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Ambient Temperature Regulates Drinking and Arterial Pressure in Eels

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ABSTRACT—Ambient temperature exerts strong influences on physiological processes in ectothermic animals. Thus, we have examined the effects of changes in water temperature on drinking and arterial blood pressure in seawater-adapted eels, *Anguilla japonica*. Temperature dependence was also examined with respect to the effects of atrial natriuretic peptide (ANP) on drinking and arterial pressure. When water temperature was altered abruptly from 18°C to 11°C or to 25°C, drinking rate consistently decreased or increased, respectively, in all fish examined. The temperature-response relationship was highly linear ($p < 0.001$) between 11°C and 25°C with a Q_{10} value of 2.45. Arterial pressure was significantly lower at 11°C compared with the level at 18°C, but no difference was observed between 18°C and 25°C. The change in hematocrit did not parallel that of temperature. Plasma Na^+ concentration did not change at different temperatures. Bolus injections of eel ANP at 10, 100, and 1000 pmol/kg decreased drinking rate and arterial pressure dose-dependently. The effects of ANP did not differ in terms of potency and efficacy at different temperatures except that the effects continued longer at lower temperatures. These results show that the ambient temperature causes profound effects on drinking rate in seawater eels even though Na^+ balance and blood volume were well maintained. The sensitivity to ANP, a physiological regulator of drinking in eels, was not altered by the temperature, suggesting an involvement of other factors in the thermogenic drinking that is demonstrated in this study.

Key words: Water intake, Blood pressure, Atrial natriuretic peptide, Eel, *Anguilla japonica*

INTRODUCTION

Temperature affects various physical properties such as the tertiary structure of proteins (enzymes and transporters) and membrane fluidity, resulting in profound changes in the metabolic rate and permeability of epithelial cells in ectothermic animals (Somero, 1978; Hazel, 1990, 1993; Rasio *et al.*, 1992; Bowden *et al.*, 1996). Since aquatic fishes, either in fresh water or in seawater, regulate water and electrolyte balance principally by fluxes across the gill epithelium, changes in ambient temperature may affect overall body fluid balance. In fact, changes in temperature have been shown to alter water and ion fluxes through cellular and paracellular pathways of the gill epithelium (Isaia, 1972; Maetz and Evans, 1972; Motaïs and Isaia, 1972; Skadhauge and Lotan, 1974; Carroll *et al.*, 1995; Nolan *et al.*, 2000). Thus, the ambient temperature appears to affect drinking and blood pressure through changes in blood volume and/or plasma osmolality in fish.

It is known that fish in fresh water drink little to avoid overhydration, whereas those in seawater drink much to cope with dehydration caused by the osmotic efflux of water across

the body surfaces (Evans, 1993). However, since drinking rate is highly variable among species, some freshwater fish drink more than seawater fish (Bentley, 1971). In *Anguilla* species, it has been recognized that *A. japonica* is generally a more copious drinker than *A. anguilla* (Maetz and Skadhauge, 1968; Hirano, 1974; Tierney *et al.*, 1995; Tsuchida and Takei, 1998). A similar difference was also observed in two closely-related elasmobranch species; the Japanese dogfish, *Triakis scyllia*, exhibits a much higher drinking rate than the European spotted dogfish, *Scyliorhinus cannicula* (Anderson *et al.*, 2001). Furthermore, we have preliminary results showing that the sensitivity to the vasodepressor effect of homologous CNP differs between the two dogfish species (N. Hazon and Y. Takei, unpublished data). These differences are most probably due to the species difference; however, ambient temperature may also be the cause because the European eel and dogfish are reared at much lower temperatures than the Japanese counterparts. A close correlation between drinking rate and ambient temperature has been observed in some teleost fishes (Motaïs and Isaia, 1972; Skadhauge and Lotan, 1974; Carroll *et al.*, 1995; see Fuentes and Eddy, 1997).

In the present study, we attempted to examine how ambient temperature affects drinking and arterial pressure in seawater-adapted *A. japonica*. To this end, water tempera-

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ture was abruptly changed from 18°C (rearing temperature of *A. japonica* in this laboratory) to 11°C (approx. rearing temperature of *A. anguilla*) or to 25°C (rearing temperature of *A. japonica* in heated culture pond). Seawater eels were used because they drink copiously at a constant rate. Changes in the effects of ANP, a possible physiological regulator of drinking in eels (Takei, 2000), were also examined on drinking and arterial pressure among the different temperatures. Plasma Na^+ concentration and hematocrit were measured to monitor the osmotic and volemic status of the fish.

MATERIALS AND METHODS

Animals:

Cultured, immature eels, *Anguilla japonica*, were purchased from a local supplier. They were maintained without feeding for a few days in a freshwater tank, and then transferred to a seawater tank and maintained there for at least two weeks before use. Water in the tank was continuously circulated, aerated, and regulated at 18°C. Since drinking rate depends on the body weight of the fish (Carroll *et al.*, 1995), eels of a similar size were used in the experiment (178.3 ± 9.2 g, $n=11$).

Surgical procedures:

Eels were anesthetized by immersion for 15 min in 0.1% (w/v) tricaine methanesulfonate (Sigma) neutralized with sodium bicarbonate. Vinyl tubes (o. d.: 1.5 mm) were inserted into the esophagus and stomach for measurement of drinking rate and for reintroduction of ingested water, respectively, as described previously (Takei *et al.*, 1998). Polyethylene tubes (o. d.: 0.8 mm) were inserted into ventral aorta for measurement of arterial pressure and into the dorsal aorta for repetitive injections and blood samplings. After surgery, eels were placed in a plastic trough through which aerated seawater continuously circulated at 18°C. The cannula in the ventral aorta was connected to a pressure transducer (DX-300, Nihon Kohden, Tokyo) and a polygraph (366 System, NEC-San-ei, Tokyo) for continuous recording of arterial pressure. Eels were allowed to recover for more than 18 hr post-operatively. The trough was covered with a black vinyl sheet to minimize the visual stress during the experimentation.

Experimental protocol:

The temperature of circulating water (ca. 20 liter) was changed abruptly in 5 min using a heating/cooling unit (HC-251A, AQUA Co. Ltd., Tokyo) as well as by replacement with heated or chilled seawater. The fluctuation of temperature was limited to $\pm 0.5^\circ\text{C}$. The temperature was changed in the following order; 18°C for 2 hr, 11°C for 2 hr, 18°C for 1 hr, 25°C for 2 hr, and 18°C for 2 hr. The periods of 18°C were placed after 11°C and 25°C to confirm that the drinking rate and arterial pressure returned to the normal level at 18°C. The drinking rate and arterial pressure became stable usually within 30 min after changes in temperature. These values were regarded as normal values of drinking rate and arterial pressure at each temperature. After the values reach equilibrium, synthetic eel ANP (Peptide Institute Inc., Osaka) was injected at 10, 100, or 1000 pmol/kg to examine its effects on drinking and arterial pressure. The injection volume was 50 μl followed by a flush of cannula with 50 μl of isotonic NaCl solution. The dead volume of cannula was ca. 30 μl . Blood (50 μl) was collected before initiation of a series of ANP injections for determination of normal values of hematocrit and plasma Na^+ concentration at each temperature. Na^+ concentrations in plasma were determined in an atomic absorption spectrophotometer (Z5300 Hitachi, Tokyo). All measurements were made in duplicate.

Calculations and Statistical analysis:

The Q_{10} value was calculated with the equation: $\log Q_{10} = (\log R(t_2) - \log R(t_1)) \times 10 / (t_2 - t_1)$, where $R(t_1)$ and $R(t_2)$ were the responses obtained at the temperature of t_1 and t_2 , respectively (Schmidt-Nielsen, 1997). Differences in drinking rate, arterial pressure, hematocrit and plasma Na^+ concentration were analyzed by ANOVA followed by Bonferroni/Dunn's test between different temperatures. Temperature-response and dose-response relationships were examined by the regression analysis followed by ANOVA to check the linearity of regression lines. Significance was determined at $p < 0.05$. All results are expressed as means $\pm$ SE of the mean.

RESULTS

Effects of temperature on drinking rate and arterial pressure

Acute alterations of ambient temperature caused profound

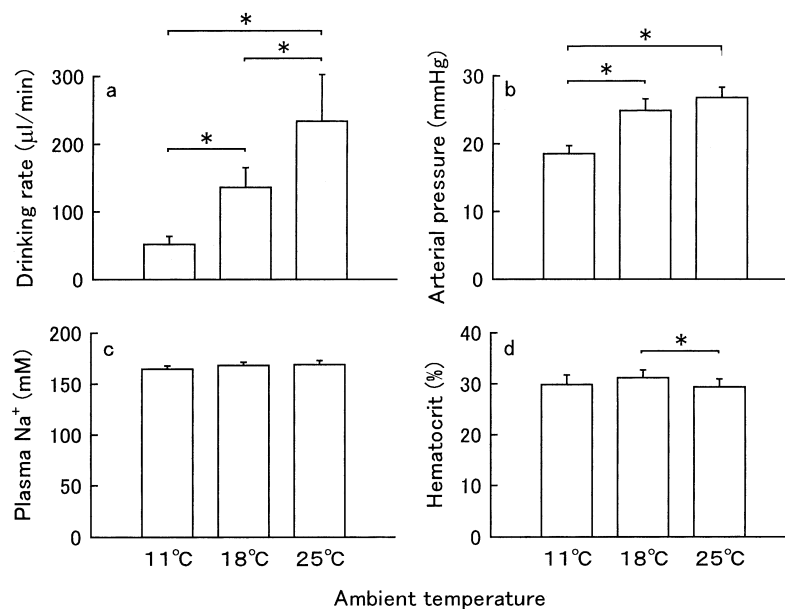


Fig. 1. Temperature-dependent changes in (a) drinking rate, (b) arterial blood pressure, (c) plasma Na^+ concentration, and (d) hematocrit in seawater-adapted eels ($n=7$). Values are means $\pm$ SE. * $p < 0.05$.

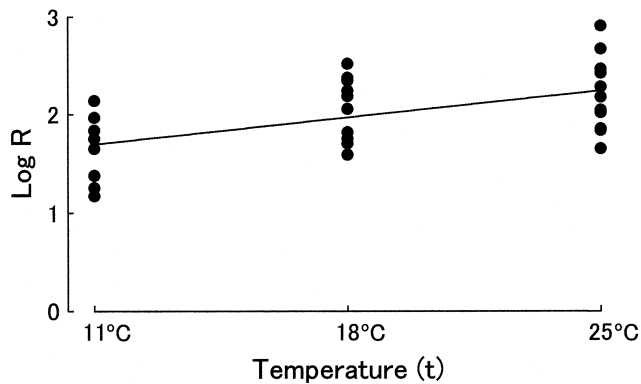


Fig. 2. Linear relationship between ambient temperature (X) and drinking rate (R) in logarithmic scale in seawater eels ($n=11$). The regression line is $\text{Log } R = 0.039t + 1.271$ ($r = 0.558$), which is highly linear ($p < 0.001$).

effects on drinking; all eels decreased drinking rate when temperature fell from 18°C to 11°C and increased it when temperature rose from 18°C to 25°C (Fig. 1a). The change in drinking rate occurred soon after changes in temperature, and the stable level, which was used as normal drinking rate at each temperature, was attained in 30 min. The stable drinking continued thereafter throughout the experimental period of 2 hr. The arterial pressure did not differ between 18°C and 25°C but it decreased after temperature dropped from 18°C to 11°C (Fig. 1b). Plasma Na^+ concentration did not change within the temperature range of 11°C and 25°C (Fig. 1c). The change in hematocrit was not temperature dependent between 11°C and 25°C (Fig. 1d).

Calculation of Q_{10} for drinking rate and arterial pressure

Since drinking rate (R) in logarithmic scale plotted against temperature (t) was highly linear ($p < 0.001$) between 11°C and

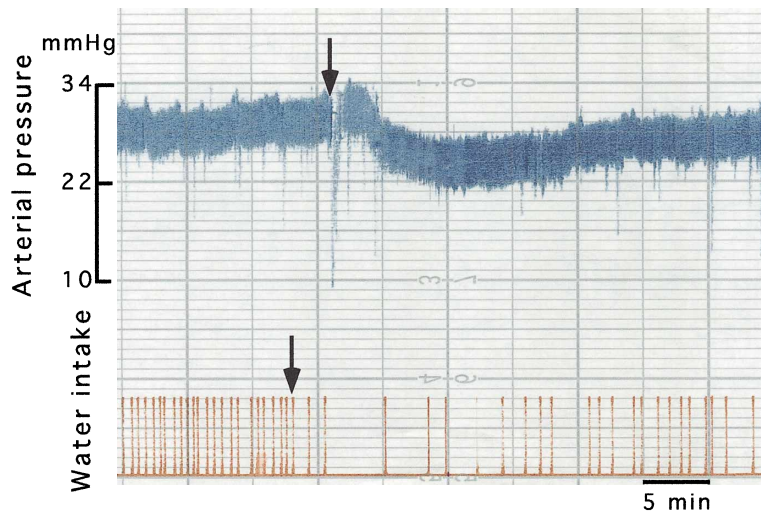


Fig. 3. An example of the recording of changes in drinking rate and arterial blood pressure after injection of 100 pmol/kg of eel atrial natriuretic peptide in a seawater eel. Arrow indicates the point of injection. Each spike for water intake represents 0.03 ml of ingested water measured by a drop counter.

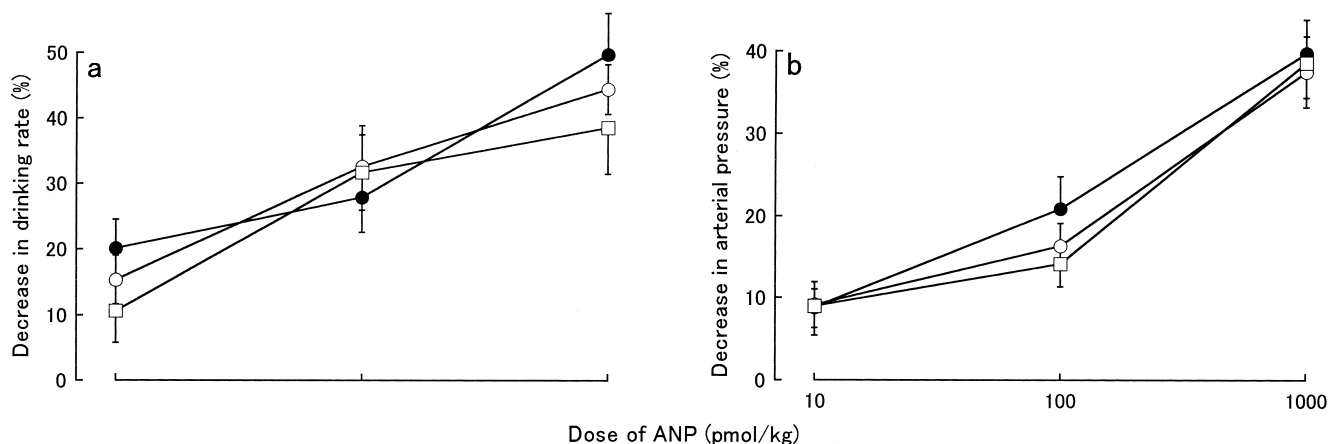


Fig. 4. Dose-response relationships of (a) antidipsogenic effect and (b) vasodepressor effect of eel atrial natriuretic peptide (ANP) in seawater eels ($n=7-11$) examined at 11°C ($\circ$), 18°C ($\bullet$), and 25°C ($\square$). Values are means $\pm$ SE. All dose-response relationships are linear at $0.004 < p < 0.02$.

25°C (Fig. 2), the Q_{10} value for drinking rate was determined based on the regression line ($\text{Log } R_{(t)} = 0.039t + 1.271$), which resulted in $Q_{10}=2.45$. The Q_{10} value for arterial pressure was 1.53 when it was calculated with the data at 11°C and 18°C where temperature-dependent changes were noted (Fig. 1b).

Temperature dependence of ANP effects

Intra-arterial injections of eel ANP inhibited drinking and decreased arterial pressure in seawater-adapted eels (Fig. 3). The effects of ANP on drinking and arterial pressure increased in a dose-dependent manner (Fig. 4a, b). However, the effects were not temperature-dependent in terms of potency and efficacy among the three temperatures examined. It was noted that the antidipsogenic and vasodepressor effects of continued longer when the temperature was lower.

DISCUSSION

It is generally believed that teleost fish in fresh water drink little while those in seawater drink abundantly to replace water lost by osmosis through the body surfaces (Evans, 1993). However, drinking rate is highly variable depending on the species. Some freshwater species drink even more than marine species if drinking rate is normalized for body weight (Bentley, 1971). This difference in drinking rate, therefore, may be due to species differences. In addition, however, it is also possible that the temperature of ambient water contributes to the difference as suggested in some teleost species (Maetz and Evans, 1972; Motaïs and Isaia, 1972; Skadhauge and Lotan, 1973; Carroll *et al.*, 1994, 1995; see Fuentes and Eddy, 1997). The present study provides further evidence to support the importance of temperature in the regulation of drinking in teleost fish.

In *Anguilla* species, it has long been recognized that Japanese eels, *A. japonica*, adapted to seawater generally drink much more than European eels, *A. anguilla* (Takei *et al.*, 1988; Tierney *et al.*, 1995). It was initially thought that the difference is due to the difference in the method of measuring the drinking rate, because an esophageal fistula was used for the measurement in Japanese eels while a radioactive tracer was used in European eels. However, recent data showed that in the dogfish, *Scyliorhinus cannicula*, the two methods measure similar drinking rate (Anderson *et al.*, 2001). It seems, therefore, that the difference in drinking rate between the two *Anguilla* species may be due to the difference in the ambient temperature. In Japanese eels, drinking was measured at 18–20°C, whereas in European eels, it was examined at 10–12°C. Since the current study shows that the drinking rate decreased to less than half at 11°C compared with at 18°C in Japanese eels, the drinking rate is almost the same between the two species if it is examined at a similar temperature.

In all teleost species thus far examined, positive relationships were always established between ambient temperature and drinking rate. However, the Q_{10} values were highly variable among species; 1–2 in the dab, *Limanda limanda* (Carroll *et al.*, 1995), 2.95 in the flounder, *Platichthys flesus* (Maetz

and Evans, 1972), 4.38–5.16 in the European eel (Motaïs and Isaia, 1972), and 4.97–9.48 in *Aphanius dispar* (Skadhauge and Lotan, 1973) if the values are calculated based on the data shown in the above papers. The Q_{10} value of 2.45 obtained in this study in the Japanese eel falls within this range. Since the temperature-response relationship of Japanese eels was highly linear between 11°C and 25°C compared with other species, the value should be highly reliable. Positive relationships have been obtained also between the ambient temperature and the water/sodium permeability across the body surfaces in some teleost fishes (Maetz and Evans, 1972; Motaïs and Isaia, 1972; Isaia, 1972). In contrast to the variability in drinking rate, the Q_{10} values were around 2 in all species examined.

In the dab, drinking rate increased as water temperature increased from 5°C to 14°C, but the rate decreased as temperature increased further to 25°C (Carroll *et al.*, 1995). Since water temperature in their natural habitat is approximately 14°C even in the summer, the decrease at high temperature may be due to the unnatural condition for the fish as shown by the increased mortality at 25°C. The eels used in the present study were cultured at 25°C in the culture pond in Japan. After purchase, they were acclimated at 18°C in the laboratory aquarium for more than 3 weeks before experimentation. Japanese eels also experience below 11°C in their natural habitat of inland water in the winter. Therefore, the temperatures between 11°C and 25°C used in the present study appear to be within a physiological range for the fish, which may explain the highly linear relationship between temperature and drinking.

In mammals, temperature-dependent increases in water intake have long been demonstrated and this phenomenon is called 'thermogenic drinking' (Fitzsimons, 1979). It is obvious that increased intake after long-term exposure to heat is caused by increased evaporative losses of water for body cooling. However, there is evidence suggesting that the heat itself is the cause of drinking (O'Connor, 1977). It is possible that thermo-sensitive neurons in the rostral hypothalamus are responsible for thermogenic drinking, although the data are still too conflicting to assess their roles (Fitzsimons, 1979).

In fish, it is not yet determined whether drinking is induced directly by increased temperature or secondarily by altered body fluid balance. The temperature dependence of permeability to water and Na^+ has been demonstrated in the gill epithelia of teleost fishes (Motaïs and Isaia, 1972; Maetz and Evans, 1972; Isaia, 1972). Since the permeability to water increases more rapidly than the permeability to Na^+ after an increase in temperature in European eels (Motaïs and Isaia, 1972), it is possible that hypovolemia occurs at higher temperature because of an enhanced loss of water across the gill of seawater fish. In contrast, hypervolemia may have occurred at high temperatures in the current study because the hematocrit decreased when ambient temperature was increased from 18°C to 25°C. An osmotic stimulus for drinking may not be involved either because plasma Na^+ concentration did not increase at higher temperatures. Therefore, enhanced drinking at higher temperature is caused by a stimulus other than

volemic and osmotic stimuli, possibly by a mechanism similar to the thermogenic drinking observed in mammals.

It is known that the potency and efficacy of hormones are vulnerable to changes in temperature in ectothermal fish because the tertiary structure of hormones and their receptors, as well as that of cytosolic enzymes responsible for information transfer from the receptors, are altered by the temperature (Somero *et al.*, 1978). In fact, it is suggested that the relative importance of angiotensin II in the regulation of drinking and arterial pressure differs depending on the ambient temperature in eels (Tierney *et al.*, 1995; Takei and Tsuchida, 2000). ANP has been shown to affect drinking and arterial pressure profoundly in eels and other teleost fishes (Duff and Olson, 1986; Lee and Malvin, 1987; Tsuchida and Takei, 1998). Since ANP is much more potent than angiotensin II for the regulation of drinking in eels (Takei, 2000), it is possible that the changes in drinking rate are related to the change in sensitivity to ANP. However, the present study showed that ambient temperature did not alter the sensitivity of eels to ANP-mediated inhibition of drinking. Further investigations are required to explore the mechanism of temperature dependence of drinking in fish.

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