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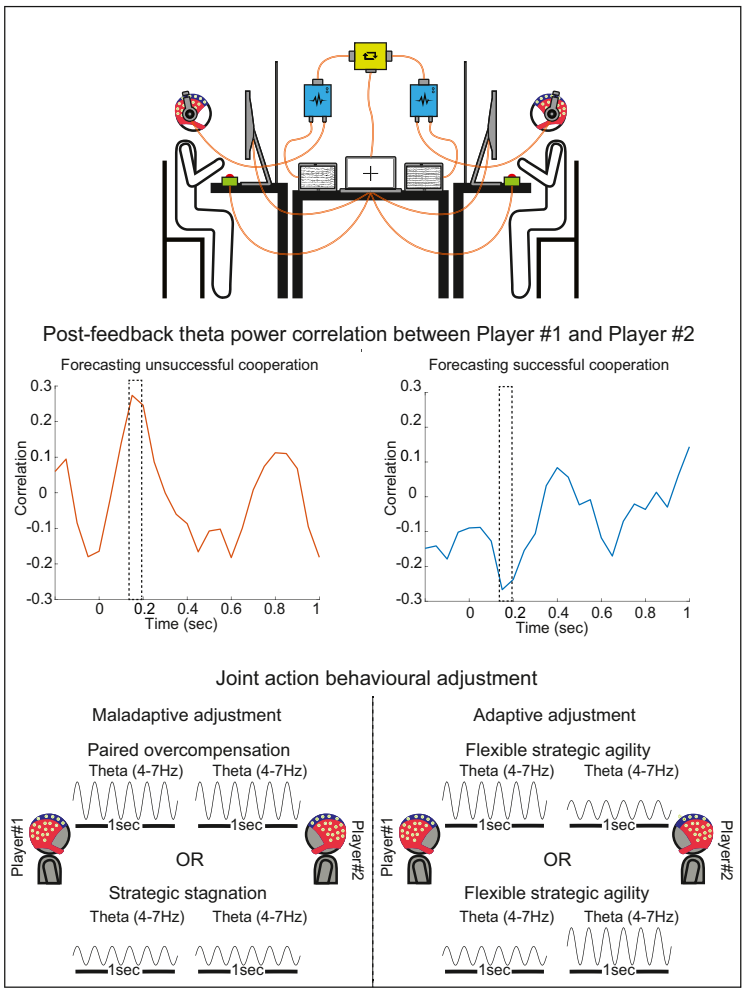

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Highlights

Cooperation was measured using a time estimation task while dual EEG was recorded

Post-feedback theta power correlation between players predicted failed joint action

Anti-correlation in theta power between players forecasted successful joint action

Successful cooperation requires flexible strategic agility from both partners

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Brain-to-brain coupling forecasts future joint action outcomes

Roksana Markiewicz,[1,2,3,4,*] Katrien Segaert,[1,2] and Ali Mazaheri[1,2]

SUMMARY

In this study, we investigated whether brain-to-brain coupling patterns could predict performance in a time-estimation task that requires two players to cooperate. The participant pairs were tasked with synchronizing button presses after converging on a shared representation of "short," "medium," and "long" time intervals while utilizing feedback to adjust responses. We employed electroencephalogram (EEG)-hyperscanning and focused on post-feedback brain activity. We found that negative feedback led to increased frontal mid-line theta activity across individuals. Moreover, a correlation in post-feedback theta power between players forecasted failed joint action, while an anti-correlation forecasted success. These findings suggest that temporally coupled feedback-related brain activity between two individuals serves as an indicator of redundancy in adjustment of a common goal representation. Additionally, the anti-correlation of this activity reflects cognitive strategic mechanisms that ensure optimal joint action outcomes. Rather than a *paired overcompensation*, successful cooperation requires *flexible strategic agility* from both partners.

INTRODUCTION

Successful joint action entails sharing a common goal and striving toward it, while also incorporating feedback when deviations from the goal occur. To successfully cooperate, it is thus crucial to process feedback and adjust behavior accordingly. While electroencephalogram (EEG)-hyperscanning has previously been used to investigate joint action,[1] no study to date has investigated the brain-to-brain coupling of neurocognitive mechanisms that drive the adjustment of shared representations of the common goal in response to feedback. In the current study, we investigate the specific brain-to-brain activity, in response to negative feedback, that can forecast the strategic cognitive mechanisms underlying adjustment of the shared representation of the task and facilitate successful performance in joint action cooperation.

The primate's brain has evolved to not only manage the demands related to cognitive abilities but more importantly to navigate and work with large social groups.[2] Joint action is a type of social interaction, in which a shared goal is achieved through the coordinated actions of at least two individuals in time and space.[3] Joint action is present in everyday life, for example when moving a heavy sofa up a flight of stairs. The success of joint action performance is reliant on creating shared representations, the ability to predict actions as well as the outcomes of one's own and others' actions, including adjustments made when the outcome of an attempt is unsuccessful.[3] A first mechanism that underlies joint action is about ensuring that the coordinating partners can *guide attention* to perceive the same event or object (like creating common ground). Secondly, for successful joint action to occur, *action observation* is required. A corresponding representation of the object/event of interest in the observer's action system is created. This aids the understanding of the action, creates "common ground" in terms of action goals, and supports prediction of each other's action outcomes. For example, it has previously been observed that the gaze of the action observer precedes the action of their partner.[4] Lastly, but perhaps the most important, is *action adjustment*, which refers to adjusting behavior in space and time to complement the action of the coordinating partner. For example, lowering your end of the sofa when you see your moving partner is getting stuck with their end (i.e., the results of the adjusted shared representation of the common goal). Joint action is influenced not just by an individual's beliefs about their own abilities but also by the beliefs about what they can achieve in collaboration with others.[5] In the present study, we will focus on using feedback to make the adjustments needed to increase joint action success. To do this, we will examine the dynamic relationship between interacting brains[6–9] using a hyperscanning approach.

In the last decade, the social neuroscience field has seen a trend toward using a "multi brain framework" to study how humans interact with each other. Hyperscanning involves the simultaneous recording of brain activity (either hemodynamic or neuroelectric) in multiple individuals during interactive task performance. It allows for investigations on how the activity dynamics of two brains (or more) underlies the continuous adaptation of one's actions in response to the changes in actions of someone else. Since first implemented,[10] two-brain science has been used to study classroom dynamics,[11] communication,[12,13] music,[14] and coordinated button presses[15–17] (see studies by Konvalinka and

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Roepstorff[7] and Czeszumski et al.[18] for detailed reviews). Also, interpersonal dynamics such as cooperation or joint action have widely been studied using hyperscanning methods.[15] Joint action relies on the postulation of anticipating and predicting other people's actions and adjusting our own actions accordingly.[19] "Coupling" between individuals can occur on motor, perceptual or cognitive levels during joint action[20] with behavioral synchrony often reflected in neural synchrony. This neural connectivity as measured by hyperscanning is the correlation between neurophysiological signals that are temporally related but spatially distinct (i.e., in two separate brains).[21]

EEG hyperscanning is particularly useful in the context of the present study due to its high temporal resolution, which allows for a real-time window into the neural processes induced by feedback in the unfolding dynamics of social interaction on a millisecond scale. Several EEG hyperscanning studies have reported inter-brain synchronous oscillatory patterns in joint action contexts, both in terms of oscillatory power as well as phase during fine motor coordination,[22,23] verbal coordination,[24] and other complex joint actions.[25] The mechanisms that support adjustment of the shared representation of the task goal in response to feedback in a joint-action context are key to explaining joint action outcomes, but they are not clear to us yet. Only two studies to our knowledge have investigated the inter-brain dynamics in tasks with an incorporated feedback element. One study reported on the heightened inter-brain alpha phase synchrony *during* a coordination task (vs. control), but not in response to feedback.[26] Conversely, another study examined directly the effect of external feedback on joint action in the context of EEG inter-brain dynamics.[27] However, in this study, feedback was superficially created and not based on the actual joint action performance. From this, it is evident that there is a clear gap in the literature: the precise neural mechanisms that facilitate adaptive responses to feedback and thus shared representation of the common goal within the context of joint action remain elusive.

The impact of feedback has been studied extensively in tasks that do not involve a joint-action component,[28] or in tasks that involved a joint-action component but only examined the neural dynamics of one of the participants.[29–31] A careful look at these studies enables us to propose precise predictions about the inter-brain mechanisms that might be involved in post-feedback adjustments in a joint-action setting. It has been established that a feedback cue induces oscillatory EEG changes, time-locked, but not necessarily phase-locked, in the 3–7 Hz (theta range) with a maximal midline frontal distribution. This feedback induced neural signature is thought to reflect the initiation of response adjustments (i.e., cognitive control) overriding "status quo" responses.[32,33] The midline theta response can be reliably measured on a trial-by-trial basis, providing valuable insights into the neural-dynamics subserving behavioral adjustment. This measure affords a real-time window into how the brain adapts and adjusts behavior based on feedback,[28] allowing us to explore the intricate relationship between neural activity and behavioral responses. In the present investigation, our focus lies on theta activity as a reflection of adjustment in the mental representation of the time intervals between the partners within a pair. However, rather than solely examining how the amplitude of feedback related theta activity in each participant (referred to as "player") relates to their performance in future trials, we, by using EEG hyperscanning, are specifically interested in how the *correlation* between these responses can effectively forecast their joint action success.

We implemented an EEG hyperscanning approach while participants completed an innovative time-estimation task. The objective of this task was to converge on a mutual representation of what a "short," "medium," and "long" interval entailed. Specifically, auditory cues instructed participants to either press a button after what they mutually judged to be a short, medium, or long time. Participants reached a successful joint action outcome if they reached a shared representation of the time intervals and thus converged on their responses. Importantly, feedback was given after each trial with respect to their joint action outcome, and if unsuccessful, about who was faster and by how much. With this, we created an ideal situation to study the inter-brain mechanisms that support feedback processing and subsequent behavioral adjustment. By utilizing this time-estimation task, we were able to study how individuals develop shared understanding and mutually converge on an idea (in this case of timing intervals) exclusively through the external feedback they received. This task included well-defined joint action outcomes, namely successful and failed cooperation, enabling us to investigate the separate neural mechanisms underlying these distinct outcomes in joint action.

In our theoretical framework, we hypothesize that the absence of strategy alteration or mutual adjustment in the mental representation of the time intervals (short, medium, and long) in both players, we refer to this as *strategic stagnation*, would result in unsuccessful joint action. Conversely, if both partners actively modify their strategies and adapt their mental representations of the time intervals, this could potentially facilitate adaptive adjustments and promote successful joint action.

However, the risk of both players attempting to adjust their strategies is that there would be a redundancy of adjustment in the mental representations of the time intervals, which could lead to *paired overcompensation* and thus maladaptive behavioral adjustment. Therefore, our alternative hypothesis posits that joint action success is more likely when players exhibit *flexible strategic agility*. In this scenario, one partner adjusts their mental representation to a greater extent than the other, allowing for asymmetry in their adaptation process. This asymmetry may manifest as one player making more pronounced changes in their mental representation compared to the other, leading to effective coordination and ultimately contributing to successful joint action. We theorize that this mechanism may strike an optimal balance, characterized by flexible strategic agility and asymmetrical adjustments in the mental representation of time intervals, and thus enable a balanced mutual convergence that facilitates successful joint action.

RESULTS

Cooperation was measured via a non-verbal task, completed in pairs, while EEG was recorded from both players simultaneously (see Figure 1 for experimental set up and trial presentation). Participants synchronized their button presses with their partner within the pair. Auditory stimuli (high, medium, or low pitch tone) at the start of each trial indicated the duration of time (referred to as "short," "medium," or "long") that participants had to wait before pressing their button and attempting to synchronize it with the other player. Participants adjusted their representations of short/medium/long and thus their button-press responses solely based on the feedback provided at the end of each trial.

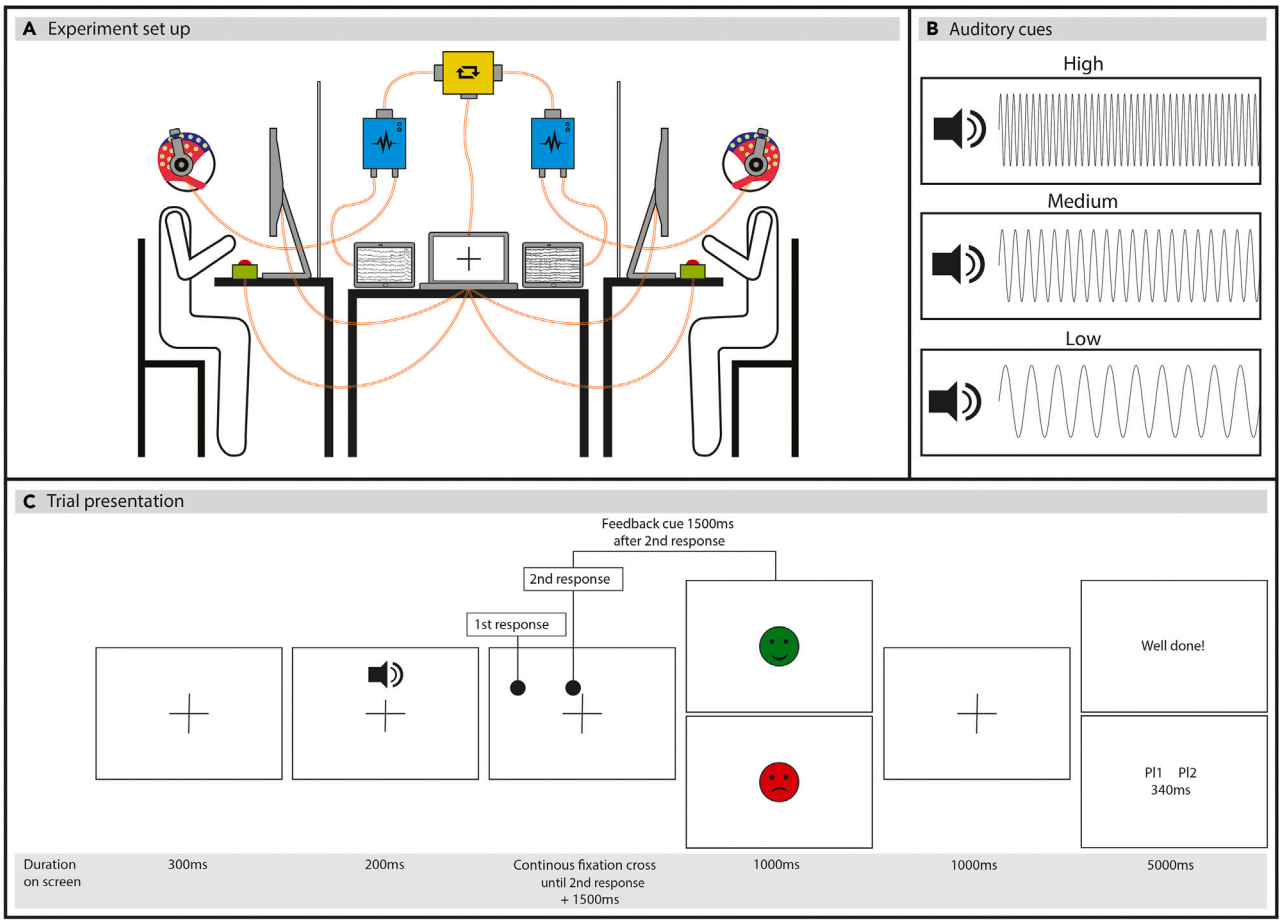

Figure 1. The experimental setup and trial presentation

(A) Participants wore Waveguard caps with 32 cap-mounted Ag/AgCI electrodes. The ANTneuro EEGsports amplifier systems amplified the signals for each participant. The EEG signals were synchronized using a parallel port splitter. The stimuli were presented on a central laptop connected to two identical monitors. Participants listened to auditory cues through noise-canceling headphones and used a button box to record their responses.

(B) The experiment used three auditory cues: high, medium, and low frequency tones, corresponding to short, medium, and long waiting times.

(C) Trial presentation involved both participants receiving the same stimuli simultaneously. The order of the button responses was completely driven by the participants and thus resulting in trial-to-trial variations of who pressed first/second. The feedback stimuli varied based on trial outcome: a green smiley face and "Well done" for successful cooperation trials, and a red sad face with feedback text indicating which player pressed the button first/second and the elapsed time for failed cooperation trials. Participants were informed of their player number to understand the feedback text.

Participants adhered to task instructions

We performed a linear mixed effects analysis between the condition type (short, medium, and long) and response times of individuals. This was to check whether participants adhered to task instructions of waiting short, medium, and long amounts of time before synchronizing their button presses (depending on the auditory cue type). We compared conditions *short* vs. *medium* and conditions *medium* vs. *long* in one model (model A), and conditions *short* vs. *long* in another model (model B). Tables 1 and 2 report the model output, showing that participants indeed adhered to waiting the respective amounts of time for each condition type before responding. Figure 2 shows the average response times (sec) and accuracy (%) for each condition across all participants, Figure S1 displays the response times of player 1 and player 2 of a representative pair in function of trial number for each condition.

Additionally, we examined whether the outcome of each trial (i.e., the time difference between the button presses) could be predicted based on the interplay of behavioral adjustments made by both players after the previous trial. To do this, we computed a multiple linear regression model, with the predictor variables being: the behavioral adjustment of player one and behavioral adjustment of player two, as well as their interaction. The outcome variable was the cooperative outcome (i.e., the time difference between the button press of player one and two); cooperative outcome ~ behavioral adjustment of player one * behavioral adjustment of player two. The model explained a statistically significant but weak proportion of variance ($F(3, 2647) = 61.40$, $p < 0.001$).The model revealed that the behavioral adjustment of player one ($\beta = -0.14$, $p < 0.001$) but not of player two ($\beta = -1.11$, $p = 0.945$) was a significant predictor of cooperative outcome. Most

Table 1. Summary of the mixed effects models for the reaction times of model A (comparison of short vs. medium and medium vs. long conditions)

	Estimate	SE	t value	*p* value
Intercept	2.077	2.039	10.19	<0.0001
Condition short vs. condition medium	−1.106	1.524	−72.58	<0.0001
Condition medium vs. condition long	1.049	1.524	68.83	<0.0001
n = 17,398				

Also see Figure S1.

importantly, the interaction between behavioral adjustment of player one and behavioral adjustment of player two significantly predicted cooperative outcome ($\beta = -0.16$, $p < 0.001$).

Given that the labels player 1 and player 2 are arbitrary, we decided to focus on the interaction term, which captures the essential dynamic interplay between both players. The interaction term in a regression model captures the combined effect of two variables on the outcome. Here the significant interaction term between player 1 and player 2's behavioral adjustments indicates that the cooperative outcome is influenced by how both players' adjustments interact, rather than by either player's adjustment alone. This highlights the importance of mutual adjustment in successful cooperation. While this model indeed confirms the significance of the interplay between the behavioral adjustments made by both players as a strong predictor of continuous cooperative outcomes (i.e., the time gap between player one's and player two's button presses), it is important to exercise caution when interpreting these findings. Our experimental design posed limitations regarding the direct calculation of behavioral adjustments occurring from one trial to the next due to the presence of intermixed trial types, making trial type (short, medium, and long) a confounding variable. Consequently, we had to establish a baseline for behavioral adjustment using the previous trial of the same condition and calculate *behavioral adjustment*, which may not fully represent the way that participants updated their mental representations of the timing intervals on the next consecutive trial. Therefore, it is important that these results are replicated using a blocked experimental design, enabling to directly examine the effect of behavioral adjustment of both players on cooperative outcome. See section Calculating behavioral adjustment (between players) for how behavioral adjustment was calculated.

Feedback related oscillatory modulations in the theta band

We compared the time-frequency representations (TFRs) of power between successful and unsuccessful cooperation conditions across all participants ($n = 59$) aligned to the onset of the feedback text. Figure 3 displays the TFRs of power locked to the onset of the feedback text for the incorrect and correct conditions, and the topographic distributions of the condition effect in the theta band. In the following, we describe the significant oscillatory differences between successful cooperation and unsuccessful cooperation conditions that were identified using non-parametric cluster-based permutation in the theta band (4–7 Hz) post-feedback text onset.

We observed significant condition differences ($p = 0.003$) in post-feedback theta activity between the successful cooperation and unsuccessful cooperation condition, which was maximal over the central and centro-parietal channels. Specifically, theta power was stronger right after the onset of the feedback text in the failed cooperation condition until around 0.4 s compared to the successful cooperation condition.

Further, we also observed significant condition differences in the feedback related activity in the delta (1–4 Hz), alpha (8–14 Hz), low beta (15–20 Hz), and high beta (20–25 Hz) frequency bands as well as event-related potential (ERP) differences (see Figure S4 for a comprehensive description of all effects).

Inter-player theta power coupling forecasts cooperative outcome on the next consecutive trial

We compared the inter-player power coupling (see section STAR Methods: Forecasting cooperative outcome analysis for how the inter-player power coupling was calculated) between two conditions: *forecasting unsuccessful cooperation* (i.e., failed cooperation trials followed by *a consecutive* unsuccessful cooperation trial) *and forecasting successful cooperation* (i.e., failed cooperation trials followed by *a consecutive* successful cooperation trial) using non-parametric cluster-based permutation tests across all pairs ($n = 29$ pairs). Figure 4 displays inter-player power coupling for (A) *forecasting unsuccessful cooperation* and (B) *forecasting successful cooperation*. We found an inter-player oscillatory power coupling signature that forecasts cooperative outcome on the next consecutive trial (i.e., local effect). Using the non-parametric cluster-based permutation tests (with a pre-defined time window of 0–4 s post-feedback based on the feedback related results in the time frequency domain), we observed a significant condition effect ($p = 0.006$) in the theta frequency band (this effect was also observed when an exploratory time window of 0 to 2 s was used in the non-parametric cluster-based permutation tests, $p = 0.051$). The effect corresponded to a cluster that spanned between 0.15 and 0.2 s and was maximal over two electrodes (Fz and FC2) that neighbored each other. The inter-player theta power coupling showed the opposite patterns of results in the two conditions. Forecasted cooperative failure was associated with a positive correlation between theta power of player one and player two (i.e., the greater the theta power in one player, the greater the theta power in the other player within a pair, or, the smaller the theta power in one player, the smaller the theta power in the other player). On the other hand, forecasted cooperative success was linked with a negative correlation between the theta power of player one and player two (i.e., the greater the theta power of one player, the lower the theta power of the other player within a pair or vice versa).

Table 2. Summary of the mixed effects models for the reaction times of model B (comparison of short vs. long condition)

	Estimate	SE	t value	*p* value
Intercept	4.176	2.039	20.48	<0.0001
Condition short vs. condition long	−2.15	1.524	−141.42	<0.0001
n = 17,398				

Also see Figure S1.

Inter-player coupling in delta, alpha, or beta bands does not forecast cooperative outcome on the next consecutive trial

We did not find any significant inter-player power coupling signatures of forecasting cooperative outcomes in the alpha band using the pre-defined 0.3 to 1.75 s time window. Further analyses using exploratory time window of 0 to 2 s post-feedback text also did not yield significant effects in any of the frequency bands (delta, alpha, low beta, and high beta).

Relationship between behavior and theta dynamics on a trial-by-trial basis

The aforementioned analysis (i.e., Inter-player theta power coupling forecasts cooperative outcome on the next consecutive trial section) treated cooperative outcomes as dichotomous variables defined by a pre-determined threshold: cooperative failure vs. success. However, we also sought to examine whether the trial-by-trial inter-player theta dynamics are predictive of *continuous* cooperative outcomes on behavioral level (i.e., the absolute difference in reaction times [RTs] between player one and player two). We carried out a multiple linear regression analysis as follows: cooperative outcome RT difference ~ averaged theta power of player one * averaged theta power of player two + absolute theta power difference between players (see Trial-by-trial analysis linking theta dynamics with behavioral outcomes in STAR Methods for further details). The model explained a statistically significant and weak proportion of variance ($F(4, 2738) = 7.64$, $p < 0.001$). The model revealed that the averaged theta power of player one ($\beta = 0.08$, $p < 0.001$), and player two ($\beta = -0.02$, $p = 0.008$) were significant predictors of cooperative outcome. Importantly, the model showed that the interaction of averaged theta power of player one and player two (i.e., averaged theta power of player one * averaged theta power of player two) significantly predicted the continuous cooperative outcome ($\beta = -0.25$, $p < 0.001$). This suggests that cooperative outcomes are significantly driven by the dynamic interplay of theta power modulations of *both* players.

Feedback related modulations in theta band do not reflect the required type of individual adjustment

We aimed to further explore the underlying mechanism responsible for the observed brain-to-brain activity in the theta power forecasting joint action outcome. Here, our aim was to examine whether the observed inter-player coupling effect originates from the *mutual* adjustment or whether it is attributed to a singular process performed independently by each individual (and thus the brain-to-brain coupling effect is merely a by-product of cognitive processing). To achieve this, we compared trials based on the individual type of adjustment required for the following trial; *unsuccessful cooperation trials that necessitated speeding up* in the subsequent trial vs. *unsuccessful cooperation trials that necessitated slowing down* in the subsequent trial.

The non-parametric cluster-based permutation tests did not yield any significant condition differences in the theta power between the unsuccessful trials that required speeding up vs. slowing down. In other words, at the *individual* level, theta power did not serve as a predictive factor for determining the type (speed up or slow down) of behavioral adjustment required in the subsequent trial. Thus, we can be confident that the brain-to-brain effects reported in the Inter-player theta power coupling forecasts cooperative outcome on the next consecutive trial section arise from the mutual adjustment of time interval representation in this joint action context and not merely as a by-product of common cognitive processing.

Inter-player power dynamics did not forecast cooperative results in the following trial of the same condition

We performed further analysis to identify power brain-to-brain signatures between participant pairs that were predictive of *global* cooperative outcomes. No significant inter-player power coupling patterns were observed when forecasting cooperative outcomes for the nearest trial of the same condition type within the theta band (utilizing the predefined time window of 0–0.4 s), nor within the alpha band (utilizing the predetermined time window of 0.3–1.75 s). Subsequent exploratory analyses involving a time window of 0–2 s post feedback similarly failed to reveal significant effects across any of the examined frequency bands, including alpha, low beta, and high beta.

Post-feedback theta power did not differ between "adjusters" and "non-adjusters"

We computed cluster-based permutation tests to examine the differences in the post-feedback theta power between adjusters and non-adjusters (see Effects of "adjusters" and "non-adjusters" on the post-feedback theta power analysis for how adjusters and non-adjusters were defined). The results revealed no significant differences in the post-feedback theta power between adjusters and non-adjusters in neither of the following: (1) successful vs. unsuccessful trials, as well as the differential theta power between successful and unsuccessful trials, and (2) failed cooperation trials followed by a consecutive successful cooperation trials vs. failed cooperation trials followed by consecutive

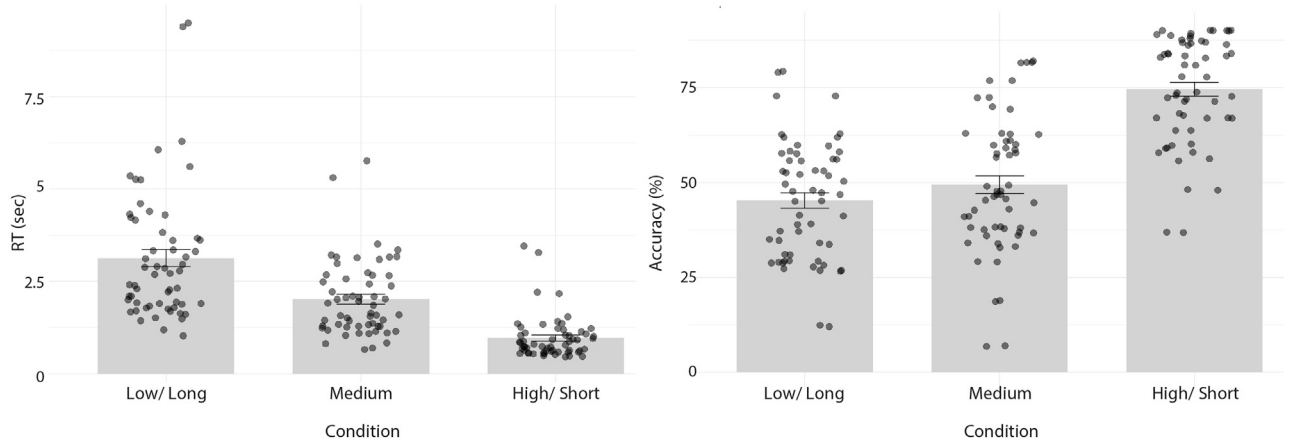

Figure 2. Average response times in seconds (left), and average accuracy in percentages (right) per condition across all participants
The error bars represent standard error and the black dots represent individual data points. Also see Figures S1–S3 and Table S1.

unsuccessful cooperation trials. Perhaps, our experimental task or the adjuster/non-adjuster definition may not effectively distinguish between adjusters and non-adjusters.

DISCUSSION

In this study, we investigated whether brain-to-brain coupling patterns in a two-player game could predict performance in a joint-cooperation task. The aim of the task for the players was, upon hearing auditory cues, to establish a shared understanding of "short," "medium," and "long" intervals and synchronize their button presses with each other. The outcome of the joint action was successful only when players converged on their responses. We found that receiving negative feedback led to increased frontal mid-line theta activity across individuals. Moreover, a correlation in post-feedback theta power between players forecasted failed joint action, while an anti-correlation forecasted success. We suggest that the temporally coupled feedback related brain activity between two individuals is an indicator of one of two strategies, either redundancy in adjustment of their representation of the task goals (i.e., *paired overcompensation*; mutual high theta power) or lack of adjustment from both partners (i.e., *strategic stagnation*; mutual low theta power). On the other hand, the anti-correlation of this activity reflects cognitive strategic mechanisms that ensure optimal joint action outcomes. We propose that our results indicate that successful joint action outcomes are achieved by the implementation of *flexible strategic agility*, whereby in a given trial one partner within the pair demonstrates greater adaptability than the other (the higher the theta power in one player, the lower the theta power in the other player). This flexible adaptive approach emerges as a key determinant for converging on the representation of the task goals and thus fostering successful cooperation. Our results emphasize the alignment of mental representations and brain interactions rather than merely adjusting motor behavior.

Our findings demonstrate how the dynamics of the brain activity induced by feedback between two players could forecast joint action outcomes. With this, we filled a crucial gap in the literature by emphasizing the significance of interpersonal neural patterns in predicting joint action outcomes on subsequent trials by focusing on the correlation of the brain-to-brain neural responses, rather than examining the feedback related neural responses on an *individual* level.

The use of the external feedback allowed the players to adjust their representations of the timing intervals and therefore responses for future trials. On an *individual* level we found distinct patterns of neural activity related to feedback: an increase in frontal midline theta activity after negative feedback and an increase in centro-posterior midline beta following positive feedback (see supplemental information for more details on feedback related modulations in *delta*, *theta*, *alpha*, and *beta* bands). The enhanced theta following negative feedback is linked with enhanced cognitive control and the need for behavioral adjustment following an error,[34–36] whereas the increased beta following positive feedback signals the requirement for strategy maintenance after a correct response. Furthermore, our analysis revealed that at the *individual* level, no significant differences emerged in theta power modulations between unsuccessful trials that required speeding up compared to those that required slowing down in the subsequent trial. This control analysis is crucial as it demonstrates that the main observed findings (i.e., theta power anti-correlation forecasts successful cooperation and theta power correlation forecasts failed cooperation) are not likely merely a reflection of common cognitive processes, but rather an inter-relational adjustment of the representations of common goal.

Most importantly, we found the correlation of brain-to-brain activity in the feedback related theta power to be a predictor of cooperative outcomes on subsequent trials. Given the well-established role of theta oscillations in adjustment following negative feedback, wherein they override "status quo" responses at individual level, it is reasonable to anticipate distinct brain-to-brain patterns within the theta frequency range, that are predictive of future joint action outcomes at a paired level. Specifically, *correlated* brain-to-brain activity in the theta power significantly increased the likelihood of an error in the subsequent trial. We speculate that this can be attributed to two potential unsuccessful cognitive strategies adopted by the players. We suggest a first unsuccessful strategy is for the two players to passively apply *strategic stagnation*, where neither of the players adjusted their representation of the timing intervals, resulting in failed joint action. Interestingly, an

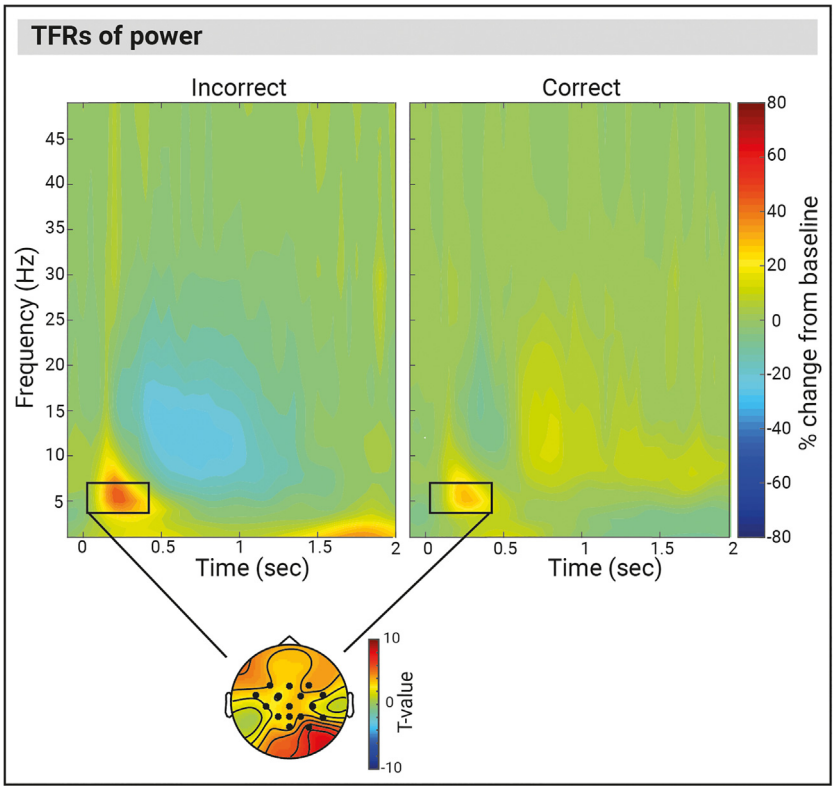

Figure 3. Time-frequency representations of power at the Cz electrode for unsuccessful trials (left), and successful trials (right) averaged over all individuals (*n* = 59), locked to the onset of the feedback text

The topoplot illustrates the clusters of electrodes that show the most pronounced condition difference. Black rectangles indicate a significant condition difference ($p < 0.05$, cluster corrected) in the theta band. Also see Figure S4.

alternative yet equally unsuccessful strategy, which we suggest is a concerted effort of strategy modification from both players (i.e., *paired overcompensation*), resulted in the redundancy of adjustment of the representation of the task goals, overcorrection, and thus subsequent failed joint action. A strategy toward success on the other hand, was *anti-correlated* brain-to-brain activity in the theta power, which forecasted successful subsequent trials. Here, our proposed interpretation is that players employed a *flexible strategic agility*, wherein one partner adjusted their cognitive strategy and the representation of the common goal to a greater extent than the other (see Figure 5 for a schematic representation of the results). This *flexible strategic agility* facilitated a harmonious balance of adaptive adjustments, resulting in mutual convergence of the time intervals, and thus successful cooperative outcome in the subsequent trial.

Our findings are consistent with the traditional view of enhanced theta power being linked with enhanced cognitive control.[28,37] Specifically mid-frontal theta is thought to be a neural marker of the adaptive response to (potential) errors.[32,34,38] Oscillatory activity in the theta band in the frontal network (including the medial frontal cortex [MFC] and lateral prefrontal cortex [pFC]) is linked to the monitoring of ongoing actions and signaling unfavorable action outcomes. A greater theta power increase has consistently been observed following errors compared to successful outcomes.[39–41] This theta band activity also extends its role to predicting learning from negative feedback suggesting its involvement in behavioral adjustment in response to feedback that arises from suboptimal actions and thus outcomes.[28] Specifically, the mPFC theta increase has been linked to predicting post-error RT slowing, suggesting greater engagement of cognitive control for identifying and fixing errors.[42] Conversely, beta oscillatory power increases have been observed following correct responses and positive feedback[35,43,44] indicating the need for strategy maintenance.[36,45] This beta band power change facilitates the reinforcement of the current motor or cognitive strategy via top-down influence.[28] We replicated and further extended literature findings in this field by demonstrating that modulations in theta and beta band activity in response to feedback are also elicited in joint action settings with the task goal being mutual convergence of timing intervals, rather than individual learned responses.

In addition, our inter-brain findings expanded the traditional view on the link between theta power modulation and cognitive control and moved this framework beyond the potential predictive nature of oscillatory activity on the individual level. Our findings demonstrated that we could apply the current theory to a joint action scenario where its success is reliant upon the convergence and creation of a mutual representation of time intervals between individuals based on the feedback provided. This view is further supported when switching from the dichotomous nature of the joint action outcome (i.e., successful vs. unsuccessful cooperation), and instead examining joint action outcomes as an

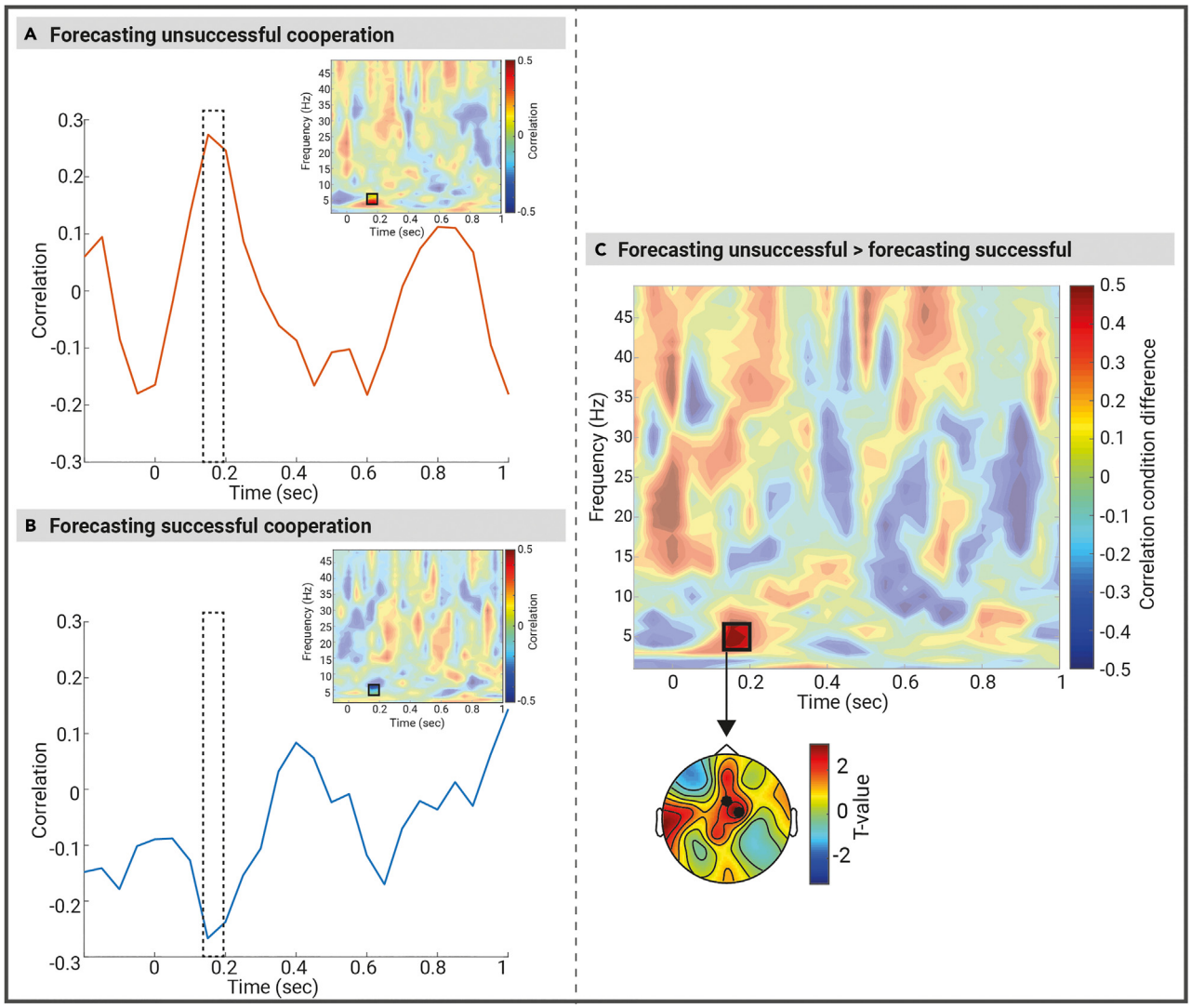

Figure 4. Forecasting joint action outcomes (successful vs. unsuccessful cooperation) on next consecutive trials based on the correlation values (Fisher Z) of oscillatory power coupling between player 1 and player 2 after the onset of feedback text in the failed cooperation condition

Line plots are representing the correlation (Fisher Z) values averaged over Fz and FC2 electrodes in the theta frequency band (4–7 Hz) forecasting (A) unsuccessful cooperation trials and (B) successful cooperation trials. The dashed rectangles indicate the time windows of the significant between condition differences (as calculated via the non-parametric cluster-based permutation tests). The heatmaps are displaying the correlation values (Fisher Z) of oscillatory power coupling averaged over Fz and FC2 electrodes between player 1 and player 2 locked to the onset of the feedback text forecasting (A) unsuccessful and (B) successful cooperation. The black rectangles indicate significant condition differences ($p < 0.05$, cluster corrected).

(C) A heatmap is representing the condition difference (forecasted unsuccessful cooperation – forecasted successful cooperation) correlation values (Fisher Z) of oscillatory power coupling (averaged across the electrode clusters that indicate maximal condition difference, i.e., Fz and FC2) between player 1 and player 2 locked to the onset of feedback text. The black rectangle indicates significant condition differences ($p < 0.0.05$, cluster corrected). Also see Figure S5.

absolute time difference between players on a trial-by-trial basis. We demonstrated that the interplay of the averaged theta power of player one and player two was a significant predictor of cooperative outcome as measured as a continuous variable (i.e., absolute difference in RTs between the players). The trial-by trial brain dynamics of two interacting players and their subsequent behavioral performance suggests a mechanistic role of the brain signatures we observed for cooperative outcomes.

We interpreted the findings as distinct strategies accompanying different joint action outcomes: successful joint action and failed joint action. We demonstrated that flexible joint action adjustment, forecasted future successful joint action. We propose that employing a *flexible strategic agility* allowed for the mutual convergence of shared representations of timing intervals to be developed among the players. The *flexible strategic agility* emerged when varying levels of adaptability among partners were developed, with one player exhibiting a greater propensity for strategic adjustment than the other. This could then lead to the harmonious balance of adaptive adjustment, and thus

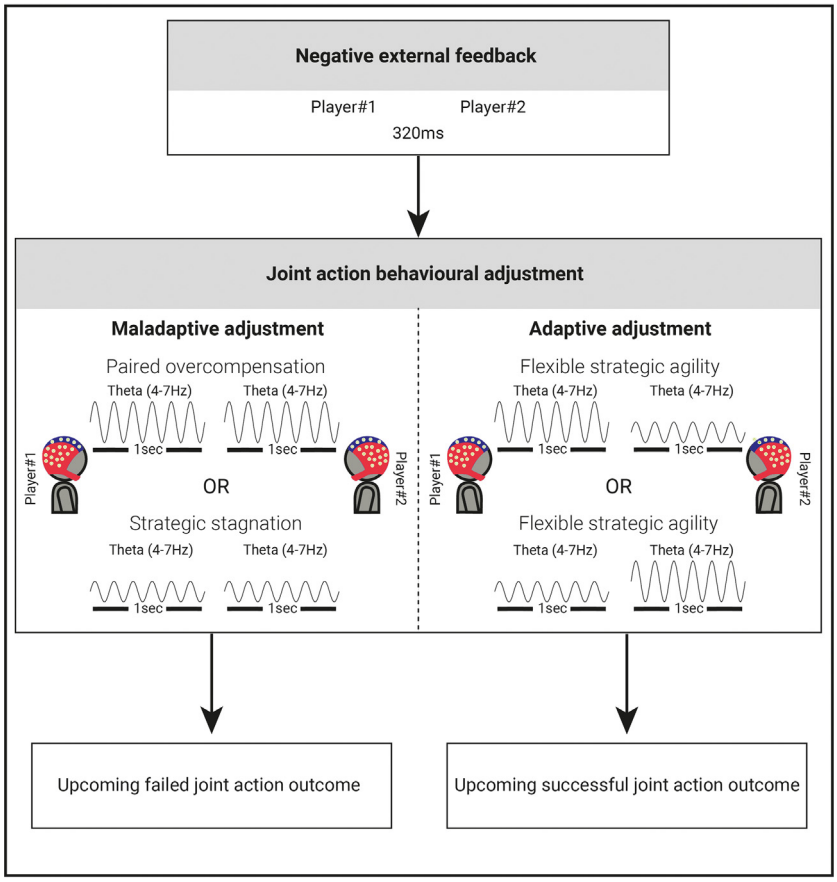

Figure 5. Schematic representation of the theta power modulation dynamics between individuals following feedback

successful cooperation. We posit that this is displayed in the anti-correlated brain-to-brain activity, wherein the higher the theta power in one player, the lower the theta power in the other player. We speculate that this *anti-correlated* brain-to-brain activity was indicative of the players engaging in rather complementary adjustment processes and increasing the likelihood of uncovering different solutions for convergence on a representation of the common goal.

On the other hand, a correlated brain-to-brain activity in the theta power was foretelling of future failed joint action. We speculate that this could be attributed to the adoption of two distinct cognitive strategies by the players. In some situations, players could have used a passive approach of *strategic stagnation*, wherein both players refrained from adjusting their representation of the timing intervals. The lack of strategic adjustment hindered effective cooperation between the players, impeding their ability to synchronize actions. In other situations, the players could have relied on a *paired overcompensation* strategy with a tendency to follow similar approaches or strategies. This redundancy in adjustment of the common goal could limit the range of perspectives and strategies applied to the task, potentially hindering performance. This flawed dynamic of maladaptive adjustment disrupted the delicate balance required for successful joint action. However, it is crucial to note here, that these speculative conclusions are our interpretations of the data and caution should be exercised when drawing conclusive remarks.

Post-error slowing has previously been observed after negative feedback and speed up following positive feedback of the same stimulus type (after some delay) and not immediately following feedback.[40] This effect was interpreted as indicative of working memory for the specific stimulus type—this is not what we see here, we see a local effect of adjustment reflected in theta power modulations in the players on trials immediately after the feedback. In contrast, we did not observe the same effect for the same condition type stimuli (i.e., the global effect; refer to supplemental information "Effects of brain-to-brain coupling on global cooperative outcomes analysis" for further details). The difference in findings potentially lies in the methodologies: the previous study[40] used a probabilistic learning task in *individual* participants, whereas our participants had to take into account the behavioral adjustment of their partner as well. Post-error slowing or speeding is not applicable in the current study. Our paradigm with its random distribution of time estimation intervals means the feedback induced activity we observe is likely not reflecting lower order motor preparation processes (i.e., slowing or increasing reaction times) but rather an adjustment in their representation of the time interval. This is evident in the current results as we observed a lack of theta modulation differences between trials that necessitated a speed up vs. slow down strategy on the next trial.

Arriving at a shared representation of time through trial-and-error in a joint task can be related to Nash's equilibrium in the context of game theory. Nash's equilibrium is a concept that describes a state in a game where each player's strategy is optimal given the strategies chosen by other players.[46] It represents a stable outcome where no player has an incentive to unilaterally change their strategy. In the case of arriving at a shared representation of time, the participants in the joint task are engaged in a cooperative endeavor where they need to coordinate their actions based on feedback. Through trial-and-error, they aim to converge on a mutually agreed-upon understanding of "short," "medium," and "long" time intervals. This process involves continuous adjustments and learning from the feedback received. The relation to Nash's equilibrium arises when the participants reach a point where their strategies, in this case, their representations of time intervals, align and are mutually optimal. It signifies that they have found a shared understanding or agreement that maximizes their joint cooperation. This equilibrium state represents a stable and satisfactory outcome in terms of their performance in the joint task.

In the context of our findings, the anti-correlated brain-to-brain activity between individuals suggests a complementary processing style, indicating that each individual is adopting different strategies or approaches. This implies that they are not in Nash equilibrium because one individual's adjustment in response to feedback is influencing the other individual's subsequent performance. Nash's equilibrium typically involves players making strategic choices based on their beliefs about the other player's actions and seeking to maximize their own outcomes. In our study, we observed that an individual player's brain activity and subsequent performance are influenced by the feedback received, rather than being solely driven by strategic decision-making based on beliefs about the other player's behavior.

As the two-brain science field continues to evolve and researchers increasingly implement neuroscientific hyperscanning methods to study social interaction, it would be important to extend the current findings pertaining the application of feedback in other social scenarios, particularly those that involve verbal communication. By doing so, we could discover valuable insights that can be applied to and improve real-world social interactions such as romantic or friendship relations, team collaborations in workplace settings or even teacher-student interactions in educational settings.[11] On the other hand, we can also explore further the specific individual characteristics that are associated with the underlying neural processes involved in successful social interactions. For example, as previously suggested,[3] what is the extent to which joint action relies on theory of mind (ToM). Building upon our previous work demonstrating a connection between ToM and cooperation,[47] the next logical step is to explore the relationship between ToM abilities and the inter-person neural correlates of joint action. Furthermore, exploring individual differences in relation to the strategies employed by players and assessing the directionality of the interaction (i.e., leader versus follower) would be an intriguing avenue for future research.[48]

In conclusion, we studied how feedback related changes in the EEG signal between two participants involved in a non-verbal cooperative task adjusted representations of the common goal to ensure optimal joint action outcomes. We showed that following external feedback, an anti-correlated brain-to-brain activity in theta power was associated with *flexible strategic agility* and adaptive adjustment, leading to successful joint action on subsequent trials. Conversely, a correlated brain-to-brain activity in theta power of the players was linked to either a *strategic stagnation* or *paired overcompensation* strategy; both of which led to maladaptive adjustment and thus failed future joint action. By focusing on the (anti-) correlation of neural responses and moving beyond an individual-level perspective, we offer novel and more comprehensive insights into how brain-to-brain coupling predicts joint action outcomes.

Limitations of the study

It is important to highlight some caveats of our work. Firstly, we did not collect information about the ancestry, ethnicity, race, or socioeconomic status of the participants. The absence of these data may limit the study's generalizability. Secondly, the inter-mixed design of our paradigm poses limitations when exploring adjustment on a behavioral level. Specifically, directly calculating sequential behavioral adjustment between consecutive trials is challenging due to the variability in experimental conditions (transitioning from a short to a long trial). Optimizing this paradigm to a block design, where each block maintains the same experimental condition (i.e., either short, medium, or long) as well as including a solo (for example with a computer) or no feedback condition could provide further support for our findings.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Dr Roksana Markiewicz (r.markiewicz@bham.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data supporting this article have been deposited on OSF and are publicly available as of the date of publication from https://osf.io/ct8jb/.
- All original code has been deposited on OSF and is publicly available as of the date of publication from https://osf.io/ct8jb/.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, R.M., K.S., and A.M.; methodology, R.M., K.S., and A.M.; software, R.M.; formal analysis, R.M.; investigation, R.M., K.S., and A.M.; resources, K.S. and A.M.; data curation, R.M.; writing – original draft, R.M.; writing – review and editing, R.M., K.S., and A.M.; visualization, R.M.; supervision, K.S. and A.M.; project administration, R.M.; funding acquisition, R.M., K.S., and A.M.

DECLARATION OF INTERESTS

The authors declare no conflicts of interest.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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REFERENCES

1. Hamilton, A.F.C. (2021). Hyperscanning: Beyond the Hype. Neuron *109*, 404–407. https://doi.org/10.1016/j.neuron.2020.11.008.
2. Dunbar, R.I.M. (1992). Neocortex size as a constraint size in primates on group ecologically. J. Hum. Evol. *20*, 469–493.
3. Sebanz, N., Bekkering, H., and Knoblich, G. (2006). Joint action: Bodies and minds moving together. Trends Cognit. Sci. *10*, 70–76. https://doi.org/10.1016/j.tics.2005.12.009.
4. Flanagan, J.R., and Johansson, R.S. (2003). Action plans used in action observation. Nature *424*, 769–771. https://doi.org/10.1038/nature01861.
5. Marsh, K.L., Richardson, M.J., Baron, R.M., and Schmidt, R.C. (2006). Contrasting approaches to perceiving and acting with others. Ecol. Psychol. *18*, 1–38. https://doi.org/10.1207/s15326969eco1801_1.
6. Dumas, G. (2011). Towards a two-body neuroscience. Commun. Integr. Biol. *4*, 349–352. https://doi.org/10.4161/cib.4.3.15110.
7. Konvalinka, I., and Roepstorff, A. (2012). The two-brain approach: How can mutually interacting brains teach us something about social interaction? Front. Hum. Neurosci. *6*, 215. https://doi.org/10.3389/fnhum.2012.00215.
8. Stolk, A., Verhagen, L., and Toni, I. (2016). Conceptual Alignment: How Brains Achieve Mutual Understanding. Trends Cognit. Sci. *20*, 180–191. https://doi.org/10.1016/j.tics.2015.11.007.
9. Hari, R., Henriksson, L., Malinen, S., and Parkkonen, L. (2015). Centrality of Social Interaction in Human Brain Function. Neuron *88*, 181–193. https://doi.org/10.1016/j.neuron.2015.09.022.
10. Montague, P.R., Berns, G.S., Cohen, J.D., McClure, S.M., Pagnoni, G., Dhamala, M., Wiest, M.C., Karpov, I., King, R.D., Apple, N., and Fisher, R.E. (2002). Hyperscanning: Simultaneous fMRI during linked social interactions. Neuroimage *16*, 1159–1164. https://doi.org/10.1006/nimg.2002.1150.
11. Dikker, S., Wan, L., Davidesco, I., Kaggen, L., Oostrik, M., McClintock, J., Rowland, J., Michalareas, G., Van Bavel, J.J., Ding, M., and Poeppel, D. (2017). Brain-to-Brain Synchrony Tracks Real-World Dynamic Group Interactions in the Classroom. Curr. Biol. *27*, 1375–1380. https://doi.org/10.1016/j.cub.2017.04.002.
12. Stolk, A., Verhagen, L., Schoffelen, J.M., Oostenveld, R., Blokpoel, M., Hagoort, P., Van Rooij, I., and Toni, I. (2013). Neural mechanisms of communicative innovation. Proc. Natl. Acad. Sci. USA *110*, 14574–14579. https://doi.org/10.1073/pnas.1303170110.
13. Schoot, L., Hagoort, P., and Segaert, K. (2016). What can we learn from a two-brain approach to verbal interaction? Neurosci. Biobehav. Rev. *68*, 454–459. https://doi.org/10.1016/j.neubiorev.2016.06.009.
14. Babiloni, C., Buffo, P., Vecchio, F., Marzano, N., Del Percio, C., Spada, D., Rossi, S., Bruni, I., Rossini, P.M., and Perani, D. (2012). Brains "in concert": Frontal oscillatory alpha rhythms and empathy in professional musicians. Neuroimage *60*, 105–116. https://doi.org/10.1016/j.neuroimage.2011.12.008.
15. Balconi, M., and Vanutelli, M.E. (2017). Cooperation and competition with hyperscanning methods: Review and future application to emotion domain. Front. Comput. Neurosci. *11*, 86. https://doi.org/10.3389/fncom.2017.00086.
16. Funane, T., Kiguchi, M., Atsumori, H., Sato, H., Kubota, K., and Koizumi, H. (2011). Synchronous activity of two people's prefrontal cortices during a cooperative task measured by simultaneous near-infrared spectroscopy. J. Biomed. Opt. *16*, 077011. https://doi.org/10.1117/1.3602853.
17. Cui, X., Bryant, D.M., and Reiss, A.L. (2012). NIRS-based hyperscanning reveals increased interpersonal coherence in superior frontal cortex during cooperation. Neuroimage *59*, 2430–2437. https://doi.org/10.1016/j.neuroimage.2011.09.003.
18. Czeszumski, A., Eustergerling, S., Lang, A., Menrath, D., Gerstenberger, M., Schuberth, S., Schreiber, F., Rendon, Z.Z., and König, P. (2020). Hyperscanning: A Valid Method to Study Neural Inter-brain Underpinnings of Social Interaction. Front. Hum. Neurosci. *14*, 39. https://doi.org/10.3389/fnhum.2020.00039.
19. Decety, J., and Sommerville, J.A. (2003). Shared representations between self and other: A social cognitive neuroscience view. Trends Cognit. Sci. *7*, 527–533. https://doi.org/10.1016/j.tics.2003.10.004.
20. Knoblich, G., Butterfill, S., and Sebanz, N. (2011). Psychological Research on Joint

Action. Theory and Data B.Ross (Academic Press). https://doi.org/10.1016/B978-0-12-385527-5.00003-6.
21. Dumas, G., Chavez, M., Nadel, J., and Martinerie, J. (2012). Anatomical connectivity influences both intra- and inter-brain synchronizations. PLoS One *7*, e36414. https://doi.org/10.1371/journal.pone.0036414.
22. Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., and Garnero, L. (2010). Inter-brain synchronization during social interaction. PLoS One *5*, e12166. https://doi.org/10.1371/journal.pone.0012166.
23. Tognoli, E., Lagarde, J., DeGuzman, G.C., and Kelso, J.A.S. (2007). The phi complex as a neuromarker of human social coordination. Proc. Natl. Acad. Sci. USA *104*, 8190–8195. https://doi.org/10.1073/pnas.0611453104.
24. Ahn, S., Cho, H., Kwon, M., Kim, K., Kwon, H., Kim, B.S., Chang, W.S., Chang, J.W., and Jun, S.C. (2018). Interbrain phase synchronization during turn-taking verbal interaction—a hyperscanning study using simultaneous EEG/MEG. Hum. Brain Mapp. *39*, 171–188. https://doi.org/10.1002/hbm.23834.
25. Astolfi, L., Toppi, J., Borghini, G., Vecchiato, G., He, E.J., Roy, A., Cincotti, F., Salinari, S., Mattia, D., He, B., et al. (2012). Cortical activity and functional hyperconnectivity by simultaneous EEG recordings from interacting couples of professional pilots. In Proceedings of the Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBS), pp. 4752–4755. https://doi.org/10.1109/EMBC.2012.6347029.
26. Mu, Y., Guo, C., and Han, S. (2016). Oxytocin enhances inter-brain synchrony during social coordination in male adults. Soc. Cognit. Affect Neurosci. *11*, 1882–1893. https://doi.org/10.1093/scan/nsw106.
27. Balconi, M., Gatti, L., and Vanutelli, M.E. (2018). EEG functional connectivity and brain-to-brain coupling in failing cognitive strategies. Conscious. Cognit. *60*, 86–97. https://doi.org/10.1016/j.concog.2018.03.001.
28. van de Vijver, I., Ridderinkhof, K.R., and Cohen, M.X. (2011). Frontal oscillatory dynamics predict feedback learning and action adjustment. J. Cognit. Neurosci. *23*, 4106–4121. https://doi.org/10.1162/jocn_a_00110.
29. Czeszumski, A., Ehinger, B.V., Wahn, B., and König, P. (2019). The social situation affects how we process feedback about our actions. Front. Psychol. *10*, 361. https://doi.org/10.3389/fpsyg.2019.00361.
30. Itagaki, S., and Katayama, J. (2008). Self-relevant criteria determine the evaluation of outcomes induced by others. Neuroreport *19*, 383–387. https://doi.org/10.1097/WNR.0b013e3282f556e8.
31. Picton, L., Saunders, B., and Jentzsch, I. (2012). "I will fix only my own mistakes" : An ERP study investigating error processing in a joint choice-RT task. Neuropsychologia *50*, 777–785. https://doi.org/10.1016/j.neuropsychologia.2012.01.011.
32. Cavanagh, J.F., and Frank, M.J. (2014). Frontal theta as a mechanism for cognitive control. Trends Cognit. Sci. *18*, 414–421. https://doi.org/10.1016/j.tics.2014.04.012.
33. Cavanagh, J.F., Eisenberg, I., Guitart-Masip, M., Huys, Q., and Frank, M.J. (2013). Frontal theta overrides Pavlovian learning biases. J. Neurosci. *33*, 8541–8548. https://doi.org/10.1523/JNEUROSCI.5754-12.2013.
34. Cohen, M.X. (2016). Midfrontal theta tracks action monitoring over multiple interactive time scales. Neuroimage *141*, 262–272. https://doi.org/10.1016/j.neuroimage.2016.07.054.
35. Cohen, M.X., Elger, C.E., and Ranganath, C. (2007). Reward expectation modulates feedback-related negativity and EEG spectra. Neuroimage *35*, 968–978. https://doi.org/10.1016/j.neuroimage.2006.11.056.
36. Spitzer, B., and Haegens, S. (2017). Beyond the status quo: A role for beta oscillations in endogenous content (RE)activation. eNeuro *4*, 1–15. https://doi.org/10.1523/ENEURO.0170-17.2017.
37. Cohen, M.X. (2011). Error-related medial frontal theta activity predicts cingulate-related structural connectivity. Neuroimage *55*, 1373–1383. https://doi.org/10.1016/j.neuroimage.2010.12.072.
38. Cohen, M.X. (2014). A neural microcircuit for cognitive conflict detection and signaling. Trends Neurosci. *37*, 480–490. https://doi.org/10.1016/j.tins.2014.06.004.
39. Cavanagh, J.F., Cohen, M.X., and Allen, J.J.B. (2009). Prelude to and Resolution of an Error: EEG Phase Synchrony Reveals Cognitive Control Dynamics during Action Monitoring. J. Neurosci. *29*, 98–105. https://doi.org/10.1523/JNEUROSCI.4137-08.2009.
40. Cavanagh, J.F., Frank, M.J., Klein, T.J., and Allen, J.J.B. (2010). Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. Neuroimage *49*, 3198–3209. https://doi.org/10.1016/j.neuroimage.2009.11.080.
41. Luu, P., Tucker, D.M., and Makeig, S. (2004). Frontal midline theta and the error-related negativity: Neurophysiological mechanisms of action regulation. Clin. Neurophysiol. *115*, 1821–1835. https://doi.org/10.1016/j.clinph.2004.03.031.
42. Crivelli-Decker, J., Hsieh, L.T., Clarke, A., and Ranganath, C. (2018). Theta oscillations promote temporal sequence learning. Neurobiol. Learn. Mem. *153*, 92–103. https://doi.org/10.1016/j.nlm.2018.05.001.
43. Marco-Pallares, J., Cucurell, D., Cunillera, T., García, R., Andrés-Pueyo, A., Münte, T.F., and Rodríguez-Fornells, A. (2008). Human oscillatory activity associated to reward processing in a gambling task. Neuropsychologia *46*, 241–248. https://doi.org/10.1016/j.neuropsychologia.2007.07.016.
44. Marco-Pallares, J., Cucurell, D., Cunillera, T., Krämer, U.M., Càmara, E., Nager, W., Bauer, P., Schüle, R., Schöls, L., Münte, T.F., et al. (2009). Genetic Variability in the Dopamine System (Dopamine Receptor D4, Catechol-O-Methyltransferase) Modulates Neurophysiological Responses to Gains and Losses. Biol. Psychiatr. *66*, 154–161. https://doi.org/10.1016/j.biopsych.2009.01.006.
45. Engel, A.K., and Fries, P. (2010). Beta-band oscillations-signalling the status quo? Curr. Opin. Neurobiol. *20*, 156–165. https://doi.org/10.1016/j.conb.2010.02.015.
46. Jin, X., Dan, M., Zhang, N., Yu, W., Fu, X., and Das, S.K. (2012). Game theory for infrastructure security: the power of intent-based adversary models. In Handbook on Securing Cyber-Physical Critical Infrastructure (Elsevier Inc.), pp. 31–53.
47. Markiewicz, R., Rahman, F., Apperly, I., Mazaheri, A., and Segaert, K. (2024). It is not all about you: Communicative cooperation is determined by your partner's theory of mind abilities as well as your own. J. Exp. Psychol. Learn. Mem. Cogn. *50*, 833–844. https://doi.org/10.1037/xlm0001268.
48. Konvalinka, I., Vuust, P., Roepstorff, A., and Frith, C.D. (2010). Follow you, follow me: Continuous mutual prediction and adaptation in joint tapping. Q. J. Exp. Psychol. *63*, 2220–2230. https://doi.org/10.1080/17470218.2010.497843.
49. R Core Team (2021). R: A Language and Environment for Statistical Computing (Preprint at R Foundation for Statistical Computing).
50. Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., et al. (2015). No T. Package "lme4". Convergence *12*, 2.
51. Delorme, A., and Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods *134*, 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009.
52. Oostenveld, R., Fries, P., Maris, E., and Schoffelen, J.M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Comput. Intell. Neurosci. *2011*, 156869. https://doi.org/10.1155/2011/156869.
53. Winkler, I., Debener, S., Muller, K.R., and Tangermann, M. (2015). On the influence of high-pass filtering on ICA-based artifact reduction in EEG-ERP. In Proceedings of the Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBS), pp. 4101–4105. https://doi.org/10.1109/EMBC.2015.7319296.
54. Markiewicz, R., Segaert, K., and Mazaheri, A. (2021). How the healthy ageing brain supports semantic binding during language comprehension. Eur. J. Neurosci. *54*, 7899–7917. https://doi.org/10.1111/ejn.15525.
55. Mazaheri, A., Segaert, K., Olichney, J., Yang, J.C., Niu, Y.Q., Shapiro, K., and Bowman, H. (2018). EEG oscillations during word processing predict MCI conversion to Alzheimer's disease. Neuroimage Clin. *17*, 188–197. https://doi.org/10.1016/j.nicl.2017.10.009.
56. Pernet, C.R., Sajda, P., and Rousselet, G.A. (2011). Single-trial analyses: Why bother? Front. Psychol. *2*, 322. https://doi.org/10.3389/fpsyg.2011.00322.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and pre-processed data	This paper	https://osf.io/ct8jb/
Software and algorithms		
Python 3.6	https://www.python.org/	RRID:SCR_008394
MATLAB 2022b	https://uk.mathworks.com/products/matlab.html	RRID:SCR_001622
R 4.3.2	https://www.r-project.org/	RRID:SCR_001905

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants

Sixty young adults (i.e., 30 participant pairs) took part in the study. These were University of Birmingham (aged 19 to 31, *M*: 21.5, *SD*: 2.3; 12 males) students who were compensated for their time with cash payments. One participant was excluded from all analyses due to excessive EEG artefacts in the recordings; while their cooperative partner's data were excluded from the *paired* analysis, they were kept in for the *individual* analysis. Subsequently, we included 59 participants in the *individual* analyses, and 29 pairs for the *paired* analyses.

All participants were native English, monolingual speakers, right-handed, with normal-to-corrected vision, and no neurological or language impairments. Information on ancestry, ethnicity, race, and socioeconomic status were not collected in this study. All participant pairs reported to not know their cooperative partner in the experiment. Participants were compensated with cash for their time. Participants signed informed consent, which followed the guidelines of the British Psychology Society code of ethics and the study was approved by the Science, Technology, Engineering, and Mathematics (STEM) Ethical Review Committee for the University of Birmingham (Ethics Approval Number: ERN_19_1661).

METHOD DETAILS

Cooperation task

Cooperation was measured via a non-verbal task, completed in pairs. Participants were instructed to synchronise button presses with their partner within the pair. One of three types of auditory stimuli was played simultaneously to both participants at the start of each trial using headphones (Sennheiser 289 HD). These stimuli indicated the duration of time (referred to as 'short', 'medium', or 'long') that participants had to wait before pressing their button and attempting to synchronise it with the other participant in the pair. Neither of the participants within a pair knew the representation of 'short', 'medium', or 'long' the other participant had. There was no verbal or non-verbal communication between participants to agree on a mutual representation of these time intervals - they adjusted their responses solely based on the feedback they received at the end of each trial.

Cooperation was considered successful when both participants pressed their buttons within a 250ms timeframe. On the other hand, a trial was classified as failed cooperation if the time elapsed between the two button presses was <250ms. Participants were provided with feedback regarding their performance, as explained below. We selected this timeframe threshold after conducting piloting of the paradigm (using a different set of participants) to attain an accuracy rate of approximately 50% across conditions. The purpose of setting the task goal with this threshold was to maintain an approximately equal number of trials per condition, including successful and failed joint action. Further, we included the three types of auditory cues for the same purpose. The inclusion of only one auditory cue type would make the task too trivial for participants resulting in uneven trial numbers (or even the lack of failed cooperation).

An analysis of the accuracy rates in the present dataset revealed that we succeeded in our purpose: the overall accuracy across all pairs was 56.39% (SD = 13.94). Moreover, the accuracy rates revealed that the task worked as expected, with accuracy being lower in the more difficult condition: A Repeated measures ANOVA (Greenhouse Geisser adjusted) revealed that there was a significant effect of condition type (high/ short, medium, and low/long) on accuracy (%) ($F(1.66, 46.469) = 76.638$, $p < .001$). Post-hoc Least Significant Difference (LSD) pairwise comparisons showed that the accuracy rates were significantly different for each condition (high vs. low, $p < .001$; high vs. medium, $p < .001$; medium vs. low, $p = .037$), with the high/ short condition having the highest accuracy (M = 74.586 , SD = 14.151), followed by the medium condition (M = 49.379, SD = 18.108), and with the low/ long condition having the lowest accuracy (M = 45.207, SD = 15.697).

The experiment was set up using Python 3.6 and incorporated in-house built scripts and PsychoPy functions. The experiment scripts can be downloaded from the following link: https://osf.io/ct8jb/. Both participants viewed identical instructions, stimuli, and trial presentations on separate screens with a resolution of 1920 x 1080. The button presses were recorded using Razer gaming keypad. This gaming pad uses high-precision mechanical keyboard switches and specialized internal circuitry that purportedly enables the keyboard state to be polled at a rate of 1000 times per second.

Each trial commenced with the appearance of a fixation cross, which remained on the screen for the entire duration of the trial. After 300ms, an auditory cue was played for 200ms to both participants. There were three distinct auditory cues used: (1) a high-frequency 'beep' (2500 Hz), (2) a medium-frequency 'beep' (1000 Hz), and (3) a low-frequency 'beep' (200 Hz). Participants were instructed to wait for a 'short' amount of time upon hearing the high tone, a 'medium' amount of time upon hearing the medium tone, and a 'long' amount of time upon hearing the low tone. Following the auditory cue, participants were required to press their buttons and synchronize their actions. Once both participants had made their button presses, the fixation cross remained on the screen for an additional 1500ms, after which a feedback symbol was displayed. Each trial had two potential outcomes: (1) successful cooperation/joint action, indicated when the elapsed time between button presses of participants within a pair was $\leq$250ms, or (2) failed cooperation/joint action, indicated when the elapsed time between button presses of participants within a pair was >250ms.

For successful cooperation, both participants were shown a green smiley face as visual feedback, while failed cooperation was represented by a red sad face for both participants. This visual feedback remained on the screen for 1000ms, followed by the presentation of a fixation cross for 1000ms. Subsequently, a feedback text was displayed to both participants for 5000ms. The text varied depending on the outcome of the trial, with participants receiving either a 'Well done!' message if their button presses were synchronized, or feedback indicating which participant pressed the button first/second and the time between the button presses (see Figure 1C).

An example of a trial presentation is depicted in Figure 1C. The experimental task consisted of 300 trials in total, divided into 10 blocks (30 trials in each block). Each block consisted of an equal number of the different auditory cues which were presented in a random (i.e., intermixed design) order (10 trials with a high beep, 10 trials with a medium beep, and 10 trials with a low beep). In total, the experiment included 100 trials of each auditory cue. Participants were given the opportunity to have a break after each block.

Procedure

Each experimental session started with the 32-electrode EEG set up of each participant. Once both participants were capped, they sat approx. 70cm from a monitor (opposite each other with a table divider in between them so that they could not see each other) (see Figure 1A for set up). Participants wore earplugs (this was to prevent hearing each other's button presses) as well as noise cancelling headphones (to hear the auditory cues). Participants read the instructions of the task and once both participants were happy to continue, the experimenter started the 'training' phase.

The training phase involved participants hearing each of the auditory tones (high, medium and low) to familiarise themselves with the tones. While each tone was played, the associated description (i.e. high, medium, low) of the tone was displayed on the screen. This was repeated twice to ensure that participants were able to distinguish between the tones.

The experimenter was not present in the room during the experiment, instead the experimenter observed the participants through a one-way mirror. The experimenter entered the room upon the completion of each block and ensured that both participants were happy to continue. The experimenter controlled the start of the next block after each break.

EEG recording

The EEG set up was the same for both participants within a pair. EEG was recorded using Waveguard caps containing 32 Ag/AgCl electrodes (10-20 layout). The EEG signal was acquired with online reference to the CPz channel. The ANTneuro EEGosports amplifier system was used to amplify the signal and the EEGo sports was used to record it. The recorded signal was sampled at 500Hz, with a 150 Hz low pass filter and a 0.05Hz high-pass filter. We aimed to keep the impedances below 10kΩ. The EEG signal of both participants was synchronized to the onset of the triggers using a parallel port splitter.

QUANTIFICATION AND STATISTICAL ANALYSIS

Ensuring participants' adherence to task instructions

We used R[49] and *lme4*[50] to perform a linear mixed effects analysis of the relationship between condition type (short, medium, and long) and response times of the individuals. This was to check whether participants adhered to task instructions of waiting short, medium, and long amounts of time before synchronising their button presses (depending on the auditory cue type). We included a fixed effect of condition type (short, medium, and long), and random effects of intercepts for pairs and subjects, as well as by-pair and by-subject random slopes for the effect of the condition type. When a model did not converge with the maximal random effects structure, we simplified the random slopes until convergence was reached. The final and simplified model specification was as follows: RT $\sim$ Condition + (1|Pair) + (1|Subject).

Calculating behavioural adjustment (between players)

We sought to examine whether the outcome of each trial could be predicted based on the interplay of adjustments made by both players on a behavioural level. However, the nature of our experimental design, which involved random interleaving of condition types within blocks rather than a block-based structure, prevented us from directly examining sequential behavioural adjustments between consecutive trials. This constraint arose because the specific condition type consistently influenced the 'change' or 'adjustment' in reaction time (RT) due to the varying wait times required (short, medium, or long).

To overcome this, we established a reference point, or 'baseline,' to facilitate the calculation of behavioural adjustments for each trial. Our reasoning centred on the notion that 'learning' occurred immediately after the present trial, coinciding with participants receiving feedback.

Consequently, for each subsequent trial following this feedback, we identified the corresponding condition type (signifying the moment of adjustment). We then located the nearest preceding trial with the same condition type, which served as our baseline. Using this approach, we computed the behavioural adjustment for each player. This adjustment was quantified as the difference between the RT of the previous trial with the same condition type and the RT of the subsequent trial with the same condition type.

With this, we were then able to fit a multiple linear regression model (estimated using Ordinary Least Squares), with the predictors being: the behavioural adjustment of player one and behavioural adjustment of player two. The outcome variable was the cooperative outcome (i.e., the time difference between the button press of player one and two); cooperative outcome ~ behavioural adjustment of player one * behavioural adjustment of player two. This was carried out on a trial-by-trial basis.

EEG pre-processing

The EEG preprocessing was performed using EEGLAB (2019.0)[51] and Fieldtrip toolbox (2021-10-16).[52] The preprocessing steps for both participants in each pair were identical. Firstly, the first 5000 data points were removed from the continuous EEG signal to remove the amplifier start up noise. The continuous signal was then filtered using a high pass filter of 0.1Hz. The notch filter was then used to eliminate the electrical noise as well as its harmonics (45 to 55Hz; 95 to 105Hz; and 145 to 155Hz). The continuous data were visually inspected, and any noisy channels were removed and then interpolated (M = .27, SD = .67, max = 2). The signal was then re-referenced to the average of all electrodes and the CPz electrode (the online reference channel) was then added back into the data.

The data were then epoched to the onset of the feedback face (-7 to 7sec) (fourth screen in Figure 1C). Ocular artefacts were removed based on the scalp distribution using independent component analysis (ICA) in EEGLAB (2019.0). To improve the signal-to-noise ratio and classification accuracy of components, the EEG signal was high pass filtered at .8Hz[53] for nine recordings prior to conducting ICA. ICA weights obtained from the filtered data were then added back to the original signal (filtered at 0.1 Hz). The average number of removed components was 2.88 (SD = 1.31) for each participant. For the subsequent analysis, the data were further epoched to the onset of the feedback text (the last screen of Figure 1C) (-4 to 4.8sec) and trials were sorted into meaningful conditions depending on the type of analysis carried out (see below).

EEG analysis

Feedback related analysis

To compare neural activity related to feedback after successful and unsuccessful cooperation, we conducted Time-Frequency representations (TFRs) of power and Event-Related Potentials (ERPs) analyses across all 59 participants. The successful condition consisted of trials (M = 155.64, SD = 41.08) in which both players within a pair pressed their buttons within 250ms of each other. The unsuccessful cooperation condition consisted of trials (M = 120.89, SD = 40.21) in which the time elapsed between the button presses of the players was greater than 250ms.

Time-Frequency representations of power analysis. The TFRs of power were calculated using the 'mtmconvol' method in Fieldtrip. In line with previous work[54] we used sliding Hanning tapers with an adaptive time window of 3 cycles per each frequency of interest. The frequency of interest range was 2-50Hz in steps of 1Hz, and the time of interest of -1 to 4.8sec in steps of .05sec locked to the onset of the feedback text of each trial. The TFRs were calculated in relation to the relative change in power from baseline, with the baseline period being -0.6sec to -0.1sec (locked to the onset of the feedback text).

The statistical significance of the differences between conditions (successful vs. unsuccessful cooperation) in feedback cue locked oscillatory power changes, specifically locked to feedback cues in the time-frequency domain, was evaluated using non-parametric cluster-based permutation tests (Maris & Oostenveld, 2007). Each channel/time/frequency data point pair (successful and unsuccessful cooperation) locked to the onset of the feedback text was compared using a dependent samples T-test with a threshold of a 5% significance level. In cases where these comparisons (successful vs. unsuccessful cooperation) exceeded the significance level, the significant pairs were then clustered based on spatial proximity (via the triangulation method – a minimum of two neighbouring electrodes were considered a cluster). The Monte Carlo simulation was then performed to obtain probability values for the clusters by randomly shuffling the condition labels 1000 times and calculating the maximum cluster level test statistic for each permutation. The permutation tests were carried out on the following pre-defined and averaged frequency range bands: delta (1-4Hz), theta (4-7Hz), alpha (8-14Hz), low beta (15-20Hz), and high beta (20-25Hz), using a time window of 0 to 4 seconds locked to the onset of the feedback text.

Event Related Potentials analysis. The ERPs were calculated by averaging the time-locked EEG activity of all trials, separately for successful and unsuccessful cooperation conditions for each participant. The baseline correction used for the ERP analysis was -0.1sec to 0 prior to the onset of the feedback text. We employed the non-parametric cluster-based permutation tests (see above for full explanation; for comparison of ERPs the frequency part is not applicable) to statistically examine condition differences (successful vs. unsuccessful) in ERP amplitudes in a 0 to 4sec time window, locked to the onset of the feedback text. See supplemental information and Figure S1 for ERP results.

Forecasting cooperative outcome analysis

Effects of brain-to-brain coupling on local cooperative outcomes analysis. To identify power brain-to-brain signatures between participant pairs that were predictive of *local* cooperative outcomes, we focused our analysis of the TFRs of power locked to feedback in failed joint action trials. Importantly, the TFRs analysis was performed on the same set of trials for both player one and player two within each pair. The

unsuccessful trials were categorized into two conditions: *forecasting unsuccessful cooperation* on the next consecutive trial (i.e., failed cooperation trials followed by unsuccessful cooperation) and *forecasting successful cooperation* (i.e., failed cooperation trials followed by successful cooperation on the next consecutive trial). The average number of trials included in the analysis was 46.24 (SD = 14.11) for the condition of forecasting successful cooperation and 48.90 (SD = 26.95) for the condition of forecasting failed cooperation.

To compare the between player coupling of power between the two conditions, we conducted a Spearman's Rho analysis on the power values between player one and player two for every time, frequency, and channel data points within each trial. To account for trial number inconsistencies between the conditions for each pair of participants, the Spearman rho values were converted to Fisher Z scores.[55] We used non-parametric cluster-based permutation tests to statistically examine condition differences (i.e., *forecasting unsuccessful cooperation* and *forecasting successful cooperation*) in the inter-player coupling of power. This is the same method as described above (in the Time-Frequency representations of power analysis *section)*, but, instead of comparing power values, we compare the Fisher Z converted correlation values (between players) at every channel/time/frequency point. These values are the "inter-player power coupling values".

We primarily focused our permutation test analyses on the theta (4-7 Hz) band. The reasoning behind this is that theta band activity has been extensively implicated in network changes underlying behavioural adjustment and signalling the need to change strategy following an error, although this has been studied in individual brains.[28,32,33] We have also *exploratively* analysed the following pre-defined and averaged frequency range bands: delta (1-4Hz), alpha (8-14Hz), low beta (15-20Hz), and high beta (20-25Hz). Based on the *feedback related* results in the Time-Frequency domain, we predefined the following time windows of interest that we used in the permutation tests: 0-0.4sec and 0.6-1.05sec in the theta band, and 0.4-1.65sec in the alpha band. In addition, we exploratively used 0-2sec time windows in the permutation tests. The permutation tests identified electrode clusters that showed the greatest inter-player power coupling differences between conditions *(forecasting unsuccessful cooperation* vs. *forecasting successful cooperation)*. We also computed similar analysis to identify brain-to-brain dynamics predictive of *global* cooperative outcomes (i.e., cooperative outcomes of subsequent trials with the same condition type; see supplemental information for further details on the analysis method and the results).

Trial-by-trial analysis linking theta dynamics with behavioural outcomes. In addition to categorizing cooperative outcomes in a dichotomous way (by using a pre-defined threshold, categorizing cooperative success within 250ms and failure beyond it), we undertook an analysis that treated the cooperative outcome as a continuous variable. The cooperative outcome as a continuous variable reflected better cooperation with a smaller absolute difference between the RT's of the button presses of player one and two. This allowed us to examine whether the trial-by-trial inter-player theta dynamics are predictive of cooperative outcomes, when the pre-defined categories of success and failure are not present. To do this, we carried out a multiple linear regression model (estimated using Ordinary Least Squares), with the outcome variable being the *continuous* cooperative outcome (i.e., time difference between the button presses of player 1 and player 2). The predictors were the averaged feedback related individual theta power values for player one and player two. The theta power values were averaged over the time window and channels (see *Feedback related results section)*, which showed significant condition differences (successful vs. unsuccessful cooperation; 0 to 0.4sec post-feedback and over central and centro-parietal electrodes) in individual feedback cue locked oscillatory power changes. Our approach here was guided by a focus on the interaction of *individual* theta powers within a regression model rather than their pairwise correlations. Thus, we utilised the cluster of electrodes identified through the cluster-based permutation tests on feedback related oscillatory modulations at an *individual* level. The proposed model was as follows: cooperative outcome ~ averaged theta power of player one * averaged theta power of player two + absolute theta power difference between players. This was carried out on a trial-by-trial basis. The merit of trial-by-trial analysis is that it can reveal information that would be lost if data were collapsed into a dichotomous mean of a condition.[56]

Individual strategy adjustment analysis. To further explore the underlying mechanism responsible for the observed brain-to-brain activity in theta power forecasting joint action outcome on a local level, we conducted additional analyses. Our aim was to determine whether this effect truly originates from the *mutual* adjustment of time interval representation in joint action context, or whether it is attributed to a singular process performed independently by each individual. The rationale behind this analysis stemmed from the hypothesis that if theta band activity on *individual* level, is associated with integrating feedback into one's actions, and considering the varying degrees of adjustments participants need to make based on their *individual* situation, correlations and anti-correlations in theta activity among individuals may arise simply due to individuals adapting their behaviour according to their own feedback, rather than any awareness of their counterparts' actions. To address this, we categorized trials based on the type of required adjustment for the subsequent trial. Specifically, using the non-parametric cluster based permutation tests (with a pre-defined time window of 0 to .4sec based on the above results) we compared the theta (4-7Hz) power of Time-Frequency Representations (TFRs) between *unsuccessful cooperation trials that necessitated speeding up* in the subsequent trial vs *unsuccessful trials that required slowing down* in the subsequent trial. The TFRs were locked to the onset of the feedback text and collapsed across all participants (n=59).

Effects of brain-to-brain coupling on global cooperative outcomes analysis. We performed further analysis to identify power brain-to-brain signatures between participant pairs that were predictive of *global* cooperative outcomes. In our experimental design, condition types (i.e., high/short, medium, and low/long) were interleaved in a randomised manner within each experimental block, meaning that successive trials frequently did not share the same condition type. Given this setup, we aimed to explore the potential for predicting cooperative outcomes of subsequent trials with the same condition types based on inter-player neural signatures – we refer to as the "global effect".

Our approach focused on examining the nearest trial of the same condition type, instead of studying consecutive trials. Specifically, we categorized unsuccessful trials into two distinct conditions: forecasting unsuccessful cooperation on the nearest trial of the same condition type (involving failed cooperation trials followed by another unsuccessful cooperation trial of the same condition type), and forecasting successful cooperation on the nearest trial of the same condition type (entailing failed cooperation trials followed by a successful cooperation trial in the subsequent non-consecutive instance). The average number of trials included in the analysis was 41.28 (SD = 12.27) for the condition of forecasting successful cooperation and 53.45 (SD = 29.58) for the condition of forecasting failed cooperation. In order to compare the two conditions, we used non-parametric cluster-based permutation tests across all pairs (n = 29 pairs). We followed the exact same steps as described in the main manuscript section "Effects of brain-to-brain coupling on local cooperative outcomes analysis".

Effects of 'adjusters' and 'non-adjusters' on the post-feedback theta power analysis. We conducted further analysis by categorising participants into 'adjusters' and 'non-adjusters'. We hypothesized that adjusters would exhibit greater variability in their response times compared to non-adjusters throughout the experiment. Consequently, we defined adjusters as those participants whose standard deviation of response times was higher than that of the non-adjusters. The average standard deviation for adjusters was 1.09 (SD = 0.631) and for non-adjusters was 0.98 (SD = 0.599). However, note that there is no significant difference between the standard deviation of RT's between adjusters and non-adjusters, $t(55.85) = 0.66$, $p = .512$. The 95% confidence interval for the difference between means ranged from -0.22 to 0.43.

We used cluster-based permutation tests to test the adjuster vs non-adjuster differences in the TFR of theta power, aligned to the onset of the feedback text within a 0 to 4 second time window. We conducted separate analyses for comparing the theta power between adjusters and non-adjusters for (1) successful vs., unsuccessful trials, as well as the differential theta power between successful and unsuccessful trials, and (2) failed cooperation trials followed by a consecutive successful cooperation trials vs., failed cooperation trials followed by consecutive unsuccessful cooperation trials.