart rate increased logarithmically with body temperature while blood pressure was comparatively stable, particularly at temperatures between 18 and 33 °C (Fig. 1). The slope of the regression line fitted to the blood pressure data in this range did not differ significantly from zero ($P > 0{\cdot}05$).

Blood pressure varied between snakes (Fig. 1) but was quite stable in any individual and, in general, followed a reproducible baseline at each stabilized body temperature. Broad fluctuations in blood pressure occurred only occasionally and almost always accompanied body movements by snakes. Minor, rhythmic oscillations of pressure were synchronous with breathing (Figs. 2, 5). Measurements from snakes that were shielded from visual stimuli by a dark cloth draped over the tube did not appear different from those obtained without the cloth. In most experiments snakes remained motionless through all angles of tilt. Data from snakes which struggled intensely were discarded.

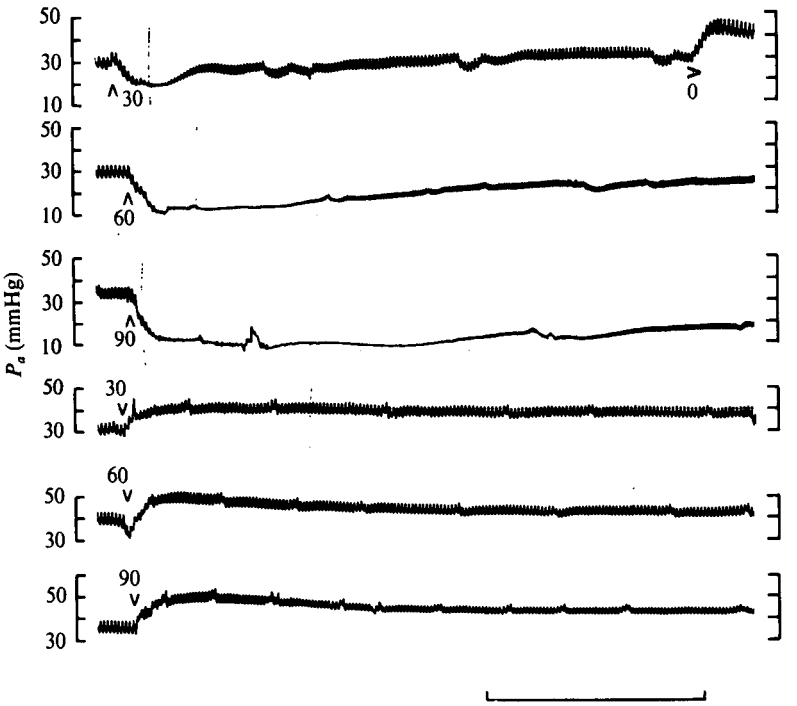

Fig. 2. Effects of tilting on aortic blood pressure (heart level) of a 380 g female tiger snake at 28 °C. Arrow marks denote the headward direction of the snake, and the small numbers identify the magnitude of tilt in degrees. Each tilt was from a horizontal position. The effect of breathing is also visible. The horizontal line denotes one minute interval.

Differences in arterial blood pressure between males and females were not statistically significant (t test, $P > 0{\cdot}05$), although the highest pressures were measured in large males (Fig. 1). There was no significant correlation between blood pressure at 33 °C and either body weight ($r = 0{\cdot}431$; $P > 0{\cdot}05$, D.F. = 13), total length ($r = 0{\cdot}264$; $P > 0{\cdot}05$, D.F. = 13), or heart rate ($r = 0{\cdot}503$; $P > 0{\cdot}05$, D.F. = 13).

(B) *Responses to tilting*

The characteristic response to head-up tilt was a brief drop in pressure (measured at the heart) followed by a slower recovery toward the pretilt pressure level (Fig. 2). The magnitude of the initial drop in pressure and both the time course and degree of recovery were variable, but after recovery the pressures were generally stable throughout the duration of tilt (from 1 to 10 min). At the cessation of tilt there was a transient overshoot of the arterial blood pressure (Fig. 2). Both the time course and magnitude of pressure recovery during tilt were related to temperature. Pressure recovery required several minutes at 10 °C, but usually occurred within a fraction of a minute at temperatures $\geqslant$ 28 °C. Responses of different snakes were variable. Three snakes failed to regulate pressure when tilt angles exceeded 45°, whereas two snakes showed almost instantaneous regulation at all tilt angles where body temperature exceeded 18 °C.

We assume that the centre of each snake approximates the passive hydrostatic indifferent point of the arterial blood column, where intravascular pressure i

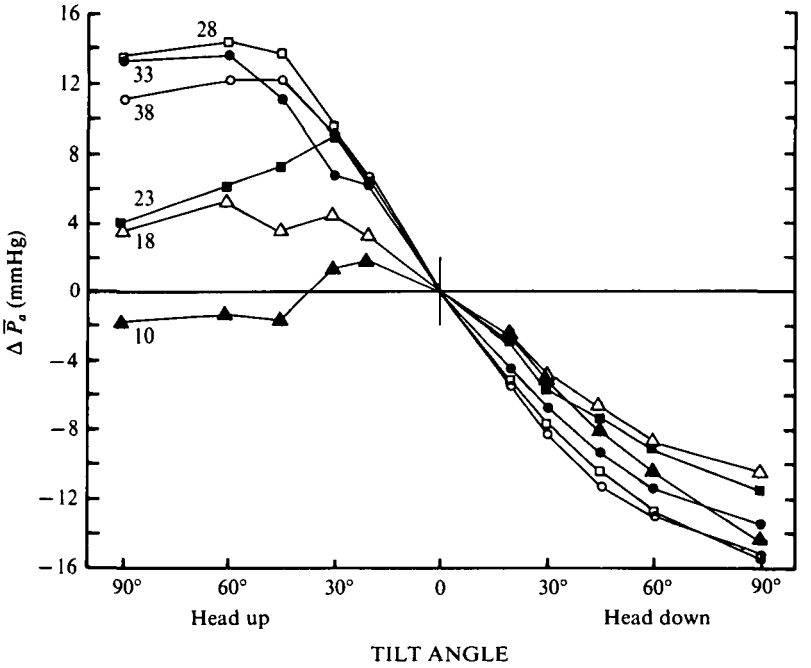

Fig. 3. Changes in mean aortic blood pressure calculated at mid-body during graded, passive tilting of tiger snakes at different body temperatures. Data points represent mean stabilized values for snakes that were inactive at all angles of tilt, and are depicted by symbols identifying the body temperature (small numbers on graph).

unaffected by tilting alone (for discussion see Gauer & Thron, 1965). Stabilized pressure changes at mid-body of tiger snakes in response to tilt thus represent arterial blood pressure adjustments which compensate for the hydrostatic shifts that occur with tilting (Fig. 3) (see Seymour & Lillywhite, 1976). Regardless of how well a snake regulated pressure during head-up tilt at high temperatures, the efficacy of regulation was consistently reduced during head-up tilt at low temperature. At 10 °C, stabilized pressure at mid-body actually decreased during head-up tilt (Fig. 3), suggesting pooling of blood in the lower vasculature. When blood pressure either dropped to very low levels (< 10 mmHg) or decreased by a proportionally large decrement ($> 50\%$), snakes frequently appeared uncomfortable and struggled inside the tube.

Tachycardia usually accompanied pressure recovery during head-up tilt (e.g. Fig. 2), but it was not essential for the restoration of arterial blood pressure in all individuals. The magnitude of increases in heart rate was positively correlated with the magnitude of head-up tilt and was maximal at higher body temperatures (Fig. 4). Heart rate at 10 °C increased little with head-up tilt. In response to head-down tilt, changes in heart rate were relatively small and occurred in either direction at all temperatures tested (Fig. 4).

During the initial and brief pressure drop following head-up tilt, decrements of systolic pressure exceeded those for diastolic pressure, and pulse pressure decreased. Stabilized pulse pressures during head-up tilt were typically reduced relative to that in pretilt controls, particularly at greater angles of tilt and at lower body temperatures (Fig. 2). The recovery of diastolic pressure during tilt generally exceeded that for

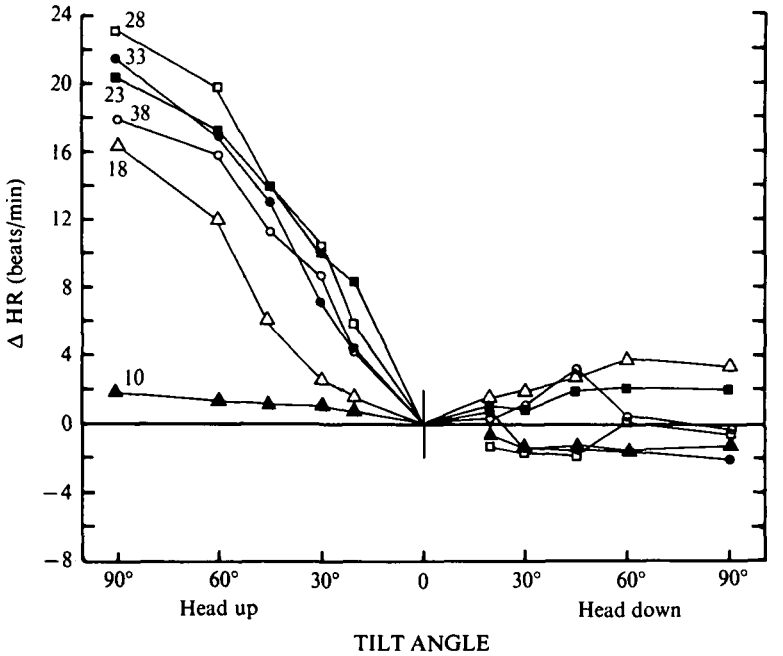

Fig. 4. Changes in stabilized heart rate during graded, passive tilting of tiger snakes at different body temperatures. Symbols as in Fig. 3.

systolic pressure, and an increased peripheral resistance was suggested particularly in cases where the runoff slope flattened in the absence of changes in heart rate.

During the initial response to head-down tilt, increments of systolic pressure usually exceeded those for diastolic pressure, suggesting a transient increase in stroke volume. As pressure recovery proceeded with head-down tilt, pulse pressure either remained unchanged from the horizontal condition or decreased somewhat, particularly at steeper angles of tilt (Fig. 2). Stabilized changes in systolic and diastolic pressures during head-down tilt were, in general, similar.

(C) *Pharmacological effects*

The effects of β-adrenergic blockade on blood pressure regulation were tested in 20 experiments on 10 snakes given propranolol (a β-adrenoreceptor antagonist) in doses from 1 to 10 mg/kg. The effects of propranolol on blood pressure were basically similar in snakes tilted with body temperatures of 18, 28, 33, and 38 °C. In horizontal snakes propranolol consistently reduced heart rate but had little effect on arterial blood pressure (Table 1). During head-up tilting, propranolol usually prevented increases in heart rate and reduced pressure control (Table 2). Responses of treated snakes to head-down tilt were generally similar to those in controls. In three experiments, atropine (0·2–1·2 mg/kg) given in combination with propranolol had effects quantitatively similar to those in snakes given propranolol alone.

The effects of α-adrenergic blockade were tested in 12 experiments involving 8 snakes given phentolamine (an α-adrenoreceptor antagonist) in doses from 1 to 5 mg/kg. The effects of this drug were similar in snakes tilted with body temperatures of 18, 33 and 38 °C. Phentolamine characteristically lowered blood pressure and

Table 1. *Effects of propranolol and phentolamine on heart rate and mean aortic blood pressure at mid-body in horizontal tiger snakes*

No. experiments/ animals	Treatment	Change from untreated control (%)	
		Heart rate	Pressure
12/7	Propranolol	−21±4	7±4
5/4	Phentolamine	39±10	−24±13

Values are mean ± standard error. Data for experiments at different T_b have been pooled (see text).

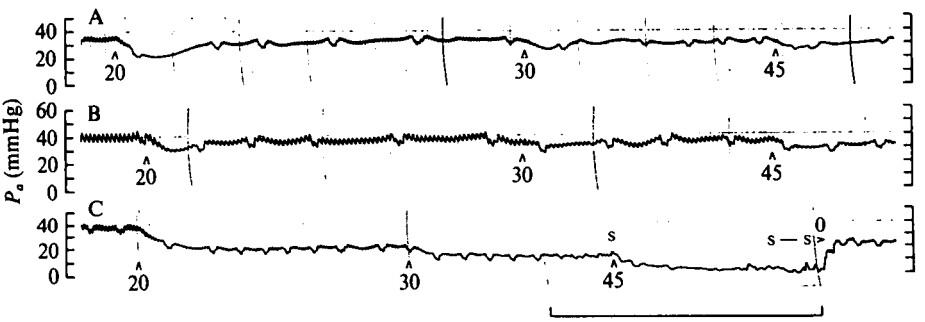

Fig. 5. Effects of graded, passive tilting on aortic blood pressure (heart level) of a 250 g female tiger snake at 33 °C. (A) Untreated control; (B) effects of 0·5 mg propranolol plus 0·06 mg atropine; (C) effects of 1 mg phentolamine. One minute intervals are indicated by the horizontal line, and 's' denotes period of struggle by snake. Note that pressure in C does not overshoot the pretilt (horizontal) level at the cessation of tilt. Tilting increased heart rate in A but had no effect on heart rate in B and C.

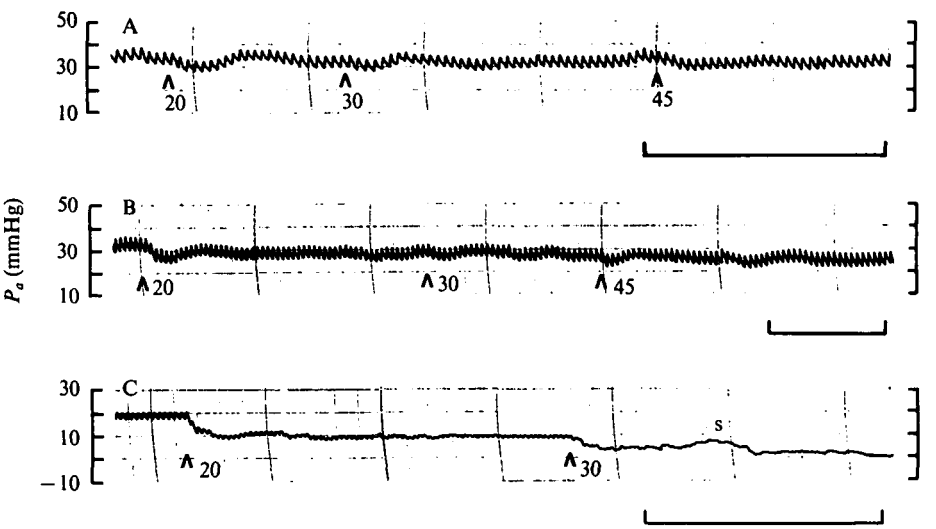

Fig. 6. Effects of graded, passive tilt on aortic blood pressure (heart level) of a 256 g male tiger snake at 33 °C. (A) Untreated control; (B) effects of 1 mg propranolol; (C) effects of 1 mg phentolamine. Symbols as in Fig. 5. Note the rapidity of pressure compensation and lack of tachycardia in A and B.

Table 2. *Effects of propranolol and phentolamine on heart rate and mean aortic blood pressure at mid-body of tiger snakes during passive 45° tilt*

No. experiments/ snakes	Treatment	Tilt	Change from pretilt control (%)	
			Heart rate	Pressure
14/8*	None	Up	23±6	24±5
12/8	Propranolol	Up	0±5	9±8
5/4	Phentolamine	Up	42†	−35±14
12/8*	None	Down	1±3	−18±3
8/7	Propranolol	Down	3±1	−23±3
3/3	Phentolamine	Down	−12±4	16±11

* Controls (no treatment) include tilting (at comparable temperatures) of all snakes subsequently tilted with drug treatments.

† Single record only (heart rates could not be told from records obscured by low pulse pressure and/or physical activity on the part of the snake).

Values are given as in Table 1. Data for experiments at different T_b have been pooled.

induced tachycardia in horizontal snakes (Table 1). Snakes given phentolamine, alone or in combination with propranolol, were unable to regulate pressure during tilting (Table 2; Figs. 5, 6).

(D) *Heating and cooling*

Eleven experiments on three snakes showed that arterial pressure was quite stable during heating or cooling, while heart rate changed with temperature (Q_{10} varied roughly between 2 and 3) (Fig. 7). Both changes in heart rate and stability of blood pressure were maximal at body temperatures greater than 20 °C. The most pronounced stability of blood pressure occurred in snake A, in which it varied by only 1 mmHg during heating (Fig. 8). In snakes B and C, pressure tended to increase between 15 and 20 °C but stabilized at temperatures between 20 and 30 °C. In all three snakes blood pressure was roughly 10–50% higher during heating than during cooling. Heart rate patterns showed no consistent differences between heating and cooling conditions.

Propranolol (1·5–4·0 mg/kg) in combination with atropine (0·75 mg/kg) reduced heart rate but did not significantly alter the level or stability of arterial pressure during heating between 15 and 30 °C (Fig. 7A, B). Phentolamine (1·5–4·0 mg/kg) elevated heart rate and reduced blood pressure 40–70% during heating (Figs. 7A, C; 8) and 5–30% during cooling (Fig. 7B).

Rates of heating and cooling between 15 and 30 °C were compared by calculating the instantaneous change in body temperature (expressed as °C/min) at 22·5 °C, the point at which the absolute difference between body temperature (T_b) and ambient temperature (T_a) was identical during both heating and cooling, from the equation

$$dT_b/dt = 2{\cdot}303S(T_b - T_a)$$

where S is the slope of the line relating the difference between T_b and T_a to time, and 2·303 is the base of natural logarithms (Bartholomew & Tucker, 1963). The slope of the line was determined from a semilogarithmic plot of the difference between T_b and T_a versus time by the method of least squares.

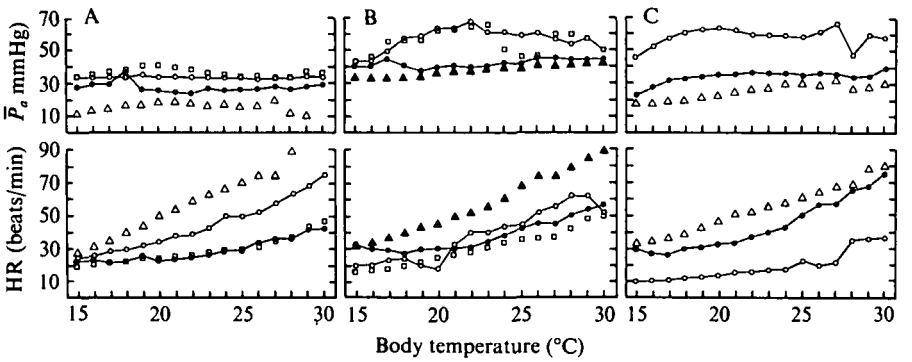

Fig. 7. Relations of heart rate and mean aortic blood pressure to body temperature in three tiger snakes (A = ♀, 250 g; B = ♂, 669 g; C = ♀, 413 g) during heating and cooling at horizontal rest. Symbol identifications are as follows: ○ = heating, no treatment; ● = cooling, no treatment; □ = heating, atropine+propranolol; △ = heating, phentolamine; ▲ = cooling, phentolamine. Note that symbols for heating or cooling are open or closed respectively. For clarity of presentation, data points for experiments without drugs (untreated controls) are connected by solid lines.

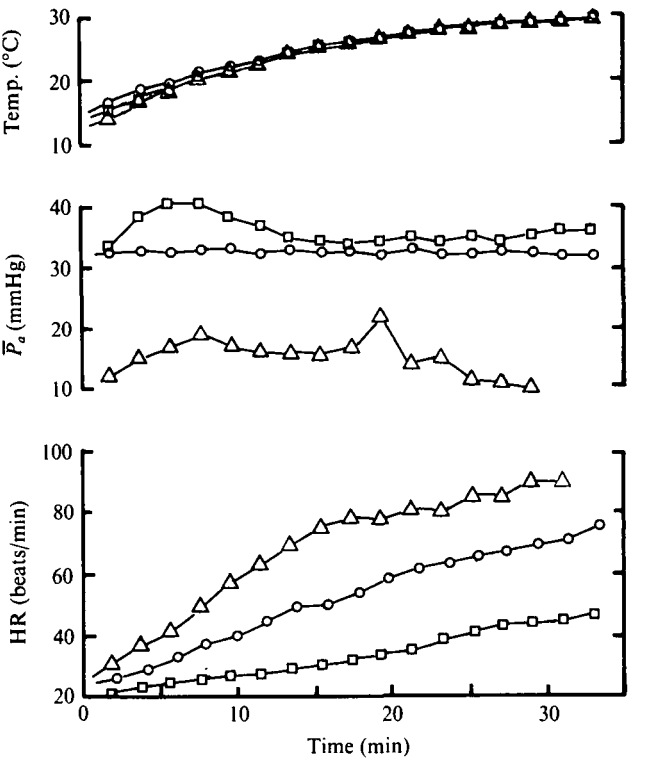

Fig. 8. Moment-to-moment changes in heart rate and mean aortic blood pressure during heating in snake A of Fig. 7 at horizontal rest, with and without drug treatment. Symbols as in Fig. 7.

Table 3. *Instantaneous rates of change in body temperature at 22·5 °C expressed as °C/min, in tiger snakes heated or cooled between body temperatures of 15 and 30 °C*

Snake	Wt. (g)	Condition	Rate	Ratio $\frac{\text{cooling}}{\text{heating}}$
A	250	Cooling	−1·10	1·21
		Heating	0·91	
		Heating P+A	0·87	
		Heating Ph	0·66	
B	669	Cooling	−0·75	1·42
		Heating	0·53	
		Cooling Ph	−0·87	
		Heating P+A	0·47	
C	413	Cooling	−0·85	1·16
		Heating	0·73	
		Heating Ph	0·74	

A = atropine. P = propranolol. Ph = phentolamine.

Rates of cooling exceeded rates of heating by as much as 42%. Drug treatments did not appear to alter rates of temperature change consistently (Table 3).

DISCUSSION

Functional properties of the cardiovascular system differ markedly in different vertebrates (Johansen, 1972). The influence of gravitational forces in air appear to have afforded important selection pressures in determining both structural and functional qualities of the cardiovascular system in snakes (Seymour & Lillywhite, 1976). The tiger snake is an active, terrestrial species characterized by relatively high levels of arterial pressure and a heart-to-head distance only 16% of the total body length; hydrostatic compensation for postural changes is superior in tiger snakes when compared with other less terrestrial snakes of close phylogenetic affinity (see also Seymour & Lillywhite, 1976).

Previous studies of blood pressure in reptiles have provided little quantitative information concerning the variability of pressure within a population of animals (Johansen, 1959; Templeton, 1964; Stephens, 1976). In the present study, mean arterial blood pressure of tiger snakes varied by as much as 50 mmHg between individuals at the same body temperature (Fig. 1), nearly extending the range of pressures known for reptiles generally (Table 4). Whether this variability is attributable to age, excitement level, genetic or other factors is not clear, but comparable variability is known in mammals (e.g. Schneider & Truesdell, 1922; Edholm, 1940). Regardless of their level, the arterial blood pressures were repeatable and were maintained by reflex mechanisms discussed below.

(A) *Regulation of arterial pressure during tilting*

The effects of passive head-up tilting on the systemic blood pressure of reptiles has been studied only in the iguana lizard (Hohnke, 1975) and in several species of aquatic and terrestrial snakes (Seymour & Lillywhite, 1976). The characteristic

Table 4. *Levels of arterial blood pressure in conscious reptiles*

Species	Temperature (°C)	Site of measurement	Pressure, mmHg (systolic/diastolic or mean)	Data source
Crocodilia				
Alligator mississippiensis	(22–27)	Femoral artery	28/17	Andersen (1961)
Chelonia				
Chelydra serpentina	Not given	Right aortic arch	19/11	Steggerda & Essex (1957)
Chrysemys picta, *Pseudemys scripta*	24–26	Axillary artery	23/18	Stephens (1976)
Chelonia oblonga	Not given	Carotid artery	27	Wooley (1959)
C. mydas	18–23	Carotid artery	47/40 s	Berkson (1966)
Squamata: Sauria				
Trachydosaurus rugosus	Not given	Carotid artery	40 s	Wooley (1959)
Tubinambis nigropunctatus	(Probably 28)	Femoral artery	48	Baker *et al.* (1972)
Iguana iguana	(Probably 28)	Femoral artery	50	Baker *et al.* (1972)
	Not given	Femoral artery	75 s	Hohnke (1975)
Sauromalus obesus	25–45	Carotid artery	38–100/30–84*	Templeton (1964)
Squamata: Serpentes				
Hydrophis ornatus	26–29	Dorsal aorta	22	Seymour & Lillywhite (1976)
Notechis scutatus	26–29	Dorsal aorta	49	Seymour & Lillywhite (1976)
Tripodonatus natrix, *Vipera berus*	Not given	Dorsal aorta	50–60/40–50* 88/66 s (highest)	Johansen (1959)
Boiga dendrophila	26–29	Dorsal aorta	74	Seymour & Lillywhite (1976)
Coluber (= *Natrix*) *natrix*	Not given	Not given	89	cited in Lehmann (1925)

s Single measurement.
* Range or average range of measurements.

response of tiger snakes to head-up tilt consists of an initial and relatively abrupt fall in pressure followed by recovery of the pressure to a stable level which is maintained for the duration of tilt (Figs. 2, 5). The recovery of pressure is usually accompanied by a reflex tachycardia and by an apparent reduction of pulse pressure; both are related in magnitude to the angle of tilt (Figs. 2, 4). The cardiovascular responses to tilting observed in snakes appear basically similar to those reported for mammals (Wald, Guernsey & Scott, 1937; Edholm, 1940; Conklin & Dewey, 1941; Mayerson, 1942; Liu *et al.* 1967; Parra & Vidio, 1969; Antonaccio, 1971; Constantine, McShane & Wang, 1971; Nolan & Bentley, 1978) and imply similar regulatory reflexes.

Three aspects of our data point convincingly to an increase of peripheral resistance during head-up tilting in tiger snakes. First, good pressure regulation was evident in a few snakes in which heart rate did not change during tilting. Secondly, the slope of the diastolic pressure curve became less steep during pressure recovery in most snakes, including those showing no change in heart rate. Third, pressure regulation was completely abolished by phentolamine (Figs. 5, 6; Table 2), which produces vasodilation both by direct action on vascular smooth muscle and by competitive α-adrenoreceptor blockade (Goodman & Gilman, 1975).

The reduction of resting blood pressure in horizontal snakes by phentolamine but not by propranolol (see below) indicates a dominant role of peripheral resistance in the maintenance of central blood pressure. Phentolamine reduced arterial blood pressure in tiger snakes despite heart rate increments of nearly similar proportional magnitude (Table 1). The latter response probably reflects 'circulatory effort' to compensate for the lowered central pressure incurred by vasodilation of the resistance vessels. During tilting, phentolamine was often an order of magnitude more effective than propranolol in reducing the ability of the cardiovascular system to regulate aortic pressure. These data parallel similar findings in mammals (Antonaccio, 1971; Nolan & Bentley, 1978).

Although a reflex increase in total peripheral resistance may be sufficient for adequate pressure compensation for tilt, changes in heart rate also contribute to pressure regulation in tiger snakes. Increases in heart rate were eliminated and (on average) pressure recovery was significantly reduced during head-up tilt in tiger snakes that were given propranolol (Figs. 5, 6; Table 2). Propranolol is a competitive β-receptor antagonist that blocks adrenergic cardiac stimulation (Goodman & Gilman, 1975; Stephens, 1976). Atropine failed to modify the effects of propranolol, suggesting that, in tiger snakes, reflex changes in heart rate during pressure regulation are predominantly sympathetically mediated, as is apparently the case in iguana lizards (Hohnke, 1975). The reduction of heart rate by propranolol in tiger snakes that were horizontal (Table 1) indicates that there is normally a significant sympathetic drive on the heart in this species.

The ability of tiger snakes to regulate blood pressure during postural change is roughly comparable in the head-up and in the head-down position (Fig. 3). Inspection of pulse pressures at the onset of head-down tilt suggest that there is, in many cases, an immediate brief increase in stroke volume as occurs in mammals (Abel, Pierce & Guntheroth, 1963; Abel & Waldhausen, 1968). It is unlikely, however, that this increase is sustained in tiger snakes, for there is a tendency for pulse pressure to decrease as mean arterial blood pressure stabilizes, particularly at steeper angles of

tilt (Fig. 2). Changes in heart rate probably do not contribute significantly to pressure regulation in tiger snakes during head-down tilt (Fig. 4; Table 2). On the other hand, vasomotor adjustments are probably important since pressure regulation is impaired by phentolamine (Table 2).

Pressure regulation during head-up posture change is probably related to a necessity for maintaining perfusion pressures at the brain. With the head down, however, pressure control possibly functions to minimize excessive pressures in the pulmonary vasculature. A plasma-like exudate may be observed flowing from the glottis of snakes when the head or anterior body is kept low (Johansen, 1972).

(B) *Effects of temperature on arterial blood pressure*

Blood pressure in tiger snakes varies little over a broad range of temperature (Figs. 1, 7, 8) and is especially stable within a thermal range (16·7–33·8 °C) encountered in this species during the seasons of activity (Heatwole, 1976). These findings are perhaps related to the influence of circulatory reflexes which act to control pressure during posture change over a comparable range of body temperature (Fig. 3). The ability of tiger snakes to regulate arterial blood pressure is maximal within a range of body temperature that includes the behaviourally 'regulated' or 'preferred' temperature (approximately 33 °C determined in laboratory gradients; Lillywhite, unpublished). The loss of effective control at 10 °C (below normal activity temperatures) is correlated with a reduced ability to increase heart rate (Fig. 4), but we do not know if this relationship is causal.

Blood pressure during changing body temperature is stable in spite of large changes in heart rate. If ventricular systemic output increases during heating, as appears likely from the magnitude of changes in heart rate, then the resistance to flow must decrease owing to the change in blood viscosity and to a probable vasodilation in the peripheral vascular beds. The regulated influence of the latter factor on arterial pressure is suggested by the data on tilting and by the observation that both the level and stability of pressure are reduced by phentolamine during heating and during cooling (Figs. 7, 8).

Differences in rates of temperature change during heating and cooling of tiger snakes either reflect biological modifications of heat transfer or possibly are accountable to physical factors relating to the holding of snakes in tubes and to the respective levels of ambient water vapour pressure during heating and during cooling (Weathers, 1972). Water was noted condensing on snakes when they were removed from the 12 °C room to the 33 °C room. Since body temperature was followed between 15 and 30 °C, the heat gained from this initial condensation was not accounted for, and subsequent heat loss by evaporation possibly diminished heating rate. However, cooling rates have been noted to exceed heating rates in the snake *Natrix taxispilota* (Moler, 1970) and in the terrestrial turtles *Gopherus polyphemus* and *Terrapene carolina* (Spray & May, 1972).

Arterial pressure in tiger snakes is consistently higher during heating than during cooling (Fig. 7). This observation is compatible with the earlier finding in turtles and lizards that localized heating of the hypothalamus, entire body or body surface induces a rapid rise of blood pressure, whereas cooling produces the converse effect (Rodbard, Sampson & Ferguson, 1950; Heath, Gasdorf & Northcutt, 1968;

Morgareidge, 1972; Baker, Weathers & White, 1972). It has been suggested that these changes in blood pressure might be causally related to corresponding changes in heart rate (White, 1976), but this is difficult to reconcile in the present study where heart rate was not consistently higher during heating than during cooling (Fig. 7). Alternatively, the greater reduction of arterial blood pressure during heating than during cooling in tiger snakes treated with phentolamine suggests that the elevated pressure observed during heating might be attributable to vasomotor changes in peripheral vascular beds. It remains to be learned whether changes in circulatory parameters during thermal change have adaptive thermoregulatory significance in these snakes, or are merely related to pressure homeostasis *per se*.

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