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Teams on the same wavelength perform better: Inter-brain phase synchronization constitutes a neural substrate for social facilitation

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ABSTRACT

Working together feels easier with some people than with others. We asked participants to perform a visual search task either alone or with a partner while simultaneously measuring each participant's EEG. Local phase synchronization and inter-brain phase synchronization were generally higher when subjects jointly attended to a visual search task than when they attended to the same task individually. Some participants searched the visual display more efficiently and made faster decisions when working as a team, whereas other dyads did not benefit from working together. These inter-team differences in behavioral performance gain in the visual search task were reliably associated with inter-team differences in local and inter-brain phase synchronization. Our results suggest that phase synchronization constitutes a neural correlate of social facilitation, and may help to explain why some teams perform better than others.

Introduction

Teamwork is a prominent feature of today's western working cultures in fields as diverse as science, healthcare, or business (Hall and Weaver, 2001; Hoegl and Gemuenden, 2001; Wuchty et al., 2007). In economics and organizational psychology much research has sought to capture the characteristics of good teamwork, to measure teamwork quality and to identify beneficial aspects of team composition (Ancona and Caldwell, 1992; Bell, 2007; Keller, 2001). Most of the empirical work in these fields did not consider neural mechanisms that facilitate teamwork, but has relied instead on interview protocols and measures of work quality. Delineating the neural mechanisms relevant for teamwork would advance our mechanistic understanding of team dynamics, including the question why working together feels easier with some people than with others.

Social neuroscience, in turn, has often focused on single individuals in 'passive' social contexts, such as observing pictures of social encounters, and has paid relatively little attention to the study of teams or groups. In recent years, however, 'hyperscanning' techniques

(Montague et al., 2002), which refer to the simultaneous assessment of the brain activity of more than one person, have helped neuroscientists to study the inter-personal dynamics of neural processes. Experiments using this technique have given rise to a body of research examining the neural processes observed in socially interacting individuals (Babiloni et al., 2007; Dumas et al., 2010; Lindenberger et al., 2009; Sänger et al., 2012, 2013). This move from 'one-body' neuroscience to 'two-body neuroscience' (Dumas et al., 2010) or 'second-person neuroscience' (Schilbach et al., 2013) was informed by theoretical concepts that emphasize the interactive nature of human cognition (Varela et al., 1992). According to these concepts, brain functions cannot be fully understood by observing neuronal subsystems or individuals in isolation; instead, the dynamic interactions among brain, behavior, and environment (Kelso, 1994; Thompson and Varela, 2001) need to be taken into account. In line with this assertion, studies of interacting individuals (Freundlieb et al., 2015; Lachat et al., 2012; Sebanz et al., 2006; Sebanz et al., 2003) have identified cognitive processes that would have gone unnoticed if individuals had been studied in isolation only. For example, Freundlieb et al. (2015)

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examined when participants adopted another's visuospatial perspective. Only if the other was perceived as an intentionally acting agent, participants consistently adopted their visuospatial perspective.

In addition to representing the partner's intention, neural mechanisms are likely to serve as a substrate for coordinated perception, action, or both. Hyperscanning studies have observed enhanced synchronization of neural processes in interactive paradigms, such as gesturing, finger tapping, guitar play, card play, or speech (for review, see Sänger et al. (2011)). It has been suggested that neural synchronization during joint action may go beyond similarities in perceptual input and motor output and also reflect the synchronization of cognitive processes. To substantiate this point, researchers have tried to extract 'functional relevance' from patterns of neural synchronization. For example synchronization between signal time courses across brains was observed to correlate with story comprehension in speaker-listener settings (Stephens et al., 2010). Similarly, neural synchronization across brains has been reported to reflect leader/follower roles of the participants (Jiang et al., 2015). Cui et al. (2012) reported increased interpersonal coherence in superior frontal cortex during cooperation but not during competition using near-infrared spectroscopy. Sänger et al. (2012) and Konvalinka et al. (2014) were able to distinguish leader/follower roles based on stronger phase locking and stronger frontal alpha suppression in leaders. These initial results fuel the hypothesis that inter-personal as well as intra-personal neural dynamics capture functional characteristics of social interaction.

So far, the majority of studies in the field of hyperscanning research ha focused on joint action. The settings explored range from highly restricted tasks such as finger tapping (Konvalinka et al., 2014) to ecologically valid tasks such as guitar duet play (Lindenberger et al., 2009; Müller et al., 2013; Sänger et al., 2012, 2013) or conversation (Jiang et al., 2015). A major critique to many of the hyperscanning studies mentioned has been the lack of a proper control condition, namely, a condition that is missing the social interactive aspect but keeps most aspects of perceptual input and motor output constant relative to the social condition. Here, we propose a paradigm that includes such a control condition by investigating an essential aspect of joint action that does not involve motor output: joint attention. Joint attention has been found to play a crucial role in social interaction (Tomasello, 1995) and particularly joint action (Sebanz et al., 2006). Joint attention entails that "two individuals know that they are attending to something in common" (Tomasello, 1995, p.106), and can be seen as providing "a basic mechanism for sharing representations of objects and events" (Sebanz et al., 2006, p.70). Hence, it constitutes a core feature of joint action, and of teamwork in general.

Joint action typically requires joint attention, but the inverse is not necessarily true, that is, there can be joint attention without joint action, such as when people are jointly looking at a photo. Also, the very same object (e.g., photo) can also be attended to alone. Thus, comparing joint attention to individual attention makes possible what hyperscanning studies have generally failed to achieve, namely, to compare two conditions, in the absence of synchronized motor activity, that vary on the social dimension without varying the perceptual setup.

The aim of the present study was to assess whether synchronization in inter-brain dynamics reflects a modulation of cognitive processes by social facilitation or merely the presence of a common driver, such as shared perceptual input. Social facilitation subsumes changes in behavioral performance associated with the passive or active presence of another person (Allport, 1920; Zajonc, 1965). For this purpose, we chose to investigate differences between individual and joint attention. We embedded individual and joint attention in a visual search task, which was carried out either individually or in dyadic teams. This setup enabled us to first analyze differences in neural dynamics between individual and joint attention and to then relate these neural differences to behavioral performance differences between individual work and teamwork. This teamwork went beyond the period of initial joint attention studied in the first step and includes the coordination of a

joint response. The current study thus explores joint attention as an important aspect of teamwork in two ways: first by analyzing intra- and inter-brain neural dynamics of joint attention and second by relating them to behavioral team performance proficiency (see Fig. 2).

To investigate the performance benefits of joint attention, we used an adaptation of Miller's Race Model Inequality (RMI; (Miller, 1982; Ulrich et al., 2007)) to separate the collaborative benefit of teamwork from the benefit that would be expected under the assumption of processing independence. Miller's RMI was originally developed to test whether two target signals were processed in one mind as a race between independent activations (with the faster signal determining the response on each occasion) or whether the signals were co-activated (signal activations were combined prior to the response decision). We apply the same logic and method here, testing whether responses by two-person teams reflect a race between independently processing individuals (with the faster person eliciting the valid response) or whether teams collaborated prior to the response (i.e., shared the task and exchanged information).

It should be kept in mind that team performance has both benefits and costs. On the one hand, cognition can be made more efficient when collaborators divide the cognitive load of the task (Houtkamp and Roelfsema, 2009). On the other hand, coordinating joint performance through speech or gesture requires effort and time (Brennan et al., 2008). Our measure of team performance captures some mix of these benefits and costs and reflects the overall collaborative benefit/cost for each team. If inter-brain dynamics indeed reflect the synchronization of cognitive processes, they should vary with the degree (and potentially the benefit) of social interaction, and might correlate (positively) with behavioral team performance. Thus, the present study was guided by two specific hypotheses: (a) Inter-brain synchronization will be greater in a social context than in a comparable setting that does not engage joint attention; (b) between-pair differences in inter-brain neural dynamics will correlate with between-pair differences in task performance.

Material and methods

Participants and data analysis

Research participants

Fifty-two healthy individuals participated in the study, forming a total of 26 non-overlapping pairs, 13 male-male pairs and 13 female-female pairs. The age of the participants ranged from 18 to 30 years (mean age = 25.2, SD = 3.43). One male pair had to be excluded from the analysis due to a technical problem, thus 25 pairs (13 female, 12 male) were retained in the EEG data analysis. Four pairs (three female, one male) had to be excluded from behavioral data analysis due to technical problems with data recording. Thus 21 pairs (10 female, 11 male) were included in the behavioral analyses, and the brain-behavior regression analyses. Participants were randomly assigned to pairs and did not know each other prior to the experimental session. At the beginning of each experimental session, participants filled out questionnaires that assessed personality (NEO Five-Factor-Inventory, Costa and McCrae, 1992) and interpersonal values (Circumplex scales of interpersonal values, Locke, 2000). While being prepared for the EEG session the two participants were placed in front of each other and asked to talk to get to know one other. All pairs talked about study subjects and hobbies/interests for ca. 10 min, after which the experimenter asked them to stop talking and to enter the EEG cabin. All pairs took part in another EEG-experiment before starting the visual search task. All participants volunteered for the experiment, and gave their written informed consent prior to their inclusion in the study. The Ethics Committee of the Max Planck Institute for Human Development approved the study. The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.
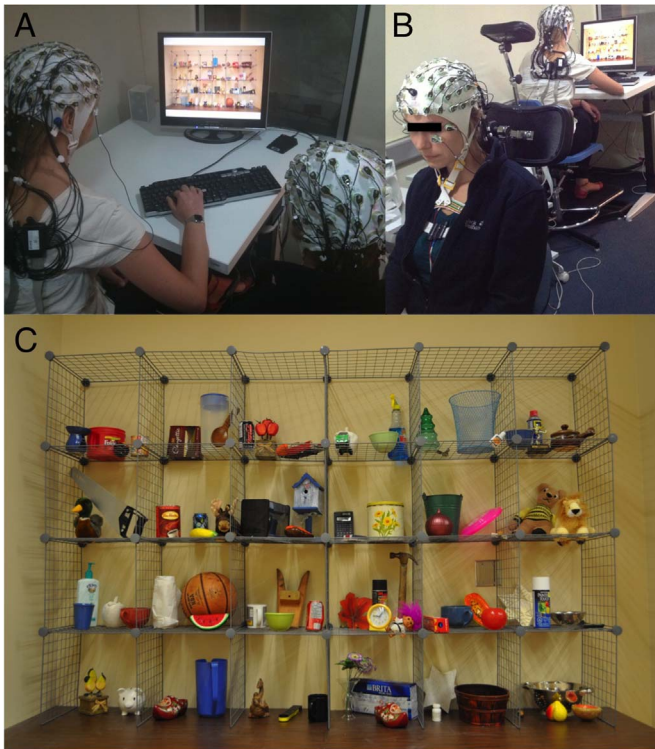
Fig. 1. Experimental set-up in the electromagnetically shielded cabin. A. EEG measurement of one participant in the individual condition. B. Two participants being measures in the social condition. C. Example of a search display.

Behavioral method: enumeration visual search task

Experimental displays depicted shelves containing objects commonly found in a home or office (see Fig. 1 for an example display). Each display contained 82 distractor objects in one of four different configurations, and zero, one, or two of four possible target objects. The same target never appeared twice in the same display and each appeared equally often in each quadrant. This generated 356 displays: four without a target, 64 with one target, and 288 with two targets. Experimental sessions consisted of a total of 42 trials: 14 trials each with zero, one, and two targets. Search displays for each session were selected using weighted random sampling of the 356 total search displays. Displays subtended 37°×30° visual angle on a 19-inch computer monitor (screen resolution 1280×1024 pixels). Matlab 2010a software and Psychtoolbox3 were used to control the experiment.

During the experiment participants indicated as rapidly and accurately as possible the number of targets present in a display by pressing keys labeled '0', '1', and '2'. Participants completed two experimental sessions: one individually (individual condition) and one as a team with another participant (social condition). Session order was randomly counterbalanced across pairs (individual first, social first). When completing the task individually, participants sat in front of their respective computers and entered responses on their respective keyboard. When completing the task as a team, participants sat side by side in front of a shared computer and entered one joint response using a shared keyboard. One participant replied during the first half of the experiment, the other participant during the second half. Teams were instructed to use whatever strategy they thought was best for working together and individuals were instructed to use whatever strategy they thought was best. Participants received feedback about their percentage of correct responses every 7 trials. Teams were allowed to interact as they wished (talking, gesturing, touching, etc.). Both teams and individuals were instructed to avoid unnecessary movements to prevent EEG artifacts. Measurements took place in an electromagnetically shielded cabin.

EEG data acquisition

The EEG was recorded with active 64 Ag/AgCl electrodes per person, placed according to the international 10–10 system, with the reference electrode at the right mastoid (actiCAP, Brain Products, Munich, Germany). Separate amplifiers (BrainAmp DC, BrainProducts, Munich, Germany) with separate grounds were used for each individual, linked to one computer. Vertical and horizontal electrooculograms (EOGs) were recorded to control for eye blinks and eye movements. All channels were recorded at a sampling rate of 5000 Hz. A 0.016–1000 Hz bandpass filter was used. Triggers were sent from the stimulus presentation computer to the EEG-recording system for stimulus onset. One stimulus computer with three synchronized screens was used for stimulus presentation. Two screens were placed inside the cabin whereas one control display was placed outside the EEG cabin to monitor stimulus presentation.

Behavioral data analysis

Following Brennan and Enns (2014), correct RT and accuracies were first subjected to a repeated measures analysis of variance (ANOVA) examining the factors of condition (team, average individual) and session order (individual first, social first). In a second step, the algorithm and MATLAB routines provided in Ulrich et al. (2007) were adapted to compare team performance to the expected performance of the two individuals under the independence assumption (Brennan, 2014; Brennan and Enns, 2014).

Team efficiency was calculated in three steps. First, cumulative density functions (CDFs) of each team's correct RTs were generated (CDF_{team}). Each CDF contained a total of 42 correct RTs, minus the errors committed. Second, CDFs of the optimal performance of two individuals under an assumption of independence were generated by combining the two individual team members' correct RTs into one distribution ($CDF_{optimal\ individual}$), and then truncating this distribution at the number of RTs in CDF_{team}. Third, a team efficiency value was generated for each team by subtracting CDF_{team} from $CDF_{optimal\ individual}$. This method approximates the statistically expected distribution of team responses if the two individuals worked independently by assuming that the faster of the two would respond in each trial, and compares it to the actual team distribution. The difference between the two distributions provides an index of team benefit.

EEG data analysis

Preprocessing

EEG data were filtered with a high-pass filter at 0.5 Hz and resampled at 1000 Hz. Thereafter, they were subjected to semi-automatic independent component analysis (Vigário, 1997) as implemented in Brain Vision Analyzer 2 as Ocular Correction ICA (Brain Products). This algorithm is optimized to detect and highlight components that likely reflect eye movements to minimize possible confusion with components reflecting, e.g., delta activity. Mean slope algorithm was used for blink detection. By using a fast ICA extended algorithm for ICA decomposition, one component was extracted per EEG channel. All EEG electrode channels were included (minus reference and eye electrode channels) yielding a total of 60 components. We visually inspected topographies and time courses of all components and rejected components that reflected blinks, horizontal eye movements, ECG, muscle activity and line noise. Across subjects on average twelve out of the 60 components were rejected. Spontaneous EEG activity was then segmented into epochs of 1200 ms (200 ms before stimulus onset until 1000 ms after stimulus onset), and we removed all epochs containing remaining artifacts from head or body movements by visual inspection. In the alone condition, on average 38 out of 45 trials (SD = 4.58) were included in the analysis as artifact-free segments; in the social condition, on average 38 trials (SD = 4.11) were included. It is important to note that the EEG data analyzed was recorded during an
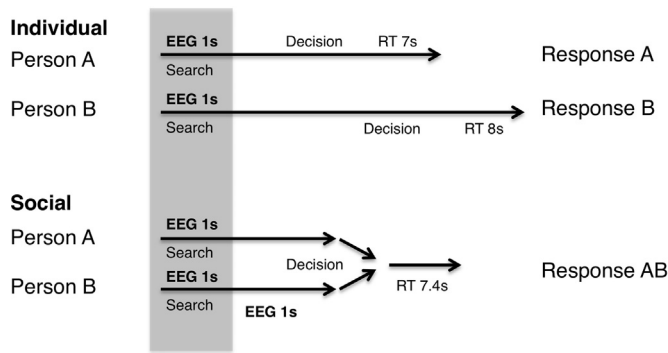
Fig. 2. Conceptualization of EEG analysis in relation to behavior. The hypothesized decision-making processes during one enumeration visual search trial in the individual and social condition is shown. Analyzed EEG epochs are highlighted in grey.

interval where no movement or decision-making was involved: only the first second after stimulus onset was analyzed out of an average trial duration of 7.4 s (see Fig. 2).

Synchronization measures

Segments were analyzed using a complex Morlet wavelet (c = 5) that transformed the EEG time series into a complex time-frequency signal for frequencies from 2 to 20 Hz, in steps of 2 Hz (10 frequency values in total). Two synchronization measures, *PLI* and *IPC*, were obtained from the corresponding time-frequency matrices (Müller et al., 2009). The phase locking index (*PLI*) reflects the invariance of phases at a single electrode across *N* trials in the time-frequency domain and is defined by

$$PLI_k(t,f) = \left| \frac{1}{N} \sum_n^N e^{j\varphi_k^n(t,f)} \right|, \quad j = \sqrt{-1}$$

where $\varphi_k^n(t,f)$ is the phase of the *n*th trial at time *t* and frequency *f* of a specific electrode *k*. The intra- and inter-brain phase coherence represents the degree of constancy in phase difference across *N* trials between two electrodes measured from one or two brains simultaneously. It is defined in a similar way as

$$IPC_{kl}(t,f) = \left| \frac{1}{N} \sum_n^N e^{j\Delta\varphi_{kl}^n(t,f)} \right|, \quad j = \sqrt{-1}$$

with the phase difference between electrodes *k* and *l* at trial *n*, time *t* and frequency *f,* being equal to:

$$\Delta\varphi_{kl}^n(t,f) = mod(\varphi_k^n(t,f) - \varphi_l^n(t,f), 2\pi)$$

The phase difference is calculated between two electrodes of the same brain for intra-brain phase coherence or between two electrodes of two different brains for inter-brain phase coherence (IPC). We selected 21 electrodes per person (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, and O2) and included all possible pairs of these electrodes in this analysis. This selection reduces a possible bias in functional connectivity findings produced by volume conduction, while still covering the entire cortex (cf. Lindenberger et al., 2009; Sänger et al., 2012). We calculated P*LI* and intra-brain phase coherence per participant and *IPC* per pair.

PLI and intra-brain phase coherence capture phase locking within one individual brain, while *IPC* captures phase locking between two brains. All measures were calculated across all trials that were included in the analysis (mean 38 trials) and for each millisecond of the 1200 ms segment length.

Statistical evaluation of synchronization measures

Partial Least Squares is a multivariate statistical method that is suitable for revealing the relationship between two blocks of datasets, and has been used extensively in the neuroimaging literature (Abdi,

2010; McIntosh et al., 1996; McIntosh and Lobaugh, 2004). Here, it was used to examine associations between synchronization measures, on the one hand, and the vectors coding for the experimental design, on the other hand. The method is based on a decomposition of the covariance of the two blocks in a set of new variables that optimally relate them, with optimality referring to explaining as much of covariance with as few dimensions as possible.

In this study, we used two versions of the method: non-rotated contrast PLS ("nr-PLS") to test the specific hypotheses that differences in brain data co-vary with differences in condition or session order and mean centering task PLS ("mc-PLS") to explore the data for additional effects, e.g., for a possible interaction between condition and session order. As we had no strong a priori hypothesis for the exact 'shape' of a potential interaction between condition and session order, we made use of the mc-PLS data-driven approach.

Both PLS versions start by constructing a brain data matrix for each experimental group. Rows in this data matrix correspond to participants within condition and, thus, in our case, to participant pairs. Consequently the data matrix is made up of NPairs×NCondition rows. Columns in the data matrix correspond to all data points or elements (i.e., in our case, *PLI* values per electrode or *IPC* values for each pair of electrodes, across all frequencies and time points in either case). Then, participants' rows are averaged column-wise within conditions, and the data matrices of all groups are concatenated into a single matrix, **M**, with rows corresponding to conditions within groups (NConditions×NGroups, in total), and data elements for columns. At this point, in the case of the mcPLS, the grand average is removed by all conditions' rows column-wise, and the modified matrix **M** undergoes a singular value decomposition **U*****S*****V** = SVD(**M**), which yields three matrices: (i) the orthonormal matrix **V** of the *saliences of the contrasts* (i.e., the *task design latent variables* describing the relations among the conditions and groups of our design for each contrast); (ii) the orthonormal matrix **U** of *element saliences* that are proportional to the covariance of each data element with each one of the task contrasts (i.e., the *brain latent variables*); and (iii) the diagonal matrix **S** of *singular values* that are proportional to the variance explained by each contrast. The number of resulting singular values, one for each contrast, depends on the degrees of freedom of the design, being, in our case, NConditions×NGroups −1 = 3. Furthermore, the multiplication **B** = **M*****U** produces a matrix of *brain scores* that indicate the strength of the task effect of each contrast per participant pair and condition. In other words, the brain score of a particular participant pair for a specific contrast and condition is the covariation of the brain data of this participant pair for that condition with the corresponding brain latent variable vector of the contrast in question.

As for the nr-PLS, instead of undergoing a SVD, it requires an orthonormal matrix **C** of predefined contrasts to be tested as a priori hypotheses. Then, $\mathbf{U} = (\mathbf{C}^T * \mathbf{M})^T$, where $(.)^T$ is the operator of matrix transposition, **V** = **C**, and $s_i = \sqrt{\sum_j u_{ji}^2}$, where s_i are the elements of the diagonal of **S** (one for each contrast) and u_{ji} are the elements of **U**. In our case, we tested the main effects of conditions and session order, i.e, contrasts [1 −1 1 −1] and [1 1 −1 −1] before normalization, respectively.

PLS addresses the problem of multiple comparisons for statistical significance via a permutation test and the problem of element-wise reliability via a bootstrap resampling test. The permutation test is performed on the singular values with resampling of the initial data matrices across conditions and groups without replacement. This permutation test yields a p-value for each task latent variable, i.e., for each contrast. For the bootstrap test, the initial data matrix is resampled with replacement within conditions and groups. For the task latent variables we plotted intervals of 95% confidence. For the brain latent variables, we calculated bootstrap ratios by dividing each element with its standard error as calculated by the corresponding bootstrap sample distribution. Bootstrap ratios greater than 2.5758
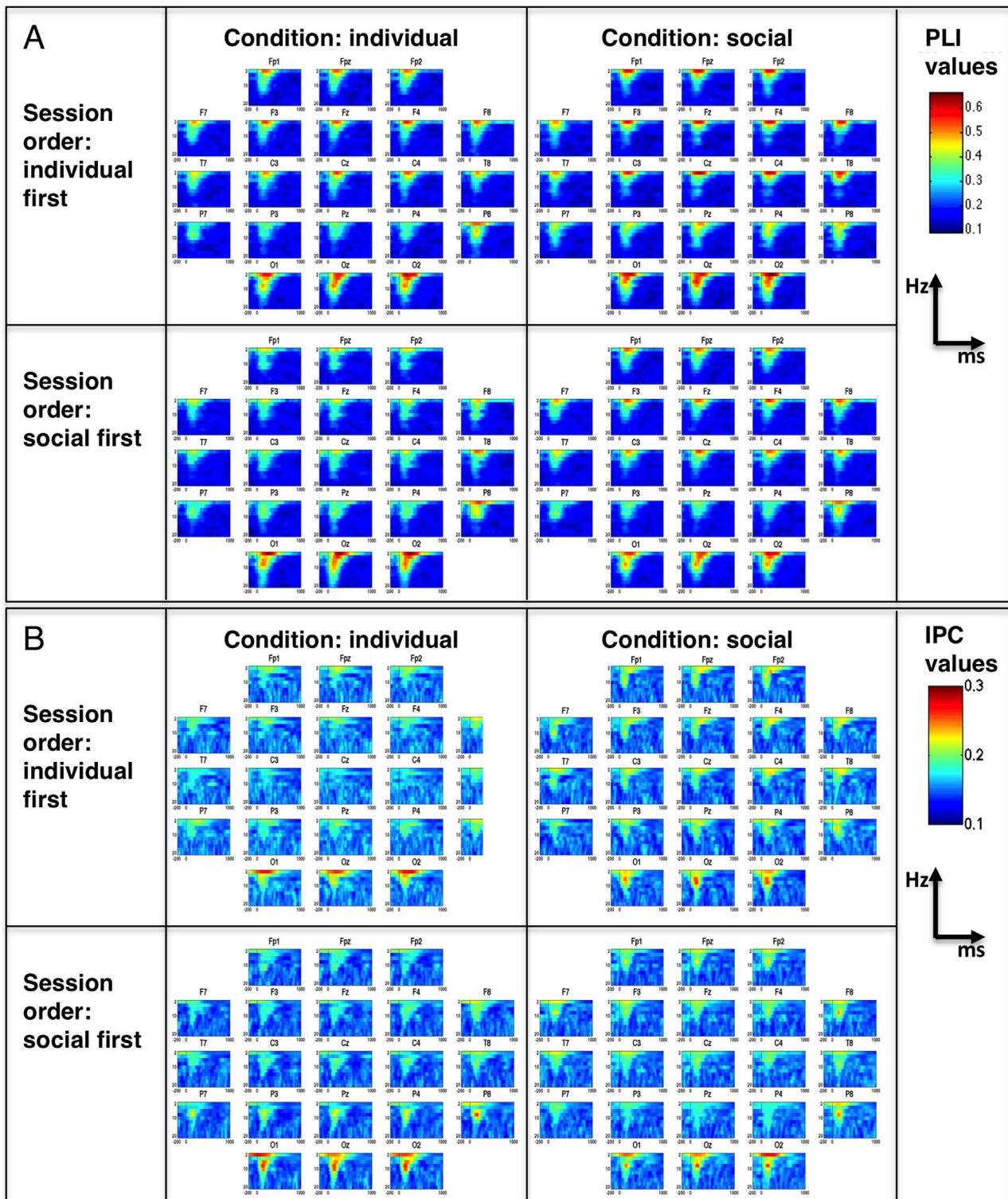
Fig. 3. Grand average *PLI* and *IPC* results, grouped by condition and session order. A. *PLI* values were averaged across all subjects at each of the 21 electrode sites for each frequency band (2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 Hz). Electrode sites are indicated above each subplot. The colormap is anchored at the lowest and highest values. B. *IPC* values from one electrode site in subject A to all other electrode sites in subject B were averaged for each frequency band (2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 Hz). This averaging procedure was repeated for all 21 electrode sites of subject A. Values were then averaged across all pairs. Electrode sites are indicated above each subplot. The colormap is anchored at the lowest and highest values.

approximate the 99th two-tailed percentile for a particular element (see Z-score table). In the connectivity plots we only plotted connections that exceeded this value. We constructed connectivity plots in Matlab, using the BrainNet Viewer software (Xia et al., 2013).

Correlations between neural and behavioral measures

PLS analyses create a latent variable similar to a factor. This latent variable represents the pattern of neural synchronization that best distinguishes the behavioral conditions across all individuals. A ,brain

score', similar to a factor score, can be computed for each pair for each condition that reflects how strongly that pair expresses the corresponding neural pattern. We computed brain scores for each pair using the latent variables identified by the PLS analyses. We then entered these brain scores into a series of three regression analyses and tested them hierarchically with model comparisons to evaluate how well brain phase synchronization predicted behavioral team performance. We also calculated mean and difference scores within dyads for the NEO-Five-Factor-Inventory (for all five domains) and for the Circumplex scales of interpersonal values (for CSIV mean) to assess correlations between personality measures, neural measures, and team efficiency.

Results

Behavioral results

Correct response time (RT) and accuracy

Teams generally responded faster (mean difference = 1.72 s, $F_{(1,194)} = 7.43$, $p < 0.01$) and less accurately (mean difference = 17%, $F_{(1,194)} = 42.73$, $p < 0.01$) than average individuals tested alone. These analyses also indicated that the condition tested first was slower in *RT* (mean difference = 2.08 s, $F_{(1,194)} = 27.94$, $p < 0.01$) and more accurate (mean difference = 12%, $F_{(1,194)} = 16.74$, $p < 0.01$) than the same condition tested second. Finally, social dimension interacted with session order in *RT*, such that when the social condition was tested second it resulted in larger gains in *RT* (mean difference = 5.30 s, $F_{(1,194)} = 19.95$, $p < 0.01$) than when the individual condition was tested second (mean difference = 0.45 s). Search accuracy did not interact in this way ($F_{(1,194)} < 1.0$).

Team efficiency

Based on RMI, we calculated and compared *RT* cumulative density functions for team and individuals to control for the statistical advantage of sampling from two instead of one response distribution. Specifically, we compared the optimal individual cumulative density function with the team cumulative density function using multiple Bonferroni-corrected paired sample t-tests at four percentiles. This analysis showed that two-person team performance was not reliably faster than optimal individual performance, ($t(21) = 0.56$, 0.38, 0.84, 3.70, -2.01, at percentiles 0.20, 0.40, 0.60, and 0.80, respectively, all $p > 0.65$). Though team performance, on average, did not surpass expectations based on individual performance, team efficiency (values are still appropriate to compare individual and team performance, and to compare different teams with one another. Importantly, team efficiency scores varied between teams (min = −8466 ms, max = 6012 ms), indicating that the benefits and collaboration outweighed the costs for some teams, while for others the costs outweighed the benefits.

EEG results

Given that we observed an interaction between social dimension and session order in the behavioral data, we approached the EEG data analysis along the same lines: separating the analysis in terms of social dimension (individual/social) as well as session order (individual condition first/ social condition first).

Phase-locking index

Grand average across pairs showed generally higher phase locking in the social condition, especially at low frequencies and frontal sites (see Fig. 3).

Fig. 4 shows PLS-based statistical significance plots. Mc-PLS contrasting *PLI* in both conditions grouped by session order did not reveal any significant differences between groups or conditions ($p > 0.1$ for all latent variables). Testing with Nr-PLS, specifically the hypothesis that differences in condition or session order co-varied
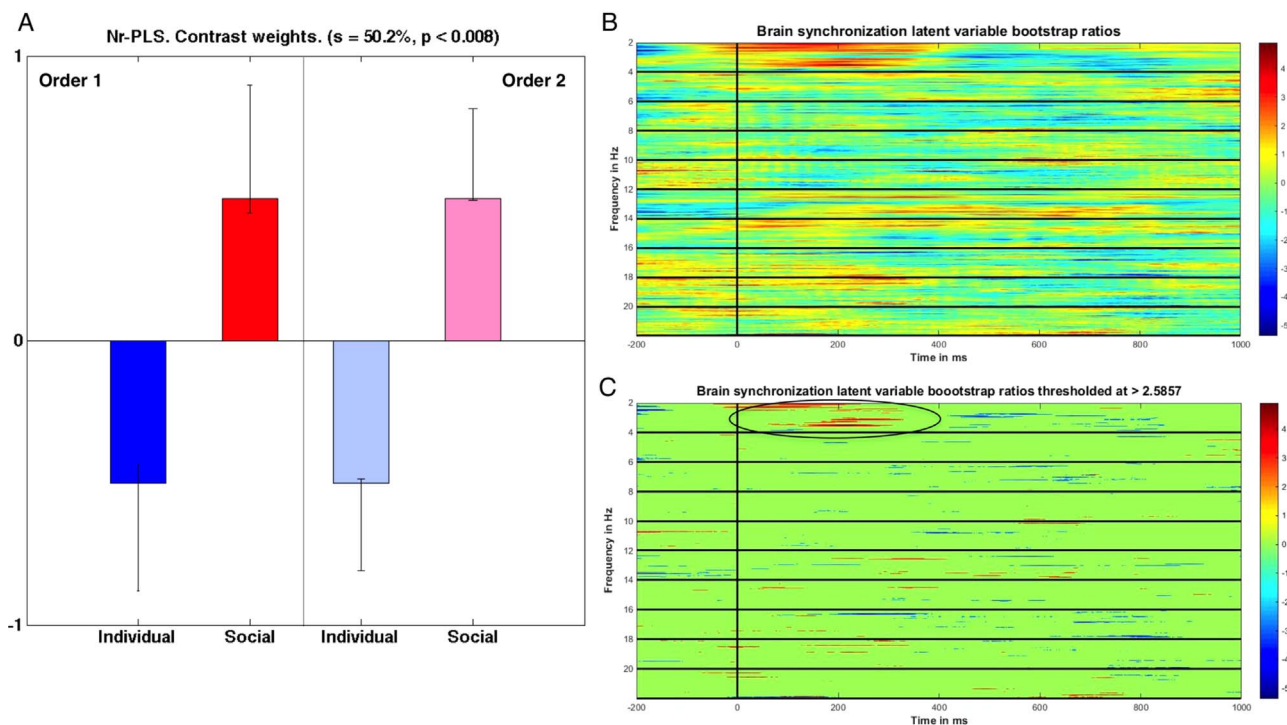
Fig. 4. Nr-PLS on *PLI* revealed higher *PLI* values in the social condition. A. Mean of subjects' brain scores per condition, mean-centered and normalized with the corresponding singular value (s), and 95% confidence intervals (CI) derived from the bootstrap test. Order 1 = session order with the individual condition first. Order 2 = session order with the social condition first. B. Brain synchronization latent variable bootstrap ratios before thresholding. Each horizontal line corresponds to one electrode at the indicated frequency (42 channels per frequency, grouped from frontal to occipital within frequencies). The colormap is anchored at the lowest and highest values. X-axis: time in ms; Y-axis: channels grouped by frequency (black lines indicate frequency boundaries) C. Analogue to (B) with brain synchronization latent variable bootstrap ratios thresholded at bootstrap ratios > 2.5857 (99% CI). Strongest effects are indicated by black ellipses.

with *PLI*, showed no significant effect for session order either (p = 0.92), but a significant main effect for condition (p < 0.01). A strong increase of synchronization during the social condition was especially observed for the 2 Hz frequency bin.

Intra- and inter-brain phase coherence

Grand average across all pairs and all electrodes showed a difference in *IPC* similar to the pattern observed for *PLI* (Fig. 3). Generally, *IPC* was increased in the social condition relative to the individual condition. As with *PLI*, we assessed *IPC* with two PLS analyses. A nr-PLS contrasting conditions and grouping by session order showed no effect for session order (p = 0.53), but a significant main effect for social condition (p < 0.01, see Fig. 5). With Mc-PLS we found a contrast that showed a difference between conditions, modulated by session order (see Fig. 5). The first latent variable depicting this interaction explained 35.5% of the variance of *IPC* at a significance level of p < 0.005. The other latent variables did not show any significant effects (p > 0.1 for all latent variables). The patterns of brain latent variables' bootstrap ratios for both PLS analyses were highly similar to each other (see Fig. 5), suggesting that social condition was indeed a major modulator of *IPC*. Consequently, we focused on the Nr-PLS results in the next steps as they reflected explicitly the effect of social condition. Unlike for *PLI*, modulation of *IPC* was not clearly stronger in one frequency bin than in others. However, similar to the *PLI* results, sustained increases of synchronization were particularly observed in the 2 Hz frequency bin at 200–600 ms post stimulus onset. Increases of *IPC* were followed by a particularly pronounced decrease of synchronization at 8 Hz 300–400 ms post stimulus presentation (see Fig. 5). Generally, initial increases of *IPC* were followed by later decreases across frequency bins.

To control for general changes in connectivity within one brain that could drive the differential *IPC* results during the social condition, we calculated intra-brain phase coherence. Neither mc-PLS (p > 0.05 for all latent variables), nor nr-PLS (p > 0.1 for all latent variables) detected any significant covariance between intra-brain phase coherence and condition or session order.

Connectivity plots

PLS results revealed a main effect for condition on both *PLI* and *IPC* that for *IPC* was also modulated by the presence of session order.

PLS results revealed a main effect for condition on both *PLI* and *IPC*, which for *IPC* was also modulated by session order. In a next step, we sought to better visualize which electrodes/connections showed the most pronounced modulation by social condition and to assess whether the electrodes that showed strong modulation of *PLI* were the same electrodes that showed strong modulation of *IPC*. We thus constructed connectivity plots on the nr-PLS results for the 2 Hz frequency bin (see Fig. 6A), as the previous analysis steps had revealed strong synchronization increases at 2 Hz for both *PLI* and *IPC* (compare Figs. 4 and 5). We additionally constructed connectivity plots for the 8 Hz frequency bin (see Fig. 6B), as in this frequency bin strongest synchronization decreases appeared (compare Fig. 5). We constructed connectivity plots based on the first latent variable identified in the nr-PLS as this contrast captured explicitly the effect of condition not modulated by session order.

Associations of intra- and inter-individual brain measures to behavioral team efficiency

Finally, we examined linear associations between changes in neural phase synchronization and changes in behavioral team performance. Our behavioral analyses showed that some teams benefited more from working together than others. Is neural phase synchronization enhanced in pairs that make better teams? To test this hypothesis we used team efficiency scores as a proxy for behavioral benefit of working together and brain scores computed by the PLS analyses (see methods

section) as a proxy of average local (*PLI*) and inter-brain (*IPC*) phase synchronization during individual and social conditions. Our behavioral analysis had revealed a strong relation between team efficiency scores and session order. To test if local phase synchronization in one player (brain scores *PLI*) and/or inter-brain phase synchronization between players (brain scores *IPC*) explained *additional* variance in team efficiency, we conducted a series of three hierarchical regression analyses and tested whether adding the relevant predictors was associated with a reliable increase in the amount of explained variance.[1]

Model No. 1:

$$y_i = \beta_0 + \beta_1 x_i + \varepsilon_i$$

Model No. 2:

$$y_i = \beta_0 + \beta_1 x_i + \beta_2 v_i + \beta_3 w_i + \varepsilon_i$$

Model No. 3:

$$y_i = \beta_0 + \beta_1 x_i + \beta_2 v_i + \beta_3 w_i + \beta_4 a_i + \beta_5 b_i + \varepsilon_i$$

where **y** denotes team efficiency values, **x** is session order, **v** is nr-PLS brain scores on *PLI* during individual condition, **w** is nr-PLS brain scores on *IPC* during individual condition, **a** is nr-PLS brain scores on *PLI* during social condition, **b** is nr-PLS brain scores on *IPC* during social condition, and **ε** is a realization of a random variable with distribution n (0, $\Sigma \varepsilon^2$).

The first model contained only session order as a predictor for team efficiency scores. As expected, session order explained a significant amount of variance in team efficiency score (F(18) = 14.29, p < 0.005, R^2 = .44, R^2 adjusted = .41, session order (social first): −3840, SE = 1016, t(18) = −3.78, p < 0.005). For the second model, brain scores obtained by nr-PLS on *PLI* and IPC during the individual condition were added as predictors. Brain scores were added as absolute values. Adding these measures of phase synchronization during the individual condition reliably increased the amount of explained variance (ΔR^2 = 0.25, ΔR^2 adjusted = 0.22, F(2) = 6.443, p < 0.01).The third model additionally contained nr-PLS brain scores on *PLI* and *IPC* during joint attention. Adding measures was again associated with a reliable increase in explained variance (ΔR^2 = 0.11, ΔR^2 adjusted = 0.10, F(2) = 4.139, p < 0.05). Table 1 reports the regression and partial correlation coefficients for the full model. As can be seen, session order, brain scores obtained by nr-PLS on *IPC* during the individual condition, and brain scores obtained by nr-PLS on *PLI* during.

the social condition uniquely predicted team efficiency score. We observed the same pattern of results when using mc-PLS brain scores instead of nr-PLS brain scores.

We also computed partial correlations between behavioral changes (team efficiency scores) and changes in local phase locking/inter-brain synchronization (nr-PLS brain scores on *PLI/IPC* during social minus nr-PLS brain scores on *PLI/IPC* during individual condition) controlling for the effect of session order. Both partial correlations were reliably different from zero (for changes in *PLI*: r(20) = 0.50, p < 0.05; for changes in *IPC*: r(20) = 0.58, p < 0.01; see Fig. 7). *PLI* and *IPC* nr-PLS brain scores for the social condition were correlated among themselves (r(18) = 0.53, p < 0.05), while *PLI* and *IPC* nr-PLS brain scores were not significantly correlated among each other for the individual condition (r(18) = 0.18, p = 0.46).

To summarize, adding measures of neural phase synchronization as predictors of behavioral change in visual search almost doubled the explanatory power compared to a regression that only included the effect of session order as a predictor (R^2 adjusted 0.41 vs. R^2 adjusted 0.74, F(4) = 6.55, p < 0.005). Neural phase synchronization between two players' brains during individual attention predicted their average behavioral benefit from working as a team. Adding measures of phase

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[1] The residuals of one dyad exceeded Cook's distance; that dyad was therefore excluded from the regression analyses.
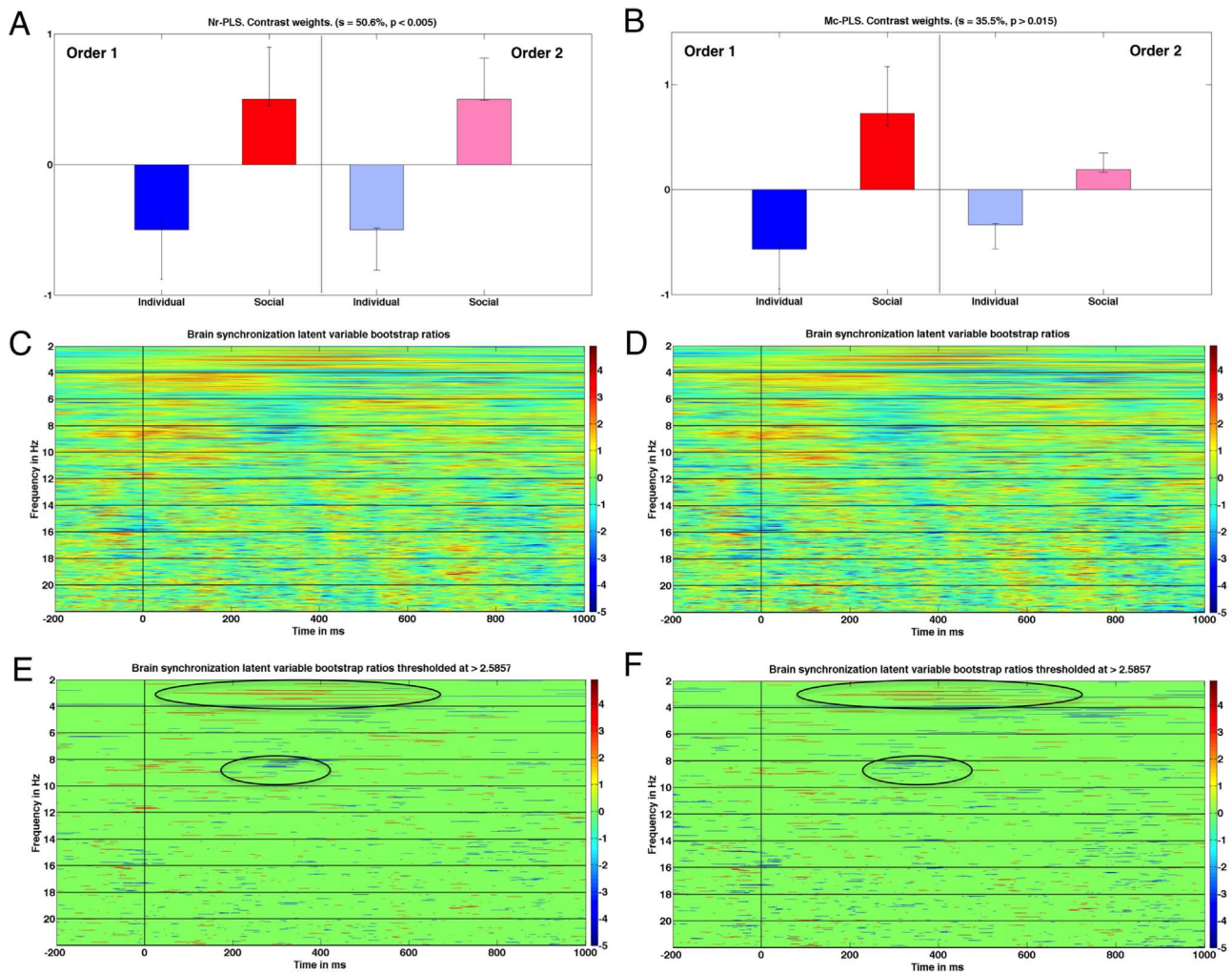
Fig. 5. Nr-PLS and Mc-PLS on *IPC* reveal higher *IPC* values in the social condition. PLS was performed twice on *IPC* values. A. Shown are the results obtained by Nr-PLS. Mean of subjects' brain scores per condition, mean-centered and normalized with the corresponding singular value (s), and 95% confidence intervals derived from the bootstrap test. B. Brain synchronization latent variable bootstrap ratios before thresholding, obtained by Mc-PLS. Each horizontal line corresponds to one electrode connection at the indicated frequency (441 connections per frequency, grouped from frontal to occipital within frequencies). The colormap is anchored at the lowest and highest values. x-axis: time in ms. y-axis: channel connections grouped by frequency (black lines indicate frequency boundaries). Panel C (for Nr-PLS results) shows brain synchronization latent variable bootstrap ratios after thresholding at bootstrap ratios > 2.5857 (99% CI). One strong synchronization and one strong desynchronization effect are indicated by black ellipses. D. Values were derived in the same way as in (A), but estimated by Mc-PLS. E. Analogue to (C), but values obtained by Nr-PLS. F. Analogue to (D) but for Mc-PLS results. Strongest effects for Nr-PLS results in (E) are indicated by black ellipses in both (E) and (F).

synchronization during dyadic performance was associated with further increments in prediction of team efficiency. Finally, change-change correlations controlling for session order confirmed that individuals showing more positive changes in *PLI* and *IPC* from individual to dyadic performance also showed more positive changes in visual search performance.

We did not observe any correlation with p-values smaller than 0.05 between personality measures, team efficiency and neural measures.

Discussion

Many earlier studies in the field of hyperscanning and social interaction have focused on interpersonal action coordination (Dumas et al., 2010; Dumas et al., 2011; Konvalinka et al., 2014; Lindenberger et al., 2009; Müller and Lindenberger, 2014; Müller et al., 2013; Sänger et al., 2012, 2013). Here, we investigated whether inter-brain synchronization can also be observed in a joint-attention setting that requires no coordinated body movements. Specifically, we addressed two main research questions: (i) Do neural processes presumably associated with joint attention manifest themselves in increased inter-brain phase synchronization? (ii) Are between-dyad

differences in performance gain from working as a team associated with between-dyad differences in phase synchronization during joint attention?

The results of the present study support positive answers to both questions. PLS analyses on local phase locking within one brain (measured by *PLI*) and phase locking between two brains (measured by *IPC*) revealed significantly higher *PLI* and *IPC* values during joint attention than during individual attention (see Figs. 4 and 5). These results suggest that within- and between-brain dynamics are susceptible to social context, resulting in higher local intra-brain as well as higher inter-brain phase synchronization when social context is made salient.

We chose to study joint attention vs. individual attention during a visual search task to improve control of condition differences in perceptual input and motor output. To address this goal, we presented identical pictures in our two experimental conditions (individual vs. team) and instructed participants to focus on the center of the screen at the beginning of each trial to reduce peripheral view of the partner in the social condition to a minimum. We further restricted the EEG data analysis to brief periods one second after picture onset to avoid potential confounds arising from finger movements. We observed
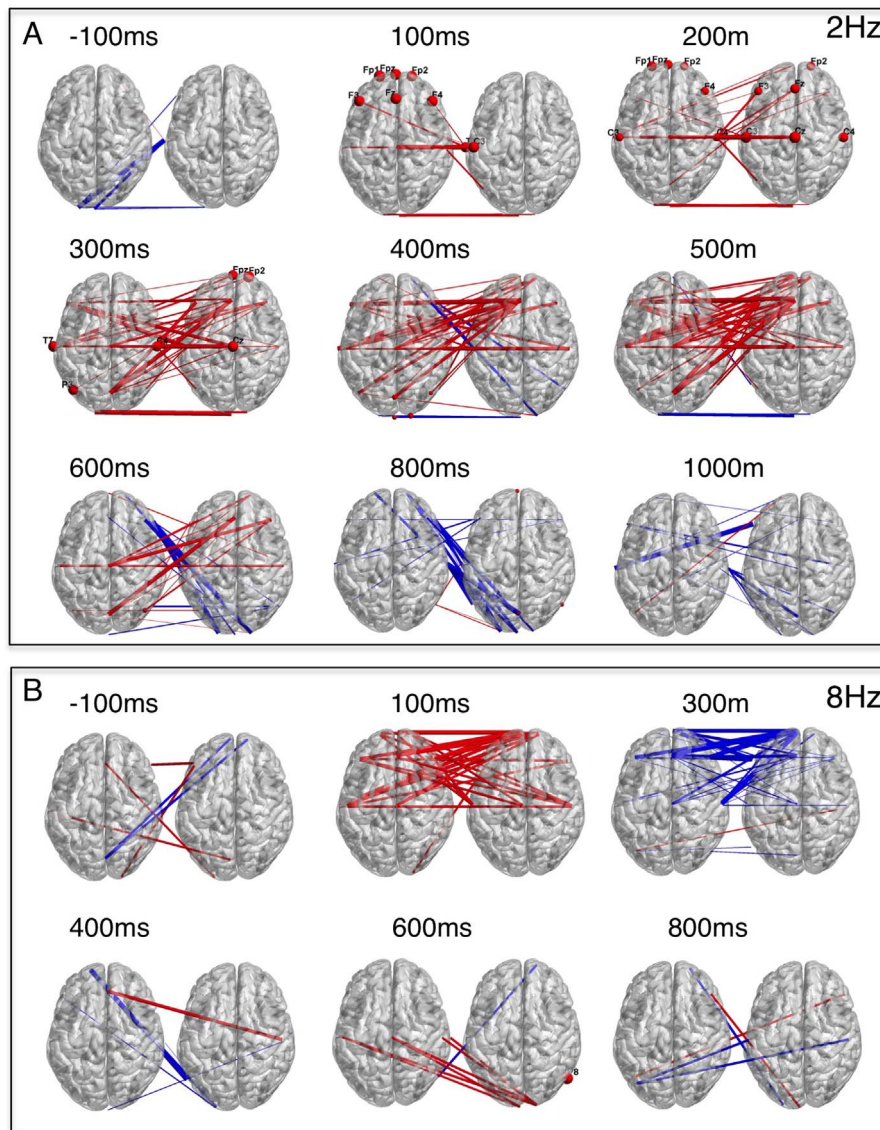
Fig. 6. Time course of *PLI* and *IPC* at (A) 2 Hz and (B) 8 Hz. A. *PLI* and *IPC* values per electrode and electrode connection at 2 Hz. B. *PLI* and *IPC* values per electrode and electrode connection at 8 Hz. Nodes = *PLI*. Edges = *IPC*. Values are thresholded at > 2.5758 bootstrap ratios (approximating 99% CI). Significant nodes are labeled with the corresponding electrode name. Blue codes for negative values. Red codes for positive values.

Table 1

Regression coefficients and semi-partial correlation coefficients estimated for the multiple linear regression model no. 3. Dependent variable = Team Efficiency Score. *PLI/IPC* individual = brainscores estimated by nr-PLS on *PLI/IPC* during the individual condition. *PLI/IPC* social = brainscores estimated by nr-PLS on *PLI/IPC* during the social condition. *B* = unstandardized regression coefficients. SE = standard error. beta = standardized regression coefficients. sr = semi-partial regression coefficients.

Variable	*B*	SE *B*	beta	sr	*t*(14)	*p*
Intercept	−9856.33	2417.49	0	0	−4.077	0.001
Session order	−2191.64	747.89	−0.38	−0.55	−2.930	0.011
PLI **individual**	14.03	66.34	0.03	0.05	0.211	0.836
IPC **individual**	364.77	107.89	0.48	0.54	3.381	0.004
PLI **social**	158.06	61.44	0.38	0.44	2.573	0.022
IPC **social**	−5.08	49.53	−0.02	−0.02	−0.102	0.920

modulation of intra- and inter-brain phase coherence during joint attention relative to individual attention across the entire 1 s interval that was analyzed (see Figs. 4,5 and Fig. 6). Particularly strong increases of inter-brain phase coherence were observed 100 to 500ms after stimulus onset (see Figs. 5 and 6) in the delta frequency band and most pronounced at frontal to parietal sites (see Fig. 6). The

strongest increase in intra-brain synchronization was also observed during the first 400 ms following stimulus onset in the delta frequency band (see Fig. 4). Increases in delta oscillations during individual EEG recordings have been observed during visual auditory stimuli detection tasks or high working memory load and have been related particularly to signal matching (Başar-Eroglu et al. 1992), which is highly relevant in our task. Also, this pattern replicates earlier studies that reported most pronounced effects in fronto-central regions for both within- and between-brain synchronization (i.e., PLI and IPC) at lower frequencies, namely in delta and theta frequency ranges during social interaction (Lindenberger et al., 2009; Delaherche et al., 2015; Sänger et al., 2012). Moreover, Sänger et al. (2012) found that within-brain synchronization (i.e., *PLI* and intra-brain strength) at lower frequencies was higher in leaders as compared to followers indicating modulation of intra-brain synchrony by musical roles, which may reflect that the role of the leader is associated with greater effort than the role of the follower. Using a graph theoretical approach, Müller and colleagues reported higher coupling strength and more connector hubs for these slow frequencies than for higher frequencies during joint musical improvisation on the guitar and suggested that slow frequency ranges generally play a bigger role in inter-brain synchronization than higher
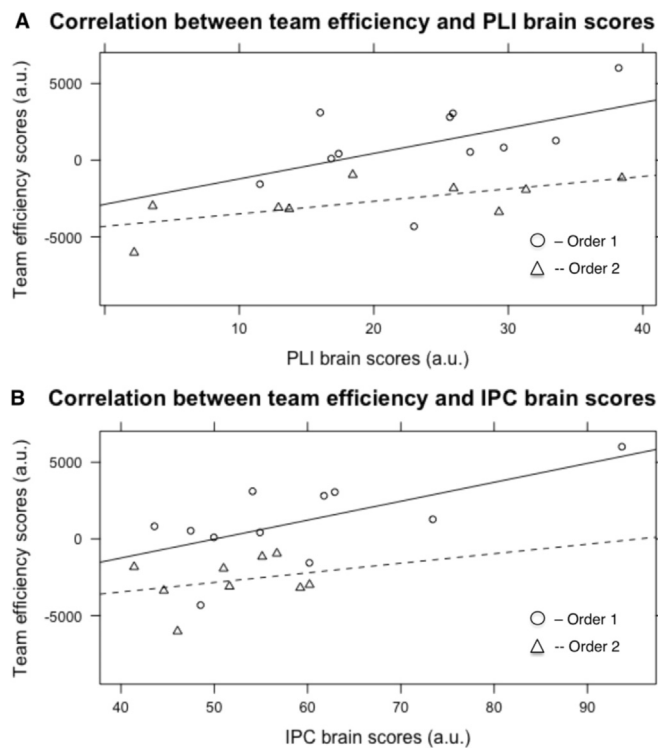
A Correlation between team efficiency and PLI brain scores

B Correlation between team efficiency and IPC brain scores

Fig. 7. Correlation between team efficiency and phase synchronization (*PLI* and *IPC*). Panel A. Correlation between team efficiency and *PLI* brain scores. Panel B. Correlation between team efficiency and *IPC* brain scores. The difference score between brain scores estimated by nr-PLS in the social condition and brain scores estimated in the individual condition was correlated with team efficiency scores. Circles indicate the session order with the individual condition first (Order 1). Triangles indicate the session order with the social condition first (Order 2). Solid line = regression line for session Order 1 Dashed line = regression line for session Order 2.

frequencies (Müller et al., 2013). Although inter-brain synchronization generally increased during joint attention, instances of reduced synchronization were observed as well (see Figs. 5 and 6). For example, we found fronto-central suppression of inter-brain phase synchronization at 8 Hz at 300 ms after stimulus onset (see Figs. 5 and 6). Attenuated power in the alpha frequency band during a joint finger-tapping task has been reported elsewhere (Konvalinka et al., 2014) and could in turn result in attenuated phase synchronization in the same frequency band. We interpret these general increases in local phase locking and inter-brain phase synchronization during joint vs. individual attention as a neural substrate of social facilitation.

The term social facilitation subsumes changes in behavioral performance associated with the passive or active presence of another person (Allport, 1920; Zajonc, 1965). Two mechanisms have been proposed to mediate social facilitation: On the one hand, automatic co-representation of the co-actors tasks (see Sebanz et al. (2003)) and on the other hand, a general increase in arousal, attention, or both (Dolk et al., 2011; Zajonc, 1965), which may reflect motivational aspects of social settings. Particularly for joint attention, the recruitment of reward-related neuronal circuits has been demonstrated (Pfeiffer et al., 2014; Schilbach et al., 2010). Our setting does not allow disambiguating the effects of task co-representation from the effects of increased attention/motivation. While participants searched two identical visual displays in the individual condition, they together searched one display in the social condition. At the beginning of the experimental session, most dyads used verbal communication to decide on splitting the visual display in halves, so that one participant would primarily search the left half and the other participant would primarily search the right half. In this situation, automatic co-representation of the co-actor's task (search left half and search right half of the display) should lead to task representation corresponding to the individual

condition (search left half and right half of the display), thus, no difference between conditions should follow from task co-representation. Our results on intra-brain dynamics, namely, local phase synchronization within one brain, might be taken to support the view that social facilitation is expressed via heightened attention. Increased local phase synchronization has been suggested to play a major role in selective attention (Womelsdorf and Fries, 2007) and in response execution and inhibition (Müller and Anokhin, 2012). We observed changes in local phase synchronization from individual to social setting in both individual brains with localization and distribution patterns paralleling the activation patterns in inter-brain synchronization reported above (see Figs. 3–5), but exhibiting a different time course: the strongest increase in *PLI* was apparent 0 to 300 ms after stimulus onset in the delta frequency band, while it manifested most strongly 300–500 ms after stimulus onset for *IPC* (see Fig. 6). Importantly phase synchronization did not increase globally within individual brains during joint attention, as we did not observe any significant modulation of intra-brain phase coherence. *IPC* and *PLI* proved further similar in their correlations with behavior (see Fig. 7).

From a conceptual perspective, attention is a key factor to visual search success. In our paradigm, teams generally responded faster than individuals. This previously observed collaborative benefit has been hypothesized to go beyond the speeding effect expected when the number of searching eyes doubles (Brennan and Enns, 2014). We interpret this increased local phase synchronization during social setting, which we found paralleled by increases in inter-brain phase synchronization, to reflect a general heightening of attention during social setting and thus interpret these changes in neural phase synchronization as neural substrates of social facilitation.

Our second research question focused on a potential relationship between measures of phase synchronization during individual and joint attention and behavioral team performance. Here, our results suggest a link between local/inter-brain phase synchronization and behavioral team performance that has not been previously reported in the literature.

We hypothesized that increases in *PLI* and *IPC* during joint attention would both correlate with behavioral performance increases, a correlation that was indeed apparent in our data (compare Fig. 7). Increases in both *PLI* and *IPC* correlated positively with team efficiency. In a hierarchical regression with *IPC*, *PLI* and session order as predictors, *IPC* during individual and *PLI* during joint attention explained variance in behavioral team performance above and beyond the variance explained by the general learning effect (session order). The observed association between higher local phase synchronization during joint attention and larger performance gains from working as a team further corroborates our interpretation of increased neural phase synchronization as heightened attention underlying social facilitation. The more two players are susceptible to the social setting, the more their attention will increase in a social setting which on the behavioral level results in larger performance gains and at the neural level is reflected as increased local phase synchronization in both individuals. The finding that behavioral gains of working together are associated with higher inter-brain synchronization in particular during individual attention but not during joint attention might reflect that for inter-brain synchronization 'more does not equal better'. If indeed inter-brain synchronization reflects synchronization of cognitive processes, inter-brain synchronization and behavioral performance should increase in teams where both players co-represent their partner and build a joint forward model (see Sänger et al. (2011)). On the other hand, as pointed out earlier, the most effective strategy in the visual search task used here seemed to split the search screen between partners and to smoothly coordinate on the joint response. Brennan and Enns (2014) have shown that degree of friendship as well as distribution of cognitive load positively correlate with team efficiency. Relating our finding on *IPC* to these results might thus suggest that partners who during individual attention 'are on the same wavelength across brains' but do

not align their cognitive processes too closely during teamwork benefit most from working as a team in this task.

It is particularly interesting to point out that we assessed phase synchronization only during an initial period of individual and joint attention (first second of trials). However, local and inter-brain phase synchronization during this initial period explained variance in a pair's reaction time several seconds later (end of trials). This finding corroborates our hypothesis that modification of neural, inter-brain patterns by social context is of general nature and not restricted to stimulus presentation. Thus, increased inter-brain phase synchronization during joint attention does not reflect shared perceptual input only but social context as a general modifying factor of brain patterns.

In summary, we suggest that social context modulates intra-, as well as inter-brain dynamics in interacting individuals, possibly reflecting a general heightening of attention in social facilitation. At the level of intra-brain dynamics, this modulation is expressed as increased local phase synchronization. At the level of inter-brain dynamics, this effect appears to be boosted and reflected as increases in inter-brain phase coherence. *PLI* and *IPC* appear to be driven by similar cognitive processes, but at least to some extent both measures might capture different dimensions of these processes.

Limitations of the study

As noted earlier, our study does not allow for clear and direct separation of task co-representation and increased attention (e.g., mediated via increased motivation) as the major forces underlying social facilitation. Also, pairs may have varied in how much they perceived the social condition as a passive or active social setting. The two subjects were exposed to the same stimulus array and knew they attended to it together. However, many dyads 'split' the search display between each other and potentially this may have weakened in some dyads the experience of co-action (active social facilitation) and instead provoked a feeling of audience (passive social facilitation), which may have limited the study's potential to maximize differences in intra- vs. inter-brain processes. Future studies using our collaborative visual search task may overcome this limitation by further differentiating explicitly between passive social facilitation (e.g. participants watch each other's individual tasks) and active social facilitation. Moreover, the similarities and differences in *PLI* and *IPC* patterns and thus the precise relationships between local phase synchronization in individual brains and phase synchronization between these brains need to be investigated further. It remains to be assessed to what extent the two measures capture different dimensions of similar or identical cognitive and neural processes.

Conclusion and future directions

Taken together, we report increased inter-brain phase synchronization and increased local phase synchronization in joint attention relative to individual attention during a visual search task and interpret these findings as neural substrates of social facilitation. We further provide some evidence for the hypothesis that this social facilitation is in turn a result of heightened attention. Though local phase synchronization in one brain and inter-brain phase synchronization between brains may reflect similar cognitive processes, we found them to differ in explanatory power of behavioral performance. In our experimental setup session, order had a strong influence on behavioral performance and teamwork benefit and accounted for 50% of inter-dyad differences in benefit of working together. Remarkably, local and inter-brain phase synchronization combined explained an additional 25% of inter-dyad differences in teamwork benefit. As a result, inter-brain phase synchronization may be considered a useful tool in the study of neural team dynamics. Future research should further assess the use of local and inter-brain phase synchronization as sensitive measures of social facilitation or as measures to detect and predict promising team

constellations. Dual eye tracking studies might be of particular interest to clarify if dyads indeed split the visual search space between each other and if spatially and/or temporally synchronized eye movements might serve as a major driver of inter-brain phase synchronization. Real-time dual eye tracking setups have been used recently to signal one person's social cues to his ore her interaction partner in the absence of any other non-verbal or verbal communication (Neider et al., 2010; Schilbach, 2015; Timmermans and Schilbach, 2014). Such setups allow for a high degree of experimental control and could be used to clarify the relation between eye movements, social gaze, and intra- and inter-brain synchronization dynamics within dyads. Another possible avenue to further disentangle the functional relevance of intra- and inter-brain dynamics for social interaction might lie within the field of psychiatry. Elsewhere, real-time dyad interaction paradigms have been suggested as a useful tool to study diseases that involve disturbances of social interaction, such as autism or schizophrenia (Schilbach, 2016). Potentially, intra- and inter-brain synchronization might be differentially altered in patient-control dyads during joint attention.

Furthermore, it would be interesting to actively manipulate inter-brain phase synchronization by means of non-invasive neural stimulation to gain more insight into the relationship between behavioral team performance and inter-brain phase synchronization patterns.

Acknowledgements

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