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14. Monkeys were trained by successive approximation to fixate within 2.0° of the fixation point. If the animal's eye position left the fixation window, the fixation light extinguished, no reward was delivered, and a 1 s time-out was imposed in addition to the intertrial interval. A trial consisted of: fixation of a centrally presented fixation point for 0.5 s, 1.0 s of visual stimulus presentation, followed by an additional 0.5 s of fixation. No behavioral response other than visual fixation was required, and stimuli were presented in a randomized order. Every neuron was tested on one or more basic sets of color stimuli presented on a computer monitor including faces, objects, and colored rectangles. Stimuli typically subtended 8° to 10° of visual angle and were presented on a monitor with 640 pixel by 400 pixel resolution and 16-bit color. In two of three monkeys, when neurons appeared to show selectivity for faces, they were then tested exhaustively with additional stimuli to assess the basis for an apparent selective response to a face stimulus.
15. The mean firing rate was calculated for five time intervals for the task: 1 s during the pretrial period preceding the onset of the fixation point, 400 ms starting 100 ms after visual fixation, 200 ms beginning 100 ms after presentation of the visual stimulus, 900 ms from 100 ms after onset of the visual stimulus, and 2000 ms starting 100 ms after offset of the visual stimulus. An analysis of variance (ANOVA) was then performed using stimulus as a factor and firing rate in the time windows as a factor with repeated measures. The ANOVA yielded *P* values for the effects of time period, stimulus, and interaction between stimulus and time period. Only neurons with a significant main effect of stimulus or a significant interaction between stimulus and time window and a significant one-way ANOVA for one of the cue periods or the postcue period at a level of $P < 0.05$ were considered selectively responsive. Using the criteria of Perret and colleagues (*20*), cells that met the ANOVA criteria and had a response magnitude to the best face stimulus that was more than twice as strong as the best response to a nonface stimulus were considered to be face-selective.
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17. Offset of response was determined by when the response returned to below (or above) a 95% confidence interval based on pretrial firing for at least 100 ms [J. M. MacPherson and J. W. Aldridge, *Brain Res.* **175**, 183 (1979)].
18. To enable an unbiased sample of neurons, and therefore meaningful intraregional comparisons, neurons were not preselected for visual responsiveness, visual selectivity, or any other form of task-related activity.
19. Flattened representations of the prefrontal cortex were constructed with methods similar to D. C. Van Essen and J. H. R. Maunsell [*J. Comp. Neurol.* **191**, 255 (1980)] as modified by H. Barbas (*4*). The location of each face-selective neuron was drawn on a tracing of the appropriate section through the monkey's brain, these sections were compared to sections of a cortical atlas, and the neurons' location was transferred to the atlas. Then the cortical atlas with the locations of the cells was flattened along the midpoint between white matter and the pial surface.
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Thermoregulation in the Mouths of Feeding Gray Whales

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Vascular structures for heat conservation in the tongue of the gray whale (*Eschrichtius robustus*) are reported here. Numerous individual countercurrent heat exchangers are found throughout the massive tongue. These converge at the base of the tongue to form a bilateral pair of retia. Temperature measurements from the oral cavity of a live gray whale indicate that more heat may be lost through the blubber layer over the body than through the tongue, despite the fact that the tongue is far more vascularized and has much less insulation. These heat exchangers substantially reduce heat loss when these whales feed in cold waters.

Because of the high thermal conductivity of water, the oceans and seas are energetically challenging environments for endotherms. Countercurrent heat exchangers in the vascular system of whales assist in the regulation of body temperature (*1*): those within the fins and flukes (*2*) function to conserve core body temperature, whereas those associated with the reproductive tracts (*3*) serve to prevent hyperthermia in these heat-sensitive organs. The mouths of baleen whales (suborder Mysticeti) are relatively large, in order to accommodate the filtering surface composed of baleen, and the oral cavity of baleen whales is a major site for heat loss during feeding. To date, there have been no measurements to quantify this loss (*4*), nor have any structures been identified that would serve to reduce it.

In each of two young gray whale calves dissected (*5*) (LACM 88981, 3.98 m long; and LACM 92044, 5.25 m long), we found numerous individual countercurrent heat exchangers spaced throughout the tongue (Fig. 1A). These periarterial venous retia (*6*) consist of a single central artery encircled by a sheath of surrounding veins and are about 0.5 cm in diameter, making them similar in size to the individual countercurrent heat exchangers within the flukes of the same animals. The groups of blood vessels are oriented in planes, so that cool venous blood returning from the surface of the tongue flows first ventrally then posteriorly toward the back of the tongue. Along the posterior half of the base of the tongue, these individual countercurrent heat exchangers converge to form a bilateral pair of large vascular retia (Fig. 1B), each composed of over 50 such heat exchangers oriented adjacent and parallel. We term each vascular bundle a lingual rete. In the 5.25-m calf, each of these lingual retia was about 13 by 2 cm in cross-section and approximately 55 cm long. The lingual retia form one of the largest countercurrent heat exchangers described in any endotherm (*2*, *3*). At the base of the tongue, these heat-exchanger retia sweep dorsally and separate into numerous individual arteries and veins that connect to the external carotid artery and jugular vein, respectively. The countercurrent vascular retia are situated in the fascial plane located between the tongue muscles (styloglossus, hyoglossus, and intrinsic tongue muscles) and the more superficial gular muscles (geniohyoideus and myohyoideus). This vascular complex is derived from the lingual arteries and veins.

The distinct lingual artery is short, bifurcating into numerous arteries about 3 cm distal to the external carotid artery. This proliferation of arteries just proximal to the lingual rete functionally increases the cross-sectional area of this vascular system and the surface area of the blood vessel walls. Both of these structural attributes function to slow blood flow in any single vessel, thereby increasing the time available for the transfer of heat from arteries to veins. This should greatly enhance the efficiency of the countercurrent heat-exchanger system.

We measured a lingual surface area of 0.325 m^2 in the 5.25-m specimen, which yields an estimated surface area of 2 m^2 for a 12-m adult. This represents approximately 5% of the surface area of the body (*7*), excluding the extremities. Because a mobile and dexterous tongue is needed to control water flow over the baleen, the tongue could not properly function if it were cloaked with a thick, semirigid adipose layer similar to the blubber encasing the body. However, the outer surface of the tongue is invested with a diffuse layer of fatty tissue about 2 cm thick.

Skin surface temperature relative to ambient temperature is a good indicator of

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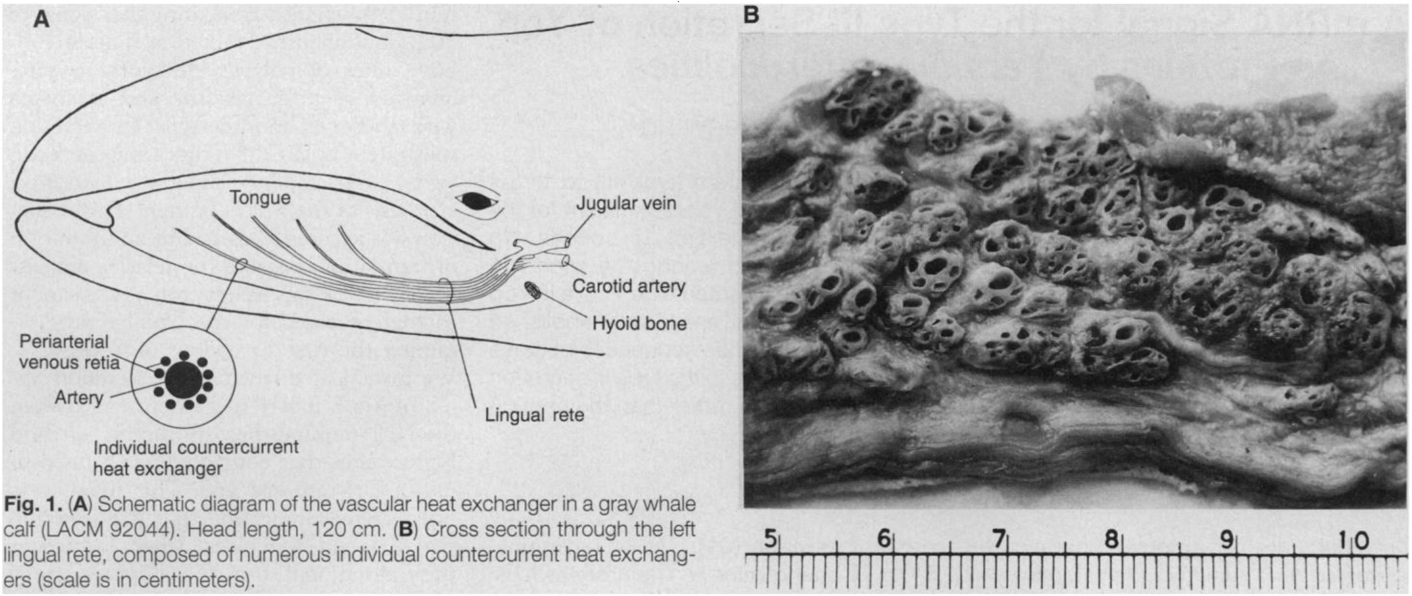

Fig. 1. (**A**) Schematic diagram of the vascular heat exchanger in a gray whale calf (LACM 92044). Head length, 120 cm. (**B**) Cross section through the left lingual rete, composed of numerous individual countercurrent heat exchangers (scale is in centimeters).

heat loss and can identify areas of regional heterothermy (*8*). We measured the surface temperature of the tongue and the skin of the body of a live gray whale calf during a series of feedings (*9*) in water temperatures of 19.5° and 12.5°C. When the calf first opened its mouth to suckle on a feeding tube, the temperature of the surface of the tongue was 1.5° to 3°C above the temperature of the skin on the dorsum of the head and cervical region. After about 1 min of suckling, with the oral cavity only slightly open to the water, the surface temperature of the tongue dropped to 0.5°C above the ambient water temperature and was 0.5° to 2.0°C below the temperature of the skin. The minor temperature differential between the tongue and the ambient water suggests that there was little heat transfer out of the tongue. During these measurements, the vivid pinkish hue of the tongue did not change noticeably, implying that the animal was not constricting blood flow to the tongue as a mechanism to conserve heat when the mouth was opened. All temperature measurements were taken when the animal briefly raised its head out of the water during feeding bouts; therefore, these measurements were not influenced directly by either water flow or boundary layer effects. Thus, we conclude that the drop in temperature on the surface of the tongue was a result of recirculation of heat back to the body core via the countercurrent heat exchanger. Although it has not been reported in the literature, it is reasonable to assume that the core body temperature of a gray whale is similar to the core temperature of the closely related balaenopterid whales, which is 35° to 36°C (*10*).

Although this test was conducted in what is for a gray whale a thermally unchallenging environment, these data suggest that gray whales can lose more heat through the blubber layer over their bodies than through the tongue, in spite of the fact that the tongue is far more vascularized and possesses much less insulation. This is due to the extreme length of the lingual countercurrent heat exchanger and the reduced rate of blood flow within each vessel because of the proliferation of blood vessels associated with the retia. The combined effect creates an extremely efficient thermal gradient over which heat can be transferred and thereby conserved.

Gray whales, like most species of baleen whales, feed in high-latitude waters during the summer. Scanty observations (*11–17*) suggest that all baleen whales possess countercurrent heat exchangers in their oral cavities, a physiological prerequisite allowing these endotherms to exploit the rich marine productivity of cold waters.

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5. The tongue of the smaller calf (LACM 88981) was transversely sectioned at about 2-cm intervals, and probes were inserted into the blood vessels to trace their course. The in situ architecture of the lingual rete of the larger calf (LACM 92044) was revealed by standard superficial-to-deep dissections in order to observe the connection of this plexus to the cranial-cervico vascular system.
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9. We measured the temperature of the tongue of a live, healthy, unrestrained gray whale calf. The first temperature measurements were made when the calf was about 4 months old in ambient water temperature of 19.5°C. The second series of measurements was taken when the calf was about 8 months old in 12.5°C water. Temperature measurements were taken with a Rayngher PM model PM3l3tru remote thermal sensor held approximately 20 cm from the target. Measurements were made when the whale calf lifted its head out of the water at the beginning and end of a feeding session. Each recording was based on several measurements made over a period of several seconds. In every case, the measurement was recorded after most of the water had dripped off and only a thin sheen of water remained on the tongue's surface. The temperature of the neck region did not change from the initial reading until at least 1 min of exposure to the air, which suggests that any biases from measuring the wet skin are minor and should apply equally to all measurements.
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17. It might seem incredible that such a large and complex vascular structure would have escaped the notice of previous workers. However, these vascular units are composed primarily of numerous small, thin-walled veins that easily collapse when the large flaccid tongue is being dissected. During most dissections, the entire heat exchanger is rather cryptic, resembling blood-invested fascia, which are plentiful within the head of a dead baleen whale.
18. We thank the staff of Sea World of California for logistical support in obtaining temperature measurements from a gray whale under their care. S. Rommel and I. Girard provided useful criticisms that improved this manuscript. The research of J.E.H. was supported by the Taylor Life Sciences Fund.

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