putting a stop to it is a different challenge. Senior women scientists must be alert to passive discrimination and work together to eradicate it.

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FURTHER INFORMATION

CORDIS: Women and Science: http://www.cordis.lu/improving/women/documents.htm
Equal Opportunities Commission: http://www.eoc.org.uk
***Journal of Cell Science*:** http://jcs.biologists.org
National Science Foundation: http://www.nsf.gov
Remarks at NBER Conference on Diversifying the Science & Engineering Workforce: http://www.president.harvard.edu/speeches/2005/nber.html
The American Society for Cell Biology: http://www.ascb.org
The Athena Project: http://www.athenaproject.org.uk
The Wellcome Trust: http://www.wellcome.ac.uk
Thomas: Legislative Information on the Internet: http://thomas.loc.gov
Access to this links box is available online.

ESSAY

Cell biology should be taught as science is practised

Stephen E. DiCarlo

Abstract | Over the past 20 years, there has been a dramatic transformation in the goals of science teaching at all levels and within all disciplines. The emphasis has moved from students obtaining a base of scientific facts to students developing a deep understanding of important concepts. This transformation requires a significant shift in the approach and attitude of the instructors and students, as well as in the procedures and techniques that are required to teach cell biology.

The American Association for the Advancement of Science (AAAS)[1] strongly recommends that "…science be taught as science is practised…" because the traditional 'lecture-then-test' format and accompanying 'cook-book' laboratories are falling short of their educational goals. The AAAS encourages a transformation from instructor-led courses to dynamic student-centred experiences that engage students in research-orientated learning[2,3]. However, many teachers are apprehensive of making this transition and are unconvinced of the need for change. Furthermore, many are not familiar with the specific strategies that could be used to achieve the goals. This article presents a review of the literature and evidence supporting the need for reform, as well as specific practical examples and resources for faculty who are considering incorporating student-centred learning into their teaching strategies.

The packed curriculum: too much content

Educators bemoan the packed curriculum in which courses have too much content and the students and teachers must learn and teach more with not enough time. The extensive course content leaves little time for students to acquire a deep understanding of the subject or to develop lifelong skills such as critical thinking, problem solving, communication and interpersonal skills. Even my children complain that it is much more difficult to learn history today than it was when I was an undergraduate, because so much more has happened since those 'ancient' times (my children believe that the USA consisted of 13 colonies when I was an undergraduate). Similarly, consider the explosion of knowledge in molecular and cellular biology over the past decade. The cell is much more complicated than was initially thought, and there is no doubt that further research will uncover additional complexity. Students of cell biology must also learn that cells function beyond their membranes and that this has broad biological implications for how complex multicellular organisms function. Furthermore, there is a greater need for cross-discussion and collaboration between cell biology and other disciplines — especially mathematics, biophysics and bioinformatics — to address comprehensively the problems that challenge our health and safety. So, few people would disagree that teachers now have access to much more factual and conceptual knowledge than our teachers had.

Too much content and not enough time

Now consider the amount of time we have in the classroom and the teaching laboratory 'to teach' this vast amount of information. Cell biology is typically taught in lecture and laboratory classes. A typical cell-biology course in the United States consists of 3 hours of lectures and 3 hours of laboratory time each week[4]. This amounts to approximately 3.6% of the total hours in a student's week.

Herein lies the problem. How do we teach this vast amount of content to students in this limited time? The logical answer is that we cannot, and therefore we should not, even attempt this Herculean task. To attempt to 'cover the content' would limit students to simply learning facts without the ability to apply their knowledge to solve new problems. This would encourage the mistaken belief that science is about learning the correct answer rather than about innovation, creativity and inquiry. In addition, this inaccurate portrayal of science is boring, and ownership and engagement by the

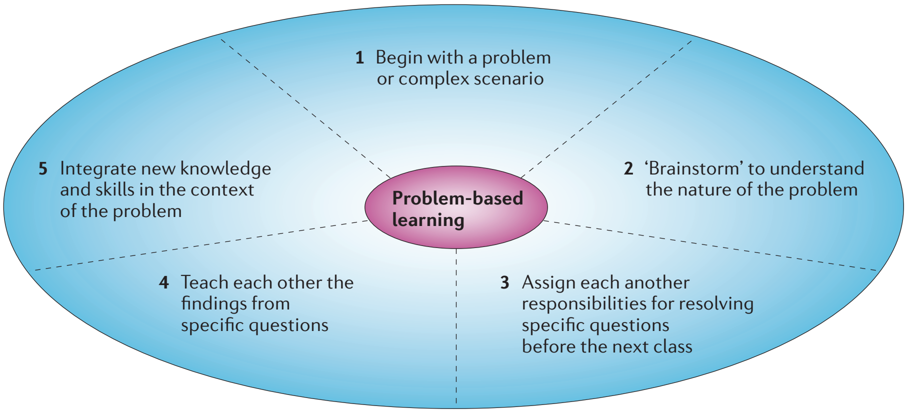

Figure 1 | **Problem-based learning.** The diagram illustrates the cycle of repeating steps that should be taken by a small group of students when solving a problem-based learning (PBL) case. Step 1: student learning begins with a problem to be solved rather than facts to be mastered. This enhances student motivation because concepts are learned in the context of their application and the students address questions that are of interest. Step 2: students gather information and consult resources to fill conceptual holes and address misconceptions. Step 3: the students and their peers learn to find and process new information and work towards resolving the problem by asking and answering each other's questions. Step 4: students define new areas of required learning (dig deeper into the problem) and learn effective communication skills while becoming influential members of a productive team. Step 5: students integrate new knowledge and skills in the context of the problem and enhance collaborative skills of acquiring, analysing and communicating information.

students in the process is low. Furthermore, covering the vast amount of material would significantly limit the time for inquiry-based laboratory and problem-solving sessions, without which students become uninspired and unchallenged by science and transfer to other disciplines or drop out of school entirely[5]. This would also reduce the time that is available for cross discussion and collaboration with other disciplines. Such activities are essential, because no problem exists in isolation, so no solution will be found by a single discipline. So, we are in the middle of a transformation of science teaching. It is moving from simply covering the material to using conceptual and integrated science learning, in which students are actively engaged in discovery and scientific inquiry[6]. A number of reports have called for educational reform[7–9], and there have been several publications on effective teaching methods to achieve these goals[3,10–12].

Unpack the curriculum

Published reports and effective teaching methods suggest that cell-biology teachers must abandon the mistaken idea that unless they 'cover the content' students will be unprepared for the future and they will have failed as teachers. Teachers must not worry about 'losing' or 'wasting' valuable lecture time for teaching activities that take time away from covering content. In-class discussion, collaborative problem solving and inquiry-based activities focus student learning on how to use scientific knowledge to solve the questions that are posed. This is important because learning is not about committing a set of facts to memory, but requires the ability to use resources to find, evaluate and apply information. As noted by the French mathematician Poincaré, "Science is built with facts, as a house is with stones. But a collection of facts is no more science than a heap of stones is a house."[13] For example, what is the use of memorizing the chemical reactions of the Krebs cycle without a deeper understanding of the relationships between these chemical reactions of cellular respiration and the organism's need to harvest energy for food[14]? Memorizing the chemical reactions of the Krebs cycle might be useful for passing the examination, however, it will not help students solve new problems and is not as important as understanding the process and how it relates to the entire organism[14]. In fact, memorizing content primarily teaches students how to take examinations (a skill not used in real life unless one is a game show contestant) and only prepares students for more school.

I can hear my colleagues argue, "Sure, but what about content mastery?"[15] These colleagues might emphasize the importance of memorizing the different amino acids or biochemical, signalling or other pathways. However, memorizing multiplication tables, for example, is not required for using mathematics to solve complex problems, but knowing when to use multiplication to solve a problem is essential[15]. Importantly, knowing the multiplication tables is likely to evolve naturally from solving problems that require multiplication[15]. So, content mastery will occur as a result of students working together, gathering evidence, learning from it, and solving novel problems. Furthermore, de-emphasizing the importance of content knowledge and concentrating on the process (for example, the ability to think, reason, analyse and communicate) will have a long-term impact on the students' lives and their ability to contribute to society.

What is the solution?

The traditional 'lecture-then-test' format might be the only experience of, and preparation for, teaching that many of us had as graduate students and postdoctoral fellows. Therefore, often, faculty members are unaware of alternative approaches for teaching. As such, many of us simply teach the way we were taught and perpetuate the process of transferring knowledge to students through lectures and note taking[16], rather than active student involvement and personal investment in the process[17]. However, there has been remarkable progress in our understanding of how people learn[8]. It is now clear that each learner must construct his/her own understanding of concepts, relationships and procedures. Teachers can encourage this process by carefully considering the type and organization of information as well as the instructional strategies that they use[17,18]. For example, we all realize that reading the recipe is not as useful as preparing the meal. How, then, do we change our approach from reading to 'doing' as far as science is concerned?

Importantly, cell biology must be taught as science is practised[4,19]. This means that the teaching approach must be consistent with the nature of scientific inquiry[20]. An essential part of scientific inquiry is collaboration[19]. Problem-based learning (PBL), case studies and concept maps are different approaches for achieving these goals[21,22] as well as increasing the students' enthusiasm and their love for learning[23,24]. Problem-based learning is initiated by, and structured around, complex problems that are rooted in situations that the learner is likely to encounter in the real world[25]. Real-world problems motivate deep conceptual learning (for example, when the learner extends what has been learned in one context to new contexts and applies the new information to solve novel problems). Students work collaboratively to identify the problem, gather

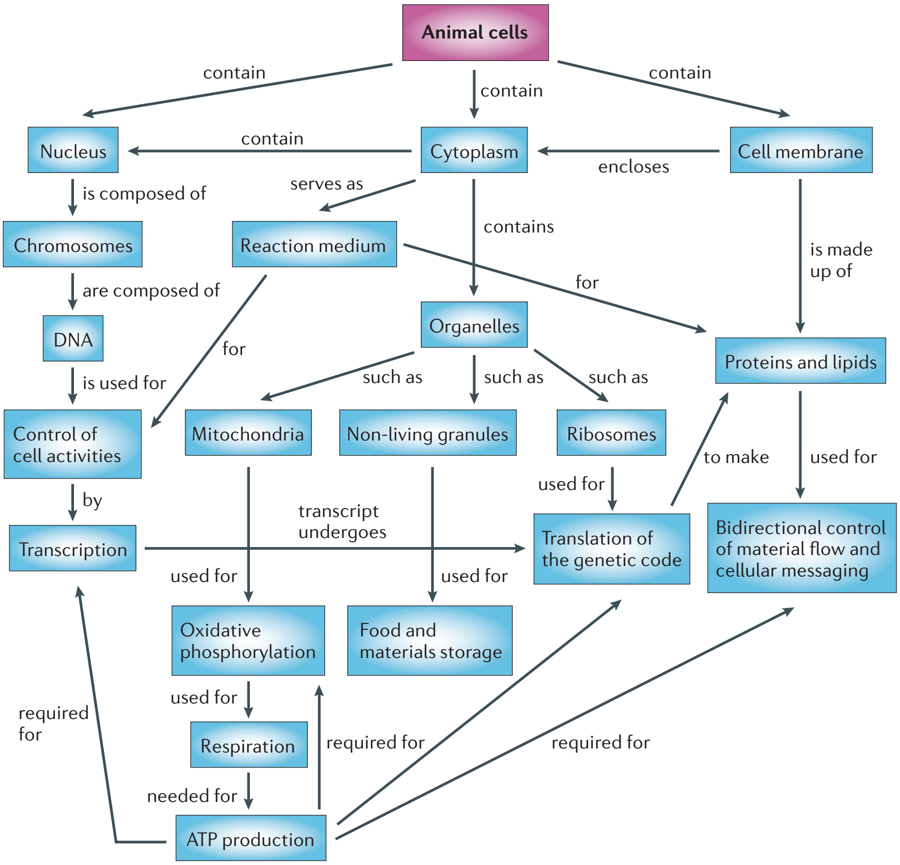

Figure 2 | **A concept map.** This concept map is a nonlinear diagrammatic representation of meaningful relationships between concepts. The concepts are linked by words that describe the relationships or connections between the concepts. Concept maps are used in various ways to enhance meaningful learning. For example, one problem that is associated with textbooks and lecture series is the fixed sequence of learning events that have been designed by the textbook's author or by the teacher. Any particular sequence can never be optimal for all students, given that every learner has a unique cognitive structure that is derived from their individual experiences. To overcome this limitation, the instructor can provide a basic, skeleton map of important concepts, which provides a 'conceptual scaffolding' that serves as a starting point for the student. Students 'fill in' and complete the map by building their knowledge structures, in their own way, and represent them in more complex and elaborate maps. Students can also be required to construct their own concept maps from each class by identifying and linking important concepts. The students' maps will become increasingly complex as their understanding progresses and they grasp the 'big picture'. An entire lecture topic, unit, course or curriculum can be elucidated by this approach when the connections between concepts are illustrated.

information, learn from it and find solutions. Specifically, students work in small groups to solve complex problems by asking and answering their own questions using their collective skills at gathering, analysing and communicating information (FIG. 1). For an outstanding description of how to implement PBL in your classes as well as a large variety of PBL-problem examples, see REF. 24.

Concept maps are an effective teaching approach that is based on Ausubel's cognitive-learning theory[26–29], which strongly encourages the construction of concepts and relationships. Ausubel's theory implies that the most important factor that influences learning is what the student already knows. The student must consciously and explicitly link new information to concepts they already know. In this way, students can identify new concepts and link them to existing concepts. This is crucial because concepts do not exist in isolation, and each concept depends on its relationship to many others for meaning. Concept maps are diagrammatic representations in which students construct meaningful relationships between concepts (FIG. 2). Concept-map construction actively engages students in searching for relationships between their existing knowledge and the new knowledge. Novak developed the use of concept maps as an effective teaching and learning strategy, and in REF. 22, he provides an outstanding description of their use, as well as several examples of concept maps.

An example of a case study is 'Dolly' the sheep[30]. Using this example, the teacher can focus attention on the process of cell cloning, the diversity of genetic material in a species, and genetic traits, as well as on the future and ethics of cloning. In addition, by introducing cloning techniques, students can learn about cell culture, cell selection and nuclear cell fusion. Online case-based and problem-learning activities are available on the BioQUEST Curriculum Consortium and Teaching Case Database Web sites (TABLE 1).

Innovative teaching

Cell biology is a creative science in which the synthesis of new ideas requires discussion and debate through student-to-student and student-to-teacher interactions, as well as constructivism (that is, constructing knowledge by asking questions, developing answers and interacting with peers, teachers and the subject). Prompt feedback by the teacher is also required to focus instruction on the points that are most difficult for the students[8]. Several studies document that those students who used interactive-engagement methods outperformed students in traditional classes. For example, peer instruction and collaborative testing — pedagogical methods that promote student participation in class and increase student interaction with each other and with the instructor — increased the performance on quizzes and exams (mastery of original material) as well as deep conceptual learning (ability to solve novel problems)[31–34].

The constructivism theory implies that learning requires constructing new knowledge from prior knowledge[29,35,36]. The theory underscores the approach that new concepts cannot be learned if alternative models already exist in a student's mind. For example, the complex and microscopic nature of cells is challenging to students who think in terms of what they can see and feel. This presents difficulties in distinguishing between cells and their molecular components. As a result, these misconceptions make it difficult to understand cell division. New concepts are learned when prior knowledge and misconceptions are uncovered and addressed[8,37]. Prompt feedback is required so that students have ample opportunities to assess their prior knowledge and make appropriate adjustments in their thinking. Just-in-time teaching (JiTT; see TABLE 1) is a technique that emphasizes these important

Table 1 | **Teaching materials and online resources in biology**

Subject*	URL	Description
Biology Brought to Life: A Guide to Teaching Students to Think Like Scientists	http://www.plantpath.wisc.edu/fac/joh/BBTL.htm	Cooperative exercises and inquiry-based laboratories
BioQUEST Curriculum Consortium	http://bioquest.org	Problem-solving and laboratory exercises
Concept mapping tool (CTOOLS)	http://www.ctools.msu.edu	Concept-mapping tools
DNA from the Beginning	http://www.dnaftb.org	Graphics and animations for teaching about DNA
DNA Interactive	http://www.dnai.org	Animations and problem solving to learn about DNA
Frog Deformities	http://www.first2.org/resources/inquiry_activities/frog_activity.htm	Experimental design and analysis
Genetics Education Center	http://www.kumc.edu/gec/	Lesson plans about genetics and the human genome project
Genome Consortium for Active Teaching (GCAT)	http://www.bio.davidson.edu/Biology/GCAT/GCAT.html	Student research on functional genomics and teaching genomics
Guppy Simulation	http://www.first2.org/resources/inquiry_activities/guppy_activity.htm	Computer-based activity on natural selection, sexual selection and fitness
Integrated Biological Science Courses Organized around Research Experience (IBSCORE)	http://www.ibscore.org/courses.htm	Material to involve students in critical thinking and communication skills
Introduction to Biological Inquiry and Analysis	http://campus.murraystate.edu/academic/faculty/terry.derting/ccli/cclihomepage.html	Ten in-class assignments of basic concepts in biology and basic statistics
LifeLines	http://bioquest.org/lifelines	Case-based learning on real-life scenarios
Microbes Count!	http://bioquest.org/microbescount	Multimedia resources and simulations for learning about microbiology
MicrobeLibrary	http://www.microbelibrary.org	Images and animations about the microbial world
Problem-based Learning	http://www.udel.edu/pbl/	Collection of problem-based-learning activities
Teaching Case Database	http://brighamrad.harvard.edu/education/online/tcd/tcd.html	Collection of online cases designed for medical students
Teams and Streams	http://surf.to/teamstreams/	Inquiry-based laboratories
Workshop Biology	http://yucca.uoregon.edu/wb/index.html	Course materials to improve biology teaching for non-biology majors
The Active Learning Site	http://www.active-learning-site.com/bib1.htm	Bibliography list of articles about active learning
Just-in-time-Teaching	http://webphysics.iupui.edu/jitt/jitt.html	Student-centred activities
Association of Biological Laboratory Education (ABLE)	http://www.zoo.utoronto.ca/able/	Course-tested investigative laboratories
National Center for Case Study Teaching in Science	http://ublib.buffalo.edu/libraries/projects/cases/case.html	Innovative materials for case teaching in science
Biology Education Online (BEoN)	http://www.accessexcellence.org/LC/BEOn/	Peer-reviewed e-journal for teaching K-16 life sciences
BioScienceEdNetwork (BEN)	http://www.biosciednet.org	Reviewed resources covering 76 biological-sciences topics
Multimedia Educational Resource for Teaching (MERLOT)	http://www.merlot.org	Open resource designed for faculty and students of higher education
National Science Digital Library	http://nsdl.org/	Online library of resources for science, technology, engineering and mathematics education and research

* These resources and classroom activities are meant to supplement the traditional lecture. Education websites are also provided where educators can access resources and links to online materials. Faculty might find some of the resources useful for their transition to student-centred learning.

requirements for deep conceptual learning. The essence of JiTT is that students respond electronically to carefully constructed Web-based assignments that are due shortly before class, and the instructor reads the students' submissions 'just in time' to adjust the classroom lesson to suit the students' needs. To learn how JiTT is used to teach cell biology at present, see the outstanding article by Marrs and Novak[38].

Innovative teaching is also facilitated by multimedia productions[39]. Multimedia-production software allows teachers to combine text, images, video, sound and animation for a cohesive learning experience. The multimedia learning experience encourages exploration, discovery and inquiry into complex processes, whilst accommodating a wide range of learning styles[40–43]. For example, computer animation is an educational tool that fosters long-term learning by allowing students to 'see' enzymes in three dimensions, and to see how a replication fork moves in ways that sketches on the blackboard or two-dimensional pictures that jump between steps simply cannot replicate[44,45]. The value of animations might be associated with the dual-coding theory[46,47], which suggests that long-term memory retention is facilitated by a

Table 2 | **Education homepages and publications of professional societies***

Professional society	URL	Comments
American Association for the Advancement of Science	http://www.aaas.org/education/	Education homepage: programmes that focus on curriculums, resources, public education, scientific-career advancement and workforce training
American Chemical Society	http://www.chemistry.org/portal/a/c/s/1/educatorsandstudents.html	Education homepage: products and services for all levels of education (K-12, undergraduate, graduate and continuing education)
	http://jchemed.chem.wisc.edu/	*Journal of Chemistry Education*: teaching methodologies and course organization in chemistry
American Physical Society	http://www.aps.org/educ/	Education homepage: programmes that focus on all areas of physics education
American Physiological Society	http://www.the-aps.org/education/	Education homepage: programmes, fellowships, and teaching resources for science education at all levels (K-12, undergraduate and graduate).
	http://www.the-aps.org/publications/advan/	*Advances in Physiology Education*: journal dedicated to the improvement of teaching and learning physiology
American Society for Biochemistry and Molecular Biology	http://www.bambed.org/	*Biochemistry and Molecular Biology Education*: journal promoting quality biochemistry, molecular-biology, microbiology and cell-biology education
American Society for Cell Biology	http://www.ascb.org/committees/edcom/index.html	Committee concerned with cell-biology education at all levels
	http://www.cellbioed.org	*Cell Biology Education*: journal carrying peer-reviewed articles on life-science education at the K-12, outreach, undergraduate and graduate levels
American Society for Microbiology	http://www.asm.org/Education/index.asp?bid=369	Education homepage: promotes access, excellence, professional development and advancement in microbiology education
	http://www.asm.org/Publications/index.asp?bid=1364	*Microbiology Education*: journal carrying articles driven by outcomes-based research in student learning; *Focus on Microbiology Education (FOME) Newsmagazine*: advice for improving teaching and learning in the microbiological sciences
Association of College and University Biology Educators	http://www.acube.org	Education homepage: undergraduate and graduate biology education
	http://acube.org/publications.html	*Bioscene* journal: *Journal of College Biology Teaching*: focus on the teaching of undergraduate biology
Ecological Society of America	http://www.esa.org/education/	Education homepage: promoting quality ecology education at all levels (K-12, undergraduate and graduate)
Faculty for Undergraduate Neuroscience	http://www.funjournal.org/	*Journal of Undergraduate Neuroscience Education:* peer-reviewed reports of innovations in undergraduate neuroscience education including laboratory exercises, new media, curricular considerations and teaching methods
National Association of Biology Teachers	http://www.nabt.org	Education homepage and journal, *American Biology Teacher*: biology and life-science education for all students
National Association for Research in Science Teaching	http://www.educ.sfu.ca/narstsite/	*Journal of Research in Science Teaching*: reports for science-education researchers and practitioners on science teaching and learning, and education policy
National Science Teachers Association	http://www.nsta.org/college	*Journal of College Science Teaching*: ideas and experiences with undergraduate, interdisciplinary science courses
Teaching Professor	http://www.teachingprofessor.com	Newsletter: discusses latest research for effective teaching in college classrooms

*This table provides a listing of education homepages and publications of professional societies for educators at all levels of teaching (K-12, undergraduate, graduate, continuing education and practitioners) across many scientific disciplines.

combination of verbal and visual clues. The World Wide Web Instructional Committee at North Dakota State University developed the Virtual Cell (VCell) animation project[48] to create high-quality animations of selected molecular and cellular processes to support student learning. Additionally, Web sites that contain animations of cell-biological processes are detailed in an article by Stith[39]. Finally, each issue of The American Society for Cell Biology publication *Cell Biology Education* (TABLE 2) has reviews of videos and animation resources.

Teaching and learning resources

With the explosive development of the Internet and other technologies, teaching resources have seen a revolution that rivals the invention of the printing press in the fifteenth century[22]. For example, several educational journals that are sponsored by national scientific societies are dedicated to the improvement of teaching and learning. The articles typically address innovative teaching approaches and pedagogically sound teaching materials (see TABLE 2 for a list of professional societies and science-education journals). Educators are encouraged to write about and share, through publication, their strategies for teaching, learning and assessment. The manuscripts should contain explicit pedagogical justification that arises from learning theory or published research findings, and include the educational content for which the teaching strategy was used. In addition, the Internet provides an enormous array of teaching materials (TABLE 1). For example, Blystone and MacAlpine described an approach for using the Internet to develop biology laboratory exercises[49]. Furthermore, Campbell[50] developed a genomics course and a consortium for hands-on genomics teaching, which uses many of the public-domain databases, research tools and journals for teaching genomics, proteomics and informatics. These resources are intended for individuals who do not want to simply read the recipe but prefer to make the meal.

Educators' concerns

Many educators might have concerns because the necessary support and recognition for innovative teaching are lacking from colleagues and administrators. In many universities, promotion and tenure is based on research productivity rather than teaching expertise and innovation. Furthermore, some faculty members generally believe that the traditional methods of teaching have 'worked' for decades, so why should they devote precious time, which could be used for research or other more valued activities, on developing and using innovative teaching methods without having the documentation that the new approach works?

To address these concerns, first, the faculty must recognize that teaching is the unique and central mission of institutions of higher learning. To quote an eloquent book on higher education[51], "Teaching is not just an addendum to research. It is not an obligation that comes along with the job. Teaching is the continuation of a culture, the continuity of what we have done and known, the substance on our intellectual life…What kills a subject is the lack of good teaching, the inability to communicate whatever once gave it vitality." Therefore, we must approach teaching with the same seriousness and effort we devote to research[52]. As we interact with several-hundred students per year, nothing we will ever do in the research laboratory is as likely to impact on so many lives. Second, the faculty must work together to put pressure on the administration to recognize the importance of the teaching mission, to provide the support to achieve the mission and to grant rewards for successful completion of this mission. Specifically, the faculty must force the administration to convert from putting a primary emphasis on research dollars to also consider teaching effectiveness and innovation as important factors in its promotion and tenure policies. Specifically, policies regarding promotion and tenure must be based on what is best for student learning, and not solely on economic considerations.

Finally, at times I have wondered what would happen if we provided students with a list of all the curricular objectives for the first two years, all the textbooks and hand-out materials, and asked them to come back in two years time and take the examinations[53]. Would their scores be significantly different? I really do not know, but I have my doubts. It seems as if students do well despite our efforts, not because of our efforts. So, the traditional methods might not have worked after all.

Conclusion

Traditionally, students experience cell-biology teaching as the memorization of facts without any relevance to the careers in which they wish to spend their working lives[14,54]. Memorization occurs when the learner makes little or no effort to relate new information to existing knowledge or novel situations. Or, a definition I prefer, memorization is what we resort to when what we are learning makes no sense. However, cell-biology teaching, when focused on conceptual and integrated science learning, leads to meaningful learning[8]. Meaningful learning[4,8,55] occurs when the learner interprets new information by relating it to and incorporating it with existing knowledge, and then applies the new information to solve novel problems. Incorporating PBL, case studies and concept maps as well as other specific strategies that have been outlined in this article can lead to meaningful learning. So, we would be wise to teach the way we learn — hands on and with application, collaboration and synthesis. Remember the words of the British mathematician, logician, and philosopher Alfred North Whitehead who said, "So far as the mere imparting of information is concerned, no university has had any justification for existence since the popularization of printing in the fifteenth century."[56]

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DEVELOPMENTAL CELL BIOLOGY — TIMELINE

Spemann's organizer and self-regulation in amphibian embryos

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Abstract | In 1924, Spemann and Mangold demonstrated the induction of Siamese twins in transplantation experiments with salamander eggs. Recent work in amphibian embryos has followed their lead and uncovered that cells in signalling centres that are located at the dorsal and ventral poles of the gastrula embryo communicate with each other through a network of secreted growth-factor antagonists, a protease that degrades them, a protease inhibitor and bone-morphogenic-protein signals.

When an embryo is cut in half, it can self-regulate to regenerate the missing part (FIG. 1). The field of experimental embryology originated in 1883 when Roux killed one of two cells in a frog embryo with a hot needle and found that the rest gave rise to only part of the embryo, usually a right or a left half[1] (TIMELINE). However, in 1891, Driesch separated the two first blastomeres of the sea urchin embryo and found that each was able to self-regulate and give rise to complete, although smaller, embryos[1]. In 1895, Thomas Hunt Morgan — who before becoming a geneticist was an experimental embryologist — repeated Roux's experiment and showed that if one of the two blastomeres is gently pipetted out of a frog embryo (instead of killing it and leaving it in place), amphibians too could self-regulate and give rise to a complete embryo from half an egg[2].

In 1903, Hans Spemann used a baby-hair loop (from his own daughter) to subdivide the cleaving amphibian (salamander) egg into two halves. If the half-embryo contained part of the future blastopore dorsal lip (the region where involution of the mesoderm starts), it formed a perfectly well-proportioned tadpole[1] (FIG. 1). In 1918, the great American embryologist Ross Harrison carried out another remarkable experiment: if the forelimb field in the mesoderm of a salamander embryo was cut in half and transplanted into the flank of a host embryo, each half could induce the formation of a complete limb, not just half a limb[3]. The part of the embryo where this phenomenon takes place was called the 'self-differentiating morphogenetic field'.

Self-regulation, as defined by these early experimental embryologists, is one of the most interesting and mysterious properties of embryos. What are the molecular mechanisms that explain the intrinsic tendency of the embryo to regulate towards the whole? Here, I recount the story of the birth, decline and revival of amphibian experimental embryology, and how recent studies have uncovered a molecular pathway of interacting extracellular proteins that explains how embryonic self-regulation works. This short review focuses on the advances made in amphibians, although great strides have also been made in other model systems, such as the fruitfly (*Drosophila melanogaster*), chick (*Gallus gallus*) and zebrafish (*Danio rerio*), as detailed elsewhere[4]. Rather than providing a comprehensive overview of the entire field of early development, this short timeline presents a personal account of the status of experimental embryology, a field that a century ago was at the very front of biological research.

Gene-fishing in Spemann's organizer

The starting point for understanding self-regulation was provided by the most famous experiment in embryology, the Spemann–Mangold organizer (hereafter referred to as Spemann's organizer) graft with salamander eggs[5] (BOX 1). This experiment established the present view that animal development results from a succession of cell–cell inductions in which groups of cells, or organizing centres, signal the differentiation of their neighbours. The dorsal-lip graft induced neighbouring cells to adopt the normal pattern of tissue types, so that a Siamese twin was formed. In 1988, a memoir recounting the heyday of experimental embryology in the Spemann laboratory was published by Viktor Hamburger[6]. At least in my case, the modern revival of studies into Spemann's organizer can be traced to this little book, which retold the excitement of discovering the inductive powers of the organizer. Hamburger was 88 years old at the time — clearly, it is never too late to impact the scientific thinking of others.

In our own laboratory, studies on Spemann's organizer were approached by cloning its molecular components: cDNA libraries were generated from manually