Adv Physiol Educ 41: 120–129, 2017;
doi:10.1152/advan.00158.2016.

SOURCEBOOK OF LABORATORY ACTIVITIES IN PHYSIOLOGY

Back to the future! Revisiting the physiological cost of negative work as a team-based activity for exercise physiology students

Matthew A. Kilgas[1,2] **and Steven J. Elmer**[1]

[1]*Department of Kinesiology and Integrative Physiology, Michigan Technological University, Houghton, Michigan; and*
[2]*Department of Biological Sciences, Michigan Technological University, Houghton, Michigan*

Submitted 6 October 2016; accepted in final form 7 January 2017

Kilgas MA, Elmer SJ. Back to the future! Revisiting the physiological cost of negative work as a team-based activity for exercise physiology students. *Adv Physiol Educ* 41: 120–129, 2017; doi: 10.1152/advan.00158.2016.—We implemented a team-based activity in our exercise physiology teaching laboratory that was inspired from Abbott et al.'s classic 1952 *Journal of Physiology* paper titled "The physiological cost of negative work." Abbott et al. connected two bicycles via one chain. One person cycled forward (muscle shortening contractions, positive work) while the other resisted the reverse moving pedals (muscle lengthening contractions, negative work), and the cost of work was compared. This study was the first to link human whole body energetics with isolated muscle force-velocity characteristics. The laboratory activity for our students (n = 35) was designed to reenact Abbott et al.'s experiment, integrate previously learned techniques, and illustrate differences in physiological responses to muscle shortening and lengthening contractions. Students (11–12 students/laboratory section) were split into two teams (positive work vs. negative work). One student from each team volunteered to cycle against the other for ~10 min. The remaining students in each team were tasked with measuring: *1*) O_2 consumption, *2*) heart rate, *3*) blood lactate, and *4*) perceived exertion. Students discovered that O_2 consumption during negative work was about one-half that of positive work and all other physiological parameters were also substantially lower. Muscle lengthening contractions were discussed and applied to rehabilitation and sport training. The majority of students (>90%) agreed or strongly agreed that they stayed engaged during the activity and it improved their understanding of exercise physiology. All students recommended the activity be performed again. This activity was engaging, emphasized teamwork, yielded clear results, was well received, and preserved the history of classic physiological experiments.

muscle contraction; oxygen consumption; metabolism; eccentric exercise; active learning

THE OBJECTIVE of this educational activity is to design and implement a team-based experiment for exercise physiology students that will shed light on the physiological responses, mechanisms, applications, and history of muscle lengthening contractions. Together, students work in teams to reenact Abbott et al.'s 1952 experiment (2), compile and analyze their data, and discuss their findings. By visiting the past, students will be inspired to go "back to the future" and connect their findings to present-day applications in rehabilitation and sport training arenas.

Address for reprint requests and other correspondence: S. J. Elmer, Department of Kinesiology and Integrative Physiology, College of Sciences and Arts, Michigan Technological University, 1400 Townsend Dr., Houghton, MI 49931 (e-mail sjelmer@mtu.edu).

Background

History. For more than a century, scientists (14, 25) have been intrigued by the observation that force produced during muscle lengthening contractions can be greater than that produced during muscle shortening contractions. In addition to this increased capacity for force production, the energy cost of muscle lengthening contractions is substantially lower compared with muscle shortening contractions (1, 13). The functional significance of these findings originally derived from isolated animal muscle preparations was not truly appreciated until 1952, when Abbott et al. (2) highlighted them during human exercise. Specifically, these authors connected two bicycles back to back via a single chain (Fig. 1). One cyclist pedaled forward as the other cyclist resisted the motion of the reverse moving pedals while O_2 consumption ($\dot{V}O_2$) was measured. During the forward pedaling condition, leg muscles produce force while shortening (i.e., positive work). Conversely, during the backward condition, leg muscles produce force while lengthening (i.e., negative work). The main finding was that the $\dot{V}O_2$ during negative work was only 1/2 to 1/5th that of positive work. The story is even more interesting as the authors piloted the experiment themselves. Most notably, the smaller Brenda Bigland was able to use considerably less effort to resist and tire out the forward pedaling efforts of the larger Murdoch Ritchie. This groundbreaking study offered a new viewpoint on muscle energetics specifically during human whole body exercise, and the story of the two-bicycle single-chain "push-me, pull-you" setup has been passed on in the literature (4, 11, 24, 27, 36, 37). Our laboratory activity not only educates students about muscle lengthening contractions, which are covered albeit briefly in exercise physiology textbooks, but also preserves the history of this original experiment.

Mechanisms and applications. "Physiologists often function as engineers in reverse in that the machines have already been built and the challenge is to decipher the primary design specifications, constraints, and material properties responsible for the machine's performance." This reverse engineering perspective in Rome and Lindstedt's chapter on the muscular system in the *Handbook of Physiology* (43) is fitting for this activity as students at our Technological University first observe that $\dot{V}O_2$ of the backward resisting cyclist is substantially lower compared with that of the forward cyclist and then have to break things down to figure out why. Some authors (16, 39) have suggested that the lower energy cost characteristics of muscle lengthening contractions might occur because the actin-

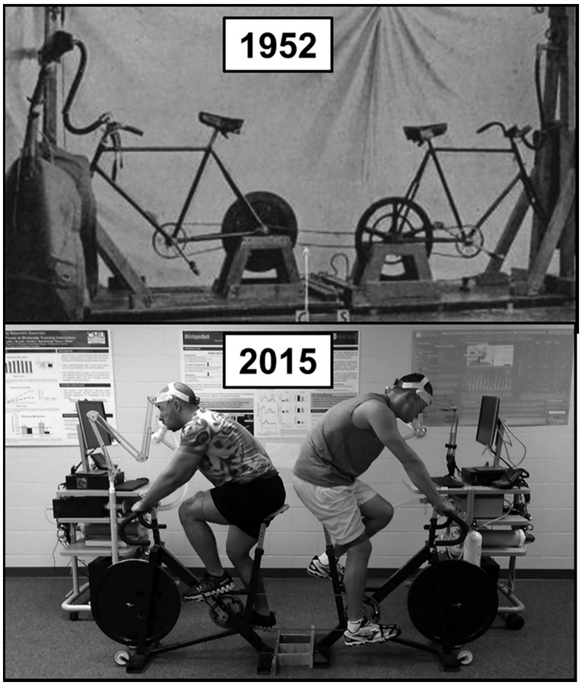

Fig. 1. *Top*: original experimental setup used by Abbott et al. in 1952. *Bottom*: setup we replicated for the present activity in 2015. The student on the right pedaled forward (positive work, quadriceps muscle shortening) while the student on the left resisted the reverse moving pedals (negative work, quadriceps muscle lengthening).

myosin bonds are disrupted mechanically rather than undergo an ATP-dependent detachment. Recently, muscle physiologists (22, 41) have proposed that the protein titin plays a critical role in enhancing force production as well. Even though many questions regarding the mechanisms responsible for muscle lengthen contractions remain unanswered (23), what is clear is that they have been successfully implemented to build muscle and enhance function without injuring muscle. Numerous investigators have demonstrated that exercise training involving muscle lengthening contractions with the lower and upper body (i.e., negative work or eccentric exercise) can be more effective than traditional exercise for improving muscle conditioning (size, strength, and power) and functional capacity in populations ranging from active individuals to individuals with advanced age and chronic diseases to competitive athletes (for reviews, see Refs. 24, 27, and 45). The novelty of negative work training in that only low to moderate levels of perceived exertion are required to generate high forces that can induce positive changes in muscular function. Given that negative work has emerged as a cutting-edge rehabilitation and sport training modality and that many of our students intend to seek professional careers in these areas (e.g., cardiac rehabilitation, physical therapy, medicine, strength, and conditioning), we emphasize the applications of muscle lengthening contractions with clinical and athletic populations.

Exercise physiology laboratory challenges. It is important to note that when delivering exercise physiology teaching laboratories, time restrictions and limited laboratory equipment (26) can make it difficult for all students to be fully engaged. For example, during a maximal $\dot{V}O_2$ ($\dot{V}O_{2max}$) test, which involves an expensive metabolic cart and cycle ergometer or treadmill, the majority of students often stand around a computer display and watch while only a handful of students actively participate with the data collection and exercise protocol. Thus, most students do not get experience with operating equipment and recording data and consequently demonstrate poor mastery of laboratory technical skills. In the Department of Kinesiology and Integrative Physiology at Michigan Technological University, we have circumvented some of these challenges by using a blended-learning approach [i.e., offloading content to self-paced video demonstrations to allow more time for laboratory activities (9)], allowing 2 wk for each laboratory topic, and strategically keeping our laboratory sections relatively small (e.g., ~8–16 students). Based on our experiences, the laboratory activity outlined below fits very well as an end-of-semester class project because it requires integration of technical skills presented in several previous laboratories, teamwork, and engagement by the entire class.

Learning Objectives

Content knowledge. After completing this activity, students will be able to:

1. Describe differences in the physiological responses (metabolic, cardiorespiratory, neuromuscular, and perceptual) between muscle shortening and lengthening contractions.
2. Identify possible underlying mechanisms contributing to these differences.
3. Experience firsthand the unique high-force, low-cost characteristics of muscle lengthening contractions.
4. Compare findings derived in class with peer-reviewed sources and apply findings to real-world scenarios in rehabilitation and sport training.

Process skills. After completing this activity, students will be able to:

1. Integrate previously learned laboratory techniques to simultaneously evaluate metabolic, cardiorespiratory, neuromuscular, and perceptual responses during exercise.
2. Gather and analyze data, present data in graphic form, and draw conclusions.
3. Reenact Abbott et al.'s original experiment (2) to preserve the history of this work.
4. Execute an individual task for successful completion of a collaborative class activity.

Activity Level

We have implemented this activity with undergraduate students enrolled in an exercise physiology laboratory course that is taken concurrently with the exercise physiology lecture. These exercise physiology courses are required for exercise science majors and also routinely attract nonmajor students from biological sciences and biomedical engineering. Before taking these courses, students had completed courses in human anatomy and physiology. At the completion of the exercise physiology laboratory course, students are expected to be able to *1*) operate laboratory equipment and administer a variety of exercise testing protocols; *2*) evaluate physiological responses to acute exercise; *3*) use Microsoft Excel to perform basic data entry, graphing, and statistical analyses; and 4) interpret and apply findings to real-world scenarios related to rehabilitation, exercise prescription, and sport training. In addition to using this activity with undergraduate students, we have implemented this in a similar manner with graduate students who are enrolled in kinesiology and physical therapy programs.

The current activity was presented as a cumulative end-of-semester class experiment. Specifically, it was designed to challenge students to integrate previously learned concepts and techniques and foster collaboration and teamwork. Thus, this activity is best suited for groups of students who have previous experience operating laboratory equipment, administering exercise testing protocols, and evaluating physiological responses to exercise.

Prerequisite and Student Knowledge or Skills

Before doing this activity, students should have a basic understanding of the following exercise physiology topics that are most often covered in lecture courses:

1. Skeletal muscle structure and function
2. Bioenergetics
3. Exercise metabolism
4. Work, power, and energy
5. Adaptations to acute and chronic exercise

Before conducting this activity, students should be able to know how to perform the following laboratory techniques:

1. Use open-circuit spirometry to measure $\dot{V}O_2$ and calculate energy cost
2. Collect blood lactate from a finger during exercise
3. Monitor subjective responses to exercise using ratings of perceived exertion

Note that during the semester, students had completed a series of laboratories that introduced each of the techniques outlined above and had time to become proficient with the techniques.

Time Required

We recommend that this activity be conducted over two consecutive laboratory sessions separated by 1 wk (Fig. 2). The time needed for each laboratory session is ~2 h, which falls within the typical range for most exercise physiology laboratories (e.g., 90 min to 3 h). The activity can also be simplified for a single session, which is described in more detail below in *Wider Applications*.

METHODS

Overview of the Activity

For each laboratory section, students are split into two teams (positive vs. negative work) and work together to carry out one experiment for the entire class. Withinin each team, students will be assigned to one of the following individual roles: *1*) the subject who performs the cycling exercise, *2*) the metabolic technician who will operate the metabolic cart, *3*) the heart rate technician who will monitor and record heart rate, *4*) the blood lactate technician who will measure blood lactate, *5*) the perceived exertion specialist who will assess rating of perceived exertion, and *6*) the master data recorder (Fig. 3). The subject from the positive work team will cycle (against the subject from the negative team) while all other students from that team collect physiological responses associated with positive work. Likewise, the subject from the negative work team will cycle (against the subject from the positive work team) while all other students from that team collect physiological responses associated with negative work. Accordingly, the class experiment yields positive and negative work data. These data are then made available to each team so that they can make their own comparisons between positive and negative work. Finally, each team has an opportunity to interpret the results of the class experiment and present their findings.

Equipment and Supplies

The following equipment and supplies are required for the entire class to carry out the laboratory activity (i.e., each positive and negative team will have one of each numbered items below):

1. Two exercise bikes
2. Two separate metabolic measurement systems
3. Two blood lactate analyzers (as wells as lactate strips, lancets, gauze, alcohol swipes, and gloves)
4. Two heart rate monitors
5. Two Borg ratings of perceived exertion scales
6. Two cooling fans

The following equipment and supplies are needed for configuring the experimental two-bike one-chain setup:

1. Two bicycle chains
2. A bicycle chain tool

Human and Animal Subjects

The procedures used were reviewed by the Institutional Review Board of Michigan Technological University, and the experiment was considered as an exempt educational activity. Educators who adopt this activity are responsible for obtaining permission for human subjects research from their home institution. For a summary of the "Guiding Principles for Research Involving Animals and Human Beings," we refer the reader to the following link: http://www.the-aps.org/mm/Publications/Ethical-Policies/Animal-and-Human-Research

Instructions

Experimental setup. Laboratory cycle ergometers or exercise bikes can be used for this activity after some minor modifications. Thus, instructors, university staff, and/or students who have bicycle maintenance knowledge can likely offer assistance with configuring the experimental setup. Moreover, we have found that a standard Monark (828 E, Monark Exercise, Vansbro, Sweden) cycle ergometer, which is used in most exercise physiology laboratories, can be easily adapted for this activity.

STEP 1. Remove the chain from the exercise bike. Many chains have a master link that enables the chain to be disconnected without

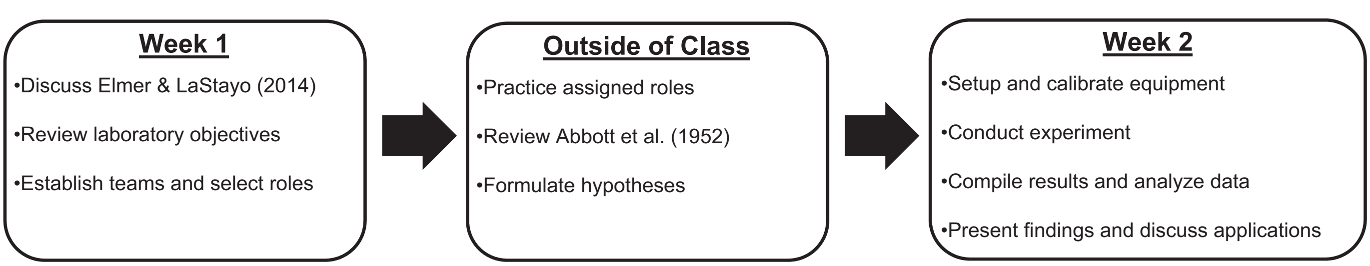

Fig. 2. Timeline and steps for carrying out the activity.

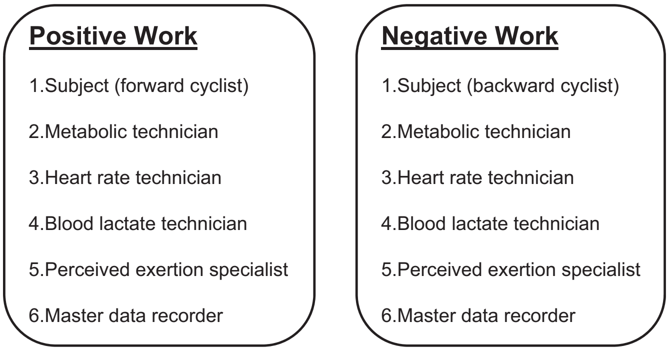

Fig. 3. Overview of team member roles. Specifically, within in each team, students are assigned to one of the indicated individual roles.

removing a link. Alternatively, a bicycle chain tool can be used to disconnect the chain and remove it from the exercise bike. Note that the plastic covering protecting the chain may first have to be removed to access the chain. Put the original chain (and master link) in a labeled Ziplock bag and set it aside for reassembling later. Repeat *STEP 1* for the second exercise bike.

STEP 2. Verify that the crank lengths are the same on both exercise bikes (e.g., ~170 mm).

STEP 3. Position the exercise bikes back to back so that they face away from each other.

STEP 4. Join the two new bicycle chains together using the chain tool.

STEP 5. Align the right crank of each exercise bike in such a way that it is 180° out of phase with the other exercise bike. While the cranks are in this position, connect the exercise bikes using the newly constructed long chain. Use the master link or chain tool to secure the chain together. Excess chain links can be removed if needed. Proper alignment of the cranks is critical to facilitate smooth coordination of movement.

STEP 6. Place a block of wood or wedge in between the two exercise bikes to help to maintain chain tension. This will also prevent the two-bike setup from moving around.

STEP 7. Ensure that the bottom bracket, crank bolts, and pedals are tight on both exercise bikes. Due to the backward motion of the one exercise bike, they tend to loosen. Thus, we recommend that these be checked frequently.

Laboratory session 1. The purpose of *laboratory session 1* is to introduce the activity, establish student teams, and have students select and practice their individual roles (Fig. 2).

STEP 1. Before class, instruct students to read the Elmer and LaStayo "Classics" Column *Journal of Experimental Biology* paper (11), which recognizes the historical significance of Abbott et al.'s original experiment (2). This will provide some background information on the topic of muscle lengthening contractions.

STEP 2. During class, explain the objectives of the activity as well as team-based approach, and split the class into two teams (i.e., the positive work team vs. the negative work team).

STEP 3. Arrange students with similar body sizes in pairs (i.e., one student from each team will pair up with one student from the other team) to practice coordinating the exercise task together. In other words, several pairs of students will try the exercise task for a few minutes so that the instructor can determine which student pair best naturally coordinates the exercise task (described below).

STEP 4. Instruct the forward cyclist to pedal at a constant pedaling rate of ~55–65 rpm. Note that the pedaling rate can be monitored by instrumenting the bike with a basic cyclo computer, having the forward cyclist pedal to the sound of a metronome, or manually counting revolutions periodically. Instruct the backward cyclist to resist the reverse moving pedals. Both cyclists have to communicate and work together to facilitate smooth pedaling. In other words, if the forward cyclist pedals too fast, it will be difficult for the backward cyclist to resist the pedals. Similarly, if the backward cyclist resists too hard, the forward cyclist will have difficulty pedaling forward at the desired pedaling rate. Thus, there is a fine balance for coordinating the system and performing the joint exercise task. Naturally, some student pairs will be able to coordinate and perform the exercise task better than others. Based on these observations, select the pair that exhibits the best coordination to perform the full experiment during the subsequent laboratory session. Note that all other students will be given specific roles for conducting the experiment. Theoretically, if the two-bike system is moving at a constant velocity (i.e., the forward cyclist is pedaling at the desired pedaling rate), the two movements and magnitude of work will be mirror opposites of one another, with the only differences being the exercise mode (forward vs. backward), work induced (positive vs. negative), and muscle contraction type (active shortening vs. active lengthening).

STEP 5. Now that the subject for each team has been identified, instruct teams (positive vs. negative work) to assign remaining team members to individual roles (Fig. 3). As stated above, within each team, students will be responsible for one of the following individual roles: *1*) the subject who cycles (already assigned by the instructor), *2*) the metabolic technician who will operate the metabolic measurement system to measure $\dot{V}O_2$, *3*) the heart rate technician who will monitor and record heart rate, *4*) the blood lactate technician who will measure blood lactate, *5*) the perceived exertion specialist who will assess rating of perceived exertion using the Borg 6–20 scale, and *6*) the master data recorder who will compile data (by hand or in Microsoft Excel). In larger laboratory sections, additional roles may be assigned, such as a team captain who is responsible for ensuring that everyone completes their job, or students may double up for *roles 2–6* so that all students are actively engaged.

Outside of class. The following steps are completed outside of class in between *laboratory sessions 1 and 2* (Fig. 2).

STEP 1. Instruct students to review Abbott et al.'s original study (2) so that they are familiar with the results of this experiment. We acknowledge that this can be a difficult read for undergraduate students due to the content and older scientific writing style. With that in mind, we direct students to focus on the METHODS and Figs. 1, 3, and 5 in that paper. Finally, based on the assigned readings and discussions in class, teams will establish their research questions and hypotheses to test before the next laboratory session.

STEP 2A. Instruct the two subjects to come in at least three times to continue to practice the exercise task. This step is critical to ensure that the subjects are adept at the cycling technique (either forward or backward) and the joint exercise task. During each practice visit, the student pair can practice for ~5–8 min. For the first 2–4 min, the backward cyclist should resist the pedals such that the forward cyclist is pedaling at a "somewhat hard" effort (Borg scale value of 13). Again, we recommend that the forward cyclist pedal between ~55 and 65 rpm. Subsequently, for the next 3–4 min, the backward cyclist should gradually start to resist harder each minute such that the forward cyclist is pedaling at a "hard" to "very hard" effort (Borg scale value of $>$15).

STEP 2B. Instruct the remaining students to come into the laboratory to practice their specific task for their team. For example, the blood lactate technician is advised to come in and practice taking a few exercise blood lactates while subjects are practicing. Similarly, the metabolic technician is advised to come in and practice calibrating the system and recording data. This serves as an important review of the technical skills developed earlier in the semester. It also requires that the students take ownership for their task so that their team is fully prepared.

Laboratory session 2. The following steps are completed during *laboratory session 2* (Fig. 2). Note that the experiment is run entirely by the students as the instructor observes.

STEP 1. Students are expected to arrive a few minutes early to begin preparing and calibrating equipment so that the class can start on time.

STEP 2. Each team will present their research questions and hypotheses to the class.

STEP 3. Subjects will begin the exercise task. For the first 5 min, subjects will perform a "steady-state" exercise trial. Based on the practice sessions, the backward cyclist will know approximately how hard to resist such that the forward cyclist is cycling at a "somewhat hard" effort. For the next 5 min, the backward cyclist will begin to resist harder and harder every minute to simulate a graded exercise test. Consequently, the forward cyclist will work harder and harder until they approach task failure and/or voluntary exhaustion. Table 1 shows a sample data sheet generated by students for recording physiological parameters during the experiment. Briefly, blood lactate is collected before exercise, during the steady-state exercise trial, and within 1 min after the completion of the graded exercise test. $\dot{V}O_2$, ventilation, heart rate, and respiratory exchange ratio data are recorded every 30 s throughout the exercise trial. The rating of perceived exertion is assessed between *minutes 4–5* and *9–10*.

STEP 4. After the experiment, subjects will be given time to fully recover while the rest of the class cleans up the laboratory area.

STEP 5. Data from each team will be made available to the other team so that both teams can separately analyze the class data and make comparisons between positive and negative work.

STEP 6. Each team will evaluate their data and calculate energy cost using the following Weir equation: energy cost (in kcal/min) = $\dot{V}O_2$ (in l/min) × (respiratory exchange ratio × 1.22 + 3.83). Students then convert and report these energy cost values (in W).

STEP 7. Each team will chart the class data in graphical format on the white board and then present their findings to the class.

Troubleshooting

The main challenges that we have encountered are *1*) ensuring that subjects can successfully coordinate the novel pedaling system and perform the exercise task and *2*) that students are prepared and organized for their specific tasks. We have found that the best approach is to include *laboratory session 1* as a preliminary introduction to the experiment and ask students to complete the outside of class practice sessions.

Safety Considerations

Students who volunteer as subjects should wear exercise clothing and footwear and be comfortable with exercising at submaximal and maximal intensities. Note that all students responsible for operating laboratory equipment and performing measurements were proficient with their specific tasks as they completed a series of introductory laboratories during the semester and reviewed these procedures again before the team-based activity. We must also emphasize that the backward resisting cycling condition can be potentially injurious in at least two ways. First, resisting the backward moving pedals with a seat position that allows the knee to reach full extension could result in injuries to the knee joint as the pedal could forcefully compress and/or hyperextend the knee. Thus, care should be taken when selecting a seat position to prevent the knee from reaching full extension. Second, because the backward condition elicits eccentric contractions involving the large muscle mass of the legs, it is easy to induce muscle damage and soreness in the lower limb, especially in eccentric-naïve individuals. Moreover, eccentric exercise-induced muscle damage and soreness can be severe, long lasting, and, in severe cases, give rise to rhabdomyolysis. With these eccentric exercise risks in mind, it is imperative that instructors *1*) provide clear instructions, *2*) require several familiarization trials at low to moderate intensities to help acquire the specific coordination for the backward motion, and *3*) limit the duration of the experiment to 5–10 min to minimize the risk of muscle damage and soreness. Indeed, our recommended familiarization protocol is consistent with eccentric exercised-based training studies that used eccentric cycle ergometry to improve muscular function without inducing muscle soreness in patient and athletic populations. Finally, as stated above, we strongly

Table 1. *Datasheet for the experiment*

Team: _______		Subject age: ____ yr			Height: ____ cm		Body mass: ____ kg	
Time, min	HR, beats/min	$\dot{V}O_2$, l/min	$\dot{V}O_2$, ml·kg^{-1}·min^{-1}	$\dot{V}E$, l/min	RER	Body RPE (scale: *6–20*)	Leg RPE (scale: *6–20*)	Energy Cost, W
0.00–0:30								
0:30–1:00								
1:00–1:30								
1:30–2:00								
2:00–2:30								
2:30–3:00								
3:00–3:30								
3:30–4:00								
4:00–4:30								
4.30–5:00								
5:00–5:30								
5:30–6:00								
6:00–6:30								
6:30–7:00								
7:00–7:30								
7:30–8:00								
8:00–8:30								
8:30–9:00								
9:00–9:30								
9:30–10:00								
Blood lactate, mmol/l								
Before exercise: ____								
Steady-state exercise: ____								
After exercise: ____								

HR, heart rate; $\dot{V}O_2$, O_2 consumption; $\dot{V}E$, minute ventilation; RER, respiratory exchange ratio; RPE, rating of perceived exertion. Energy cost was calculated based on $\dot{V}O_2$ and RER values. Blood lactate was measured before exercise, during the steady-state exercise portion (*minute 4–5*), and within 1 min after exercise.

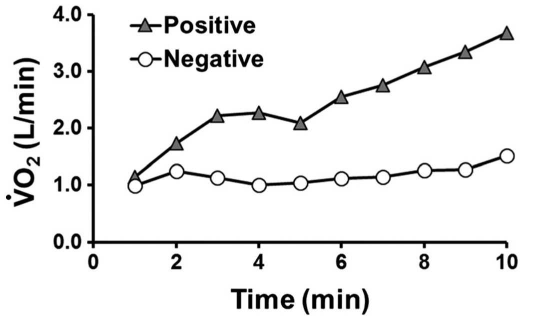

Fig. 4. Volume of O_2 consumption ($\dot{V}O_2$) measured during positive and negative work (representative data). For the first 5 min, the exercise task was performed such that the forward cyclist performing positive work was exercising at a "steady-state" intensity. During the remaining time, the backward cyclist increased the resistance every minute to exhaust the forward cyclist. Consequently, $\dot{V}O_2$ for the forward cyclist steadily increased and approached maximal $\dot{V}O_2$.

advise that the bottom bracket, crank bolts, and pedals on the exercise bikes be checked frequently to ensure they are tight.

RESULTS

Expected Results

The backward cyclist performing negative work will be able to resist and exhaust the forward pedaling efforts of the cyclist performing positive work. Indeed, during the final minute of exercise, $\dot{V}O_2$ values for the forward cyclist often approach previously established maximum values (determined earlier in the semester), indicating that the forward cyclist was exercising very close to $\dot{V}O_{2max}$. Representative results obtained by students are shown in Figs. 4 and 5. Students will discover that $\dot{V}O_2$ during negative work will be substantially lower compared with that of positive work. We typically observe values of 1/2 to 1/3rd of positive work, which is consistent with Abbott et al.'s original experiment (2) (Figs. 4 and 5).

Students will also discover that the negative work condition will elicit lower-end exercise values for several other metabolic, cardiorespiratory, and perceptual responses. For example, end-exercise whole blood lactate levels for negative work are often slightly above resting baseline values (~2 mmol/l), whereas positive work values can increase by up to 10-fold (~10 mmol/l; Fig. 5). Furthermore, heart rate and ventilation are considerably lower during negative work compared positive work. It will also be clear that negative work will require less effort compared with positive work. Indeed, the representative data indicate that the student performing negative work was exercising at a "very light" intensity compared with the student performing positive work who was exercising at a "very hard" intensity (Borg scale value of 9 vs. 17; Fig. 5). Finally, a strength of this activity is that the experiment yields clear results even if things do not go perfectly.

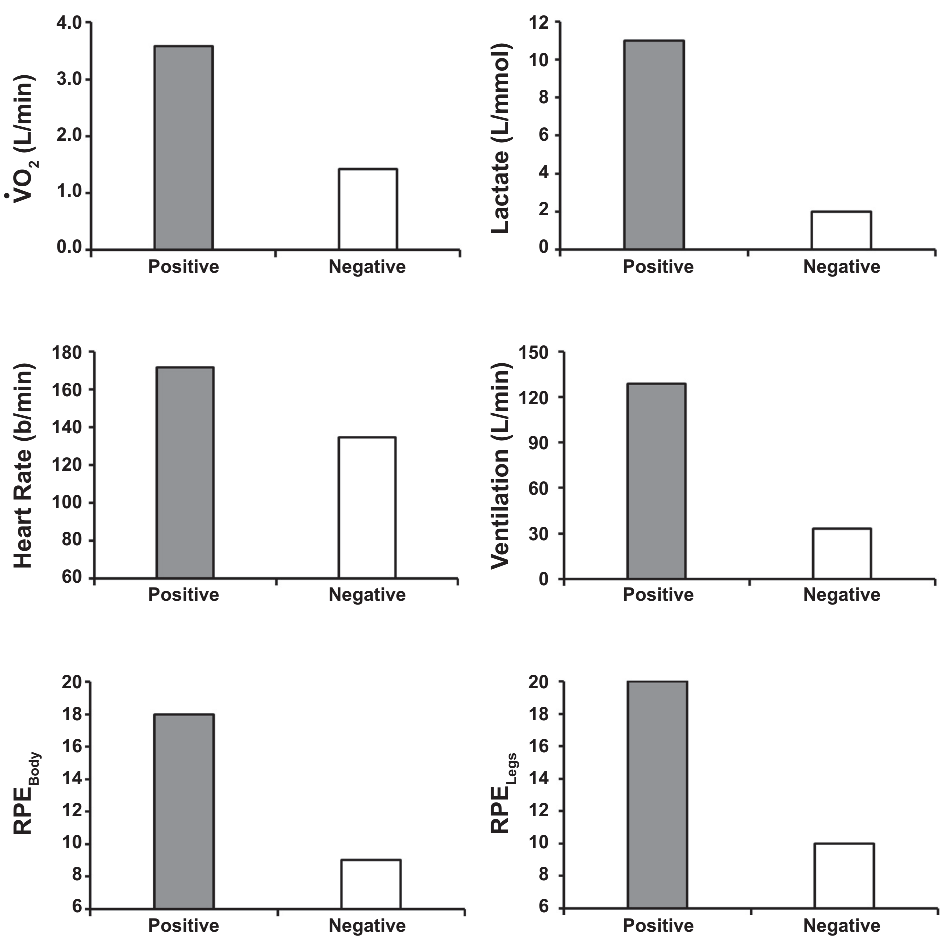

Fig. 5. Representative metabolic, cardiorespiratory, and perceptual responses assessed during the final minute of the exercise task.

Misconceptions

When learning about the structure and function of skeletal muscles, students, by no fault of their own, will often predict that muscle lengthening contractions would simply be the opposite of muscle shortening. That is, the chemical reactions that consume ATP during muscle shortening contractions might be reversed during muscle lengthening contractions. For this activity, students can observe and experience firsthand that muscle lengthening contractions are not the same and exhibit different responses. Importantly, these unique characteristics can have applications in rehabilitation and sport training and are discussed at the end of the activity to highlight real-world applications.

Evaluation of Student Work

We emphasize to students that this laboratory activity is very technically demanding and requires each student to take responsibility for his/her specific role. With adequate preparation and teamwork, the class will be able to successfully reenact Abbott et al.'s original experiment. With this in mind, we do not evaluate individual student work. Rather, we evaluate the success of each team and the entire class. To date, this approach has been well received by students and yielded positive outcomes each semester. Alternatively, instructors could choose to evaluate student work through a traditional laboratory report or assignment.

To further evaluate the effectiveness of the activity, a brief survey was administered to 35 students (24 undergraduate and 11 graduate students) to obtain student perceptions related to the laboratory format, level of engagement, and perceived learning. Questions were quantified using a Likert scale ranging from *1* to *5* (i.e., unable to comment, strongly disagree, disagree, agree, and strongly agree). As shown in Table 2, the majority of students (>90%) agreed or strongly agreed that the laboratory activity *1*) required them to come prepared for the experiment, *2*) integrated materials from previous laboratory activities, *3*) kept them engaged, *4*) enhanced their learning, and *5*) facilitated teamwork. Moreover, all 35 students recommended that the laboratory activity be performed again next year.

Questions and Discussion Points

Question 1. Which participant was working harder and were they close to reaching $\dot{V}O_{2max}$*?* The metabolic ($\dot{V}O_2$ and blood lactate), cardiorespiratory (heart rate and ventilation), and perceptional (rating of perceived exertion) data are all considerably lower during negative work compared with positive work. Therefore, the forward cyclist performing positive work will be working much harder. Furthermore, the general physiological criteria (8, 21) below can be used to verify whether the forward cyclist was exercising close to $\dot{V}O_{2max}$:

1. Plateau in $\dot{V}O_2$ (despite the increase in resistance provided by the backward cyclist)
2. Heart rate within 10 beats/min of the age-predicted maximal heart rate
3. Respiratory exchange ratio value of >1.15
4. Body rate of perceived exertion of >17 (using a Borg scale of *6–20*)
5. High postexercise lactate value (e.g., >8.0 mmol/l)

Question 2. How do results from class compare with those reported by Abbott et al.? As stated above, we typically observe values that are 1/2 to 1/3rd of positive work, which is consistent with Abbott et al.'s original experiment (2) (Figs. 4 and 5). Note that the effect of pedaling rate can influence these ratios (as shown in Table 1 of Abbott et al.'s paper), and thus we simply emphasize the large differences between the two conditions.

Question 3. What is the energy cost associated with positive and negative work? Using the $\dot{V}O_2$ data (average over *minutes 4–5* of exercise) and Weir equation, students will be able to calculate energy cost. Energy cost values for negative work are also ~1/2 to 1/3rd of that for positive work. Students will then be able to appreciate the difference between $\dot{V}O_2$ (in l/min) and energy cost (in W) and gain experience performing metabolic calculations used for exercise prescription.

Question 4. Why is the energy cost of muscle lengthening contractions lower? Mechanistically, the reduced energy cost might occur because the actin-myosin bonds are disrupted mechanically rather than undergo an ATP-dependent detachment (16, 39). However, this hypothesis has not been directly tested. Through the assigned papers and discussion period, we also explain to students that the reduced $\dot{V}O_2$ during negative work (along with reduced muscle activity findings from the literature) indicate that fewer muscle fibers are recruited and suggest that the recruited muscle fibers consume less O_2. Thus, muscle lengthening contractions are unique and not simply the opposite of muscle shortening contractions. Additionally, the lower cost of negative work may be further explained by the spring like

Table 2. *Student perceptions related to the laboratory activity expressed as a percentage of the total comments*

Question	Unable to Comment	Strongly Disagree	Disagree	Neutral	Agree	Strongly Agree
All of my team members were fully prepared to conduct their assigned roles.	0	0	0	0	17	83
The team-based final experiment required students to integrate exercise physiological concepts and techniques from several previous laboratory activities.	0	0	0	0	11	89
Overall, this team-based final experiment enhanced my learning.	0	0	0	3	31	66
I participated and stayed engaged throughout the experiment.	0	0	0	6	17	77
I felt like my team worked together in a cohesive manner to conduct our part of the experiment	0	0	0	0	6	94

Values are percentage; n = 35 total comments.

characteristics of the protein titin and the winding filament hypothesis (41). While a complete discussion of these mechanisms goes beyond the scope of this laboratory experiment, instructors may want to discuss these in more detail in the lecture course particularly with graduate students.

Question 5. Regarding rehabilitation, which clinical populations would be able to benefit from performing negative work training? Negative work (eccentric exercise) training is a well-established and highly effective rehabilitation modality for improving lower- and/or upper-body muscle conditioning and functional capacity in individuals with cardiovascular, respiratory, neuromuscular, and orthopedic disorders (for extensive reviews, see Refs. 27 and 34 and Table 3). Briefly, the novelty of negative work training is that it couples high forces (the stimulus for muscle adaption) with very low energy costs; hence, minimal perceived exertion is required (32, 33). This high-force, low-energy cost combination yields high levels of exercise adherence in even the most deconditioned patient groups (e.g., cancer survivors, frail elderly individuals, or individuals with chronic obstructive pulmonary disease) while building muscle and improving strength. These exercise-induced changes in muscle conditioning are reflected in improved leg power, balance, and mobility (24, 27). Importantly, while muscle lengthening contractions are often associated with muscle injury, damage, and soreness, none of these are required to stimulate improvements (15).

Question 5. Regarding sport training, which athletic populations would be able to benefit from performing negative work training? Negative work training offers a useful training adjunct for athletes and coaches. Specifically, it has produced significant improvements in muscle conditioning and functional capacity in healthy recreationally active individuals, competitive basketball players, and junior alpine ski racers (for extensive reviews, see Ref. 45 and Table 3).

Question 6. Why was Abbott et al.'s experiment so groundbreaking? It was the first study to link human whole body energetics with isolated muscle force-velocity characteristics previously measured in isolated animal muscles. It also inspired the fabrication of negative work ergometers and implementation of negative work training in rehabilitation and sport training settings.

Inquiry Applications

This activity is at the "methods" level of inquiry as the instructor designs the experiment. There are also components of "facilitated inquiry" as teams decide how to carry out the proposed experiment by assigning individual student roles, practicing these roles outside of class, and preparing for the activity ahead of time (e.g., equipment setup and calibration as well as creating data sheets). Based on the two required readings (2, 11), teams also develop their research questions and hypotheses to test before the class activity. To increase the level of inquiry, the instructor could pose the following general question: "Is the energy cost of performing positive and negative work the same?." Students could then use PubMed (https://www.pubmed.com) to find key papers that address this question and design an experiment similar to Abbott et al.'s original experiment (2).

Wider Applications

We have adapted this activity for educational outreach efforts including use with high school science fairs and department laboratory tours. To simplify the activity, we include only the two bikes and one chain. As described above, younger students are divided into teams, provided time to practice coordinating the exercise task, assigned roles (subject, heart rate recorder, perceived effort, master time keeper, etc.), and carry out the experiment for ~5 min. Students manually record heart rate from the carotid pulse and rating of perceived exertion using the Borg scale. Subsequently, they work together to graph their results and draw conclusions. The activity takes ~30–45 min. This activity not only exposes students to the scientific method but also generates enthusiasm and provides a source of physiological entertainment.

The activity also has potential to be implemented in other courses, such as biomechanics, because it includes aspects of muscle energetics and mechanics. For example, incorporation of surface electromyography to record quadriceps muscle activity during the activity would enable students to examine the relationship between motor unit recruitment and energy cost to better understand muscle contraction. Finally, for those instructors who can measure mechanical power directly from the two-bicycle setup (e.g., SRM power meter), the activity could be further strengthened by discussing the link between energy cost and mechanical power and calculating efficiency.

Additional Resources

For additional information on this topic, we direct the reader to the following references:

Table 3. *Effects of negative work training on lower-body muscle conditioning and functional capacity in clinical and athletic populations*

Population	Training	Intensity	Primary Outcomes
Frail elderly (26)	3 times/wk for 12 wk	RPE = 13 (somewhat hard)	↑ Muscle size, strength, and balance
Cancer survivors (27, 28)	3 times/wk for 12 wk	RPE = 13 (somewhat hard)	↑ Muscle size and walking distance
Heart disease (38)	3 times/wk for 8 wk	60% of peak $\dot{V}O_2$	↑ Muscle strength and peak $\dot{V}O_2$
Chronic obstructive pulmonary disease (40)	3 times/wk for 5 wk	60% of peak $\dot{V}O_2$	↑ Total work output
Parkinson's (5)	3 times/wk for 12 wk	RPE = 13 (somewhat hard)	↑ Muscle size and walking distance
Total knee replacement (29)	3 times/wk for 12 wk	RPE = 13 (somewhat hard)	↑ Muscle size, strength, and power
Anterior cruciate ligament surgery (16–18)	3 times/wk for 12 wk	RPE = 13 (somewhat hard)	↑ Muscle size and strength
Healthy (9, 30, 31, 33)	3 times/wk for 6–8 wk	58–66% of peak HR	↑ Muscle size, strength, power, and leg spring function
Basketball players (36)	3 times/wk for 6 wk	Not reported	↑ Jumping height
Alpine skier racers (19)	3 times/wk for 6 wk	Not reported	↑ Muscle size and jumping height

- Abbott et al.'s original experiment (2)
- Followup experiments (3, 6, 7, 12)
- Historical perspectives (4, 11)
- Mechanisms of lengthening contractions (16, 22, 39, 41)
- Negative work training with clinical (5, 17–19, 28–31, 40, 42, 44) and athletic (10, 20, 32, 33, 35, 38) populations
- Review articles (24, 27, 34, 45)

ACKNOWLEDGMENTS

The authors sincerely thank the undergraduate and graduate exercise physiology students for allowing us to improve this class activity and the Michigan Tech Center for Teaching and Learning for their support.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

M.A.K. and S.J.E. performed experiments; M.A.K. and S.J.E. analyzed data; M.A.K. and S.J.E. interpreted results of experiments; M.A.K. and S.J.E. prepared figures; M.A.K. and S.J.E. drafted manuscript; M.A.K. and S.J.E. edited and revised manuscript; M.A.K. and S.J.E. approved final version of manuscript.

REFERENCES

1. **Abbott BC, Aubert XM, Hill AV.** The absorption of work by a muscle stretched during a single twitch or a short tetanus. *Proc R Soc Lond B Biol Sci* 139: 86–104, 1951. doi:10.1098/rspb.1951.0048.
2. **Abbott BC, Bigland B, Ritchie JM.** The physiological cost of negative work. *J Physiol* 117: 380–390, 1952. doi:10.1113/jphysiol.1952.sp004755.
3. **Bigland-Ritchie B, Woods JJ.** Integrated electromyogram and oxygen uptake during positive and negative work. *J Physiol* 260: 267–277, 1976. doi:10.1113/jphysiol.1976.sp011515.
4. **Bigland-Ritchie BR.** Looking back. *Adv Exp Med Biol* 384: 1–9, 1995. doi:10.1007/978-1-4899-1016-5_1.
5. **Dibble LE, Hale TF, Marcus RL, Droge J, Gerber JP, LaStayo PC.** High-intensity resistance training amplifies muscle hypertrophy and functional gains in persons with Parkinson's disease. *Mov Disord* 21: 1444–1452, 2006. doi:10.1002/mds.20997.
6. **Dufour SP, Doutreleau S, Lonsdorfer-Wolf E, Lampert E, Hirth C, Piquard F, Lonsdorfer J, Geny B, Mettauer B, Richard R.** Deciphering the metabolic and mechanical contributions to the exercise-induced circulatory response: insights from eccentric cycling. *Am J Physiol Regul Integr Comp Physiol* 292: R1641–R1648, 2007. doi:10.1152/ajpregu.00567.2006.
7. **Dufour SP, Lampert E, Doutreleau S, Lonsdorfer-Wolf E, Billat VL, Piquard F, Richard R.** Eccentric cycle exercise: training application of specific circulatory adjustments. *Med Sci Sports Exerc* 36: 1900–1906, 2004. doi:10.1249/01.MSS.0000145441.80209.66.
8. **Duncan GE, Howley ET, Johnson BN.** Applicability of $\dot{V}O_{2max}$ criteria: discontinuous versus continuous protocols. *Med Sci Sports Exerc* 29: 273–278, 1997. doi:10.1097/00005768-199702000-00017.
9. **Elmer SJ, Carter KR, Armga AJ, Carter JR.** Blended learning within an undergraduate exercise physiology laboratory. *Adv Physiol Educ* 40: 64–69, 2016. doi:10.1152/advan.00144.2015.
10. **Elmer S, Hahn S, McAllister P, Leong C, Martin J.** Improvements in multi-joint leg function following chronic eccentric exercise. *Scand J Med Sci Sports* 22: 653–661, 2012. doi:10.1111/j.1600-0838.2011.01291.x.
11. **Elmer SJ, LaStayo PC.** Revisiting the positive aspects of negative work. *J Exp Biol* 217: 2434–2436, 2014. doi:10.1242/jeb.092247.
12. **Elmer SJ, Marshall CS, McGinnis KR, Van Haitsma TA, LaStayo PC.** Eccentric arm cycling: physiological characteristics and potential applications with healthy populations. *Eur J Appl Physiol* 113: 2541–2552, 2013. doi:10.1007/s00421-013-2687-7.
13. **Fenn WO.** The relation between the work performed and the energy liberated in muscular contraction. *J Physiol* 58: 373–395, 1924. doi:10.1113/jphysiol.1924.sp002141.
14. **Fick A.** *Mechaniche Arbeit und Warmeentwicklung b.d. Muskelthatigkeit*. Leipzig, 1882.
15. **Flann KL, LaStayo PC, McClain DA, Hazel M, Lindstedt SL.** Muscle damage and muscle remodeling: no pain, no gain? *J Exp Biol* 214: 674–679, 2011. doi:10.1242/jeb.050112.
16. **Flitney FW, Hirst DG.** Cross-bridge detachment and sarcomere 'give' during stretch of active frog's muscle. *J Physiol* 276: 449–465, 1978. doi:10.1113/jphysiol.1978.sp012246.
17. **Gerber JP, Marcus RL, Dibble LE, Greis PE, Burks RT, LaStayo PC.** Effects of early progressive eccentric exercise on muscle size and function after anterior cruciate ligament reconstruction: a 1-year follow-up study of a randomized clinical trial. *Phys Ther* 89: 51–59, 2009. doi:10.2522/ptj.20070189.
18. **Gerber JP, Marcus RL, Dibble LE, Greis PE, Burks RT, Lastayo PC.** Safety, feasibility, and efficacy of negative work exercise via eccentric muscle activity following anterior cruciate ligament reconstruction. *J Orthop Sports Phys Ther* 37: 10–18, 2007. doi:10.2519/jospt.2007.2362.
19. **Gerber JP, Marcus RL, Dibble LE, Greis PE, LaStayo PC.** Early application of negative work via eccentric ergometry following anterior cruciate ligament reconstruction: a case report. *J Orthop Sports Phys Ther* 36: 298–307, 2006. doi:10.2519/jospt.2006.2197.
20. **Gross M, Lüthy F, Kroell J, Müller E, Hoppeler H, Vogt M.** Effects of eccentric cycle ergometry in alpine skiers. *Int J Sports Med* 31: 572–576, 2010. doi:10.1055/s-0030-1254082.
21. **Haff GG, Dumke C.** *Laboratory Manual for Exercise Physiology*. Champaign, IL: Human Kinetics, 2012.
22. **Herzog W.** Mechanisms of enhanced force production in lengthening (eccentric) muscle contractions. *J Appl Physiol* 116: 1407–1417, 2014. doi:10.1152/japplphysiol.00069.2013.
23. **Hoppeler H, Herzog W.** Eccentric exercise: many questions unanswered. *J Appl Physiol* 116: 1405–1406, 2014. doi:10.1152/japplphysiol.00239.2014.
24. **Isner-Horobeti ME, Dufour SP, Vautravers P, Geny B, Coudeyre E, Richard R.** Eccentric exercise training: modalities, applications and perspectives. *Sports Med* 43: 483–512, 2013. doi:10.1007/s40279-013-0052-y.
25. **Katz B.** The relation between force and speed in muscular contraction. *J Physiol* 96: 45–64, 1939. doi:10.1113/jphysiol.1939.sp003756.
26. **Kolkhorst FW, Mason CL, DiPasquale DM, Patterson P, Buono MJ.** An inquiry-based learning model for an exercise physiology laboratory course. *Adv Physiol Educ* 25: 117–122, 2001.
27. **LaStayo P, Marcus R, Dibble L, Frajacomo F, Lindstedt S.** Eccentric exercise in rehabilitation: safety, feasibility, and application. *J Appl Physiol* 116: 1426–1434, 2014. doi:10.1152/japplphysiol.00008.2013.
28. **LaStayo PC, Ewy GA, Pierotti DD, Johns RK, Lindstedt S.** The positive effects of negative work: increased muscle strength and decreased fall risk in a frail elderly population. *J Gerontol A Biol Sci Med Sci* 58: M419–M424, 2003. doi:10.1093/gerona/58.5.M419.
29. **Lastayo PC, Larsen S, Smith S, Dibble L, Marcus R.** The feasibility and efficacy of eccentric exercise with older cancer survivors: a preliminary study. *J Geriatr Phys Ther* 33: 135–140, 2010.
30. **LaStayo PC, Marcus RL, Dibble LE, Smith SB, Beck SL.** Eccentric exercise versus usual-care with older cancer survivors: the impact on muscle and mobility--an exploratory pilot study. *BMC Geriatr* 11: 5, 2011. doi:10.1186/1471-2318-11-5.
31. **LaStayo PC, Meier W, Marcus RL, Mizner R, Dibble L, Peters C.** Reversing muscle and mobility deficits 1 to 4 years after TKA: a pilot study. *Clin Orthop Relat Res* 467: 1493–1500, 2009. doi:10.1007/s11999-009-0801-2.
32. **LaStayo PC, Pierotti DJ, Pifer J, Hoppeler H, Lindstedt SL.** Eccentric ergometry: increases in locomotor muscle size and strength at low training intensities. *Am J Physiol Regul Integr Comp Physiol* 278: R1282–R1288, 2000.
33. **Lastayo PC, Reich TE, Urquhart M, Hoppeler H, Lindstedt SL.** Chronic eccentric exercise: improvements in muscle strength can occur with little demand for oxygen. *Am J Physiol Regul Integr Comp Physiol* 276: R611–R615, 1999.
34. **LaStayo PC, Woolf JM, Lewek MD, Snyder-Mackler L, Reich T, Lindstedt SL.** Eccentric muscle contractions: their contribution to injury, prevention, rehabilitation, and sport. *J Orthop Sports Phys Ther* 33: 557–571, 2003. doi:10.2519/jospt.2003.33.10.557.
35. **Leong CH, McDermott WJ, Elmer SJ, Martin JC.** Chronic eccentric cycling improves quadriceps muscle structure and maximum cycling power. *Int J Sports Med* 35: 559–565, 2014. doi:10.1055/s-0033-1358471.
36. **Lindstedt SL.** Skeletal muscle tissue in movement and health: positives and negatives. *J Exp Biol* 219: 183–188, 2016. doi:10.1242/jeb.124297.
37. **Lindstedt SL, LaStayo PC, Reich TE.** When active muscles lengthen: properties and consequences of eccentric contractions. *News Physiol Sci* 16: 256–261, 2001.

38. **Lindstedt SL, Reich TE, Keim P, LaStayo PC.** Do muscles function as adaptable locomotor springs? *J Exp Biol* 205: 2211–2216, 2002.
39. **Menard MR, Penn AM, Lee JW, Dusik LA, Hall LD.** Relative metabolic efficiency of concentric and eccentric exercise determined by ^{31}P magnetic resonance spectroscopy. *Arch Phys Med Rehabil* 72: 976–983, 1991.
40. **Meyer K, Steiner R, Lastayo P, Lippuner K, Allemann Y, Eberli F, Schmid J, Saner H, Hoppeler H.** Eccentric exercise in coronary patients: central hemodynamic and metabolic responses. *Med Sci Sports Exerc* 35: 1076–1082, 2003. doi:10.1249/01.MSS.0000074580.79648.9D.
41. **Nishikawa K.** Eccentric contraction: unraveling mechanisms of force enhancement and energy conservation. *J Exp Biol* 219: 189–196, 2016. doi:10.1242/jeb.124057.
42. **Rocha Vieira DS, Baril J, Richard R, Perrault H, Bourbeau J, Taivassalo T.** Eccentric cycle exercise in severe COPD: feasibility of application. *COPD* 8: 270–274, 2011. doi:10.3109/15412555.2011.579926.
43. **Rome LC, Lindstedt SL.** Mechanical and metabolic adaptation of the muscular system. In: *Handbook of Physiology. Comparative Physiology*. Bethesda, MD: American Physiological Society, 1997, sect. 13, vol. II, chapt. 23, p. 1587–1652.
44. **Steiner R, Meyer K, Lippuner K, Schmid JP, Saner H, Hoppeler H.** Eccentric endurance training in subjects with coronary artery disease: a novel exercise paradigm in cardiac rehabilitation? *Eur J Appl Physiol* 91: 572–578, 2004. doi:10.1007/s00421-003-1000-6.
45. **Vogt M, Hoppeler HH.** Eccentric exercise: mechanisms and effects when used as training regime or training adjunct. *J Appl Physiol (1985)* 116: 1446–1454, 2014. doi:10.1152/japplphysiol.00146.2013.