How We Teach

Assessment outcome is weakly correlated with lecture attendance: influence of learning style and use of alternative materials

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Horton DM, Wiederman SD, Saint DA. Assessment outcome is weakly correlated with lecture attendance: influence of learning style and use of alternative materials. Adv Physiol Educ 36: 108–115, 2012; doi:10.1152/advan.00111.2011.—The relation between lecture attendance and learning is surprisingly weak, and the role of learning styles in this is poorly understood. We hypothesized that 1) academic performance is related to lecture attendance and 2) learning style influences lecture attendance and, consequently, affects performance. We also speculated that the availability of alternative resources would affect this relationship. Second-year Bachelor of Science physiology students (n = 120) self-reported their lecture attendance in a block of 21 lectures (attendance not compulsory) and use of alternative resources. Overall self-reported lecture attendance was 73 ± 2%. Female students (n = 71) attended more lectures (16.4 ± 0.6) than male students (14.3 ± 0.8, n = 49) and achieved a higher composite mark in all assessments (73.6% vs. 69.3%, P < 0.02). Marks in the final exam were not statistically different between the sexes and correlated only weakly with lecture attendance (r = 0.29, n = 49, P < 0.04 for male students; r = 0.10, n = 71, P = not significant for female students; and r = 0.21, n = 120, P < 0.02 for the whole class). Of the students who passed the exam, poor attenders (<11 lectures) reported significantly more use of lecture recordings (37 ± 8%, n = 15, vs. 10 ± 1%, n = 85, P < 0.001). In a VARK learning style assessment (where V is visual, A is auditory, R is reading/writing, and K is kinesthetic), students were multimodal, although female students had a slightly higher average percentage of the R learning style (preferred read/write) compared with male students (28.9 ± 0.9%, n = 63, vs. 25.3 ± 1.3%, n = 32, P < 0.03). Lecture attendance was not correlated with measured learning style. We concluded that lecture attendance is only weakly correlated with academic performance and is not related to learning style. The substitution of alternative materials for lecture attendance appears to have a greater role than learning style in determining academic outcomes.

However, the degree to which lecture attendance influences academic performance is often unclear. For example, a positive correlation between lecture attendance and exam score has been shown in dental students, but the correlation was weak (r = 0.28, P = 0.03) (8). Gatherer and Manning (11), in a 1998 study of first-year biological science students, reported the correlation between lecture attendance and performance. This was substantially stronger for ethnic minority students (r = 0.603, P < 0.005) than for Anglophone students in the same class (r = 0.276, P < 0.005). They suggested that this might reflect the more effective substitution of alternatives by the latter group, but did not assess this. This illustrates that a range of factors may impinge on the effectiveness of different teaching strategies. For example, Clayton et al. (5) found that a majority of students (73%) preferred “traditional” learning environments, and they ascribed this to differences in motivation of the students.

Students have varied learning styles, or combinations of styles, usually assessed as the degree to which the student prefers visual (V), auditory (A), reading/writing (R), and kinesthetic (K) modes of learning [the “VARK” classification (10)]. Preferred learning styles have been shown in some cases to be correlated with academic outcomes. Palloff and Pratt (16) suggested that online learning might not match many students’ preferred learning style and that this has implications for the increasing shift toward online course delivery. In a survey of 901 applied human physiology students (of both sexes), Dobson (7) found that K learning style students performed significantly worse in the lecture portion of the course compared with V, R, and A styles. In a later, smaller study (6) of 64 exercise Physiology students, the majority of students (36%) nominated the V learning style as their preferred sensory modality, although other modalities were also well represented, with a “very nearly significant” sex-related difference. Perceived sensory modality correlated with course scores by ANOVA (6). In a group of 57 dental students, El Tantawi (8) showed a significant relationship between final exam scores (in a biostatistics and research design course) and learning style preferences.

However, very few studies have addressed the question as to whether the preferred learning style influences the choices that students make in their source of information and whether this may disadvantage some students compared with others. In particular, few studies have asked whether lecture attendance influences learning and whether this might interact with learning style. Whether the students can substitute the use of alternative materials for lecture attendance, and the interaction of this with learning style, is similarly poorly understood.

Here, we examined the correlation between lecture attendance and student performance in a second-year physiology course, in which lecture attendance was not compulsory. In the

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course, the subject matter was delivered in a variety of formats; lectures were recorded and made available online and in downloadable format, and lecture notes were available online 1 wk before the lecture. Students were surveyed as to the degree to which they used these alternative formats. Differences between male and female students in performance and in preferred learning styles were assessed. Importantly, actual learning style (as measured by VARK analysis) was distinguished from the students’ self-assessed, or predicted, learning style.

We hypothesized that lecture attendance would affect performance in assessments. Given this, we further hypothesized that the student’s preferred learning style and the availability of alternative materials would influence their degree of lecture attendance and consequently affect performance in assessments.

METHODS

This study had prior approval from the University of Adelaide Faculty of Science Learning and Teaching Committee.

The Discipline of Physiology at the University of Adelaide teaches Medical and Dental programs and also teaches physiology to science students [a mix of Bachelor of Health Science (BHSci) and Bachelor of Science (BSc) degree program students]. The cohort of these latter students (BHSci and BSc; n = 141) taking second-year physiology was invited to participate in the study. The purpose of the study was explained to the students in an information lecture during an orientation week. The subject consisted of a block of 21 lectures in the first semester of 2009 covering cellular, neuromuscular, cardiovascular, and respiratory physiology, which were given by two experienced lecturers (professorial level, one male professor and one female professor). Students were aware before the start of semester that attendance at the lectures was not compulsory, and attendance was not monitored. Lecture notes for all lectures were posted online at least 1 wk before each lecture. All lectures were recorded (slides and synchronous audio) and posted immediately afterward. Each lecturer was available for questions by e-mail and at regular “open office” times. After the lecture block, students were asked to complete a questionnaire in which they self-reported the number of lectures they attended on scale between 0 and 21. The questionnaire also asked them to report the time they spent using alternative resources to supplement their learning. The questionnaire was distributed in a practical class at which attendance was compulsory and collected by the demonstrator, so students not attending lectures would still be captured in the data set. Before they completed the questionnaire, students were informed that participation was voluntary and that all data would be deidentified.

In the same setting on a separate occasion, students were also given a 12-point VARK questionnaire based on that used by Fleming (10) to assess their preferred learning style. After completing the VARK questionnaire, students were given a brief explanation of the VARK assessment and asked to predict what their own preferred style would be by assigning percentages to V, A, R, and K modalities. Prediction by students was based on the following four statements:

- V learner: uses flowcharts, color coding/highlighting, and recalling information with the aid of diagrams.
- A learner: listens to recordings and finds information in lectures easy to recall.
- R learner: makes notes from textbooks and compares those in lectures, rote learning of your notes or from text works best.
- K learner: has good recall in practical classes, case studies, or specific real-life examples.

All student data were collected anonymously and deidentified by a member of staff not involved in the assessment of this cohort.

At the end of the semester, assessment scores in a variety of tasks through the semester for each student were added to the data set, again blinded to the project personnel. The assessment tasks were as follows:

1. Exams. A-3 h exam near the end of the semester, directly related to the lecture material, with mostly short-answer questions designed to test recall and the ability to synthesize information (50% of the total mark).
2. Tutorials. These were online questions on practical theory and revision questions (25% of the total mark). The material was only peripherally related to the lectures. Students could work through the material in groups outside of formal teaching hours.
3. Practicals. Students attended a working research laboratory for one afternoon per fortnight and participated in a guided research project as part of a group of six to eight students total. The overall score for the practical component was derived from a mix of group and individual written assessments (25% of the total mark, with 11.25% coming from the written individual final report). The final data set consisted of a list of anonymous coded student identification numbers, with assessment scores in each of the tasks noted above, VARK preferred learning style, self-reported lecture attendance, and self-reported use of alternative information sources for each student.

Statistical analysis. Any sex-related differences were analyzed by a Student’s unpaired t-test. Differences between students’ VARK scores for those attending <11 lectures and those attending >11 lectures were analyzed by a Student’s unpaired t-test. Correlation analysis [Pearson’s correlation (r)] was used to examine the associations between lecture attendance and grade outcome in exams, tutorials, and practicals. Correlation analysis was also used to determine associations between learning style and grade outcome. Students’ actual and predicted VARK percentages were analyzed by a paired t-test. Bonferroni’s correction was performed for multiple t-tests. The students’ predicted VARK percentages were also correlated with their actual VARK score as determined by the 12-point questionnaire to determine their ability to “self-assess” their own learning style. Quadranet analysis of alternate resources used as well as actual and predicted VARK percentages were by ANOVA. Statistical analysis was done with SPSS version 13.

RESULTS

Survey participation. Of the 141 students, 120 students (85.1%) completed the questionnaire on their lecture attendance. One hundred and nineteen of these students (84.4%) also reported the percentage of study time they spent using

![Fig. 1. Study design and numbers of students participating in each part.](http://advan.physiology.org/10.1152/advan.00222.2011)
other methods throughout the semester. Ninety-five students (67.4% of the total) completed the VARK assessment. Ninety students completed the VARK questionnaire and had submitted all assignments/assessments, and 86 students completed all questionnaires and had all assessment tasks completed. Three students did not complete the predicted VARK form correctly and therefore were excluded from all predicted VARK analysis, leaving $n = 83$ students (see Fig. 1 for survey participation).

Associations between lecture attendance and grade outcomes. Students attended, on average, 73.2% of the lectures. The mean number of lectures attended was significantly greater for female students ($16.4 \pm 0.06, n = 71$) compared with male students ($14.3 \pm 0.08, n = 49, P < 0.03$). Overall, female students performed better in the aggregate grade score compared with male students ($73.6 \pm 1.1, n = 78$; male students: $69.3 \pm 1.4, n = 63, P < 0.02$).

Where there was a significant difference between the sexes, female students performed better than male students: tutorials ($82.2 \pm 1.2\%$ vs. $75.9 \pm 1.8\%, P < 0.05$), total practical assessment ($77.7 \pm 0.9\%$ vs. $74.2 \pm 1.2\%, P < 0.03$), individual practical components of peer review ($79.1 \pm 1.3\%$ vs. $68.4 \pm 2.3\%, P < 0.0005$), and literature reviews ($82.2 \pm 1.2\%$ vs. $75.9 \pm 1.8\%, P < 0.05$). However, there were no differences between exam marks between the sexes [female students: $67.4 \pm 1.7\%$ vs. male students: $63.5 \pm 1.4\%$, not significant (NS)].

The associations between lecture attendance and marks in practicals, tutorials, exams, and overall composite grades for these students (49 male students and 71 female students) are shown in Fig. 2. Practical grades correlated positively with lecture attendance in male students ($r = 0.32, P < 0.03$) and overall ($r = 0.29, P < 0.002$) but not for female students when considered separately ($r = 0.20, NS$; Fig. 2A). Grades in tutorials correlated positively with lecture attendance overall ($r = 0.35, P < 0.0005$) and when male students ($r = 0.29, P < 0.05$) and female students ($r = 0.33, P < 0.005$) were considered separately (Fig. 2B). Exam grades correlated positively with lecture attendance in male students ($r = 0.29, P < 0.04$) and overall ($r = 0.21, P < 0.02$) but not for female students considered separately ($r = 0.10, NS$; Fig. 2C). Similarly, overall grades correlated positively with lecture attendance in male students ($r = 0.35, P < 0.01$) and overall ($r = 0.31, P < 0.001$) but not when female students were considered separately ($r = 0.20, NS$; Fig. 2D).

Use of alternative materials. The self-reported use of alternative sources of information by the students was aggregated for those students who attended fewer than 11 lectures and

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**Fig. 2.** Relationship between outcome in Practicals (A), Tutorials (B), Exams (C) and Overall Grade (D) and lecture attendance for male (closed circles, solid line, $n = 49$) and female (open circles, dashed line, $n = 71$) students.
passed the exam \((n = 15)\), those who attended more than 11 lectures and passed the exam \((n = 84)\), those who attended fewer than 11 lectures and failed the exam \((n = 5)\), and those who attended more than 11 lectures and failed the exam \((n = 15)\) (the “quadrants” in Fig. 3). Although the small numbers in some of the quadrants meant that any differences did not reach statistical significance, some trends were apparent. Of the students who passed the exam, those who attended fewer than 11 lectures reported significantly greater use of lecture recordings \((37.8\% \text{ vs. } 10.1\%, n = 15 \text{ vs. } 85, P < 0.001)\) with apparently less use of textbooks, the internet, or their peers. Of the students who failed the exam, it appears that those who attended fewer than 11 lectures made more use of lecture notes. Notably, of the students attending fewer than 11 lectures, those who passed the exam tended to make greater use of recordings \((P < 0.08)\). In addition, there was an obvious cohort of students who attended very few lectures but still achieved good marks (top left quadrant in Fig. 2C). These students reported a tendency to higher use of lecture recordings than those who attended a similar number of lectures but failed the exam \((53 \pm 17\% \text{ vs. } 24 \pm 7\%, P = 0.08)\). They also reported that they spent less time studying from their notes \((24 \pm 11 \text{ vs. } 48 \pm 5, P = 0.05)\).

**VARK analysis.** Students were overwhelmingly multimodal (Table 1, “actual” results). Only slight sex-related differences were seen in the actual learning preference: female students had a greater percentage of the R (actual) component to their preferred learning style \((28.9 \pm 0.9\% \text{ vs. } 25.3 \pm 1.4\%, n = 59 \text{ vs. } 31, P < 0.03)\). There were no differences in the proportions of V, A, and K learning styles between the sexes (data not shown).

Students were very poor at assessing their own learning style: for all learning styles, students significantly under- or overpredicted their actual style (Table 1). They overpredicted their percentage of V and R styles while underpredicting their percentage of A and K styles.

<table>
<thead>
<tr>
<th>VARK analysis</th>
<th>Actual</th>
<th>Predicted</th>
<th>(P) Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent V</td>
<td>22.2 ± 0.7</td>
<td>28.0 ± 1.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Percent A</td>
<td>24.6 ± 0.8</td>
<td>17.9 ± 1.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Percent R</td>
<td>27.8 ± 0.8</td>
<td>33.1 ± 1.9</td>
<td>&lt;0.015</td>
</tr>
<tr>
<td>Percent K</td>
<td>25.4 ± 0.6</td>
<td>20.3 ± 1.6</td>
<td>&lt;0.015</td>
</tr>
</tbody>
</table>

Values are means ± SE for each percentage score and were analyzed by a paired t-test; \(n = 90\) students total. V, visual; A, auditory; R, reading/writing; K, kinesthetic. \(P\) values were determined after the Bonferroni correction for multiple t-tests.

Fig. 3. Alternative learning materials used in students who attended <11 lectures and passed the exam \((n = 15)\) (A), in those who attended >11 lectures and passed the exam \((n = 84)\) (B), in those who attended <11 lectures and failed the exam \((n = 5)\) (C), and in those who attended >11 lectures and failed the exam \((n = 15)\) (D).
Relation between lecture attendance and VARK scores. There were no significant differences in the actual VARK scores of those students attending fewer than 11 lectures compared with those attending more than 11 lectures (Table 2). However, students attending fewer than 11 lectures had a significantly higher predicted percentage of the V learning style (37.3 ± 4.7% vs. 26.8 ± 2.2%, $P < 0.02$) and lower predicted percentage of the R learning style (23.5 ± 2.8% vs. 34.0 ± 2.2%, $P < 0.05$) than those attending 12–21 lectures (Table 2).

Associations among VARK score, lecture attendance, and grade outcome. The findings shown in Table 2 were reflected in the “quadrant” analyses of lecture attendance and exam performance. The distribution of the students’ actual VARK percentages are shown in Fig. 4. Numeric analysis did not reveal any statistically significant differences, and visual inspection of the pie charts revealed no obvious trends between the cohorts of students. These data were further analyzed using correlation analysis. There were no correlations between actual percentages of V, A, or K learning styles and any assessment.

### Table 2. Number of lectures attended and proportion of actual and student-predicted VARK percentage scores in Physiology 2 students

<table>
<thead>
<tr>
<th>Lectures Attended</th>
<th>Number of Students</th>
<th>Percent V</th>
<th>Percent A</th>
<th>Percent R</th>
<th>Percent K</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actual VARK scores</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–11 lectures attended</td>
<td>15</td>
<td>24.2 ± 1.9</td>
<td>22.2 ± 2.4</td>
<td>26.6 ± 2.1</td>
<td>26.9 ± 1.9</td>
</tr>
<tr>
<td>12–21 lectures attended</td>
<td>71</td>
<td>22.3 ± 0.7</td>
<td>24.4 ± 0.8</td>
<td>28.3 ± 0.9</td>
<td>25.0 ± 0.7</td>
</tr>
<tr>
<td>$P$ value</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Predicted VARK scores</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–11 lectures attended</td>
<td>13</td>
<td>37.3 ± 4.7</td>
<td>15.0 ± 2.9</td>
<td>23.5 ± 2.8</td>
<td>22.1 ± 4.0</td>
</tr>
<tr>
<td>12–21 lectures attended</td>
<td>70</td>
<td>26.8 ± 1.5</td>
<td>19.0 ± 1.5</td>
<td>34.0 ± 2.2</td>
<td>20.0 ± 2.0</td>
</tr>
<tr>
<td>$P$ value</td>
<td>&lt;0.02</td>
<td>NS</td>
<td>&lt;0.05</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

Values are means ± SE for each percentage score. Data were analyzed by an unpaired two-tailed $t$-test. NS, not significant.

Fig. 4. Distribution of the actual VARK percentage for those students who attended <11 lectures and passed the exam ($n = 13$) (A), in those who attended >11 lectures and passed the exam ($n = 65$) (B), in those who attended <11 lectures and failed the exam ($n = 2$) (C), and in those who attended >11 lectures and failed the exam ($n = 7$) (D).
outcome. The percentage of the R learning style was weakly correlated with exam marks ($r = 0.22, n = 90, P < 0.03$).

The same quadrant analysis repeated using the students’ own predicted learning style is shown in Fig. 5. Again, although statistical analysis was inconclusive, the results shown in Table 2 were reflected here; for the students attending fewer than 11 lectures and having a higher predicted percentage of the V learning style and a lower predicted percentage of the R learning style (compared to those attending more than 11 lectures), there were no apparent differences between those who passed the exam and those who failed. The largest apparent difference was that those who attended more than 11 lectures and passed the exam had a higher predicted percentage of the R learning style than any other group. However, correlation analysis revealed no relations between the predicted VARK style and exam outcome.

**DISCUSSION**

*Lecture attendance.* The correlation between lecture attendance and performance in the various assessment tasks, although sometimes statistically significant, was consistently weak, with correlation coefficients of $\sim 0.25–0.35$. This is consistent with other reports (e.g., Refs. 8 and 11), although some have reported values as low as 0.17 (18). This low correlation may be a reflection of the availability of alternative sources of the information; students may be able to substitute these sources for lectures and still achieve good learning outcomes. This is supported by the observation that the cohort of students who attended very few lectures but still achieved good marks (top left quadrant in Fig. 2C) reported a tendency for higher use of lecture recordings than those who attended a similar number of lectures but failed the exam. These students also reported that they spent less time studying from their notes. However, no differences in VARK percentages were found in this subset.

Visual inspection of the results shown in Fig. 2C also revealed that there was a cohort of five female students who attended almost all lectures but who nevertheless performed very poorly in the exam (bottom right quadrant). We initially suspected that these students may be English as a Second Language students, but inspection (anonymized through a third party) indicated no obvious ethnic differences (as inferred from names) and nothing remarkable about this cohort in the use of alternative sources. However, of the students who did attend >11 lectures, these poorly performing students had a lower percentage of the actual R learning style (19 ± 3% vs. 28 ±

![Fig. 5](http://advan.physiology.org/)

Fig. 5. Distribution of the predicted VARK percentage for those students who attended <11 lectures and passed the exam ($n = 11$) (A), in those who attended >11 lectures and passed the exam ($n = 65$) (B), in those who attended <11 lectures and failed the exam ($n = 2$) (C), and in those who attended >11 lectures and failed the exam ($n = 7$) (D).
How We Teach

LECTURE ATTENDANCE, ASSESSMENT OUTCOMES, AND LEARNING STYLES

1%, \( P = 0.03 \), with no other differences found. Notably, this cohort performed reasonably well in the other assessment tasks. It is not clear, in the absence of individual survey data, why these particular students apparently found the lectures so unhelpful, or the exam so challenging, but it may be related to their lower percentage of the R preferred style.

There also appeared to be a cohort of “midrange” students, predominantly male, who attended about half of the lectures but did very poorly. This same cohort appeared to have performed badly in tutorials and hence in the overall grade. Investigation of the anonymous data revealed nothing unusual about this group of students.

Learning styles. The students in this study were multimodal (Table 1, “actual” results), with only a small difference between the sexes (female students had a slightly greater percentage of the R learning style). This is consistent with most reports of learning styles (1, 3, 12), although reported sex-related differences in learning styles are inconsistent. Breckler et al. (4) found that more female premedical students had multimodal preferred styles compared with male premedical students (4), whereas Wehrwein (20) found that female students were mostly K learners and male students were mostly multimodal. In contrast, Dobson (7) found that both male and female students preferred the V learning style equally (49% and 46%, respectively), with the distribution of the other styles being significantly different between the sexes. Slater (19) found no sex-related difference in learning styles. We surmise that, if there are sex-related differences in actual learning styles, they are likely minor.

With the introduction of blended learning environments, in which students can choose a variety of formats for learning, it becomes more important that students chose the most effective strategy for their own learning, that is, one most suited to their learning style. In our data, the students’ actual preferred learning style was not related to attendance, with no significant differences in the distribution of VARK between those who attended fewer than 11 lectures compared with those who attended more than 11 lectures (Table 2). However, it is the student’s own (perhaps unconscious) assessment of their learning style that influences their choice to attend lectures (since they were unaware of their actual VARK style until after these lectures). At first sight, the result here appears counterintuitive: those students predicting that they had a higher percentage of the V learning style were less likely to attend lectures. This may be because the recorded lectures show the slides on screen and, for some recordings, are interactive and, hence, a highly visual experience. This is consistent with the observation in the quadrant analysis showing that those attending fewer lectures but passing the exam made far greater use of recordings. Similarly, those students who predicted they had a higher preference for the R learning style attended more lectures. We surmise that the students interpreted the R learning style as being the use of lecture notes taken during lectures for revision purposes in concert with textbooks.

Implications. It has been suggested that student learning is enhanced when information is presented in the style that students prefer (14, 15), so this “self-selection,” if it is operating, may well enhance student outcomes. However, the idea that students are “self-selecting” their sources of information implies that they are aware of their own learning style. On the contrary, our data show that students are poor at assessing their learning style before they have been exposed to the concept, and so they cannot be making “informed” choices in how to learn. This implies that a better introduction to learning styles and their implications for student learning could be provided to the students earlier in their higher degree studies. This might enable students to tailor their learning strategies better [the “meshing” hypothesis (2)], although it is worth noting that the idea of matching of learning styles and mode of teaching is not without its critics (17).

Limitations of the study and suggestions for future work. There are other factors that may influence a student’s choice to attend lectures or not. They may lack motivation, find the lectures (or lecturers) boring, or be otherwise disengaged. Some of these factors have been discussed in a study on a cohort of commerce students (13). However, it has become apparent in recent years that students are increasingly constrained by work and family commitments, such that although they may wish to attend lectures, they find it difficult to do so. Presumably these students, provided they are motivated, are the ones who substitute other learning resources and hence still achieve good learning outcomes. In the absence of individual surveys designed to test these possibilities, we could not, in this study, ascertain the reasons for nonattendance.

Conclusions. Lecture attendance was only poorly correlated with performance in assessment tasks, apparently because the students could substitute alternative sources of material for the lectures. Learning style, based on actual VARK analysis, was not related to lecture attendance and, consequently, was not correlated with performance.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

D.M.H. performed experiments; D.M.H. analyzed data; D.M.H., S.D.W., and D.A.S. interpreted results of experiments; D.M.H. and S.D.W. prepared figures; D.M.H., S.D.W., and D.A.S. drafted manuscript; D.M.H., S.D.W., and D.A.S. edited and revised manuscript; D.M.H., S.D.W., and D.A.S. approved final version of manuscript; D.A.S. conception and design of research. D.A.S. edited and revised manuscript; D.M.H., S.D.W., and D.A.S. approved final version of manuscript; D.M.H. performed experiments; D.M.H. analyzed data; D.M.H., S.D.W., and D.A.S. interpreted results of experiments; D.M.H. and S.D.W. prepared figures; D.M.H., S.D.W., and D.A.S. drafted manuscript; D.M.H., S.D.W., and D.A.S. edited and revised manuscript; D.M.H., S.D.W., and D.A.S. approved final version of manuscript; D.A.S. conception and design of research.

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