

Functional brain connectivity when cooperation fails

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ABSTRACT

Functional connectivity during cooperative actions is an important topic in social neuroscience that has yet to be answered. Here, we examined the effects of administration of (fictitious) negative social feedback in relation to cooperative capabilities. Cognitive performance and neural activation underlying the execution of joint actions was recorded with functional near-infrared spectroscopy (fNIRS) on prefrontal regions during a task where pairs of participants received negative feedback after their joint action. Performance (error rates (ERs) and response times (RTs)) and intra- and inter-brain connectivity indices were computed, along with the ConIndex (inter-brain/intra-brain connectivity). Finally, correlational measures were considered to assess the relation between these different measures. Results showed that the negative feedback was able to modulate participants' responses for both behavioral and neural components. Cognitive performance was decreased after the feedback. Moreover, decreased inter-brain connectivity and increased intra-brain connectivity was induced by the feedback, whereas the cooperative task pre-feedback condition was able to increase the brain-to-brain coupling, mainly localized within the dorsolateral prefrontal cortex (DLPFC). Finally, the presence of significant correlations between RTs and inter-brain connectivity revealed that ineffective joint action produces the worst cognitive performance and a more 'individual strategy' for brain activity, limiting the inter-brain connectivity. The present study provides a significant contribution to the identification of patterns of intra- and inter-brain functional connectivity when negative social reinforcement is provided in relation to cooperative actions.

1. Introduction

The 'social brain' has become a central focus of interest in neuroscience research in order to define the neurophysiological basis of social behavior and inter-subjective interactions (Toppi et al., 2016). Cooperation, in particular, can be considered as a social interaction between two or more agents who intend to share their performance and produce a common behavioral outcome. In this perspective, their joint actions are directed towards the achievement of specific common in-interests that provide significant advantage to all participants involved (Balconi & Pagani, 2014, 2015; Vanutelli, Nandrino, & Balconi, 2016; Balconi & Vanutelli 2017). Earlier work investigated how self-representation, perceived self-efficacy in social interactions, and social cognition are modified by cooperative tasks. Findings showed that a cooperative instruction is able to support a sense of ingroup, and may increase self-efficacy representation, interpersonal cohesion, and general social well-being (Knoblich, Butterfill, & Sebanz, 2011; Liu, Saito, & Oi, 2015).

Concerning the neural networks involved during cooperative behaviors, involvement of relevant prefrontal areas has been noted (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Schilbach, 2010; Vanutelli et al., 2016). Specifically, limbic regions and the pre-frontal cortex (PFC) support emotional, cognitive, and behavioral components of social interactions during cooperation (Holper, Scholkmann, & Wolf, 2012). It was observed that both the dorsal (DLPFC) and orbital (VLPFC) part of the PFC are generally engaged during social conditions that involve a cooperative task (Liu et al., 2015; Nozawa, Sakaki, Sakaki, Yokoyama, & Kawashima, 2016). It was suggested that these brain mechanisms probably reflect the recruitment of top-down control processes over specific emotional and cognitive responses to social contexts, as a way to regulate appropriate behavior (Balconi & Vanutelli, 2016a).

However, as noted in many previous studies, a critical aspect that is able to mediate these brain circuits and their activity is the perception of the efficacy of shared strategies; that is, the effects when cooperation goes wrong, or when it goes well. In fact, this feedback can be analyzed as a way to reinforce or not reinforce behavior toward a common direction, and is a relevant tool to train the brain to work synergistically or, on the other hand, to reduce the synergy. Previous studies have explored the effects of positive interpersonal feedback on self-representation (Balconi & Pagani, 2014; Balconi & Vanutelli, 2016b), performance (Balconi & Pagani, 2015, 2014; Balconi & Vanutelli, 2016a, 2016b; Monterosso, Ainslie, Mullen, Pamela Toppi Mullen, & Gault, 2002), and brain responsiveness in cooperative or competitive tasks (Balconi & Vanutelli, 2016b). It was found that positive feedback in relation to the outcomes reinforces efficient performance, activates the PFC, and in many cases, elicits a left-lateralized effect, since the generated positive emotions are linked to the experience of a positive and reinforcing condition for cooperation (Balconi, Brambilla, & Falbo, 2009; Balconi, Grippa, & Vanutelli, 2015a). Further, brain-to-brain coupling was considered in this regard, showing that good self-representation related to positive feedback on joint performance re-inforces brain effectiveness and neural synchronization between the inter-agents (Baker et al., 2016). However, no previous studies have simultaneously explored the effects of negative feedback on behavioral performance and brain correlates during interactions. That is, when we perceive that our co-operative actions are not efficient, what kind of brain and behavioral responses are produced?

A second critical point is related to the distinction between a one-person and a two-person perspective in explaining cooperative behavior. Indeed, a second perspective emphasizes that a deep understanding of cooperative processes can be obtained by including all interacting actors as a whole system (Hasson et al., 2012; Johnson & Johnson, 2005). Nonetheless, the majority of previous research within social neuroscience has explored this construct by means of single-brain paradigms, in which individual participants interact with a computer, or two people interact one at a time in turn-taking tasks, with off-line measurements (Balconi & Pagani, 2014; Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004). Such paradigms cannot explain the complexity of these processes in real-time, and cannot offer a complete understanding of brain-to-brain coupling. More recently, an increased number of researchers have shifted towards a 'wo-person perspective' (Schilbach, 2010) thanks to the creation of the hyperscanning paradigm. This technique permits the simultaneous recording of neural activity from different participants interacting together (Montague, 2002). The underlying idea is that, during joint actions, people become implicitly synchronized (Knoblich et al., 2011), as shown in previous studies that have revealed typical patterns of inter-brain synchronization with correlated cortical responses. For example, Cui and colleagues (2011) recorded the simultaneous brain responses of two people while they performed a computer-based game in which they were required to cooperate or compete; the authors then calculated inter-brain activity coherence. Results showed increased coherence between the two time series in the right superior frontal cortices, during cooperation only, but not during the competitive condition. Similarly, Holper et al. (2012) analyzed between-brain

connectivity during an imitation task and found increased coherence with respect to the control condition. Moreover, Nozawa et al. (2016) found increased neural synchronization within the frontopolar cortex between inter-agents performing co-operative verbal communication.

Nevertheless, no previous study has detailed the effect of negative feedback or failing cooperation on functional connectivity, taking into account the hyperscanning perspective.

The effect of negative feedback on goal pursuit has been previously studied with respect to motivational theories, which attest that positive feedback is more effective in supporting goal pursuit than negative feedback, since it can reinforce outcome expectancy of the goal and perceived self-efficacy (Bandura & Cervone, 1983; Zajonc & Brickman, 1969). According to this view, positive feedback increases people's confidence about the possibility of pursuing their goals, thus leading them to expect successful goal achievement. On the contrary, negative feedback undermines people's confidence in their ability to pursue their goals and the opportunity to succeed (Fishbach, Eyal, & Finkelstein, 2010). Based on this evidence, in the present paper we hypothesized that obtaining a negative external evaluation could influence subjects' dyadic strategies, both at a behavioral and neural level. In fact, we hypothesized that receiving negative feedback as a couple could lead to discouragement, and subsequently, to the adoption of dysfunctional goal orientation.

Accordingly, we expected that the brain responses would be similar to those found in a competitive situation, because of the implementation of self-centered, rather than joint, neural strategies. In fact, as already found by Liu and colleagues in a recent paper (Liu, Saito, Lin, & Saito, 2017), although cooperation and competition share the same brain networks due to the interdependent nature of the tasks, competition requires additional mentalizing resources because of its clear self-other distinction.

In the present context, we considered functional connectivity. Functional connectivity is calculated as the simultaneous coupling between two time series (Friston, 2011), and provides a temporal correlation between neurophysiological events that are spatially remote (Zhao, Xi, Wang, Li, & He, 2014). By using functional infrared spectroscopy (fNIRS) we were able to address the functional connectivity effects and temporal course of brain activation. Indeed, whereas classical imaging (i.e., functional magnetic resonance imaging; fMRI) measures do not seem to completely describe the real nature of social interpersonal processes, fNIRS measurements allow for direct examination of hemodynamic aspects of brain activation in line with social dynamics (Balconi, Grippa, & Vanutelli, 2015b; Biallas, Trajkovic, Haensse, Marcar, & Wolf, 2012). Experimental contexts that imply social interactions are characterized by a fast temporal evolution. For this reason, it is preferable to apply imaging methods that offer good resolution in both temporal and spatial domains, in order to provide an ecological setting to acquire event-related hemodynamic responses, such as fNIRS (Elwell et al., 1993).

Finally, a third critical point is that no previous studies have considered in depth the specific contributions of intra- and inter-brain connectivity during cooperation. That is, the contribution of both individual (intra-brain) and intersubjective (inter-brain) connectivity is unexplored. Earlier work has investigated inter-brain connectivity in romantic partners (Pan, Cheng, Zhang, Li, & Hu, 2017), or when playing a cooperative ecological dyadic game (Liu et al., 2016); however, to the best of our knowledge, no previous study has directly compared inter- and intra-brain connectivity. When analyzing a co-operative task, it is important to explore the activation of specific brain areas, and their connections within each brain alone, as well as the inter-brain connections. Moreover, we propose a new computation, the ConIndex, which allows calculation of inter-brain synchronization. This procedure has already been applied in our recent paper describing positive cooperative social dynamics (Balconi, Pezard, Nandrino, & Vanutelli, 2017). Results showed that the experimental conditions were associated differently with activation of frontal and prefrontal networks, in single and joint brains. Thus, a further objective of the present work was to explicitly compare intra- and inter-brain connectivity when cooperation goes wrong.

Therefore, in the present study we aimed to investigate the relationship between intra- and inter-brain functional connectivity during cooperation, within a hyperscanning paradigm in which participants were required to synchronize their behavioral performance. Halfway through the task, participants received feedback on their performance, manipulated ad hoc by the experimenter, in order to induce a negative perception of self-efficacy that would in turn influence the construction of joint strategies. We hypothesized that, at the cognitive level, increased cognitive effort would result in the post-feedback condition being characterized by poor performance (increased RTs and ERs), when compared to the first part of the task where there was no specific social feedback. At the brain level, we assume that external negative social feedback will increase intra-brain and inter-brain functional connectivity. In fact, improved synchronization could be considered a strategic way to reinforce and restore cooperation that was previously failing. Alternatively, it is also possible that discomfort and a negative attitude toward the ineffective cooperation by the inter-agents will affect the subjects' performance. Therefore, in this case, we may also expect a reduction in inter-brain connectivity in favor of intra-brain functional connectivity. Finally, we expected that both intra- and inter-connectivity would involve a specific contribution by the prefrontal regions, and mainly by the DLPFC, which was previously demonstrated to be relevant in social and cooperative tasks (Balconi et al., 2017; Cui, Bryant, & Reiss, 2012; Nozawa et al., 2016).

2. Methods

2.1. Participants

Thirteen dyads of subjects (twenty-six subjects in total) were recruited. All subjects were volunteer undergraduate students ($M = 25.89$, $SD = 1.21$). Each dyad was composed of two individuals of the same sex, matched for age. They did not meet and did not know each other before the experiment. The exclusion criterion was history of psychopathology (Beck Depression Inventory, BDI-II (Beck, Steer, & Brown, 1996) and State-Trait-Anxiety-Inventory (STAI) (Spielberger, Gorsuch, Lushene, Vagg & Jacobs, 1970)) among the subjects and their immediate families. No neurological or psychiatric pathologies were revealed, as assessed in a preliminary screening phase. One clinician evaluated the general psychiatric and neurological condition of the subjects. All participants were right-handed, presented with normal or corrected-to-normal visual acuity, and provided informed written consent to participate in the study. The research was conducted in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee of the Department of Psychology of the Catholic University of Milan, following the internal process of the Committee. No payment was provided for subjects' participation.

2.2. Procedure

The task consisted of a selective attention game where subjects were required to recognize target stimuli among non-targets by pressing two different keys. Stimuli varied based on color and shape: triangles and circles were colored blue and green. At the beginning of each experimental block, the target stimulus was presented for 500 ms.

The task comprised three different experimental conditions: each condition comprised 100 trials, subdivided into four blocks of 25 trials. A new target was presented within each block. Thus, blocks were separated by a brief pause. Each trial was composed of a series of three stimuli to categorize as target or non-target. Each stimulus remained on the screen for 500 ms, with a 300 ms inter-stimulus interval (ISI).

The three conditions differed based on the experimental instruction: the first one (t0) was a control condition where subjects were not asked to cooperate, but were simply required to individually execute the attention task. In the following two sessions, subjects were instructed to cooperate. In fact, participants were not required to be the fastest and most accurate possible, but simply to answer jointly.

After each trial, feedback (trial feedback) appeared on the screen to inform participants about their performance; feedback was provided in the form of two up-arrows (high cooperation score), a dash (mean performance), or two down-arrows (low cooperation score). This feedback was presented for 5000 ms and then an inter-trial interval (ITI) occurred for another 5000 ms (Fig. 1). From a total of 200 trials, 140 trials (70%) were presented as bad cooperation, represented by down-arrows. For the remaining 60 trials (30%), the feedback reported good or average performance, in order to make the paradigm more plausible.

However, condition 1 (t1) and 2 (t2) also differed with respect to another feature. At the end of condition 1, participants received a more general evaluation about their cooperative performance (general feedback). This involved a fictitious report about the participant's performance, stating that only 27% of responses were made jointly in terms of speed and 32% in terms of accuracy (either correct or incorrect). This manipulation was made to induce a psychological framework related to perceived self-efficacy to perform as a couple and be constructive. Together with the report, the participants were also encouraged to change and improve their performance level during t2, which was thus characterized by a new cognitive framework. To recap, the experimental flow was managed as follows:

- T0: 100 trials, 4 blocks. Instruction: not cooperative.
- T1: 100 trials, 4 blocks. Instruction: answer jointly according to the trial feedback.
- MANIPULATION: "you're not good cooperators".
- T2: 100 trials, 4 blocks. Instruction: answer jointly according to the trial feedback.

The task was modified from the version described in our recently published paper (Balconi et al., 2017). First, the previous paradigm was meant to induce a positive framework due to manipulation of good cooperation, while the present one refers to inefficient cooperation. Second, the present version was improved and integrated with a control condition, which allowed us to better distinguish the experimental effects.

The task was conducted in a moderately darkened room where subjects participated in randomly assigned dyads. They were seated at the same table in front of two computer screens, one each, which were located about 50 cm from their eyes (modified from the previous version to allow a better perceptual setting). A black panel was positioned in a way so as to separate the two participants and avoid any possible visual contact between them, in order to exclude the possibility that synchronization could derive from simple mirroring mechanisms.

To obtain high engagement, subjects were told that their subjective skills would be screened with several questionnaires that are usually used in a business context to screen future professional career success and teamwork capabilities. Further, the cooperative and joint nature of the game was highly stressed; subjects were informed that their scores were based on their ability to synchronize their responses with their dyad pair, in terms of both accuracy (correct responses, measured as error rates; ERs) and response times (RTs). In addition, after each block of 25 trials, subjects were required to assess their performance and efficacy on a seven-point Likert scale (from 1 = most decreased performance, to 7 = most improved performance).

Participants were strongly engaged in the cooperative context, as indicated by the post-experiment debriefing. Indeed, 95% of the participants reported that they were strongly engaged ("I was strongly engaged and motivated in performing the joint-task"). Subjects were also required to self-report their degree of trust in the exact performance feedback; the result indicated high trust (93%) ("I considered the task highly relevant and truthful"), and participants reported that the task had high relevance in terms of social status representation (97%) ("The present performance is relevant to test my future ability to collaborate").

2.3. Performance scoring

The RTs (msec) were recorded from the stimulus onset, and ERs were calculated as the total number of incorrect detections out of the total trial (therefore higher values represented increased incorrect responses).

2.4. fNIRS

fNIRS measurements were acquired with NIRScout System (NIRx Medical Technologies, LLC. Los Angeles, California) using an 8-channel array of optodes (4 light sources/emitters and 4 detectors) positioned over the frontal and prefrontal area. Emitters were placed on positions FC3-FC4 and F1-F2, while detectors were placed on FC1-FC2 and F3-F4 (Fig. 2). The distance between emitters and detectors was kept at 30 mm for contiguous optodes and a near-infrared light of two wave-lengths (760 and 850 nm) was used. NIRS optodes were positioned on the subject's head using a NIRS cap according to the international 10/5 system. Acquired channels are the following: Ch 1 (FC3-F3) and Ch 3 (FC4-F4) correspond to the left and right (respectively) DLPFC (Brodmann Area 9). Ch 2 (FC3-FC1) and Ch 4 (FC4-FC2) correspond to the left and right (respectively) dorsal pre-motor cortex (DPMC, Brodmann Area 6). Ch 5 (F1-F3) and Ch 7 (F2-F4) correspond to the left and right (respectively) frontal eye fields (FEF, Brodmann Area 8). Ch 6 (F1-FC1) and Ch 8 (F2-FC2) correspond to the left and right (respectively) superior frontal gyrus (SFG, Brodmann Area 6) (Koessler et al., 2009).

With NIRStar Acquisition Software it was possible to calculate the changes in the concentration of oxygenated (O2Hb) and deoxygenated hemoglobin (HHb) during the task, starting from a 120 s resting base-line. The sampling rate was 6.25 Hz. The signals obtained from the 8 channels were then analyzed and transformed with nirsLAB software (v2014.05; NIRx Medical Technologies LLC, 15Cherry Lane, Glen Head, NY, USA), based on their wavelength and location, resulting in values for the changes in the concentration of O2Hb oxy and HHb for each channel, scaled in mmol * mm.

The raw O2Hb and HHb data from each channel were digitally band-pass filtered at 0.01–0.3 Hz. Then, the mean concentration of each channel was computed by averaging data across the trials, starting from the feedback onset for the following 5 s. The mean concentration value of 5 s before the experimental session was used as event-related base-line. Although NIRS raw data were originally relative values and could not be directly averaged across subjects or channels, effect sizes normalized data could be averaged regardless of the unit since the effect size is not affected by differential pathlength factor (DPF) (Matsuda & Hiraki, 2006; Schroeter, Zysset, Kruggel, & Von Cramon, 2003; Shimada & Hiraki, 2006). Therefore, the effect size was calculated in every condition, for each channel and subject, based on oxy/deoxy variations in the time series. The effect sizes (Cohen's d) were

calculated as the difference of the means of the baseline and trial divided by the standard deviation (sd) of the baseline: $d = (m1 - m2)/s$, with $m1$ and $m2$ being the mean concentration values during baseline and trial, respectively, and s the SD of the baseline. Then, the effect sizes calculated from the 8 channels were averaged to increase the signal-to-noise ratio. Finally, signs have been inverted to interpret the hemodynamic responses evoked by the trial feedback as an increase/ decrease with respect to each baseline.

2.5. Functional connectivity analysis

In a preliminary phase to exclude a possible learning effect due to pre-/post feedback condition, an analysis was conducted comparing distinctly the first set of four intervals (pre feedback intervals) and the second set of four intervals (post feedback feedback) for all the dependent measures (RTs, ERs, O2Hb). No significant differences among the four intervals (respectively for the four intervals before and the four after the feedback) were found. Therefore we did not include this factor (eight time intervals) in the successive analysis.

Three sets of analyses were performed with respect to behavioral (ERs; RTs) and neurophysiological (fNIRS: O2Hb measures) measures.

Firstly, repeated measure ANOVAs with independent factor Condition (Cond: control vs pre vs. post feedback) were applied to ER, and RTs.

Secondly, a set of analysis was applied to the neurophysiological level which consisted in four different phases: at first, to obtain intra- and inter-brain connectivity, the partial correlation coefficient Π_{ij} was computed to calculate functional connectivity indices. They were obtained by normalizing the inverse of the covariance matrix $\Gamma = \Sigma^{-1}$:

$$\Gamma = (\Gamma_{ij}) = \Sigma^{-1} \text{ inverse of the covariance matrix}$$

It quantifies the relationship between two signals (i, j) independently from the other (Wheland et al., 2012). A successive phase included the calculation of a specific ConIndex as the ratio between inter-brain and intra-brain connectivity ($\text{Inter}_{\text{CON}}/\text{Intra}_{\text{CON}}$) to directly compare the two connectivity levels across the experimental conditions.

Then, we applied ANOVAs to intra-brain, inter-brain and ConIndex dependent measures. For all these ANOVAs, independent repeated factors were Condition (Cond, 3), Localization (Loc: DLPFC, DPMC, FEF, SFG, 4) and Lateralization (Lat: left vs. right, 2). For all of the ANOVA tests, the degrees of freedom were corrected using Greenhouse-Geisser epsilon where appropriate. Post-hoc comparisons (contrast analyses for repeated measures ANOVAs) were applied to the data. The Bonferroni test was applied for multiple comparisons. In addition, the normality of the data distribution was preliminarily tested (kurtosis and asymmetry tests). The normality assumption of the distribution was supported by these preliminary tests.

Finally, a third step of analysis included correlational analyses to compare behavioral (RTs and ERs) and neurophysiological (intra-brain connectivity; inter-brain connectivity; ConIndex) measures to verify the relationships of these different levels on each other.

3. Results

3.1. ERs and RTs

For ERs measurement, ANOVA revealed significant effects for Cond ($F[1, 25] = 10.66, p \leq .001, \eta^2 = .42$), with increased ERs for post-feedback condition compared with both control and pre-feedback condition ($F[1, 25] = 9.89, p \leq .001, \eta^2 = .40$ and ($F[1, 25] = 9.60, p \leq .001, \eta^2 = .39$, respectively). Similarly, about RTs, ANOVA indicated significant main effect for Cond ($F[1, 25] = 9.05, p \leq .001, \eta^2 = .39$), with increased RTs during post-feedback compared to control ($F[1, 25] = 8.76, p \leq .001, \eta^2 = .37$) and pre-feedback ($F[1, 25] = 9.01, p \leq .001, \eta^2 = .38$) condition (Fig. 3). We also found significant decreased RTs for pre-feedback condition compared to control condition ($F[1, 25] = 9.60, p \leq .001, \eta^2 = .39$).

3.2. Intra-brain connectivity

The statistical analyses were applied to intra-brain indices for O2Hb and HHb-concentration. Since the analysis on HHb did not reveal significant effects, we report only results for O2Hb-values. As shown by ANOVA Localization and Condition x Localization effects were significant (Localization: $F[1, 83] = 11.34, p \leq .001, \eta^2 = .40$; Condition x Localization: $F[1, 83] = 9.07, p \leq .001, \eta^2 = .37$). Firstly, as revealed by post hoc analysis, intra-brain functional connectivity was generally higher in DLPFC than in other areas (respectively compared with DPMC $F[1, 25] = 8.09, p \leq .001, \eta^2 = .38$, FEF $F[1, 25] = 8.77, p \leq .001, \eta^2 = .39$, SFG $F[1, 25] = 9.54, p \leq .001, \eta^2 = .40$) (Fig. 4). In addition, intra-brain connectivity was higher in post-feedback with respect to the other two conditions (respectively control $F[1, 25] = 7.80, p \leq .001, \eta^2 = .37$ and pre-feedback $F[1, 25] = 8.11, p \leq .001, \eta^2 = .39$) within DLPFC. No other simple or interaction effect was significant.

3.3. Inter-brain connectivity

The ANOVA applied to inter-brain indices for the dyads showed significant Condition and Condition x Localization effects (Condition: $F[1, 12] = 10.45, p \leq .001, \eta^2 = .33$; Condition x Localization: $F[1, 36] = 8.76, p \leq .001, \eta^2 = .37$). Indeed, concerning the main effect, a general decreased inter-brain connectivity was observed in post-feedback with respect to pre-feedback condition ($F[1, 12] = 10.03, p \leq .001, \eta^2 = .42$). In addition, as revealed by significant interaction (simple effects), inter-brain connectivity decreased in post-feedback if compared to pre-feedback ($F[1, 12] = 10.45, p \leq .001, \eta^2 = .41$); and in post-feedback than control ($F[1, 12] = 10.45, p \leq .001, \eta^2 = .41$) condition within DLPFC. In addition inter-brain connectivity increased in pre-feedback than control condition ($F[1, 12] = 9.67, p \leq .001, \eta^2 = .40$) (Fig. 5). No other effect was statistically significant.

3.4. ConIndex

The ANOVA revealed significant Cond x Localization interaction effect ($F[1, 12] = 9.18, p \leq .001, \eta^2 = .38$). Indeed, a decreased Index was observed in post-feedback than pre-feedback ($F[1, 12] = 9.55, p \leq .001, \eta^2 = .40$) and control ($F[1, 12] = 8.84, p \leq .001, \eta^2 = .38$) condition within the DLPFC. Therefore, as shown by the Index, we may conclude in favor of a general decreased inter-brain than intra-brain

connectivity in DLPFC for the post-feedback condition compared to the other two conditions (Fig. 6).

3.5. Correlational analysis

Correlation analyses (Pearson coefficients, Bonferroni correction was multiple comparisons) were applied to behavioral indices (ERs; RTs) and neurophysiological measures (intra- and inter-brain connectivity; ConIndex) by also considering brain region and lateralization. We report only significant effects. RTs revealed significant negative correlation with the inter-brain connectivity within left and right DLPFC in post-feedback condition (respectively $r^2 = -.576, p \leq .001$; $r^2 = -.507, p \leq .001$): in fact, a decreased right and left DLPFC connectivity was related to higher RTs values in post-feedback condition. Similar effects were found for ERs: significant negative correlations were found between ERs and the inter-brain connectivity within left and right DLPFC in post-feedback condition (respectively $r^2 = -.516, p \leq .001$; $r^2 = -.553, p \leq .001$). No other effect was statistically significant.

Significant effects were also found between ConIndex and RTs: correlational coefficients showed a negative correlation ($r^2 = -.532, p \leq .001$). Therefore the increased ConIndex values (more inter-brain connectivity than intra-brain) were related to decreased RTs (Fig. 7).

4. Discussion

The present research explored the effects of inefficient cooperation during joint action, focusing on behavioral performance and intra-/ inter-brain functional connectivity. Specifically, we considered several cognitive variables (RTs and ERs), functional connectivity for intra- and inter-brain coupling (fNIRS), and correlational measures between cognitive and brain levels. Although there are some limitations of the present study, we consider it a valid and innovative contribution. Indeed, this study considered only a limited number of couples. However, we applied the pertinent statistical analyses to provide reliable results. Secondly, the analyses were able to isolate the contribution of intra- and inter-brain connectivity, and future studies could directly compare other kinds of inter-subjective conditions which are able to induce competitive strategies. Such a comparative analysis could better clarify the role of negative feedback versus real competition. We believe that these procedures could expand and deepen our analyses, without diminishing the main message of the present work. Further, we believe our results were not affected by these limitations and that the results can be interpreted with confidence.

First, the results showed that the external feedback modulated both the behavioral and brain responses. In line with our hypotheses, the perception of negative outcomes, and subsequently the perception of less joint efficacy, induced significant modification of behavioral performance. In fact, from a cognitive point of view, generally poorer performance was observed, with higher ERs and RTs, in the post-feedback condition, as compared to both the control condition (individual task) and the pre-feedback condition (cooperative task). An unsuccessful strategy, although in a cooperative context, may require an increased demand on cognitive resources in order to update the ineffective joint action. This condition may produce an increase in the cognitive load related to the necessity to recalibrate one's own strategy and to implement a more efficient cognitive plan. Moreover, there was an improvement in performance between the individual task (control condition) and the joint task, where cooperation was relevant. That is, the perception of a cooperative condition (pre-feedback) resulted in optimization of cognitive performance within the couple, as shown in previous studies (Balconi & Pagani, 2015).

Secondly, behavioral performance was also related to activation of prefrontal sites (DLPFC); this area was associated with systematic brain-to-brain coupling (Baker et al., 2016). Thus, the decreasing trend in subjects' performance could be ascribed to both a general subjective 'cognitive cost', but also to a blockage of the inter-brain functional connectivity. Specifically, the negative feedback could have triggered a frustrated response, which encouraged subjects to perform better, thus leading to intensification of resource allocation. At the same time, the joint strategy could have been impaired after receiving an evaluation suggesting poor cooperative skills with the paired participant, thus influencing the joint strategy and the interpersonal bond. In fact, a significant effect was observed in terms of functional connectivity, considering both intra- and inter-brain connectivity, which was marked by a feedback effect. Indeed, brain-to-brain coupling was modulated by negative feedback, with consistently decreased inter-brain connectivity compared to the control and pre-feedback conditions. A relevant and concomitant effect was observed with gradually higher intra-brain connectivity seen in the post-feedback condition. The absence of a functional strategic plan (as artificially communicated by the external feedback) may have induced the subject to act as an individual instead of as a co-agent in the interaction. This recalibration due to the contextual constraints may have acted as a powerful incentive to think about alternative ways to manage the interaction, where the individual strategy was prevailing over the inter-subjective one. Therefore, the present results appear to suggest that negative cooperation is more similar to a competitive task, and this may be due to increasing difficulty in creating a shared mental strategy (Balconi & Pagani, 2015). This difficulty may be fundamentally based on the increased work load required to change the cognitive plan (the request of higher performance). Alternatively, it may be due to the negative emotional condition that negative feedback may create (Balconi & Vanutelli, 2016). Activity patterns in the frontal cortices were found to be crucially involved in the processing of emotional conditions, which are characterized by negative feedback and negative emotions (Balconi, Falbo, & Conte, 2012). However, few studies have tried to connect the emotional effects of unsuccessful cooperation, taking into account the impact of the emotional conditions on the cortical network when it responds to specific social situations. This could be of fundamental importance in situations that require good synergy to promote better outcomes and wellbeing, for example, in the workplace, in romantic bonds, and more generally, interpersonal bonds; there are important clinical implications of such work.

In contrast, when the couples were required to be cooperative, in the absence of specific positive feedback (as in the pre-feedback condition), an increase in brain-to-brain coupling emerged, as marked by an increased level of inter-brain connectivity compared to intra-brain connectivity (ConIndex). In other words, when subjects pass from an individual perspective (control condition) to an inter-personal perspective (cooperative task), they change their brain state; this results in a switch from a one-person to an inter-agent representation, as the joint-brain findings indicate. Similarly, the transition from a cooperative state to an inefficient cooperation condition induces a consistent decrease in brain coupling, indicating a renewed individual perspective when the couple's connection may be partially disrupted. The ConIndex further highlights this effect, with a significant decrease in inter-brain functional connectivity compared to intra-brain connectivity for the post-feedback condition as compared to the control and pre-feedback conditions. That is, the individual (and intra-brain connectivity) reaches its highest value when negative feedback is received about their joint action; when the common action fails, this intra-brain synergy is even higher than when the subject is acting alone (in the control condition with an individual task). Therefore, it appears that there is an 'individual' attempt to go on with an alternative solution when the interpersonal approach is ineffective.

Moreover, it has been demonstrated that only the effective 'two-player connection', compared to single subject performance in the pre-feedback condition, may guarantee efficient performance, as revealed by the presence of a significant improvement in performance (ERs and RTs) and inter-brain connectivity indices. That is, it appears that the cooperation task acts as an implicit reinforcement for effective joint behavior inside the couple, with relevant convergence of increased cognitive performance and brain inter-activity by the two inter-agents.

Finally, considering the brain areas involved, in the present research we verified the contribution of frontal areas and, importantly, the modulation of brain connectivity according to our experimental manipulation. More specifically, we found that the cortical synchrony or asynchrony was primarily localized within the DLPFC. This is particularly important since both intra-brain and inter-brain indices underlined the recruitment of a brain network involved in social exchange, such as perspective taking and theory of mind (Kalbe et al., 2010). The same area was also found to be involved during the suppression of ‘ego-centered’ behavior (Baeken et al., 2010) and commitment in significant relationships (Petrican & Schimmack, 2008); this was also evident in inter-brain patterns after the social reinforcement. Therefore, it is plausible to assume that this area possesses specialized mechanisms to perceive joint actions in conditions of success or failure.

To summarize, behavioral connectivity and functional connectivity effectively signal the response to reinforcing feedback, when subjects perceive themselves to be an inefficient team. Secondly, it appears that they also share a similar responsiveness to external cues. Indeed, it could be assumed that the experimental instruction reinforced the joint significance of inter-subjective actions. In addition, the interplay between intra- and inter-brain connectivity is calibrated as a function of the subject’s representation of the need to adopt a more ‘individual’ or ‘inter-subjective’ perspective. That is, the cooperative task is able to produce significant brain-to-brain coupling, followed by a relevant re-duction in this synergic activity when the cooperation is perceived to be going wrong. In other words, only with real cooperation in mind are subjects able to functionally operate with synchronized brains and behaviors.

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