

# Precedence of head homoeothermia over trunk homoeothermia in dehydrated men

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Summary. Three male humans were subjected repeatedly to 20 min exercise on a bicycle ergometer: twice when hydrated normally and twice when dehydrated. Tympanic  $(T_{ty})$  and oesophageal  $(T_{es})$ temperatures were recorded and sweat rates on forehead and back were measured. Dehydration did not change the forehead sweat rate, but on the back it reduced significantly, resulting in an increase of  $T_{es}$ . However,  $T_{ty}$  was decreased by dehydration. 20 min after the end of exercise subjects were allowed to drink water in order to trigger the potohidrotic response. A potohidrotic response was noted on the back of dehydrated subjects only. It is concluded that dehydration results in active inhibition of sweating on the body but not on the forehead, where evaporation is needed for selective cooling of the brain.

**Key words:** Dehydration — Sweating — Hyperthermia — Selective brain cooling — Potohidrotic response

# Introduction

Dehydration in the heat is a challenge for the temperature regulatory system because of water shortage for evaporative cooling. Under these conditions sweat secretion decreases and as a consequence, body temperature increases in both humans (Adolph 1947; Greenleaf and Sargent

1965; Hertzman and Ferguson 1960; Nadel 1984) and other mammals (Dmi'el 1986; Maloiy 1970; Maloiy 1973; Robertshaw and Dmi'el 1983; Taylor 1970; Taylor 1972). Such a reduction in sweat rate is indicative of the higher emergency rank of water saving over temperature defence. Panting, however, is less or not at all inhibited in dehydrated animals (Dmi'el 1986; Maloiy 1970; Maloiy 1973; Robertshaw and Dmi'el 1983; Taylor 1970; Taylor 1972). This is why a biological compromise between water economy and evaporative cooling needs has been suggested (Caputa 1981). The compromise would be an abandonment of the evaporative cooling of the whole body and limiting thermoregulatory use of water to keep the heat-susceptible brain cooler than the rest of the body. According to its role in selective brain cooling (Cabanac and Caputa 1979a and b; Caputa et al. 1978; McCaffrey et al. 1975a and b) facial sweating in dehydrated humans is analogous to panting in dehydrated animals (Dmi'el 1986: Maloiy 1970; Maloiy 1973; Robertshaw and Dmi'el 1983; Taylor 1970; Taylor 1972). Sweating on the face should be, therefore, inhibited less than sweating on the trunk. The aim of this study was to identify the partitional effects of dehydration on facial and trunk skin sweating in humans. A preliminary report of this study has been published (Cabanac et al. 1981).

#### Methods

Three volunteers participated each in four experimental sessions: two control sessions and two sessions in the dehydrated state. Dehydration was achieved by abstaining from drinks and liquid foods for a period of 24 to 36 h, with occasional spitting, and by sweating during exercise on a cycle ergometer. The duration of this dehydration was comparable to that of experiments conducted by other authors, and resulted in the

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same clinical syndrome: severe thirst, tiredness, cutaneous plicature and a rise in rectal temperature. Blood samples were taken, once in each subject just before the beginning of an experimental session. The mean ( $\pm$ SE) increase in blood osmolarity was 9.3  $\pm$  1.4 m osmol.

Temperature recordings. Oesophageal  $(T_{es})$ , tympanic  $(T_{ty})$ , forehead, flank, and hand temperatures were recorded using copper-constantan thermocouples. The oesophageal thermocouple was passed through the nose down the oesophagus 0.45 m below the nares so as to eliminate any respiratory cooling influence during exercise (Caputa 1980). Contact of the tympanic thermocouple with the membrane itself was indicated by sharp pain. The auditory canal was then filled with cotton wool and taped so that no movement of air could occur inside the canal. Forehead skin temperature and flank temperature were measured by unprotected thermocouples fixed by adhesive tape.

Sweat measurement. Sweating was measured by a sudorimeter (evaporimeter EPI/Servomed AB) every 2 min on the fore-head and on the back alternately throughout the experimental session.

*Potohidrotic response.* The potohidrotic response is a large increase in sweat secretion in the minutes following water ingestion; the response is independent of salt content and temperature of the water (Nicolaidis 1964, 1970). In both experimental sessions the subject drank water ad libitum and the measurement of sweat continued until all variables monitored reached a steady state.

*Experimental procedure.* The subject, fitted with thermocouples, was placed in a climatic chamber at 24°C, on a cycle ergometer. Each session was divided into 4 parts:

A- 10 min control period at rest on the cycle;

B-20 min work in order to achieve hyperthermia. The exercise was maintained constant for each subject throughout each session; each subject pedalled at a different power ranging between 80 and 150 W depending on his work capacity;

C- a resting period, lasting until oesophageal and tympanic temperatures reached a new steady state;

D— potohidrotic response: the subject drank water ad libitum, usually more than 1 l, and remained under observation until the variables monitored reached a steady state.

Statistics. All the mean values presented in the results were calculated, first within subjects, and then for the group. This suppressed any nesting effect but reduced the degrees of freedom to two. The means were compared using the Student paired *t*-test. The number of subjects was small but sufficient to reach significance (Still 1982).

### Results

# The effect of dehydration on body temperatures and on sweating

In the dehydrated subjects tympanic temperature was lowered and oesophageal temperature was elevated both during the rest period before exercise and during cycling work as compared with the control condition (Figs. 1 and 3). The dehydra-



Fig. 1. Evolution of local sweat secretion and deep body temperatures before, during and after 20 min of work on a cycle ergometer. Each curve is the mean of six sessions (3 subjects taken twice each). Back, forehead: locus where sweating was measured. Control, dehydrated: data obtained during experiments on control or dehydrated subjects



Fig. 2. Mean sweating rate on the forehead and on the back (left side) and mean tympanic ( $T_{ey}$ ) and oesophageal ( $T_{es}$ ) temperature (right side) in the exercise period during control sessions (empty column) and during dehydration (grey column). \*\* P < 0.01; \*\*\* P < 0.001 (paired Student's *t*-test)



Fig. 3. Left: Mean tympanic temperature during the dehydrated sessions (ordinate) plotted against its values under the control condition (abscissae). A fall in tympanic temperature during dehydration is to be noted. Right: mean oesophageal temperature during the dehydrated sessions (ordinate) plotted against its values under the control condition (abscissae). An increase in  $T_{es}$  throughout the session is to be noted. Plotted values were paired according to their time courses from the beginning of the experiments. The broken line represents an isotherm

tion-induced increase in  $T_{es}$  and decrease in  $T_{ty}$  were highly significant (P < 0.001) during the exercise period (Fig. 2). Thus dehydration clearly dissociated  $T_{ty}$  from  $T_{es}$ .

Sweating on the back in dehydrated subjects was significantly reduced (P < 0.001) (Fig. 1 and 2); on the other hand, sweating on the forehead was not modified by dehydration in either the resting or the exercising subjects (Fig. 1 and 2).

In the control sessions  $T_{ty}$  at rest was higher than  $T_{es}$ , but this difference did not reach statistical significance, and during exercise  $T_{es}$  and Tty remained practically superimposed.

In the dehydrated subjects at rest  $T_{ty}$  was about 0.2 ° C lower than  $T_{es}$ . During exercise this difference tended to increase up to a mean maximal value of 0.6 ° C. Over the whole exercise period the mean difference was 0.43 ° C (P < 0.001) (Fig. 2).

#### Potohidrotic response

When internal temperatures reached a steady state at the end of the sessions no significant difference was observed in sweating on the forehead between the control and dehydrated subjects (Fig. 4). On the back of dehydrated subjects, the low sweat rate observed at rest and during exercise still persisted. Sweating was measured after drinking: twice on the forehead (6 min and 14 min), and twice on the back (8 min and 16 min).

Neither in the hydrated nor the dehydrated



Fig. 4. Upper: potohidrotic response measured on the forehead 6 and 14 min after drinking (T) in control (left) and dehydrated sessions (right). Lower: Potohidrotic response measured on the back 8 and 16 min after drinking (T) in control (left) and dehydrated sessions (right). In the controls forehead and back sweating decreased. In dehydrated subjects back and forehead sweating increased after drinking but only back sweating increased significantly, on account of a large decrease during dehydration (\* P < 0.05 Paired Student's t-test)

subjects did drinking affect the sweating rate on the forehead. The same was the case concerning back sweating in hydrated subjects. On the other hand, drinking enhanced back sweating, which reached the same value as under control conditions (Fig. 4).

# Discussion

### Deep body temperature and sweating

In control experiments,  $T_{ty}$  was usually higher than  $T_{es}$ . During dehydration, however,  $T_{es}$  was higher than  $T_{ty}$  both at rest and during exercise. In dehydrated subjects during rest a dissociation between sweating on the forehead and sweating on the back was observed. Sweating on the back was low, whereas sweating on the face was not reduced. This dissociation between sweat rates on the back and on the forehead was caused by active inhibition of sweat secretion on the back but not on the forehead when in the state of dehydration, as shown by intense and instantaneous sweating on the back during the potohidrotic response.

It is likely that the dissociation between oesophageal and tympanic temperatures was related to the inhibition of sweating on the back. The higher  $T_{es}$  can be explained by the lower sweat rate on the trunk (Fig. 5). On the other hand, the unimpaired sweat rate on the forehead kept the



**Fig. 5.** Left: Sweating on the back (Ordinate) as a function of oesophageal temperature during exercise under control conditions (solid line-according to equation:  $y=96.98 \times 3549$ ; r=0.86; P<0.001) and during exercise in the dehydrated state (broken line-equation:  $y=84.42 \times -3121$ ; r=0.906; P<0.001). Right: Sweating on the forehead as a function of tympanic temperature during control exercise (continuous line-equation:  $y=109.56 \times -40.19$ ; r=0.885; P<0.001), and during exercise in dehydrated subjects (broken line-equation:  $y=85.58 \times -3116$ ; r=0.817; P<0.01)

tympanic temperature lower than  $T_{es}$ . In Figure 3 both core temperatures in normally hydrated subjects (abscissae) were plotted against respective values in dehydrated subjects (ordinates). The broken lines represent the isotherms. It can be seen that there was little difference in  $T_{tv}$  between hydration and dehydration, and that  $T_{es}$  was higher during dehydration. It can therefore be hypothesized that the elevated core temperature reported in dehydrated subjects (Adolph 1947; Greenleaf and Sargent 1965; Hertzman and Ferguson 1960; Nadel 1984; Nadel et al. 1980; Nielsen 1974; Strydrom and Holdsworth 1968) concerned only the trunk temperature, recorded rectally or oesophageally. Such higher trunk temperature, therefore, may be due not to resetting the hypothalamic thermostat, but rather to open loop drift visible only in the trunk and not in the head. Indeed there is some indication that dehydrated goats also inhibit sweating on the body to switch evaporative heat loss to panting and sweating on the head, which cools the head selectively (Dmi'el 1986; Robertshaw and Dmi'el 1983). Figs. 1, 2 and 3 show a comparable response in humans.

#### Selective brain cooling

The present results are compatible with the hypothesis of selective brain cooling in hyperthermic humans. Such a mechanism has been repeatedly demonstrated in all the mammalian species studied so far (Baker 1982; Caputa 1981). There is inM. Caputa and M. Cabanac: Dehydration and brain temperature

direct evidence that it also occurs in humans (Cabanac and Brinnel 1985; Cabanac and Caputa 1979a and b; Cabanac et al. 1987; Caputa 1981; Caputa et al. 1978). The anatomical basis of human selective brain cooling is based upon the flow in the ophthalmic and other emissary veins of the head, in which blood flows inwards abundantly during hyperthermia (Cabanac and Brinnel 1985; Caputa et al. 1978). The decisive role of facial skin in selective brain cooling in primates has recently been directly confirmed in squirrel monkeys, which sweat and do not pant (Fuller and Baker 1983). During dehydration, selective brain cooling was permitted by the sustained sweat evaporation on the face observed in this experiment. During work, in dehydrated subjects the difference between Tes and Tty increased whereas no difference was visible in the control subjects. This can be explained by the inhibition of sweating on the back observed only in the dehydrated subjects, whereas there was no difference in face sweat rate in the dehydrated or the control subjects. The selective brain cooling in dehydrated subjects and their capacity to resist heat can be prolonged by the saving of water resulting from sweat inhibition on the remainder of the body.

# Different nervous control of heat loss for the head and the rest of the body?

The inhibition of sweating on the trunk but not on the head during dehydration implies different nervous controls of the sweat glands of the head and of the rest of the body. It is quite remarkable from this point of view that these two skin areas project their thermal inputs to different nuclei of the thalamus (Dickenson 1977; Dickenson and Hellon 1979; Dickenson et al. 1979; Dostrovsky and Hellon 1978). It is possible, therefore, that there are two loops for the control of heat loss: one consisting of facial and cerebral thermal inputs, and cranial effectors of heat dissipation, and the other containing sensors and effectors of heat dissipation of the rest of the body. Under optimal conditions they operate in consonance, but under the conditions of physiologically conflicting stresses (dehydration vs temperature regulation) they can operate in dissonance. Strong evidence confirming this suggestion is the existence of a competition for cool nasal blood between the brain and the trunk in hyperthermic goats when their brain and trunk temperatures are artificially changed independently of each other (Caputa et al. 1986). More evidence for opposite trends in M. Caputa and M. Cabanac: Dehydration and brain temperature

head and trunk thermolytic responses is given by the increase in sweating on the head and decrease in sweating on the trunk in dehydrated goats (Dmi'el 1986). Therefore there are good reasons to focus on facial sweating as a function of  $T_{ty}$ and on trunk sweating as a function of  $T_{es}$ . Our results are presented from this point of view in Fig. 5. They show that in the dehydrated subjects the threshold of  $T_{es}$  for trunk sweating was elevated and the gain of the response slightly reduced. On the other hand, dehydration decreased the threshold of  $T_{ty}$  for facial sweating, but the gain of this response was also slightly reduced.

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#### References

- Adolph EG, and associates (1947) Physiology of man in the desert. Adolph EF (ed) Interscience, New York
- Baker MA (1982) Brain cooling in endotherms in heat and exercise. Ann Rev Physiol 44:85-96
- Caputa M (1980) Thermal gradients in the esophagus of man during exercise and passive warming. J Therm Biol 5:249-251
- Caputa M (1981) Selective brain cooling: an important component of thermal physiology. In: Szelenyi Z, Szekely M (eds) Contributions to thermal physiology. Akademiai Kiado, Budapest, pp 183–192
- Cabanac M, Caputa M (1979a) Natural selective cooling of the human brain: evidence of its occurence and magnitude. J Physiol 286:255-264
- Cabanac M, Caputa M (1979b) Open loop increase in trunk temperature produced by face cooling in working humans. J Physiol 289:163-174
- Cabanac M, Brinnel H (1985) Blood flow in the emissary veins of the human head during hyperthermia. Eur J Appl Physiol 54:172-176
- Cabanac M, Massonnet B, Caputa M (1981) Independence of head and trunk temperature regulation in dehydrated humans. Fed Proc: 1642
- Cabanac M, Germain M, Brinnel, H (1987) Tympanic temperatures during hemiface cooling. Eur J Appl Physiol 56:534-539
- Caputa M, Feistkorn G, Jessen C (1986) Competition for cool nasal blood between trunk and brain in hyperthermic goats. Comp Biochem Physiol 85A:423-427
- Caputa M, Perrin G, Cabanac M (1978) Ecoulement sanguin réversible dans la veine ophthalmique: mécanisme de refroidissement sélectif du cerveau humain. CR Acad Sci 28:1011-1014
- Dickenson AM (1977) Specific responses of cat raphe neurones to skin temperature. J Physiol 273:277-293

- Dickenson AM, Hellon RF (1979) Falicitation and suppression of antidromic invasion by orthodromic impulses in the cat. J Physiol 289:57-58
- Dickenson AM, Hellon RF, Taylor DCM (1979) Facial thermal input to the trigeminal spinal nucleus of rabbits and rats. J Comp Neurol 185:203-210
- Dmi'el R (1986) Selective sweat secretion and panting modulation in dehydrated goats. J Therm Biol 11:157-159
- Dostrovsky JO, Hellon RF (1978) The representation of facial temperature in the caudal trigeminal nucleus of the cat. J Physiol 277:29-47
- Fuller CA, Baker MA (1983) Selective regulation of brain and body temperatures in the squirrel monkey. Am J Physiol 245:R293-R297
- Greenleaf JE, Sargent F (1965) Voluntary dehydration in man. J Appl Physiol 20:719-724
- Hertzman AB, Ferguson ID (1960) Failure in temperature regulation during progressive dehydration. US Armed Forces Med J 11:542--560
- Maloiy GMO (1970) Water economy of the Somali donkey. Am J Physiol 219:1522-1527
- Maloiy GMO (1973) The water metabolism of a small East African antelope: the dik-dik. Proc R Soc Lond B 184:167-178
- Mc Caffrey TV, Mc Cook RD, Wurster RD (1975a) Effect of head skin temperature on tympanic and oral temperature in man. J Appl Physiol 39:114–118
- Mc Caffrey TV, Geis GS, Chung JM, Wurster RD (1975b) Effect of isolated head heating and cooling on sweating in man. Aviat Space Environ Med 46:1353-1357
- Nadel ER (1984) Effects of dehydration on heat transfer mechanisms in humans. Abstract 106, 10th Int Congr of Biometeorology, Toyko
- Nadel ER, Fortney SM, Wenger CB (1980) Effect of hydrative state on circulatory and thermal regulation. J Appl Physiol 49:715-720
- Nicolaidis S (1964) Etude d'une réponse de sudation après ingestion d'eau chez le sujet deshydraté. CR Acad Sci (Paris) 259:4370-4372
- Nicolaidis S (1970) Réflexe potohidrotique et son rôle dans la régulation thermique et hydrominérale. Arch Sci Physiol 24:397-408
- Nielsen B (1974) Effect of changes in plasma volume and osmolarity on thermoregulation during exercise. Acta Physiol Scand 90:725-730
- Robertshaw D, Dmi'el R (1983) The effect of dehydration on the control of panting and sweating in the black Bedouin goat. Physiol Zool 56:412-418
- Still AW (1982) On the number of subjects used in animal behaviour experiments. Anim Behav 30:873-880
- Strydom NB, Holdsworth LD (1968) The effect of different levels of water deficit on physiological responses during heat stress. Int Z Angew Physiol Arbeitphysiol 26:95-102
- Taylor CR (1970) Dehydration and heat: effects on temperature regulation in East African ungulates. Am J Physiol 219:1136-1139
- Taylor CR (1972) The desert gazelle: a paradox resolved. Symp Zool Soc Lond 31:215-227

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