Brain-to-Brain Synchrony and Learning Outcomes Vary by Student–Teacher Dynamics: Evidence from a Real-world Classroom Electroencephalography Study

Dana Bevilacqua[1*], Ido Davidesco[1*], Lu Wan[2], Kim Chaloner[3], Jess Rowland[1,4], Mingzhou Ding[2], David Poeppel[1,5], and Suzanne Dikker[1,6]

Abstract

■ How does the human brain support real-world learning? We used wireless electroencephalography to collect neurophysiological data from a group of 12 senior high school students and their teacher during regular biology lessons. Six scheduled classes over the course of the semester were organized such that class materials were presented using different teaching styles (videos and lectures), and students completed a multiple-choice quiz after each class to measure their retention of that lesson's content. Both students' brain-to-brain synchrony and their content retention were higher for videos than lectures across the six classes. Brain-to-brain synchrony between the teacher and students varied as a function of student engagement as well as teacher likeability: Students who reported greater social closeness to the teacher showed higher brain-to-brain synchrony with the teacher, but this was only the case for lectures—that is, when the teacher is an integral part of the content presentation. Furthermore, students' retention of the class content correlated with student–teacher closeness, but not with brain-to-brain synchrony. These findings expand on existing social neuroscience research by showing that social factors such as perceived closeness are reflected in brain-to-brain synchrony in real-world group settings and can predict cognitive outcomes such as students' academic performance. ■

INTRODUCTION

Methodological advances in neuroscience research have enabled novel approaches to investigating how the brain supports dynamic real-world social interactions. For example, researchers have begun to study the neural basis of social interactions by comparing the brain responses of multiple individuals during a variety of seminaturalistic tasks (for a review, see Hasson & Frith, 2016; Babiloni & Astolfi, 2014; Scholkmann, Holper, Wolf, & Wolf, 2013; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012). Research involving turn-taking in gestural (Schippers, Roebroeck, Renken, Nanetti, & Keysers, 2010) as well as verbal (Dikker, Silbert, Hasson, & Zevin, 2014; Stephens, Silbert, & Hasson, 2010) communication have demonstrated a relationship between brain synchrony and comprehension as well as the predictability of another person's communicative act. Further work has shown that complex audio-visual stimuli (e.g., natural movies) elicit similar brain activity among viewers and emotional responses and, crucially, vary as a function of participants' attentional engagement (Ki, Kelly, & Parra, 2016; Chang et al., 2015; Nummenmaa et al., 2012; Jääskeläinen et al., 2008; Hasson, Nir, Levy, Fuhrmann, & Malach, 2004).

Although these experiments explore the similarities and differences in neural activity across participants as they engage in similar or pseudointeractive tasks, they do not capture the dynamic nature of real-world settings. Methodological constraints limit the ways in which researchers have been able to explore the brain basis of social interactions as they occur in real world. Although providing promising results, these studies are still largely confined to the laboratory, mostly limited to dyads, and typically use neuroimaging technology with low temporal resolution (e.g., functional near-infrared spectroscopy). We know that the direct study of face-to-face exchanges is critical to fully understand social interactions, yet there is a gap in the research exploring the underlying neural mechanisms of joint behavior as it naturally unfolds (Dumas, 2011). To be able to investigate how the brain supports interactions that resemble the complexity of the interactions we encounter in everyday life, hyperscanning research will have to accommodate more ecologically valid situations (Babiloni & Astolfi, 2014; Schilbach et al., 2013; Dumas, 2011). In the current study, we investigated the neuroscience of real-world classroom

learning using mobile electroencephalography (EEG) headsets to simultaneously record participants in support of previous experimentation by Dikker et al. (2017).

Increasingly, research shows that, during joint actions, people become "coupled" at motor, perceptual, and cognitive levels in both planned and improvised coordination (Knoblich, Butterfill, & Sebanz, 2011). Participants during synchronized motor activity modify their own actions in response to their partners (Dumas, Nadel, Soussignan, Martinerie, & Garnero, 2010). Hyperscanning neuroscience research has shown not only a relationship between synchrony at the motoric and neural levels (Dumas et al., 2010) but also that face-to-face interactions moderate the relationship between social factors and brain-to-brain synchrony (Dikker et al., 2017; Jiang et al., 2015; Hari, Himberg, Nummenmaa, Hämäläinen, & Parkkonen, 2013; Scholkmann et al., 2013; Jiang, Dai, Peng, Liu, & Lu, 2012; Dumas et al., 2010). Specifically, joint action tasks demonstrate that synchronous motor activity within interactive partners leads to increased feelings of affiliation and social cohesion (Valdesolo, Ouyang, & DeSteno, 2010; Hove & Risen, 2009; Bernieri, 1988), particularly in cooperative versus competitive contexts, and that this is reflected at the neural level (Cheng, Li, & Hu, 2015; Cui, Bryant, & Reiss, 2012; Yun, Watanabe, & Shimojo, 2012).

The classroom setting is an exemplary environment to systematically investigate group interactions—between students and students with their teacher—under semi-controlled conditions, while measuring behavioral and cognitive outcomes (e.g., academic performance and student engagement; Scholkmann et al., 2013; Watanabe, 2013). The dynamic interaction between a teacher and a group of students is fundamental to classroom learning and has been shown to affect both student engagement and academic achievement (Watanabe, 2013; Hughes, Wu, Kwok, Villarreal, & Johnson, 2012; Walton & Cohen, 2011; Hamre & Pianta, 2001; Bernieri, 1988). Teaching and learning can be viewed as a joint action between the teacher and the students such that features of the interactive partner and the event are treated as stimuli in a reciprocal exchange (Sensevy, Gruson, & Forest, 2015). Research into student–teacher relationship exchanges in the classroom suggests that exploring underlying neural activity may support understanding and predicting educational outcomes from the perspective of the teacher and the student (Holper et al., 2013). Recently, researchers have used portable EEG equipment in the classroom to record nine students simultaneously during natural movie viewing and reproduced findings from similar, laboratory-based, experimental designs with commercial-grade equipment, demonstrating the potential for real-world measurement of students' attentional engagement (Poulsen, Kamronn, Dmochowski, Parra, & Hansen, 2017).

In further recent classroom-based experimentation, which forms the foundation for the current work, authors report that brain-to-brain synchrony (quantified as total interdependence [TI] or interbrain coherence; Wen, Mo, & Ding, 2012) between students during class activities was correlated with student engagement and classroom social dynamics (Dikker et al., 2017). Students' synchrony to the group was higher in their preferred teaching style (e.g., video over lecture) and related to greater student focus, group affinity, and empathy (Dikker et al., 2017). In addition, findings in group social dynamics speak directly to the presence of others as a moderator of student synchrony during class. For example, higher student ratings of their teacher correlated with a smaller difference between video (where the teacher played no role) and lecture conditions (where the teacher was central), and students who engaged in prelesson face-to-face baseline recordings showed the highest pairwise synchrony during class with their mutual gaze partner compared with other random students in the group (Dikker et al., 2017). Together, their results suggest that brain-to-brain synchrony is driven by a combination of (i) stimulus properties, (ii) individual differences, and (iii) social dynamics.

The Current Study

In the context of classroom learning, attention is known to play a critical role in learning and maintaining information (Reyes, Brackett, Rivers, White, & Salovey, 2012), and student attention is a challenge even for the most experienced teachers (Evertson & Weinstein, 2013). If brain-to-brain synchrony indeed increases as a function of shared attention (to the teacher, the lesson content, peers), as suggested by the research summarized above (Dikker et al., 2017; Ki et al., 2016), and attention increases retention (Cohen & Parra, 2016), we can then ask whether a student's neural synchrony to the rest of the group or with the teacher predict their retention of the content.

To capture the unique underlying neural activity of the social and behavioral factors in the class, we simultaneously recorded students and their teacher during their usual high school biology lessons, which included both video and lecture components, and tested students' retention postlesson. These teaching styles generated data that were relatively free of motion artifacts, a considerable concern in real-world EEG research (see Dikker et al., 2017, supplementary materials for an extensive discussion and evidence showing that motion artifacts do not explain brain-to-brain synchrony). We aimed to address two research questions, pertaining to the relationship between brain-to-brain synchrony (TI; Wen et al., 2012) on the one hand and classroom learning and student–teacher relationships on the other.

1. Does brain-to-brain synchrony between a student and their peers predict their retention of the class content?
2. Is there a relationship between student–teacher brain-to-brain synchrony, classroom learning, and student–teacher relationships, respectively?

In Dikker et al. (2017), both student ratings (e.g., engagement) and brain-to-brain synchrony between students were higher when students viewed lesson-related videos compared with lectures, which allows us to ask if such a parametric difference also exists for content retention (Research Question 1). In addition, as the teacher plays a pivotal role during lectures but not during videos, we ask whether the student–teacher relationship matters more when the teacher is present (Research Question 2). To address these questions, we employed a similar setup as the classroom EEG findings from Dikker et al. but included two metrics in addition to student-to-group synchrony: (1) student performance and (2) student–teacher brain-to-brain synchrony.

METHODS

Overall Procedure

This experiment took place between February 2016 and May 2016. We collaborated with a New York City high school biology class composed of juniors and seniors. Students received an introduction to neuroscience and the experimental background in the fall semester preceding the experiment and then a refresher in the spring semester right before the classroom EEG sessions (Figure 1A). Students were also introduced and trained to use the wireless EEG equipment to assist in presession setup and postsession breakdown procedures (see vimeo.com/212150060 for an impression of the classroom EEG setup in a different school). Pre-experimental questionnaires were electronically mailed to students and the teacher for completion before recording sessions. After all recording sessions, we returned for a nonrecording session to administer the same preexperiment electronic questionnaires.

During six classroom sessions, 80 min each, we visited the class to record neurophysiological activity as the students and their teacher engaged in semiregular classroom activities (Figure 1B and C). Class content followed the teacher's preplanned biology curriculum. For every session, to preserve time, participants and experimenters worked together to set up the mobile EEG headsets and test connectivity across all channels. Students also filled out presession questionnaires during this time (see below). EEG was recorded from students and their teacher simultaneously for all conditions.

For each session, students and their teacher's EEG activity was recorded during a preexperimental baseline in three conditions (e.g., facing the wall, facing a partner, and facing the group; 2 min each). Afterward, all participants were simultaneously EEG-recorded during the lesson, which was composed of two lecture blocks and two video blocks (interleaved) of approximately 5 min each, with 20 min per lesson. The final EEG recording was a repeated baseline condition also for 2 min each through altering the sequence of conditions. After
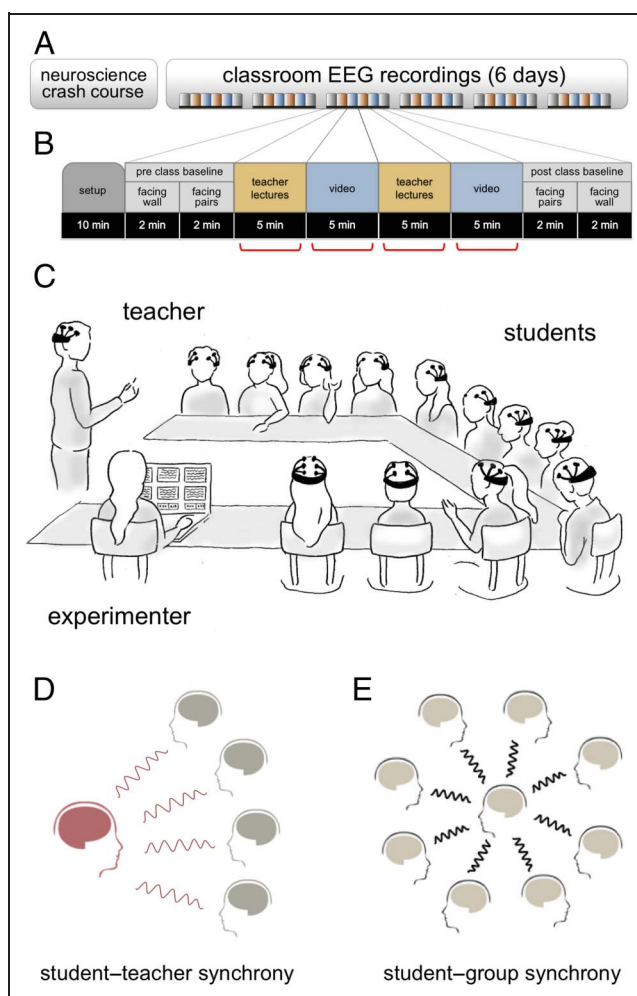

Figure 1. Experimental setup, procedure, and synchrony. (A) Experimentation was preceded by a neuroscience crash course to introduce students to the foundations for the current study. EEG recordings occurred over six sessions. (B) Each session was 80 min and composed of setup, pretesting and posttesting baseline EEG recordings, and four blocks of experimental conditions (two lectures interleaved with two videos). After EEG recordings, students were tested for lesson content retention with quizzes (five questions per lesson block) and finished with a postsession self-report questionnaire. (C) Illustration reproduced from Dikker et al. (2017) of the general classroom recording setup for each session. Synchrony between student-to-teacher (D) and student-to-group (E) can be explored using TI in relation to performance and social factors.

removing EEG equipment, students completed a post-lesson multiple-choice quiz as a measure of students' lesson content retention and a self-report questionnaire for students' engagement, focus, and likability of the teaching style (e.g., lecture vs. video; see details below).

Participants

Participants of this study were 12 healthy high school students (seven girls and five boys, aged 16–18 years), randomly chosen from the entire class of 19 (one student of 19 declined participation altogether and was assigned the role of experimental assistant). Consent forms were

distributed to all students and the teacher (including parental consent for students under the age of 18 years) before the beginning of data collection. The institutional review board of New York University approved all experimental procedures for this study. One student (a girl) was not included in the statistical analysis reported below because of limited TI values (e.g., only student-to-group TI for three lecture blocks in total for all EEG recording sessions, and no student-to-teacher TI, was available for computation).

Teaching Styles

Classroom activities included two "teaching styles"—the teacher's lectures and lesson-related educational videos. Before each recording session, we designed lesson content with the teacher based on her normal curriculum for the class and semester so as to maintain continuity and normalcy in relation to the overall class structure. Before each session, the researcher collaborated with the teacher to design lectures and choose relevant educational videos suited to the level of the class, structuring content to fit the session time constraints (~5 min per condition). In each session, the teacher lectured for approximately 5 min and then presented the students with a 5-min instructional video, and after a short break, this sequence was repeated in the same order. Data analyses were performed for each student on each day for each teaching style. Thus, there was one TI (see below) value per student per day per teaching style (Lectures 1 and 2 were averaged together and compared with the average of Videos 1 and 2).

Student Retention

Students completed a 20-question multiple-choice knowledge quiz immediately after each recording session (six in total) to test retention of core concepts from the day's lesson. The knowledge quiz included five questions for each lecture or video unit (thus 20 questions in total). The teacher and the researchers codesigned quizzes before recording sessions to ensure that quiz content was adequately paired to the students' general comprehension level. Scores were computed as an average per teaching style per session to assess information retention for lectures compared with videos. Outlier (<0.2) and at-ceiling performance (1) was removed in the statistical analyses reported below.

Questionnaires

Two types of questionnaires were administered to students: (i) before and after all recording sessions and (ii) before and after each recording session. The prestudy and poststudy questionnaires included demographic information (gender and age), class and content likability, and closeness ratings toward the teacher and each student in the class. Before and after the recording session, students filled out brief self-report items including their engagement and general likability of the day's lesson and experimental experience. Students were asked directly how much they enjoyed and felt engaged in both teaching styles separately for comparison. All self-report questionnaires were on a scale of 1–7 and were max–min normalized in all figures for presentation purposes.

Data Collection, Preprocessing, and Analysis

EEG Data Collection

Recordings were collected over six class sessions throughout the spring semester (February 2016 through May 2016). Students were briefed on basic EEG technology and uses and were aware of movement, speech, and eye blink artifacts. Further instructions to minimize movement and speech during recording segments were given before each lesson, and students were instructed to reserve questions and discussion for after the recording session was over. Thus, minimal to no conversational exchange occurred between students and their teacher during the EEG recordings. EEG activity was recorded simultaneously from 12 students and their teacher using Emotiv wireless EMOTIV EPOC EEG headsets (14 channels; sampling rate = 128 Hz, online notch filter; mastoid reference locations; Debener, Minow, Emkes, Gandras, & de Vos, 2012). Custom software built using the Open-Frameworks software package (www.openframeworks. com) was used to record EEG data from all 13 participants simultaneously onto a single computer (MacBook Pro). Individual laptops (a combination of students' personal computers and those provided by the school) were set up at the beginning of each session to test each participant's headset connectivity and electrode impedance before data collection. For a detailed discussion of the software and experimental setup and evaluation of the EEG data quality, see Dikker et al. (2017; supplemental materials).

Analysis: Quantifying Brain-to-Brain Synchrony

EEG Preprocessing

The raw EEG data for students and the teacher for each class and each teaching style (videos and lectures) were filtered and preprocessed using EEGLAB (Delorme & Makeig, 2004). The signals were band-pass filtered between 0.5 and 35 Hz and divided into 1-sec epochs for artifact rejection and EEG analysis. Artifacts in the data were both automatically and manually excluded. We first set a rejection threshold in EEGLAB of ±100 μV for all channels and then visually inspected each 1-sec epoch to further exclude eye, muscle, and speech-related artifacts. This resulted in an average rejection rate (across students and days) of 59% of EEG-recorded epochs during lecture lessons and 54% of EEG-recorded epochs

during video lessons. Subsequently, channels with average amplitude diverging from the mean channel amplitude by 4 SDs were excluded from analysis.

Computing Brain-to-Brain Synchrony: TI

Brain-to-brain synchrony was computed using the method of TI (Dikker et al., 2017; Wen et al., 2012). Spectral coherence was computed based on the Welch method to limit bias in coherence estimation (Dikker et al., 2017; Burgess, 2013). For every student–student and student–teacher pair during each 1-sec epoch recorded per teaching style, TI was computed for a pair of simultaneously acquired time series (e.g., (x_1, y_1), (x_2, y_2),… (x_3, y_3)) as:

$$TI_{x,y} = -\frac{1}{2\pi} - \frac{1}{2\pi} \int_{-\pi}^{\pi} ln \int_{-\pi}^{\pi} ln \left(1 - C_{xy}^2(\lambda) \left(1 - C_{xy}^2(\lambda) \right) d\lambda$$

where $C_{xy}(\lambda)$ is the coherence between the two signals, x and y, at frequency $f = \lambda/2\pi$.

In this study, six preselected channels, which were most often free of noise across students in Dikker et al. (2017), were used for computing TI. These included two occipital channels (O1, O2), two frontal channels (F3, F4), and two parietal channels (P7, P8)—unless electrodes have been rejected based on artifacts. TI was assessed according to the methodology of Dikker et al. First, we computed the magnitude-squared coherence using the Welch method for the six preselected one-on-one paired combinations of electrodes from two participants. This coherence was calculated for the frequency range between 1 and 20 Hz by tapering nonoverlapping 1-sec epochs with a Hanning window (zero-padded to 4 sec; Mäki & Ilmoniemi, 2010; Lalor et al., 2005) and performing the Fourier transform with a 0.25-Hz frequency resolution. A minimum of 30 artifact-free mutual epochs for pairs was required to be included in the analysis for the corresponding teaching style per day. For each pair of participants, TI values across all paired electrodes were averaged. Then, student-to-group TI was calculated by averaging all possible pairwise combinations between one participant and the rest of the group. Student-to-teacher TI was a pairwise value between the student and their teacher. Student-to-group TI and student-to-teacher TI were then entered in the multilevel models for statistical analysis (Figure 1D and E) to evaluate students' synchrony with the group and their teacher in relation to the performance and social factors.

Analysis Strategy

To investigate the relationship between student-to-group TI, student-to-teacher TI, quiz scores, and questionnaire metrics across days, we created multilevel models (Goldstein, 1995), with days nested within students. Multilevel models were implemented in the SAS PROC MIXED procedure (random effects were modeled wherever possible; Singer, 1998). Table 1 summarizes the repeated-measures analyses that were conducted and their corresponding research questions.

RESULTS
Student-to-Group Synchrony and Memory Retention

We first tested whether brain-to-brain synchrony between a student and their peers predicted content retention. Overall, students retained content presented in videos better than content from the lectures (video:

Table 1. Repeated-Measures Multilevel Models and Corresponding Research Question (Related to Figures 2 and 3)

Analysis	Research Question
(1) Repeated-measures multilevel regression analysis assessing effects of Teaching Style × Quiz Scores on student-to-group TI	Do quiz scores vary by teaching style and as a function of student-to-group TI?
(2) Repeated-measures multilevel regression analysis assessing effects of Teaching Style × Engagement on student-to-teacher TI	Does student-to-teacher TI vary by teaching style and as a function of engagement?
(3) Repeated-measures multilevel regression analysis assessing effects of teacher-modulated student-to-group TI on student-to-teacher TI and any possible interaction by teaching style	Does any effect of the teacher in student-to-group TI covary with student-to-teacher TI? Is this the case only for the (teacher-relevant) lecture teaching style?
(4) Repeated-measures multilevel regression analysis assessing effects of student-to-teacher closeness on student-to-teacher TI and any possible interaction by teaching style	Does student-to-teacher closeness predict student-to-teacher TI? Is this the case only for the (teacher-relevant) lecture teaching style?
(5) Repeated-measures multilevel regression analysis assessing effects of student-to-teacher closeness on quiz scores and any possible interaction by teaching style	Does student-to-teacher closeness predict quiz scores? Is this the case only for the (teacher-relevant) lecture teaching style?
(6) Repeated-measures multilevel regression analysis assessing effects of student-to-teacher TI on quiz scores and any possible interaction by teaching style	Does student-to-teacher TI predict quiz scores? Is this the case only for the (teacher-relevant) lecture teaching style?

0.78 ± 0.02; lecture: 0.70 ± 0.03; Teaching Style × Quiz Scores: $F(1, 10) = 6.40, p = .029$; Figure 2A, right). However, contrary to our prediction based on previous findings (Cohen & Parra, 2016), there was no significant relationship between student-to-group brain synchrony and lesson content retention (Student-to-Group TI × Quiz Scores: $F(1, 70) = 1.16, p = .2847$; Figure 2B; Table 1, Cell 1).

Brain-to-Brain Synchrony, Student–Teacher Dynamics, and Learning

Similar to our previous findings (Dikker et al., 2017), students reported higher daily engagement for videos compared with lectures (video: 5.05 ± 0.21; lecture: 3.63 ± 0.18; Daily Engagement × Teaching Style: $F(1, 9) = 14.67, p = .004$). In addition, student-to-teacher TI suggests variations according to teaching style where brain synchrony with the teacher was significantly higher for videos compared with lectures (video: 0.65 ± 0.02; lecture: 0.39 ± 0.03; Student-to-Teacher TI × Teaching Style: $F(1, 10) = 35.33, p = .0001$; Figure 2C, left), and there was a strong interaction between the two variables (Student-to-Teacher TI × Daily Engagement: $F(1, 43) = 10.33, p = .003$; Figure 2D; Table 1, Cell 2). Interestingly,

daily student engagement was not correlated with student-to-group brain synchrony (not shown), replicating similar findings from Dikker et al. (2017), who found that postsemester engagement ratings, but not daily engagement ratings, correlated with student-to-group TI. This suggests that students' relationship to their teacher may be a stronger predictor of class engagement than a student's peer.

We next explored whether "teacher-relevant" factors varied as a function of teaching style. As pointed out above, a major distinction between video and lecture teaching styles is that the teacher plays a pivotal role during lectures, whereas this is not the case for videos. Dikker et al. (2017) found that a student's teacher likeability rating was significantly correlated with the difference between a student's student-to-group TI during video as opposed to lecture content (i.e., student-to-group TI during videos was used as a "baseline" condition): The greater the teacher likeability, the smaller the difference between conditions (recall that video sessions overall show larger TI values, because of a combination of stimulus properties and engagement factors; see Dikker et al., 2017). Here, we extend this finding to student-to-teacher TI: As shown in Figure 3A and B, the correlation between student-to-teacher TI during lectures, on the one hand,
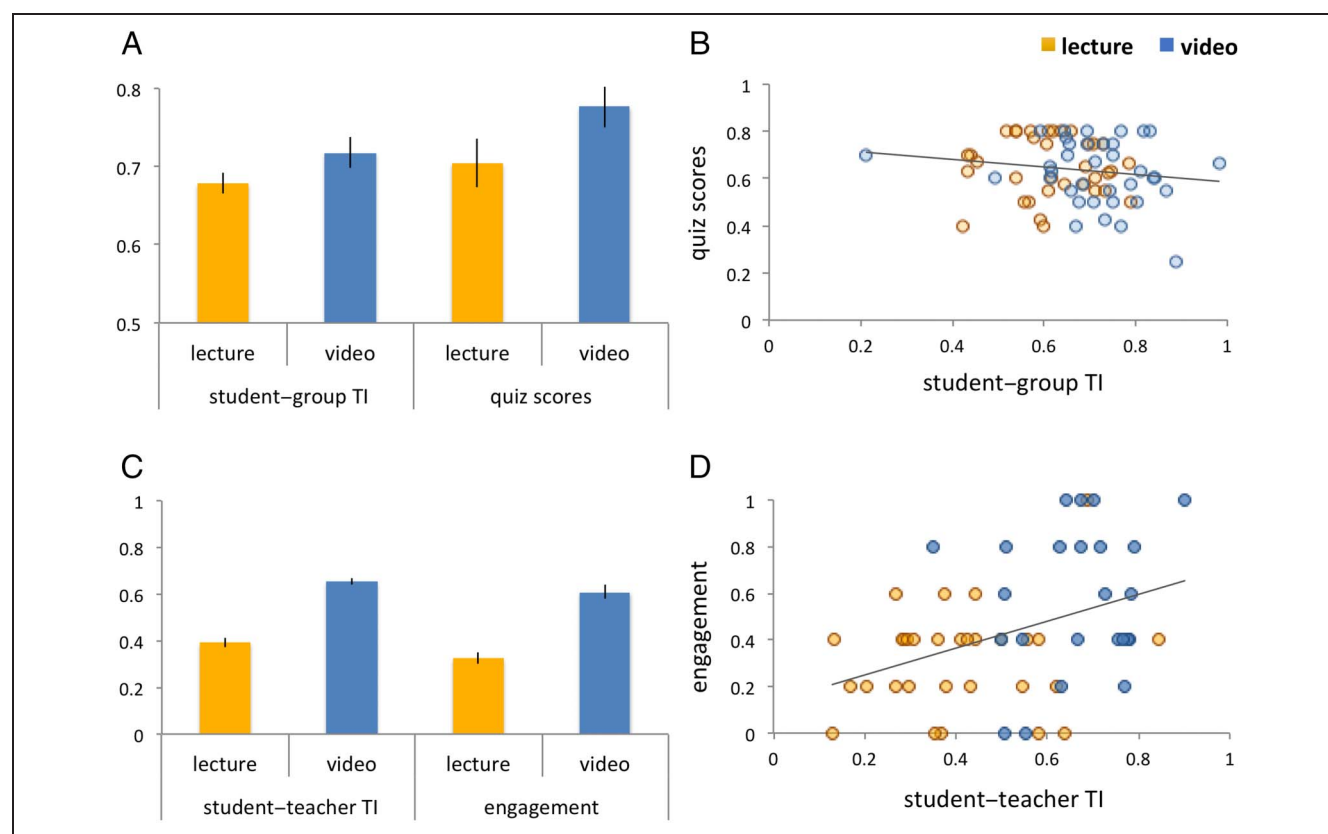
Figure 2. Brain-to-brain synchrony, student retention, and individual differences. (A) Average student-to-group TI (left) and average quiz scores (right) for two teaching styles (videos vs. lectures). Students' brain synchrony with the group did not correlate with performance on a knowledge quiz (B). (C) Student-to-teacher TI (left) and students' day-to-day self-reported engagement (right). Students' daily engagement predicted student-to-teacher TI (D).
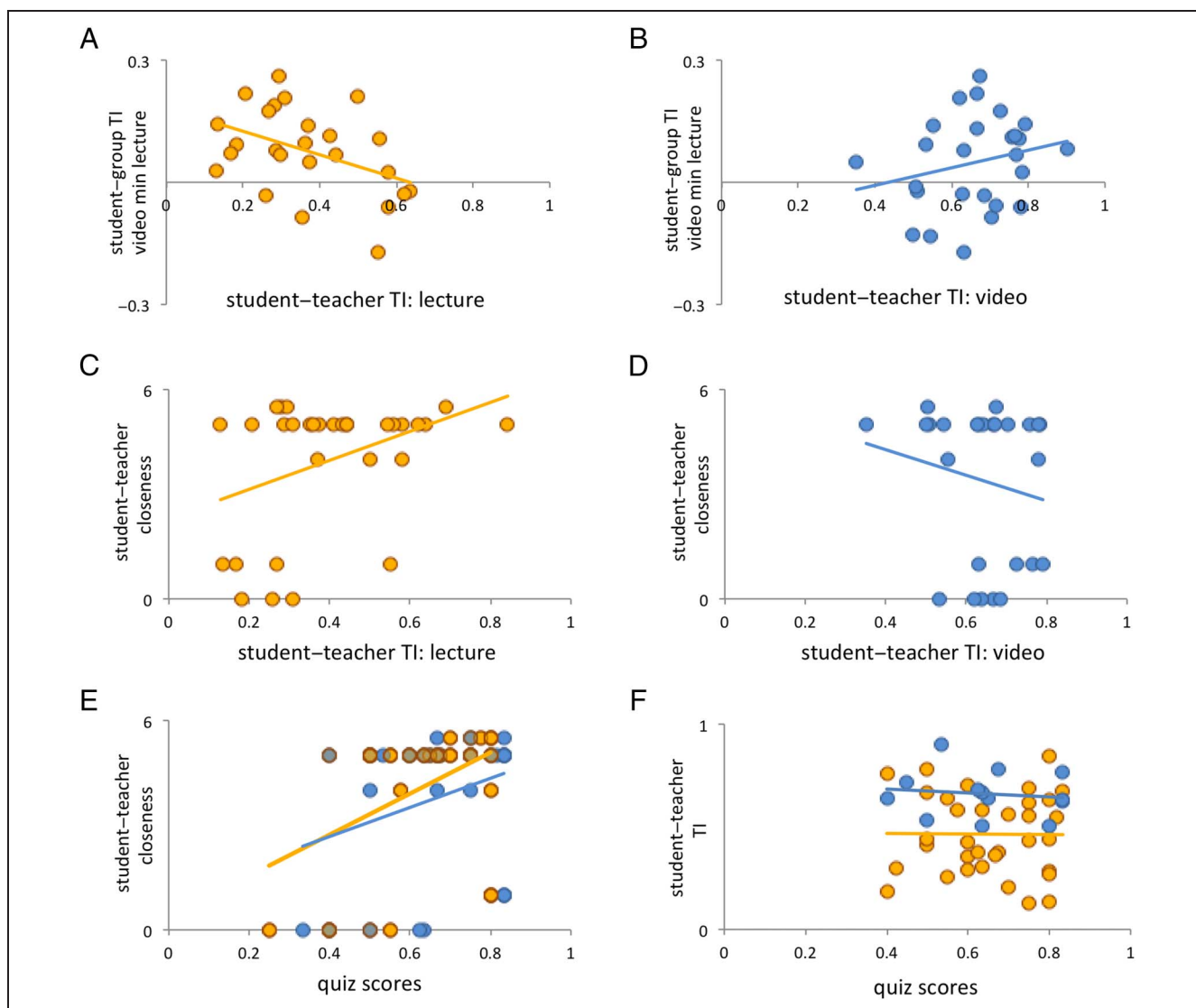
Figure 3. Social dynamics predict student–teacher synchrony and retention. (A) The difference in student-to-group TI (video TI minus lecture TI) predicted greater synchrony with the teacher during lectures, but not during videos (B). (C) Student–teacher closeness predicted student-to-teacher synchrony during lectures, but not during videos (D). Student–teacher closeness predicted better quiz scores (E), but student-to-teacher TI did not (F).

and the video–lecture difference between student-to-group TI, on the other, suggests significant variations by teaching style (Student-to-Teacher TI × Student-to-Group $TI_{video-lecture}$: $F(1, 28) = 6.48, p = .0167$; Table 1, Cell 3). There was a negative correlation between the two variables during lectures ($r = -.426, p < .05$), but not during videos ($r = .23, p = .258$). These exploratory analyses suggest that students who showed greater brain synchrony with their teacher during the lecture conditions also showed less of a relative reduction in their synchrony with the group for lectures compared with videos.

We observed a similar interaction for the correlation between student–teacher closeness and student-to-teacher TI ($r = .382, p < .05$): Student–teacher closeness ratings only predicted student-to-teacher TI during lectures, not videos (student–teacher closeness: 3.94 ±

0.26; Student-to-Teacher Closeness × Teaching Style: $F(1, 39) = 3.98, p = .05$; Figure 3C and D; Table 1, Cell 4). Interestingly, there was a significant correlation between student–teacher closeness and quiz scores ($r = .352, p = .003$; Figure 3E; Table 1, Cell 5). However, like student-to-group TI, student-to-teacher TI did not predict quiz scores for either condition (Student-to-Teacher TI × Quiz Scores: $F(1, 35) = 0.05, p = .818$; Figure 3F; Table 1, Cell 6).

DISCUSSION

In an effort to understand the neural basis of student–teacher interactions and explore the relationship between brain-to-brain synchrony and classroom learning, we recorded simultaneous EEG from a group of high school students and their teacher during their normally

scheduled biology classes. EEG data were analyzed in conjunction with a set of behavioral measures, including quiz scores, self-reported engagement, and student–teacher closeness.

We show that quiz scores were higher for videos than lectures, as was brain synchrony. However, although prior work has already demonstrated that brain-to-brain synchrony relates to successful communication (Dikker et al., 2014; Stephens et al., 2010), memory formation (Hasson, Furman, Clark, Dudai, & Davachi, 2008), and information retention (Cohen & Parra, 2016), there was no relationship between student retention and brain-to-brain synchrony: Neither student-to-group synchrony nor student–teacher synchrony predicted quiz scores. It is worth emphasizing that we did see a similar overall pattern where quiz scores, student-to-group synchrony, student–teacher synchrony, and engagement were all higher for videos as compared with lectures, and we know from past research that social factors such as student–teacher closeness and student engagement are related to student learning (Holper et al., 2013; Hughes et al., 2012).

There are multiple possible reasons as to why we failed to replicate previous findings between neural activity and students' performance (Cohen & Parra, 2016). First, measuring neurophysiological activity in the real world comes with its own unique limitations, for example, the trade-off between preserving naturalistic exchanges to the greatest degree and minimizing artifacts in data. Classroom exchanges are often dynamic and expressive, and although we instructed participants to minimize movement and speech during recording segments (recall that only the teacher spoke during lectures), a certain amount of natural gesturing was inherent to the design and environment compared with laboratory-based research. Second, and most important, prior laboratory-based research that has linked neural activity and learning used a larger sample of participants and longer quizzes (Cohen & Parra, 2016). Here, we were constrained by class duration and class size.

Furthermore, we estimated the overall relationship between retention and synchrony during different teaching activities. This means the synchrony values included moments in which learned items were presented as well as moments with concepts that were later forgotten. This may have been too coarse as an approach for measuring students' learning: Most past research has compared synchrony during the presentation of remembered versus forgotten items (Battro et al., 2013; Holper et al., 2013). Thus, to accurately quantify the relationship between brain synchrony and learning, it might be necessary to reconstruct when the content featured on the quizzes was presented during class and relate student retention of that information to group synchrony during those specific "learning" moments (along the lines of, e.g., Kang & Wheatley, 2017; Wagner, Kelley, Haxby, & Heatherton, 2016). Unfortunately, this information was unavailable in the current study as lectures were not scripted verbatim or videotaped, and the onset of the instructional videos was not synchronized with the EEG recordings. Finally, the EEG equipment we used is less precise than laboratory-grade EEG equipment used in classic experimentation, maybe resulting in failing to capture subtle effects. As technology advances in wireless EEG recording options (e.g., affordable headsets with more electrodes), isolating neurophysiological activity in relation to specific stimuli events will be discernible and should be explored more fully in student-to-group and student-to-teacher interactions.

Our second research goal concerned the relationship between student–teacher brain-to-brain synchrony, classroom learning, and student–teacher social closeness. We observed that student–teacher synchrony was predicted by teacher closeness during lectures, but not videos. One way to interpret this result is that the teacher is a greater "attractor" of synchrony during lectures than videos, independent of students' preferences for videos over lectures. More simply put: The teacher is the "stimulus" during lectures, but not during videos.

The finding that brain synchrony reflects student–teacher closeness relates to a growing body of literature about how social networks are represented in the brain (Curley & Ochsner, 2017; Parkinson, Kleinbaum, & Wheatley, 2017; Zerubavel, Bearman, Weber, & Ochsner, 2015). It was recently demonstrated that similarity in fMRI responses to video stimuli across individuals varies with distance in a social network, with close friends exhibiting the highest degree of neural similarity (Parkinson, Kleinbaum, & Wheatley, 2018). Another study found that information about social network position was spontaneously activated when participants viewed familiar individuals (Parkinson et al., 2017). Similarly, in our study, student–teacher closeness was predicted by brain synchrony during lectures, when the students (presumably) were not actively thinking about their relationship with the teacher.

The student–teacher results also support an indirect relationship between synchrony and performance. Although student–teacher synchrony did not directly relate to students' quiz scores, student–teacher closeness did, supporting previous findings (Dikker et al., 2017; Watanabe, 2013). Given the relationship between student–teacher closeness and quiz scores, future research may further elucidate whether students better retain information from lectures than videos over time, as prior research tested information retention after a period of 3 weeks from presentation (Cohen & Parra, 2016). In addition, student-to-teacher synchrony, but not student-to-group synchrony, was predicted by students' daily engagement ratings, suggesting that students' relationship to their teacher, rather than to their peers, may be a stronger predictor of engagement. This also suggests a crucial link between attention, identifying the relevant stimulus features for interpretation, and retention of information related to the target

stimuli—specifically, as attending to different features of stimuli can alter interpretation and is reflected in changes in neural activity (Cooper, Hasson, & Small, 2011).

It is important to clarify that significant correlations in brain-to-brain synchrony research do not indicate that brains are "physically linked" (Babiloni & Astolfi, 2014). Rather, brain-to-brain synchrony is a neural marker, across all participants, that is a quantifiable reflection of underlying cognitive psychological processes. One proposal, with growing support (Dikker et al., 2017; Poulsen et al., 2017; Ki et al., 2016), is that brain-to-brain synchrony increases as shared or joint attention modulates entrainment by "tuning" neural oscillations to the temporal structure of our surroundings. Temporally aligned entrainment to the oscillatory features of external stimuli (e.g., teacher's voice) is thought to support information extraction from the stimulus, such as in parsing continuous speech into syllables (Giraud & Poeppel, 2012) and attentional selection of relevant information (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). Thus, stimulus-evoked responses drive the relationship between similar brain activity in groups and naturalistic stimuli, and multiple perception-related processes, such as attentional engagement as well as structural features of the stimuli, modulate this relationship (Ki et al., 2016; Poulsen et al., 2017).

It is widely shown that stimulus entrainment heavily depends on attention (Fiebelkorn, Saalmann, Kastner, 2013; Zion Golumbic et al., 2013; Lakatos et al., 2008). For example, several recent studies demonstrated that, in the "cocktail party effect," when confronted with two speakers and paying attention only to one of them, oscillations in high-order auditory areas track only the attended speaker's voice (Zion Golumbic et al., 2013; Mesgarani & Chang, 2012). In social interactions, joint attention and mutual gaze drive the defining characteristics of the exchange: initiator and responder roles, shared intention and motivation, and the interactive context (Koike et al., 2016). Stimulus properties (e.g., teaching style or richness of the audiovisual environment; Hasson et al., 2004), individual differences (e.g., focus, engagement, personality traits; Nummenmaa et al., 2012), and social dynamics (e.g., social closeness and social interaction; Koike et al., 2016) each mediate attention and brain-to-brain synchrony.

In our analyses of student-to-group and student-to-teacher synchrony, we begin to see how neural synchrony reflects the complex interaction between attention and social dynamics. During the lectures, student–teacher closeness varied with student–teacher synchrony. Still, videos overall generated stronger student–teacher synchrony than lectures overall. This may be due to low-level differences between the two types of stimuli (e.g., stronger audiovisual cues in the videos), in line with prior findings suggesting that correlated neurophysiological activity is partially driven by low-level visual features (Poulsen et al., 2017). Together, these findings are readily explained

within a stimulus entrainment account: When the teacher is the stimulus, student–teacher synchrony increases as a function of increased attention-modulated stimulus entrainment (indirectly measured via student–teacher closeness in our study). Independently, videos are a stronger "entrainer stimulus" than lectures because of their rich (and spatially constrained) audiovisual content, resulting in an increase of brain-to-brain synchrony (Ki et al., 2016). As discussed, a classroom has complex sensory features and dynamics, such as educational videos, group projects and discussion, and interactions with the teacher. This increases variability of how students may receive and retain information. Although the student–teacher relationship mimics more classically explored leader–follower dynamics (Jiang et al., 2015), little research has directly investigated the specific nuanced features of this complex social exchange to provide insight into the neural underpinnings of attentional engagement in the real world (Ki et al., 2016).

The interaction between students and their teacher is implicit and explicit, is social, flows bidirectionally and continually, and is influenced by behavioral contagion as individuals automatically imitate each other (Watanabe, 2013)—all with the added component of performance-based evaluations and assessments. In this study, we replicated previous findings (Dikker et al., 2017) showing that students reported higher daily engagement for video lessons compared with lectures and built upon these findings by showing that students also performed better in quizzes measuring content retention in the lesson type they preferred (i.e., videos). In summary, in addition to the nature of the stimulus (here, lectures vs. videos), social dynamics, specifically student–teacher social closeness, appear to drive brain-to-brain synchrony. Our findings on brain-to-brain synchrony in a group setting marry two lines of prior research, namely, studies investigating neural entrainment to engaging stimuli (e.g., Poulsen et al., 2017) and studies linking social connectedness to brain responses (Parkinson et al., 2017, 2018).

Further investigating these complex dynamics as they occur naturally—such as those between students, peers, and their teacher in relation to class content—can reveal more about the nuanced interplay of the various factors that affect learning in the real world.

Acknowledgments

REFERENCES

Babiloni, F., & Astolfi, L. (2014). Social neuroscience and hyperscanning techniques: Past, present and future. *Neuroscience & Biobehavioral Reviews, 44,* 76–93.

Battro, A. M., Calero, C. I., Goldin, A. P., Holper, L., Pezzatti, L., Shalóm, D. E., et al. (2013). The cognitive neuroscience of the teacher–student interaction. *Mind, Brain, and Education, 7,* 177–181.

Bernieri, F. J. (1988). Coordinated movement and rapport in teacher–student interactions. *Journal of Nonverbal Behavior, 12,* 120–138.

Burgess, A. P. (2013). On the interpretation of synchronization in EEG hyperscanning studies: A cautionary note. *Frontiers in Human Neuroscience, 7,* 881.

Chang, W., Jääskeläinen, I. P., Belliveau, J. W., Huang, S., Hung, A., Rossi, S., et al. (2015). Combined MEG and EEG show reliable patterns of electromagnetic brain activity during natural viewing. *Neuroimage, 114,* 49–56.

Cheng, X., Li, X., & Hu, Y. (2015). Synchronous brain activity during cooperative exchange depends on gender of partner: A fNIRS-based hyperscanning study. *Human Brain Mapping, 36,* 2039–2048.

Cohen, S. S., & Parra, L. C. (2016). Memorable audiovisual narratives synchronize sensory and supramodal neural responses. *eNeuro, 3.*

Cooper, E. A., Hasson, U., & Small, S. L. (2011). Interpretation-mediated changes in neural activity during language comprehension. *Neuroimage, 55,* 1314–1323.

Cui, X., Bryant, D. M., & Reiss, A. L. (2012). NIRS-based hyperscanning reveals increased interpersonal coherence in superior frontal cortex during cooperation. *Neuroimage, 59,* 2430–2437.

Curley, J. P., & Ochsner, K. N. (2017). Neuroscience: Social networks in the brain. *Nature Human Behaviour, 1,* 0104.

Debener, S., Minow, F., Emkes, R., Gandras, K., & de Vos, M. (2012). How about taking a low-cost, small, and wireless EEG for a walk? *Psychophysiology, 49,* 1617–1621.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134,* 9–21.

Dikker, S., Silbert, L. J., Hasson, U., & Zevin, J. D. (2014). On the same wavelength: Predictable language enhances speaker–listener brain-to-brain synchrony in posterior superior temporal gyrus. *Journal of Neuroscience, 34,* 6267–6272.

Dikker, S., Wan, L., Davidesco, I., Kaggen, L., Oostrik, M., McClintock, J., et al. (2017). Brain-to-brain synchrony tracks real-world dynamic group interactions in the classroom. *Current Biology, 27,* 1375–1380.

Dumas, G. (2011). Towards a two-body neuroscience. *Communicative & Integrative Biology, 4,* 349–352.

Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., & Garnero, L. (2010). Inter-brain synchronization during social interaction. *PLoS One, 5,* e12166.

Evertson, C. M., & Weinstein, C. S. (2013). *Handbook of classroom management: Research, practice, and contemporary issues.* New York: Routledge.

Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic sampling within and between objects despite sustained attention at a cued location. *Current Biology, 23,* 2553–2558.

Giraud, A., & Poeppel, D. (2012). Cortical oscillations and speech processing: Emerging computational principles and operations. *Nature Neuroscience, 15,* 511–517.

Goldstein, H. (1995). *Multilevel statistical models.* London: Edward Arnold.

Hamre, B. K., & Pianta, R. C. (2001). Early teacher–child relationships and the trajectory of children's school outcomes through eighth grade. *Child Development, 72,* 625–638.

Hari, R., Himberg, T., Nummenmaa, L., Hämäläinen, M., & Parkkonen, L. (2013). Synchrony of brains and bodies during implicit interpersonal interaction. *Trends in Cognitive Sciences, 17,* 105–106.

Hasson, U., & Frith, C. D. (2016). Mirroring and beyond: Coupled dynamics as a generalized framework for modelling social interactions. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 371,* 20150366.

Hasson, U., Furman, O., Clark, D., Dudai, Y., & Davachi, L. (2008). Enhanced intersubject correlations during movie viewing correlate with successful episodic encoding. *Neuron, 57,* 452–462.

Hasson, U., Ghazanfar, A. A., Galantucci, B., Garrod, S., & Keysers, C. (2012). Brain-to-brain coupling: A mechanism for creating and sharing a social world. *Trends in Cognitive Sciences, 16,* 114–121.

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject synchronization of cortical activity during natural vision. *Science, 303,* 1634–1640.

Holper, L., Goldin, A. P., Shalóm, D. E., Battro, A. M., Wolf, M., & Sigman, M. (2013). The teaching and the learning brain: A cortical hemodynamic marker of teacher–student interactions in the Socratic dialog. *Science Direct, 59,* 1–10.

Hove, M., & Risen, J. (2009). It's all in the timing: Interpersonal synchrony increases affiliation. *Social Cognition, 27,* 949–960.

Hughes, J. N., Wu, J., Kwok, O., Villarreal, V., & Johnson, A. Y. (2012). Indirect effects of child reports of teacher–student relationship on achievement. *Journal of Educational Psychology, 104,* 350–365.

Jääskeläinen, I. P., Koskentalo, K., Balk, M. H., Autti, T., Kauramäki, J., Pomren, C., et al. (2008). Inter-subject synchronization of prefrontal cortex hemodynamic activity during natural viewing. *Open Neuroimaging Journal, 2,* 14–19.

Jiang, J., Chen, C., Dai, B., Shi, G., Ding, G., Liu, L., et al. (2015). Leader emergence through interpersonal neural synchronization. *Proceedings of the National Academy of Sciences, U.S.A., 112,* 4274–4279.

Jiang, J., Dai, B., Peng, D., Liu, L., & Lu, C. (2012). Neural synchronization during face-to-face communication. *Journal of Neuroscience, 32,* 16064–16069.

Kang, O., & Wheatley, T. (2017). Pupil dilation patterns spontaneously synchronize across individuals during shared attention. *Journal of Experimental Psychology: General, 146,* 569–576.

Ki, J. J., Kelly, S. P., & Parra, L. C. (2016). Attention strongly modulates reliability of neural responses to naturalistic narrative stimuli. *Journal of Neuroscience, 36,* 3092.

Knoblich, G., Butterfill, S., & Sebanz, N. (2011). Psychological research on joint action: Theory and data. In B. Ross (Ed.), *The psychology of learning and motivation* (pp. 59–101). Cambridge, MA: Academic Press.

Koike, T., Tanabe, H. C., Okazaki, S., Nakagawa, E., Sasaki, A. T., Shimada, K., et al. (2016). Neural substrates of shared attention as social memory: A hyperscanning functional magnetic resonance imaging study. *Neuroimage, 125,* 401–412.

Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science, 320,* 110–113.

Lalor, E. C., Kelly, S. P., Finucane, C., Burke, R., Smith, R., Reilly, R. B., et al. (2005). Steady-state VEP-based brain–computer interface control in an immersive 3D gaming environment.

EURASIP Journal on Applied Signal Processing, 2005, 3156–3164.

Mäki, H., & Ilmoniemi, R. J. (2010). EEG oscillations and magnetically evoked motor potentials reflect motor system excitability in overlapping neuronal populations. *Clinical Neurophysiology, 121,* 492–501.

Mesgarani, N., & Chang, E. F. (2012). Selective cortical representation of attended speaker in multi-talker speech perception. *Nature, 485,* 233–236.

Nummenmaa, L., Glerean, E., Viinikainen, M., Jääskeläinen, I. P., Hari, R., & Sams, M. (2012). Emotions promote social interaction by synchronizing brain activity across individuals. *Proceedings of the National Academy of Sciences, U.S.A., 109,* 9599–9604.

Parkinson, C., Kleinbaum, A., & Wheatley, T. (2017). Spontaneous neural encoding of social network position. *Nature Human Behaviour, 1,* 1–7.

Parkinson, C., Kleinbaum, A., & Wheatley, T. (2018). Similar neural responses predict friendship. *Nature Communications, 9,* 332.

Poulsen, A. T., Kamronn, S., Dmochowski, J., Parra, L. C., & Hansen, L. K. (2017). EEG in the classroom: Synchronised neural recordings during video presentation. *Scientific Reports, 7,* 43916.

Reyes, M. R., Brackett, M. A., Rivers, S. E., White, M., & Salovey, P. (2012). Classroom emotional climate, student engagement, and academic achievement. *Journal of Educational Psychology, 104,* 700–712.

Schilbach, L., Timmermans, B., Reddy, V., Costall, A., Bente, G., Schlicht, T., et al. (2013). Toward a second-person neuroscience. *Behavioral and Brain Sciences, 36,* 393–414.

Schippers, M. B., Roebroeck, A., Renken, R., Nanetti, L., & Keysers, C. (2010). Mapping the information flow from one brain to another during gestural communication. *Proceedings of the National Academy of Sciences, U.S.A., 107,* 9388–9393.

Scholkmann, F., Holper, L., Wolf, U., & Wolf, M. (2013). A new methodical approach in neuroscience: Assessing inter-personal brain coupling using functional near-infrared imaging (fNIRI) hyperscanning. *Frontiers in Human Neuroscience, 7,* 813.

Sensevy, G., Gruson, B., & Forest, D. (2015). On the nature of the semiotic structure of the didactic action: The joint action theory in didactics within a comparative approach. *Interchange, 46,* 387–412.

Singer, J. D. (1998). Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *Journal of Educational and Behavioral Statistics, 23,* 323–355.

Stephens, G. J., Silbert, L. J., & Hasson, U. (2010). Speaker–listener neural coupling underlies successful communication. *Proceedings of the National Academy of Sciences, U.S.A., 107,* 14425–14430.

Valdesolo, P., Ouyang, J., & DeSteno, D. (2010). The rhythm of joint action: Synchrony promotes cooperative ability. *Journal of Experimental Social Psychology, 46,* 693–695.

Wagner, D. D., Kelley, W. M., Haxby, J. V., & Heatherton, T. F. (2016). The dorsal medial prefrontal cortex responds preferentially to social interactions during natural viewing. *Journal of Neuroscience, 36,* 6917.

Walton, G. M., & Cohen, G. L. (2011). A brief social-belonging intervention improves academic and health outcomes of minority students. *Science, 331,* 1447.

Watanabe, K. (2013). Teaching as a dynamic phenomenon with interpersonal interactions. *Mind, Brain, and Education, 7,* 91–100.

Wen, X., Mo, J., & Ding, M. (2012). Exploring resting-state functional connectivity with total interdependence. *Neuroimage, 60,* 1587–1595.

Yun, K., Watanabe, K., & Shimojo, S. (2012). Interpersonal body and neural synchronization as a marker of implicit social interaction. *Scientific Reports, 2,* 959.

Zerubavel, N., Bearman, P. S., Weber, J., & Ochsner, K. N. (2015). Neural mechanisms tracking popularity in real-world social networks. *Proceedings of the National Academy of Sciences, U.S.A., 112,* 15072–15077.

Zion Golumbic, E., Ding, N., Bickel, S., Lakatos, P., Schevon, C., McKhann, G., et al. (2013). Mechanisms underlying selective neuronal tracking of attended speech at a "cocktail party". *Neuron, 77,* 980–991.