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**Journal**

AJP: Advances in Physiology Education, 36(1)

**ISSN**

1043-4046 1522-1229

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**Publication Date**

2012-03-01

**DOI**

10.1152/advan.00094.2011

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Peer reviewed

# A laboratory exercise using a physical model for demonstrating countercurrent heat exchange

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**Loudon C, Davis-Berg EC, Botz JT.** A laboratory exercise using a physical model for demonstrating countercurrent heat exchange. *Adv Physiol Educ* 36: 58–62, 2012; doi:10.1152/advan.00094.2011.—A physical model was used in a laboratory exercise to teach students about countercurrent exchange mechanisms. Countercurrent exchange is the transport of heat or chemicals between fluids moving in opposite directions separated by a permeable barrier (such as blood within adjacent blood vessels flowing in opposite directions). Greater exchange of heat or chemicals between the fluids occurs when the flows are in opposite directions (countercurrent) than in the same direction (concurrent). When a vessel loops back on itself, countercurrent exchange can occur between the two arms of the loop, minimizing loss or uptake at the bend of the loop. Comprehension of the physical principles underlying countercurrent exchange helps students to understand how kidneys work and how modifications of a circulatory system can influence the movement of heat or chemicals to promote or minimize exchange and reinforces the concept that heat and chemicals move down their temperature or concentration gradients, respectively. One example of a well-documented countercurrent exchanger is the close arrangement of veins and arteries inside bird legs; therefore, the setup was arranged to mimic blood vessels inside a bird leg, using water flowing inside tubing as a physical proxy for blood flow within blood vessels.

thermal biology; circulatory system; diffusion; physiology; bird

THIS LABORATORY EXERCISE was developed for use in an organismal physiology course taught at the undergraduate level for Biology majors. The purpose of this laboratory exercise was to teach the students about countercurrent exchange, one of the classic and ubiquitous mechanisms encountered in physiology. Countercurrent exchange of heat, respiratory gases, or nutrients is an important feature of the functional design of organisms, is covered in most undergraduate physiology textbooks (e.g., Refs. 19, 21, and 22), and is even mentioned in some introductory biology texts (e.g., Refs. 1 and 6). In countercurrent exchange, transport occurs between fluids moving in opposite directions on either side of a barrier (Fig. 1*A*). The mechanism for transport across the barrier is diffusion for chemicals or conduction for heat. Therefore, the rate and type of transport between the two fluids depend on the chemical or temperature gradients that exist across the barrier and the relevant conductivities of the barrier. Transport will also occur across the barrier if the fluids are moving in the same direction (concurrent exchange; Fig. 1*B*), but the rate of transport across the barrier will be much less than in the countercurrent case

because the gradient between the two fluids diminishes downstream when the fluids are moving in the same direction, and the rate of transport at any location is directly proportional to the local gradient. Therefore, countercurrent exchange leads to increased transport between fluid compartments. The function of countercurrent exchangers varies tremendously depending on the nature and location of the two fluid compartments; for example, the countercurrent exchanger may consist of part of the circulatory system doubling back on itself (Fig. 1*C*). Countercurrent exchange helps keep the testes cool in dolphins (16), promotes the uptake of oxygen from water to fish gills (18) and from the mother to the fetus in placental mammals (29), keeps muscles warm in swimming tuna (2), and minimizes heat loss to the environment from the feet of birds standing in cold water (20) and from the tail flukes of cetaceans swimming in cold water (4). Additional discussions of countercurrent mechanisms may be found in Refs. 13 and 28.

In our experience, many undergraduate Biology majors do not understand how flow in opposite directions promotes transport during countercurrent exchange after simply reading about it or hearing a short lecture on it. Because this is an important concept for students that is needed to understand many physiological processes, a hands-on laboratory exercise can be of great assistance to the instructor. Structure-function relationships and transport along gradients have been identified as core principles in physiology teaching (5, 15), and Biology majors or premedical students will need these concepts for either the Medical College Admission Test or Biology Graduate Record Examination. Active learning via laboratory exercises has repeatedly been shown to help students learn more effectively than simple lecturing (e.g., Refs. 14 and 26). We were therefore interested in developing a simple and inexpensive physical model that would allow students to directly measure the results of countercurrent exchange as part of a laboratory exercise to facilitate their understanding of mass and heat transport in biological systems.

Physical modeling is extremely useful to promote the understanding of the physical basis of physiological concepts and has repeatedly been used in hands-on undergraduate instruction; examples include physical modeling of parts of the gastrointestinal system (11), respiratory system (24, 25), and circulatory system (23). Countercurrent heat exchange may be physically modeled using two adjacent sections of tubing through which liquid is flowing in opposite directions, such as the two arms of a "U-shape" in which the tubing bends back on itself (Fig. 1*C*). Students find it challenging to make the conceptual connection between a physical model and its biological counterpart. We made the conceptual leap easier for

## A counctercurrent

fluid 1

40                                          6

35                                          1

fluid 2

## B current

fluid 1

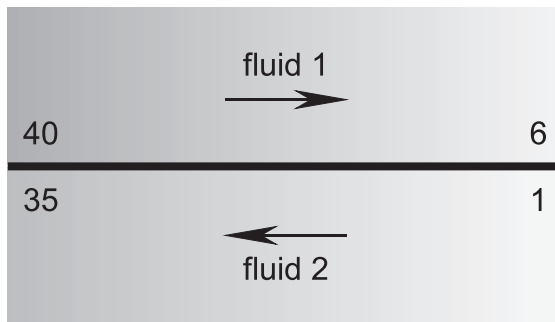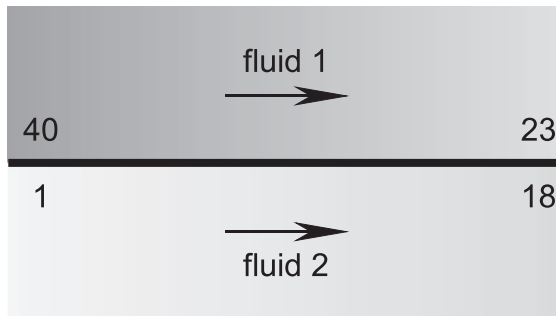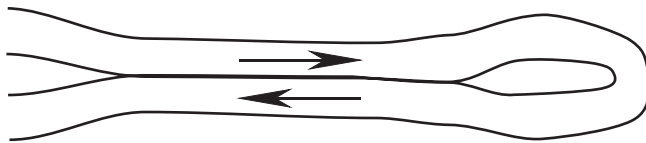40                                          23

1                                           18

fluid 2

## C counctercurrent

Fig. 1. *A*: in countercurrent exchange, two fluids (*fluid 1* and *fluid 2*) separated by a barrier flow in opposite directions. *Fluids 1* and *2* enter the area of exchange with temperatures of 40 and 1°C, respectively. Heat moves across the barrier down the local temperature gradient (from *fluid 1* to *fluid 2*). *Fluid 1* exits the exchanger chilled to a temperature of 6°C, and *fluid 2* was warmed to a temperature of 35°C. *B*: in concurrent exchange, *fluids 1* and *2* flow in the same direction on either sides of the barrier. As in *A*, *fluids 1* and *2* enter the area of exchange with temperatures of 40 and 1°C, respectively. However, *fluid 1* exits the exchanger chilled only to a temperature of 23°C, and *fluid 2* was warmed only to a temperature of 18°C. *C*: example of countercurrent exchange in which the flow doubles back on itself; this allows heat to take a different route than the moving fluid and bypass the end of the loop.

them by making the physical model explicitly resemble the biological system. We chose heat exchange within bird legs as our example of countercurrent exchange and, therefore, encased the tubing (which represented blood vessels) inside a plastic structure that resembled a bird leg and foot (Fig. 2).

## MATERIALS AND METHODS

### Overview

The physical model consists of a reservoir of water at a constant temperature (representing the "body") that supplies water (representing "blood") that flows through a thin-walled piece of tubing (dialysis tubing) to a site at which the water is chilled and returns to the body through a second piece of dialysis tubing (Fig. 2). The two sections of dialysis tubing (the outgoing and returning sections) are brought

together in close proximity to allow countercurrent heat exchange to take place. Controls are run for comparison by separating and insulating the outgoing and returning tubing. The water is chilled by passing it through a copper coil that is placed in ice water. Students collect the returning water and measure its temperature for the two cases of countercurrent exchange and the control. To remind students that the physical model represents a part of an organism, the plastic holder through which the dialysis tubing runs is shaped like a bird's foot.

### Experimental Details: Practical Tips and Suggestions

*Tubing.* Two pieces of dialysis tubing, each of 20-cm length, were used for the area of exchange because dialysis tubing walls are extremely thin and would therefore be less insulating, allowing heat transfer between the separated but adjacent water compartments flowing within the two pieces of tubing. It was difficult to make connections between the dialysis tubing and the other parts of the apparatus (such as the copper cooling coil); we made secure connections by folding back the edge of the dialysis tubing over the adjacent part and using a few short lengths of tygon tubing as external clamps. The dialysis tubing must be examined for kinks or twisting, because this will impede flow. Bubbles in the tubing can be a problem; they can be avoided by first clearing the tubing with a rapid flow of water and thereafter making sure that the tubing system does not empty. It is useful to have a clamp at the end of the tubing system (where the exiting water is collected for temperature measurement) to stop the flow between measurements.

*Generating and measuring flow.* The flow can be driven by gravity or by a pump. A gravity-fed flow is smooth, but the reservoir must be replenished regularly or must be fairly large, so that the flow rate does not decrease as the level in the reservoir falls. Gravity-fed flows also have the advantage of being low cost. We had better luck using a peristaltic pump to drive the flow, which made it easier for the students to change flow rates or keep the flow rate constant, although inexpensive aquarium pumps are also likely to work. The resistance to flow (of the tubing setup) can differ between the countercurrent and control cases; therefore, we had the students take measurements for four different flow rates to facilitate valid comparisons between the countercurrent exchange and the control. Students calculated the volume flow rate by measuring the volume of the collected water (after measuring its temperature) and the time during which it was collected (using a stopwatch).

*Temperature measurement and gradient generation.* Temperature measurements at two locations are sufficient to characterize the overall performance of the exchanger: the water in the reservoir before entering the exchanger and the water exiting the exchanger. The simplest way to measure temperature is to use thermometers; for the water exiting the system, collection in a styrofoam cup worked well, and we used styrofoam chips floating at the surface to limit heat exchange with the room air. One could also insert thermocouples at various locations in the tubing system and monitor their output to characterize the exchanger temperature gradients directly. Students can get a qualitative impression of the heat exchanger gradient by simply holding the dialysis tubing on the warm and cool sides between their fingers (before wrapping it in insulation). A water temperature of 40°C more closely represents the body temperature of a bird, but without a lot of insulation, the water chilled to room temperature before entering the exchanger. Our students had more consistent results when the water in the reservoir was at room temperature (~22–25°C). However, even when starting with room temperature water, it is crucial to insulate the exchanger from its surroundings, and, therefore, the entire exchanger was wrapped in insulation (a soft closed cell foam such as neoprene or minicel). For the control (no countercurrent exchange), the two antiparallel parts of the exchanger were insulated from each other with soft foam before the entire exchanger was wrapped in insulation. Insufficient insulation
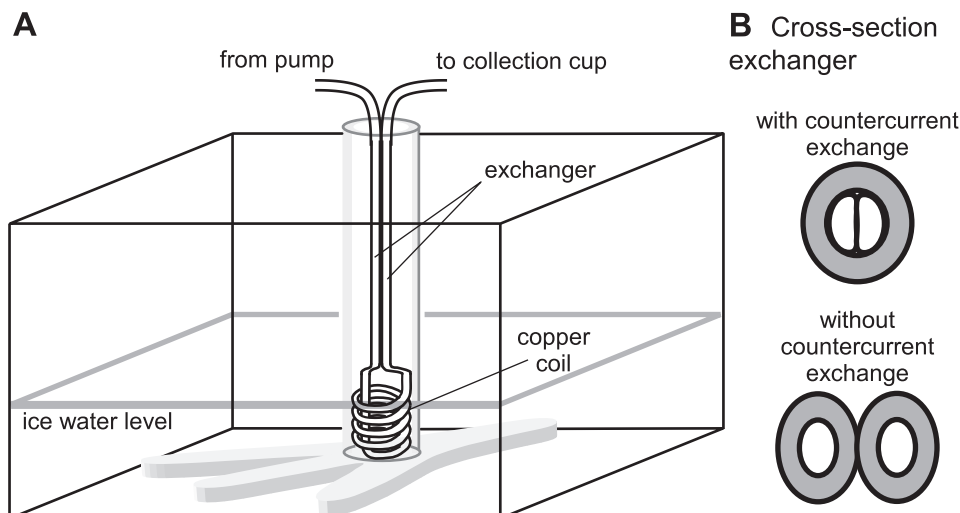
Fig. 2. *A*: diagram of the countercurrent exchange setup. Water enters from the reservoir, flows down the outgoing dialysis tubing to the copper coil, enters the copper coil, ascends back through the returning dialysis tubing , and exits. For countercurrent exchange, the two pieces of dialysis tubing were pressed together along their full length. For the control, the two pieces of tubing were insulated from each other. In both cases, additional insulation was placed around the dialysis tubing pair. The insulation is not shown. The exchanger (wrapped in insulation) was placed in a plastic holder that resembled a bird foot in shape, and the bird foot was placed in an ice bath in a styrofoam box with a stirbar mixing the ice water. Slits in the bottom of the holder allowed access of the surrounding ice water to the copper coil. *B*: cross section of the tubing (white) and the first layer of surrounding insulation (shaded) in the exchanger showing how the tubing was pressed together to facilitate countercurrent exchange (*top*) and insulated separately to minimize it (*bottom*).

is indicated if the water exiting the exchanger is at room temperature. Chilling was accomplished by passing the water through a copper coil (made by wrapping a piece of copper tubing smoothly around a pen for several turns). The insulated exchanger was placed within a plastic holder ("bird foot") consisting of a 25-cm length of polycarbonate tubing (transparent and stiff; internal diameter: 3 cm ) glued to a Plexiglas base (Fig. 2). The bird foot (housing the insulated exchanger) was placed in ice water inside a styrofoam box; the ice water was sufficiently deep to cover the copper coil but not the exchanger itself. Slits several millimeters in width and 3-cm high at the base of the polycarbonate tubing brought the ice water into contact with the copper coil. We found that rotation of a stir bar in the styrofoam box was critical to keep the ice water moving; otherwise, the water immediately surrounding the copper coil warmed up and the coil no longer adequately chilled the water flowing through it. A more porous base might lessen the need for ice water agitation.

**RESULTS**

Students were given data sheets (Table 1) on which to record the results for three replicates for each of four volume flow rates for each of the two experimental conditions (with and without countercurrent exchange). They recorded the volume of water collected (in ml), the time during which that volume was collected (in s), the average temperature of the collected water (in °C), and the starting temperature of the water (in °C). Students were given the information that 1 cal is required to raise the temperature of 1 g of water by 1°C, 1 ml of water has

a mass of (approximately) 1 g, and the term "Calorie" used in nutrition (with a capital "C") is the energy equivalent to 1,000 cal or 1 kcal. From this, students calculated the following: the volume flow rate (in ml/s), the difference in temperature (average temperature of the collected water − starting temperature of the water), the Calories (equal to kcal) lost due to cooling, and the rate of heat loss (in Cal/h). Students graphed the rate of heat loss (in Cal/h) as a function of flow rate and the temperature of the returning water (the chilled blood returning to the bird's body) as a function of flow rate (Fig. 3). We used Calories rather than joules as our energy unit to emphasize that the heat lost by the bird standing in cold water must ultimately be replaced by energy from catabolized food, requiring foraging by the bird. There was great consistency in the student measurements; Fig. 4 shows the data from 20 laboratory groups collected over a 2-yr period.

**DISCUSSION**

*What the Students Should Learn*

After completing this exercise, students should have a better understanding of the movement of heat down its gradient via conduction from areas of higher temperature to areas of lower temperature (and, by analogy, nutrients or respiratory gases via diffusion). By considering countercurrent exchange, the students should also be able to appreciate the role of convection

Table 1. *Column headings on the data sheets provided to the students*

| A | B | C | D | E | F | G | H |
|---|---|---|---|---|---|---|---|
| Volume of water collected, ml | Time during which volume (*column A*) was collected, s | Volume flow rate (*column A/ column B*), ml/s | Average temperature of water collected, °C | Starting temperature of water, °C | Difference in water temperature (*column D − column E*) | Calories lost by bird due to cooling, kcal | Rate of heat loss, Cal/h |

One data sheet was labeled "without countercurrent heat exchange" and the other data sheet was labeled "with countercurrent heat exchange."
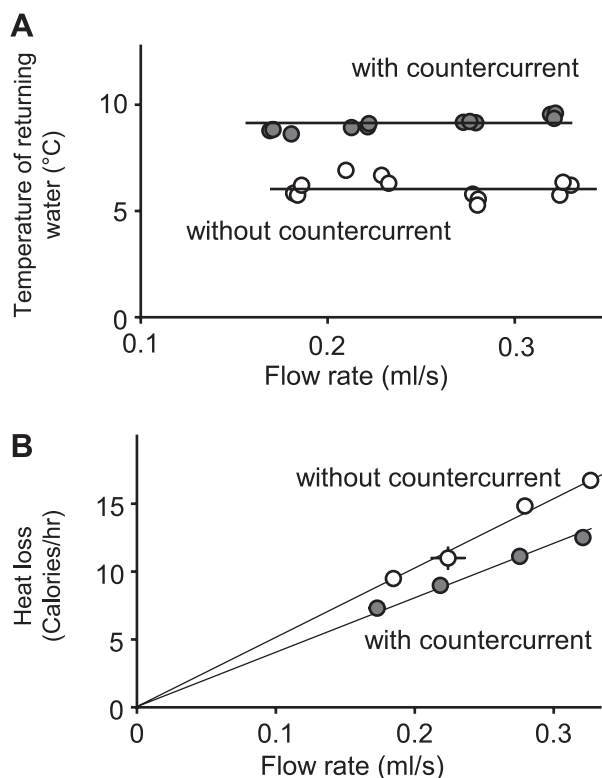
**A**



**B**



Fig. 3. Examples of student data. *A*: measured flow rates and water temperatures for three replicates for each of four different flow rates with and without countercurrent exchange. Global means are indicated by the horizontal lines. The temperature of the water returning from the chilling section was typically a few degrees warmer with countercurrent exchange than without and was independent of flow rate within the experimental range. *B*: heat loss was directly proportional to flow rate. Each point is the average of three replicates; error bars are $\pm 1$ SD for heat loss and flow rate. In most cases, the error bars lie within the marker. Linear regression through the origin resulted in $y = 52x$ without countercurrent exchange ($r^2 = 0.99$) and $y = 40x$ with countercurrent exchange ($r^2 = 0.99$).

(or bulk flow) of body fluids in heat transport and its interplay with transport via conduction. Because this exercise provides an example in which conduction occurs at right angles to bulk flow (convection), the differences between these two transport processes (conduction vs. convection) are highlighted. And, finally, students should have a better appreciation for the importance of the geometry or arrangement of blood vessels in changing the pattern of net transport. This exercise will be more valuable if it is made clear to the students that these are general principles that illustrate common features that they should be able to recognize and apply in different circumstances (15). The students also did some simple calculations (volume flow rate and rates of heat loss) and made graphs, as described above. Statistical tests may also be performed by the students, although many of these students had not yet had statistics courses and would need step-by-step instructions. The described setup (with tubing that loops back on itself) allows the comparison of countercurrent exchange with a control of no exchange at all, but an instructor wanting to compare countercurrent with concurrent exchange explicitly could devise a double-loop system, using a setup such as that described in Ref. 28 for inspiration.

We also wanted the students to think about the consequences or benefits of countercurrent exchange at the level of the whole

organism. Because we chose the biological context of heat loss to a cold environment from extremities (more specifically, countercurrent exchange in bird legs decreasing heat loss for birds standing in cold water), we linked the heat loss data to predictions of increased foraging and food intake by the bird (see the example questions below). This was also an opportunity to expose the students to classic papers (such as Ref. 20). An instructor may also want the students to consider why fluctuating blood flow to cold extremities may be important to minimize cold damage (8).

*Example questions*

Below is a list of questions that our students were required to answer after completing the laboratory exercise.

*Question 1.* If blood circulating to a bird's feet standing in ice water cooled to 2°C and was then returned to the bird's core without the heat savings that occurs with a countercurrent heat exchanger, how many calories would the bird lose every day (24-h period)? You may assume that the bird's core temperature is 40°C, that 100 ml of blood are circulated through the feet every 5 min, and that the bird is constantly standing in the cold water.

*Question 2.* The primary prey item for the bird in *question 1* is fish, which has ~1 Cal/g. How many grams of fish must this bird capture and consume every day to offset the losses from standing in cold water? How many pounds of fish is this (1 lb = 454 g)?

*Question 3.* In *part I* (without countercurrent exchange), how was "blood" temperature (returning from the foot) affected by the blood flow rate? Is this what you expected? Why or why not?

*Question 4.* In *part II* (with countercurrent exchange), how was "blood" temperature (returning from the foot) affected by the blood flow rate? Was this the same as what you found in *part I*? Would you expect this? Why or why not?

*Question 5.* Why is it important to have a stir bar rotating in the ice water bath in which the bird foot is immersed?

*Possible Extensions and Modifications*

For instructors wanting to provide a more mathematical treatment in countercurrent transport for the students, a very useful mathematical solution for concentration gradients in countercurrent exchange has been provided by Keener and
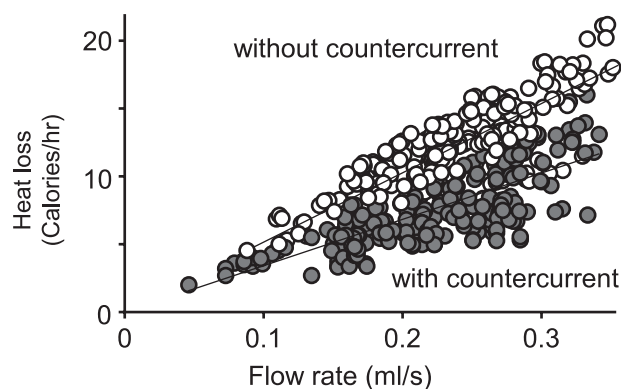


Fig. 4. Compilation of student data from 2 yr of this laboratory exercise. Open circles are data without countercurrent exchange; shaded circles are data with countercurrent exchange. Linear regression through the origin resulted in $y = 51x$ without countercurrent exchange ($r^2 = 0.64$) and $y = 34x$ with countercurrent exchange ($r^2 = 0.58$).

Sneyd (10). Assuming that the volume flow rate is identical in the two tubes and in opposite directions and that the concentration gradients within the tubes are one-dimensional (i.e., the concentration is a function of distance along each tube but does not vary radially within each tube) and in steady state (not changing in time), the concentration at the exit of one of the tubes of length $L$ can be given by *Eq. 20.22* (10), as follows:

$$\frac{C_1(L)}{C_1^0} = \frac{q_1 + \gamma dL}{q_1 + dL}$$

where $C_1(L)$ is the concentration in *tube 1* at distance $L$ (output concentration), $C_1^0$ is the input concentration of the same tube (*tube 1*), $q_1$ is the volume flow rate inside *tube 1* (equal to the volume flow rate in *tube 2*), $d$ is a lumped parameter related to the conductivity between the two tubes ($d$ equals the rate of change of $C_1$ caused by local transport between the two tubes divided by the local concentration difference between the two tubes), and $\gamma$ is the ratio of the input concentrations of the two tubes ($C_2^0/C_1^0$). Rewriting this equation by analogy between heat and mass transfer results in the following:

$$\frac{T_1(L)}{T_1^0} = \frac{q_1 + \gamma d'L}{q_1 + d'L}$$

where $T_1(L)$ is the temperature in *tube 1* at distance $L$ (output temperature), $T_1^0$ is the input temperature of the same tube (*tube 1*), $d'$ is the thermal analog of $d$ (related to the thermal conductivity between the two tubes), and $\gamma$ is the ratio of the input temperatures of the two tubes ($T_2^0/T_1^0$). The lumped parameter $d'$ may be estimated by the students from their data using the supplied equation, which may also be used to explore the influence of changing tube length or flow rates on expected heat transfer. Mathematical treatments are especially sought after in interdisciplinary physiology courses such as those taught by teams of engineers and biologists (3), but the challenge for the instructor is often ensuring that the students truly understand the relationship between the mathematical equation and the physical analog.

Another opportunity for extension of this countercurrent exercise is to discuss the more complicated renal countercurrent system. Classic papers (such as Ref. 7) may be used (17, 27), or the heterogeneity of the renal system may be considered (12). Katz (9) provides many useful suggestions for effective and creative teaching of this complex subject.

## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

## AUTHOR CONTRIBUTIONS

Author contributions: C.L. and J.T.B. conception and design of research; C.L., E.C.D.-B., and J.T.B. analyzed data; C.L. and J.T.B. interpreted results of experiments; C.L. and E.C.D.-B. prepared figures; C.L. and E.C.D.-B. drafted manuscript; C.L., E.C.D.-B., and J.T.B. edited and revised manuscript; C.L. approved final version of manuscript; E.C.D.-B. and J.T.B. performed experiments.

## REFERENCES

1. **Campbell NA, Reece JB.** *Biology*. San Francisco, CA: Benjamin Cummings, 2007.
2. **Carey FG, Teal JM, Kanwisher JW, Lawson KD, Beckett JS.** Warm-bodied fish. *Integr Comp Biol* 11: 137–143, 1971.
3. **Clase KL, Hein PW, Pelaez NJ.** Demand for interdisciplinary laboratories for physiology research by undergraduate students in biosciences and biomedical engineering. *Adv Physiol Educ* 32: 256–260, 2008.
4. **Elsner R, George JC, O'Hara T.** Vasomotor responses of isolated peripheral blood vessels from bowhead whales: thermoregulatory implications. *Marine Mammal Sci* 20: 546–553, 2004.
5. **Feder ME.** Aims of undergraduate physiology education: a view from the University of Chicago. *Adv Physiol Educ* 29: 3–10, 2005.
6. **Freeman S.** *Biological Science*. San Francisco, CA: Benjamin Cummings, 2010, p. 1320.
7. **Gottschalk CW, Mylle M.** Micropuncture study of the mammalian urinary concentrating mechanism: evidence for the countercurrent hypothesis. *Am J Physiol* 196: 927–936, 1959.
8. **Johansen K, Millard RW.** Vascular responses to temperature in the foot of the giant fulmar, *Macronectes giganteus. J Comp Physiol* 85: 47–64, 1973.
9. **Katz SA.** Some teaching tips on the mechanisms of urinary concentration and dilution: countercurrent multiplication be damned. *Adv Physiol Educ* 20: 195–205, 1998.
10. **Keener J, Sneyd J.** *Mathematical Physiology*. New York: Springer, 1998, p. 625195–635.
11. **Lawson DM.** A model for visualizing fluid handling by the gastrointestinal tract. *Adv Physiol Educ* 27: 87–88, 2003.
12. **Layton AT, Layton HE, Dantzler WH, Pannabecker TL.** The mammalian urine concentrating mechanism: hypotheses and uncertainties. *Physiology* 24: 250–256, 2009.
13. **McNeill AR.** *Animals*. Cambridge: Cambridge Univ. Press, 1990, p. 364250–366.
14. **Michael J.** Where's the evidence that active learning works? *Adv Physiol Educ* 30: 159–167, 2006.
15. **Michael J, Modell H, McFarland J, Cliff W.** The "core principles" of physiology: what should students understand? *Adv Physiol Educ* 33: 10–16, 2009.
16. **Rommel SA, Pabst DA, McLellan WA, Mead JG, Potter CW.** Evidence for a countercurrent heat exchanger associated with dolphin testes. *Anatom Rec* 232: 150–156, 1992.
17. **Schafer JA.** *Editorial Focus. Essays on APS Classic Papers. Experimental Validation of the Countercurrent Model of Urinary Concentration* (online). http://ajprenal.physiology.org/content/287/5/F861.full.
18. **Scheid P, Hook C, Piiper J.** Model for analysis of counter-current gas transfer in fish gills. *Respir Physiol* 64: 365–374, 1986.
19. **Schmidt-Nielsen K.** *Animal Physiology: Adaptation and Environment*. Cambridge: Cambridge Univ. Press, 1997, p. 264–267.
20. **Scholander PF.** Evolution of climatic adaptation in homeotherms. *Evolution* 9: 15–26, 1955.
21. **Sherwood L, Klandorf H, Yancey P.** *Animal Physiology: from Genes to Organisms*. Belmont, CA: Brooks Cole, 2004, p. 816.
22. **Silverthorn DU.** *Human Physiology: an Integrated Approach*. San Francisco, CA: Benjamin Cummings, 2010, p. 992.
23. **Smith AM.** A model circulatory system for use in undergraduate physiology laboratories. *Adv Physiol Educ* 22: 92–99, 1999.
24. **Stockert B.** Pulmonary ventilation teaching aid. *Adv Physiol Educ* 27: 41–42, 2003.
25. **Stockert B.** Pulmonary ventilation teaching aid: part 2. *Adv Physiol Educ* 27: 86–87, 2003.
26. **Taraban R, Box C, Myers R, Pollard R, Bowen CW.** Effects of active-learning experiences on achievement, attitudes, and behaviors in high school biology. *J Res Sci Teach* 44: 960–979, 2007.
27. **Tauck DL.** Using a classic paper by Gottschalk and Mylle to teach the countercurrent model of urinary concentration. *Adv Physiol Educ* 30: 63–66, 2006.
28. **Vogel S.** *Vital Circuits: on Pumps, Pipes, and the Workings of Circulatory Systems*. New York: Oxford Univ. Press, 1992, p. 186.
29. **Wilkening RB, Meschia G.** Current topic: comparative physiology of placental oxygen transport. *Placenta* 13: 1–15, 1992.