

Innovations in Teaching Undergraduate Biology and Why We Need Them

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active learning, concept inventories, course transformation, discipline-based educational research, formative assessment, pedagogy

Abstract

A growing revolution is under way in the teaching of introductory science to undergraduates. It is driven by concerns about American competitiveness as well as results from recent educational research, which explains why traditional teaching approaches in large classes fail to reach many students and provides a basis for designing improved methods of instruction. Discipline-based educational research in the life sciences and other areas has identified several innovative promising practices and demonstrated their effectiveness for increasing student learning. Their widespread adoption could have a major impact on the introductory training of biology students.

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DEFINING THE CHALLENGE

Two principal forces are generating momentum for a revolution in the way biology and other sciences are taught in high schools, colleges, and universities (DeHaan 2005). First, there are deep concerns about American international competitiveness, amid indications that the U.S. is doing a relatively poor job at retaining and training students in the science, technology, engineering, and mathematics (STEM) disciplines (DoE 2000, NAS 2004). Too many talented students get the impression from introductory courses that science is simply a collection of facts to be memorized and consequently drop out of STEM majors with little understanding or appreciation of what science is all about (Seymour & Hewitt 1997). For students who do major in life sciences, there is concern that future research biologists are being inadequately trained (NRC 2003, AAMC-HHMI 2009).

The second driving force for reform is recent research from educators and cognitive scientists into how students learn. This research, discussed further below, provides strong evidence that the traditional teaching methods employed in most secondary-school and undergraduate introductory courses are far from optimal for promoting student learning. Alternative research-based teaching methods have been developed and shown to be more effective, and a small but growing number of informed STEM faculty and administrators are pushing for their adoption.

Beyond the general findings about how students learn, there is now a substantial body of discipline-based educational research (DBER) dealing with teaching and learning of specific STEM disciplines. This review refers to some of the more important general findings on how students learn, but it primarily highlights results and applications from recent DBER and,

STEM: science, technology, engineering, and mathematics

DBER: discipline-based educational research

more specifically, life sciences education research. It focuses on teaching and learning for undergraduates, particularly in large courses, where innovation is most needed.

HISTORY AND CURRENT STATE OF DISCIPLINE-BASED EDUCATIONAL RESEARCH

DBER grew out of the efforts of physicists in the mid-1980s, who discovered that most undergraduate students in their introductory courses were gaining only very superficial knowledge from traditional methods of instruction (Halloun & Hestenes 1985, Hestenes et al. 1992). Rather than integrated conceptual understanding and creative problem solving, students were learning fragmented factual information and rote problem solving methods, while retaining many misconceptions about physical phenomena. To gain some measure of student understanding, physicists developed the Force Concept Inventory (FCI), a simple multiple-choice test of basic concepts and common misconceptions about Newtonian physics of everyday events written in simple language and requiring no sophisticated mathematics (Hestenes et al. 1992). By administering the FCI at the beginning and the end of an introductory course, instructors could obtain a measure of gains in student conceptual learning. They could then experiment with different instructional approaches and test them for efficacy. These physicists showed that adopting a small number of nontraditional promising practices in course design and implementation could substantially increase student learning gains. These practices, and their basis in more general educational research on how people learn, are described in the following sections.

After a lag of several years, instructors in other STEM disciplines began to make similar observations about their students and to initiate similar efforts at improving instruction. The empirical approach of varying instructional methods and measuring effects on student learning has been called “scientific teaching” (Handelsman et al. 2004, Wieman 2007).

Many DBE researchers doing this work are practicing scientists trained in their disciplines who have also learned educational research methods and taken up DBER as a sideline. Some schools of education have added DBER practitioners trained as educators to their faculties. In addition, some university science departments, particularly in physics but increasingly in other STEM disciplines, now include staff or tenure-track DBE researchers (NAS 2005) and are beginning to offer graduate training and degrees in DBER.

DBER is published in a variety of education journals, some general and some that are discipline-specific, sponsored by STEM professional societies. A few scientific journals, including *Nature*, *Science*, *PLoS Biology*, and *Genetics*, have also begun publishing DBER articles, generally in an education section. **Table 1** lists some of the more widely read general and discipline-specific educational journals that publish DBER in life sciences.

HOW STUDENTS LEARN

New ideas about teaching and learning began to receive public attention in the 1960s. Popular iconoclasts such as Holt (1964, 1967) and Kozol (1967), building on earlier ideas (Dewey 1916, Ausubel 1963), pointed out the shortcomings of passive learning environments for learners of all ages and advocated instead more student-centered, open classrooms that promoted active learning through hands-on experience, by doing rather than by simply listening, reading, and watching. These writers, considered radicals in their time, articulated ideas about optimal conditions for meaningful learning that have since been tested and validated by a large body of educational research. Also during the past three decades, advances in cognitive science have begun to elucidate the neural activities and synaptic changes that accompany learning. Results of research in both education and cognition were reviewed in the seminal National Research Council (NRC) report *How People Learn: Brain, Mind, Experience, and School* (NRC 1999). The

FCI: force concept inventory

Table 1 A partial list of journals that publish life sciences education research^a

General scientific journals

Genetics
Nature
Science
PLoS Biology^b

Education journals (sponsored by professional societies)

Advances in Physiology Education, 2001- (Amer. Physiol. Soc.)^{*†}
Biochemistry and Molecular Biology Education, 2006- (Amer. Soc. Biochem. and Mol. Biol.)[†]
CBE-Life Sciences Education, 2002- (Am. Soc. Cell Biol.)^{b,c}
Journal of Biological Education, 1990- (Brit. Inst. Biol.)^b
Microbiology Education Journal (Amer. Soc. Microbiol.)^c
Frontiers in Ecology and the Environment (Ecol. Soc. Am.)

General education journals

American Biology Teacher (Natl. Assoc. Biol. Teach.)^{b,c}
Bioscene: Journal of College Biology Teaching^b
BioScience (Am. Inst. Biol. Sci.)
International Journal of the Scholarship of Teaching and Learning^{b,c}
Journal of College Science Teaching (Natl. Sci. Teach. Assoc.)

^aFor additional journal listings, see Dolan (2007).

^bOpen access.

^cHigher standards: Research articles require assessment and outcome evidence for efficacy of a new course or intervention rather than simple descriptions of practice.

Constructivist: the view that individual learners must build their own knowledge structures, from experience and instruction, on a foundation of prior knowledge

Formative assessment: frequent, ongoing testing, usually during class, with the goal of monitoring understanding and providing feedback rather than judging performance

Summative assessment: high-stakes testing at the end of an instructional unit or course to judge student performance, e.g., mid-term and final exams

major conclusions from this research can be summarized as follows:

- Learning involves the elaboration of knowledge structures in long-term memory. According to this constructivist view of education (Dewey 1916; Ausubel 1963, 2000), effective instruction must begin at the level of a student's prior knowledge (which may include misconceptions). New information unrelated to prior knowledge is difficult to learn and remember.
- No two learners are the same: Learners differ in previous experience, previous instruction, preferred styles of learning, family background, cultural background, and so on. Diversity is an asset for collaborative work because different members of a group bring different perspectives and skills to bear, but it can hamper learning for some students unless the level and mode of instruction are appropriate for all.
- Learning is promoted by frequent feedback, that is, ongoing testing of new knowledge as students are acquiring it. Educators call this formative assessment, as opposed to summative assessment, which refers to high-stakes exams given after an extended period of instruction. Formative assessment provides valuable feedback to both instructor and students: Do students understand the concept just presented or discussed? Can they transfer this understanding to apply the concept in a new situation?
- Effective learning requires awareness and questioning of one's own learning process: How well do I understand this? What information do I need to understand it better? What do I not understand yet? Do I understand it well enough to transfer it, that is, apply it to a new situation? Educators call this awareness metacognition.

- Learning is enhanced in a community of learners who value the knowledge that is being learned. In early childhood this community is the family; at the university it could be a group of students working together to solve a problem or complete a research project.
- Learning changes the structure of the brain, and the extent of change increases with the degree of complexity, stimulation, and emotional involvement in the learning environment (Zull 2002). Active learning, in which a student's levels of motivation, curiosity, and attention are high, for example during a group effort to solve an intriguing problem, will be better retained than learning from relatively passive activities such as reading a text or listening to a lecture.
- Learning in a particular area of knowledge such as life sciences can be viewed as a continuum from novice to expert status, along which we would like to help our students progress. The knowledge of an expert constitutes a coherent structure into which new concepts can easily fit and from which relevant information can be efficiently retrieved. In contrast, new knowledge for the novice often appears to be a collection of unrelated facts, which are difficult to memorize and retain. In other words, experts see and make use of meaningful patterns and relationships in the information they possess, whereas novices cannot.

APPLICATION TO THE COLLEGE CLASSROOM

These general conclusions apply to teaching and learning of STEM disciplines at the undergraduate level:

- Effective instruction must build on students' prior knowledge (which may include misconceptions that require correction).
- Instructors should be aware of the student diversity in their classrooms and use

a variety of teaching modes to optimize learning for all students.

- Classes should include frequent formative assessment to provide feedback to both instructors and students.
- Students should be encouraged to examine and monitor their own understanding of new concepts, for example, by explaining these concepts to their peers.
- Students should be encouraged to work cooperatively and collaboratively in small groups.
- In order to bring about the neurological changes that constitute learning, students should spend time actively engaged with the subject matter, for example, discussing, diagramming, solving problems, working on a research project, etc., in addition to or in place of listening passively to a lecture, reading the textbook, or consulting Web sites.

Most undergraduate college STEM classes, particularly in large introductory courses, are not designed around these principles, and it can be argued that this is one reason for the high attrition rates and generally superficial learning among introductory students in STEM disciplines. Educators have shown that effective instruction requires not only disciplinary content knowledge, for example, expertise in life sciences, but also pedagogical content knowledge, that is, understanding of and ability to apply known educational principles. Because graduate and postdoctoral training in STEM disciplines seldom includes any instruction in pedagogical practice, most university faculty are unaware of new knowledge about learning that could make their teaching more effective. Therefore, they simply teach the way they were taught in large classes, by traditional lecturing. We need to improve the way we teach undergraduates. The remainder of this article discusses evidence that applying the above principles to college classrooms can make a difference in how much and how well our students learn.

Transfer: application of knowledge learned in one context to a problem in a different context

Metacognition: the process of monitoring one's own learning process and level of understanding

EVIDENCE THAT RESEARCH-BASED TEACHING AT THE COLLEGE LEVEL INCREASES STUDENT LEARNING

Our best undergraduates, sometimes with little help from faculty, develop learning skills that incorporate the above principles, allowing them to progress toward expert knowledge regardless of how we teach them. However, many students, for whom studying means highlighting phrases in their textbooks and memorizing disconnected facts, fail to develop effective learning skills and consequently learn very little. Is there evidence that changes in teaching practices at the college level can significantly enhance student learning?

Physicists were the first to obtain such evidence, using the Force Concept Inventory (FCI; Hestenes et al. 1992) described above. The FCI became nationally accepted among physics instructors during the 1990s as a way to gauge student learning of Newtonian mechanics. Administering the FCI as a pre-test at the start of a course and then again as a post-test at the end yielded a raw learning gain for each student. For comparison of students with different levels of incoming knowledge, each raw gain was divided by the maximum possible gain for that student to arrive at a percentage normalized gain: $\langle g \rangle = 100(\text{post-test score} - \text{pre-test score}) / (100 - \text{pre-test score})$.

In attempts to increase the generally low normalized gains seen in traditional introductory courses, physics education researchers transformed their courses with new teaching approaches following the principles described above: more class time devoted to active learning, more group problem solving, frequent formative assessment, and so on. They carried out controlled studies, for example, the same instructor teaching the same syllabus through traditional lectures in one semester and then using the new approaches in the following semester (e.g., Beichner 2008). Study after study indicated that students in the transformed courses substantially outperformed those in traditional courses. In a compelling landmark

meta-analysis combining data from many such studies, Hake (1998) showed that for a sample of over 6000 students in 55 introductory physics courses nationwide, the average learning gains were nearly twice as high in transformed courses as in traditional courses.

Other STEM disciplines have lacked widely accepted assessment instruments comparable to the FCI until recently (see below). Nevertheless, several studies using some form of pre- and post-testing have also yielded results showing the greater efficacy of transformed courses. In the life sciences, an early study from the University of Oregon showed that students in the traditional introductory course learned substantially less than students in a workshop biology course, in which lecturing was almost entirely replaced by student group problem solving and other projects during class time (Udovic et al. 2002). Knight & Wood (2005) showed in a quasi-controlled study that even an incremental change, substituting 30–40% of lecturing during class time with more engaging student-centered activities (described below), led to increases in normalized learning gains averaging about 30% in a large upper-division developmental biology course. Similar results have been reported in large introductory biology courses (e.g., Smith et al. 2005, Armstrong et al. 2007, Freeman et al. 2007).

Clearly, concept inventories in life sciences would be valuable for continuation of this research (Garvin-Doxas et al. 2007) and several have recently been published for various subdisciplines including general biology (Klymkowsky et al. 2003), genetics (Bowling et al. 2008, Smith et al. 2008), and natural selection (Anderson et al. 2002). Libarkin (2008) has compiled a comprehensive current listing and comparison of concept inventories in STEM disciplines.

PROMISING PRACTICES FOR INCREASING STUDENT LEARNING

Many college faculty use Socratic dialog and student-centered group work in small classes

and seminars, but they believe there is no alternative to lecturing when confronted with hundreds of students in an auditorium with fixed seats. However, innovative instructors pursuing DBER have developed and tested alternative teaching approaches that prove to be substantially more effective than traditional lectures. This research has identified several promising practices for transforming large classes in ways that enhance student learning and conceptual understanding (reviewed in Handelsman et al. 2007).

Froyd (2008) has introduced a useful rating of promising practices based on two criteria: (a) practicality of implementation (breadth of applicability to STEM courses, freedom from resource constraints, ease of transition for instructors) and (b) evidence for efficacy in promoting increased student learning (from strongest evidence, i.e., multiple high-quality comparison studies, to weakest evidence, i.e., descriptive application studies only). The following paragraphs, summarized in **Table 2**, compare these practices with their counterparts

Table 2 Comparison of traditional practices with corresponding research-based promising practices for nine aspects of large course design and implementation in STEM disciplines

Course aspect	Traditional practice	Research-based promising practice
1. Content organization	Prepare a syllabus describing the topics that the instructor will present in class.	Formulate specific student learning objectives, in the form of “after this course, students will be able to. . .”
2. Student organization	Most student work is done individually and competitively.	Most student work is done cooperatively in small groups.
3. Feedback	Grading based primarily or entirely on summative assessments, i.e., midterm and final exams.	Feedback to instructor and students provided continually through in-class formative assessments.
4. In-class learning activities	Instructor transmits information by lecturing. Some questions may be posed to students, but only a small subset of the class is likely to participate in discussion.	All students spend most or all class time engaged in various active-learning activities (see text) facilitated by instructors and TAs. These activities also provide formative assessment.
5. Out-of-class learning activities	Students read the text and may do assigned homework to practice application of concepts previously presented in class.	Students read and do assigned homework on new topics and post results online for the instructor to review before the class on those topics.
6. Student-faculty interaction in class	Students are expected to accept the teaching mode chosen by the instructor and to infer how they should study and what they should learn from the instructor’s lectures and assignments.	Instructor explains the pedagogical reasons for the structure of course activities to encourage student buy-in, and explicitly and frequently communicates the course learning goals to students.
7. Student-faculty interaction out of class	Students must initiate out-of-class interaction with each other and with the instructor, e.g., by coming to office hours.	Instructor facilitates interaction with and among students by setting up online chat rooms, encouraging group work on homework assignments, and communicating with students electronically.
8. Use of teaching assistants (TAs)	TAs grade assignments and exams and may conduct recitation sessions to demonstrate problem solving methods or further explain lecture material.	TAs receive some initial instruction in basic pedagogy and serve as facilitators for in-class group work and tutorial sessions for small student groups to work out problems on their own.
9. Student laboratories	Students carry out exercises that demonstrate widely used techniques or verify important principles by following a prescribed protocol (“cookbook labs”).	Students are required to solve a research problem, either defined (e.g., identify an unknown) or more open-ended (e.g., determine whether commonly used cosmetic products are mutagenic), and learn necessary experimental techniques and concepts in the process (inquiry-based labs).

Instructor-centered:

designed around the knowledge the instructor wishes to transmit to students; focused on the instructor's teaching process

Student-centered:

designed around the needs, abilities, prior knowledge, and diversity of students; focused on the student's learning process

MCAT: medical college admission test

in traditional instruction and rate them on Froyd's two criteria. The practices are organized under nine aspects of course organization.

Content Organization: The Syllabus versus Specific Learning Goals

The difference between preparing a course syllabus and formulating learning objectives is more profound than it may appear (Allen & Tanner 2007). The typical syllabus is instructor-centered; it lists the topics on which the instructor will lecture and assign out-of-class work, but it gives students little information about the level of understanding they should strive for or the skills they are to learn. In molecular biology, for example, the process of transcription can be understood at many levels, which are generally not distinguished in a syllabus. In contrast, learning objectives are student-centered and more explicit; they describe what a successful student should be able to do at the end of the course or unit. For example, students should be able to "name the principal enzyme that catalyzes transcription," "explain the nucleotide sequence relationships between the two strands of the template DNA and the RNA transcription product," "diagram a step in the elongation of an RNA transcript showing the local nucleotide sequences and strand polarities of both DNA strands and the RNA," or "predict the consequences for the transcription process if one of the four nucleoside triphosphates is unavailable."

The learning objectives above demand different levels of understanding. A half century ago, the American educator Benjamin Bloom developed a convenient scheme for classifying these levels (Bloom & Krathwohl 1956), which became known as Bloom's taxonomy of the cognitive domain (Figure 1). Each of Bloom's six levels of understanding can be associated with verbs appropriate for a learning goal at that level. For example, the ability to name an enzyme or describe a process requires only memorization of the relevant information (level 1), whereas ability to predict an outcome (level 3) or defend a principle based on evidence (level 6)

require deeper conceptual understanding. The verbs employed (Figure 1) describe an action or ability that can be assessed by asking students to carry it out. Importantly, statements such as "students should understand," "appreciate," or "be aware of" are inappropriate learning objectives because their achievement cannot be tested without more explicit performance-based criteria. Because lower Bloom's levels are easier to assess with multiple-choice and short-answer exams, many instructors in large STEM courses neither demand nor test for higher levels of understanding. In a survey of over 500 final exams from a variety of introductory undergraduate and medical school biology courses, most questions were rated at Bloom's levels 1 and 2, and questions on the Medical College Admissions Test (MCAT) and Graduate Record Examination (GRE) ranked only slightly higher (Zheng et al. 2008). Another ongoing research study on assessment in introductory biology courses indicates that the overwhelming majority of test items on final exams are Bloom's level 1 (D. Ebert-May, personal communication). Because most students learn at the level assessed on summative exams, it is small wonder that they derive only superficial knowledge from such courses. Instructors can remedy this situation by aiming for higher Bloom's levels in formulating course learning goals and assessing student knowledge with appropriately challenging questions on exams (Crowe et al. 2008).

Course design around learning goals follows the principle of backward design (Wiggins & McTighe 1998). The instructor first formulates broad learning goals for students in the course and then more specific learning objectives. Once these are defined, she designs assessments (both formative and summative) to test for their achievement. Only then does she choose the most appropriate text or other reference materials and plan the learning activities in and outside of class that will most effectively lead to fulfillment of the objectives. At the start of the course, she will explicitly apprise students of the learning objectives, which may include rubrics (Allen & Tanner 2006) demonstrating

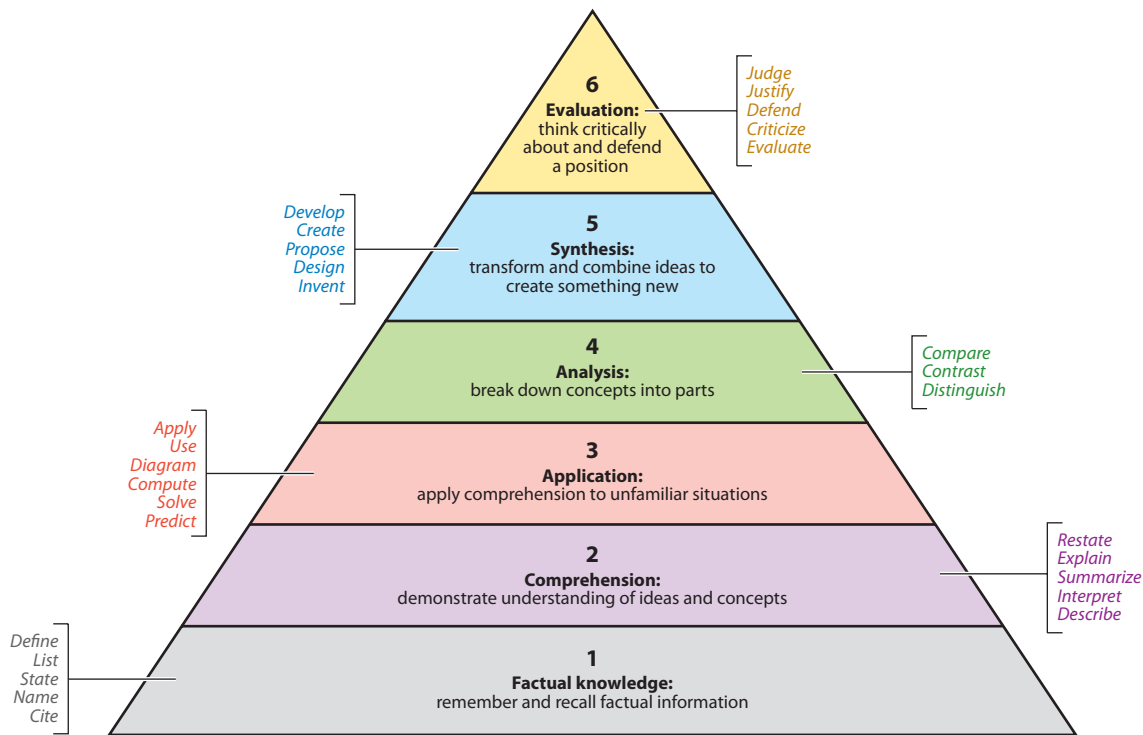


Figure 1

Bloom's levels of understanding. Originally termed Bloom's taxonomy of the cognitive domain, this schema defines six levels of conceptual understanding according to the intellectual operations that students at each level are capable of (Bloom & Krathwohl 1956). The italicized verbs have been added to the original hierarchy; they indicate performance tasks that test achievement of learning goals at each level. Fine distinctions in the hierarchy are difficult, and some educators prefer to classify goals on only three levels: low (1, 2), medium (3, 4), and high (5, 6). (Based on Allen & Tanner 2002.)

what achievement of the objectives would look like. **Figure 2** compares traditional and backward design of STEM courses.

Froyd's (2008) implementation rating for the practice of course design around learning objectives is high (applicable to any STEM course, no significant resource constraints, no need for radical change in instructor's teaching methods). As for efficacy rating, there are no empirical studies (known to this author) that compare student learning in courses taught from syllabi and those built around learning objectives. However, it seems self-evident that more learning will occur in courses that explicitly set goals for higher levels of conceptual

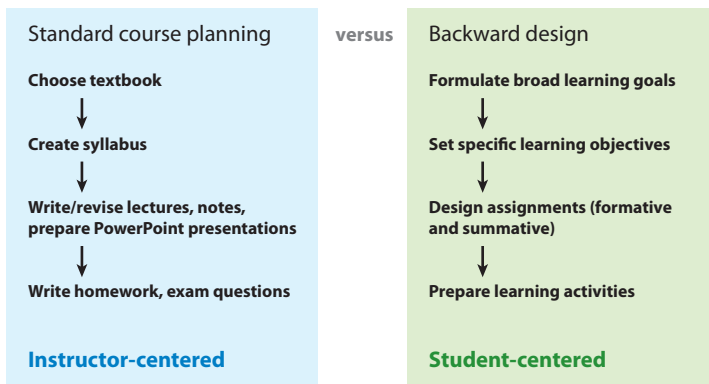


Figure 2

Schematic comparison of standard and backward course design.

understanding and require that students demonstrate achievement of these goals on exams and other course work.

Student Organization: Individual versus Group Work

Organizing students into small groups for in-class and out-of-class work can transform the course experience from competitive to collaborative, allow students to learn from each other as well as from instructors, and help to involve students who might not otherwise become actively engaged with the course content (Tanner et al. 2003). Groups can collaborate on regular homework assignments, longer-term projects such as researching a topic and developing a poster presentation, and in-class work if the course includes problem solving and other active learning activities during class time.

The implementation rating for group organization is lower than for learning objectives, because it involves additional instructor effort and decision making regarding, for example, how to form effective groups, facilitate their function, and help students develop collaborative skills (for specific references, see Froyd 2008). With regard to efficacy, much research in social science has shown that groups in general are more effective at complex problem solving than individuals (e.g., Brophy 2006) and that a group's effectiveness increases with the diversity of its members (Cox 1993, McLeod et al. 1996, Guimera et al. 2005). Comparative studies and meta-analyses provide strong evidence that group work in STEM courses contributes to increased student learning (e.g., Johnson et al. 1998, Springer et al. 1999). There is additional evidence in connection with in-class active learning in groups, discussed in the context of practice 4 below.

There are also other arguments for encouraging group work. With the increasing popularity of distance learning, the opportunity for student collaborative intellectual endeavor is one of the major advantages that resident universities can provide, and these universities should exploit it. As Astin (1993) concluded in his book

of the same name, *What Matters in College* are the relationships students build with each other and with their instructors. Moreover, the development of group-work skills is important in preparing students for the real world. When students who are comfortable with the traditional individual and generally competitive learning mode object to group work, the instructor can point out that when they join the workforce, they will probably be part of a team whose members they did not choose and that they need to learn how to work effectively with a group as an important part of their education.

Feedback: Summative versus Formative Assessment

One of the key aspects of effective instruction identified in *How People Learn* (NRC 1999) is feedback to students during the learning process. Traditional courses provide feedback by returning graded homework and exams to students, often too late to be of optimal use because the class has moved on to other topics. In contrast, in-class formative assessment provides immediate feedback to both students and instructors on how well a concept under discussion is being understood. The results can be eye-opening, particularly for instructors who are considered engaging and effective lecturers, when they find that only a fraction of their students have understood a seemingly lucid explanation (see Hrepic et al. 2007). Students may be surprised as well because the concept as presented may have seemed clear until they were asked to explain or apply it. But most important, awareness of a problem in understanding allows the class to address it immediately and in context when it is most meaningful to students.

In the 1990s, the physicist Eric Mazur began to obtain this kind of feedback by posing to his class multiple-choice questions ("ConcepTests") that required application of the concept under discussion (Mazur 1997, Crouch & Mazur 2001). Initially, students indicated their choices by a show of hands or by holding up different colored cards. More recently the audience response devices known

as clickers, developed originally for TV game shows, have made this kind of formative assessment more convenient and powerful (Wood 2004, Caldwell 2007, Bruff 2009). Each student has a clicker, generally with five buttons labeled A–E, and a receiver is connected to the instructor’s computer. When students answer a multiple-choice question using the clickers, their answers are recorded electronically, and a histogram of the results is displayed to the instructor and, eventually, to the class. How the instructor can respond to this information is discussed in the following section on active learning, but the benefits for formative assessment are clear: Student responses are independent and anonymous, responses are recorded for later analysis by the instructor if desired, problems with understanding are immediately apparent, and the class can address these problems on the spot.

Frequent quizzes can also serve as formative assessment, and research has shown that taking tests after studying leads to significantly more learning than studying alone (Karpicke & Roediger 2008, Klionsky 2008). Moreover, the results of quizzes (and in-class concept questions) are valuable to the instructor in designing appropriate exam questions for future summative assessments. Another kind of formative assessment is the “one-minute-paper” (Angelo & Cross 1993, Stead 2005), in which students are asked to write down and hand in anonymously a brief statement of what they found most difficult and what they found most interesting during the preceding class. This exercise encourages immediate reflection on the part of students and informs the instructor of possible problems. Students can also be asked to comment, positively or negatively, about general aspects of the course. Additional types of formative assessment are considered in the following section on in-class active-engagement activities. Any activity that requires students to apply concepts just discussed can provide useful feedback about conceptual understanding to both students and instructors.

The ease of implementing formative assessment is high; instructors do not need to

change the way they teach to obtain occasional feedback during class, although the results of such feedback may well change their teaching approaches as discussed further below. Clickers are an added expense for students who generally purchase a clicker at the bookstore and can resell it if they wish at the end of the course (Barber & Njus 2007). With regard to evidence for efficacy, formative assessment is generally coupled with in-class activities and so cannot be easily evaluated in isolation. Studies demonstrating the value of both these practices in combination are discussed in the following section.

In-Class Learning Activities: Listening and Note-Taking versus Active Engagement

In large STEM classes, the traditional learning activity is the lecture. Even students who are paying close attention to the lecturer are engaged primarily in the passive recording of information with little time for reflection. There is compelling evidence from all STEM disciplines that replacing some or all lecturing with in-class activities that actively engage students can substantially increase their learning gains. Of the promising practices reviewed here, this one, especially when combined with practice 2, students working in groups, and practice 3, frequent formative assessment, has produced the most impressive improvements in study after study. Many possible in-class activities—brainstorming, reflection followed by discussion with a neighbor and reporting to the class (“think-pair-share”), concept mapping, group problem solving, and more—are well described in the excellent book *Scientific Teaching* (Handelsman et al. 2007) and in the series of features titled “Approaches to Biology Teaching and Learning” by D. Allen & K. Tanner in the online journal *CBE-Life Sciences Education* (Allen & Tanner 2002; 2003a,b; 2005). **Table 3**, adapted from Handelsman et al. (2007), compares the traditional lecture presentation of a few topics with corresponding active-learning alternatives.

Table 3 Comparisons between presentation of topics in traditional lecture format and corresponding active learning activities

Concept	Passive lecture	Active class
Differential gene expression	Every cell in an organism has the same DNA, but different genes are expressed at different times and in different tissues. This is called differential gene expression.	If every cell in an animal has the same DNA, then how can cells of different tissues be so different? Discuss this question with your neighbor and generate a hypothesis.
DNA structure and replication	Complementary base pairing is the basis for the mechanism of DNA replication.	What do you know about the structure of DNA that suggests a mechanism for replication? Think about this for a minute and then discuss it with your neighbor.
Data analysis and interpretation	Based on the data shown in this slide, researchers concluded that <i>Snarticus inferensis</i> is the causal agent of the disease.	Consider these data from the experiment I just described. Which of the following conclusions can you draw from them? Think about it for a minute, and then we will take a vote and discuss the results.
Biology and society	Many people have concerns about genetically modified organisms (GMOs). Some of these concerns are well founded, and others are not. You have to decide for yourself.	I would like to split the class into two groups. One group will brainstorm about the potential benefits of GMOs and the other about possible harmful consequences. Then we will have a debate.

In-class concept questions, particularly when used with clickers, can be a powerful active learning tool. When a challenging multiple-choice concept question is presented to the class and the initial response is about evenly split between the correct choice and one or more incorrect choices (distracters), a teachable moment occurs: Students may be amused or surprised, but they want to know who is right and who is wrong, and they have become emotionally involved (Wood 2004). Rather than revealing the correct answer or trying to explain the concept again, the instructor, if interested in promoting active learning, should ask the students to discuss their answers in small groups, trying to convince their neighbors of the correct choice. Following a few minutes of discussion, the instructor calls for another vote, and almost invariably, the majority of students will now choose the correct answer, which is then revealed and discussed. Students are often better able than the instructor to identify flawed reasoning by their peers and convince them of the correct reasoning. Mazur named this phenomenon peer instruction in his delightful book of the same name (Mazur 1997, Crouch & Mazur 2001). It could be argued that less knowledgeable students are simply influenced during discussion by peer pressure from neighbors they perceive to be more knowledgeable,

but a recent study indicates that, on the contrary, students are actually learning during the discussion, even when no one in a group initially knows the correct answer (Smith et al. 2009).

Clicker questions, to be effective, must be conceptual and challenging. Ideally they should include distracters based on known student misconceptions, and they should assess higher Bloom's levels of understanding (Modell et al. 2005, Lord & Baviskar 2007, Crowe et al. 2008). Writing good questions is challenging but essential; questions that simply test factual recall of recently presented information do not engage students and are of little pedagogical use. Clicker questions are also not helpful if the instructor, after the initial vote, simply indicates the correct answer and then moves on. Student discussion before revealing the correct answer as well as after is key to learning. For additional guidance on writing good clicker questions and their effective use, see Beatty et al. (2006), Wieman et al. (2008), and Bruff (2009).

Clicker questions generally pose well-defined, discrete problems that are directly related to the immediate class content. Other valuable problem-based activities can be based on larger, more open-ended questions that groups of students may work on for a larger fraction of the class period and continue outside of class (see following section). But all

Distracters: the incorrect choices in a multiple-choice question

are examples of building instruction around student engagement with a problem, rather than around a body of factual information. Prince & Felder (2007) have contrasted deductive teaching—transmitting facts, abstract concepts, and finally (maybe), discussing their application to real-world problems—with inductive teaching—posing a real-world problem to students at the start, and letting them uncover the relevant concepts and facts in the process of solving it. When teaching is deductive, student motivation to learn facts and concepts is often primarily extrinsic, driven by desire to obtain a good grade, and the instructor must try to keep students engaged with assertions that this knowledge will be important in their future studies or careers. By contrast, when teaching is inductive, the students are presented with a real-world scenario (relevant to the particular group of students being taught) that they are likely to find interesting, and their motivation is intrinsic, based on desire to find a solution. Inductive approaches have been given a variety of labels including inquiry-based, problem-based, project-based, case-based, question-driven, and discovery learning (reviewed in Prince & Felder 2007). Their scope can range from a series of related clicker questions in a single class period (Beatty et al. 2006) to a complex problem requiring several weeks of work, in which new information is provided in response to requests from students for data or results of specific experimental tests. Disease-related, problem-based, and case-based activities, in which students are presented with a set of symptoms and asked to arrive at a diagnosis, are used extensively in medical education (Albanese & Mitchell 1993).

Instructors who wish to introduce more active learning into their classes may confront several problems. Implementing this mode of teaching can involve more up-front effort than the promising practices discussed above. Although designing a new course around the active learning model may require no more effort than preparing the lectures for a new traditional course, transforming a traditional course requires the additional work of creating

effective in-class activities and formative assessments. Another problem is that traditional auditorium-style classrooms with fixed seating are poorly suited for interactive group work. A few institutions have installed large classrooms with café-style seating, which greatly facilitates student-centered teaching (see Beichner 2008), and more such classrooms are needed to encourage course transformation. A final problem, perhaps most difficult for some instructors, is that teaching effectively in the new mode requires both a willingness to let go of some control in the classroom and a change in perspective from instructor-centered teaching to student-centered learning. Instructors must give up the widely held transmissionist view that students must be told everything they need to know and instead realize that not only are students in a stimulating and supportive environment capable of learning a great deal on their own (the constructivist viewpoint), but that they must develop this ability in order to become either successful scientists or well-informed citizens.

Balanced against the above potential difficulties is the clear evidence from DBER that moving toward more active learning in a more student-centered classroom can substantially increase student learning gains. And complete restructuring is not necessary; even incremental changes can have a significant effect (e.g., Knight & Wood 2005). Other evidence from the life sciences has been mentioned (Udovic et al. 2002, Armstrong et al. 2007, Freeman et al. 2007), and additional references can be found in Froyd (2008).

Out-of-Class Learning Activities: Instructor versus Student Responsibility for Learning

A frequent concern of instructors contemplating introduction of clickers and other active-learning activities into their classrooms is that they will no longer be able to cover all the necessary content. First of all, this may not be a bad thing. More coverage does not necessarily mean more learning, and it can be argued that deep student understanding of a few important

Transmissionist: the view that learning can or must occur by transmission of knowledge from an instructor to the learner

concepts is more valuable than superficial exposure to many concepts. Nevertheless, the content issue is real because it can affect student preparation for subsequent courses and standardized tests such as the MCAT. A solution to this dilemma lies in placing more of the responsibility on the students themselves for learning basic concepts, and again, recent technology makes this solution more practical. Using an approach that physicists have called Just-in-Time Teaching (JiT) (Novak et al. 1999), students are assigned reading and required to submit homework online to a course Web site before a topic is considered in class. The instructor can then scan the results (sampling randomly if the class is large), determine which concepts students seem to have grasped on their own, and then focus activities in the upcoming class on concepts they found difficult. Students may resist taking this responsibility, but again, learning to do so is essential preparation for later advanced study as well as for the real world, where one cannot expect to receive a lecture whenever a new concept must be learned. An extension of JiT, which may be more palatable to students, is the inverted classroom approach (Lage et al. 2000). Students are provided in advance of class with access to podcasts of a PowerPoint lecture by the instructor or some other multimedia presentation that serves the information transmission function of the traditional in-class lecture. Class time can then be devoted to clicker questions, solving problems, interpreting data, or other active learning activities without concerns about decreased content coverage.

The implementation of these approaches is quite simple using the Internet and one of the Web-based course management programs that are now available at most universities to instructors of large classes. Many faculty have reported not only increased student learning with these methods but also strong endorsement by students once they realized how much they were learning (e.g., Klionsky 2004, Silverthorn 2006).

In general, the practice of assigning homework is underutilized in teaching biology. Homework may not be of much help for

assimilating factual information but, in transformed courses designed to help students achieve higher Bloom's levels of understanding, homework assignments that require students to practice applying concepts, solving problems, predicting outcomes, analyzing data, and designing experiments can be an invaluable supplement to similar in-class exercises. In addition to more traditional forms of homework, interactive simulations (e.g., <http://phet.colorado.edu/index.php>) and educational video games (Mayo 2009) seem likely to become increasingly useful as out-of-class learning activities.

Student-Faculty Interaction in Class: Making Pedagogy Explicit

Many students, who have become comfortable with traditional instruction, may object to the new teaching approaches and the demands that are placed on them in transformed courses: more responsibility for learning outside of class, the need to attend class regularly, the emphasis on group work, refusal of the instructor to tell them all the things they need to know, and so on. The best way to confront these objections, in the author's experience as well as in the literature (e.g., Silverthorn 2006), is to encourage buy-in by being open with students about the pedagogical reasons for new approaches and the benefits they bring. For example, the instructor can spend a few minutes introducing the concept of Bloom's levels and remind students that the skills likely to determine their success in graduate work and the job market correspond to levels 3–6, not levels 1 and 2 (**Figure 1**). Instructors can show students evidence from DBER that group work and active learning can substantially increase learning gains and point out, as mentioned above, that these activities will better prepare them for life in the real world. But instructors should also be sympathetic and supportive of students struggling with these changes, because students, like instructors, must shift their perceptions about teaching and learning in order to succeed with the new instructional approaches (Silverthorn 2006).

The active learning activities discussed above greatly increase the amount of student-faculty interaction in comparison with traditional lecture settings. Use of clickers with peer instruction, in particular, is an easy way to move classes from one-way transmission of information to interactive dialogs between instructor and students, and between students, with instructional benefits that have been documented by research as described in the preceding paragraphs.

Student-Faculty Contact Out of Class: Office Hours versus Enhanced Communication

Umbach & Wawrzynski (2005) cite several studies showing that, in general, student learning is enhanced by increased student-faculty contact, suggesting that faculty, as time permits, should provide more opportunities for interaction than simply holding office hours for those (often few) students who will make use of them. Additional interactions can include brief get-acquainted visits by invitation to the instructor's office or, for larger courses, virtual communication through emails to the class, moderated discussion forums, or use of social networking Web sites. Aside from requiring some additional faculty time, this practice is easy to implement and its efficacy is supported by the studies referenced above.

Use of Teaching Assistants: Grading and Recitation versus Facilitation of Student Learning

Many instructors of large STEM courses have help from one or more teaching assistants (TAs), whose principal tasks are grading of homework and exams and perhaps conducting recitation sessions to go over lecture material and solutions to homework problems. If TAs are made part of the course transformation process and given minimal pedagogical training (e.g., reading of Handelsman et al. 2007), they can serve as valuable facilitators in class for discussion of clicker questions or group work on problems. In addition, they will

have gained a new kind of teaching experience that can serve them well in the future if they should go on to become faculty themselves. Many institutions, for example those involved in the Center for the Integration of Research, Teaching, and Learning (CIRTL) Network (<http://www.cirtl.net/>), provide such training to STEM graduate students in Preparing Future Faculty programs (e.g., Miller et al. 2008). This practice is quite easy to implement, and research to evaluate its efficacy is in progress at the author's institution and elsewhere (personal communications).

Student Laboratories: Cookbook Exercises versus Inquiry

As one solution to the problem of inadequate STEM education for undergraduates, the Carnegie Foundation's Boyer Commission Report (Boyer 1998) recommended that research universities integrate their research and teaching missions by involving more students in the process of research. In traditional "cookbook labs" associated with many large introductory lecture courses, students perform prescribed exercises in which they may learn some laboratory techniques but generally gain little understanding of scientific inquiry. At the other end of the lab experience spectrum (see **Figure 3**), some undergraduates become apprentices in faculty laboratories, learning how science is done by working alongside graduate students and postdocs on research projects that often result in publication. Although this experience is highly desirable, most departments can provide it to only a fraction of their majors. Between these extremes, some departments have developed a variety of inquiry-based laboratory courses designed to introduce large numbers of students to the process of research (reviewed in Weaver et al. 2008). These courses range from guided inquiry labs to open-ended group research projects that may result in publications by undergraduates (e.g., Hanauer et al. 2006). Faculty who supervise these courses often design them to yield results that can contribute directly to their own research programs.

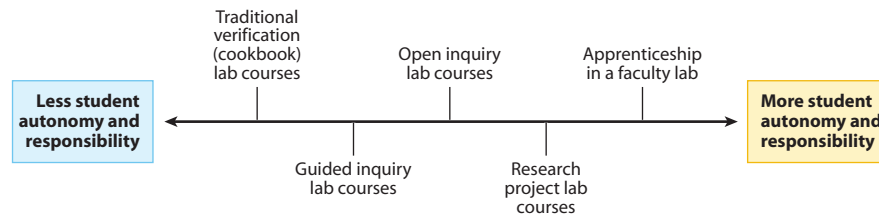


Figure 3

The range of student laboratory experiences from verification exercises (“cookbook labs”) to apprenticeship in a faculty research laboratory. Levels of student responsibility and autonomy increase from left to right. (Adapted from Weaver et al. 2008.)

Implementation of inquiry-based courses in place of traditional labs may require additional resources including more extensive training for TAs. Although Froyd (2008) rates this promising practice low in terms of evidence for efficacy, several studies, in addition to the two cited above, have shown that engagement of students with real research problems is one of the most effective ways to move students along the path from novice to expert (Nagda et al. 1998, Lopatto 2004, Luckie et al. 2004, Seymour et al. 2004). Compared to students who experience only traditional lab courses, reported benefits to students in inquiry-based curricula include deeper understanding of content, increased confidence in their ability to understand and perform science, more positive attitudes about science, and lower attrition rates. These gains are particularly evident among under-represented minority students (Nagda et al. 1998, Russell et al. 2007). Thus, the benefits of this promising practice can include not only increased student learning and higher retention of students in the major (especially if inquiry-based labs are introduced early in the curriculum) but also contributions to faculty research.

CONCLUSION: THE DUAL FUNCTIONS OF BIOLOGY EDUCATION

There are two important purposes for the introductory biology courses we teach. One is

to attract, motivate, and begin preparing the next generation of biologists including the research stars of the future. The other is to help the large majority of our students who will not become biologists or even scientists to achieve minimum biological literacy and to understand the nature of science, the importance of empirical evidence, and the basic principles that underlie biological systems. They will need this knowledge as twenty-first century citizens of the United States and the world to make intelligent decisions about issues such as personal health, conflicting claims in the media, energy policy, climate change, and conservation of natural resources.

Traditional teaching methods do not prevent the progress of superior students from introductory courses to upper-level courses to graduate training, where they may become experts in their fields and develop into skilled researchers. But the traditional methods fail the majority of students who leave our introductory courses viewing biology as a large collection of disconnected facts that have little relevance to their daily lives and will soon be forgotten. Part of the problem, as described in this review, lies not in what we teach these students (though this is also a concern; see NRC 2003, AAMC-HHMI 2009) but in how we teach it. We must do better! Widespread adoption of the research-based promising practices described here will help.

SUMMARY POINTS

1. We must improve the undergraduate teaching of biology and other STEM disciplines to remain competitive in the global economy and educate American citizens adequately.
2. Recent research in educational psychology, cognitive science, and neurobiology has yielded important new insights into how people learn and the optimal conditions for learning.
3. Discipline-based educational research (DBER) has led to the development of teaching approaches based on these insights (promising practices) and has provided extensive evidence that these approaches can be substantially more effective than traditional lecturing even in large classes.
4. These promising practices vary in their ease of implementation but even their partial adoption can lead to significant gains in student learning.
5. Applying these promising practices widely in STEM classes can have a major impact on better preparing our undergraduate biology students for their future endeavors.

DISCLOSURE STATEMENT

The author is Editor-in-Chief of *CBE-Life Sciences Education*.

LITERATURE CITED

- AAMC-HHMI Committee. 2009. *Scientific Foundations for Future Physicians*. Washington, DC: Assoc. Amer. Med. Coll. and Howard Hughes Med. Inst.
- Albanese M, Mitchell S. 1993. Problem-based learning: a review of the literature on its outcomes and implementation issues. *Acad. Med.* 68:52–81
- Allen D, Tanner K. 2002. Approaches to cell biology teaching: questions about questions. *Cell Biol. Educ.* 1:63–67
- Allen D, Tanner K. 2003a. Approaches to cell biology teaching: learning content in context–problem-based learning. *Cell Biol. Educ.* 2:73–81
- Allen D, Tanner K. 2003b. Approaches to cell biology teaching: mapping the journey–concept maps as signposts of developing knowledge structures. *Cell Biol. Educ.* 2:133–36
- Allen D, Tanner K. 2005. Infusing active learning into the large-enrollment biology class: seven strategies, from the simple to complex. *Cell Biol. Educ.* 4:262–68
- Allen D, Tanner K. 2006. Rubrics: tools for making learning goals and evaluation criteria explicit for both teachers and learners. *CBE-Life Sci. Educ.* 5:197–203
- Allen D, Tanner K. 2007. Putting the horse back in front of the cart: using visions and decisions about high-quality learning experiences to drive course design. *CBE-Life Sci. Educ.* 6:85–89
- Anderson DL, Fisher KM, Norman GJ. 2002. Development and evaluation of the conceptual inventory of natural selection. *J. Res. Sci. Teach.* 39:952–78
- Angelo TA, Cross PK. 1993. *Classroom Assessment Techniques: A Handbook for College Teachers*. San Francisco: Jossey-Bass
- Armstrong N, Chang SM, Brickman M. 2007. Cooperative learning in industrial-sized biology classes. *CBE-Life Sci. Educ.* 6:163–71
- Astin AW. 1993. *What Matters in College: Four Critical Years Revisited*. San Francisco: Jossey-Bass
- Ausubel D. 1963. *The Psychology of Meaningful Verbal Learning*. New York: Grune and Stratton
- Ausubel D. 2000. *The Acquisition and Retention of Knowledge: A Cognitive View*. Boston: Kluwer Acad. Publ.
- Barber M, Njus D. 2007. Clicker evolution: seeking intelligent design. *CBE-Life Sci. Educ.* 6:1–8

The articles by Allen & Tanner, plus another by Tanner et al. 2003, provide excellent practical introductions to several of the promising practices discussed in the text.

- Beatty ID, Leonard WJ, Gerace WJ, Dufresne RJ. 2006. Question driven instruction: teaching science (well) with an audience response system. In *Audience Response Systems in Higher Education: Applications and Cases*, ed. DA Banks. Hershey, PA: Inf. Sci. Publ.
- Beichner R. 2008. *The SCALE-UP Project: a student-centered active learning environment for undergraduate programs*. Presented at BOSE Conf. Promis. Pract.—Innov. Undergrad. STEM Educ., Washington, DC. http://www7.nationalacademies.org/bose/PP_Commissioned_Papers.html
- Bloom BS, Krathwohl DR. 1956. *Taxonomy of Educational Objectives: The Classification of Educational Goals. Handbook 1: Cognitive Domain*. New York: Longmans
- Bowling BV, Acra EE, Wang L, Myers MF, Dean GE, et al. 2008. Development and evaluation of a genetics literacy assessment instrument for undergraduates. *Genetics* 178:15–22
- Boyer Commission on educating undergraduates in the research university. 1998. *Reinventing Undergraduate Education: A Blueprint for America's Research Universities*. Stony Brook, NY: Carnegie Found.
- Brophy DR. 2006. A comparison of individual and group efforts to creatively solve contrasting types of problems. *Creativity Res. J.* 18:293–315
- Bruff D. 2009. *Teaching with Classroom Response Systems: Creative Active Learning Environments*. San Francisco: Jossey-Bass
- Caldwell JE. 2007. Clickers in the large classroom: current research and best-practice tips. *CBE-Life Sci. Educ.* 6:9–20
- Cox J. 1993. *Cultural Diversity in Organizations: Theory, Research, and Practice*. San Francisco: Berrett-Koehler Publ.
- Crouch CH, Mazur E. 2001. Peer instruction: ten years of experience and results. *Am. J. Phys.* 69:970–77
- Crowe A, Dirks C, Wenderoth MP. 2008. Biology in bloom: implementing Bloom's taxonomy to enhance student learning in biology. *CBE-Life Sci. Educ.* 7:368–81
- DeHaan RL. 2005. The impending revolution in undergraduate science education. *J. Sci. Educ. Technol.* 14:253–59
- Dewey J. 1916. *Democracy and Education*. New York: Macmillan
- DoE. 2000. Before it's too late (the Glenn Report). Dept. Educ., Washington DC. <http://www.ed.gov/americaaccounts/glenn>
- Dolan EL. 2007. Grappling with the literature of education research and practice. *CBE-Life Sci. Educ.* 6:289–96
- Freeman S, O'Connor E, Parks JW, Cunningham M, Hurley D, et al. 2007. Prescribed active learning increases performance in introductory biology. *CBE-Life Sci. Educ.* 6:132–39
- Froyd J. 2008. *White paper on promising practices in undergraduate STEM education. Presented at BOSE Conf. Promis. Pract.—Innov. Undergrad. STEM Educ., Washington, DC.* http://www7.nationalacademies.org/bose/PP_Commissioned_Papers.html
- Garvin-Doxas K, Klymkowsky M, Elrod S. 2007. Building, using, and maximizing the impact of concept inventories in the biological sciences: report on a National Science Foundation sponsored conference on the construction of concept inventories in the biological sciences. *CBE-Life Sci. Educ.* 6:277–82
- Guimera R, Uzzi B, Spiro J, Amaral LA. 2005. Team assembly mechanisms determine collaboration network structure and team performance. *Science* 308:697–702
- Hake RR. 1998. Interactive-engagement versus traditional methods: a six-thousand-student survey of mechanics test data for introductory physics courses. *Am. J. Phys.* 66:64–74
- Halloun IA, Hestenes D. 1985. Common-sense concepts about motion. *Am. J. Phys.* 53:1056–65
- Hanauer DI, Jacobs-Sera D, Pedulla ML, Cresawn SG, Hendrix RW, Hatfull GF. 2006. Inquiry learning. Teaching scientific inquiry. *Science* 314:1880–81
- Handelsman J, Ebert-May D, Beichner R, Bruns P, Chang A, et al. 2004. Scientific teaching. *Science* 304:521–22
- Handelsman J, Miller S, Pfund C. 2007. *Scientific Teaching*. New York: W.H. Freeman**
- Hestenes D, Wells M, Swackhamer G. 1992. Force concept inventory. *Phys. Teach.* 30:141–58
- Holt J. 1964. *How Children Fail*. New York: Pitman
- Holt J. 1967. *How Children Learn*. New York: Pitman
- Hrepic Z, Zollman DA, Rebello SJ. 2007. Comparing students' and experts' understanding of the content of a lecture. *J. Sci. Educ. Technol.* 16:213–24
- Johnson DW, Johnson RT, Smith KA. 1998. Cooperative learning returns to college: What evidence is there that it works? *Change* 30:26–35

A good summary of the evidence with additional references for most of the promising practices described in this review.

An excellent, brief practical guide to most of the promising practices described in this review. Highly recommended for all STEM instructors.

- Karpicke JD, Roediger HL III. 2008. The critical importance of retrieval for learning. *Science* 319:966–68
- Klionsky D. 2004. Talking biology: teaching outside the textbook, and the lecture. *Cell Biol. Educ.* 3:204–11
- Klionsky D. 2008. The quiz factor. *CBE-Life Sci. Educ.* 7:265–66
- Klymkowsky MW, Garvin-Doxas K, Zeilik M. 2003. Bioliteracy and teaching efficacy: what biologists can learn from physicists. *Cell Biol. Educ.* 2:155–61
- Knight JK, Wood WB. 2005. Teaching more by lecturing less. *Cell Biol. Educ.* 4:298–310
- Kozol J. 1967. *Death at An Early Age*. Boston: Houghton-Mifflin
- Lage MJ, Platt GJ, Treglia M. 2000. Inverting the classroom: a gateway to creating an inclusive learning environment. *J. Econ. Educ.* 31:30–43. <http://www.sba.muohio.edu/plattgj/eco201>
- Libarkin J. 2008. Concept inventories in higher education science. Presented at BOSE Conf. Promis. Pract.—Innov. Undergrad. STEM Educ., Washington, DC. http://www7.nationalacademies.org/bose/PP_Commissioned_Papers.html
- Lopatto D. 2004. Survey of undergraduate research experiences (SURE): first findings. *Cell Biol. Educ.* 3:270–77
- Lord T, Baviskar S. 2007. Moving students from information recitation to information understanding: exploiting Bloom's taxonomy. *J. Coll. Sci. Teach.* 36:40–44
- Luckie DB, Maleszewski JJ, Loznak SD, Krha M. 2004. Infusion of collaborative inquiry throughout a biology curriculum increases student learning: a four-year study of "Teams and Streams." *Adv. Physiol. Educ.* 28:199–209
- Mayo MJ. 2009. Video games: a route to large-scale STEM education? *Science* 323:79–82
- Mazur E. 1997. *Peer Instruction: A User's Manual*. Upper Saddle River, NJ: Prentice Hall
- McLeod PO, Lobel SA, Cox TH. 1996. Ethnic diversity and creativity in small groups. *Small Group Res.* 27:248–65
- Miller S, Pfund C, Pribbenow CM, Handelsman J. 2008. Scientific teaching in practice. *Science* 322:1329–30
- Modell HM, Michael J, Wenderoth MP. 2005. Helping the learner to learn: the role of uncovering misconceptions. *Am. Biol. Teach.* 67:20–26
- Nagda BA, Gregerman SR, Jonides J, von Hippel W, Lerner JS. 1998. Undergraduate student-faculty research partnerships affect student retention. *Rev. Higher Educ.* 22:55–72
- Natl. Acad. Sci. 2004. *Rising Above the Gathering Storm: Energizing and Employing America for a Brighter Economic Future*. Washington DC: Natl. Acad. Press. <http://books.nap.edu/catalog/11463.html>
- Natl. Acad. Sci. 2005. Natl. Acad. Worksh. Educ. Res. Positions STEM Discipl. Dep. Washington, DC. http://www7.nationalacademies.org/cfe/STEM_Disciplines_Agenda.html
- Natl. Res. Council. 1999. *How People Learn: Brain, Mind, Experience, and School*. Bransford JD, Brown AL, Cocking RR, eds. Washington, DC: Natl. Acad. Press
- Natl Res. Council. 2003. *Bio2010: Transforming Undergraduate Education for Future Research Biologists*. Stryer L, ed. Washington, DC: Natl. Acad. Press
- Novak G, Gavrin A, Christian W, Patterson E. 1999. *Just-in-Time Teaching: Blending Active Learning with Web Technology*. San Francisco: Benjamin Cummings. <http://webphysics.iupu.edu/jitt/jitt.html>
- Prince M, Felder R. 2007. The many faces of inductive teaching and learning. *J. Coll. Sci. Teach.* 36:14–20
- Russell SH, Hancock MP, McCullough J. 2007. The pipeline. Benefits of undergraduate research experiences. *Science* 316:548–49
- Seymour E, Hewitt S. 1997. *Talking About Leaving: Why Undergraduates Leave the Sciences*. Boulder, CO: Westview Press
- Seymour E, Hunter AB, Laursen SL, Diatonic T. 2004. Establishing the benefits of research experiences for undergraduates in the sciences: first findings from a three-year study. *Science Educ.* 88:493–534
- Silverthorn DU. 2006. Teaching and learning in the interactive classroom. *Adv. Physiol. Educ.* 30:135–40
- Smith AC, Stewart R, Shields P, Hayes-Klosteridis J, Robinson P, Yuan R. 2005. Introductory biology courses: a framework to support active learning in large enrollment introductory science courses. *Cell Biol. Educ.* 4:143–56
- Smith MK, Wood WB, Adams WK, Wieman C, Knight JK, et al. 2009. Why peer discussion improves student performance on in-class concept questions. *Science* 323:122–24
- Smith MK, Wood WB, Knight JK. 2008. The genetics concept assessment, a new concept inventory for gauging student understanding of genetics. *CBE-Life Sci. Educ.* 7:422–30

Classic review of educational and cognitive science research on how learning occurs and the conditions that foster it.

Review of instructional approaches that present real-world problems to students and challenge them to discover the facts and concepts they need for a solution.

A good review of inquiry-based curricular innovations and their utility for introducing more students to the process of research.

A useful introductory guide to clickers and their effective use to promote active learning through in-class concept questions.

A book for educators on the neurobiology of learning.

- Springer L, Stanne ME, Donovan SS. 1999. Effects of small-group learning on undergraduates in science, mathematics, engineering, and technology: a meta-analysis. *Rev. Educ. Res.* 69:21–51
- Stead DR. 2005. A review of the one-minute paper. *Active Learn. Higher Educ.* 6:118–31
- Tanner K, Chatman LS, Allen D. 2003. Approaches to cell biology teaching: cooperative learning in the science classroom—beyond students working in groups. *Cell Biol. Educ.* 2:1–5
- Udovic D, Morris D, Dickman A, Postlethwait J, Wetherwax P. 2002. Workshop biology: demonstrating the effectiveness of active learning in an introductory biology course. *Bioscience* 52:272–81
- Umbach PD, Wawrzynski MR. 2005. Faculty do matter: the role of college faculty in student learning and engagement. *Res. Higher Educ.* 46:153–84
- Weaver GC, Russell DB, Wink DJ. 2008. Inquiry-based and research-based laboratory pedagogies in undergraduate science. *Nature Chem. Biol.* 4:577–80**
- Wieman C. 2007. Why not try a scientific approach to science education? *Change* 39:9–15
- Wieman C, Perkins K, Gilbert S, Benay F, Kennedy S, et al. 2008. *Clicker Resource Guide: An Instructors Guide to the Effective Use of Personal Response Systems (Clickers) in Teaching*. Vancouver, BC: Univ. British Columbia. http://www.cwsei.ubc.ca/resources/files/Clicker_guide_CWSEI-CU-SEI.04-08.pdf**
- Wiggins G, McTighe J. 1998. *Understanding by Design*. Alexandria, VA: Assoc. Superv. Curric. Dev.
- Wood WB. 2004. Clickers: a teaching gimmick that works (resource review). *Dev. Cell* 7:796–98
- Zheng AY, Lawhorn JK, Lumley T, Freeman S. 2008. Application of Bloom's taxonomy debunks the "MCAT myth." *Science* 319:414–15
- Zull JE. 2002. *The Art of Changing the Brain*. Sterling, VA: Stylus



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Errata

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