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SOME FACTORS REGULATING WATER INTAKE BY THE EEL, *ANGUILLA JAPONICA*

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SUMMARY

1. Internal as well as external factors affecting water ingestion in the eel were analysed using oesophagus-cannulated eels.

2. Acute withdrawal of the blood induced an immediate drinking response in the freshwater eel, whereas infusion of a large amount of hypertonic saline interrupted the copious drinking observed in the seawater eel.

3. The freshwater eel responded to slow infusion of hypertonic NaCl solution by constant drinking.

4. Inhibition of drinking was observed in the seawater eel by distension of the stomach or intestine with isotonic mannitol solution.

5. The freshwater eel started drinking immediately after transfer to sea water, and stopped drinking immediately after return to fresh water.

6. Application of various salt solutions revealed that chloride ions are responsible for the induction of drinking in sea water.

7. Stimulation of drinking by chloride ions and inhibition by fresh water may be an anticipatory drinking behaviour, which facilitates adaptation of eels to both sea water and fresh water.

INTRODUCTION

It is well accepted that water ingestion is one of the essential ways in which teleosts maintain water balance in sea water, where they lose water osmotically across the body surface. On the other hand, in fresh water they are continually faced with the need to dispose of water which enters through the body surface, and drink little water (Maetz, 1970; Bentley, 1971). Transferring the eels, *Anguilla japonica* or *A. anguilla*, from fresh water to sea water results in an increase in plasma electrolytes and a decrease in body weight; maximal changes are observed 2 days after transfer (Oide & Utida, 1968; Mayer & Nibelle, 1970; Kirsch, 1972; Kirsch & Mayer-Gostan, 1973). Concomitantly a gradually increasing ingestion of sea water is observed, with a maximum between the 4th and 7th day after transfer, followed by a reduction and stabilization after 2–3 weeks (Oide & Utida, 1968; Kirsch & Mayer-Gostan, 1973). Increased drinking rate is observed after increasing the external salinity in *Tilapia mossambica* (Potts, Foster, Ruddy & Parry Howells, 1967), *Xiphister atropurpureus* (Evans, 1967), *A. anguilla* (Maetz & Skadhauge, 1968) and *Salmo gairdneri* (Shehadeh & Gordon, 1969). In the stenohaline *Carassius auratus*, an augmentation of the drinking rate is

also observed during adaptation to slightly hypertonic medium (Lahlou, Henderson & Sawyer, 1969). Water ingestion is induced in the freshwater eel by transferring to hypertonic sucrose solution (Sharratt, Bellamy & Chester Jones, 1964), and in the flounder when kept in hypertonic mannitol solution (Motais, 1967). These results suggest that ingestion is induced by reduction in extracellular fluid volume and/or elevation of plasma osmolality resulting from dehydration in a hypertonic environment.

Recently, Kirsch (1972) and Kirsch & Mayer-Gostan (1973) observed considerable ingestion of water at the moment of transfer to sea water, suggesting that the drinking reflex is triggered by a sensory stimulus or local dehydration. However, no further information seems to be available on the control mechanisms of drinking by teleosts. The present investigation was undertaken to clarify some regulatory factors in water intake by the Japanese eel, *Anguilla japonica*. Drinking rate was measured by cannulating the oesophagus, and effects of changes in external salinity, extracellular fluid volume, plasma osmolality and fullness of stomach and intestine were examined. Seawater-adapted eels were used to observe inhibition of drinking and freshwater-adapted eels to observe its induction. In addition, experiments which show induction of drinking by chloride ions in sea water, and inhibition by fresh water or the absence of chloride ions in the medium are also described. A preliminary account of parts of this work has been presented (Utida, Hirano & Kamiya, 1972).

MATERIAL AND METHODS

Japanese cultured eels, *Anguilla japonica*, weighing about 200 g, were purchased from a commercial source, and kept in a freshwater tank at 20 °C for at least a week before use. Some eels were then transferred to a seawater tank and kept there also for at least a week. After anaesthesia with a 0·1 % solution of methane tricaine sulphonate (MS 222), an incision was made longitudinally in the abdominal wall along the posterior half of the liver. A vinyl tube (1·5 mm in inner diameter) was inserted into the oesophagus at the entrance to the stomach and tied in place with cotton thread. The incision was then stitched and the eel was transferred to a plastic trough which was adjusted to the size of the eel. The cannula was connected to a drop counter and/or fraction collector for continuous recording of drinking or swallowing rate. Swallowed water did not enter the stomach. Well-aerated fresh water or sea water at 20 °C was passed through the trough from a cistern and returned to the cistern through a large reservoir with a filtering and thermoregulating system. The trough water could be changed from fresh water to sea water or *vice versa*, without disturbing the animal, by reversing a three-way valve and discarding the flowing water for about a 3-min period. In the experiments dealing with effects of various salt and mannitol solutions, however, the trough water was removed by suction pump and replaced with the new solution, which was not circulated but aerated directly.

In order to examine the effects of a decrease in extracellular fluid volume, blood was withdrawn from freshwater eels through a thin polyethylene cannula inserted into the pneumogastric artery. Expansion of extracellular fluid volume or elevation of plasma osmolality was induced in freshwater eels and in seawater eels by infusing hypertonic saline through a cannula in the pneumatic duct vein at various speeds using a miniflow pump (RP-V Furue Sci., Tokyo). Effects of fullness of stomach or intestine were

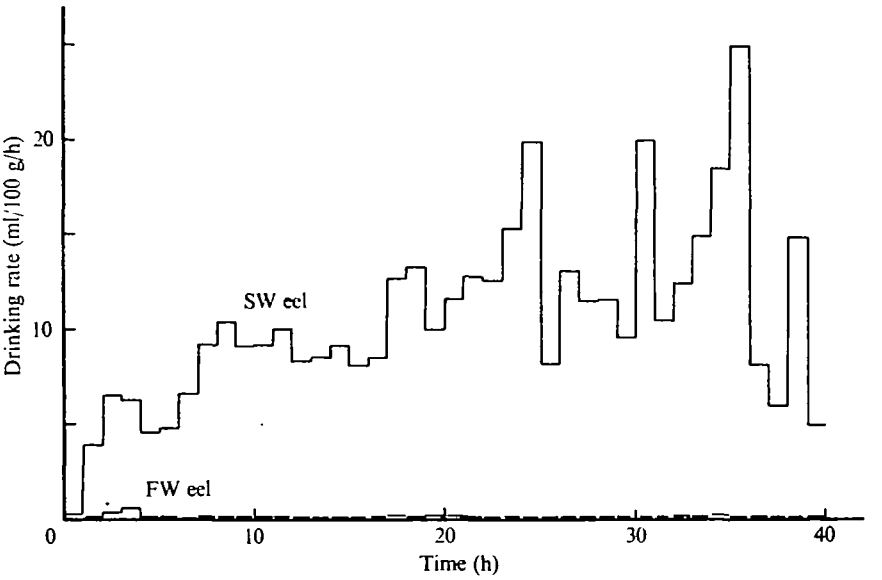

Fig. 1. Time course of change in drinking rate in a seawater-adapted eel (195 g) placed in the seawater trough (SW eel) and in a freshwater-adapted eel (210 g) placed in the freshwater trough (FW eel).

examined in seawater eels by introducing isotonic mannitol (0·35 M) through a vinyl tube (1·5 mm in inner diameter) inserted into the stomach from the oesophageal end, or into the intestine from the cloaca. In both cases, the stomach and the intestine were separated by ligating the stomach at the entrance of the intestine with cotton thread. In general, the experiments were repeated using at least three different preparations; the findings were consistently reproducible and representative results are presented.

RESULTS

Drinking behaviour of the oesophagus-cannulated eel

When the oesophagus of freshwater eels was cannulated and the eels were placed in a freshwater trough, they started drinking water 2–3 h after the operation at a rate of 0·3–0·5 ml/100 g.h, which usually lasted for 3 h. They scarcely drank during the rest of the period, and drinking rate during the first 24 h after operation was 20–40 μl/100 g.h. Seawater eels, when placed in a seawater trough, started drinking sea water immediately after recovery from anaesthesia at a rate of 0·3–0·5 ml/100 g.h for the first 1–2 h; then in contrast to the freshwater eel, drinking rate increased greatly, being maintained at more than 10 ml/100 g.h as long as the eels were in sea water (Fig. 1). Eventually they died after 3 or 4 days in sea water, losing about 15 % of their body weight. Maximum drinking rate observed in sea water was more than 100 ml/100 g.h.

Effects of modification of internal environments

Water ingestion was induced in freshwater eels by withdrawing the blood through the cannula in the pneumogastric artery. A typical example is illustrated in Fig. 2. Total blood volume of the eel is assumed to be about 3 % of the body weight. Immediately

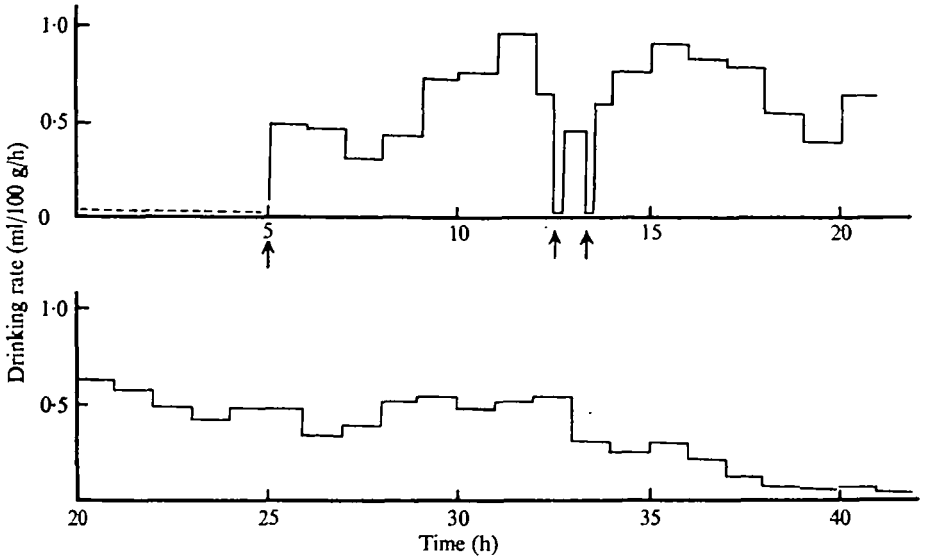

Fig. 2. Effect of acute withdrawal of 2 ml of blood (arrow at 5 hr point) from the pneumogastric artery on drinking rate of a freshwater eel (200 g). 1 ml of isotonic 0·9 % (154 mM) NaCl was infused through the cannula into the pneumatic duct vein 7–8 h after blood withdrawal (second and third arrows). The dashed line before the 5 hr point indicates no water drinking during this period.

after the withdrawal of 2 ml of blood (about 30 % of the total blood), the eel started drinking at a rate of 0·5–1·0 ml/100 g.h for the next 15 h, and gradually returned to the original drinking rate after about 40 h. Intravenous infusion of 2 ml of 0·9 % (154 mM) NaCl solution resulted in interruption of drinking only for a few minutes. On the other hand, the copious drinking observed in seawater eels was interrupted by intravenous infusion of a large amount (2·3–4·6 ml) of a hypertonic 2 % (342 mM) NaCl solution (Fig. 3). The duration of interruption seemed to depend on the volume of infused solution; the larger the infused volume, the longer the interruption.

In the next experiment, the effects of a slower reduction in body water were examined by placing freshwater eels in hypertonic mannitol or sucrose solution. Fig. 4 shows the time course of changes in drinking rate after the trough water was changed from fresh water to a hypertonic 0·7 M mannitol solution. The eels did not drink water until 8–10 h after application of mannitol solution. The drinking rate was about 0·3–0·5 ml/100 g.h, which is much less than the rate in eels placed in a seawater trough; the eels died after 14–16 h, losing about 12 % of their body weight. A similar response was also observed when fresh water in the trough was replaced with 0·7–0·9 M sucrose solution; in this case the eel died after 12 h.

Fig. 5A shows the effect of intravenous infusion of 10 % (1·71 M) NaCl into the freshwater eel placed in the freshwater trough. The infusion was made at a rate of 1·75 ml/h for 90 min. The eel responded by drinking 2·8 ml of water during the first 30 min, but ingested only 0·1 ml for the following 60 min. However, it started drinking again 2 h after the end of infusion; drinking lasted for the next 3 h at a rate of 0·12 ml/100 g.h. Since the lack of drinking response during the latter half of the infusion is

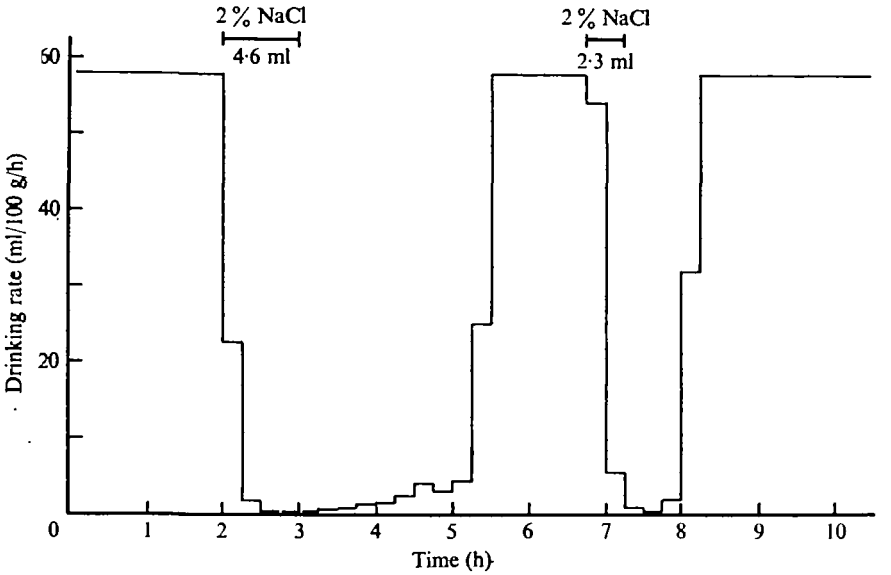

Fig. 3. Effect of infusion of 2 % (342 mM) NaCl into pneumatic duct vein on drinking rate of a seawater eel (190 g). Two infusions were made at a rate of 4·6 ml/h for 60 and 30 min.

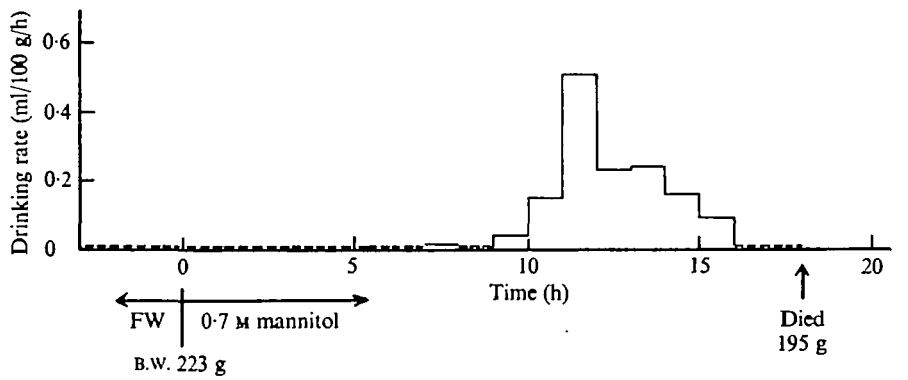

Fig. 4. Effect of change in trough water from fresh water to 0·7 M mannitol solution on drinking rate of a freshwater eel.

probably due to the expansion of the extracellular fluid volume, a slower infusion rate was employed in the next experiment. When the freshwater eel was infused with 0·2 ml of 20 % (3·42 M) NaCl over 8·5 h, constant drinking at a rate of about 0·15 ml/100 g.h was induced during the infusion (Fig. 5B).

Immediately after the introduction of isotonic 0·35 M mannitol solution into the stomach of the seawater eel, the drinking rate decreased greatly, and the eel kept drinking at a low rate for another 40 min. When the mannitol solution was withdrawn, the drinking rate gradually returned to the original copious rate after 40 min (Fig. 6). The inhibition of drinking by distension of the stomach and its initiation by emptying were reproducible. Similar inhibition of drinking was observed in the sea water eel by distending the intestine with mannitol solution.

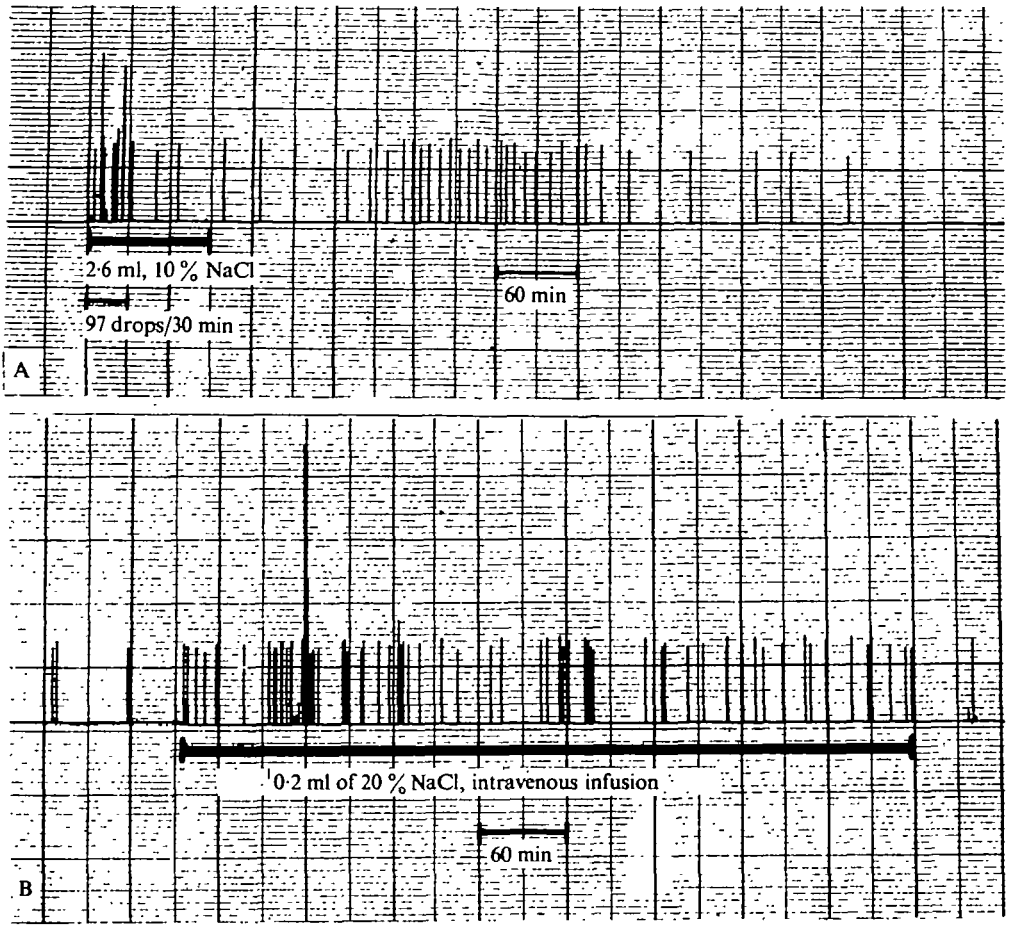

Fig. 5A. Effect of infusion of 10 % (1·71 M) NaCl into the pneumatic duct vein on drinking rate of a freshwater eel (200 g). Infusion was made for 1·5 h at a rate of 1·7 ml/h. B. Effect of slow infusion of 20 % (3·42 M) NaCl into the pneumatic duct vein on drinking rate of a freshwater eel (195 g). Infusion was made for 8·5 h at a rate of 0·024 ml/h. Each spike represents 0·03 ml of swallowed water.

Effects of external salinity changes

In the next experiment, freshwater eels were kept in a freshwater trough for at least 18 h, and the trough water was replaced by sea water or by various salt solutions. As shown in Fig. 7A, the eel started drinking immediately after the trough water was changed from fresh water to sea water, and kept drinking for an hour at a rate of 1·3 ml/100 g.h. The trough water was then changed back to fresh water, and the eel stopped drinking immediately. The inhibition of drinking in fresh water was always observed if the previous exposure to the salt solutions lasted for 60–90 min. The response to fresh water after longer exposure to sea water was variable depending on duration of the exposure. When eels were returned to fresh water after being kept in sea water for several hours, the inhibition was observed only for the first 30 min or less: when they were kept in sea water for more than 24 h, the inhibition of drinking was usually not observed.

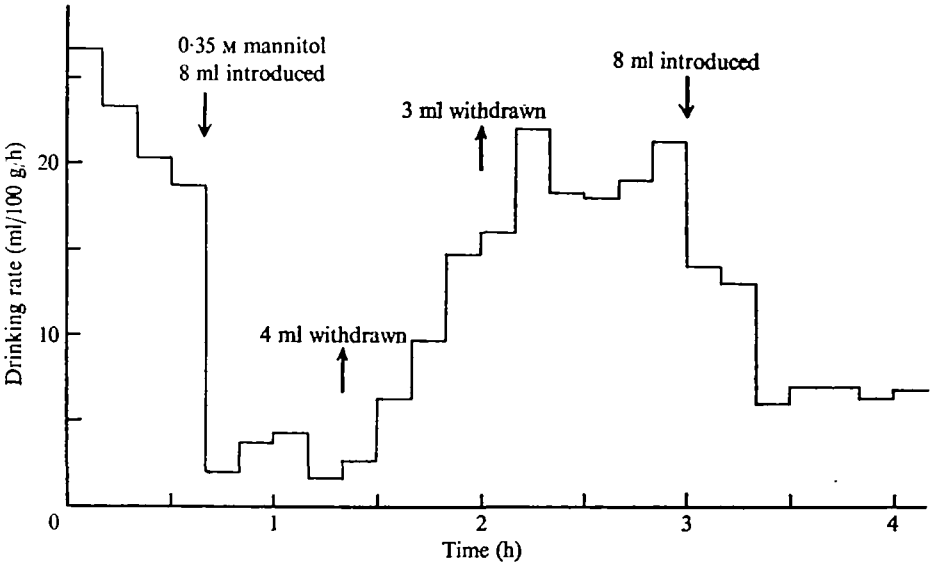

Fig. 6. Effect of distension of the stomach with 0·35 M mannitol solution on drinking rate of a seawater eel (200 g).

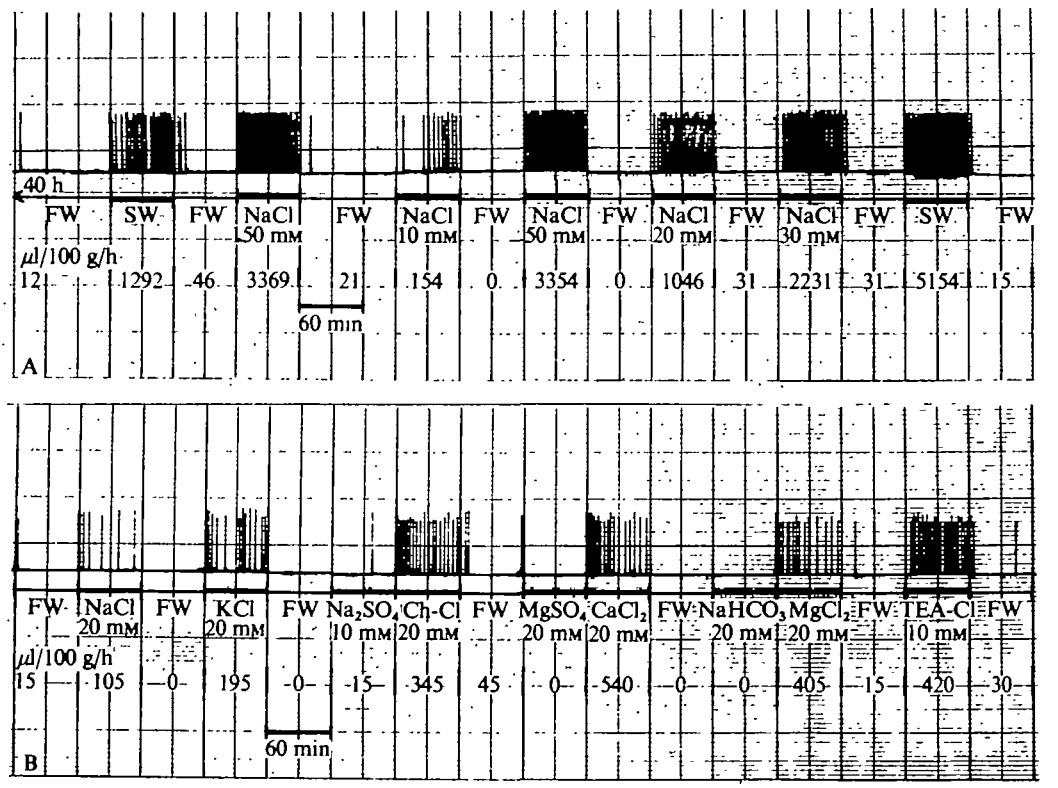

Fig. 7(A). Effect of sea water (SW), fresh water (FW) and various concentrations of NaCl solutions on drinking rate of a freshwater eel (139 g). (B) Effect of various salt solutions on drinking rate of a freshwater eel (200 g). Each spike represents 0·03 ml of swallowed water.

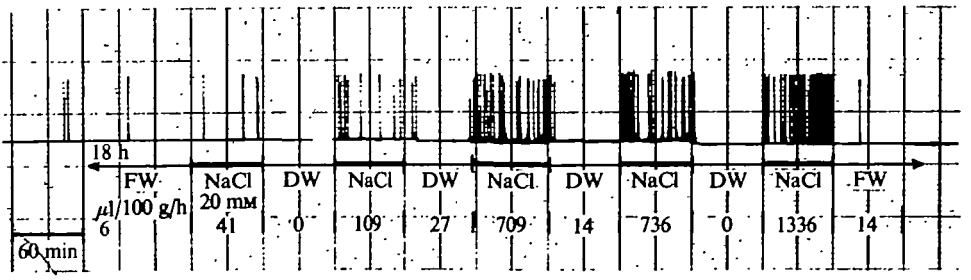

Fig. 8. Effect of repeated application of 20 mM NaCl and deionized water (DW) on drinking rate of a freshwater eel (214 g). Each spike represents 0·03 ml of swallowed water.

The immediate induction and inhibition of drinking were also observed by alternate introduction of NaCl solutions and fresh water into the trough. The minimum effective concentration of NaCl was 10 mM, and the drinking rate increased with increasing concentrations of NaCl. Most eels continued to drink in response to NaCl for at least an hour. In a few preparations, however, adaptation or refractoriness to stimuli was observed after one or two minutes.

10 or 20 mM solutions of the salts which are the main components of sea water were next tested (Fig. 7B). The eel responded to NaCl, KCl, $CaCl_2$, but not to Na_2SO_4 and $NaHCO_3$. In another eel, K_2SO_4 and Na_2HPO_4 were ineffective. Eels also responded to choline-Cl and tetraethylammonium-Cl. The chloride ion seemed specifically effective in inducing water ingestion in the eel at a threshold concentration of less than 20 mequiv/l, whereas freshwater or the absence of chloride ion in the environment seemed to act in an inhibitory fashion. Although other halides are only present in trace amounts in sea water, water ingestion was also induced by KBr and NaI at equivalent molar concentrations.

As also shown in Fig. 7A, although the amounts of salt water swallowed during exposure to NaCl or other salt solutions were roughly proportionate to the ionic concentrations of the solutions, there was a tendency for facilitation in response to salts: the drinking rate (5·1 ml/100 g.h) in response to sea water after a series of salt and fresh water treatments was greater than that at the initial application of sea water (1·3 ml/100 g.h). Facilitation of drinking by repeated exposure to salt solutions was also observed during alternative applications of 20 mM NaCl solution and deionized water (Fig. 8).

DISCUSSION

In the present study, the drinking rate of the eel was measured by cannulating the oesophagus, and allowing ingested water to escape. The swallowed water did not enter the stomach. The drinking rate (or swallowing rate) thus measured is far from that in an intact eel in sea water, being more than 10 ml/100 g.h; far greater than the average drinking rate of 0·3 ml/100 g.h in the intact eel in sea water (Oide & Utida, 1968; Maetz & Skadhauge, 1968; Gaitskell & Chester Jones, 1971; Motais & Isaia, 1972; Kirsch, 1972; Hirano, Satou & Utida, 1972; Kirsch & Mayer-Gostan, 1973). Since they are unable to absorb swallowed water from the intestine and are consequently exposed to severe dehydration, it is conceivable that the eels are in urgent need to drink water. In fresh water, however, the cannulated eel scarcely drinks water, except for a few hours after the operation. This short drinking spell may result from th

loss of a small amount of blood during the operation. The absence of drinking in fresh water is in accord with previous reports on *A. japonica* (Oide & Utida, 1968; Hirano *et al.* 1972). Therefore, the oesophagus-cannulated eel seems to be under constant pressure to drink while in sea water, but not in fresh water. This preparation seems suitable for the analysis of the factors affecting the drinking behaviour.

In mammals, there is substantial experimental work showing that thirst or water ingestion is caused by an intracellular or an extracellular deficit of fluid (see recent review by Fitzsimons, 1972). As shown in the present study, the eel also seems to regulate its drinking rate following the changes in extracellular fluid volume: the eel in sea water responded to expansion of extracellular fluid by limiting the amount of water swallowed, and the freshwater eel responded to acute loss of blood by immediate initiation of drinking. Slow infusion of hypertonic NaCl also elicited the drinking response in freshwater eels, suggesting the presence of an internal ionreceptor(s) or osmoreceptor(s) in the eel. Effects of haemodilution were not tested in the present study. The inhibitory effect of distension of stomach and intestine as observed in seawater eels seems also essential for the maintenance of their water balance. Since the ingested water is hypertonic to the body fluid, it is first diluted and subsequent reabsorption of water follows as a consequence of ionic absorption (Smith, 1932; Sharratt *et al.* 1964; Utida, Isono & Hirano, 1967; Skadhauge, 1969). A rate of water ingestion more rapid than the rate of intestinal absorption would result in more pronounced dehydration. Distension of the stomach with water or with an inflated balloon has also been shown to inhibit drinking in some mammalian species (Towbin, 1949; Adolph, 1950).

Infusion of a hypertonic NaCl solution into seawater eels caused only temporary inhibition of drinking: hypertonicity of the plasma and/or the presence of chloride ions in the environment seemed to override the inhibitory effect of expansion of extracellular fluid volume. Similarly, infusion of a large volume of hypertonic solution did not produce a full response in the freshwater eel, which could also be explained by the effect of volume overriding salt or osmotic stimuli. On the other hand, the eel in fresh water responded immediately to acute loss of blood, and continued drinking for more than 40 h, during which time extracellular fluid volume seemed to have been restored by osmotic influx of water from the hypotonic environment, resulting in a halt in drinking. Slower reduction in body water during exposure of the eel to hypertonic mannitol or sucrose solutions induced drinking only after 8–10 h. The drinking rate was much less than the rate in the seawater eel, which may be a result of the absence of salts in the environment. Thus, 'summation' and 'balancing' of above-threshold facilitatory and inhibitory stimuli seem to lead to a net stimulatory or net inhibitory modification of drinking activity.

It is striking that the eel started drinking immediately after the change in the trough water from fresh water to sea water. Immediate drinking response to seawater transfer has also been observed in the intact *A. anguilla* by Kirsch (1972) and Kirsch & Mayer-Gostan (1973). They ascribed this drinking reflex, which lasted for about 1 h after transfer, to a local dehydration or a sensory stimulus; overall dehydration and increase in plasma osmolality are unlikely to occur in such a short period. However, this immediate response to sea water is not due to changes in osmotic pressure, since hyperosmotic mannitol and sucrose did not induce drinking until after 8–10 h of exposure,

and also since a similar response can be induced by hypotonic NaCl (10–150 mM) as well as by hypertonic sea water. As shown in the present study, it is the chloride ion in sea water which seems responsible for the reflex. The fact that the eel responded also to KBr and NaI suggests the presence of chemoreceptor(s) specific to halide ions. It is also to be noted that the eel stopped drinking immediately in response to the change in the trough water from sea water to fresh water or from salt solutions containing chloride ions to those containing no chloride ions. However, the inhibition of drinking by fresh water was not observed, when eels were returned to fresh water after being kept in sea water for more than 24 h. This suggests the participation of internal stimulatory factors which override the inhibitory influence of fresh water or the absence of chloride ions in the environment. Similar induction of drinking by chloride ions and inhibition by fresh water is observed in *A. anguilla* (Hirano, unpublished).

Electrophysiological evidence indicates that the palatal chemoreceptors of the carp are highly sensitive to NaCl and other salt solutions, and anions are suggested to be important in the stimulation of the receptors (Konishi, 1967). In contrast to the drinking response of the eel, however, the palatal organ of the carp does not respond specifically to halide ions. The olfactory systems of the goldfish (Hara & Gorbman, 1967) and the lateral-line organ of some teleosts (Katsuki, Hashimoto & Kendall, 1971) also respond to NaCl, but inorganic anions are ineffective in both systems. On the other hand, specific water receptors have been shown to occur on the tongue of a frog (Andersson & Zotterman, 1950). Therefore, some of the chemoreceptors in the gustatory organ or taste buds may be responsible for the chloride-induced drinking and inhibition in fresh water, although the presence of chemoreceptors specific to halide ions and to distilled water on other parts of the body surface remains a possibility.

It has been shown in some mammals that drinking often precedes the meal or occurs early during it, and that taste or smell of food or its physical presence in the mouth or stomach could cause drinking. There are a number of anticipatory drinking behaviours to various stimuli; preabsorptive mechanisms operate to stop drinking in some species long before any significant absorption of water has taken place, and passage of water through the oropharynx seems to cause this temporary satiety. Moreover, the idea that dryness of the mouth and throat may be an essential component in thirst is one of the classical theories of thirst (see Fitzsimons, 1972). The initiation of drinking by chloride ions and inhibition by water observed in the eel may be a primitive type of the anticipation reflex. With this reflex, the eel would be able to anticipate the long-term consequences of its drinking behaviour and to take appropriate action to forestall such consequences, namely, to drink when in sea water and not to drink when in fresh water, thus facilitating its adaptation to the full spectrum of salinity changes in its environment. In a previous report, it has been shown that the hypothalamus of the eel, unlike in mammals, may not be involved in regulation of drinking, but that a neural reflex at the level of the medulla oblongata seems essential (Hirano *et al.* 1972). Therefore, the need for water ingestion may not be a 'conscious' sensation in the eel. At any rate, the integration of the facilitatory and inhibitory stimuli by the central nervous system which determines drinking behaviour must be a complex process. Further studies, notably on the nature and location of the receptors involved and on the central integrative mechanisms, are called for.

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