

1 **Title:** Dissecting social interaction: Dual-fMRI reveals patterns of interpersonal brain-
2 behaviour relationships that dissociate among dimensions of social exchange.

3

4 **Running title:** Interpersonal brain-behaviour dependencies.

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21 behaviour dependencies

1 **Abstract**

2 During social interactions, each individual's actions are simultaneously a consequence of and
3 an antecedent to their interaction partner's behaviour. Capturing online the brain processes
4 underlying such mutual dependency requires simultaneous measurements of all interactants'
5 brains during real-world exchange ("hyperscanning"). This demands a precise characterisation
6 of the type of interaction under investigation, however, and analytical techniques capable of
7 capturing interpersonal dependencies. We adapted an interactive task capable of dissociating
8 between two dimensions of inter-dependent social exchange: goal structure (co-operation vs.
9 competition) and interaction structure (concurrent vs. turn-based). Performing dual-fMRI
10 hyperscanning on pairs of individuals interacting on this task, and modelling brain responses in
11 both interactants as systematic reactions to their partner's behaviour, we investigated
12 interpersonal brain-behaviour dependencies (iBBD) during each dimension. This revealed
13 patterns of iBBD that differentiated among exchanges: In players supporting the actions of
14 another, greater brain responses to the co-player's actions were expressed in regions implicated
15 in social cognition, such as the medial prefrontal cortex, precuneus, and temporal cortices.
16 Stronger IBBD during concurrent competitive exchanges was observed in brain systems
17 involved in movement planning and updating, however, such the supplementary motor area.
18 This demonstrates the potential for hyperscanning to elucidate neural processes underlying
19 different forms of social exchange.

20

21 **Keywords:** Social interaction; hyperscanning; co-operation; competition; interpersonal brain-
22 behaviour dependencies.

1 **1. Introduction**

2 Humans engage in a variety of social exchanges on a daily basis; we interact not only with
3 friends and loved ones, but also with rivals and strangers. Despite our proficiency in negotiating
4 such interactions, each one emerges through a highly complex and dynamic process; even in a
5 simple dyadic exchange, for instance, the actions of each individual are mutually and directly
6 influenced by the prior and present behaviour of their interaction partner, and, simultaneously,
7 serve to mutually and directly influence the other's behaviour. In this sense, social interactions
8 between two individuals comprise a "two-in-one" dynamic, whereby the actions of each person
9 are simultaneously a consequence of and antecedent to their partner's behaviour (Koike *et al.*,
10 2015). Furthermore, each interactant can alternate between different roles during the course of
11 a dyadic exchange. Understanding the brain processes that give rise to such mutual dependency
12 within the non-linear context of social interaction is central to social neuroscience, but this
13 remains somewhat of a "dark matter" (Schilbach *et al.*, 2013).

14 To investigate the neural processes underlying social behaviour, neuroscientists have
15 turned typically to the classic sensory neuroscience approach – individuals' brain responses are
16 measured while they evaluate experimental social stimuli in isolation. While this has unveiled
17 numerous brain systems underlying social information processing (Van Overwalle, 2009), such
18 a "spectator science" offers little insight into how these systems are modulated during social
19 interaction; by considering individuals as detached observers, we cannot investigate how they
20 respond online to the behaviour of our interaction partners (Hari *et al.*, 2015; Konvalinka &
21 Roepstorff, 2012; Schilbach, 2014). Indeed, increasing awareness that social cognition differs
22 fundamentally during real interaction compared to mere observation has led to calls for "real-
23 world", "*in situ*" or "two-person" social neuroscience (Hari *et al.*, 2013; Kasai *et al.*, 2015;
24 Schilbach *et al.*, 2013), whereby the brains of two or more interactants are measured
25 simultaneously while they engage with one another in real-time social exchanges. This
26 "hyperscanning" technique requires a number of methodological and technical developments

1 before it can be used to advance the field of social neuroscience, however, and this was the
2 focus of the present study.

3 Liu and Pelowski (2014) propose that three distinct dimensions of interaction must be
4 delineated: the goal structure (competitive vs. co-operative), interaction structure (concurrent
5 vs. turn-based), and task structure (independent vs. interdependent). For example, although
6 sporting activities share the common characteristics of a competitive goal, they differ in both
7 interaction and task structure: while opposing tennis players take turns to return a ball, and each
8 individual's shot is directly dependent upon the prior move of their opponent, individuals in a
9 race compete with one another concurrently and independently. Similarly, although members
10 of a band must co-operate with one another to achieve harmony, they can do so by aligning
11 instrumental outputs simultaneously (concurrent) or in a sequential (turn-based) manner, and
12 independently (solo) or interdependently (duet). Since the main benefit of hyperscanning is the
13 ability to explore interaction *in vivo*, it is essential to dissociate among these discrete forms of
14 social exchange (Konvalinka & Roepstorff, 2012). To our knowledge, however, all existing
15 hyperscanning studies have focused on either the goal or task structure – none have explored
16 the interaction structure. In order to understand the neural systems through which the mutual
17 dependency of behaviour emerges during social interaction, we must first elucidate the brain
18 processes that are modulated online during these dissociable dimensions of social exchange.

19 Hyperscanning has undergone a number of technical developments: it has been
20 performed successfully with functional magnetic resonance imaging (fMRI),
21 electroencephalography (EEG), functional near-infrared spectroscopy (fNIRS) and
22 magnetoencephalography (MEG; for reviews see Scholkmann et al., 2013; Babiloni & Astolfi,
23 2014). With these techniques, neuroscientists have been able to identify neural processes
24 engaged during various forms of social exchange, from interpersonal motor synchronisation
25 (Naeem *et al.*, 2012; Osaka *et al.*, 2014) and joint-action tasks (Funane *et al.*, 2011; Cui *et al.*,
26 2012) to verbal communication (Jiang *et al.*, 2012; Spiegelhalder *et al.*, 2014) and economic

1 exchanges (King-Casas *et al.*, 2005; Chung *et al.*, 2008; Shaw *et al.*, 2018). Further, a range of
2 analytical techniques have been developed to detect mutual dependencies in the brain responses
3 of interacting individuals, from inter-subject correlation (Liu *et al.*, 2015; Koike *et al.*, 2016;
4 Shaw *et al.*, 2018) to sophisticated measures of inter-brain coherence (Babiloni & Astolfi, 2014;
5 Liu *et al.*, 2016; Nozawa *et al.*, 2016; Stolk *et al.*, 2014; Tang *et al.*, 2016; Toppi *et al.*, 2016;
6 for reviews see Babiloni & Astolfi, 2014; Hasson & Frith, 2016). Although these analytical
7 techniques are capable of measuring symmetrical brain responses between two interacting
8 individuals (“neural alignment”), this might fail to capture other forms of neural inter-
9 dependencies during social exchange; while such symmetry might be expected between brains
10 exposed to the exact same stimulus, indicating shared processing or meaning extraction (Hasson
11 & Frith, 2016), interpersonal brain responses are unlikely to take this form during the sequential
12 and non-linear dynamic of naturalistic dyadic exchange. In such contexts, the brain responses
13 of each interactant are likely to reflect a reaction to their partners’ behaviour, which might give
14 rise to temporally lawful but *asymmetric* inter-dependencies. It is therefore necessary to develop
15 and optimise new analytical techniques that are capable of capturing the brain responses of one
16 individual that are modulated by, or dependent upon, the behaviour of their interaction partner
17 (Burgess, 2013; Hari *et al.*, 2015); that is, interpersonal brain-behaviour dependencies (iBBD).

18 In this study, we measured the brain responses of two individuals simultaneously with
19 dual-fMRI while they interacted with one another in a task capable of distinguishing between
20 different dimensions of social interaction – namely, an adaptation of the interactive Pattern
21 Game (Decety *et al.*, 2004). By measuring both players’ brains simultaneously during this
22 game, we were able to capture neural responses in both interactant’s brains that were modulated
23 online by their co-player’s behaviour during an ecologically valid social context; one in which
24 an exchange emerged through the participation of *both* individuals (Schilbach *et al.*, 2013). To
25 investigate brain responses that underlie the mutual dependency characterising naturalistic
26 dyadic exchange, we considered only the interdependent level of task structure; that is, when

1 the task outcome is dependent upon the performance of both interactants, and the performance
2 of each interactant is mutually dependent upon their interaction partner. We then measured
3 iBBD by modelling the brain responses of one individual as systematic reactions to the other's
4 behaviour (Hasson & Frith, 2016). By separating both interaction and goal structure, we were
5 able to investigate whether iBBD differed across combinations of concurrent and turn-based,
6 co-operative and competitive interactions. Based on previous research (Krill & Platek, 2012),
7 we predicted strong brain responses to the behaviour of an interaction partner in the reward
8 system (e.g., ventral striatum, anterior cingulate cortex) during co-operative compared with
9 competitive exchanges. In contrast, we expected stronger iBBD in brain areas implicated
10 consistently in socio-cognitive capacities (e.g., mentalising) during competition given the
11 increased need to predict an opponent's upcoming moves (e.g., medial prefrontal cortex;
12 Carlson et al., 2013). Finally, since there is a higher demand on attention and movement
13 planning during concurrent relative to turn-based interpersonal behaviour, we hypothesised that
14 there would be greater iBBD in brain regions associated with attention and movement planning;
15 specifically, the frontoparietal attention network and the supplementary motor area (Cona &
16 Semenza, 2017). Conversely, in turn-based exchanges we expected stronger brain responses to
17 an opponent's behaviour in brain areas implicated in behavioural inhibition (e.g., pre-
18 supplementary motor cortex; Nachev et al., 2008) and self-other distinction (e.g., tempo-
19 parietal junction, precuneus; Brass et al., 2009; Reniers et al., 2014).

20

21 **2. Methods**

22 ***2.1. Participants***

23 We recruited 44 individuals (22 males) from Brno, Czech Republic. The mean age of this
24 sample was 22.37 (SD=1.91) years. These participants were paired into same-sex dyads (11
25 male-male) matched on self-evaluated handedness (40 right-handers), age (mean difference =
26 6.27 [SD=4.32] months) and education (highest qualification achieved). Importantly, the

1 participants comprising each dyad were unacquainted with each other prior to the day of the
2 experiment; they were introduced to one another for the first time upon their arrival to the
3 scanning facility, and instructed together about the task and the scanning procedure. The study
4 was approved by the Research Ethics Committee of Masaryk University, and all participants
5 gave their informed consent prior to the scanning procedure. Participation was rewarded with
6 200 CZK (approx. €8).

7

8 ***2.2. The Pattern Game***

9 In the Pattern Game (PG), two players either co-operated or competed with one another over
10 recursive rounds to reconstruct patterns comprised of blue and yellow tokens (see Figure 1). At
11 the beginning of the game, each player was assigned to one colour – either blue or yellow –
12 which remains fixed throughout. On any given round, one player was assigned the role of the
13 Builder, whose goal was to recreate the target pattern as closely as possible. Due to the
14 characteristics of the patterns, however, the Builder could never recreate the pattern perfectly
15 on their own. The second (“Other”) player was instructed to either help the Builder (“Helper”)
16 or prevent them from reconstructing the pattern (“Hinderer”), and this instruction defined two
17 experimental conditions – Co-operation and Competition, respectively. In a Control condition,
18 the Other was instructed to simply observe the Builder without contributing any tokens.
19 Participant roles alternated on each round.

20 Before each round, an instruction was presented for three seconds that allocated each
21 participant to a player role (e.g., “*Yellow builds, Blue helps*”). This was followed immediately
22 by a white fixation cross visible for one second, before the round began. Every round began
23 with the players’ tokens presented on either side of the monitor above the playing board (e.g.,
24 a blue token on the left side of the monitor, and yellow token on the right; see Figure 1). Players
25 then moved their respective token either left or right to the desired columnar location, and then
26 dropped the token into the lowest empty row. In our adaptation, rounds were played iteratively

1 in two separate blocks: In the first block, players took turns sequentially to place their tokens
2 (Turn-based); in the second, participants were free to place their tokens simultaneously
3 (Concurrent). In the Turn-based block, the Builder always placed the first token, immediately
4 after which another token appeared for the Other. In the Concurrent condition, the Builder's
5 token was always in the lower row, closer to the playing board; as such, if both players
6 attempted to place their token at the same columnar position at the same time, the Builder's
7 token always dropped to the lowest row and the Other's token was positioned above it (see
8 Figure 1F). In every round of the game, each participant had five tokens to place and every
9 round lasted for a maximum of 25 seconds. After this time limit, a new round began regardless
10 of how many tokens had been placed. Both the Turn-based and Concurrent block consisted of
11 16 Co-operative, 16 Competitive, and 16 Control rounds. These 48 rounds were presented in
12 pseudorandom order, such that no single round type occurred more than three times in a row.
13 It is important to stress that, since all players played an equal number of rounds as Builders and
14 Others, we were able to assess iBBD during this interactive game in all 44 individuals.

15 Players moved their tokens via four-button response boxes, on which the buttons were
16 organised horizontally in a single row; the left- and right-most buttons moving tokens one
17 column to the left or right, respectively, and either of the two centre buttons caused the token
18 to be dropped into the lowest available row. Before the scanning session, both participants
19 performed four practice Control rounds of the Pattern Game to familiarise themselves with the
20 task. The entire protocol was coded using MATLAB (v2016b, The MathWorks, Inc.;
21 RRID:SCR_001622), and the Cogent 2000 toolbox (developed by the Cogent 2000 team at the
22 FIL and the ICN and Cogent Graphics developed by John Romaya at the LON at the Wellcome
23 Department of Imaging Neuroscience; RRID:SCR_015672).

24

25 ***2.3.MRI Data Acquisition***

1 Brain images were acquired using two identical 3T Siemens Prisma scanners located in adjacent
2 rooms within the same facility; and a 64 channel HeadNeck coil. High resolution T1-
3 weighted structural images were first recorded (MPRAGE, TR/TE=2300/2.33 msec; flip
4 angle 8°; matrix = 240x224x224, 1 mm³ voxels). Functional imaging data were then recorded
5 in two sequential runs, each containing 570 volumes (approx. 20 minutes) – the Turn-based
6 block was always followed by the Concurrent block. Blood-oxygen-level dependent (BOLD)
7 images were obtained with T2*-weighted echo planar imaging (EPI), with parallel acquisition
8 (i-PAT; GRAPPA acceleration factor = 2; 34 axial slices; TR/TE=2000/35 msec; flip angle =
9 60°; matrix=68x68x34; 3x3x4 mm voxels). Axial slices were acquired in interleaved order. To
10 ensure the synchronisation of the scanners we used an external programmable signal generator
11 to begin the acquisition sequence (Siglent SDG1025, www.siglent.com). Scanners were
12 connected to a stimulation computer via parallel ports, through which radio frequency pulse
13 timings were recorded (mean asynchrony in volume acquisition = 1.69 [SD=0.65] msec).

14

15 ***2.4. Behavioural data***

16 For each round of the PG we recorded all button presses by both players and the final layout of
17 tokens on the playing board. We could then recreate offline the moves of each player in every
18 round. Since Turn-based and Concurrent rounds may have differed in length and, therefore, the
19 number of total moves afforded, we expressed the number of successful placements as a
20 proportion of all moves. For each participant, we calculated the proportion of successful moves
21 they made in both roles under each condition: For Builders, a successful move was defined as
22 any placement that served to partially recreate the target pattern; for Helpers it was any token
23 placed in a position that provided support to the Builder, while for Hinderers it was any
24 placement within the desired pattern (thus preventing the Builder from making that same
25 successful placement; see Figure 1). For example, in the Turn-based block each participant
26 played eight Co-operation rounds in the role of Builder; with five tokens in each round they had

1 the opportunity make 40 successful placements over the course of the game. Since each
2 participant played the role of Builder and Other on alternating rounds, proportions of successful
3 placements for each player role in each condition were assessed with a 2 (Role: Builder vs.
4 Other) x 2 (Goal structure: Co-operate vs. Compete) x 2 (Interaction structure: Turn-based vs.
5 Concurrent) within-subject ANOVA.

6

7 ***2.5. Neuroimaging data***

8 Functional and structural brain images were analysed using the variety of utilities packaged
9 within FMRIB's software library (FSL; Jenkinson et al., 2012; SCR_002823).

10

11 ***2.5.1. Pre-processing***

12 Each of the four functional time-series for a given pair (two players x two blocks of PG rounds)
13 were pre-processed separately: First, motion correction was performed with MCFLIRT
14 (Jenkinson *et al.*, 2002). To remove any residual motion artefacts, or signal caused by
15 physiological noise (e.g., heart rate, respiration), we performed independent component
16 analysis with MELODIC (Beckmann & Smith, 2004) to identify 50 spatial and temporal
17 components of the BOLD signal. Artefactual components were identified automatically using
18 the Spatially Organized Component Klassifikator (SOCK; Bhaganagarapu et al., 2013), and
19 any signal corresponding to these problematic components was regressed out of the time-series
20 using *fsl_regfilt*. Slice-timing correction for interleaved slice acquisition was then applied to
21 these cleaned functional images, and each time-series was then high-pass filtered across time
22 (Gaussian-weighted least-squares straight-line fitting; sigma=50.0 secs) and spatially smoothed
23 with a 5mm full-width half-maximum Gaussian kernel. Using FLIRT, the time-series were
24 registered to a corresponding high resolution structural image using Boundary-based
25 Registration, and this, in turn, was registered linearly to the MNI-152 template (12 DOF).

26

1 2.5.2. *General Linear Modelling*

2 With FEAT, General Linear Modelling (GLM) was used to identify brain signals in each of the
3 44 participants that were elicited as a direct response to their interaction partner's prior
4 behaviour; specifically, in an event-related fashion we modelled the brain activity of each
5 individual in the 1-second period immediately following each of their partner's token
6 placement. In a two-step process, fixed-effect analyses were performed for the following
7 parameter estimations at the individual level: Builders' responses to the moves of the Other
8 under the Co-operation ($COO_{Builder}$) or Competition condition ($COM_{Builder}$); Others' responses
9 to the moves of Builders under the Co-operation (COO_{Other}) or Competition condition
10 (COM_{Other}); and, in the Control condition, the individual's brain responses while playing the
11 role of Builder and attempting to recreate the pattern without any help or hindrance ($CTL_{Builder}$).
12 Importantly, by modelling brain responses recorded during a player's own token placement in
13 the Control condition we were able to distinguish between those reflecting a reaction to their
14 partner's token placement and those elicited during their own subsequent action (see below).
15 Event-related responses were modelled as stick functions with 1-sec duration, convolved with
16 a double-gamma hemodynamic response function. Through combinations and comparisons of
17 these first-level parameters estimates, we then performed group-level whole-brain random-
18 effects analyses with FLAME to examine the main effects of Role, Goal, and Interaction; the
19 two-way interactions of Role-by-Goal, Role-by-Interaction, and Goal-by-Interaction; and the
20 three-way interaction of Role-by-Goal-by-Interaction (see Supplementary Materials for full
21 contrast specifications). Since non-parametric permutation inference offers more precise
22 control over false positives than other methods of multiple-comparison correction (Eklund *et*
23 *al.*, 2016), group-level statistical maps were corrected across space using *randomise* (Winkler
24 *et al.*, 2014) with 5000 permutations and threshold-free cluster enhancement (Smith & Nichols,
25 2009).

26

3. Results

3.1. Behaviour

First, for each participant we computed the proportion of all moves that served as successful token placements in the Builder or Other role. There was no main effect of Role ($F[1,43]=.73$, $p=.40$; $\eta_p^2=.13$), but a main effect of Goal confirmed that players made more successful placements in both roles under the Co-operation relative to the Competition condition (.95 [$\pm.01$] vs .41 [$\pm.01$]; $F[1,43]=3655.31$, $p<.001$, $\eta_p^2=1.00$). A main effect of Interaction structure demonstrated a higher proportion of successful placements on Concurrent compared with Turn-based rounds (.69 [$\pm.01$] vs .66 [$\pm.01$]; $F[1,43]=7.36$, $p=.010$, $\eta_p^2=.76$). A Role-by-Goal interaction ($F[1,43]=14.23$, $p<.01$, $\eta_p^2=.96$) revealed an increased success rate for Helpers compared with Builders in the Co-operation condition (.96 [$\pm.01$] vs .94 [$\pm.01$]) but greater success for Builders relative to Hinderers in the Competition condition (.39 [$\pm.01$] vs .42 [$\pm.01$]). There was no interactive effect of a Role-by-Interaction ($F[1,43]=1.66$, $p=.205$, $\eta_p^2=.04$). Further, a significant Goal-by-Interaction effect ($F[1,43]=12.09$, $p=.001$, $\eta_p^2=.93$) revealed that, while the increased proportion of successful placements made during Concurrent relative to Turn-based rounds was significant under the Competition condition (.43 [$\pm.01$] vs .38 [$\pm.01$]; $p<.01$), this was not the case under the Co-operation condition (.95 [$\pm.01$] vs .95 [$\pm.01$]; $p=.63$). We also found no interactive Role-by-Goal-by-Interaction effect ($F[1,43]=.10$, $p=.756$; $\eta_p^2=0.06$). These results are illustrated in Figure 2.

3.2. GLM results

Interpersonal brain-behaviour dependencies (iBBD) were measured by modelling the brain responses of one individual in the 1 sec period following the preceding token placement of their co-player. The mean (\pm SD) duration between a co-player's preceding token placement and the player's own subsequent move was 2.96 (\pm 2.14) sec in the Turn-based conditions, and 2.12 (\pm 1.69) sec in the Turn-based conditions. Importantly, by subtracting brain responses measured

1 during the Control condition from those recorded in the experimental conditions, we were able
2 to identify the brain responses reflecting reactions to a co-partner's token placements
3 independently of those elicited during a player's own moves. Localised brain signals reflecting
4 these neural responses to a co-players's moves (iBBD) expressing the contrasts between
5 different dimensions of interaction are detailed in Tables 1-3, and illustrated in Figure 3.
6 Clusters expressing each contrast were identified according to FSL's *cluster* utility.

7

8 **3.2.1. Role**

9 Consistent with the behavioural data, we observed no differences when contrasting iBBD brain
10 responses between roles of Builders and Others.

11

12 **3.2.2. Goal structure**

13 Brain responses that represented iBBD differentiated between co-operative and competitive
14 exchanges. Greater brain responses to the behaviour of a co-player were observed in the Co-
15 operation compared with the Competition condition throughout the bilateral orbito-frontal
16 cortices, medial prefrontal (mPFC) and anterior cingulate cortices (ACC), putamina and pallida,
17 precunei (extending into the posterior cingulate cortex [PCC]), frontoparietal rolandic opercula,
18 temporal corticies, and hippocampi (extending into the amygdalae). In the reverse contrast, we
19 observed differential iBBD throughout bilateral pre-supplementary motor area (pre-SMA),
20 triangularis of the inferior frontal cortex, and anterior insulae.

21

22 **3.2.3. Interaction structure**

23 Brain responses reflecting iBBD were greater in the Concurrent relative to the Turn-based
24 condition in the bilateral precentral gyri, temporo-parietal cortices and thalami; the right
25 anterior insula, and bilateral superior temporal sulci (STS). No differential expressions of iBBD
26 were revealed in the reverse contrast.

1

2 **3.2.4. Role-by-Goal**

3 Builders exhibited greater differential iBBD compared with Others in the Co-operation relative
4 to the Competition condition throughout the frontal and parietal cortices, and the cuneus. In
5 Others, however, greater reactive brain responses during the Co-operation condition were
6 observed in the mPFC and left ACC, cunei, calcarine cortices and the lingual gyri.

7

8 **3.2.5. Role-by-Interaction**

9 In line with the pattern of behavioural data, no differences were observed in interpersonal brain-
10 behaviour dependencies when contrasting player roles in each level of Interaction structure.

11

12 **3.2.6. Goal-by-Interaction**

13 We observed stronger iBBD during competitive exchanges under the Concurrent but not the
14 Turn-Based condition; specifically, this was exhibited within the SMA, bilateral precentral and
15 postcentral gyri, supramarginal gyri and occipital cortices. No brain responses expressed this
16 contrast, or the reverse, more in the Turn-Based compared with the Concurrent condition.

17

18 **3.2.7. Role-by-Goal-by-Interaction**

19 As with the behavioural data, the three-way interaction between Role, Interaction and Goal
20 structure revealed no differential iBBD after thresholding with nonparametric permutations.

21

22 **4. Discussion**

23 Using a dual-fMRI protocol, this study investigated whether discrete dimensions of dyadic
24 social exchange elicit dissociable patterns of inter-dependency between the behaviour of one
25 interactant and the resultant brain responses of another – that is, interpersonal brain-behaviour
26 dependencies (iBBD). To this end, we adapted the Pattern Game (PG; Decety et al., 2004) to

1 be an experimental paradigm for two-person hyperscanning capable of delineating between
2 different interaction dimensions. Building on Liu and Pelowski's framework of social
3 interaction (2014), this is the first research to dissociate between more than one dimension of
4 dyadic exchange, and to examine interpersonal brain and behavioural processes between both
5 interactants during concurrent and turn-based exchanges. By modelling the brain responses in
6 each interactant as neural reactions to their partner's behaviour, we able to measure iBBD
7 online – that is, interpersonal brain processes that emerge between two individuals whose active
8 participation combines to give rise to a dynamic, non-linear, real-world social exchange. Our
9 results reveal that specific patterns of player behaviour under each dimension were mirrored by
10 discrete patterns of iBBD.

11 It might be argued that the interpersonal brain-behaviour relationships we have observed
12 in the present study could have been investigated in a simpler, more classic neuroimaging
13 protocol, whereby the brain of one individual was scanned while they played with another
14 person who was not scanned. While this would capture brain signals that are modulated online
15 by the behaviour of an interaction partner, it would present an incomplete picture that considers
16 iBBD to be a unidirectional process; we would not know how the brain of the other player is
17 modulated by the resultant reciprocal actions. Naturalistic dyadic exchanges are defined by the
18 active participation of both interactants; both competitive and cooperative interactions emerge
19 through a bidirectional to-and-fro of mutually contingent behavioural exchanges that
20 communicate intentional states, giving rise to unique non-linear dynamics that are created by
21 the two players *together*. As such, iBBD reflects brain processes that are simultaneously both
22 a cause and an effect of an interaction partner's prior and present behaviour, and will emerge
23 in a unique fashion during each exchange. By scanning both interactants brains simultaneously,
24 we have measured iBBD as a bidirectional process of *mutual* dependency as it unfolds online
25 over the course of unique social interactions, thereby capturing the shared intentionality
26 between players (Tomasello, Carpenter, Call, Behne, & Moll, 2005; Schilbach et al., 2013).

1 Furthermore, the conditions under which participants interacted with one another were highly
2 similar; both interactants knew that their co-player was in a similar context, allowing for a more
3 ecologically valid context (Schilbach, Wilms, Eickhoff & Romanzetti, 2010).

4 Beginning with goal structure, players achieved greater success in the Co-operative
5 relative to the Competition condition. This was reflected in the brain, and in a manner consistent
6 with our hypothesis: reactive brain responses were greater during co-operative than competitive
7 rounds in neural systems implicated in reward processing; namely, the putamen and ventral
8 pallidum (Haber & Knutson, 2010). This converges with previous studies in which co-operative
9 tasks are reported to engage the left caudate and putamen (Krill & Platek, 2012). Co-operation
10 is discussed widely in various evolutionary settings, and is generally considered beneficial to
11 individuals (Kurzban et al., 2015; Rilling et al., 2002; Tomasello & Vaish, 2013). Interpersonal
12 brain-behaviour dependencies exhibited within the basal ganglia might therefore represent the
13 reward experienced during such co-operative dyadic exchange (Haber & Knutson, 2010). This
14 interpretation is in line with the results of Schilbach et al. (2010), who used interactive task to
15 compare pleasantness ratings and brain responses during joint-attention task. These authors
16 report that higher ratings of pleasantness were accompanied by stronger engagement of the
17 ventral striatum, associating subjective experiences with neural systems implicated in reward
18 processing. The second set of reactive brain responses constituted brain areas linked repeatedly
19 to socio-cognitive and -emotional processes; specifically, the anterior cingulate (ACC) and
20 medial prefrontal cortex (mPFC), and the amygdalae (Bickart *et al.*, 2014; Twining *et al.*, 2017).
21 A previous study has also reported the involvement of the ACC during co-operative tasks
22 (Chaminade *et al.*, 2012). Interestingly, the ACC is engaged consistently in tasks that require
23 performance monitoring and adaptive behaviour during changing environmental demands, and
24 evaluating the decisions of others during social interactions (e.g., Apps et al., 2013). This has
25 led to the proposal that the ACC processes reward in an “other-oriented” reference frame, which
26 can be used to estimate the motivation and, in turn, predict the behaviour of others (Apps *et al.*,

1 2016). This pattern of iBBD also included the posterior cingulate cortex (PCC), which
2 converges with the pattern of activations observed by Decety et al. (2004) during co-operative
3 rounds of the PG. Strong brain responses to an interaction partner's behaviour in this region
4 during our interactive task suggests that it is involved in the adaptation of our own behaviour
5 in response to the inferred intentions of our interaction partner(s). Contrary to our prediction,
6 then, this finding might indicate that individuals attempt to infer the intentional state of their
7 interaction partner more during co-operative than competitive exchanges.

8 Interpersonal brain-behaviour dependencies elicited during the Competitive condition
9 was observed throughout brain areas involved predominantly in movement planning and
10 attention processes: pre-supplementary motor area (pre-SMA), inferior frontal cortex and
11 anterior insula. Previous research has shown that the pre-SMA is activated reliably during tasks
12 that require response inhibition or switching between stimulus-response rules (Nachev *et al.*,
13 2008). This may reflect the need for players to respond more adaptively during competitive
14 exchanges, changing their plans in response to their co-player's behaviour. The reactivity of the
15 inferior frontal gyrus may represent the functioning of neural mirroring systems implicated in
16 action understanding (Rizzolatti & Craighero, 2004), which would support motor planning
17 performed by the pre-SMA. The response of the anterior insula during competitive exchanges
18 is also consistent with previous research (Takahashi *et al.*, 2015). Given the well-documented
19 role of this brain area in subjective feelings states (Walter, 2012; Morelli *et al.*, 2014; Hari *et*
20 *al.*, 2015), this focus of neural reactivity might reflect affective reactions when monitoring and
21 adapting to another's behaviour.

22 An important novel aspect of this study is the focus not only on goal but also interaction
23 structure. To our knowledge, all existing hyperscanning experiments have employed interactive
24 tasks that afford *either* turn-based (e.g., Tomlin. et al., 2006; Babiloni et al., 2007) or concurrent
25 exchanges (e.g., Tognoli et al., 2007; Lindenberger et al., 2009; Cui et al., 2012), but our
26 modified PG enabled us to compare these two types of interaction structure directly. Our data

1 demonstrate important differences between these types of exchange: First, we recorded a higher
2 rate of successful placements during concurrent compared with turn-based rounds.
3 Furthermore, we observed a parallel pattern of stronger iBBD during concurrent relative to turn-
4 based exchanges, particularly in the right superior temporal sulcus (STS) and temporo-parietal
5 cortices. Since these brain regions are associated frequently with mentalizing processes
6 (Carlson et al., 2013; Frith & Frith, 2006; Van Overwalle, 2009; Walter, 2012), we suggest this
7 reflects the greater need for individuals to infer their opponent's intentions in real time during
8 concurrent compared with sequential interactions.

9 Second, while the success rate was comparable on concurrent and turn-based exchanges
10 in the Co-operative condition, players were significantly more successful in concurrent rounds
11 of the Competition condition. Congruently, increased iBBD expressed during competitive
12 compared with co-operative rounds was greater under the Concurrent relative to the Turn-Based
13 condition. This was exhibited within the SMA, bilateral precentral and postcentral gyri – brain
14 areas linked strongly to movement planning. One possible explanation is that competitive
15 exchanges afforded multiple strategies; players may have spent more time evaluating the
16 playing space and second-guessing their opponent's upcoming move in the Turn-based
17 condition, rather than reacting dynamically to their opponent. On concurrent rounds of the
18 Competition condition, however, in which the quicker player often made more successful token
19 placements, there was less time for such strategic planning. Conversely, under the Co-operation
20 condition there is no such plurality of strategies to consider; both players work towards the
21 same shared goal in both concurrent and turn-taking exchanges.

22 Although we observed no differences when comparing Builders and Others directly, a
23 role-by-goal interaction revealed different patterns of brain reactivity evoked in each role:
24 While, Builders achieved less successful placements than Others in the Co-operation condition,
25 the opposite effect was present under the Competition condition. This likely reflects
26 fundamental differences in the nature of the task for Helpers and Hinderers: A single strategy

1 for success was illustrated explicitly to Helpers, since only three token placements enabled the
2 Builder to form the target pattern. In contrast, a number of implicit strategies were available to
3 Hinderers in their impedance of the Builder – they could hinder actively through obstructive
4 placements, for instance, or passively through no placements at all. This is an important aspect
5 of our interactive paradigm, and of social exchanges more generally: while both interactants
6 might pursue the same goal, different social contexts may afford different strategies for each
7 individual. We observed a stronger iBBD during co-operative exchanges in the Builder
8 compared with the Other throughout frontal and parietal brain regions, and the precuneus. The
9 precuneus is thought to be involved in self-referential processes and self-other distinction
10 (Cabanis *et al.*, 2013; Reniers *et al.*, 2014), which suggests the recruitment of these processes
11 when one individual (the Builder) must infer the co-operative intentions behind the actions of
12 another (the Other). On the other hand, iBBD in the Other during co-operative exchanges were
13 expressed in other brain areas associated with socio-cognitive processes, such as the mPFC and
14 ACC (Völlm *et al.*, 2006; Reniers *et al.*, 2014).

15 Our findings illustrate the need for social neuroscience research to operationalise
16 carefully the specific dimension(s) of social interaction under investigation. In doing so,
17 hyperscanning permits a characterisation of the specific dimensions along which clinical
18 disorders exhibit dysfunctional social behaviour, and the identification of underlying inter-brain
19 neuromarkers. To develop our results further, future studies should investigate how these
20 dissociable, role-specific patterns of iBBD emerge spontaneously during naturalistic
21 exchanges. One way to achieve this is to modify our paradigm by removing the fixed task
22 structure. In many interactive paradigms used for hyperscanning studies, such as those
23 employing economic games (e.g., Ultimatum Game; Shaw *et al. in press*), the asymmetry of
24 player roles is enforced by the very nature of the task. In others, however, such asymmetry is
25 allowed to emerge spontaneously; in the synchronized finger-tapping task used by Konvalinka
26 *et al.* (2014), for example, pairs of participants either mutually adjusted to each other or

1 followed a computer metronome. These authors report a spontaneous emergence of leader-
2 follower relationship, which was accompanied by differential brain responses between players.
3 We instructed interactants about the type of exchange they should perform at any one time, but
4 real interactions are often characterised by a degree of uncertainty about how the other person
5 is going to behave – for example, whether they will decide to co-operate or not. Our interactive
6 task could be adjusted such that players are free to choose their role on a given round, affording
7 an interactive context that resembles real-world dyadic exchange even more closely.

8

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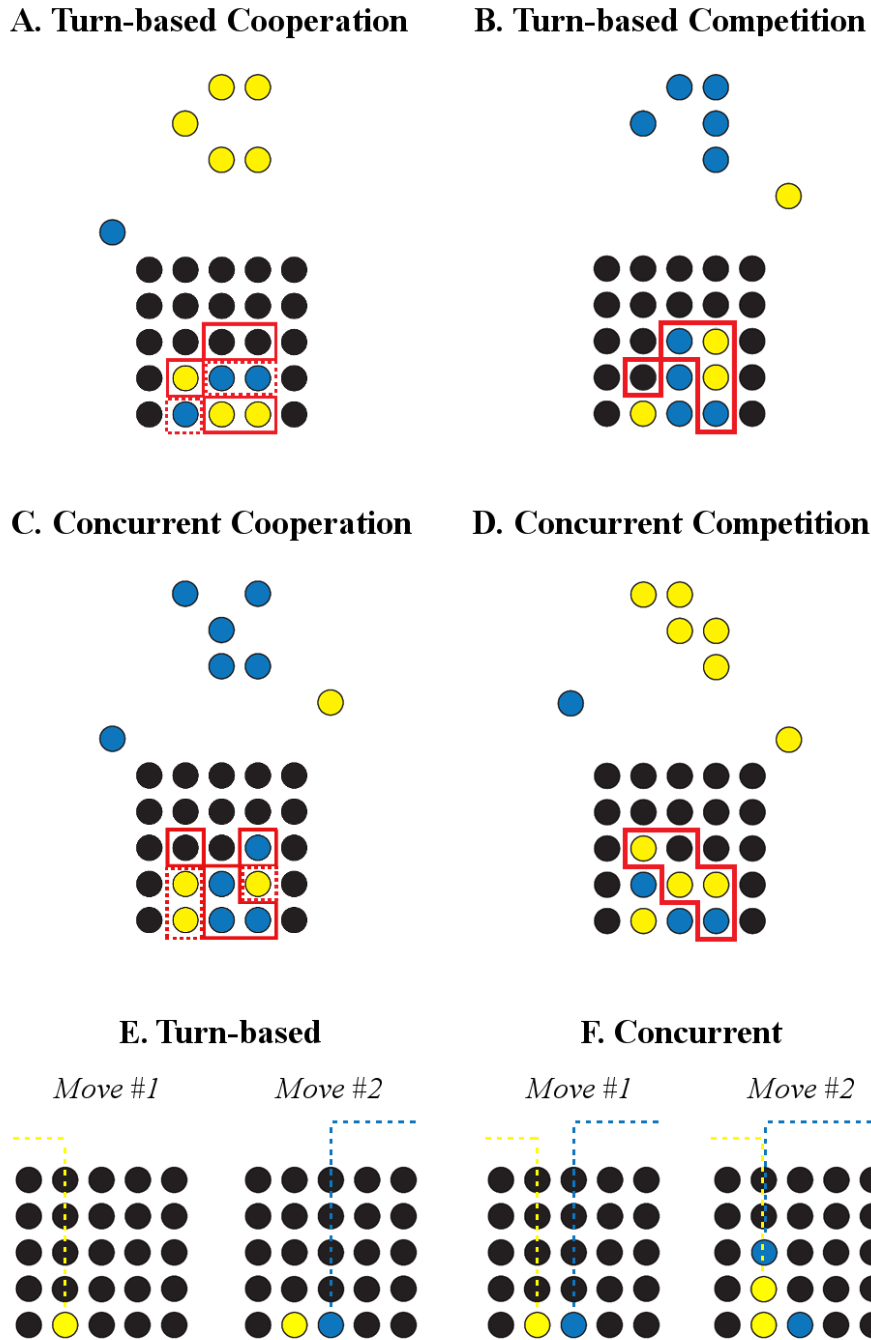
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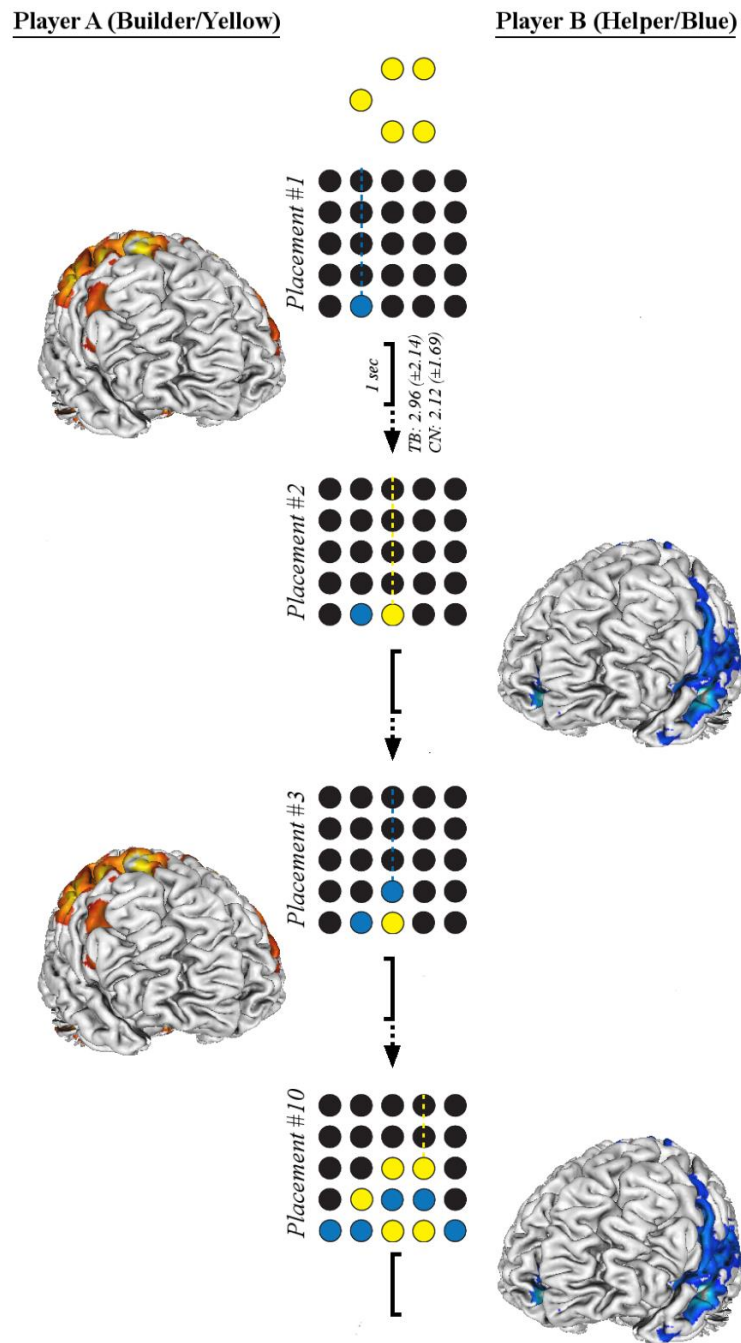
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1 **Figures**



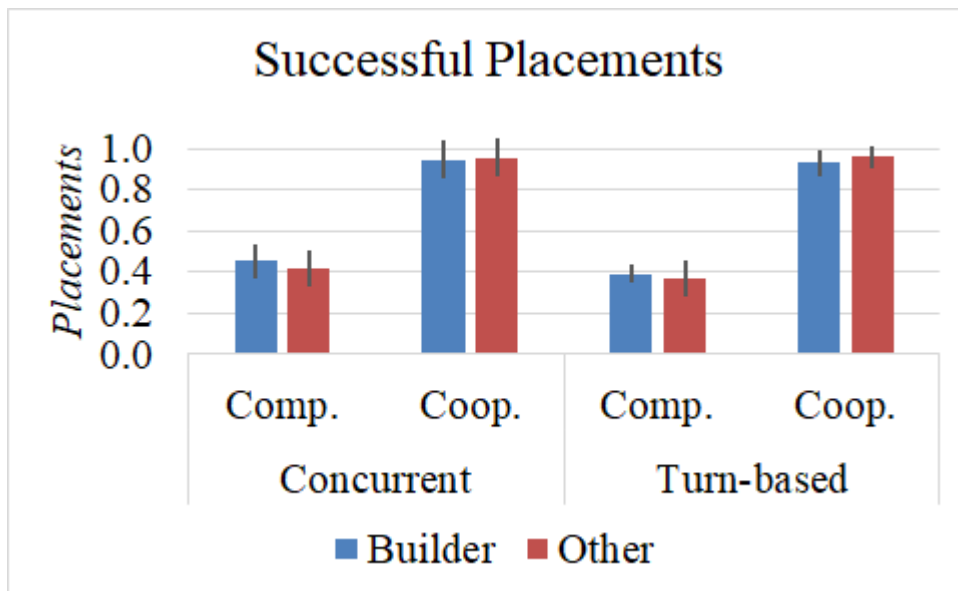
2

3 Figure 1. Snapshots of Turn-based Co-operation (A) and Competition rounds (B), and Concurrent Co-operation (C) and
 4 Competition rounds (D); and schematics of sequential player moves in Turn-taking (E) and Concurrent rounds (F). In panels
 5 A-D, the Builder is assigned the same colour as the depicted target pattern, and scores by placing tokens in locations that
 6 recreate the pattern (indicated by solid red lines). The Other scores by placing their tokens in locations that serve to help (dashed
 7 red lines) or hinder the Builder; since the latter is achieved by placing tokens within the pattern space, thereby obstructing the
 8 Builder, the scoring location of Others and Builders are the same in Competitive rounds (solid red lines). In E, players take
 9 turns to move their tokens. In F, both players can move simultaneously; if both players chose move their token to the same
 10 location then the Builder's token (*lower*) is positioned in the first available space, and the Other's token is positioned above it.



1

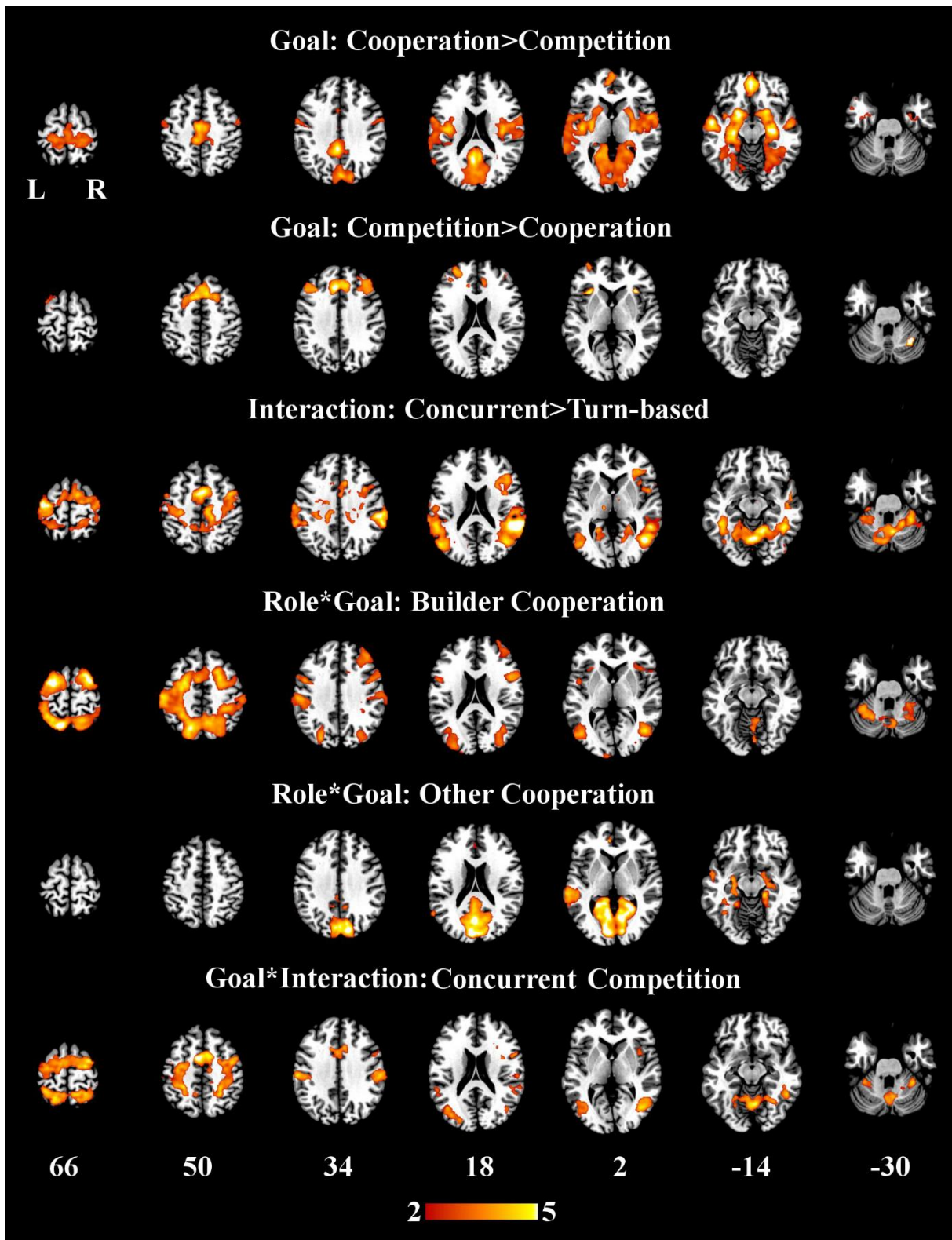
2 Figure 2. Schematic of the General Linear Modelling procedure. This illustrates the timings of four token
 3 placements during an example Turn-based Co-operation round, in which Helper (*blue*) takes turns with a Builder
 4 (*yellow*) to assist them in re-creating the target pattern. The brain responses of each player are modelled in the 1
 5 second period immediately following their co-player's token placement. The mean (\pm SD) interval between the co-
 6 player's token placement and the individual's own subsequent placement are shown for both Turn-based (TB) and
 7 Concurrent (CN) rounds. On CN rounds particularly, the individual's own placement sometimes occurred within
 8 this 1 second period, but brain responses specific to an opponent's token placement and independent of the player's
 9 own moves were identified by subtracting those modelled during a Control condition (see text for further details).



1

2 Figure 3. Behavioural data. Mean (\pm SE) proportions of successful token placements achieved by

3 Builders (*blue*) and Others (*red*) in both levels of goal and interaction structure.



1
 2 Figure 4. Neuroimaging data from group analyses. Rows present selected axial slices illustrating z-maps in which
 3 clusters of BOLD response expressed differential Interpersonal brain-behaviour dependencies (iBBD) among
 4 conditions after thresholding ($p < 0.05$) with non-parametric permutation bootstrapping. *Note:* z-maps are overlaid
 5 onto the Colin27 template (Holmes *et al.*, 1998). Values at the bottom of the image present z-coordinates of
 6 corresponding axial slices, in MNI space.

1 Table 1. Clusters iBBD expressing the main effect of Goal.

Co-operation > Competition								Competition > Co-operation							
Cluster	Voxels	Label		Max	x	y	z	Cluster	Voxels	Label		Max	x	y	z
3	36910	Putamen	L	8.07	-18	8	-8	5	3770	dmPFC	L	7.49	-4	24	42
			R	7.1	20	14	-6				R	6.48	4	26	44
		MTG	L	7.4	-56	-6	-14					6.89	10	24	44
		Hippocampus	R	7.38	30	-18	-12					6.55	10	32	40
		Precuneus	L	6.87	-4	-58	20			SMA	L	6.48	-8	16	46
		Rolandic Operculum	L	6.59	-40	-14	16			MCC	L	7.03	-4	28	36
2	1492	vmPFC	L	6.67	0	42	-10	4	1165	MFG	L	5.54	-30	54	10
				6.58	-2	50	-12					5.21	-46	34	28
				6.4	0	56	-8					5.09	-44	24	40
		dmPFC	L	5.13	0	62	0					4.64	-36	26	36
				4.33	-2	54	6			IFG	L	4.54	-36	28	28
		ACC		4.18	0	36	8			SFG	L	4.43	-22	48	22
1	7	Orbito-frontal cortex	R	6.04	28	34	-10	3	218	Insula	L	7.95	-34	18	-4
				5.99	32	34	-12	2	106		R	6.8	34	22	2
												6.7	30	24	-4
								1	74	Cerebellum	R	7.39	32	-58	-30

2

3 *Note:* Coordinates are given at 3mm³ resolution in MNI space, and max values present peak *t*-
4 value from non-parametric permutation inference. *Abbreviations:* MTG=middle temporal
5 gyrus, v/dmPFC=ventro-/dorso-medial prefrontal cortex, ACC=anterior cingulate cortex,
6 SMA=supplementary motor area, MCC=mid cingulate cortex,
7 I/M/SFG=inferior/middle/superior frontal gyrus.

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1 Table 2. Clusters of iBBD expressing the Goal-by-Role interaction.

Builder (COO>COM) > Other (COO>COM)							
Cluster	Voxels	Label		Max	x	y	z
2	27005	Precuneus	L	9.04	-12	-62	62
		SFG	L	8.36	-28	-2	66
				8.25	-24	-6	66
			R	8.18	26	0	62
		SPL	L	8.33	-16	-68	56
		MFG	L	8.21	-26	-2	56
1	4733	Cerebellum	L	7.12	-38	-44	-46
				6.03	-24	-34	-42
				5.85	-36	-50	-30
				5.84	-12	-52	-48
			R	6.56	14	-54	-50
				6.34	30	-40	-46

Other (COO>COM) > Builder (COO>COM)							
Cluster	Voxels	Label		Max	x	y	z
3	11776	Calcarine	L	7.96	-10	-86	2
				7.54	-22	-48	4
			R	7.83	24	-50	6
		Cuneus	L	7.56	-2	-86	28
				7.52	-6	-88	24
		Lingual	R	7.52	12	-70	0
2	1337	MTG	L	5.58	-64	-32	4
				5.47	-52	-26	0
				5.28	-66	-30	0
				5.14	-60	-38	8
				5.12	-58	-12	-6
		STG	L	4.91	-54	-10	-8
1	217	Frontal Med Orbital	L	6.18	-4	50	-4
		ACC	L	6.17	-2	44	8
				5.77	0	40	14

2

3 *Note:* Coordinates are given at 3mm³ resolution in MNI space, and max values present peak *t*-
4 value from non-parametric permutation inference. *Abbreviations:* SFG=superior frontal gyrus,
5 SPL=superior parietal lobule, MFG=middle frontal gyrus, MTG=middle temporal gyrus,
6 STG=superior temporal gyrus, ACC=anterior cingulate cortex.

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- 1 Table 3. Clusters of iBBD expressing the main effect of Interaction (*left*) and the interactive
- 2 Goal-by-Interaction effect (*right*).

Concurrent > Turn-based							
Cluster	Voxels	Label		Max	x	y	z
4	36386	STG	R	7.35	58	-44	18
		MTG	R	6.96	54	-52	12
				6.55	46	-64	6
		Precentral	L	6.77	-30	-18	70
				6.5	-38	-18	68
		Cerebellum	L	6.76	-14	-76	-36
3	335	Thalamus	L	5	-16	-12	12
				4.38	-8	-16	-2
			R	4.46	8	-22	0
		STG	R	5.05	46	-16	-8
				4.02	52	-2	-14
		Insula	R	4.15	40	-10	-6
2	275	Temporal Pole	R	3.9	54	4	-16
		Thalamus	R	4.38	16	-8	14
				3.96	8	-8	4
				3.88	18	-22	14
1	120			3.87	12	-12	10

Turn-based (COO>COM) > Concurrent (COO>COM)							
Cluster	Voxels	Label		Max	x	y	z
3	14191	SMA	L	6.37	-8	2	48
			R	5.59	10	2	48
		Supramarginal gyrus	L	6.09	-58	-24	30
		Precentral gyrus	L	5.5	-28	-12	54
		SPL	L	5.42	-20	-54	62
		Postcentral gyrus	R	5.36	56	-22	32
2	8060	MOG	L	5.8	-40	-70	12
		Vermis		5.67	-2	-62	-8
				5.18	4	-64	-12
				5.05	2	-66	-18
		MTG	R	4.87	42	-68	4
		Cerebellum	L	4.85	-8	-72	-42
1	3	Postcentral	R	2.94	36	-32	72

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- 4 *Note:* Coordinates are given at 3mm³ resolution in MNI space, and max values present peak *t*-
- 5 value from non-parametric permutation inference. *Abbreviations:* STG=superior temporal
- 6 gyrus, MTG=middle temporal gyrus, SMA=supplementary motor area, SPL=superior parietal
- 7 lobule, MOG=middle occipital gyrus.

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