Human attachments shape interbrain synchrony toward efficient performance of social goals

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ABSTRACT

The human brain has undergone massive expansion across primate evolution through life amidst multi-layered social attachments; within families, among friends, and between clan members and this enabled humans to coordinate their brains with those of others toward the execution of complex social goals. We examined how human attachments facilitate efficient, resource-sensitive performance of social goals by balancing neural and behavioral synchrony. Using hyperscanning EEG, we collected neural data from male-female pairs in three groups (N=158, 79 pairs); long-term couples, best friends, and unfamiliar group members, during two ecologically-valid naturalistic tasks; motor coordination and empathy giving. Across groups and tasks, neural synchrony was supported by behavior coordination and orchestrated multiple neural rhythms. In the goal-directed motor task, interbrain synchrony implicated beta and gamma rhythms localized to sensorimotor areas. Couples showed the highest neural synchrony combined with greatest behavioral synchrony and such brain-behavior *linkage* resulted in speedy performance, conserving energy in the long run. The socially-oriented empathy task triggered neural synchrony in widely-distributed sensorimotor and bilateral temporal regions, integrated alpha, beta, and gamma rhythms, and implicated brain-behavior *complementarity*; couples displayed the highest behavioral synchrony combined with lowest neural synchrony toward greatest felt support while strangers exhibited the opposite pattern. Findings suggest that human attachments provide a familiar backdrop of temporal regularities, required for the brain's allostatic function, and interbrain and behavioral synchrony are sculpted by familiarity and closeness toward resource-sensitive performance of survival-related social goals, toiled by two.

1. Introduction

Humans are fundamentally social and their complex social skills, including the capacity to understand others' mental states, empathize with others' affect, and collaborate to execute joint motor goals have led to the supremacy of our species among the animal kingdom (de Waal and Preston, 2017; Levy et al., 2020). Models in social neuroscience postulate that the human brain has undergone massive expansion across primate evolution through life within multi-layered social attachments: within families, among friends, and between clan members, and this enabled humans to synchronize their brains with those of others while performing complex social אא tasks (Dunbar, 2014; Hari and Parkkonen, 2015). Such social embeddedness of the human brain implies that

the brain's natural mode of operation is in response to natural, live, and dynamic social exchanges, not to static and socially-removed stimuli (Sonkusare et al., 2019); hence, research in social neuroscience should focus on how human brains synchronize during real-life, natural social moments to sustain distinct social goals. Emerging research using hyperscanning methods, which simultaneously collect data from two or more brains to measure synchronized activity (Czeszumski et al., 2020; Montague et al., 2002) and conceptual models such as "two-person neuroscience" (Redcay and Schilbach, 2019; Schilbach et al., 2013), or the brain's "we mode" (Gallotti and Frith, 2013) are beginning formulate a perspective that perceives the human brain as rooted in social action and in the ebb-and-flow of daily social life. However, while neural synchrony is a feature of interpersonal relationships and depends on familiarity and

closeness (Ben-Naim et al., 2013; Feldman, 2020), no study to date has tested how the various human attachments shape neural synchronization. The current study utilized hyperscanning EEG to measure neural synchrony during two naturalistic interactions: joint motor activity and empathy-giving, in male-female pairs who were either long-term couples, best friends, or strangers. We aimed to measure neural coupling in relation to behavioral synchrony when partners are interacting as naturally as possible and test the effects of task and relationship status on brain synchronization.

Interbrain processes emerge within the parent-infant bond and are a feature of the protracted maturity and social regulation of the mammalian brain (Feldman, 2017). Mammalian young are born with an immature brain and require the external regulation of the mother's mature brain for the development physiological and behavioral systems that sustain participation in social life (Dunbar, 2014; Feldman, 2020). A core mechanism underpinning such regulation is *biobehavioral synchrony*, the coordination of physiological and behavioral processes during moments of social contact (Feldman, 2020, 2017). During episodes of social behavioral synchrony, mother and infant synchronize their heart rhythms (Feldman et al., 2011), hormonal release (Feldman et al., 2010), and brain activation patterns (Nguyen et al., 2020), indicating that behavioral synchrony provides the template for interbrain processes. The early experience of biobehavioral synchrony prepares infants to synchronize with other attachment partners throughout life: with partners, close friends, and group members (Feldman, 2017). However, whereas biobehavioral synchrony in infancy is expressed as brain-behavior *linkage,* with greater behavioral synchrony links with tighter physiological coupling to support optimal outcome, beginning in adolescence, naturalistic interactions among attachment partners often follow a pattern of *complementarity*, characterized by greater behavioral synchrony combined with looser physiological coupling (Ben-Naim et al., 2013; Motsan et al., 2020). Possibly, these two expressions of biobehavioral synchrony, *linkage* and *complementarity*, reverberate in the adult attachment relationships and can be flexibly employed according to the task at hand.

A key feature of interbrain processes is their role in allostasis. Models on allostasis view the brain's primary role as a resource-regulator that applies anticipatory predictions to foresee, prioritize, and deliver resources to fulfil survival-related needs in a "just enough" and "just in time" fashion (Sterling, 2012). Toward this goal, the brain utilizes all physiological and behavioral systems at its disposal as regulated by a hypothalamic clock that synchronizes rest-activity cycles in every tissue of the body, including neural oscillations (Schulkin and Sterling, 2019). Long-term attachments provide a familiar backdrop against which partners can coordinate performance toward the smooth execution of survival-related social goals and co-regulate social needs to maximize well-being and thriving. Interbrain processes based on the entrainment of such familiar rhythms can economically balance neural and behavioral synchrony toward allostatic performance of survival-related social goals.

Overall, survival-related social acts across human evolution fall into two distinct categories. The first describes goal-directed joint motor tasks that typically involve tool use (e.g., cutting wood for fire, lifting water from well, or rowing a boat). These mark a well-defined task, require energy and intent, follow a familiar sequence of actions, improve by practice, and terminate when goal is reached. In such daily motor tasks, interbrain synchrony relies on behavioral coordination, and, similar to the coupling of physiological and behavioral processes in eusocial species such as ants or bees (Wilson, 2012), the linkage of neural and behavioral synchrony leads to better performance. When partners have ample opportunities for practice, for instance, among cohabitating couples, behavioral patterns become familiar, leading to greater automaticity and smoother performance (Seth and Friston, 2016). In such cases, brain-behavior *linkage,* the combination of high neural synchrony with high behavioral synchrony, while requiring substantial energy expenditure may result in more efficient performance and quicker execution in tasks where speed and accuracy carry clear survival advantage.

The second category of human social-collaborative acts taps behaviors directed toward the formation, cementing, and maintenance of affiliative bonds with group members, which carry survival advantage by promoting food and resource sharing and consolidating the ingroup to protect against external danger (Feldman, 2016). Non-human primates spend significant effort in socially directed act; grooming, repairing social bonds after aggressive conflicts, or mimicking to increase social resonance, and these function to enhance group living (Arlet et al., 2015; Dunbar, 2014; Preis et al., 2018). With the evolution of human empathy, which combines the automatic resonance of other primates with humans' cognitive empathy, empathy-giving acts permeate social relationships. Humans discuss daily hassles, share joyous moments, and console others in grief, and these social acts create the fabric of social life, weave individuals into close affiliations, and cement the sense of belonging to social groups (Bickart et al., 2011; Lambert et al., 2013; Walton et al., 2012). Empathy-giving marks a core aspect of long-term attachments but can also occur with unfamiliar group members; humans easily share distress with a stranger on the train. Similar to motor coordination, empathy giving involves interbrain processes that rely on behavioral coordination; yet, the lack of a clear goal and predetermined action pattern may recruit a different interbrain process that is less localized, more widely-distributed, and, due to allostatic considerations, may trigger *complementarity* of neural and behavioral synchrony.

Interbrain processes are sustained by neural oscillations, a highly conserved and pervasive feature of neuronal activity (Buzsáki and Draguhn, 2004). The temporal consistency of brain rhythms builds a model of self and partner's behavior that can guide the allostatic regulation of neural activity toward resource-sensitive performance (Seth and Friston, 2016; Theriault et al., 2020). The various neural rhythms have been proposed to sustain distinct phases of this process, although empirical evidence is still needed; alpha is thought to sustain the construction of predictions, beta the accuracy of predictions, while gamma is implicated in prediction errors and the reorganization of predictions vis-à-vis incoming sensory information (Sedley et al., 2016). Complex social tasks orchestrate multiple rhythms and the integration of alpha, beta, and gamma rhythms in sensorimotor and associative areas has been shown to support complex social skills, such as empathy (Levy et al., 2017) and attachment (Pratt et al., 2018).

Interbrain studies, especially those employing conversations in more naturalistic settings, implicated alpha, beta, and gamma rhythms in central and temporal regions. Using hyper-scanning EEG, alpha synchrony in central regions was found between infant and adult when singing nursery rhymes, which increased during live interactions (Leong et al., 2017). Hyperscanning EEG studies showed gamma synchrony in temporal regions during positive discussion (Kinreich et al., 2017) and alpha and beta synchrony during conversation (Pérez et al., 2017). An fNIRS study showed greater activity in left superior and temporal gyri and pre-and supplementary motor cortices during eye-to-eye, compared with eye-to-picture condition (Hirsch et al., 2017) and a MEG study showed gamma synchrony in right STS in mothers and children observing their own interaction, which was embedded in behavioral synchrony (Levy et al., 2017).

In comparison, motor coordination studies described a more localized pattern of interbrain matching, mainly limited to sensorimotor areas. Szymanski et al., (2017) showed that during a visual search, team participants showed higher synchronizations in central regions and Mu et al., (Mu et al., 2017) found increased gamma synchronization during a coordination task. Imitation of hand movement triggered alpha- and beta-band coordination in central regions (Dumas et al., 2010). Notably, none of these studies included observation of the partners' behavioral coordination. Since gamma oscillations in motor cortex are particularly important for movement execution and imitation (Nowak et al., 2018), gamma synchrony in sensorimotor areas may be particularly salient during joint motor tasks in daily life (van Wijk et al., 2012).
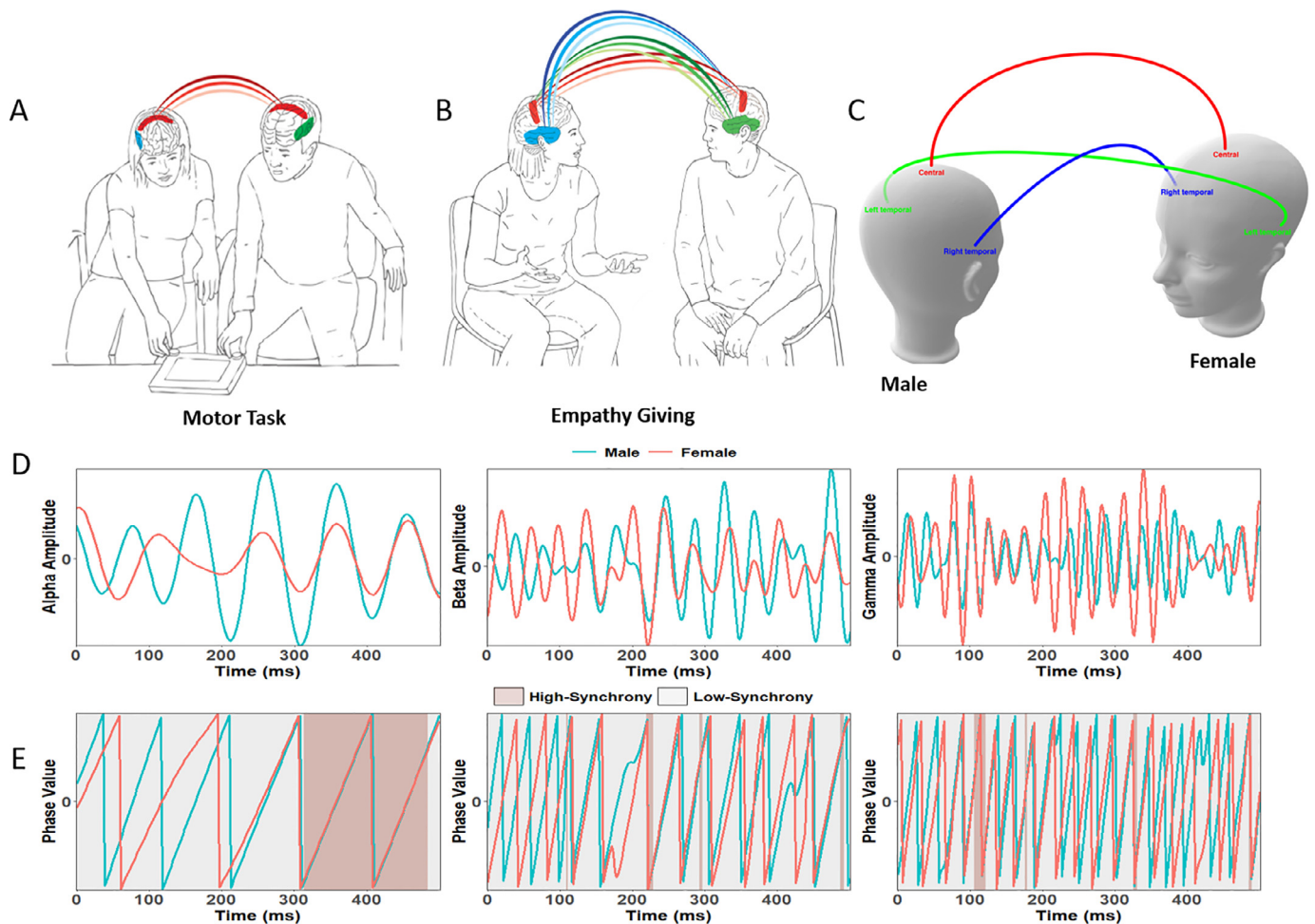
Fig 1. Illustrations for the motor and empathy giving tasks, brain areas and neuronal signals.
Figures (A) - (C) illustrates the motor and empathy giving tasks, and the hypothesized ROIs. (D) illustrate 500_{ms} neural signal amplitudes for male and female in alpha, beta, and gamma frequencies. (E) illustrates the signals' phase value and areas of high and low synchrony.

In light of the above, the goal of the current study was to examine how neural synchronization, as supported by behavior synchrony, is shaped by human attachments to sustain specific social goals. Our two ecologically-valid paradigms aimed to tap the prototypical collaborative acts utilized across human evolution; motor coordination and empathy giving. We tested how attachment bonds facilitate the most efficient balance between neural and behavioral synchrony toward successful performance.

To pinpoint the role of human attachments in neural synchronization, we recruited the largest sample to date of paired adults (N=158; 79 male-female pairs) organized in three groups: (1) *Couples*- long-term romantic couples within a committed relationship and at least 1 year of cohabitation; (2) *Friends*- close friends who considered each to be among their top five friends (Dunbar, 2014) and their familiarity period matched the couples'; and (3) *Strangers*- demographically-matched unfamiliar group members. Brain and behavioral synchrony were measured during a "motor task", when partners coordinated their manual action (Yirmiya et al., 2018) and an "empathy giving" paradigm where partners shared in turn a recent distressing event (Fig 1).

Because neural synchronization is a feature of human brain evolution, we expected to find brain synchrony across all groups and in both tasks (Hypothesis 1). Due to the complexity of the tasks, we expected each to integrate neural synchronization in alpha, beta, and gamma rhythms (Hypothesis 2). The motor task tapped a patterned process found in eusocial species, where rapid cycles of sensory-neurocircuitry coupling are locked with behavioral matching toward efficient performance. Such activity may have achieved specialization across animal evolution and recruit neural coupling primarily in sensorimotor regions. Since joint motor acts are perfected by practice, we expected cohabitating couples to exhibit brain-behavior *linkage* of highest neural synchrony combined with greatest behavioral synchrony, and to show the best performance in terms of speed and accuracy (hypothesis 3). In comparison, the empathy-giving task defines a more evolutionary-recent skill that incorporates humans' complex social abilities of emotional identification, affect sharing, and mentalization (Levy et al., 2017); hence, interbrain synchrony would recruit both sensorimotor and temporal regions. Since the evolutionary goal of this interaction is to cement social bonds, allostatic considerations may express in brain-behavior *complementarity*. Among couples, whose bond has already been established and are familiar with each other's behavioral patterns, highest behavioral synchrony may combine with low neural coupling and result in highest "felt support" (Hypothesis 4).

2. Materials and methods

All procedures used in this study including paradigms, questionnaires, and equipment were approved by the ethical committee of Bar-Ilan University and all participants signed an informed consent. All procedures were explained to the participants before the study and were performed in accordance with ethical guidelines. Participants were free to leave the experiment at any time with full compensation.

2.1. Participants

Participants included 158 young adults in male-female pairs recruited in accordance to three groups (1) *Couples* - committed romantic couples living together for at least a year (time together: M=3.83, SD = 2.85 years), (2) *Friends* - Consistent with Dunbar (Dunbar, 2014), friends considered each other among their top five "best friends" but have never been involved romantically (time of close friendship: M=4.10, SD=2.39, no different than couples', $t_{(38)}$=-0.31, *p*=0.76), (3) *Strangers* – demographically-matched male and female from the same in-group who met for the first time during the experiment (Table S1).

Only dyads with good data were included and participant attrition was due to equipment malfunction. No significant differences were found in any demographic variables among those included and not included in the final analysis. The final sample included 134 participants (67 couples): 46 romantic partners (23 pairs, age 25.67±5.75), 34 best-friends (17 pairs, age 25.17±4.14), and 52 strangers (27 pairs, age 25.04±3.06). Exclusion criteria included medication intake, physical or psychiatric condition, and self-reported health problems (such as asthma, blood pressure, head injuries, etc.). No significant differences were found between groups in age, education or depression (Table S1, *p*>0.05).

2.2. Procedure

Participants were recruited using ads posted at a university campus, surrounding areas, and via the internet. Prior to arrival, participants completed self-report questionnaires related to general demographics, health information (*e.g.*, weight, height, smoking, medication, etc.), and Back Depression Inventory (BDI). Upon arrival, participants were seated next to each other with a dividing screen between them during the EEG preparation and were guided not to talk. While the purpose of this process was to maintain unfamiliarity between the strangers, we followed the same procedure with the couples and friends. A general explanation about the experiment was given, participants signed informed consent, and the dual electroencephalography (EEG) was placed by trained experimenters.

Participants engaged in two naturalistic interactions (Fig 1A-B). For the *motor task* and similarly to previous study in our lab (Yirmiya et al., 2018), participants were given an "Etch A Sketch", a mechanical drawing toy. The toy has two twisting knobs, one for drawing up-down and the other to draw left-right. Participants were asked to draw only with one knob each a pre-defined abstract picture (a X and a house). Each participant was allowed to use only one knob and talking was allowed. An example of how to use the toy was given by the experimenter. For the *empathy giving task,* similarly to previous study in our lab (Schneiderman et al., 2014), participants were asked to share, in turn, a distressing or troubling event that was unrelated to their relationship (for couples and friends). After 5 minutes, the experimenter stopped the conversation and asked the participants to reverse roles. From each paradigm, the first 3 minutes were analyzed, consistent with prior research (Kinreich et al., 2017). At the end of the experiment, participants rated how comfortable they were in each task and rated how empathic, supportive, and helpful their partner was during the support giving task.

2.3. Dual-EEG data acquisition and preprocessing

Neuroelectric activity in the two participants was simultaneously and continuously recorded while they engaged in the two tasks and the specific paradigm segments were edited for processing and analyses. Data acquisition was performed using a 64-channels BrainAmp standard amplifier from the Brain Products Company (Germany) to enable the computation of millisecond-range synchrony between the two EEG recordings. The system was composed of two Acticap helmets with 32 active electrodes arranged according to the international 10/20 system with analog 0.1–500 Hz band-pass filtering. Data was sampled at 1000Hz. The impedances were maintained below 10kOhm and reference was placed on FCz and ground on AFz.

The preprocessing was conducted using Python 3.7.3 in Anaconda (v4.6.11) with MNE software suite (v0.18.1) (Jas et al., 2018). We first visually inspected the data in order to evaluate the types of artifacts which present in our data. Next and similarly to (Dumas et al., 2010; Jas et al., 2018), bandpass "fir" filter ranging from 1 to 48 was used and a division into 1000ms windows with 500ms overlap. In order to remove trials containing transient jumps in isolated EEG channels, and eyeblink artifacts affecting groups of channels Autoreject v0.2 was used (Jas et al., 2018). While Autoreject is an unsupervised algorithm which minimizes the cross-validation error, measured by the Frobenius norm between the average signal of the training set and the median signal of the validation set, it does not necessarily work well for a systematic physiological artifact that affects multiple sensors. For these purposes, we used MNE's implementations of FastICA and CORRMAP (Campos Viola et al., 2009). Because our analyses are done on a large number of participants, CORRMAP allows us to manually select an IC (independent component) for exclusion in one participant and use the chosen component as template for selecting and excluding similar component in other participants. The general idea behind the CORRMAP algorithm is that artifact patters are generally similar over large number of participants. Therefore, correlation between the template IC and each ICA solution, enables to choose the IC with the highest correlation. Thus, excluding similar components. We identified and removed components mainly containing ocular movements (e.g. blinks, saccades) and muscle artifacts (mean of 3 components with maximum of 4 per participant). Prior to running FastICA and CORRMAP, data was average referenced. Finally, a visual examination was used to assess the goodness of the data.

Based on prior research and to avoid large number of multiple comparisons, we choose to use a theory-driven ad-hoc approach and to focus on interbrain synchrony only between homologies areas (Balconi et al., 2017; Kawasaki et al., 2013; Koike et al., 2020; Kuhlen et al., 2012; Liu et al., 2017). Consistent with much prior interbrain research (Dumas et al., 2010; Mu et al., 2017; Pérez et al., 2017), we used phase locking value (PLV) to estimate the amount of synchrony between each electrode two electrodes (Dumas et al., 2010). PLV ranges between 0 and 1, were 0 indicates no synchrony and 1 full synchrony. We used the mean of PLV values of the electrodes in the left temporal, right temporal, and central areas (Fig 1C-E). We also used phase lag index (PLI; Fig S1) to better validate our main findings.

2.4. EEG synchronous calculation

In order to assess the brain synchrony between the couples, data was bandpass to alpha (8–12Hz), beta (13–30Hz) and gamma (31–48Hz), and phase-locking value (PLV) was calculated between each pair of between-subject electrodes and for every frequency (Dumas et al., 2010; Pérez et al., 2017).

Where N is the number of samples considered in each 1000_{ms} window, w is the phase and | | the complex modulus. Thus, the PLV values of two signals can range from 0 (fully unsynchronized) to 1 (fully synchronized).

Since these calculations results with a high number of comparisons, we divided the cap into a pre-defined areas and frequency of interest based on our hypotheses: left temporal (FT9, T7, TP9), right temporal (FT10, T8, TP10), and central (Cz, C3, C4). In addition, based on previous studies and as the level of neural activity network can predict the same network in the other brain (Anders et al., 2011; Kawasaki et al., 2013), we choose to focus on synchrony only between homologies areas. Finally, in order to further validate the differences between our groups in neural synchrony, we also used PLI (Czeszumski et al., 2020). Similar to the PLV, PLI values are on the same scale.

2.5. Social behavior coding

Interactive Behavior manual (CIB), a well-validated rating system for coding social interactions (Kinreich et al., 2017; Schneiderman et al., 2014; Yirmiya et al., 2018) with multiple codes integrated into theoretically-based constructs. The synchrony construct of the CIB consists of codes related to reciprocity of interaction, fluency and rhythmicity of the interaction, mutual adaptation and regulation by the two partners, positive and relaxed mood, and partners' ability to give each other space and expand on each other's actions and communication. Coding was conducted by trained coders a blind to any other information. Reliability was conducted on 15% of the interaction with reliability exceeding 95% (intraclass r = .93). In addition to the synchrony coding, we also coded for the motor task whether participants completed the first task and the time (in seconds) it took to complete the task to assess accuracy and speed.

2.6. Statistical analyses

Our statistical analyses were hypotheses driven and focused on the three brain areas (central, left temporal, and right temporal) and three frequency bands (alpha, beta, gamma). Even though, we hypothesis about specific area-band, we used conservative measure and used bootstrapped (5,000 samples) or permutation (5,000 iterations) analyses. All statistical analyses were done in R version 3.5.3 (R Core Team, 2014).

3. Results

3.1. Demonstrating interbrain synchrony during live social interactions

To demonstrate the existence of neural synchronization during real life social interactions, we created surrogate data, similar to prior interbrain research (Pérez et al., 2017). Surrogate data were calculated from pairing shuffled 30 "partners" to each participant. Each surrogate "partner" was selected from the opposite sex in same paradigm, to eliminate spurious findings and show that the effects present "real life" interactions, not the result of the laboratory settings itself. Using Wilcoxon test we compared the real and surrogate data across paradigms, ROIs, and frequency bands. Interbrain synchrony in the real data was significantly higher than the surrogate data in all groups, ROIs, and oscillatory bands ($p<0.05$; Table S2), confirming our first hypothesis.

3.2. Linkage and complementarity in neural and behavioral synchrony

To examine patterns of linkage and complementarity in the balance between neural and behavioral synchrony in the motor coordination (linkage) and empathy giving (complementarity) tasks, for each task we describe four sets of analysis. In the first, we assess behavioral synchrony in the three groups. In the second, we present data on neural synchronization in the various oscillatory bands and ROIs. In the third, we use bootstrap regression to predict neural synchronization (PLV values) from behavior synchrony for each group, and in the fourth, we address objective (motor task) and subjective (empathy task) indices of task performance in the three groups.

3.3. Motor coordination: Linkage of neural and behavioral synchrony

3.3.1. Behavioral synchrony

We used bootstrapped Analysis of variance (ANOVA) to test group differences in behavioral synchrony (CIB scores) during the motor task. Results showed significant group effect ($F_{(2,48)}=5.78$, $p=0.025$, $\eta_p^2=0.194$; Fig 2A) and Bonferroni post-hoc analysis revealed that *Couples* (M=3.40, SD=0.34) showed higher synchrony than *Strangers* (M=3.04, SD=0.39, $p=0.001$) with *Friends* scoring at mid-point with no significant differences from either group.

3.3.2. Neural synchrony

Neural synchrony was hypothesized in central regions during the motor task. Using permutation ANOVA test with 5,000 iterations we found a significant effect for group in central beta synchrony ($F_{(2,50)}=5.5$, $p=0.007$, $\eta_p^2=0.18$) and central gamma synchrony ($F_{(2,50)}=5.8$, $p=0.005$, $\eta_p^2=0.19$). Post-hoc comparisons showed significant difference in beta between *Couples* and *Strangers* ($p<0.05$, Bonferroni corrected; Fig 2B. Please see Fig S1 for the same analysis with PLI values) with *Couples* showing higher interbrain synchrony than *Strangers*. Post-hoc comparison for gamma synchrony showed differences between *Couples* and *Strangers*, as well as between *Couples* and *Friends*: couples showed the highest gamma synchrony, friends exhibited lower gamma synchrony than couples, and strangers showed the lowest gamma synchrony ($p<0.05$, Bonferroni corrected).

3.3.3. Balance of neural and behavioral synchrony

Lastly, we assessed how attachment bonds moderate the relationship between behavioral synchrony and neural synchrony. Bootstrapped regression analysis with 5,000 samples and group as moderator showed overall significant models for both central beta synchrony ($F_{(6,45)}=4.10$, $p=0.001$, $R^2=0.31$) and gamma synchrony ($F_{(6,45)}=3.33$, $p=0.01$, $R^2=0.27$). However, only among *Couples* significant moderation emerged between behavioral and neural synchrony ($p<0.01$; Fig 2C) in both beta-band and gamma-band synchrony. This implies that among co-habitating couples, the greater the behavioral synchrony the higher the neural synchrony, demonstrating *linkage* of brain and behavioral synchrony.

3.3.4. Task performance

Two aspects of task performance were measured, speed and accuracy. Bootstrapped logistic regression assessed the likelihood to complete the task (Fig 2D-E). Using C*ouples* as reference, *Strangers* were significantly less able to finish the task in time (OR=0.17, $p=0.027$). Bootstrapped ANOVA examined differences in speed between groups and found significant group differences ($F_{(2,50)}=3.32$, $p=0.04$, $\eta_p^2=0.112$); *Couples* (M=113.81, SD=36.89) finished significantly faster than *Strangers* (M=141.97, SD=32.45, $p<0.05$). No differences emerged between *Couples* and *Friends* in accuracy and speed ($p>0.05$; Bonferroni corrected*)*. Lastly, while behavioral synchrony was not significantly associated with accuracy (r=0.18, $p>0.05$), greater behavioral synchrony correlated with speed (r=-0.34, $p<0.05$).

3.4. Empathy giving: Complementarity of neural and behavioral synchrony

3.4.1. Behavioral synchrony

Bootstrapped ANOVA revealed an effect for group ($F_{(2,64)}=3.94$, $p=0.037$, $\eta_p^2=0.11$; Fig 3A). Bonferroni post-hoc analysis revealed that *Couples* (M=3.55, SD=0.37) exhibited higher behavioral synchrony compared to *Strangers* (M=3.28, SD=0.34, $p=0.03$). *Friends* scored at mid-point showing no differences with the other two groups.

3.4.2. Neural synchrony

Here we hypothesized a widely-distributed neural synchronization across the three ROIs (central, left temporal, and right temporal) and three frequency bands (alpha, beta, gamma). Multiple bootstrapped (5,000 samples) t-tests between the interbrain connectivity (PLV) during male and female empathy-giving showed no significant effect (Table S3) thus we used the mean interbrain connectivity of the two activities. Using permutation ANOVA with 5,000 iterations, significant group effect emerged (Table S4, Fig 3B, Please see Fig S1 for the same analysis with PLI values). Significant differences were found between *Couples* and *Strangers*. Significant differences were also found between *Couples* and *Friends* in central alpha and gamma and right temporal alpha, beta and gamma ($p<0.05$, Bonferroni corrected; see Tables S4-5). Overall, across ROIs and oscillatory bands, *Couples* showed lowest interbrain synchrony, *Strangers* exhibited the highest neural synchrony and *Friends* scored at
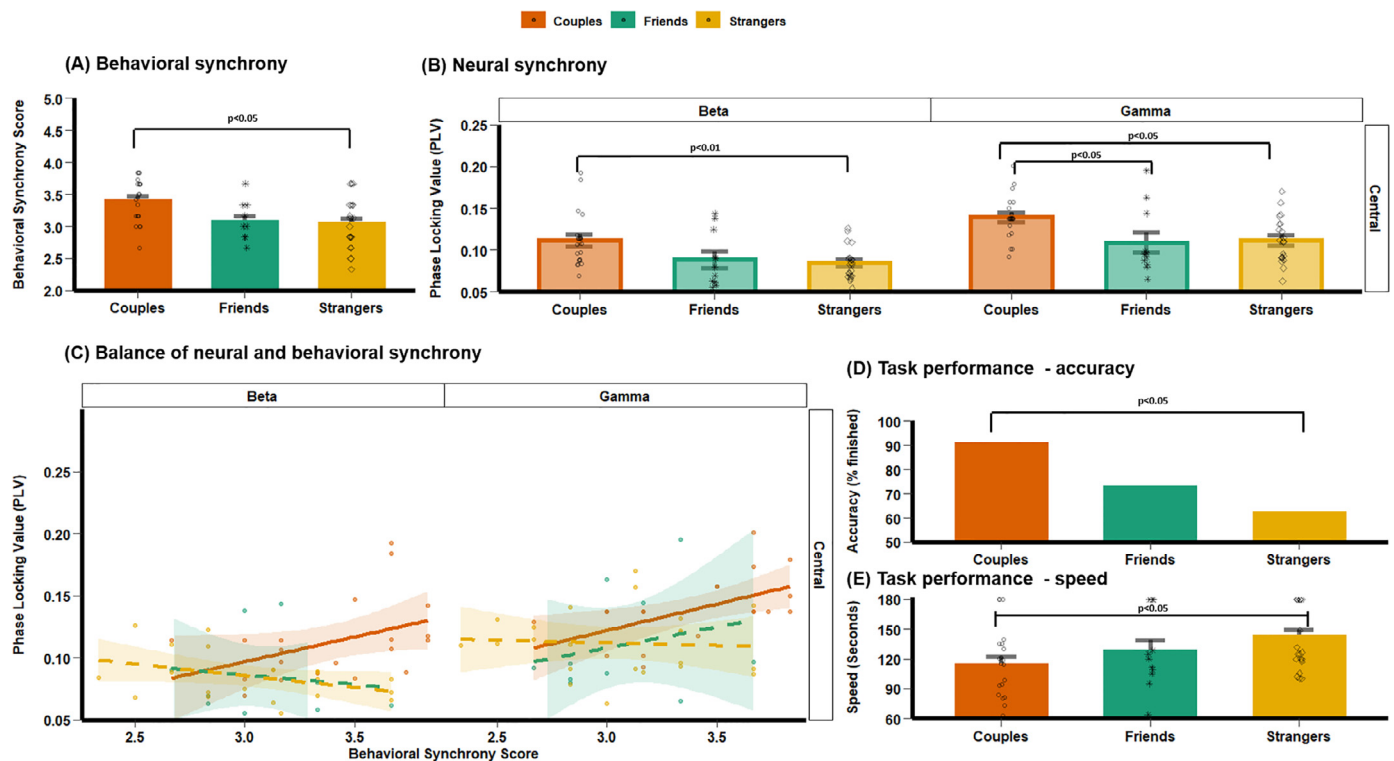
Fig 2. Mechanisms of brain-behavior linkage – motor task.
(A) Behavioral synchrony. Bootstrapped ANOVA revealed a significant effect between the groups ($F_{(2,48)}$=5.78, p=0.025, η_p^2= 0.194). Bonferroni correction revealed that couples' behavior was significantly higher than strangers (p<0.001). (B) Neural synchrony. Differences between groups in interbrain connectivity (PLV) by brain area, frequency and task. All differences were Bonferroni corrected. (C) Balance of neural and behavioral synchrony. Prediction of interbrain connectivity (PLV) by behavioral synchrony score for each group by frequency and task. Significant slopes are marked with straight line. Non-significant slopes are marked with dashed lines. (D) Task performance – accuracy. Differences between groups in accuracy. In order to assess participants accuracy, bootstrapped logistic regression was used using *Couples* as reference group. *Strangers* were significantly less able to finish the task in time (OR=0.17, p=0.027). (E) Task performance - speed. Differences between groups in speed during motor task. Bootstrapped Analysis of variance reveled significant differences between the groups ($F_{(2,50)}$=3.32, p=0.04, η_p^2= 0.112), with *Couples* (M=113.81, SD=36.89) finishing the task significantly faster than *Strangers* (M=141.97, SD=32.45, p<0.05; Bonferroni corrected). Whiskers indicate standard error of the mean.

mid-way, at time showing significant differences from the other two groups.

3.4.3. Balance of neural and behavioral synchrony

Bootstrapped regression analysis with 5,000 samples showed that all models were significant, (p<0.05; Table S6). However, full moderation was found only for *Strangers* (p<0.05; Fig 3C, Table S7), the greater the behavioral synchrony, the higher the neural synchrony, but such links were not found for couples or friends.

3.4.4. Task performance

Success in the empathy task is defined by the degree to which individuals reported feeling supported by their partner. No difference was found for the felt support measure between episodes when males or females gave support giving ($t_{(100)}$=1, p>0.05), thus we used the averaged measure. Bootstrapped ANOVA showed a significant main effect ($F_{(2,64)}$=16.6, p=0.001, η_p^2= 0.342; Fig 3D). *Strangers* (M=4.04, SD=0.56) felt significantly less supported than *Couples* (M=4.64, SD=0.29, p<0.01) and *Friends* (M=4.61, SD=0.34, p<0.01; Bonferroni corrected). No differences were found in *felt support* between couples and friends (p>0.05).

We found that higher behavioral synchrony was associated with grater felt support (r=0.37, p<0.01). Due to the complementary nature of brain-behavior coupling, we measured moderation of group and neural synchrony. Bootstrapped regression analysis with 5,000 samples and group as moderator was significant for all ROIs and frequencies (p<0.01). However, only among *Strangers* significant moderation was

found between the degree of felt support and the level of neural synchrony emerged, with higher felt support in this group predicting neural synchrony (Fig S2; Table S8).

4. Discussion

Humans' exquisite social abilities are thought to have evolved on the basis of social interactions within complex, multi-layered affiliative bonds; within families, among friends, and between clan members during daily interactions that refined the neural processing of survival-related social goals. In this study, we aimed to elucidate how neural synchronization during natural social moments is shaped by human attachments toward efficient, resource-sensitive performance. As social brain maturation occurs within natural contexts, we focused on familiar, ecological, and daily social interactions and targeted the interplay of neural and behavioral synchrony as it is mediated by the various attachment bonds. Our tasks tapped the two prototypical social-collaborative acts utilized across human evolution: the capacity to collaborate in the planning and execution of complex motor tasks and the ability to emotionally resonate and empathically share others' misfortunes and joys. We found that during natural social exchanges interbrain processes are pervasive, sustained by behavioral coordination, and are shaped by attachment bonds toward efficient performance of survival-related social goals. Overall, our results show that in both tasks, cohabitating partners employed the most efficient two-brain-two-behavior balance toward best performance, detailing how attachment bonds shape interbrain processes in the service of allostasis.
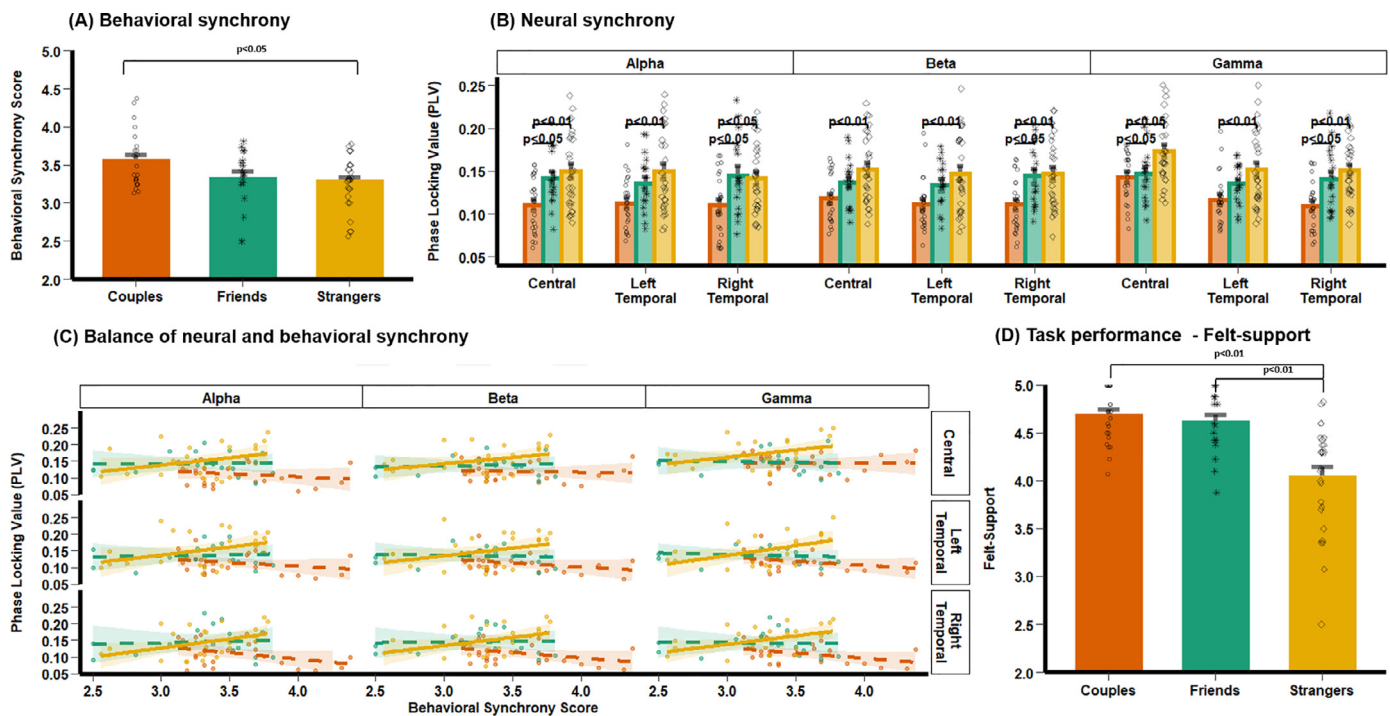
Fig 3. Mechanism of complementarity – empathy giving.
(A) Behavioral synchrony. Bootstrapped ANOVA revealed a significant effect between the groups ($F_{(2,64)}$=3.94, p=0.037, η_p^2 = 0.11). Bonferroni correction revealed that couples' behavior was significantly higher than strangers (p<0.05). (B) Neural synchrony. Differences between groups in interbrain connectivity (PLV) by brain area, frequency and task. All differences were Bonferroni corrected. (C) Balance of neural and behavioral synchrony. Prediction of interbrain connectivity (PLV) by behavioral synchrony score for each group by frequency and task. Significant slopes are marked with straight line. Non-significant slopes are marked with dashed lines. (D) Task performance – felt-support. Differences between groups in felt-support. Bootstrapped ANOVA for the differences between the groups in levels of felt-support showed a significant main effect ($F_{(2,64)}$=16.6, p=0.001, η_p^2 = 0.342). *Strangers* (M=4.04, SD=0.56) rated their partners significantly lower in empathy giving compering to *Couples* (M=4.64, SD=0.29, p<0.01) and *Friends* (M=4.61, SD=0.34, p<0.01). Couples and friends were not significantly different (p>0.05). Whiskers indicate standard error of the mean.

In addition to pervasiveness, we found that both motor coordination and empathy giving integrated interbrain processes across multiple brain rhythms; beta and gamma in the motor task, and alpha, beta, and gamma during empathy giving. This indicates that the two tasks index complex social competencies that have been shown to orchestrate multiple brain rhythms (Levy et al., 2017; Pratt et al., 2018). The balance between neural and behavioral synchrony differed according to the social goal. In the well-defined joint motor task, synchrony was localized to sensorimotor areas and followed a pattern of brain-behavior *linkage*, wherein brain and behavioral coupling are coordinated. Couples exhibited the highest interbrain and greatest behavioral synchrony with a gradient decrease in both neural and behavioral synchrony in friends and strangers and a full moderation of brain and behavioral synchrony found only in couples. In contrast, the empathy giving task triggered neural synchrony across widely-distributed brain areas, including central and bilateral temporal regions and the balance of neural and behavioral synchrony followed a pattern of *complementarity*, with couples showing the highest behavioral synchrony combined with lowest neural synchrony and strangers exhibiting the opposite patterns. Our two tasks tapping these two distinct yet inter-related prototypical social-collaborative acts are consistent with conceptual models on the inter-relatedness of infant social and motor development. For instance, Bowlby's (1969) attachment theory (Bowlby, 1969) highlights the key role of social reciprocity within the mother-infant attachment for the infant's motor exploration; the biobehavioral synchrony frame (Feldman, 2017, 2012) describes the two forms of synchrony infants learn during early "social" and "exploratory" interactions and addresses the distinct contributions of mothering and fathering to each; and Adolph's model on motor development underscores the embeddedness of infant motor action in social relationships and cultural contexts (Adolph and Hoch, 2019).

Neural synchrony develops within the parent-infant bond and from this initial relationship becomes a facet of other attachments in a manner based on a gradient of the two key attributes of attachment relationships: exclusivity and endurance (Feldman, 2017). The "best friends" group was included to disentangle the "exclusive" component of romantic relationships from the "enduring" component on which the two groups were matched and pinpoint their differential effect on interbrain and behavioral synchrony. Consistent with the model, we found that across interactive tasks, oscillatory bands, and brain regions and in both neural and behavioral markers of synchrony, the same gradient was consistently observed; from couples, to friends, to strangers with significant differences mainly found between couples and strangers and friends scoring at mid-point. This suggests that each attachment bond plays a distinct role in allostasis and the differences between long-term romantic partners and strangers are not the result of mere familiarity but link with other aspects of long-term romantic love, such as cohabitation, sexuality, intersubjectivity, centrality of the relationship to the sense of self, or more opportunities for practice. Long-term couple relationships afford predictability of the partner's behavioral patterns and communicative intent, which enables the consolidation of accurate neural predictions and better processing of incoming stimuli, presumably consolidating both the alpha-gamma and beta-gamma platforms (Sedley et al., 2016). We suggest that attachment bonds provide the most parsimonious context for anticipatory co-regulation (*i.e.* allostasis) and, if the brain's primary function is to "turn energy into offspring" (Pontzer, 2015), long-term couple relationships may have evolved as the most efficient allostatic context toward this evolutionary goal.

The motor task elicited beta and gamma synchrony over sensorimotor regions, which was highest in couples and lowest in strangers. The cortical motor system has undergone massive evolution in primates and

further expansion in humans, particularly in its connectivity to higher-order associative areas, diversity of cell types that enable imitation and attention augmentation, projections to interoceptive targets, and overlap of perceptual and motor functions that support goal directed actions that necessitate constant scrutiny of incoming signals (Mendoza and Merchant, 2014). During the execution of motor tasks, the agranular primary motor area (M1) relays predictions on anticipated proprioceptive and kinesthetic aspects of movement to the granular sensory area S1, which feed-forwards exteroceptive prediction errors from the environment via gamma activity in pyramidal cells as well as descending information about the state of the body through an active inference process (Seth and Friston, 2016; Shipp et al., 2013). Active inference leverages proprioceptive predictive models to control sensory inputs toward the smooth execution of motor action and our findings on the beta-gamma interplay during the motor task are consistent with the role of sensorimotor beta and sensorimotor gamma in refining action through sensory input (Haegens et al., 2011; Kilavik et al., 2013). It is important to note, however, that while predictive coding model may provide a conceptual frame for our data, the exact functioning of distinct neural rhythms in interbrain processes requires much further validation in both single brain and two-brain studies.

Couples showed the highest interbrain synchrony in both beta and gamma rhythms. Long-term cohabiting couples likely engage in countless daily episodes of joint motor action and are better able to form accurate predictions of the partner's action and coordinate information online via beta and gamma synchrony. Furthermore, both beta and gamma activity in sensorimotor areas have been implicated in pain perception (Levy et al., 2018) and our findings show that interbrain sensorimotor beta and gamma, apart from their well-known involvement in empathy (which is corroborated here), are also implicated in joint motor action. The high interbrain beta and gamma synchrony in couples was combined with high behavioral synchrony and, similar to other eusocial species, the linkage of brain and behavior assisted in cementing the automaticity of survival-related motor tasks and improving the speed of performance, playing an allostatic function by saving energy in the long run. Such brain-behavior coupling among cohabiting partners may have played an important role across human evolution in the formation of the human family and in sustaining the parents' effort to jointly care for infants. Consistent with findings in other bi-parental species, the joint care of offspring by mother and father confers significant evolutionary benefits to infants, as seen in both human and other mammalian species (Feldman et al., 2019).

The empathy task triggered a different pattern of interbrain and behavioral synchrony which integrated alpha, beta, and gamma oscillations in central and bilateral temporal areas. In this widely spread, multi-rhythmic, metabolically expensive endeavor, brain and behavior followed a mechanism of complementarity; couples exhibited high behavioral synchrony combined with low neural synchrony whereas strangers displayed the opposite pattern of high neural and low behavioral coordination. The allostatic role of this mechanism may be understood in light of the evolutionary goal of empathy-giving, which is to form and maintain social bonds that can facilitate food and resource sharing and consolidate the in-group to protect against intruders. Models on allostasis (Hutchinson and Barrett, 2019; Schulkin and Sterling, 2019) suggest that toward efficient predictive regulation, the brain uses broad complementary patterns that integrate prior knowledge (prediction) with sensory data (prediction error) to anticipate the precise amount of energy needed for specific action (Schulkin and Sterling, 2019). Among long-term couples, the attachment bond has already been established and the evolutionary goal here is to cement the relationship so that it can foster anabolism, the relaxation of vigilance in the service of the brain's upkeep and reparatory mechanisms, which are sustained by human attachments and cultural activities (Schulkin and Sterling, 2019). In cases when this survival-related goal is achieved by the high behavioral coordination, a widely-distributed, multi-rhythmic neural entrainment may be less efficient and our results demonstrate that the use of such parsi-

monious brain-behavior mechanism resulted in better performance, in terms of the partners' felt support, the goal of the social act. However, when meeting an in-group stranger, who can become a potential mate or ally but can also be hurtful and demeaning, there is a need for greater investment of energy in the detection of unfamiliar patterns and vigilance against potential insult. Indeed, among strangers, only when both neural and behavioral coupling was high, individuals reported a sense of felt support.

Empathy is a complex human achievement. It involves the integration of two processes; affect sharing and the ability to assume the vicarious stance, the first more automatic, bottom up, and implicates sensorimotor regions that enable the representations of others' motions in one's brain, the other higher order, top down, and underpinned by temporal areas such as the STS, temporoparietal junction, and temporal pole (Bernhardt and Singer, 2012). Unlike most research on the human empathic neural response, which employed static stimuli of physical pain or emotional distress, ours study is the first to employ live interactions of empathy giving and to utilize a two-brain approach to unravel the neural basis of empathy. Notably, our findings support prior work on the brain basis of empathy and its two-tier sensorimotor and temporal underpinnings. We show that when two humans share an empathic dialogue that is person-specific, emotional, and associative, both the sensorimotor resonance and mentalization components of empathy coordinate between their brains to underpin the neural basis of empathy in real life. We further found that this two-person empathy integrates alpha, beta, and gamma rhythms. Gamma oscillations in agranular associative regions is thought to integrate higher-order information by using interoceptive representations of one's own bodily milieu in the service of the vicarious stance (Seth and Friston, 2016), and our findings are the first to demonstrate such process between two brains in the service of in-the-moment, real-life empathy.

Overall, our findings can add to the rapidly growing hyper-scanning literature. To complement prior research on motor synchrony during mimicking or computer tasks (Dumas et al., 2010; Konvalinka et al., 2014; Naeem et al., 2012a, 2012b; Tognoli et al., 2007), we observed motor synchrony in a more naturalistic and daily context, yet found the same brain areas and neural rhythms to underpin interbrain synchrony. We further expanded our analysis from motor coordination to naturalistic empathy-giving. While previous studies (Ciaramidaro et al., 2018; Goldstein et al., 2018; Hu et al., 2017) examined how brain-to-brain synchronization and joint motor tasks impact prosocial behavior via computer paradigms or physical proximity and touch, our participants acted naturally in an empathy-giving situation in a real life face-to-face setting. This shift of paradigm from abstract or non-social interactions to a daily social exchange may expand our knowledge on how two brains synchronize during real-life social moments.

Interbrain processes are only beginning to receive empirical attention and require much further research in order to untangle the brain areas, neural rhythms, behavioral markers, and molecular processes that underpin the complex unfolding of neural synchrony in real time among dyads and within groups. Limitations of our study also should be noted; we included only homologous regions in our brain-to-brain analysis and further research should explore all possible connectivity patterns. Similarly, inclusion of a structured task would have provided additional valuable information, and there are other methods of data analysis, each with its own drawbacks and benefits.

Much further research across developmental stages, brain areas, and experimental tasks is required to shed further light on the mechanisms by which the human brain responds online to social signals, collaborates to accomplish social goals, reads the intentions of others in real time, and resonates with the feelings of fellow humans. We need much more research to understand how love and friendship, as well as conflict and hatred, turn into distinct interbrain processes underpinned by specific behavioral markers. We are only beginning to understand how interbrain processes play a role in allostasis and how co-regulatory processes may sustain efficient resource allocation to maximize performance and

save metabolic cost. Finally, much further research is required to understand how these processes mature from infancy to adulthood and what are the specific disruptions that may compromise the individual's capacity to engage fully in human social life in order to build two-brain interventions that can facilitate a mature participation in two-brain social experiences.

Ethics statement

The experimental protocol was approved by the Institutional Review Board (IRB) of Bar-Ilan University. All procedures were explained to the participants before the study and were performed in accordance with ethical guidelines. Participants gave written informed consent and were free to leave the experiment at any time with full compensation.

Data and materials availability

The data that support the findings of this study are available on request from the corresponding author, R.F. The data are not publicly available due to its nature – questionnaires and videos of interactions containing information that could compromise the privacy of research participants.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2020.117600.

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