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Brain-to-brain synchrony predicts long-term memory retention more accurately than individual brain measures

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Abstract

Multi-person neuroscience studies have demonstrated that synchrony across participants' brains ('brain-to-brain synchrony') can predict a range of cognitive and social phenomena. However, it is unclear whether brain-to-brain synchrony can predict individual outcomes, specifically long-term memory retention, better than intra-brain measures. Here we recorded EEG in a laboratory classroom from groups of four students and a teacher during a science lesson. We show that alpha-band (8-12Hz) brain-to-brain synchrony, but not alpha power or intra-brain alpha synchrony, significantly predict students' performance in both an immediate and a delayed post-test. Remarkably, moment-to-moment variation in alpha-band brain-to-brain synchrony during the lesson were found to indicate what specific information was retained by the students a week later. Whereas student-to-student brain synchrony was instantaneous, student-to-teacher brain synchrony best predicted learning when adjusting for a ~200 millisecond lag in the students' brain activity relative to the teacher's brain activity, suggesting a sequential, lagged transfer of information from teachers to students. These findings provide key new evidence for the importance of brain data collected simultaneously from groups of individuals using ecologically-valid materials and substantially extend the brain-as-predictor approach by demonstrating that the predictive value of two brains can exceed that of individual brains.

Significance Statement

The brain mechanisms that underlie how people learn while interacting with one another are not well understood. Here, we concurrently measured EEG activity from groups of four students and a teacher during a science lesson. Our findings revealed that both student-to-student and student-to-teacher brain synchrony can predict how much information students retained after one week.

Furthermore, brain-to-brain synchrony predicted retention above and beyond measures derived from individual brains. These results provide critical evidence for the importance of brain data collected simultaneously from groups of individuals using ecologically-valid materials.

Introduction

We know little about the human brain mechanisms that underpin learning while we interact with others in ecologically-valid environments (1). The reason is that typical cognitive neuroscience methods limit the research on the human brain to studies in which one participant at a time conducts a task in a highly constrained environment (e.g., inside a brain scanner). In the past few years, researchers have begun comparing brain responses *across* individuals (2-4). In pioneering research, Hasson and colleagues (5) used functional Magnetic Resonance Imaging (fMRI) to demonstrate that the brains of viewers who watch the same movie show similar activation patterns over time. Since then, a growing number of studies have demonstrated - using different methodologies (fMRI, electroencephalography (EEG), and functional near-infrared spectroscopy (fNIRS)) - that synchrony in brain activity across individuals (i.e. brain-to-brain synchrony) can predict a range of cognitive and social outcomes, including the degree of engagement in a task (6-9), memory retention (7, 10, 11), communication quality (12, 13), pain reduction (14), social closeness (6, 8, 15), and audience preferences (16).

The growing body of research on second-person and group neuroscience (1) raises many new questions. For example, it is unclear whether brain-to-brain synchrony can predict real-world outcomes better than measures derived from individual brains. Previous research suggests that brain-to-brain synchrony might provide unique information compared to individual brain measures. For example, using fMRI, Simony et al. (17) reported that inter-subject functional correlations (where inter-region correlations are computed *across* brains) have much higher sensitivity to the structure of a real-life story compared to traditional functional connectivity analysis (where inter-region correlations are calculated *within* individual brains), potentially because inter-subject functional correlations filter out intrinsic neural dynamics and non-neural artifacts that are consistent *within* a brain but not *across* brains (17). In another study, using fNIRS, inter-brain but not intra-brain synchronization was shown to predict behavioral performance in a cooperative task (18). However, the restricted spatial coverage and low temporal resolution of fNIRS limit the generalizability of these findings. Here we used EEG to simultaneously record brain activity from groups of four students and a teacher to investigate whether brain-to-brain synchrony, both between students and between the students and the teacher, can predict learning outcomes (Fig. 1A). Students' content knowledge was assessed a week before the EEG session, immediately following each one of four mini-lectures, and one week later (Fig. 1B).

Recent EEG research in classrooms found that brain-to-brain synchrony was associated with student engagement (6, 8, 19), but not with learning outcomes (6). This is surprising because brain-to-brain synchrony is hypothesized to be driven, at least partially, by shared attention (8), and shared attention has been shown to affect subsequent memory (20). Indeed, a recent laboratory study demonstrated that brain synchrony across participants who individually watched educational videos was associated with memory retention immediately after the videos were presented (7). The discrepancy between laboratory- and classroom-based studies might be due to the small sample size and lower quality EEG equipment used in the latter. While it is possible that moment-to-moment variations in brain synchrony might be a more sensitive measure to reveal what information will be remembered or forgotten (10, 17), previous studies have only assessed the overall brain synchrony measured across the entire duration of a lecture or a video (6, 7). Furthermore, whereas previous studies have only assessed immediate memory retention (6, 7), the more relevant outcome for education systems is long-term retention of knowledge (21).

The current study addressed the following questions: First, do student-to-student and student-to-teacher brain synchrony predict delayed memory retention? Second, does synchrony *across* brains predict delayed retention more accurately than measures within individual brains? Third, do moment-to-moment variations in brain synchrony indicate what information will be successfully retained or forgotten? We focused on the neurophysiological alpha frequency band (8-12 Hz) because it is well characterized as an index of attention (22-26) and has been shown to be the most robust frequency range for brain-to-brain synchrony (27).

Results

Behavioral results. Students' content knowledge significantly increased from the pre-test (0.43±0.02; mean ± standard deviation of the mean) to the immediate post-test (0.73±0.02; $F(1,30)=210.76$; $p<10^{-13}$), and from the pre-test to the delayed post-test (0.64±0.02; $F(1,30)=93.48$; $p<10^{-10}$; Fig. 2A). The retention of content knowledge significantly declined over the course of the week between the immediate and delayed post-tests ($F(1,30)=46.00$; $p<10^{-6}$). Both immediate retention (the difference between the pre- and immediate post-test scores) and delayed retention (the difference between the pre- and delayed post-test scores) were considered as outcome variables in subsequent analyses.

Student-to-student brain synchrony, individual brain measures, and memory retention. For each student dyad in a given group, Circular Correlation values (CCorr; (28))

were computed for all combinations of EEG electrodes (32*32 electrodes) and then averaged across dyads (8) (Fig. 2B). Similarly, CCorr values were computed between each EEG electrode and all the other electrodes *within* individual students as a measure of intra-brain synchrony. Statistical significance was assessed by comparing CCorr values to surrogate datasets generated by shuffling the lectures (29) (Fig. S1). CCorr values were then averaged across all statistically significant electrode pairs (see Materials and Methods).

We first assessed whether student-to-student brain synchrony as well as intra-brain synchrony can predict memory retention. Since students were nested within groups, we constructed a multilevel model wherein both brain-to-brain synchrony and intra-brain synchrony were considered level 1 predictors (see Materials and Methods). This analysis revealed that memory retention was significantly predicted by alpha-band *brain-to-brain* synchrony (immediate retention: $F(1,13.79)=5.57$; $p=0.034$; delayed retention: $F(1,13.03)=6.66$; $p=0.023$), but not by alpha-band *intra-brain* synchrony (immediate: $F(1,26.24)=.26$; $p=0.613$; delayed: $F(1,25.55)=.31$; $p=0.582$) (Fig. 3A-B and Fig. S2). As expected, due to volume conductance (30), the number of significant electrode pairs was much higher in the intra-brain analysis (all 992 pairs) than the brain-to-brain analysis (only 11 pairs; Table S1). To account for this difference, we computed the correlation between intra-brain synchrony and memory retention across 10,000 randomly sampled subsets of 11 electrode pairs. As can be seen in Fig. 3C and Fig. S2C, the correlation between brain-to-brain synchrony and memory retention was well outside the distribution of correlation values between intra-brain synchrony and retention. As the results for immediate and delayed retention were comparable, we focused on delayed retention in all subsequent analyses.

Since the power of alpha oscillations has been associated across many studies with task-related processing (22-26), we next examined the relationship between overall alpha power and delayed retention. In contrast to alpha-band student-to-student brain synchrony, overall alpha power did not significantly predict delayed retention ($F(1,27.72)=.17$; $p=0.681$; Fig. 3D). To equate the number of electrodes and the way they were selected, we repeated this analysis while assessing brain synchrony only between matched electrodes (e.g. O1 with O1; (8)). In this analysis, for both brain-to-brain synchrony and alpha power all 32 electrodes were examined without any a priori electrode selection. The results of this analysis were almost identical to the previous analysis (brain-to-brain synchrony: $F(1,13.88)=6.56$; $p=0.023$; alpha power: $F(1,27.94)=0.39$; $p=0.537$). Out of three frequency bands that were examined (theta, alpha and beta), only alpha-band brain-to-brain synchrony significantly predicted delayed retention (Fig. S3). Further, alpha-band brain synchrony, but not alpha power, significantly predicted delayed retention at the individual electrode level. Three of 32 electrode pairs (C3-C3, C4-C4 and FC1-FC1) significantly predicted delayed retention ($p<0.05$; false-discovery-rate (FDR) corrected; Fig. 3E), whereas, for alpha power, no individual electrode reached significance (Fig. 3F).

Moment-to-moment variations in brain synchrony predict delayed retention. Typically, brain-to-brain synchrony is computed over an extended period of time (e.g. the entire duration of a lecture or a video; (6-8)). In order to examine whether moment-to-moment variations in synchrony can indicate what specific information students learned, we transcribed all the lectures and identified *when* the teacher provided information to answer each one of the test questions (Fig. 4A). Then, for each question in the post-test, we computed the corresponding brain-to-brain synchrony and alpha power during the lecture. Student-to-student brain synchrony was significantly higher for questions that students answered incorrectly in the pre-test and correctly in the delayed post-test compared to questions where students' answers have not changed (learned: 0.075±0.002; not learned: 0.065±0.002; $F(1,30.16)=15.13$; $p=0.0005$; Fig. 4B). In contrast, alpha power did not significantly discriminate between learned and not learned information (learned: 1.124±0.040; not learned: 1.120±0.037; $F(1,30)=.28$; $p=0.60$; Fig. 4C).

Student-to-teacher brain synchrony. So far, we have only considered brain-to-brain synchrony between students rather than between the students and the teacher. As students only listened to the lectures, we hypothesized that student-to-student brain synchrony would best predict delayed retention at lag 0 (i.e. instantaneous synchronization). In contrast, because the teacher served as the speaker and the students as listeners, we expected student-to-teacher brain synchrony would be best predict delayed retention at a non-zero lag (13). On average, the correlation between student-to-student synchrony and delayed retention indeed peaked for zero-lagged synchrony (Fig. 5A). The correlation between student-to-teacher synchrony and delayed retention, on the other hand, showed a clear peak at ~200 msec lag between the student and the teacher (i.e. teacher's brain activity preceding students' by about 200 msec; Fig. 5B). Intriguingly, central and frontal electrodes showed the reverse pattern, where the correlation between student-to-teacher synchrony and delayed retention peaked when the student's brain activity preceded the teacher (Fig. 5C). This finding is in line with previous fMRI research and might reflect predictive anticipation by the students (12, 13).

Discussion

Brain measures are widely used to understand and predict human behavior. This brain-as-predictor approach (31) has been effective in elucidating a wide range of real-world outcomes, such as economic decisions and clinical outcomes. The aim of this study was to test whether information measured *across* brains can predict long-term memory retention better than information within *individual* brains. Our results show that alpha-band brain-to-brain synchrony, but not individual brain measures, significantly predicted students' immediate and delayed memory retention (Fig. 3 and Fig. S2). Furthermore, moment-to-moment variations in brain-to-brain synchrony significantly discriminated between information that was learned and not learned (Fig. 4). These results substantially extend the brain-as-predictor approach, demonstrating that the predictive value of two brains can be greater than that of individual brains.

Traditionally, psychology and neuroscience data are collected from individual participants in controlled laboratory environments. In the past few years, researchers have begun to approach the neural basis of social interactions by comparing the brain responses of multiple individuals during a variety of tasks. This line of research shows that cognitive and social factors are reflected in the brain-to-brain synchrony between participants (2-6, 8, 10, 13-15, 18, 27, 29). However, most of these studies are limited to dyads, in many studies participants were not measured concurrently, and others are limited in their ecological validity. Importantly, the vast majority of these studies have not assessed what can be learned from synchrony across brains that *cannot* be revealed by measuring individual brains. Our findings extend previous research, which suggested that measuring synchrony across brains can yield complementary information to individual brain analysis (10, 17, 18, 32, 33). Hasson et al. (10) examined how brain synchrony across individuals during movie viewing predicted subsequent memory. The fMRI response in several brain regions was significantly more correlated across individuals during portions of the movie that were later remembered compared to those that were forgotten. These regions only partially overlapped with those revealed by traditional individual brain analyses, but the predictive power of the two analyses (within and across brains) was not directly compared. More recently, Simony et al. (17) demonstrated that inter-subject functional correlations, but not within-brain connectivity, are modulated by narrative structure. Furthermore, inter-subject correlations within the default-mode network predicted immediate recall of story elements, but the predictive value of inter-subject correlations was not contrasted with that of intra-subject measures. In another study, inter-brain, but not intra-brain, synchronization was shown to predict behavioral performance in a laboratory cooperative task (18). However, intra-brain synchrony in this study might have been underestimated due to the limited spatial coverage and low temporal resolution of fNIRS.

From a methodological perspective, brain-to-brain synchrony can offer better signal-to-noise ratio than intra-brain synchrony (17). In addition to stimulus-driven effects, intra-brain synchrony is influenced by: (a) non-task related intrinsic neural dynamics; and (b) non-neural artifacts (e.g. ocular and movement artifacts). Both (a) and (b) are consistent *within* a brain, but not *across* brains. Intra-brain connectivity analysis is particularly problematic in EEG research because of the spreading of electrical signals from the neuronal sources to scalp electrodes and because of the dependence of phase measures on the way data has been referenced (30, 34, 35).

The current study quantified the brain dynamics of students and teachers in a laboratory classroom. While brain-to-brain synchrony has been associated with several classroom-related variables (mainly students' engagement and social closeness; (6, 8)), there are conflicting results about its relationship with learning outcomes. Bevilacqua et al. (6) collected EEG data from a group of 12 high school students and their teacher during regular biology lessons. Student-to-teacher brain synchrony predicted how engaged students were and how close they felt toward the teacher, but it was not significantly associated to how well students retained class content (6).

Cohen et al. (7) measured brain-to-brain synchrony between students who watched instructional videos individually. Even though the students were not measured concurrently, brain-to-brain synchrony was found to predict their immediate memory retention (7). These contradicting findings might be explained by methodological differences. While Bevilacqua et al. (6) used commercial-grade EEG devices in a classroom environment, Cohen et al. (7) used research-grade EEG devices in a lab setting. In another recent study, student-instructor brain synchrony was measured using fNIRS during song learning. Brain-to-brain synchrony was found to predict learning outcomes, but only when there were turn-taking interactions between the student and the instructor (36). The current study substantially extends previous research by demonstrating that both student-to-student and student-to-teacher brain synchrony are associated with long-term memory retention. Whereas student-to-student brain synchrony best predicted learning outcomes at zero-lag, delayed retention was best predicted for student-to-teacher brain synchrony when students' neural activity was compared to the neural activity of the teacher that preceded the students' by roughly 200 msec (Fig. 5). This finding is consistent with previous research on speaker-listener brain synchrony, which demonstrated that listeners' brain activity is coupled with speakers' at a delay (13, 37). However, these previous studies used methods with low temporal resolution (fMRI and fNIRS), and thus could not accurately estimate the speaker-listener delay. A delay of roughly 200 msec is consistent with the time scale of speech processing (38). In line with previous fMRI research (12, 13), we found that in central and frontal EEG electrodes, the correlation between student-to-teacher synchrony and delayed retention peaked when the student's brain activity preceded the teacher (Fig. 5C), possibly reflecting students' anticipation of upcoming input (39).

While the phenomenon of brain-to-brain synchrony is not yet fully understood, Dikker et al. (8) proposed that shared attention plays a crucial role. At the most basic level, brain-to-brain synchrony is driven by stimulus entrainment: as all students are presented with the same input (e.g. teacher's voice), their brain activity becomes entrained to that stimuli. Critically, since stimulus entrainment is modulated by attention (40, 41), brain-to-brain synchrony increases when students are engaged in a task and decreases when students disengage (6-8). The hypothesis that brain-to-brain synchrony is partially driven by shared attention is consistent with the current study: when students pay attention to information provided by a teacher, their brain synchrony with the teacher and other students increases, as does their tendency to retain information. The current study focused on brain-to-brain synchrony in the alpha band (8-12 Hz) since there is extensive research linking the alpha rhythm to attention. While traditionally associated with cortical idling (42), it is currently thought that the alpha rhythm is involved in actively suppressing task-irrelevant processing (22-26). There is substantial evidence that the phase and amplitude of alpha-band oscillations prior to and during stimulus presentation influences subsequent stimulus processing (43, 44). Indeed, in the current study, the association between alpha power and immediate retention approached significance ($p=0.058$; Fig. S2). There is also evidence that alpha-band phase synchrony across brain regions is correlated with task performance (45-49). Surprisingly, the current study demonstrates that alpha-band phase synchrony *across* brains, rather than within individual brains, predicts learning outcomes.

However, more research, possibly in more controlled experiments, is needed to understand the neural dynamics that give rise to brain-to-brain synchrony. Future research might examine not only what conditions enhance brain synchrony, but also under what circumstances brain synchrony is diminished, and what the behavioral consequences of decreased neural synchrony are. It should go without saying that the methods we have to study the human brain do not permit more neurobiologically granular, mechanistic characterization. That being said, the measures that we have used here yield unanticipated new insights into how learning in a group context is reflected in the brain dynamics of teachers and learners.

Materials and Methods

Participants. 42 participants (28 females) were recruited and measured in groups of three or four students. All participants satisfied the following criteria: (i) native English speaker; (ii) right hand dominant; (iii) between the ages of 18 and 30 (mean age: 20.6; s.d.: 3.0 years); (iv) non-science major, if applicable; (v) no known history of neurological abnormalities. All participants completed high school, with the majority (76.2%) being current college undergraduates. All participants provided written informed consent, and the experimental protocol was approved by the Institutional Review Board of New York University. In two of the 11 groups, due to technical issues, only two participants had usable EEG data; as student-to-student brain synchrony could not be determined for all dyads, all participants within these two sessions were excluded from analysis (N=7). Four additional subjects were omitted from analysis: two due to poor quality EEG data and the other two since they scored higher in the pre- than the post-test for the majority of lectures (i.e. they did not demonstrate any learning gains). Thus, the final sample consisted of 31 participants (21 female).

The two teachers (1 female) were professional high school science teachers. The female teacher led four sessions, and the male teacher led five of the nine lessons included in analysis. The teachers had no prior acquaintance with the students.

Procedure. Students were seated evenly and randomly around a table, and the teacher was seated at the head of the table (Fig. 1). The experiment took place in a laboratory classroom equipped with a projector and three video cameras. Following EEG set up, baseline EEG recordings (eyes-open and eyes-closed) were taken to test data quality. The lesson comprised of four teacher-led lectures (6:43.26±0:45.93 minutes-long; mean±s.d.) on discrete topics in Biology and Chemistry: Bipedalism, Insulin, Habitats and Niches, and Lipids. Slides were projected onto a screen behind the teacher and controlled by the teacher via a tablet computer (see Fig. 1). In order to minimize speaking- and movement-related artifacts, students were instructed to sit still, minimize head motion, and refrain from asking questions during the lectures. Each lecture was preceded by either no activity or one of three brief pre-lecture activities, where students could interact more freely with one another and with the teacher: a discussion-based activity, a short quiz where students answered three topic-related questions and then observed the distribution of answers across their group, or a short video related to the lecture topic. Activity–lecture combinations and order were randomly pre-assigned and counterbalanced across groups. Each lecture was immediately followed by a brief topic-specific assessment to gauge lecture engagement and content knowledge (see below). Assessments were administered via a tablet computer that was placed next to each student. The lesson concluded with one final three-minute eyes-open baseline recording. The same four content knowledge assessments were given to participants individually both one week prior to (pre-test) and one week following (delayed post-test) his or her corresponding group session (Fig. 1B).

EEG hardware and data collection. Participants' EEG activity was recorded using a 32-channel Neuroelectrics Enobio 32 5G gel sensor system (sampling rate: 500Hz). A dual earclip electrode served as a common unipolar reference. Electrode placement followed the standard 10-10 EEG system. The Neuroelectrics Instrument Controller (NIC2) software application was used to record data and assess signal quality. Data was aligned between students and the teacher post-hoc at the millisecond level using wireless triggers that were sent every second by a tablet computer via Lab Streaming Layer (50).

Quantifying memory retention. For each lecture, memory retention was measured using 10 multiple-choice questions and one short answer question (only the multiple-choice questions were used in the current analysis). Questions were developed by the two participating teachers and reviewed by an independent education specialist (see Table S2). In order to measure changes in content knowledge at the individual question level, the same content questions were used in the pre-test, immediate, and delayed post-test. Note that in order to minimize priming effects, the pre-test was administered a week before the EEG session (Fig. 1B). The difference in student scores between the pre-test and immediate post-test as well as between the pre-test and delayed post-test were averaged across lectures and used as the main outcome variables throughout this study.

All the lectures were audio recorded and synced to the EEG data via LSL. The lectures were transcribed and for each content question, time intervals in which information necessary to answer the question were identified. This enabled matching question-specific EEG data with students' answers to these questions (Fig. 4).

EEG Preprocessing. All preprocessing was carried out using Matlab R2018b in conjunction with EEGLAB 14.1.1b (51). Only data recorded during lecture presentation was included in the analysis. After band-pass filtering (0.5 to 35 Hz), noisy channels were identified and removed using a combination of automatic channel rejection (kurtosis, z-score=3) and inspection of channel power spectra. Continuous EEG data were then epoched into 1-second intervals and visually inspected for non-neural artifacts. Independent component analysis (ICA) was then conducted to identify and remove components that were associated with eye blinks and eye movements (52). Finally, abnormal residual epochs with signals outside of -100 to 100 µV range were automatically tagged and visually inspected. It should be noted that due to the nature of this experiment, teacher data were inherently noisier than those of students. As a result, a more stringent data removal approach was required to obtain high-quality teacher data (See Table S3).

EEG analysis. The data were analyzed using custom-built Matlab code and the FieldTrip toolbox (53). Following preprocessing, EEG data were filtered between 8- and 12-Hz using Butterworth filters of order four, and Hilbert transform was used to compute the instantaneous phase. For each 1-second epoch and for each combination of EEG electrodes (total of 1024 electrode pairs), CCorr (28) was calculated. CCorr was chosen because it has been shown to be the least sensitive to spurious couplings of EEG hyperscanning data (54). CCorr values were calculated for each pair of students within a group and between each student and the teacher (see Fig. 2B). Calculated CCorr values were normalized by Fisher's Z transformation and averaged across epochs, lectures, and electrode pairs. For intra-brain synchrony analysis, CCorr values were computed within each student dataset between each EEG electrode and all the other electrodes (total of 992 electrode pairs). For power analysis, the 1-second epochs were multiplied with a Hanning taper, and power spectra (4–30 Hz) were computed using a fast Fourier transform. Power spectra were then averaged across all epochs within each lecture. In order to normalize the data, the power of each frequency band of interest (theta: 4-7Hz; alpha: 8-12Hz; beta: 13-20Hz) was divided by the averaged power in the 4-20Hz band (referred to as "relative power" in the main text).

Moment-to-moment analysis (Fig. 4): In this analysis, rather than averaging CCorr and alpha power values across the entire duration of each lecture, data were averaged across question-specific epochs identified based on the lecture transcript (Fig. 4A). A question was categorized as "learned" if a student answered it correctly in the delayed post-test, but not in the pre-test. A question was categorized as "not learned" if a student's answer has not changed between the pre- and the delayed post-test (i.e. the student either already knew the answer to the question before the lecture, or answered it correctly before the lecture and incorrectly after the lecture).

Time-lagged cross-correlation analysis (Fig. 5): For each student-student dyad, the time course of one of the students was shifted either backward or forward in the range of -500 msec to +500 msec in steps of 50msec. Similarly, for each student-teacher dyad, the time course of the teacher was shifted between -500 msec to +500 msec in steps of 50 msec with respect to the time course of the student. For each electrode pair and temporal lag, we computed the correlation between student-to-student or student-to-teacher brain synchrony and delayed retention.

Statistical analysis. Following Perez et al. (29), the significance of CCorr values was assessed by constructing surrogate datasets with data taken from different lectures within the same student-student dyads. For example, the EEG data of Student A in the *bipedalism* lecture was paired with the EEG data of Student B in the *lipids* lecture (Fig. S1). By shuffling the lectures, 9 possible combinations were examined. Then, a non-parametric bootstrap test with 10,000 random samplings was used to assess statistical differences between the real and surrogate datasets. An FDR correction (55) was applied to the p-values obtained by the bootstrap test (q=0.05). For intra-brain synchrony, surrogate datasets were constructed by shuffling lectures within each student (for example, the EEG data of Student A in the *bipedalism* lecture was paired with EEG data of same student in the *lipids* lecture).

Since students were nested within groups, data were analyzed using multilevel modeling treating group as the unit of analysis to control for nonindependence in student responses. The MIXED procedure in SPSS was used. Both alpha-band brain-to-brain synchrony and alpha-band intra-brain synchrony or alpha power were included as level 1 predictors. Immediate or delayed retention were treated as the outcome variable.

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References

1. Schilbach L, *et al.* (2013) Toward a second-person neuroscience. *Behavioral and brain sciences* 36(4):393-414.
2. Babiloni F & Astolfi L (2014) Social neuroscience and hyperscanning techniques: past, present and future. *Neuroscience & Biobehavioral Reviews* 44:76-93.
3. Hasson U, A Ghazanfar A, Galantucci B, Garrod S, & Keysers C (2012) *Brain-to-Brain Coupling: A Mechanism for Creating and Sharing a Social World* pp 114-121.
4. Shamay-Tsoory SG, Saporta N, Marton-Alper IZ, & Gvirts HZ (2019) Herding Brains: A Core Neural Mechanism for Social Alignment. *Trends in cognitive sciences* 23(3):174-186.

5. Hasson U, Nir Y, Levy I, Fuhrmann G, & Malach R (2004) Intersubject synchronization of cortical activity during natural vision. *science* 303(5664):1634-1640.
6. Bevilacqua D*, et al.* (2019) Brain-to-Brain Synchrony and Learning Outcomes Vary by Student-Teacher Dynamics: Evidence from a Real-world Classroom Electroencephalography Study. *Journal of cognitive neuroscience* 31(3):401-411.
7. Cohen SS*, et al.* (2018) Neural engagement with online educational videos predicts learning performance for individual students. *Neurobiology of Learning and Memory* 155:60-64.
8. Dikker S*, et al.* (2017) Brain-to-Brain Synchrony Tracks Real-World Dynamic Group Interactions in the Classroom. *Current Biology* 27(9):1375-1380.
9. Cohen SS, Henin S, & Parra LC (2017) Engaging narratives evoke similar neural activity and lead to similar time perception. *Scientific reports* 7(1):4578.
10. Hasson U, Furman O, Clark D, Dudai Y, & Davachi L (2008) Enhanced Intersubject Correlations during Movie Viewing Correlate with Successful Episodic Encoding. *Neuron* 57(3):452-462.
11. Cohen SS & Parra LC (2016) Memorable audiovisual narratives synchronize sensory and supramodal neural responses. *eNeuro* 3(6).
12. Dikker S, Silbert LJ, Hasson U, & Zevin JD (2014) On the same wavelength: predictable language enhances speaker-listener brain-to-brain synchrony in posterior superior temporal gyrus. *The Journal of neuroscience : the official journal of the Society for Neuroscience* 34(18):6267-6272.

13. Stephens GJ, Silbert LJ, & Hasson U (2010) Speaker–listener neural coupling underlies successful communication. *Proceedings of the National Academy of Sciences* 107(32):14425.

14. Goldstein P, Weissman-Fogel I, Dumas G, & Shamay-Tsoory SG (2018) Brain-to-brain coupling during handholding is associated with pain reduction. *Proceedings of the National Academy of Sciences* 115(11):E2528.

15. Parkinson C, Kleinbaum AM, & Wheatley T (2018) Similar neural responses predict friendship. *Nature communications* 9(1):332.

16. Dmochowski JP*, et al.* (2014) Audience preferences are predicted by temporal reliability of neural processing. *Nature communications* 5:4567.

17. Simony E*, et al.* (2016) Dynamic reconfiguration of the default mode network during narrative comprehension. *Nature communications* 7:12141.

18. Balconi M, Pezard L, Nandrino J-L, & Vanutelli ME (2017) Two is better than one: The effects of strategic cooperation on intra- and inter-brain connectivity by fNIRS. *PloS one* 12(11):e0187652.

19. Bhattacharya J (2017) Cognitive neuroscience: synchronizing brains in the classroom. *Current Biology* 27(9):R346-R348.

20. Shteynberg G (2015) Shared attention. *Perspectives on Psychological Science* 10(5):579-590.

21. Custers EJ (2010) Long-term retention of basic science knowledge: a review study. *Advances in Health Sciences Education* 15(1):109-128.

22. Haegens S, Händel BF, & Jensen O (2011) Top-Down Controlled Alpha Band Activity in Somatosensory Areas Determines Behavioral Performance in a Discrimination Task. *The Journal of Neuroscience* 31(14):5197.

23. Palva S & Palva JM (2007) New vistas for alpha-frequency band oscillations. *Trends in neurosciences* 30(4):150-158.

24. Haegens S, Nácher V, Luna R, Romo R, & Jensen O (2011) α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences* 108(48):19377-19382.

25. Jensen O & Mazaheri A (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Frontiers in human neuroscience* 4:186.

26. Klimesch W, Sauseng P, & Hanslmayr S (2007) EEG alpha oscillations: the inhibition–timing hypothesis. *Brain research reviews* 53(1):63-88.

27. Dumas G, Nadel J, Soussignan R, Martinerie J, & Garnero L (2010) Inter-Brain Synchronization during Social Interaction. *PLOS ONE* 5(8):e12166.

28. Jammalamadaka S & Sengupta A (2001) *Topics in circular statistics* (World Scientific Publishing, Singapore).

29. Pérez Fernández A, Carreiras M, & Duñabeitia JA (2017) Brain-to-brain entrainment: EEG interbrain synchronization while speaking and listening. *Scientific reports* 7:4190.

30. Michel CM & Murray MM (2012) Towards the utilization of EEG as a brain imaging tool. *Neuroimage* 61(2):371-385.

31. Berkman ET & Falk EB (2013) Beyond brain mapping: Using neural measures to predict real-world outcomes. *Current directions in psychological science* 22(1):45-50.

32. Ben-Yakov A, Honey CJ, Lerner Y, & Hasson U (2012) Loss of reliable temporal structure in event-related averaging of naturalistic stimuli. *Neuroimage* 63(1):501-506.

33. Dumas G, Chavez M, Nadel J, & Martinerie J (2012) Anatomical connectivity influences both intra-and inter-brain synchronizations. *PloS one* 7(5):e36414.

34. Guevara R, *et al.* (2005) Phase synchronization measurements using electroencephalographic recordings. *Neuroinformatics* 3(4):301-313.

35. Schiff SJ (2005) Dangerous phase. *Neuroinformatics* 3(4):315-317.

36. Pan Y, Novembre G, Song B, Li X, & Hu Y (2018) Interpersonal synchronization of inferior frontal cortices tracks social interactive learning of a song. *Neuroimage* 183:280-290.

37. Liu Y, *et al.* (2017) Measuring speaker–listener neural coupling with functional near infrared spectroscopy. *Scientific reports* 7:43293.

38. Giraud A-L & Poeppel D (2012) Cortical oscillations and speech processing: emerging computational principles and operations. *Nature neuroscience* 15(4):511.

39. Dikker S & Pylkkänen L (2013) Predicting language: MEG evidence for lexical preactivation. *Brain and language* 127(1):55-64.

40. Golumbic EMZ, *et al.* (2013) Mechanisms underlying selective neuronal tracking of attended speech at a "cocktail party". *Neuron* 77(5):980-991.

41. Lakatos P, Karmos G, Mehta AD, Ulbert I, & Schroeder CE (2008) Entrainment of neuronal oscillations as a mechanism of attentional selection. *science* 320(5872):110-113.

42. Pfurtscheller G, Stancak Jr A, & Neuper C (1996) Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. *International journal of psychophysiology* 24(1-2):39-46.

43. Busch NA, Dubois J, & VanRullen R (2009) The phase of ongoing EEG oscillations predicts visual perception. *Journal of Neuroscience* 29(24):7869-7876.

44. Mathewson KE, Gratton G, Fabiani M, Beck DM, & Ro T (2009) To see or not to see: prestimulus α phase predicts visual awareness. *Journal of Neuroscience* 29(9):2725-2732.

45. Doesburg SM, Green JJ, McDonald JJ, & Ward LM (2009) From local inhibition to long-range integration: a functional dissociation of alpha-band synchronization across cortical scales in visuospatial attention. *Brain research* 1303:97-110.

46. Freunberger R, Fellinger R, Sauseng P, Gruber W, & Klimesch W (2009) Dissociation between phase-locked and nonphase-locked alpha oscillations in a working memory task. *Human brain mapping* 30(10):3417-3425.

47. Lobier M, Palva JM, & Palva S (2018) High-alpha band synchronization across frontal, parietal and visual cortex mediates behavioral and neuronal effects of visuospatial attention. *Neuroimage* 165:222-237.

48. Palva S & Palva JM (2011) Functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Frontiers in psychology* 2:204.

49. Bhattacharya J, Petsche H, & Pereda E (2001) Long-range synchrony in the γ band: role in music perception. *Journal of Neuroscience* 21(16):6329-6337.

50. Kothe C (2014) Lab Streaming Layer (LSL). Available at: https://github.com/sccn/labstreaminglayer

51. 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(1):9-21.

52. Jung T-P, *et al.* (1998) Extended ICA removes artifacts from electroencephalographic recordings. *Advances in neural information processing systems*, pp 894-900.

53. Oostenveld R, Fries P, Maris E, & Schoffelen J-M (2011) FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational intelligence and neuroscience* 2011:1.

54. Burgess AP (2013) On the interpretation of synchronization in EEG hyperscanning studies: a cautionary note. *Frontiers in human neuroscience* 7:881.

55. Benjamini Y & Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B (Methodological)* 57(1):289-300.

Figure Legends

Figure 1. Experimental setup and timeline. (A) Four students and a teacher were concurrently measured with EEG during a science class; (B) The lesson comprised four mini-lectures, each followed by a post-test. Pre-test and delayed post-tests were administered one week prior to and one week following the EEG recording session.

Figure 2. Behavioral results and calculation of brain-to-brain synchrony.

(A) Proportion of correct answers (content knowledge) for the pre-test, immediate post-, and delayed post-tests. Each dot corresponds to one participant, horizontal black lines depict the mean for all students; grey regions represent one standard deviation; (B) Brain-to-brain synchrony (CCorr) values were computed between each student and all other students in the group.

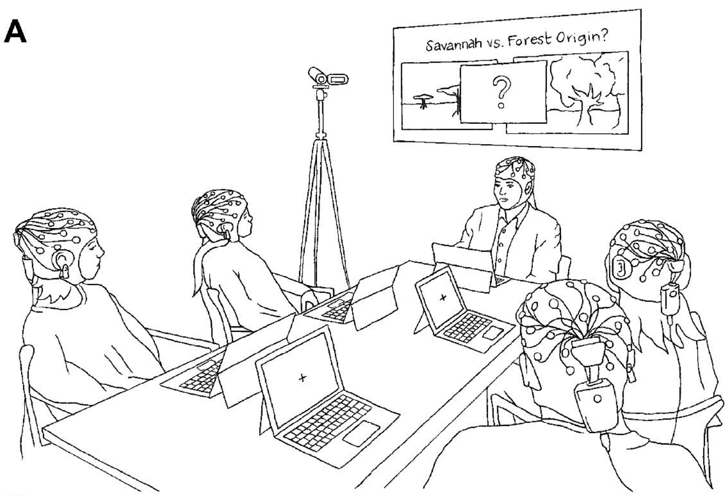
Figure 3. Brain-to-brain synchrony better predicts delayed retention than individual brain measures. Alpha-band brain-to-brain synchrony (A), but not alpha-band intra-brain synchrony (B), significantly predicted delayed retention; (C) The distribution of correlation values between alpha-band intra-brain synchrony and delayed retention generated by randomly resampling 11 electrode pairs; (D) The relationship between relative alpha power and delayed retention; (E-F) Spatial distribution of the relationship between delayed retention and alpha-band brain-to-brain synchrony (E) or alpha power (F). The color bar displayed applies to both (E) and (F). Electrodes circled in pink were found to significantly predict delayed retention ($p<0.05$; FDR corrected).

Figure 4. Moment-to-moment variations in alpha-band brain-to-brain synchrony and learning. (A) Question-specific time intervals where relevant content was delivered by the teacher were identified based on the lecture transcript. Moment-to-moment variations in alpha-band brain-to-brain synchrony (B), but not alpha power (C), significantly discriminated between information that was learned and not learned at the individual question level.

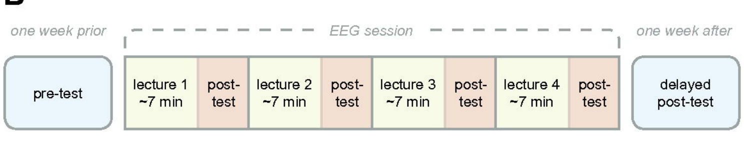
Figure 5. Time-lagged cross-correlation between brain-to-brain synchrony and delayed retention. (A) Correlation between student-to-student brain synchrony and delayed retention as a function of temporal lag between students' brain activity; (B) Correlation between student-to-teacher brain synchrony as a function of temporal lag between the student's and teacher's brain activity. For both (A) and (B), cross-correlation was computed for each electrode pair and then

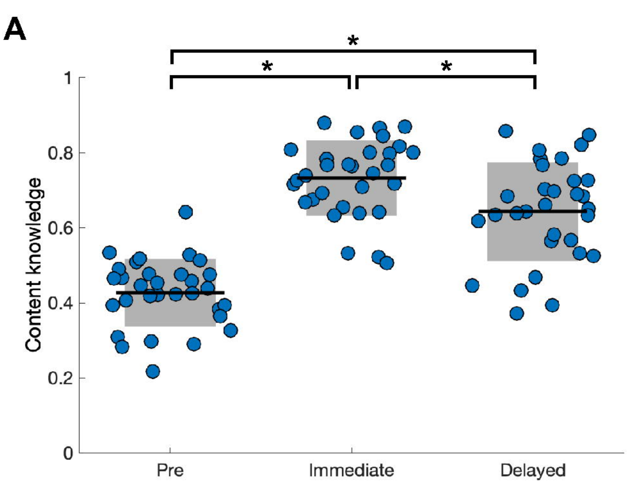
averaged across pairs (total of 1024 pairs). (C) Spatial distribution of the temporal lag that produced the highest correlation between student-to-teacher brain synchrony and delayed retention. For this analysis, synchrony was computed only between matched electrodes (e.g. O1-O1). Electrodes are color coded by temporal lag: student precedes (yellow) to teacher precedes (blue).

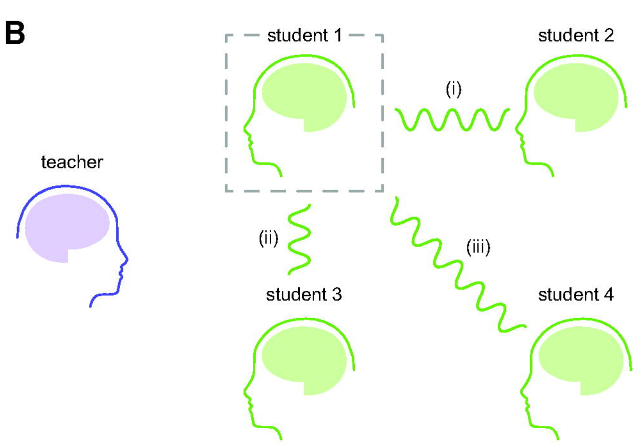
A

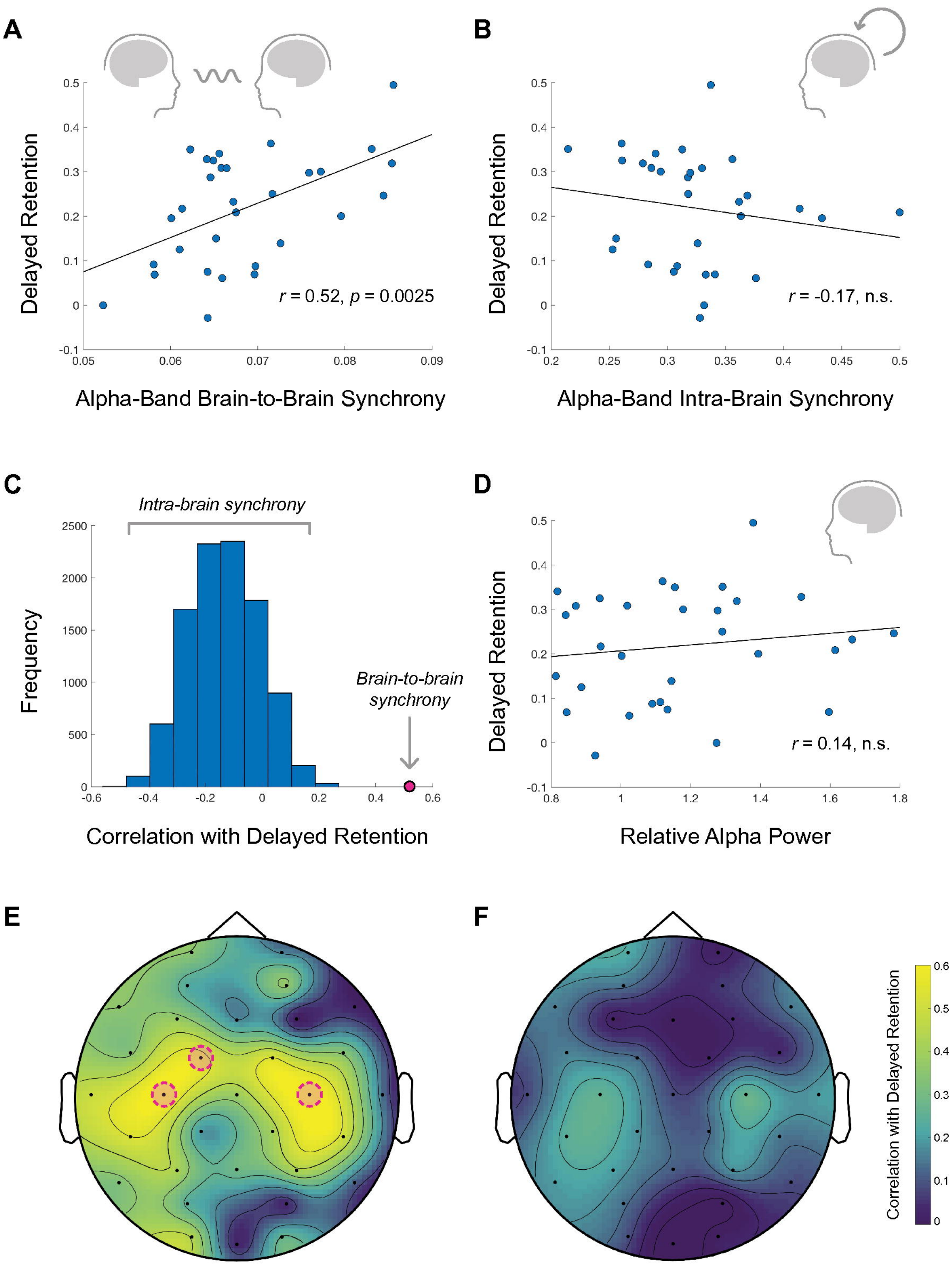

Savannah vs. Forest Origin?
?

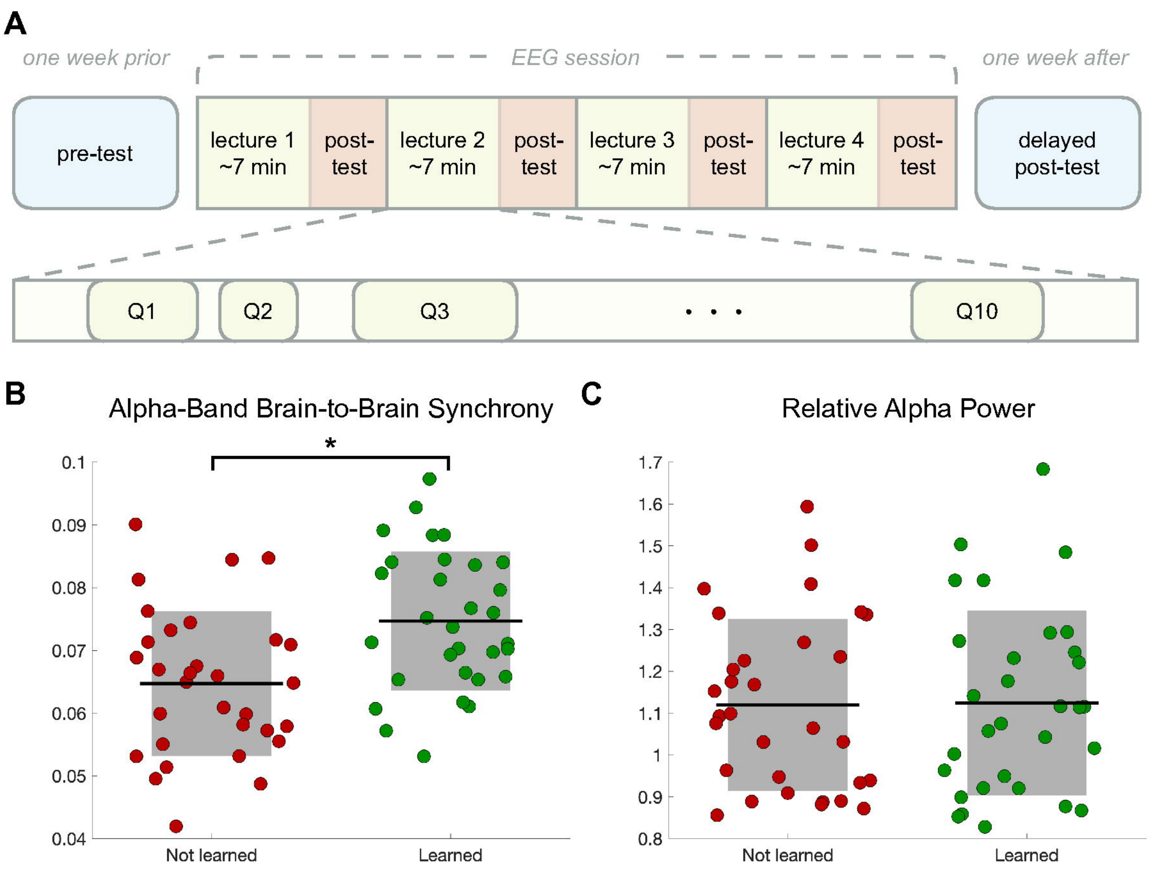
B

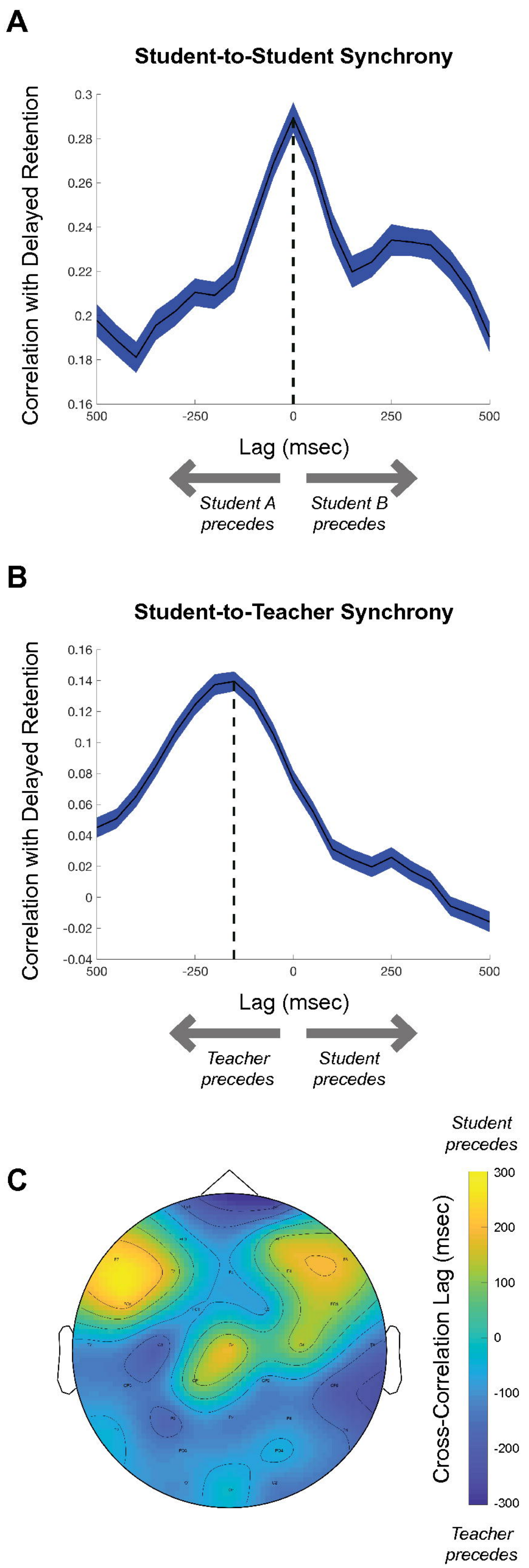

one week prior
EEG session
one week after
pre-test
lecture 1 ~7 min
post-test
lecture 2 ~7 min
post-test
lecture 3 ~7 min
post-test
lecture 4 ~7 min
post-test
delayed post-test


A
*
*
*
1
0.8
0.6
0.4
0.2
0
Content knowledge
Pre
Immediate
Delayed


B
student 1
student 2
(i)
teacher
(ii)
(iii)
student 3
student 4


A
B
Delayed Retention
r = 0.52, p = 0.0025
Alpha-Band Brain-to-Brain Synchrony
r = -0.17, n.s.
Alpha-Band Intra-Brain Synchrony
C
D
Intra-brain synchrony
Frequency
Brain-to-brain synchrony
Correlation with Delayed Retention
r = 0.14, n.s.
Relative Alpha Power
E
F
Correlation with Delayed Retention


A
one week prior
EEG session
one week after
pre-test
lecture 1 ~7 min
post-test
lecture 2 ~7 min
post-test
lecture 3 ~7 min
post-test
lecture 4 ~7 min
post-test
delayed post-test
Q1
Q2
Q3
Q10
B
Alpha-Band Brain-to-Brain Synchrony
*
0.1
0.09
0.08
0.07
0.06
0.05
0.04
Not learned
Learned
C
Relative Alpha Power
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
Not learned
Learned


A
Student-to-Student Synchrony
Correlation with Delayed Retention
0.3
0.28
0.26
0.24
0.22
0.2
0.18
0.16
500
-250
0
250
500
Lag (msec)
Student A precedes
Student B precedes
B
Student-to-Teacher Synchrony
Correlation with Delayed Retention
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
500
-250
0
250
500
Lag (msec)
Teacher precedes
Student precedes
C
Student precedes
Cross-Correlation Lag (msec)
300
200
100
0
-100
-200
-300
Teacher precedes