Teaching skeletal muscle adaptations to aerobic exercise using an American Physiological Society classic paper by Dr. Philip Gollnick and colleagues

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**Brown, Gregory A.** Teaching skeletal muscle adaptations to aerobic exercise using an American Physiological Society classic paper by Dr. Philip Gollnick and colleagues. *Adv Physiol Educ* 30: 113–118, 2006; doi:10.1152/advan.00054.2005.—The use of primary research in the classroom enhances the critical thinking abilities of students. The present article describes a strategy for using the American Physiological Society classic paper “Enzyme activity and fiber composition in skeletal muscle of untrained and trained men” by Dr. Philip D. Gollnick and colleagues to enhance the students’ ability to understand research, increase their knowledge of the adaptations to exercise, and learn computer skills in data analysis and presentation. By having students read, study, prepare graphs, and discuss the data from a classic paper, they gain an improved understanding of the factors that influence aerobic exercise ability. This study is especially useful for illuminating the exercise-specific differences in bioenergetic enzymes, muscle fiber type, and fitness characteristics that exist between untrained and trained individuals.

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The feats of great athletes regularly arouse interest in the factors that determine athletic success. For example, with Lance Armstrong’s recent seventh consecutive victory in the Tour de France, there has been considerable interest in the physiological characteristics that make him such a great athlete. This interest is exemplified by the Discovery Channel’s production of a documentary entitled “The Science of Lance Armstrong,” which explores how training, engineering, and biology have combined to maximize the potential of this outstanding athlete (2). The American Physiological Society (APS) classic paper “Enzyme activity and fiber composition in skeletal muscle of untrained and trained men” by Gollnick et al. (6) provides an excellent cross-sectional overview of many of the skeletal muscle characteristics that are related to successful athletic performance.

This study by Gollnick et al. (6) explores the differences in skeletal muscle fiber histochemistry, bioenergetic enzymes, and maximal aerobic capacity [maximal oxygen consumption (V\textsubscript{O2\text{max}})] between aerobically trained, untrained, and resistance-trained men. Other notable data include the enhanced muscle glycogen storage capacity and differences in muscle fiber size between trained and untrained men. In addition, there is excellent coverage of the principle of specificity when the characteristics of upper-body dominant versus lower-body dominant athletes (e.g., canoeists and bicyclists) are compared. Finally, this study presents students with an excellent point of discussion regarding the effects of training and genetics on muscle fiber composition and histochemistry.

Although the data to be examined do not differ, the expectations for data analysis, interpretation, and presentation can easily be tailored to suit students ranging from those with little background in the adaptions to exercise to those who well understand the adaptations but may need more experience with their presentation or critical thinking skills. By using this study as the backbone for a directed in-class discussion and take-home assignment in either an introductory, advanced undergraduate, or graduate exercise physiology class, the instructor can deliver an effective instructional experience for students studying the effects of exercise on the human body.

**TEACHING POINTS**

*Preparing the students.* Before discussing the study by Gollnick et al. (6) with a class, the students need to have an understanding of the processes of aerobic and glycolytic bioenergetics within the body, the role of enzymes in regulating energy transfer, the role of muscle glycogen in exercise, and the purposes and implications derived from the assessment of aerobic capacity by V\textsubscript{O2\text{max}}. The students must also have an understanding of the different types of skeletal muscle fibers [e.g., slow twitch (type I) and fast twitch (type II), at a minimum].

Recently, Stavrianeas and Silverstein (20) presented an effective technique on using electrical power generation as an analogy to teach students about the regulation of glycolysis. A similar analogy can be used for the aerobic processes of bioenergetics as well as overall metabolic regulation by altering the discussion to include regulation of other pathways, such as the tricarboxylic acid (TCA) cycle, or discussing the regulation of the interaction of metabolic pathways, such as the entry of pyruvate into aerobic metabolism. As for teaching students about fiber types, it would be ideal if students could perform histochemical analysis of muscle fibers as described...
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by Sweeney et al. (22). However, it has been the experience of the author that many institutions lack sufficient facilities for students to perform muscle fiber histochemistry outside of a research endeavor. So, if laboratory analysis of muscle fibers is not possible, one method that has always been successful in past experience and to which the students can relate is to discuss the differences between white meat and dark meat in poultry leading into a discussion of the characteristics of different skeletal muscle fiber types, as presented in many exercise physiology textbooks (3, 15, 23). Finally, it would be ideal if the students have had first-hand experience with the assessment of VO₂max. Hopefully, the students have been sufficiently exposed to these concepts in their introductory physiology or biology courses or previously in their present course, so that only a brief discussion of some specific enzymes [e.g., the role of phosphofructokinase (PFK) and succinate dehydrogenase (SDH)] is necessary to help the students understand the importance of these enzymes in understanding the findings of Gollnick et al. (6).

Once students have been prepared with the appropriate background in bioenergetics, assessing aerobic capacity, and characteristics of different muscle fiber types, the students should now be prepared to explore and discuss the biochemical and morphological adaptations that occur within the skeletal muscle cells in response to different types of exercise stimuli.

Discovery learning exercise. After the aforementioned background information has been covered sufficiently in class and/or the laboratory, the students should be provided with the classic article (6), the recreated table (Table 1), and the questions in Table 1 as a “discovery learning” exercise (which is easily accomplished using a web-based system such as Blackboard or WebCT). To help the students visualize muscle fiber analysis, some internet sites (which have been provided after the discovery learning questions) are given to the students, and it is suggested that the students visit those websites to see examples of muscle fiber typing images. It has been the experience of the author that 1 wk provides sufficient time for the students to complete the assignment, so that is when the classic article (6), recreated Table 1, and questions should be provided to the students. For instance, if an instructor is using Physiology of Sport and Exercise (23), chapter 4 is “Metabolism, Energy, and the Basic Energy Systems,” whereas chapter 5 is “Hormonal Regulation of Exercise,” and chapter 6 is “Metabolic Adaptations to Exercise,” so the assignment should be distributed while there is 1 wk remaining in the discussion of chapter 5.

If the class structure is conducive to having students make in-class presentations (e.g., if the class size is small or if there is an emphasis on presentation skills), the students, either in small groups or individually, should be assigned to prepare graphs that illustrate the differences between the various categories of persons. The students then present their graphs using PowerPoint or another medium and lead a brief discussion of the meaning of the data presented during the appropriate class meeting. If this is to be used as a more traditional “homework” assignment, the students may answer the questions and make their graphs, which are then turned in and graded. In this way, this study can be effectively used in small graduate classes as well as larger undergraduate courses.

Depending on the size of the class and ability of the students, the instructor may ask the students to graph percentage of slow twitch muscle fibers, SDH activity, PFK activity, and VO₂max for only legs, only arms, or any combination (Table 1; for examples of some finished graphs, see Figs. 1–3) or use other data from Gollnick et al. (6), such as muscle fiber size and muscle glycogen content, as presented in the original article. Instructors can assign students to prepare all of the graphs or divide the class such that each student or group of students prepares only one graph. In the author’s experience, by requiring the students to prepare the graphs, they become more actively involved in their study of the differences in skeletal muscle histochemistry between trained and untrained persons.

Data presentation. It is explained to the students that graphing the information contained in Table 1 from Gollnick et al. (6) is very easily accomplished by using the “Stock Chart” selection on Microsoft Excel, but, instead of using closing stock prices, the data for high, low, and mean values are graphed (Fig. 4). The students are then shown an example graph from Figs. 1 to 3 and sent forth to complete the assignment on their own (an added benefit to this type of assignment is that it encourages students who are not familiar with using Excel to visit this instructor for assistance, thereby increasing instructor-student interactions).

For a more in-depth analysis of the data, the students produce a scatter graph of two data sets (for instance, SDH activity and VO₂max; Fig. 5) and use simple linear regression (insert a trendline in MS Excel) and then have the students display the R² value when making their graphs. Unfortunately, it seems that most undergraduate students are not sufficiently familiar with statistics to perform in-depth correlation analyses. However, the students have readily grasped the simple explanation that linear regression is an effort to predict one variable (e.g., VO₂max) from another (e.g., SDH activity). The students also easily understand that an R² value close to 1 indicates a close relationship between the two variables, whereas an R² value close to 0 indicates very little relationship.

In-class discussion. If this has been used as a presentation exercise, the students who have prepared the graphs relevant to the data should be called upon to present their graph(s) at the appropriate time and lead the discussion. Otherwise, at the class meeting during which the adaptations to exercise will be discussed, an introductory discussion and attention activity begins by simply posing the question “Why are endurance-trained athletes better at their sport than untrained persons?” with the student responses being listed on the chalk board, white board, or other type of visual medium. The answers given by students have in the past varied from the utterly ridiculous (e.g., “athletes are taller”) to the absolutely correct (e.g., “training has increased their ability to form ATP aerobically”). However, because the goal is a discussion of the classic study by Gollnick et al. (6), some reasons why trained athletes are better at their sport than untrained persons that need to be highlighted include that 1) aerobically trained athletes have a higher VO₂max, 2) a greater percentage of slow twitch muscle fibers, and 3) enhanced aerobic bioenergetic enzyme activity than do untrained persons (9, 10). Each of these reasons for enhanced performance in sport should be followed up with clarification questions and asking of the students to find the data in the Gollnick et al. study (6) to support their statements. It should be pointed out that the data in the Gollnick et al. study (6) is of a cross-sectional nature. However, other studies have confirmed the changes in bioenergetic enzymes (8–10), aero-
Table 1. Physical characteristics, fiber populations, enzyme activities, and VO\textsubscript{2}\text{max} of the groups studied

<table>
<thead>
<tr>
<th>Group</th>
<th>Age, yr</th>
<th>n</th>
<th>Height, cm</th>
<th>Weight, kg</th>
<th>Type of Work</th>
<th>%ST Fibers</th>
<th>Enzyme Activities, \text{mmol} \cdot \text{g}^{-1} \cdot \text{min}^{-1}</th>
<th>VO\textsubscript{2}\text{max}, \text{ml} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Untrained</td>
<td>27 (24–30)</td>
<td>12</td>
<td>179 (166–187)</td>
<td>76.5 (66.4–105.5)</td>
<td>Arm</td>
<td>46.0 ± 6.8 (14.3–59.8)</td>
<td>3.6 ± 0.4 (2.1–6.0)</td>
<td>21.6 ± 3.7 (19.8–28.6)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Leg</td>
<td>36.1 ± 5.0 (13.0–50.8)</td>
<td>4.3 ± 0.6 (2.7–6.5)</td>
<td>25.3 ± 2.1 (17.7–38.0)</td>
</tr>
<tr>
<td>Untrained</td>
<td>39 (31–52)</td>
<td>14</td>
<td>178 (168–191)</td>
<td>75.6 (63.2–88.6)</td>
<td>Arm</td>
<td>45.2 ± 2.7 (33.5–58.3)</td>
<td>3.5 ± 0.4 (1.9–6.6)</td>
<td>23.0 ± 1.9 (16.5–32.3)</td>
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<tr>
<td></td>
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<td></td>
<td></td>
<td>Leg</td>
<td>43.9 ± 4.8 (24.0–72.9)</td>
<td>4.4 ± 0.3 (2.3–6.5)</td>
<td>25.2 ± 1.9 (14.3–36.6)</td>
</tr>
<tr>
<td>Trained*</td>
<td>25 (17–30)</td>
<td>12</td>
<td>179 (165–189)</td>
<td>68.8 (59.6–76.0)</td>
<td>Arm</td>
<td>54.8 ± 3.4 (45.5–66.2)</td>
<td>4.0 ± 0.5 (2.7–5.3)</td>
<td>19.1 ± 1.8 (13.3–24.6)</td>
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<td></td>
<td></td>
<td>Leg</td>
<td>52.3 ± 6.8 (26.0–62.5)</td>
<td>6.0 ± 0.3 (4.0–8.0)</td>
<td>19.9 ± 3.6 (14.3–28.3)</td>
</tr>
<tr>
<td>Bicyclists</td>
<td>24 (18–33)</td>
<td>4</td>
<td>182 (175–189)</td>
<td>74.5 (74.0–75.0)</td>
<td>Arm</td>
<td>50.7 ± 4.4 (39.5–63.8)</td>
<td>6.1 ± 0.2 (5.5–6.7)</td>
<td>24.0 ± 4.0 (19.4–32.0)</td>
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<tr>
<td></td>
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<td></td>
<td></td>
<td>Leg</td>
<td>61.4 ± 5.9 (47.9–73.2)</td>
<td>11.0 ± 1.0 (8.2–12.4)</td>
<td>23.9 ± 1.4 (21.4–32.0)</td>
</tr>
<tr>
<td>Canoeists</td>
<td>26 (25–27)</td>
<td>4</td>
<td>181 (179–186)</td>
<td>74.0 (71.0–79.0)</td>
<td>Arm</td>
<td>58.4 ± 3.8 (48.2–65.9)</td>
<td>7.9 ± 0.6 (7.1–9.2)</td>
<td>25.0 ± 6.8 (19.0–42.0)</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td>Leg</td>
<td>61.4 ± 6.2 (45.0–72.4)</td>
<td>5.8 ± 0.9 (3.3–8.0)</td>
<td>22.2 ± 4.7 (11.3–35.1)</td>
</tr>
<tr>
<td>Runners</td>
<td>23 (19–33)</td>
<td>8</td>
<td>177 (168–185)</td>
<td>69.5 (59.1–80.8)</td>
<td>Arm</td>
<td>58.9 ± 3.7 (52.7–70.0)</td>
<td>6.4 ± 0.4 (4.3–8.2)</td>
<td>20.1 ± 2.5 (10.3–26.5)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Leg</td>
<td>74.3 ± 5.7 (65.9–85.3)</td>
<td>8.6 ± 0.7 (6.2–9.9)</td>
<td>22.7 ± 0.4 (21.0–23.2)</td>
</tr>
<tr>
<td>Swimmers</td>
<td>21 (18–23)</td>
<td>5</td>
<td>181 (175–189)</td>
<td>78.3 (70.0–78.6)</td>
<td>Arm</td>
<td>57.7 ± 9.3 (37.2–79.7)</td>
<td>7.6 ± 0.5 (5.5–8.5)</td>
<td>29.3 ± 0.4 (28.0–29.7)</td>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Leg</td>
<td>52.6 ± 7.7 (42.6–66.7)</td>
<td>2.6 ± 0.4 (2.0–3.2)</td>
<td>21.1 ± 4.8 (12.1–29.0)</td>
</tr>
<tr>
<td>Weight lifters</td>
<td>25 (23–29)</td>
<td>4</td>
<td>171 (159–186)</td>
<td>81.3 (52.0–107.0)</td>
<td>Arm</td>
<td>46.1 ± 10.5 (25.3–59.7)</td>
<td>3.0 ± 0.3 (2.5–3.7)</td>
<td>24.7 ± 1.7 (20.8–29.4)</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Leg</td>
<td>63.1 ± 5.1 (31.0–98.7)</td>
<td>4.1 ± 0.4 (1.8–6.6)</td>
<td>41.3 ± 1.4 (30.3–50.4)</td>
</tr>
<tr>
<td>Weight lifters</td>
<td>52 (47–58)</td>
<td>11</td>
<td>176 (161–184)</td>
<td>72.7 (59.5–88.0)</td>
<td>Arm</td>
<td>68.8 ± 5.2 (46.5–98.7)</td>
<td>5.7 ± 0.3 (3.9–7.9)</td>
<td>50.7 ± 2.2 (37–62)</td>
</tr>
</tbody>
</table>

Values are means ± SE, with values in parentheses being the highest and lowest observations; n, no. of subjects/group. ST, slow twitch; SDH, succinate dehydrogenase; PDK, phosphofructokinase; VO\textsubscript{2}\text{max}, maximal oxygen consumption. *This group was composed of athletes competing in several different events. †Average of 3 values.

Discovery Learning Questions

1. Explain how each of the following factors will influence athletic success and respond to aerobic endurance training.
   A. SDH activity
   B. PFK activity
   C. Muscle fiber type
   D. Muscle fiber size
   E. Muscle glycogen content

2. What determines the oxidative potential of muscle fibers, fiber type distribution, and VO\textsubscript{2}\text{max}: genetics or exercise training or both? How would you conduct research to determine the effects of genetics and exercise training on muscle fiber histochemistry?

3. Why would it be incorrect to categorize muscle fiber type based solely on oxidative capacity? What characteristics would you use to determine fiber type?

4. Based on the data shown in Table 1 and the conclusions of Gollnick et al. (6), what factors likely limit VO\textsubscript{2}\text{max} in most people?
bic capacity (1), and cardiorespiratory fitness that occur with aerobic training (4).

**Answering the discussion/learning questions.** As a result of aerobic exercise, there is enhanced development in the size and functioning of the mitochondrial reticulum and an increase in the activity of aerobic bioenergetic enzymes, all of which combine to increase exercise endurance and performance by enhancing the aerobic formation of ATP (9). This is illustrated in the larger concentrations of SDH (Fig. 1), a TCA cycle enzyme, in the aerobically trained subjects shown in Table 1. Aerobically trained people also tend to have lower concentrations and activities of PFK and higher concentrations of muscle glycogen (9). As a result of these adaptations, aerobically trained persons are better suited to provide the needed ATP to sustain exercise. Additionally, trained individuals utilize fat for ATP formation during exercise more effectively than their untrained counterparts, which delays the onset of fatigue (10).

In general, aerobically trained athletes have a greater percentage and size of slow twitch fibers in their skeletal muscles than do untrained persons (Fig. 2), which favors their successful exercise endurance and performance. However, as is well illustrated in Table 1, there is considerable interindividual variation in the muscle fiber type composition within a population of similarly trained athletes. This brings up a particularly interesting discussion point regarding the effects of training versus genetics on muscle fiber type composition (11). Although we now realize that skeletal muscles do not exist as merely two, or even three, discrete types but instead along a very pliable continuum (11), and that a modest transition of type II to type I fiber type can occur with endurance training (17), there is still discussion as to the extent that training can alter muscle fiber type from fast twitch to slow twitch (7, 11). Students should be encouraged to discuss whether they think that training can cause a meaningful change in muscle fiber type or whether persons are naturally drawn toward the type of activity to which their muscle fiber composition is best suited.

It is useful to point out to students that the question of fiber type conversion due to training in humans has yet not been conclusively answered. Some possible reasons why the issue of fiber type conversion has not been decisively answered include the difficulties in conducting long-term studies, the concept that young persons may exhibit an ability to alter fiber type that is less prominent in older individuals (7), and variations in the exercise stimulus applied during research (11).

As a person trains aerobically, their $\dot{V}O_2_{max}$ increases. Increases in $\dot{V}O_2_{max}$ are due to changes in the muscle’s ability to use and extract oxygen and to changes in cardiac size and contractility. As pointed out by Gollnick et al. (6), the activity of SDH in trained athletes indicates that a small portion of the skeletal muscle could be responsible for the whole body oxygen consumption. Therefore, the cardiovascular system limits aerobic adaptations to exercise in most people (1). Changes in cardiovascular function associated with aerobic exercise include increased ventricular capacity and cardiac contractility, which lead to increased stroke volume but not an increased maximal heart rate, resulting in enhanced maximal cardiac output. Of course, the effects of exercise on the cardiovascular system may have been discussed in detail dur-

![Fig. 1. Succinate dehydrogenase (SDH) activity as measured in the vastus lateralis in persons of different athletic training. The solid squares represent mean values, whereas the bars represent the ranges of values. The average ages of the subjects are indicated on the x-axis. [Adapted from Ref. 6.](http://advan.physiology.org/)

![Fig. 2. Slow twitch (ST) muscle fiber distribution as measured in the vastus lateralis in persons of different athletic training. The solid squares represent mean values, whereas the bars represent the ranges of values. The average ages of the subjects are indicated on the x-axis. [Adapted from Ref. 6.](http://advan.physiology.org/)

![Fig. 3. Maximal aerobic capacity [maximal oxygen consumption ($\dot{V}O_2_{max}$)] as measured with a leg ergometer task in persons of different athletic training. The solid squares represent mean values, whereas the bars represent the ranges of values. The average ages of the subjects are indicated on the x-axis. [Adapted from Ref. 6.](http://advan.physiology.org/)
ing a previous section of the course or may be discussed in a subsequent section.

Other adaptations to exercise noted by Gollnick et al. (6) include enhanced muscle glycogen concentrations, which allows for delayed fatigue during prolonged endurance exercise or a greater reliance on glycolysis for energy production during shorter-duration exercise (8). Aerobic exercise also causes hypertrophy of type I and type IIA muscle fibers and a decrease in the size of type IIB muscle fibers (4). This is demonstrated by the increased muscle fiber size reported by Gollnick et al. (6). However, it has been reported that the classification of type IIB fiber in humans may be incorrect because the myosin heavy chain type IIB gene is not expressed in humans, and so it may be more correct to classify these as type IIX/d fibers (19).

As the discussion progresses, students should be constantly asked to support their assertions with the data from Gollnick et al. (6). When the students cannot find the data, the instructor could point out where the data can be found in the study (whether it is in Tables 1, 2, 3, or 4 or if the evidence is mentioned in the discussion or in text) or allow the students time in class to find the data themselves, depending on the students’ abilities, the time available for this topic, and sometimes merely on the collective personality of the class. As the end of the class draws near, if the students are provided with a few minutes of reflection to review their understanding and ask questions about the key adaptations observed, the students’ comprehension is further enhanced.

CONCLUSIONS

Of course, it would be ideal if students could replicate the study by Gollnick et al. (6) and conduct histochemical analysis of the skeletal muscles of trained and untrained persons to gain first-hand knowledge of the adaptations to exercise training. However, this process is far beyond the scope of most under-
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graduate or graduate exercise physiology classes due to the time-intensive and invasive nature and the cost factor for obtaining, slicing, and staining of sufficient muscle samples to elucidate the adaptations to training. The considerable variation in fiber characteristics observed by Gollnick et al. (6) indicates the difficulties in observing differences between trained and untrained persons if only a few samples are analyzed. Also, it takes quite a bit of practice to become sufficiently proficient at muscle fiber histochemistry to produce reliable, accurate, and precise results. Therefore, this assignment has been developed and successfully used to help students gain enhanced understanding of the differences in muscle fiber characteristics between trained and untrained persons.

The purpose of this exercise is not to replace a laboratory exercise or lecture on muscle fiber analysis and characteristics but to have the students gain familiarity with reading and understanding scientific literature, with a particular emphasis on an example of classic research that continues to shape contemporary investigations and theories. The students then apply this information to an example to which they can relate. By merely having the students read a paper and answer some questions, many students do not really delve into the study beyond merely searching for answers to the questions and essentially paraphrasing the statements from the original text. Furthermore, the old axiom that “a picture is worth a thousand words” is true when it comes to illustrating the differences between trained and untrained persons demonstrated by Gollnick et al. (6). Therefore, by including an assignment that requires the students to closely examine and then present the data in another format (such as by converting the textual data into graphs, as explained herein), the students’ learning of the material is enhanced. Even though college students are skilled in the casual or recreational use of information technology, many students lack applied career-related computer skills (5, 16). So, by having the students prepare graphs using MS Excel and conduct some simple statistical analysis of the data, the students develop applied computer skills that will serve them well in the future. Also, by having the students read the original literature, we reinforce what is presented in the textbook, increase their understanding of how research is incorporated into learning, and also demonstrates to the students that “older” literature may still be worth reading as they prepare assignments and conduct literature searches. Enhanced understanding of the literature based on the assignment described herein is reflected in comments on instructor evaluations, such as student comments stating that the assignment “. . .helped stimulate thoughts” and that it could “. . .definitely help us expand our knowledge and give a different learning component to the class.”

In conclusion, by using the APS classic paper “Enzyme activity and fiber composition in skeletal muscle of untrained and trained men” by Gollnick et al. (6) as the basis for an in-class discussion of the adaptations to exercise with the accompanying graphing assignment, students increase their ability to read and understand primary research as well as gain an understanding of the adaptations to exercise. Finally, even though the study by Gollnick et al. (6) was published over 30 years ago, it remains a classic piece of exercise physiology literature that continues to shape the thinking and research emphasis of scientists today.

REFERENCES


