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Selective brain cooling and its vascular basis in diving seals

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SUMMARY

Brain (T_{brain}), intra-aorta (T_{aorta}), latissimus dorsi muscle (T_m) and rectal temperature (T_r) were measured in harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals during experimental dives in 4°C water. The median brain cooling was about 1°C during 15 min diving, but in some cases it was as much as 2.5°C. Cooling rates were slow for the first couple of minutes, but increased significantly after about 5 min of diving. The onset of cooling sometimes occurred before the start of the dive, confirming that the cooling is under cortical control, like the rest of the diving responses. T_{aorta} also fell significantly, and was always lower than T_{brain}, while T_m was fairly stable during dives. Detailed studies of the vascular anatomy of front flippers revealed that brachial arterial blood can be routed either through flipper skin capillaries for nutritive purposes and return through sophisticated vascular heat exchangers to avoid heat loss to the environment, or, alternatively, through numerous arterio-venous shunts in the skin and return by way of large superficial veins, which then carry cold blood to the heart. In the latter situation the extent to which the brain is cooled is determined by the ratio of carotid to brachial arterial blood flow, and water temperature, and the cooling is selective in that only those organs that are circulated will be cooled. It is concluded that T_{brain} is actively down-regulated during diving, sometimes by as much as 2.5°C, whereby cerebral oxygen requirements may be reduced by as much as 25% during extended dives.

Key words: hooded seal *Cystophora cristata*, harp seal *Pagophilus groenlandicus*, vascular heat exchange, arterio-venous shunt, rete, hypoxia.

INTRODUCTION

When seals undergo experimental dives they reduce their cardiac output to about 10% of the pre-dive value, primarily as a result of a profound bradycardia, to compensate for a selective peripheral arterial vasoconstriction. This ensures that the oxygen in the blood is delivered to hypoxia-sensitive tissues, like the brain, while the rest of the body has to subsist on local stores of oxygen and/or anaerobiosis (Ramirez et al., 2007). In this situation it is of obvious importance that brain metabolism, and hence brain oxygen requirements, are kept as low as possible to extend the animal's diving capability, and it follows that a reduction of brain temperature would meet this end.

Scholander and colleagues (Scholander et al., 1942) reported a drop in brain temperature of harbour seals (*Phoca vitulina*) during experimental diving, but their results were obtained by use of mercury thermometers and were generally regarded with scepticism and soon largely forgotten. Some 40 years later, however, Kooyman and colleagues (Kooyman et al., 1980) showed that the central arterial temperature of freely diving Weddell seals (*Leptonychotes weddelli*) decreased about 3°C during a 53 min dive, and Hill and coworkers (Hill et al., 1987) found that the aortic temperature of freely diving Weddell seals was reduced by about 2°C in periods of active diving. Finally, in preliminary reports we (Blix et al., 2002; Odden et al., 1999) confirmed the results of Scholander et al. (Scholander et al., 1942) showing that seals may indeed reduce their brain temperature, even during relatively short experimental dives.

Any reduction of brain temperature will normally lead to vigorous shivering in mammals (Simon et al., 1986), and if so this thermoregulatory response would compromise the brain cooling and in that context be rather counterproductive. However, Kvadsheim and colleagues (Kvadsheim et al., 2005) have previously shown that the normal shivering response to brain cooling is inhibited as part of the response package that is elicited upon diving. In the present study we add new insight about selective brain cooling in seals and endeavour to explain how it is achieved.

MATERIALS AND METHODS

Animals

A total of 4 harp seals (*Pagophilus groenlandicus*, Erxleben 1777) and 9 hooded seals (*Cystophora cristata*, Erxleben 1777), aged from 1 to 3 years, of both sexes, were used in this study. Information on the diving behaviour of harp (Folkow et al., 2004) and hooded seals (Nordoy et al., 2008; Folkow and Blix, 1999) is available elsewhere. The animals used in the present study were originally caught as pups in the pack-ice of the Greenland Sea and raised in captivity at Tromsø in 5.5 m×5.5 m×1.2 m seawater pools with wooden ledges, where they were offered herring (*Clupea harrengus*) or capelin (*Mallotus villosus*) supplemented with a vitamin complex (Blix et al., 1973). The animals were taken under permits issued by The Royal Norwegian Ministry of Fisheries and The Royal Danish Ministry of Foreign Affairs, and the experiments were carried out under permit from the Norwegian Animal Research Authority. Animals used for morphological studies were killed for other purposes by overdoses of pentobarbital (Nembutal, 40 mg kg^{-1}) injected into the extradural intravertebral vein.

Experimental protocol

Diving procedure

In preparation for the experiments the animal was placed on a specially designed restraining board of classic design and accustomed to experimental dives in water of 3–4°C over a period of several days. The duration of these preparatory dives was varied over the range of 10–20 min to avoid habituation. Before each experimental session, the animal was instrumented with electrodes for measurement of heart rate and thermocouples for measurement of brain, intra-aortic, musculus latissimus dorsi and rectal

temperature. Before diving, the animal was allowed to equilibrate with its body immersed to the neck in the water for at least 1 h, whereafter it was submerged three times for periods of 10, 15 or 20 min separated by recovery periods of 40–60 min while still immersed to the neck in water.

Temperature measurements

Brain temperature was measured in 4 harp seals and 5 hooded seals as described previously (Odden et al., 1999): a 30 mm long and 1.5 mm thick blind-ended stainless steel tube was surgically implanted into the brain of the animals under full isoflurane anaesthesia. The steel tube was placed 10 mm lateral to the midline into the left cerebral hemisphere, near the third ventricle (as verified *post mortem*). Animals were not used in any experiments until at least 48 h after implantation of the tube. Before each experiment, a 0.5 mm isolated copper–constantan thermocouple was introduced into the tube under light sedation [0.6 mg kg^{-1} i.m. injection of Zoletil forte vet (tiletamin–zolazepam); Virbac, Carros Cedex, France]. The thermocouple was connected through a thermocouple amplifier with internal temperature reference (AD 595 CD: Analog Devices, Norwood, MA, USA) to an A/D converter and data acquisition system that stored the data every 20 s (Lab-Acq Pro and Insta-Trend Pro; Dianachart, Oak Ridge, NJ, USA). After sedation, the animals rested in air for at least 1 h to allow complete recovery before the series of diving experiments commenced.

Aorta blood temperature was measured in 2 harp seals by exposing a small section of the brachial artery at the base of the fore-flipper under full isoflurane anaesthesia and inserting a 0.5 mm sterile copper–constantan thermocouple transmurally and advancing it retrograde to the level of the aorta. The temperature was recorded as described for brain temperature. Again the animals were not used in any experiments until at least 48 h after completion of the surgery.

Musculus lattissimus dorsi temperature was measured in 1 harp seal by inserting a hypodermic needle under local anaesthesia [subcutaneous injection of 2–3 ml Xylocaine (10 mg ml^{-1}); AstraZeneca, Södertälje, Sweden] and introducing a 0.5 mm copper–constantan thermocouple 2 cm into the lattissimus dorsi muscle through the hypodermic needle which was subsequently withdrawn. The temperature was recorded as described for brain temperature.

Rectal temperature was recorded in 4 harp seals and 5 hooded seals with a copper–constantan thermocouple probe that was inserted 20 cm into the rectum of the animal. The temperature was recorded as described for brain temperature.

All thermocouples were calibrated at 0 and 40°C, and the recorded temperatures were linearized according to Tøyen (Tøyen, 1992).

Heart rate

During all diving experiments, heart rate was recorded using two subcutaneous electrodes placed anterior and posterior to the heart along the dorsal mid-line, and a third reference electrode was placed laterally on the animal. The electrodes were connected to a monitoring unit (CM-4008; Medi-Stim, Oslo, Norway) where data were stored digitally, or recorded on a printer (TA 4000; Gould, Valley View, OH, USA).

Vascular anatomy

Micro-anatomy

The brachial arteries of 3 dead hooded seals were perfused first with saline and then with McDowell's fixative (McDowell and Trumph, 1976) immediately after death, whereupon tissue samples were excised from the ventral side of the fore-flippers, cut into smaller blocks and immersed in fresh fixative until further processing. In preparation for further processing all samples were rinsed in 2.5% glutaraldehyde in 0.1 mol l^{-1} phosphate buffer adjusted to pH 7.2. Samples intended for light microscopic examination were subsequently dehydrated in graded series of ethanol up to 100% and embedded in Epon (Electron Microscopy Sciences, Hatfield, PA, USA), then cut on an Ultracut UCT microtome (Leica, Wetzlar, Germany) and examined using a Colour View Camera with accompanying software (Soft Imaging System, Münster, Germany). Samples intended for scanning electron microscopy were dehydrated in graded series of ethanol and critical point dried with carbon dioxide, then attached to metal stubs with silver paste, sputter coated with a 30 nm platinum layer and examined in a Phillips XL 30 ESEM (Eindhoven, The Netherlands).

Plastic corrosion casts

Vascular injections of quick-setting polyester (Ashland, Porsgrunn, Norway) were made into the brachial artery of 4 dead hooded seals under 0.4–0.5 atm (~40.4–50.5 kPa) pressure. Pressure was maintained for different periods in the different animals to obtain casts of the arterial part alone, and in combination with the venous part of the vasculature. After hardening of the cast the tissue was removed by digestion in concentrated HCl.

Angiography

Photographs were taken of the arteries and veins in the fore-flippers of 2 dead hooded seals after rinsing of the vessels with saline and subsequent injection of radio-opaque fluid (Mixobar Colon, Astra Meditec, Göteborg, Sweden; 1 g ml^{-1}) into the brachial artery or the veins of the digits, using OEC 9600 (OEC Medical Systems Inc., Salt Lake City, UT, USA) X-ray equipment.

Statistics

Temperature data were subjected to statistical analyses to test for significant differences in changes in temperature in connection with diving. The distribution of temperatures for repeated measurements in one animal was approximately symmetric, but with somewhat heavy tails. Therefore, the results are presented as Wilcoxon medians with corresponding 95% Wilcoxon's signed rank confidence intervals (Hollander and Wolfe, 1999). Different animals of both species showed very similar temperature responses to diving, as confirmed by ANOVA, where drop in temperature was the dependent variable and species and different animals and different dives were potential independent variables. Only a large random effect between different dives by the same animal was found. Dive series from different species and animals were therefore combined in one non-parametric presentation of the results. A P-value of <0.05 was taken to indicate statistically significant differences.

RESULTS

Heart rate

Heart rate always fell promptly from about 90 beats per minute (b.p.m.) to 8–10 b.p.m. upon submergence, stayed at this level throughout the dive, except for occasional brief episodes of muscle movement, and rose promptly to about 100 b.p.m. upon emergence (Fig. 1).

Body temperatures

Brain temperature (T_{brain}) always fell significantly upon submergence (Fig. 2), in some cases as much as 2.5°C, but that was unusual (Tables 1 and 2). The drop in T_{brain} was not linear throughout

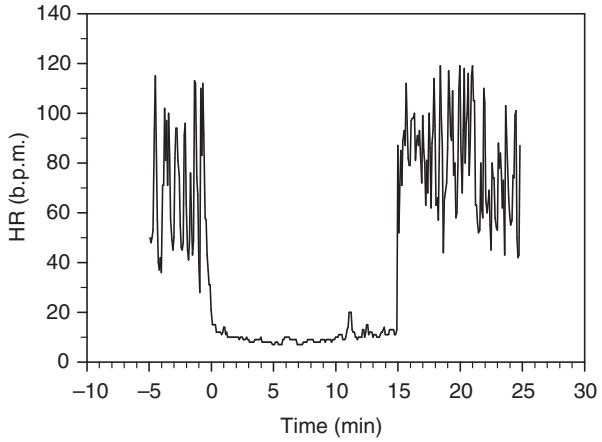

Fig. 1. Typical example of the changes in heart rate (HR; b.p.m.) in a harp seal during a 15 min experimental dive in water of 4°C, showing very variable heart rate before the dive, caused by spontaneous episodes of apnoea during sleep, and a profound bradycardia in response to submergence, followed by a return to pre-dive values upon emergence.

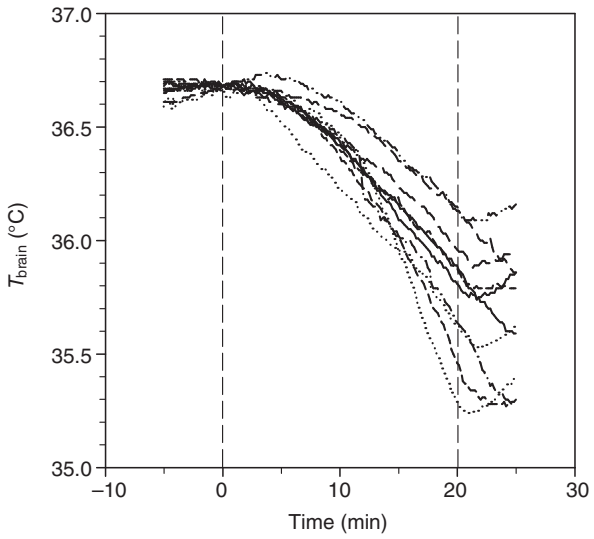

Fig. 2. Changes in brain temperature (T_{brain}; °C) of a hooded seal during 10 experimental dives lasting 20 min (between vertical dashed lines) and during the first 5 min of the recovery period. The lines for the individual dives were normalized to fit the median brain temperature at the start of diving (t=0). See Table 2 for statistics.

the dive. It was slow during the first few minutes, but dropped quite linearly, and significantly more (P>0.001), after about 5 min of diving (Figs 2 and 3; Table 1). In some cases we noted that T_{brain} fell progressively during series of three consecutive dives (Fig. 4), but this was not always the case. On a few occasions we also noted that T_{brain} started to fall prior to the commencement of the dive. The lowest T_{brain} ever recorded was 34.2°C.

Intra-aortic temperature (T_{aorta}) fell by and large in parallel with T_{brain}, but was always significantly (about 0.5°C, P=0.002) lower than T_{brain}, and the difference tended to decrease throughout the dive (Fig. 5; Table 2).

Musculus lattissimus dorsi temperature (T_m) was fairly stable throughout the dives (Fig. 5; Table 2).

Rectal temperature (T_r) dropped very significantly (Table 2) during dives. In fact, in some cases it dropped even more than T_{brain} (Fig. 5), but overall significantly less (P=0.025; Table 1).

Vascular anatomy

Angiography (Fig. 6) as well as the plastic casts revealed that the brachial artery of the hooded seal consists of one prominent vessel with few significant side branches until it splits up to the five digits of the fore-flipper. However, at the base of the flipper a conspicuous

Table 1. Median values for brain temperature (T_{brain}; Fig. 3) and rectal temperature (T_r) from the same dives in 4 harp seals and 5 hooded seals during 10 min experimental dives, and brain temperature (T_{brain}) during 15 min experimental dives in 1 harp and 1 hooded seal

				95% confidence interval		
	n	*N*	Median	Lower	Upper	*P*
T_{brain} at t=0 min	9	88	37.54	37.25	37.64	
T_{brain} at t=5 min	9	88	37.47	37.08	37.51	
T_{brain} at t=10 min	9	88	37.15	36.66	37.15	
T_r at t=0 min	9	86	36.70	36.41	36.78	
T_r at t=5 min	9	85	36.55	36.23	36.60	
T_r at t=10 min	9	85	36.14	35.80	36.28	
ΔT_{brain} from 0 to 5 min	9	88	0.15	0.12	0.18	
ΔT_{brain} from 5 to 10 min	9	88	0.32	0.32	0.44	
ΔT_{brain} from 0 to 10 min	9	88	0.50	0.50	0.64	
ΔT_r from 0 to 10 min	9	85	0.29	0.28	0.50	
ΔT_{brain} 5–10 min – ΔT_{brain} 0–5 min	9	88	0.21	0.18	0.26	<0.001
ΔT_{brain} 0–10 min – ΔT_r 0–10 min	9	85	0.15	0.02	0.20	0.025
T_{brain} at t=0 min	2	32	37.65	37.10	37.72	
T_{brain} at t=5 min	2	32	37.63	37.02	37.66	
T_{brain} at t=10 min	2	32	37.29	36.78	37.35	
T_{brain} at t=15 min	2	32	36.92	36.49	37.02	

Temperature is in °C. The medians are the observed medians. The 95 % confidence intervals for the medians are Wilcoxon's signed rank confidence intervals. The significance values (p) refer to test of a null hypothesis that the median is zero against a two-sided alternative, using Wilcoxon's signed rank test. n=number of animals, N=number of dives.

Table 2. Statistics based on changes in brain (T_{brain}), aorta blood (T_{aorta}), musculus lattissimus dorsi (T_m) and rectal temperature (T_r) in 2 harp seals during the first 8 min of 13 experimental dives of various duration, except muscle temperature, which was recorded in 6 dives

			95% confidence interval		
	N	Median	Lower	Upper	*P*
T_{brain} at t=0 min	13	36.51	36.41	36.78	
T_{brain} at t=8 min	13	35.75	35.64	35.99	
T_{aorta} at t=0 min	13	36.21	35.61	36.27	
T_{aorta} at t=8 min	13	35.53	34.94	35.72	
T_m at t=0 min	6	34.82	34.47	35.69	
T_m at t=8 min	6	34.79	34.31	35.31	
T_r at t=0 min	13	36.09	35.93	36.23	
T_r at t=8 min	13	35.41	35.03	35.79	
ΔT_{brain} from 0 to 8 min	13	0.74	0.69	0.83	0.002
ΔT_{aorta} from 0 to 8 min	13	0.69	0.47	0.84	0.002
ΔT_m from 0 to 8 min	6	0.16	0.00	0.38	0.059
ΔT_r from 0 to 8 min	13	0.74	0.41	0.91	0.002
$T_{brain} - T_{aorta}$ at t=0 min	13	0.49	0.37	0.91	0.002
$T_{brain} - T_{aorta}$ at t=8 min	13	0.35	0.24	0.74	0.002

Temperature is in °C. The 95% confidence intervals for the medians are Wilcoxon's signed rank confidence intervals. For the six lower lines in the table a null hypothesis that the median is zero has been tested against a two-sided alternative.

arterial rete is shunted in parallel with the brachial artery. The light and scanning electron microscopical examination of tissue from this area (Fig. 7) revealed that the blood in the arterial rete runs in parallel with blood in an even more conspicuous venous rete, creating what appears to be an ideal counter-current heat exchanger.

Angiography (Fig. 6) also revealed a system of prominent superficial veins which may lead the venous effluent from the flippers outside the heat exchanger described above and thereby provide cold blood to the heart.

DISCUSSION

Brain cooling in diving seals

This study has shown that seals respond to experimental diving not only with the well known host of cardiovascular responses (Ramirez et al., 2007), as reflected in a profound bradycardia (Fig. 1), but also with a controlled cooling of their brain (Figs 2–5). The median cooling recorded in this study was of the order of 1°C over 15 min, but brain cooling of 2.5°C was recorded in single experiments, confirming the old and defamed results of Scholander and colleagues (Scholander et al., 1942). Moreover, our finding of a blockade of the thermoregulatory responses of hooded seals during diving (Kvadsheim et al., 2005) strongly supports the notion that the brain cooling is indeed intended and under physiological control. This also includes reduction of the thermoregulatory 'set-point' for body temperature, as part of the diving response package. This is basically a medullary reflex package, but in expert divers it may be profoundly affected by cortico-hypothalamic input, such as the controlled blockade of the thermoregulatory responses to hypothermia. It is

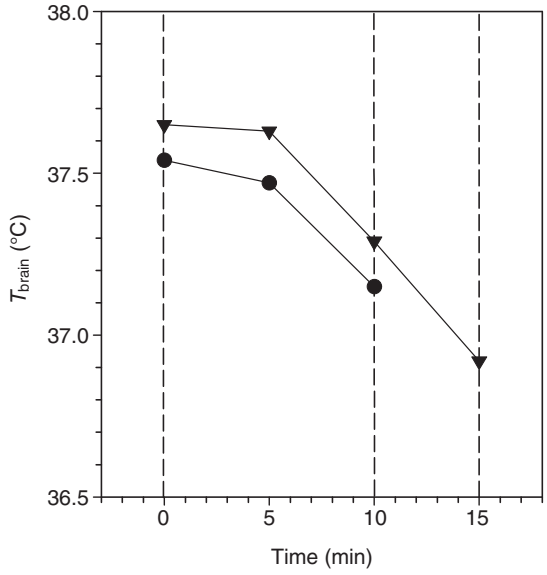

Fig. 3. Median values for brain temperature (T_{brain}; °C) in 4 harp and 5 hooded seals during 10 min experimental dives (filled circles; N=88 dives) and during 15 min experimental dives in 1 harp and 1 hooded seal (filled triangles; N=32 dives). See Table 1 for statistics.

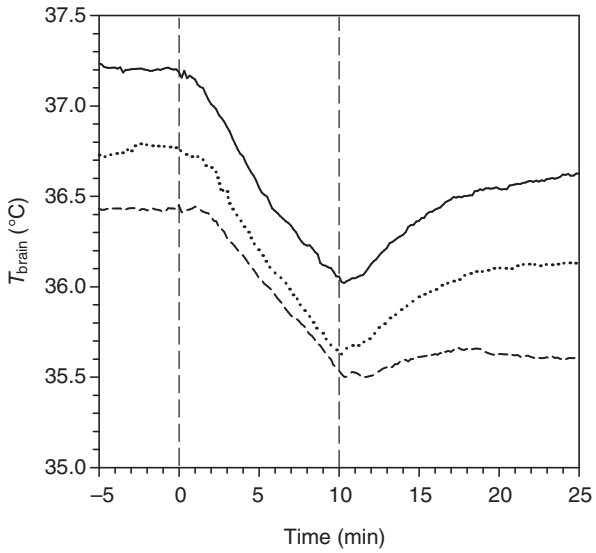

Fig. 4. Changes in brain temperature (T_{brain}; °C) of a harp seal during a series of three consecutive experimental dives of 10 min (between vertical dashed lines) with the first 15 min of the recovery period, which was always of 1 h duration between each dive. Dive 1, solid line; dive 2, dotted line; dive 3, dashed line.

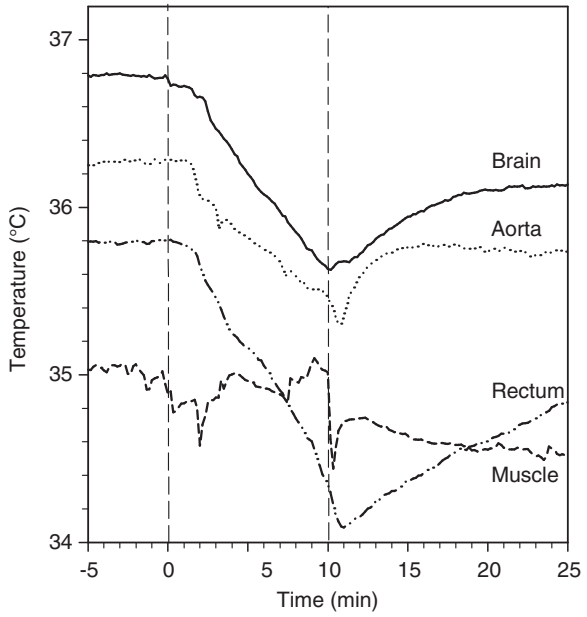

Fig. 5. Changes in the temperature of brain (solid line), aorta blood (dotted line), rectum (dashed and double dotted line) and musculus lattissimus dorsi (dashed line) in a harp seal before a dive, during a 10 min experimental dive (between dashed vertical lines) and during the first 15 min of the recovery period.

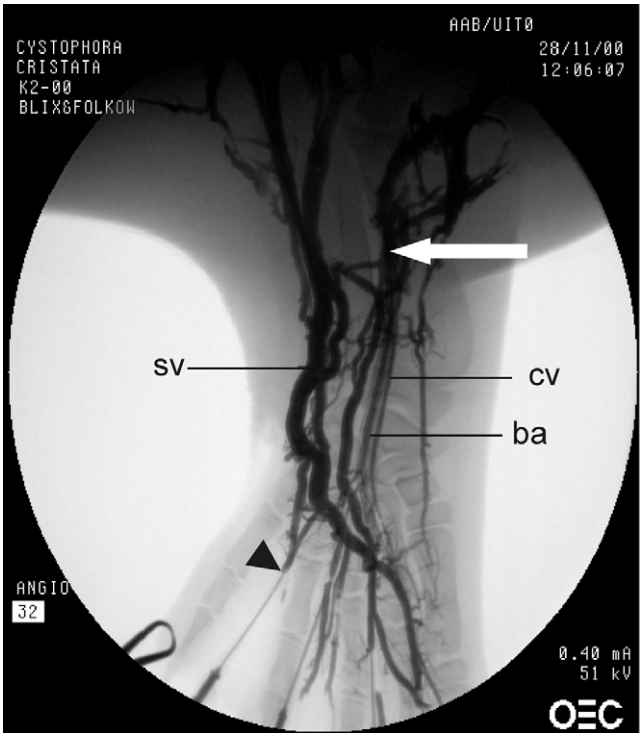

Fig. 6. Angiogram of the great superficial veins (sv) of a fore-flipper of a hooded seal. The point of contrast medium injection is indicated by the arrowhead. ba, brachial artery; cv, deep central veins. The location of the counter-current vascular heat exchanger shown in Fig. 7 is indicated by a white arrow.

by now also quite clear that expert divers may decide to what extent they will activate their (diving) defence responses depending on the challenge of the dive to come (Blix and Folkow, 1983; Folkow and Blix, 2010).

Without the recorded cooling, brain temperature is likely to increase during diving because of increased insulation of the head caused by vasoconstriction in skin and blubber and a marked reduction in cerebral blood flow (Blix et al., 1983a), which reduces the removal of heat from the brain during the early part of the dive. This is further supported by the fact that the difference between brain and aorta blood temperature was gradually reduced towards the end of the dive (Fig. 5), when cerebral blood flow is supernormal (Blix et al., 1983a). Moreover, assuming that Q_{10} is the same in seals as in piglets (Busija and Leffler, 1987; Laptook et al., 1995), a reduction in brain temperature of 2.5°C in the seal should lead to a reduction in brain oxygen demand of about 25%. In cases of prolonged diving, when the brain is pretty much the sole consumer of haemoglobin-bound oxygen in seals, this obviously represents a very significant expansion of diving capacity. Hindell and colleagues (Hindell et al., 1992), and others, have pondered over the fact that several species of seals, notably the southern elephant seal, repeatedly exceed their calculated aerobic dive limit, and brain cooling may well, at least in part, also be the explanation for this.

In any case, all this begs the question, will the brain work adequately at such reduced temperatures? This is of course anybody's guess in seals, but Moser and Andersen (Moser and Andersen, 1994) found that spatial learning in rats is unimpaired at brain temperatures as low as 30°C, and we therefore boldly suggest that a cool head is a great advantage in diving seals.

How is brain cooling achieved?

This study suggests that when brachial arterial blood flow to the fore-flippers is directed to the capillaries of the tissues for nutritional purposes, the blood may return in the deep central veins through a sophisticated counter-current vascular heat exchanger at the base of the flippers (Figs 6–8). This heat exchanger contains elements of an arterial and a venous rete which are reminiscent of structures described from the tail fluke and dorsal fin of the porpoise (*Lagenorhynchus acutus*) by Scholander and Schevill (Scholander and Schevill, 1955). This structure was later erroneously represented as a venous rete around the brachial artery, as the sole elements of (fore-) flipper circulation by Schmidt-Nelsen (Schmidt-Nelsen, 1975), and because of the prominence of his book and probably because of the simplicity of the concept, it unfortunately has become the general conception of marine mammal fluke and flipper circulation. However, at least in hooded seals, the arterial rete, which runs in parallel with the venous rete, is shunted in parallel with the prominent brachial artery, in much the same way as described in mallard ducks (*Anas platyrhynchos*) by Midtgård (Midtgård, 1980), and this difference is not trivial from a brain cooling point of view, as elaborated upon below. In any case, the counter-current vascular heat exchanger ensures that any capillary blood in the flippers may return to the body core at a temperature very close to core temperature and thereby avoid any body cooling in circumstances when that is undesirable. In that case the numerous cutaneous arterio-venous (A–V) shunts in the skin of the flippers (Bryden, 1978) will be closed and the entire venous drainage routed through the heat exchanger. The A–V shunts are under the control of the thermoregulatory 'centre' in the hypothalamus. They are not activated as part of the medullary controlled cardio-vascular diving responses if the animal is in positive thermal balance, as first shown by Djojosugito and colleagues (Djojosugito et al., 1969) in the duck,

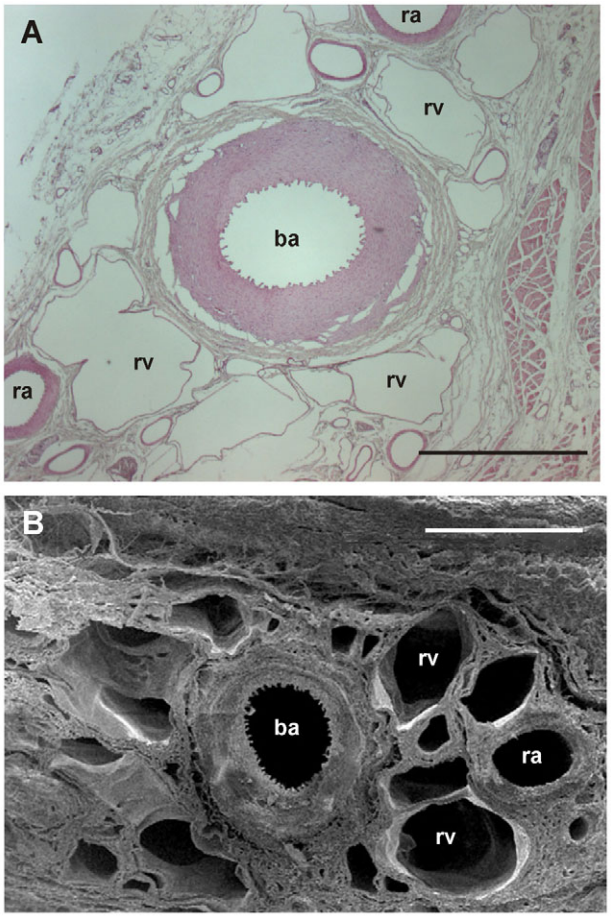

Fig. 7. Light (A) and scanning electron (B) microscopical representation of a cross-section through the counter-current heat exchanger at the base of the fore-flippers of hooded seals, showing the prominent brachial (thoroughfare) artery (ba) in the centre, with several rete arteries (ra) and numerous rete veins (rv) surrounding the brachial artery. The great superficial veins are outside the field of vision and are therefore not shown. Scale bars=1 mm.

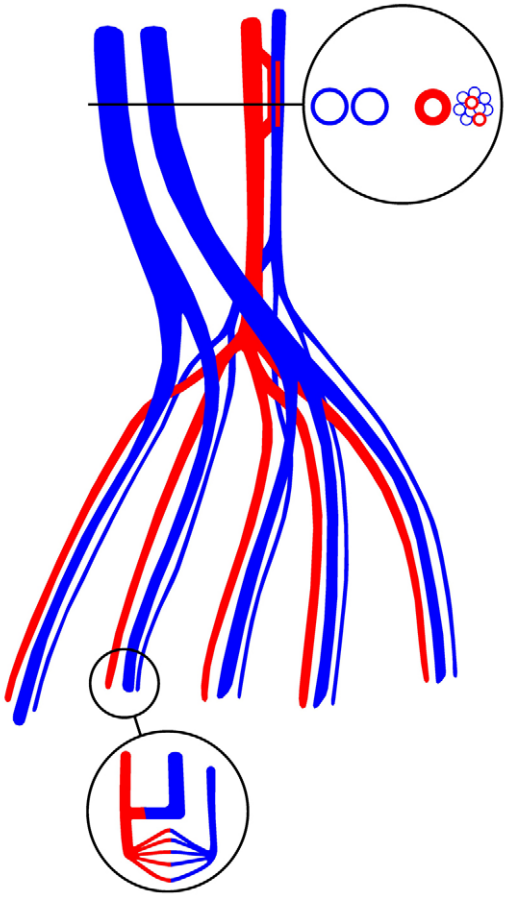

Fig. 8. Schematic drawing of the flipper vasculature shown in Fig. 6, indicating that the nutritive arterial inflow to the flipper leaves by way of the deep internal veins and exchanges heat with the incoming arterial blood in the counter-current vascular (rete) heat exchanger at the base of the flipper (Fig. 7) to avoid cooling of the body when there is need for heat conservation. When the animal wants to cool its brain, or cool off in general, a much increased arterial inflow may be routed through A–V shunts in the skin and the cold blood routed back to the heart by way of the large superficial veins (left) whereby those organs, notably the brain, that are circulated will be cooled.

and later by Hammel and coworkers (Hammel et al., 1977) in the harbour seal, and A–V shunts are not affected by chemoreceptor activation later in the dive (Chalmers and Korner, 1966; Löfving, 1961).

When, on the other hand, the A–V shunts are opened, venous drainage occurs through the huge superficial veins (Figs 6 and 8) and thereby bypasses the vascular heat exchanger at the base of the flippers and provides cold blood from the cold flipper skin (Irving and Hart, 1957) to the heart. It follows that the cold blood will henceforth be delivered selectively to those tissues that are circulated, notably the brain, and the cooling rate of the brain will be determined by the ratio of carotid to brachial arterial blood flow, and of course water temperature, during diving. We (Blix et al., 1983a) have shown that A–V shunts are indeed open during experimental dives. This is not only because of the need for brain cooling but also because of the need for some A–V shunt flow in the hind flippers to allow the considerable oxygen-containing venous depots (Hol et al., 1975) to reach the heart in a situation when most organs are shut off from the circulation. The latter is clearly supported by the finding of maintained saphenous venous flow during experimental diving in the harp seal (Hol et al., 1975). This will inevitably bring some cold blood from the hind-flipper venous plexuses (Tarasoff and Fisher, 1970) to the venous plexuses of the pelvic region (Blix et al., 1983b). This is most likely the reason for the decrease in the temperature recorded in the rectum (Fig. 5), but the effect of this cooling on brain temperature will be minor, since this blood will be heated by its passage through the central venous blood pool. The muscles, on the other hand, are not circulated during experimental dives (e.g. Blix et al., 1983a) and the temperature of the lattissimus muscle was stable or tended to rise during the dive in the present study (Fig. 5; Table 2). This is in accordance with Ponganis and coworkers (Ponganis et al., 1993) who found stable muscle temperatures in the Weddell seal diving voluntarily in the Antarctic.

Then why is the degree of brain cooling variable from dive to dive in the same animal? This is quite certainly due to the fact that the phenomenon depends on the control of the cutaneous A–V shunts and that emotional stimuli exert profound effects on the vascular tone in these shunts. Thus, any transient or permanent apprehension on

one side, and any degree of habituation on the part of the animal on the other, are bound to cause less cooling than would have been the case under natural conditions at high sea, when the animal is in control.

We conclude that the brain temperature may be actively down-regulated by at least as much as 2.5°C by the use of cold blood from the fore-flippers in the diving seal. By the Q_{10} effect (e.g. Schmidt-Nielsen, 1975) alone cerebral oxygen requirements may as a result be reduced by as much as 25% and diving capacity thereby substantially extended. This may explain, at least in part, how seals diving voluntarily repeatedly exceed their calculated aerobic dive limit.

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