Why Peer Discussion Improves Student Performance on In-Class Concept Questions
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plored by combining models and further empirical data, but geology offers a stronger constraint because circumstances under which sulfate can be preserved in terrestrial sedimentary records are uncommon.

Although various aspects of Neoproterozoic glaciations are intensely disputed (*25*), our results confirm a profound difference from Phanerozoic ice ages. A near-global distribution of glaciated continents during the Marinoan phase ending ~635 million years ago is supported by evidence of low palaeomagnetic latitudes (*26*). The snowball Earth model (*27*) predicts a progressive accumulation of volcanic volatiles in the atmosphere that are not removed by weathering until the rapid demise of the ice age as the ice-albedo feedback reverses. If sulfate with large negative $\Delta^{17}O$ signals derived from oxidative weathering could only be generated in a large quantity after melting of the "snowball" and exposure of continents, then the diamictites above W2 had to be deposited during final glacial retreat, a hypothesis that should prompt a re-examination of their sedimentology. The alternative "slushball" model, in which parts of the ocean area are ice-free (*28*), would also permit accumulation of sulfate from prolonged oxidative weathering in certain continental "oases" where arid but cold conditions prevailed. This study provides an effective way to study the dynamics of sedimentation and atmospheric-hydrosphere-biosphere interactions during a global glaciation and highlights the need for further stratigraphically constrained $\Delta^{17}O_{SO4}$ data on continental carbonate precipitates to ground-truth flux-balance models.

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3. Reference units for stable isotope compositions: VSMOW for sulfate $\delta^{18}O$, $\delta^{17}O$, and $\Delta^{17}O$; VPDB for carbonate $\delta^{13}C$ and $\delta^{18}O$; and Vienna Canyon Diablo Troilite for sulfate $\delta^{34}S$.
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29. H.B. and I.J.F. designed research and led the writing of the manuscript; H.B. performed CAS extraction and triple oxygen isotope measurements; I.J.F secured samples from field expeditions and conducted sedimentological, petrographic, mineralogical and elemental studies; P.M.W. conducted preliminary CAS extraction and performed $\delta^{34}S_{CAS}$ analysis; and C.S. carried out $\delta^{13}C$ and $\delta^{18}O$ analysis of host carbonates. We thank G. Halverson for discussion and Y. Peng for analytical assistance. Financial and facility supports were provided by Louisiana State University, NSF, and Chinese Academy of Science (H.B.), Natural Environment Research Council (NERC) standard grant (GR3/C511805/1) and NERC inductively coupled plasma mass spectrometry facilities (I.J.F.), and Austrian Science Funds (C.S.). The authors declare no competing financial interests.

Supporting Online Material

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Why Peer Discussion Improves Student Performance on In-Class Concept Questions

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When students answer an in-class conceptual question individually using clickers, discuss it with their neighbors, and then revote on the same question, the percentage of correct answers typically increases. This outcome could result from gains in understanding during discussion, or simply from peer influence of knowledgeable students on their neighbors. To distinguish between these alternatives in an undergraduate genetics course, we followed the above exercise with a second, similar (isomorphic) question on the same concept that students answered individually. Our results indicate that peer discussion enhances understanding, even when none of the students in a discussion group originally knows the correct answer.

In undergraduate science courses, conceptual questions that students answer using personal response systems or "clickers" are promoted as a means to increase student learning [e.g. (*1*, *2*)], often through peer instruction (PI) (*3*). Instructors using this approach break up their lectures with multiple-choice questions to test understanding of the concepts being presented. When PI is used, students are first asked to answer a question individually, and then a histogram of their responses may be displayed to the class. If there is substantial disagreement among responses, students are invited to discuss questions briefly with their neighbors and then revote before the correct answer is revealed. The instructor then displays the new histogram and explains the reasoning behind the correct answer. Most instructors report that the percentage of correct answers, as well as students' confidence in their answers, almost always increases after peer discussion (*2*–*4*).

It is generally assumed that active engagement of students during discussion with peers, some of whom know the correct answer, leads to increased conceptual understanding, resulting in improved performance after PI. However, there is an alternative explanation: that students do not in fact learn from the discussion, but simply choose the answer most strongly supported by neighbors they perceive to be knowledgeable. We sought to distinguish between these alternatives, using an additional, similar clicker question that students answered individually to test for gains in understanding. Our results indicate that peer discussion enhances understanding, even when none of the students in a discussion group originally knows the correct answer.

In an undergraduate introductory genetics course for biology majors at the University of Colorado–Boulder (additional demographic in-

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formation in table S1), we asked an average of five clicker questions per 50-min class throughout the semester and encouraged students to discuss questions with their neighbors. Students were given participation points for answering clicker questions, regardless of whether their answers were correct. Exam questions were similar to the clicker questions, so that students had an incentive to take clicker questions seriously.

Sixteen times during the semester we assessed how much students learned from peer discussion by using a paired set of similar (isomorphic) clicker questions. Isomorphic questions have different "cover stories," but require application of the same principles or concepts for solution (*5*, *6*). Sample isomorphic question pairs are shown in fig. S1. In class, students were first asked to answer one question of the pair individually (Q1). Then they were invited to discuss the question with their neighbors and revote on the same question ($Q1_{ad}$ for "Q1 after discussion"). Finally, students were asked to answer the second isomorphic question, again individually (Q2). Neither the answers to the two questions ($Q1/Q1_{ad}$ and Q2) nor the histograms of student answers were revealed until after the voting on Q2, so that there was minimal instructor or whole-course peer influence on the Q2 responses. The isomorphic questions were randomly assigned as $Q1/Q1_{ad}$ or Q2 after both questions were written. Data analysis was limited to students who answered all three questions of an isomorphic pair with a total of 350 students participating in the study (*7*) (see supporting online text).

Two results indicate that most students learned from the discussion of Q1. First, using data pooled from individual mean scores on Q1, $Q1_{ad}$, and Q2 for all 16 question pairs, the average percentage correct for Q2 was significantly higher than for Q1 and $Q1_{ad}$ (Fig. 1A and Table 1). Second, of the students who answered Q1 incorrectly and $Q1_{ad}$ correctly, 77% answered Q2 correctly (Fig. 2). This result suggests that most students who initially did not understand a concept were able to apply information they learned during the group discussion and correctly answer an isomorphic question. In contrast, almost all students who answered Q1 correctly, presumably because they understood the concept initially, did not change their votes on $Q1_{ad}$ and went on to answer Q2 correctly (Fig. 2).

In addition, students who answered both Q1 and $Q1_{ad}$ incorrectly still appeared to learn from discussions with peers and answering a second question on the same topic. Of these students, 44% answered Q2 correctly, significantly better than expected from random guessing (Fig. 2; on average, the questions in our 16 isomorphic pairs had four answer choices each). This result was unexpected because when students answered Q2, they had not been told the correct answer to $Q1/Q1_{ad}$, had not seen histograms of student responses, and had not discussed Q2 with their peers. We speculate that when this group of students discussed Q1, they were making sense of the information, but were unable to apply their new knowledge until presented with a fresh question on the same concept (Q2). There may also be a learning benefit to considering successive clicker questions on the same topic (*8*).

Although the difficulty of the question pairs varied, as judged by the percentage of correct answers on Q1 (see supporting online text), students performed significantly better on $Q1_{ad}$ and Q2 compared to Q1 for each difficulty level (Fig. 1B and Table 1). On the most difficult questions there was another significant increase between $Q1_{ad}$ and Q2, suggesting that there was an additional delayed benefit to the group discussions.

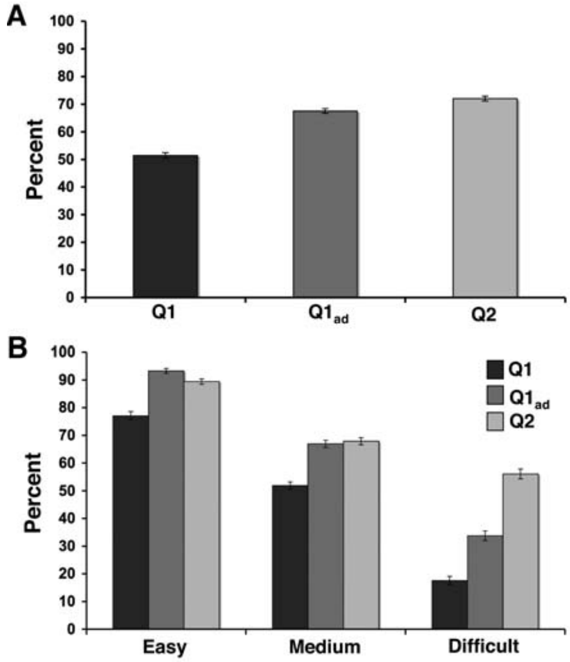

Fig. 1. The percentage of students who can correctly answer a question as individuals increases after peer discussion of a similar (isomorphic) question. Q1: One question of an isomorphic pair was voted on individually; $Q1_{ad}$: the same question was voted on again after peer discussion; Q2: the second isomorphic question was voted on individually. (**A**) Results for all 16 question pairs were averaged for each individual (n = 350 students), and the class averages of these scores are shown. (**B**) The 16 paired questions were grouped according to difficulty based on the percentage of correct answers for Q1 (five easy questions, seven medium questions, and four difficult questions), and performance results were again averaged for each individual (n = 343 students for easy, 344 for medium, and 337 for difficult) before computing the averages shown. Error bars show the SEM.

Table 1. Mean differences between Q1, $Q1_{ad}$, and Q2. The SEM is in parentheses.

Question category	$Q1_{ad}$ − Q1* (%)	Q2 − Q1* (%)	Q2 − $Q1_{ad}$* (%)
All questions	16(1)	21(1)	5(1)
Easy questions	16(1)	12(2)	−4(1)†
Medium questions	15(1)	16(2)	1(1)†
Difficult questions	16(2)	38(2)	22(2)

*Mean values are the averages of the differences between $Q1_{ad}$-Q1, Q2-Q1, and Q2-$Q1_{ad}$ for each student. †No significant improvement between these questions.

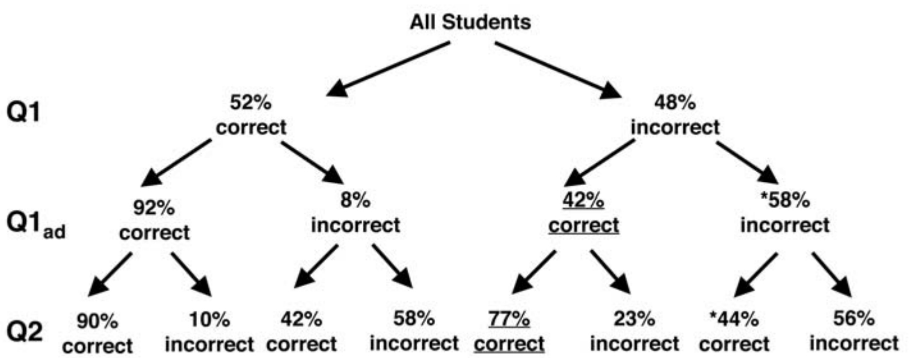

Fig. 2. Breakdown of student responses for the pool of 16 Q1, $Q1_{ad}$, and Q2 questions. Percentages of the category are connected by arrows from the preceding line. Underlined entries represent students who initially did not answer Q1 correctly but did so after group discussion; entries with an asterisk represent students who did not answer either Q1 or $Q1_{ad}$ correctly, but nevertheless were able to correctly answer the isomorphic question Q2. Of the 32 questions in our 16 question pairs, 7 had 5 answer choices, 5 had 4 choices, 3 had 3 choices, and 1 had 2 choices.

Our results suggest that peer discussion can be effective for understanding difficult concepts even when no one in the group initially knows the correct answer. In a postsemester survey (n = 98 responding), students reported an average of three participants in their peer discussion groups. If students who knew the answer to Q1 were randomly distributed throughout the classroom, then on the difficult questions (Fig. 1B), more than half of the 84 groups would have included no one who knew the correct answer to Q1 (naïve groups). Statistical analysis (see supporting online text) shows that some students who answered Q2 correctly must have come from naïve groups.

Student opinion supported the view that having someone in the group who knows the correct answer is unnecessary. On an end-of-year survey (n = 328 responding), 47% of students disagreed with the statement: "When I discuss clicker questions with my neighbors, having someone in the group who knows the correct answer is necessary in order to make the discussion productive." Representative comments from these students included the following: "Often when talking through the questions, the group can figure out the questions without originally knowing the answer, and the answer almost sticks better that way because we talked through it instead of just hearing the answer." "Discussion is productive when people do not know the answers because you explore all the options and eliminate the ones you know can't be correct."

This study supports the substantial value of student peer discussion as an effective means of active learning in a lecture class. Our findings are consistent with earlier demonstrations of social learning, including the value of discussion with peers (*9–13*). The significant increases in performance between Q1 and $Q1_{ad}$ confirm results from earlier classroom studies (*2–4*). In addition, we have presented new evidence showing that these increases result primarily from student gains in conceptual understanding rather than simply from peer influence.

Previous explanations for the value of PI have maintained the "transmissionist" view (*14*) that during discussion, students who know the right answer are explaining the correct reasoning to their less knowledgeable peers, who consequently improve their performance on the revote (*3*, *4*). Our finding that even students in naïve groups improve their performance after discussion suggests a more constructivist explanation: that these students are arriving at conceptual understanding on their own, through the process of group discussion and debate.

Some instructors who use clicker questions skip peer discussion entirely, believing that instructor explanation of the correct reasoning will be more clear and accurate than an explanation by peers, and will therefore lead to more student learning. Although our current work does not directly compare the benefits of instructor versus peer explanation, research in physics has shown that instructor explanations often fail to produce gains in conceptual understanding (*15*). We have shown that peer discussion can effectively promote such understanding. Furthermore, justifying an explanation to a fellow student and skeptically examining the explanation of a peer provide valuable opportunities for students to develop the communicative and metacognitive skills that are crucial components of disciplinary expertise.

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Supporting Online Material

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Regulation of Neuronal Survival Factor MEF2D by Chaperone-Mediated Autophagy

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Chaperone-mediated autophagy controls the degradation of selective cytosolic proteins and may protect neurons against degeneration. In a neuronal cell line, we found that chaperone-mediated autophagy regulated the activity of myocyte enhancer factor 2D (MEF2D), a transcription factor required for neuronal survival. MEF2D was observed to continuously shuttle to the cytoplasm, interact with the chaperone Hsc70, and undergo degradation. Inhibition of chaperone-mediated autophagy caused accumulation of inactive MEF2D in the cytoplasm. MEF2D levels were increased in the brains of α-synuclein transgenic mice and patients with Parkinson's disease. Wild-type α-synuclein and a Parkinson's disease–associated mutant disrupted the MEF2D-Hsc70 binding and led to neuronal death. Thus, chaperone-mediated autophagy modulates the neuronal survival machinery, and dysregulation of this pathway is associated with Parkinson's disease.

In neurodegenerative diseases, certain populations of adult neurons are gradually lost because of toxic stress. The four myocyte enhancer factor 2 (MEF2) transcription factors, MEF2A to MEF2D, have been shown to play an important role in the survival of several types of neurons, and a genetic polymorphism of the MEF2A gene has been linked to the risk of late onset of Alzheimer's disease (*1–3*). In cellular models, inhibition of MEF2s contributes to neuronal death. Enhancing MEF2 activity protects neurons from death in vitro and in the substantia nigra pars compacta in a mouse model of Parkinson's disease (PD) (*4*). Neurotoxic insults cause MEF2 degradation in part by a caspase-dependent mechanism (*5*), but how MEF2 is regulated under basal conditions without overt toxicity is unknown. Autophagy refers to the degradation of intracellular components by lysosomes. Relative to macro- and microautophagy, chaperone-mediated autophagy (CMA) selectively degrades cytosolic proteins (*6*). This process involves binding of heat shock protein Hsc70 to substrate proteins via a KFERQ-like motif and their subsequent targeting to lysosomes via the lysosomal membrane receptor Lamp2a. Dysregulation of autophagy plays a role in neurodegeneration (*7–9*). However, the direct mechanism by which CMA modulates neuronal survival or death is unclear.

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