AMAZING PAPERS IN NEUROSCIENCE
Three Scientific Controversies to Engage Students in Reading Primary Literature

DJ Brasier
Department of Biological Sciences, Carnegie Mellon University, Pittsburgh, PA 15213.

In this review, three sets of papers are presented. Each of the sets presents a historical or active controversy in neuroscience ranging from cell biology and cell signaling, to developmental neuroscience, to cognitive neuroscience. The first set captures a historical controversy about whether the beta/gamma subunit of G-proteins can be active in opening ion channels. The second set represents a modern instantiation of the oldest debate in neuroscience: are our minds and brains the product of innate factors or environmental influences. This debate plays out in a series of papers on the development of the visual system. The third set contrasts the view that the hippocampus and surrounding structures primarily function to represent our location in space (a position for which the 2014 Nobel Prize in Physiology or Medicine was awarded to three investigators) with the perspective that the hippocampus is a general-purpose structure for declarative memories, spatial or non-spatial. The first and third controversies feature publications of virtually identical experiments that show opposing results. All three controversies are discussed in regards to the individual scientists who did the experiments and debated directly with each other. The first (beta/gamma subunits) emphasizes the value of reproducibility in scientific research, the second (visual cortex development) emphasizes the value of new techniques and updating scientific models, and the third (hippocampus) exposes students to an ongoing, albeit under discussed, debate.

Key words: pedagogy; controversy; science process; interpretation of data; debate; GPCR; nature; nurture; synapses; place cells

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The story of science is not merely a story of facts and theories; it is a story of the lives and passions of scientists. It has been demonstrated that focusing some class time and assignments on humanizing scientists can improve students' perceptions of science and of themselves as potential future scientists, especially for students in underrepresented groups (Schinske et al., 2016). Another way to humanize scientists is to expose the controversies that occur in science; this allows students to see the passion scientists have for their work and the emotion we can bring as scientists. Additionally, while this reveals scientists to not always be completely dispassionate in our pursuit of knowledge, the criticisms scientists make of each others' work ultimately serves an invaluable purpose: encouraging each other to be more rigorous in our experiments and in the interpretation of our data (Osborne, 2010).

When presenting these controversies, I discuss them as competing theories. This provides me with an opportunity to discuss with students what a well-established scientific theory (such as climate change, evolution, the atomic theory, or the theory of quantum electrodynamics) is, and how theories often begin as hypotheses with one or two experiments in support of them (for more on this, instructors can refer students to watch Anticole, 2015). We then further discuss how multiple lines of evidence taken together can cause what was once a hypothesis to become a working theory. Occasionally, theories are refined: for example, in the first controversy discussed here (G-protein signaling), the dominant theory had been that only the alpha subunit participates in intracellular signaling; new evidence (met initially with skepticism, but ultimately widely accepted) led to a refined theory with more diverse mechanisms of intracellular signaling. Sometimes, there are two competing theories for how a biological process or brain area functions: each of which has a body of many pieces of evidence to support it. A historical example of this in neuroscience is the decades during which there were two competing theories for how neurons communicate: electrically or chemically (Eccles, 1982). At any time, the competing theories have their own body of data that they explain and may have some data for which they have incomplete explanations. For example, during the 1980s and 1990s, the presynaptic theory of LTP easily explained changes in synaptic reliability but struggled to explain changes in NMDA-mediated synaptic currents; while the converse was true for the postsynaptic theory of LTP (reviewed by Brasier in Harrington et al., 2015).

The second and third controversies presented here fall into the latter category: current competing theories. In the second controversy I present here (ocular dominance columns), the "nature" theory easily explains the observations of Crowley and Katz (1999 & 2000), but struggles to explain the observations of LeVay et al. (1978) as well as the work of von Melchner et al., (2000; also reviewed by Olivo in Harrington, et al., 2015); the converse is true of the "nurture" theory. In the third controversy I present here (function of the hippocampus), the "declarative memory" theory easily explains why patients with hippocampal damage can navigate familiar neighborhoods well but struggle to form a variety of new declarative memories (Insausti et al., 2013), but struggles to explain why rodent recordings in the hippocampus reveal unambiguous place cells (Moser et al., 2008).

During periods in which there are competing theories, each with their own body of supporting evidence and evidence that is more difficult for them to explain, there are at least two ways that the scientific debate proceeds (reviewed more in Osborne, 2010). First, scientists can

challenge the experimental validity of their competitors' approaches. For example, Birnbaumer and Brown (1987) pointed out several possible sources of experimental error in the original work of Logothetis et al. (1987); this criticism, while not always dispassionate or even civil, does prompt researchers to develop more rigorously controlled experiments (Osborne, 2010). Second, scientists can accept each others' data, but can question whether there is a way to explain the "other side's" data within the context of their own theory. For example, Eichenbaum (2000) argues that place cells are observed in rats' brains when they are exploring an environment precisely because the rats are learning the environment and remembering locations in it and that other kinds of activity (e.g., "odor cells") can be identified in the hippocampus of rats when they are learning or remembering odors, thus making place cells a subset of memory-encoding functions. Conversely, Burgess et al. (2002) argue that contextualization of experiences is critical for formation of declarative memory, and the hippocampus' primary function is to contextualize experience, with amnesia being a secondary consequence of the loss of this capacity. I discuss with students that when two competing theories have different explanations for the same data sets, the challenge scientists face does not end with explaining each others' data in the context of their own theory, but rather with finding experiments that make different empirical predictions under the two theories. I frequently remind my students that a clever idea can start a scientific controversy, but clear predictions and data that unambiguously support one theory over another is what can finally end a controversy.

As a final note, during these periods of debate, each side would like to hold up their own idea as a theory and call the opposing idea a hypothesis. In my discussion of these ideas (in my classes and in this article), I refer to them as competing theories because they each have a body of work that supports them. Sometimes, what was once a competing theory or even a widely accepted theory begins to fail to explain large numbers of results and becomes a discredited or outdated (or just plain wrong) theory as with phlogiston (Kuhn, 1962) or the idea that the beta/gamma subunits of G-proteins cannot act as intracellular signals (see the first controversy below). Sometimes we find ourselves in an exciting period of scientific controversy where some questions are settled [neurons mostly communicate via chemical synapses, see Eccles, 1982)], and others are still actively being debated (see the second and third controversy below). Many times during the course of teaching this material, I remind my students that during times of scientific controversy, while disagreements can reveal the passion scientists have for their work, the act of disagreement does not challenge the edifice of established knowledge in science, but instead serves to strengthen it (Osborne, 2010).

Here I review three sets of scientific papers that I have used in freshman seminars [see Willard and Brasier (2014) for full description of seminar style and assessments used] to teach core concepts in neuroscience through the perspective of historical and active scientific controversies. The use of primary literature as a pedagogical tool, even in introductory courses, has been reviewed elsewhere (Hoskins et al., 2011; Harrington et al., 2015; Hartman et al., 2017).

Is the beta/gamma subunit of G-protein an active signaling molecule?

Topics: cell biology; synaptic transmission; ion channels; GPCRs

Key References: Logothetis et al., 1987; Birnbaumer and Brown, 1987; Yatani et al., 1988; Reuveny et al., 1994; Wickman et al., 1994.

Description: In the late '80s and early '90s, the field of cell-signaling was gripped by a debate about the role of the beta/gamma subunits of G-proteins in signaling. The traditional view had been that after a ligand binds to G-protein coupled receptors (GPCRs), the alpha subunit exchanges GDP for fresh GTP and actively signals to downstream effectors, while the beta/gamma subunits function as additional regulatory controls for the alpha subunit. (This model continues to be the only model presented in most introductory biology textbooks today; see chapter 11 in Freeman et al., 2017, for example.) Once students have learned about G-proteins and G-protein coupled receptors (GPCRs), the module begins with the presentation of Logothetis et al. (1987), which first demonstrated evidence that binding of acetylcholine to muscarinic acetylcholine receptors can cause the opening of K^+ channels via the beta/gamma, rather than the alpha, subunit of G-proteins. Students then read the scathing response by Birnbaumer and Brown (1987) in which several concerns about the study by Logothetis et al. (1987) are raised. Even in a large introductory course with no prerequisites, students easily pick up on the fierce tone of this response with comments including "Why didn't they just discuss peacefully?" and "The 'rebuttal' just sounds like a condescending rant." Among the criticisms raised by Birnbaumer and Brown (1987) is the possibility that the procedure for purification of beta/gamma subunits could have been imperfect. This serves as an ideal jumping-off point for a discussion of recombinant DNA technology as a source for proteins that can often be more free from contaminants than purifying the protein from a native source (see chapter 20 in Freeman et al., 2017). Following up on this discussion, students read one study that presents data using recombinant proteins indicating that the alpha subunit is the active signal that activates K^+ channels (Yatani et al., 1988) and two studies from different labs that use recombinant proteins, for both the G proteins and channel, to demonstrate that the beta/gamma, and not the alpha, subunit is the active signal (Wickman et al., 1994; Reuveny et al., 1994). The latter paper was a landmark in resolving the debate and developing the modern consensus that the beta/gamma subunit is the active signal in this process in large part because it was done in a separate lab that was not one of the two main labs (Clapham and Birnbaumer) who were fueling the debate. These papers can serve as a launch point for discussing the value of reproducibility in scientific research. For a full discussion of this lesson and sample questions to ask, see Supplemental Materials.

Value: When presented at any level, these studies can teach students about the complexity of biological processes and give them insight into levels of detail of G-protein function that go beyond traditional introductory textbook material. Furthermore, in working through data, students develop not only a nuanced appreciation of the science process but also a better retention of science facts (Hoskins et al., 2011; Willard and Brasier, 2014; Hartman et al., 2017). Additionally, this work is a perfect starting point for discussions about the uses and the value of recombinant DNA technology in research as well as in medicine. It can also prompt a discussion on how each technique has limitations that are often overlooked or minimized. Also, it is interesting and useful to discuss how science self-corrects when multiple labs address the same question. Finally, in addition to providing students a compelling view of scientists as passionate individuals deeply invested in their work, this also can serve as a starting point for discussions about reproducibility in science and the dramatic effects of subconscious bias on the experimental outcomes even in well-established experimental approaches.

Audience: This work can be effectively presented to students in introductory biology or neuroscience courses, which is where I have experience teaching it (See Supplemental Materials). It can also be taught to advanced undergraduates and has been taught effectively to graduate students (which is where I first encountered it). Depending on the sophistication of the students, the instructor may assign more or less reading for students to do on their own. For introductory students, typically only abstracts are assigned before class and data figures are walked through during class time. This unit should be taught immediately after a textbook introduction to cell signaling and GPCRs. Ideally, students should have worked through a classical G-protein model. The ideal model is adrenaline because it speeds up heart rate (as opposed to acetylcholine which slows it down). Students should have a basic understanding of the following topics: ligand binding, receptor activation and GTP exchange in the alpha subunit, dissociation from beta/gamma subunits, alpha subunit binding to adenylyl cyclase, cAMP production, protein kinase A activation, signal amplification, and GTP hydrolysis and signal termination. Students should also understand the basics of recombinant DNA technology. Ideally, students will also understand the basics of active transport and Na^+/K^+ pumps, electrochemical gradients, and ion channels (minimally, these should not be completely foreign concepts). Additionally, students should understand membrane excitability well enough to be able to describe that as positive potassium ions leave the cell, the cell becomes less excitable.

Do ocular dominance columns initially develop because of an innate genetic pathway or because of visual experience?

Topics: vision; neural plasticity; nature vs. nurture; cortical wiring

Key References: LeVay et al., 1978; Stryker and Harris, 1986; Crowley and Katz, 2000; Katz and Crowley, 2002.

Description: This module can stand on its own or be paired with an additional module on the relative contributions of genetic vs. environmental factors in other kinds of neural plasticity (Flinn, 2016). Students begin by discussing experiments which visualize ocular dominance patches using transneuronal injection of radioactive proline in one eye over the first two weeks of life. In early development, ocular dominance patches emerge over the first 2-4 weeks of life (LeVay et al., 1978) which happens to be the same age at which the critical period for monocular deprivation peaks (Katz and Crowley, 2002). This correlative evidence suggests that there is a competitive process of "sorting out" each eye, and that altered activity during this period is why that time window is the classical critical period. The instructor can then ask students the following: "Based on this observation, what would you predict would happen if you blocked activity during this time window with tetrodotoxin?" Class discussions should come to the conclusion that this would result in a failure to develop ocular dominance patches. Then the class can read Stryker and Harris (1986) in which exactly that experiment was done and exactly that result was obtained, confirming the hypothesis. However, in the early 21st century, this theory began to be questioned, initially by some of the last work Larry Katz did before he passed away from cancer. Together with Justin Crowley, Katz observed that injection of another anterograde tracer into the thalamus in very young animals gave rise to ocular dominance patches that could be visualized in primary visual cortex (Crowley and Katz, 2000; Katz and Crowley, 2002); this effect could even be observed in animals who had no eyes and therefore no visual activity from birth (Crowley and Katz, 1999). These results indicate the opposite theory: that thalamocortical synapses have already segregated into ocular dominance zones prior to experience (Katz and Crowley, 2002). The early work by Wiesel and Hubel (1963) is accounted for as a revision of the initial pattern laid down before sensory experience. The reason for the results observed by LeVay et al. (1978) ends up being more technical: early in development retinofugal synapses are poorly segregated and immature, allowing radioactive proline to spill out into neighboring areas in the lateral geniculate nucleus of the thalamus, causing the possibility for diffuse signal in primary visual cortex even if the thalamocortical projection is already segregated prior to experience.

Value: This can lead into a discussion about the contingent nature of scientific theories and the value of improved tools to trace neural circuits. An important additional point I make when discussing this is that what settles a scientific controversy is not merely ideas, but data (Osborne, 2010). Additionally, in contrast to the GPCR controversy described above and to the hippocampus controversy described below, the model proposed by Crowley and Katz (2002) provides a full account of the earlier data. This allows students to experience some cognitive dissonance as new data apparently conflict with old interpretations, but then the updated methodology allows a satisfying conclusion which accounts for all data. For a more detailed illustration of how this can be a useful pedagogical tool, see Hoskins (2008). Depending on the course and the instructional goals, many instructors will want to emphasize that this is one chapter in

the perennial nature vs. nurture debate (see Flinn, 2016).

Audience: Prior to beginning this module, students should have a basic understanding of transneuronal tracing of ocular dominance patches and also functional recording of ocular dominance physiology. That material can be introduced via textbook (see chapters 10 and 23 in Bear et al., 2016) or as another literature-based discussion that can lead into this one (see Olivo: "Structure and function of the mammalian visual cortex" in Harrington et al., 2015). This module can be taught in any neuroscience course that has such a background, and I have successfully taught it in large (80+ student), introductory-level (freshman and non-majors) courses. If the students are more advanced and have a basic background in immuno staining techniques, a more recent genetic correlate of ocular dominance in early development can be presented (Tomita et al., 2013). For some more recent evidence on the side of experience, students can move on to discuss the work of Mriganka Sur's lab in the early 21st century with rewired ferrets (von Melchner et al., 2000; Sharma et al., 2000; discussed by Harrington in "Seeing with a rewired auditory cortex" in Harrington et al., 2015). Additionally, advanced students may also benefit from further discussion of spontaneous activity in the retina that proponents of the idea that neural activity, rather than genetics, instructs circuit formation have studied over the last decade (reviewed in Feller, 2009).

Is the hippocampus a structure for spatial awareness or for declarative memory formation?

Topics: Memory; navigation; neural plasticity; cognitive neuroscience

Key References: Milner et al., 1998; Eichenbaum, 2000; Moser et al., 2008; Milner et al., 1968; Morris et al., 1982; Burton et al., 2000; Alvarez et al. 2001; Shrager et al., 2008.

Description: Popular press references to the hippocampus abound, calling it the "brain's GPS" (Gallagher, 2014), and also the area "responsible for new memories" (Lucas, 2015), and sometimes just an area devoted to "spatial memory" (Span, 2011). However, these vague descriptions actually hide a debate that has been ongoing for nearly 35 years. On the one hand, some argue that the hippocampus is primarily an area that is devoted to spatial awareness and the amnesic effects of its loss comes from an absence of orientation (Miller et al., 2013); on the other hand, some maintain that the hippocampus' primary job is to help consolidate declarative memories and the reason place cells show up is because of the memories an animal is forming or accessing as it explores an environment (Jeneson and Squire, 2011). An overview of the controversy published by Eichenbaum (2000) is a useful guide for students and instructors. When I teach this, I begin with a description of patient H.M., the most influential patient in 20th century neuroscience. The landmark paper studying H.M. by Milner et al. (1968) simultaneously established the two major distinctions that my students already know when arriving in college freshman classes. 1. that memory can be divided into short- and long-term; and 2. that memory can be divided into declarative and non-declarative forms (see also chapter 24 in Bear et al., 2016). The work done on H.M. and other human patients (Insausti et al., 2013) led to the model that the hippocampus is a key feature in the formation of all types of new declarative memory. However, with the discovery of place cells in the late 20th century, many neurophysiologists began to reconsider the primary role of the hippocampus in spatial navigation (O'Keefe and Dostrovsky, 1971; Moser et al., 2008). The crux of this controversy lies in interpretation of the work by Morris et al. (1982) – work which established the now well-used "Morris water maze" which demonstrated that rats with hippocampal lesions could not learn to find a submerged platform. Morris et al. (1982) interpreted this in light of the discovery of place cells (O'Keefe and Dostrovsky, 1971) as being a deficit of navigation, while others believed that the animals know perfectly well how to navigate, but could not remember the location of the platform (Jeneson and Squire, 2011). The question, then, is how to interpret the following three pieces of data:

#1) Animals with hippocampal damage struggle to find their way to a hidden platform that they have recently found (Morris et al., 1982).

#2) Humans with hippocampal damage struggle to form new declarative memories (e.g., Insausti et al., 2013).

#3) Animals exploring an environment show activity in CA1 neurons of the hippocampus in specific locations in space (reviewed in Moser et al., 2008).

Those who believe the hippocampus is primarily a navigation structure account for #1 because of a failure to navigate (Morris et al., 1982), #2 because the patients with hippocampal damage cannot form new memories when there is no spatial context (Miller et al., 2013), and #3 is the cornerstone observation of their theory of hippocampal function (Moser et al., 2008). Conversely, proponents of the idea that the hippocampus is a declarative memory structure account for #1 because of a failure to remember the location of the platform (Jeneson and Squire, 2011), #2 is the cornerstone of their theory of hippocampal function (Jeneson and Squire, 2011), and #3 is thought to be because when a rodent is exploring an environment the only thing it can be learning or recalling are locations visited (Broadbent et al., 2007). After introducing the 3 core pieces of evidence described above, students can brainstorm about how to resolve this controversy. Ultimately, the challenge is that each theory accounts for the data available: most notably each theory has a separate explanation for data #1. Through class discussion, students should arrive at the conclusion that what is needed is an experiment for which the two theories make different predictions. After my students discuss ideas, often two main flavors of experiment come up: 1. devise an experiment that requires the ability to remember some fact that is independent of any spatial features; and 2. devise an experiment that requires the ability to navigate without requiring a subject to remember something beyond short-term memory. Indeed, in the first two years of the 21st century, a pair of publications attempted to do the former. Briefly, rats were divided into two groups: control and rats with damage to the hippocampus and subiculum (the surrounding area). Animals were trained on an odor recognition and memory task. The 'navigation' theory of hippocampal function would predict no difference between groups, whereas the 'memory' theory of hippocampal function would predict hippocampal damage to

impair this non-spatial memory task. In one study on which the discoverer of place cells, O'Keefe, was senior author, no difference was found (Burton et al., 2000), despite multiple variants on this paradigm; in another study published the following year, another group found a significant deficit among the animals with hippocampal damage (Alvarez et al., 2001). The second flavor of experiment (testing the ability to navigate without taxing memory) has been tested most by Larry Squire, a proponent of the theory that the hippocampus is a declarative memory structure (Jeneson and Squire, 2011). In these experiments, Squire and colleagues have consistently found that patients with damage to their hippocampus perform comparably to controls in their ability to navigate, provided that the navigation task does not require them to remember something new beyond the capacity of their working memory (Shrager et al., 2008; Urgolites et al., 2013). Indeed, one experiment done by Teng and Squire (1999) demonstrates that a patient with severe damage to the hippocampus and surrounding areas has the ability to navigate very well in his childhood home, an experiment that was specifically designed to show that as long as new facts are not being learned, the hippocampus has no role in navigation ability. However, in other studies it has been shown that hippocampus-dependent recollection in humans does have a distinctly spatial component (Miller et al., 2013) as well as evidence for spatial processing in human imaging (Jacobs et al., 2013). In working through this controversy with students, I start with the data from H.M. (Milner et al., 1968), the discovery of place cells (O'Keefe and Dostrovsky, 1971), and the Morris water maze (Morris et al., 1982). I then move on to brainstorm with the class about possible experiments to distinguish between the competing theories, letting the students' ideas guide my choice for additional papers to present among those referenced. Once the key references have been worked through as a class, students are assigned to review the data on either side of the debate, propose a model for hippocampal function, and propose a new experiment (see Supplemental Materials).

Value: After introducing the three core pieces of evidence just described students learn collaboratively about what makes a good experiment that cleanly distinguishes two theories. In seeing that two theories can sometimes account for one set of data, what is needed is not just a good idea, but an experiment that makes distinct predictions for the two theories. Although a large number of research groups have attempted this and the results either directly disagree (Burton et al., 2000; Alvarez et al., 2001) or lead to opposite conclusions by studying different populations (e.g., Shrager et al., 2008 and Miller et al., 2013), the act of deciding what makes for a useful vs. not useful experiment to distinguish theories is valuable to students. Although the two sides of the controversy have many different experiments, there was one attempt made by researchers on both sides of the debate to do the same experiment in each lab. In particular, the experiment was to train rats on a declarative memory task that did not require spatial awareness: to remember odors independent of where the animals experienced those odors. As with the G-protein controversy described above, the two different groups reached contradictory results: the lab that previously believed the hippocampus to be a spatial navigation structure observed no deficiency in the ability of rats with hippocampal lesions to remember this non-spatial information (Burton et al., 2000), while the lab that previously believed that the hippocampus was a general-purpose declarative memory structure confirmed their prediction that rats with hippocampal lesions cannot remember this non-spatial information (Alvarez et al., 2001). However, unlike the G-protein controversy, no consensus has been reached about which of those two results is most reproducible. Thus, there is no widely-accepted consensus – although both the awarding of the Nobel Prize to O'Keefe, Moser, and Moser in 2014 (Gallagher, 2014) and the slight outnumbering of PubMed hits for "hippocampus spatial navigation" over "hippocampus declarative memory" (1020 vs. 747, PubMed, May 20, 2017), indicate that more researchers may favor the former; furthermore, the navigation theory has generated other lines of research including grid cells (Fyhn et al., 2004; Moser et al., 2008). In either case, students are able to use this as a starting point for exploring their own ideas for designing new experiments to resolve this controversy (see Supplemental Materials).

Audience: Because of the collaborative way in which I typically teach this material and explore possible experiments to resolve the controversy, I have had the most success teaching this to small seminar-style classes (see Willard and Brasier, 2014). With instructor guidance through the experimental methods, the techniques are not beyond the capacity of introductory-level students with minimal science background and I have been successful teaching it to first year students (Willard and Brasier, 2014). More advanced students will need less guidance through the techniques in the research articles. As a cognitive neuroscience controversy in which most of the experimental results discussed are either behavioral or single unit recordings, this controversy requires the least understanding of challenging biochemistry or neuroanatomy techniques of the three I have discussed in this review.

As an extension to this activity, students can also look into the neuroanatomy of patient H.M. Since his death, some researchers have begun to vigorously debate the extent of lesion in his brain and who has the rights to study his brain (Dittrich, 2016).

Conclusion

I have presented three different controversies that instructors can adapt to teach to their students. When taught to first year students, all three (especially the first two) require some background work to be done by the instructor on neuroscience techniques and basic neurobiology functions. However, I have had success teaching these to college freshmen with no neuroscience or biology background, provided sufficient time is spent preparing students to understand the techniques (Willard and Brasier, 2014). The first controversy (G-proteins and ion channels), provides an opportunity for students to get beyond an introductory-level understanding of the interactions between G-proteins and neurophysiology. It also provides a starting point for the discussion of reproducibility and bias in scientific investigation. The second controversy

(thalamocortical development in the visual cortex), provides a view into the age-old debate of nature vs. nurture; it motivates the value of questioning the technical limitations of experiments and can serve as a touch point for themes discussed by other undergraduate educators (see Olivo and Harrington in Harrington et al., 2015 and also Flinn 2016). The third controversy (hippocampal function) gives students an opportunity to see what makes for a useful experiment to test between competing theories; students can also use it as a launch point for designing an experiment to resolve an ongoing scientific debate. Each of these asks students to reconsider the idea of science as a series of established, received facts and instead prompts them to consider science as a progressing, but ultimately somewhat messy enterprise. In addition to giving students a more nuanced understanding of true scientific progress and debate (Osborne, 2010), each controversy also encourages students to see themselves as potential future contributors to the growth of science as a field.

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Address correspondence to: Dr. DJ Brasier, Department of Biological Sciences, Mellon Institute, 4400 Fifth Ave, Pittsburgh, PA 15213. Email: dbrasier@cmu.edu