

Leader–follower behavioural coordination and neural synchronization during intergroup conflict

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Hejing Zhang¹, Jiaxin Yang^{1,2}, Jun Ni ^{1,2}, Carsten K. W. De Dreu ^{3,4,5} & Yina Ma ^{1,2,6} 

Leaders can launch hostile attacks on out-groups and organize in-group defence. Whether groups settle the conflict in their favour depends, however, on whether followers align with leader's initiatives. Yet how leader and followers coordinate during intergroup conflict remains unknown. Participants in small groups elected a leader and made costly contributions to intergroup conflict while dorsolateral prefrontal cortex (DLPFC) activity was simultaneously measured. Leaders were more sacrificial and their contribution influenced group survival to a greater extent during in-group defence than during out-group attacks. Leaders also had increased DLPFC activity when defending in-group, which predicted their comparatively strong contribution to conflict; followers reciprocated their leader's initiatives the more their DLPFC activity synchronized with that of their leader. When launching attacks, however, leaders and followers aligned poorly at behavioural and neural levels, which explained why out-group attacks often failed. Our results provide a neurobehavioural account of leader–follower coordination during intergroup conflict and reveal leader–follower behavioural/neural alignment as pivotal for groups settling conflicts in their favour.

Intergroup polarization and conflict abound¹. From shouting contests on social media to political protests and violent riots, individuals coalesce into groups to fight other groups for resources, political influence or ideological supremacy. They contribute metabolic energy, insights and material resources to create a collective 'fighting capacity' that, if strong enough, may settle the conflict in their favour. Along the way, however, energies get wasted, people get hurt and resources are destroyed.

Individuals involved in intergroup conflicts differ in their motivation and ability to fight, and some are more intimately involved

than others^{2,3}. Attacks on rivaling out-groups are often initiated and orchestrated by a few key individuals who stand out for their boldness of character or gain comparatively more from the conflict. Likewise, group members who stand out for their bravery or may lose comparatively more from group defeat often lead the in-group defence against out-group enemies^{2,4,5}. Having such key individuals in the group can help. For example, groups with leaders are more likely to resolve intergroup conflict in their favour than leaderless groups^{4,6,7}, and groups using sequential decision-making, in which one randomly selected member moves first, are more likely to win intergroup contests than

¹State Key Laboratory of Cognitive Neuroscience and Learning, and IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing, China.

²Beijing Key Laboratory of Brain Imaging and Connectomics, Beijing Normal University, Beijing, China. ³Social, Economic, and Organizational Psychology, Leiden University, Leiden, the Netherlands. ⁴Leiden Institute for Brain and Cognition, Leiden University, Leiden, the Netherlands. ⁵Center for Research in Experimental Economics and Political Decision Making, Amsterdam School of Economics, University of Amsterdam, Amsterdam, the Netherlands.

⁶Chinese Institute for Brain Research, Beijing, China. ✉e-mail: yina@bnu.edu.cn

groups where all members move simultaneously without knowing decisions of other members^{8,9}.

What remains puzzling is why group members align with leader initiatives and directives. Whereas groups are more likely to settle the conflict in its favour the more group members contribute to collective fighting capacity, participating in conflict can be risky and is often personally costly. Accordingly, individuals may be tempted to ‘lay low’ and free ride on the cooperative efforts of fellow group members^{7,10,11}. In such settings and all else being equal, first moves and norm setting by key individuals and group leaders do not alter the personal costs associated with contributing to conflict. Group members have as strong an incentive to ‘lay low’ in groups with and without first movers or group leaders. Whereas following leader signals and initiatives may make groups more successful competitors^{12–14}, following leaders can be at odds with the individual’s personal best interest.

Here we aimed to better understand leader behaviour and leader–follower coordination during intergroup conflict at both the behavioural and neural levels. We nested every 6 individuals in two 3-person groups and gave them an endowment from which they could contribute to their group’s capacity to win resources from rivaling out-groups (henceforth out-group attack) or to defend the in-group against such out-group attacks (henceforth in-group defence^{8,9}). Following a series of contest interactions, individuals within each group elected their group leader and continued for another series of intergroup contests. Leaders in our experiments were strictly symbolic, that is, they could not sanction followers and they could not communicate other than signalling their own contributions to the collective fighting capacity. Leaders in our experiments thus model after ‘key individuals’ in coalitional conflict^{4,5}, or what political scientists refer to as ‘opinion leaders’^{15,16}. Across rounds, we observed (changes in) contributions to out-group attack and in-group defence by leaders and followers, the degree to which these contributions were (mis)aligned, and how this influenced personal and group outcomes. This set-up thus allowed us to address three questions to which we currently lack answers. First, how do group leaders engage in intergroup conflict? Second, when and how do followers align their costly contributions to intergroup conflict with those made by their group leader? Finally, how does the group’s position in the conflict—engaging in out-group attacks versus in-group defence—shape leader behaviour and leader–follower alignment and coordination?

Recent studies on leadership in intergroup conflict scaled leader behaviour from sacrificial on the one hand, to extractive on the other^{17–19}. Sacrificial leaders engage in and contribute comparatively much to collective fighting and compensate for possible lack of participation from followers (viz. compensatory alignment). Extractive leaders, in contrast, may initiate conflict without making substantial contributions themselves, that is, they contribute when followers do not yet withhold contributions when followers do participate (viz. free-riding misalignment^{17–19}). For two reasons, leaders may be more sacrificial (and less extractive), and followers and leader may align better during in-group defence than during out-group attack. First, out-group attacks pose threats to both individual group members and the group as a whole. Under such collective threat, individual and group survival are interdependent, and group members, especially group leaders, have strong motivations to contribute to conflict^{20,21}; incentives to free ride are weaker during in-group defence than during out-group attack²². Second, collective threats increase group cohesion and feelings of ‘common fate’ among group members^{23–25}, and this increases parochial cooperation and intragroup coordination^{26–28}. Importantly, aligning and coordinating with first movers or group leaders have been shown as an efficient way for group coordination and fighting against rivals^{8,9,29,30}. Indeed, group members show more support for the leader and follow leader initiatives more during collective crises^{25,31}. We thus expected better alignment and coordination with the leader during in-group defence than during out-group attack.

In addition to behavioural decisions, we concurrently measured leader and follower neural responses in the right dorsolateral prefrontal cortex (rDLPFC) and right tempo-parietal junction (rTPJ) using functional near-infrared spectroscopy (fNIRS)^{32–34}. This brain imaging technology allowed us to identify (changes in) neural activity when leaders and followers made decisions and processed what others did contribute. Crucially, it also allowed us to examine to what degree leader and followers within the same group synchronized their neural activity and whether such leader–follower neural synchronization predicted contribution decisions and conflict outcomes. We focused on the rDLPFC as earlier work has linked neural activity in the rDLPFC to updating beliefs about and adapting to another person’s risk-preferences^{35,36}, to compliance with social norms for cooperation^{37–39}, and to perceiving greater influence and valuing dominance hierarchies^{40–42}. Recent studies also found within-group neural synchronization in the prefrontal cortex during intergroup conflict, and that the degree of synchronization predicted how much group members contributed to group fighting capacity^{1,33,34}. In addition, we included the rTPJ as a region of interest because of its central role in mentalizing and the theory of mind^{43,44}, and its involvement in the anticipation of others’ decisions⁴⁵ and in the alignment with group members in emotional responses and forming group norms^{44,46}.

Results

We organized each set of 6 individuals into 3-vs-3-person contests between attacker and defender groups (Methods and Supplementary Table 1). Individuals were fixed in their group and groups were fixed in the intergroup contest for two blocks of 24 rounds (Fig. 1a). For each round, individuals were given an endowment e of 20 monetary units (MU). Individuals in the attacker (defender) group could contribute x (y) out of e to their group’s fighting capacity C . Contributions were non-recoverable. However, when $C_{\text{attacker}} \leq C_{\text{defender}}$, defender groups survived the attack from their out-group and members of both groups would keep their non-invested monetary units (that is, $e - \{x, y\}$). In contrast, when $C_{\text{attacker}} > C_{\text{defender}}$, the attacker group ‘won’ and earned the non-invested resources from the defender group (that is, $3e - C_{\text{defender}}$). These ‘spoils of war’ were then added in equal shares to the three individuals in the attacker groups, regardless how much they had contributed to their group’s attack capacity (Supplementary Table 2).

In the first block of 24 contest rounds, participants simultaneously made their contribution decisions and received feedback about others’ contributions and the contest outcomes after each round. Results for this first block were reported elsewhere³³ and are subsequently ignored here. Following the first block, groups engaged in a 4-min computer-mediated chat to elect among themselves a group leader (Methods). Once each 3-person group had elected their leader, groups continued the intergroup contest for another 24 consecutive contest rounds. Individuals made their investments simultaneously and without communication. However, individuals were provided with feedback detailing what their group leader and followers had contributed and earned from each round (Fig. 1b), allowing leader and followers to adapt their subsequent contribution decisions.

Behavioural results

Consistent with earlier work^{3,8,9,33}, individuals in defender groups contributed on average more than individuals in attacker groups (main effect of role, $F_{1,86} = 254.350$, $P = 2.021 \times 10^{-27}$, $\eta^2_p = 0.747$ (90% confidence interval (CI): 0.669, 0.796)). Moreover, group leaders contributed more than their followers (main effect of leader, $F_{1,86} = 29.056$, $P = 6.069 \times 10^{-7}$, $\eta^2_p = 0.253$ (90% CI: 0.128, 0.368)). Crucially, this difference between leaders and followers was stronger in defender groups ($F_{1,86} = 24.555$, $P = 3.579 \times 10^{-6}$, $\eta^2_p = 0.222$ (90% CI: 0.103, 0.338)) than in attacker groups ($F_{1,86} = 8.222$, $P = 0.005$, $\eta^2_p = 0.087$ (90% CI: 0.015, 0.190)) (Fig. 1c; leader \times role interaction: $F_{1,86} = 6.906$, $P = 1.017 \times 10^{-2}$, $\eta^2_p = 0.074$ (90% CI: 0.010, 0.173)).

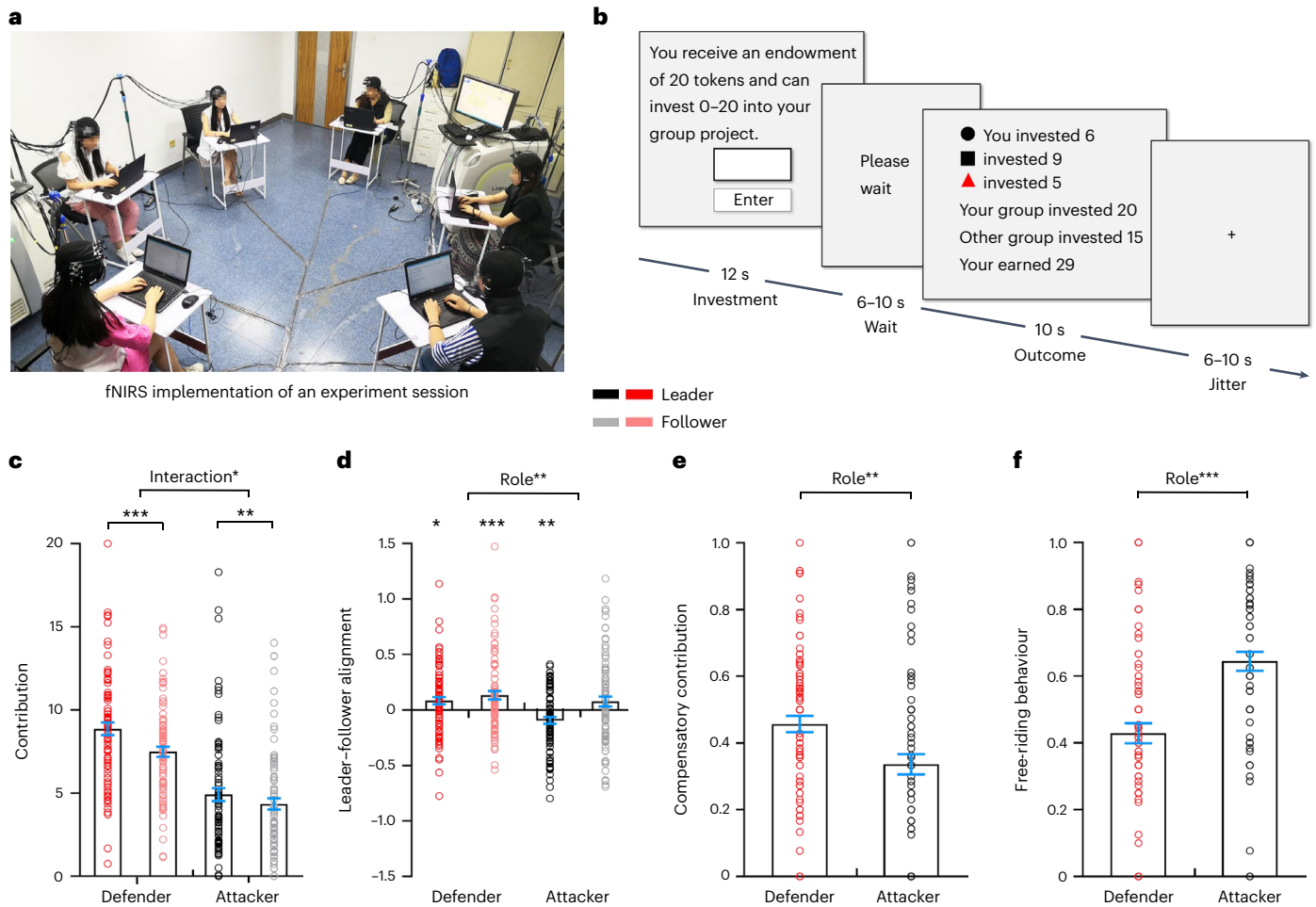


Fig. 1 | Experimental settings and behavioural results. **a**, During the intergroup contest, individual neural activity in the rDLPFC and rTPJ was recorded using fNIRS. Shown here is a snapshot of a session between the 3-person attacker group (data simultaneously recorded by the same fNIRS system) and the 3-person defender group (data simultaneously recorded by another identical fNIRS system). **b**, The timeline of a contest round with a feedback screen for an individual in the attacker group (symbols identify each individual in the group; red triangle is the elected leader). The leader and follower roles were fixed in groups and groups were fixed in the intergroup contest during the entire 24-round contest. Contributions were wasted, and full feedback on contributions and earnings concluded each contest round. Endowments were reset after each contest round. **c**, Contributions to intergroup conflict, showing stronger difference between leaders and followers in defender groups (contribution,

leaders: 8.866 ± 0.372 ; followers: 7.490 ± 0.302) than in attacker groups (leaders: 4.914 ± 0.388 ; followers: 4.343 ± 0.341). **d**, Leader–follower alignment in contributions. Defender leaders and followers aligned contributions with each other (alignment parameter β , leaders: 0.084 ± 0.033 ; followers: 0.132 ± 0.039). In attacker group, followers did not track their leader’s contributions ($\beta \pm \text{s.e.m.} = 0.076 \pm 0.044$) and leaders decreased contributions the more their followers contributed in the previous round ($\beta \pm \text{s.e.m.} = -0.094 \pm 0.030$). **e, f**, Behavioural alignment patterns. Defender leaders displayed more compensatory contributions than attacker leaders (0.456 ± 0.028 vs 0.337 ± 0.030) (**e**), whereas attacker leaders displayed more free-riding behaviours than defender leaders (0.643 ± 0.031 vs 0.402 ± 0.029) (**f**). $n = 88$ 3-vs-3-person intergroup contest sessions. Data are shown as mean \pm s.e.m. with overlaid dot plots. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

To probe how leader and follower contributions to intergroup conflict influenced round-by-round defender survival (1, otherwise 0) and attacker victory (1, otherwise 0), we performed logistic regressions in which we respectively regressed leader and follower contributions within defender (attacker) groups onto group survival (victory) across the 24 rounds. On average, defender groups survived 77.899% (s.e.m.: 1.494%) of the contests. Crucially, group survival in defender groups was better predicted by leader than by follower contributions ($F_{1,79} = 5.008, P = 0.028, \eta^2_p = 0.060$ (90% CI: 0.003, 0.158)). Victory for attacker groups, in contrast, was better predicted by follower than leader contributions ($F_{1,79} = 7.524, P = 0.008, \eta^2_p = 0.087$ (90% CI: 0.013, 0.194)) (role \times leader interaction on the regression parameter predicting contest success: $F_{1,79} = 13.405, P = 4.517 \times 10^{-4}, \eta^2_p = 0.145$ (90% CI: 0.044, 0.262)).

Next we set out to examine how group leader and followers coordinated their contributions during intergroup contest. To probe

leader–follower alignment in contributions, we first regressed leader (follower) contribution on any round onto followers (leader) contributions in the previous round. We then examined the effects of role and/or leader on the leader–follower alignment while controlling for the autocorrelation of one’s own contributions across 24 rounds. The tracking of others’ last round contributions differed as a function of role (defender > attacker: $F_{1,79} = 7.401, P = 0.008, \eta^2_p = 0.086$ (90% CI: 0.013, 0.193)), leader (follower-align-to-leader > leader-align-to-follower: $F_{1,79} = 11.321, P = 1.185 \times 10^{-3}, \eta^2_p = 0.125$ (90% CI: 0.033, 0.240)) and their interaction ($F_{1,79} = 6.004, P = 0.016, \eta^2_p = 0.071$ (90% CI: 0.007, 0.173)) (Fig. 1d). In defender groups, both leaders and followers increased their contributions the more followers and leaders contributed in the previous round (leaders: $t_{86} = 2.535, P = 0.013$, Cohen’s $d = 0.272$ (95% CI: 0.057, 0.485); followers: $t_{86} = 3.426, P = 9.404 \times 10^{-4}$, Cohen’s $d = 0.367$ (95% CI: 0.149, 0.583)). In attacker groups, we observed a different pattern. Followers did not track their leader’s contributions

($t_{82} = 1.741, P = 0.085$, Cohen's $d = 0.191$ (95% CI: $-0.027, 0.408$)), and leaders in attacker groups even misaligned with followers by decreasing contributions the more their followers contributed on the previous contest round ($t_{82} = -3.120, P = 0.002$, Cohen's $d = -0.343$ (95% CI: $-0.563, -0.120$)). In short, in defender groups, leaders and followers mutually adjusted and aligned their behavioural contributions over contest rounds; in attacker groups, leaders and followers coordinated less well and there is little evidence for behavioural alignment across contest rounds.

The pattern of leader behaviour and leader–follower alignment during in-group defence is reminiscent of compensatory alignment, where leaders increase or keep their contribution to conflict even when follower contributions fell below that of the leader on earlier contest rounds. The patterns during out-group attack, in contrast, reflect a leader's free riding on followers, where leaders keep or even decrease their contributions to conflict when follower contributions on the previous rounds exceeded that of the leader. We further directly examined the differential patterns in defender leaders and attacker leaders. Indeed, defender leaders displayed more (sacrificial) compensatory contributions than attacker leaders ($F_{1,81} = 10.106, P = 0.002, \eta^2_p = 0.111$ (90% CI: 0.026, 0.222)) (Fig. 1e), whereas attacker leaders displayed more (extractive) free-riding behaviours than defender leaders ($F_{1,70} = 34.423, P = 1.342 \times 10^{-7}, \eta^2_p = 0.330$ (90% CI: 0.183, 0.451)) (Fig. 1f).

To understand what made a group more or less successful besides the obvious factor of group contribution, we performed stepwise regressions with contest success as the criterion and leader–follower behavioural alignment, leaders' compensatory contributions and free-riding behaviours, and leader or follower influence on round-level success from both defender and attacker, as predictors. The model explained 11.1% of the variance in defender survival rate ($F_{2,67} = 5.304, P = 0.007, \eta^2_p = 0.137$ (90% CI: 0.023, 0.250)). Defender survival depended on the degree to which leader contributions influenced the round-level success ($\beta = 0.345, t_{69} = 2.947, P = 0.004$) and on less free-riding behaviour in defender leaders ($\beta = -0.242, t_{69} = 2.069, P = 0.042$). Taken together, whether in-groups survive out-group attacks depends not only on the in-group and out-group fighting capacity but also on how leaders contribute and how much they influence group dynamics.

The differential contributions by leaders and followers in defender and attacker groups influenced not only contest success but also individual earnings. Whereas leaders earned less than followers in both defender and attacker groups ($F_{1,86} = 27.631, P = 1.055 \times 10^{-6}, \eta^2_p = 0.243$ (90% CI: 0.120, 0.359)), this effect was stronger in defenders ($F_{1,86} = 23.351, P = 5.836 \times 10^{-6}, \eta^2_p = 0.214$ (90% CI: 0.097, 0.329)) than in attackers ($F_{1,86} = 8.222, P = 0.005, \eta^2_p = 0.087$ (90% CI: 0.015, 0.190)); leader \times role interaction: $F_{1,86} = 4.239, P = 0.043, \eta^2_p = 0.047$ (90% CI: 0.001, 0.136)). Combined, these results suggest that followers use their leader as a focal point and that leaders display self-sacrificial tendencies especially in defender groups; they positively adapt to their follower contributions, they contribute more than their followers and while they disproportionately impact group survival probability, they earn less than their followers. Conversely, followers in attacker groups

use their leader less as a focal point, and leaders in attacker groups display opportunistic tendencies; across rounds, they misalign their contributions with those of their followers, have little impact on the likelihood of winning the conflict and earn comparatively more than leaders in the defender groups.

Neural results

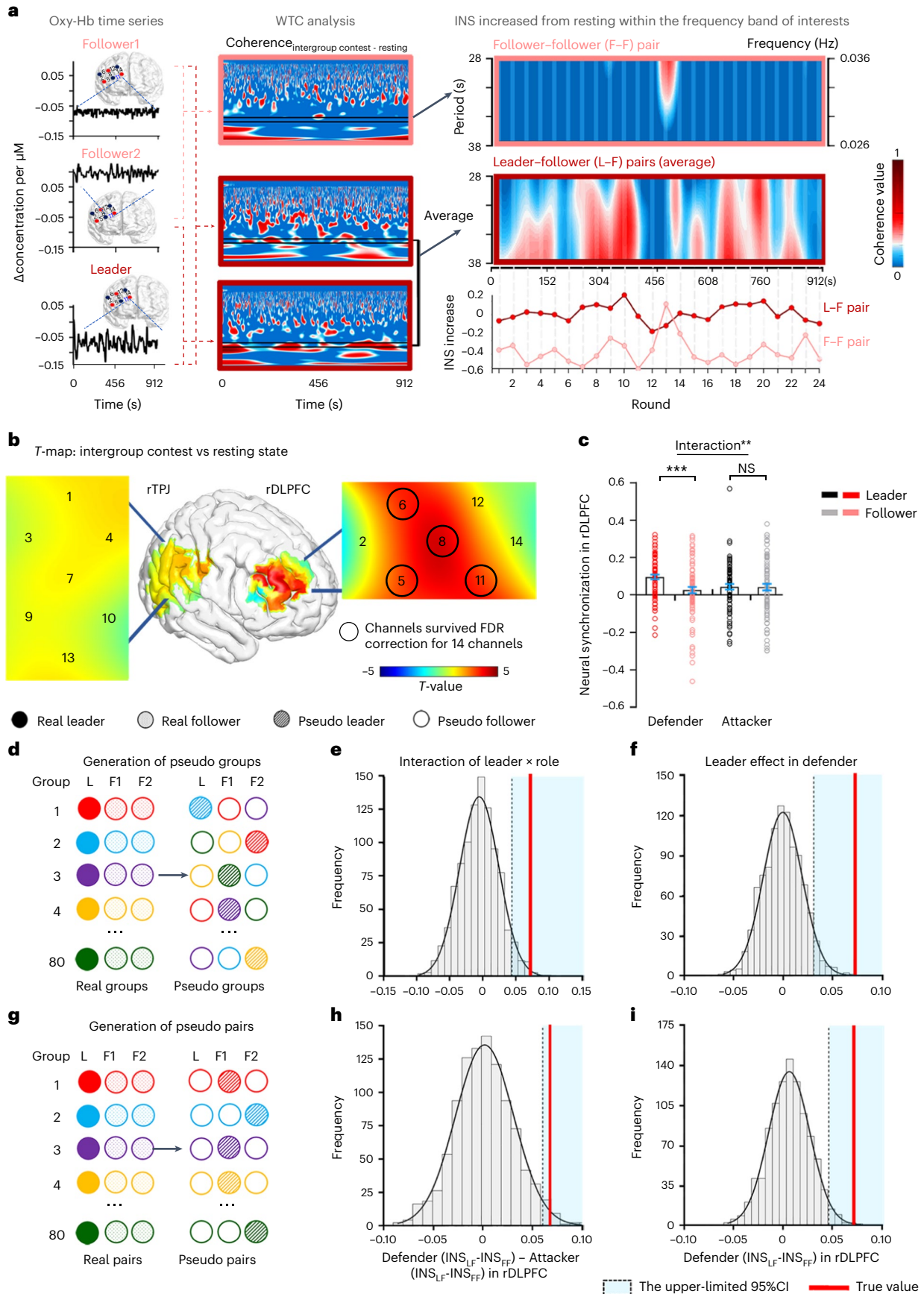
Neural activity in the rDLPFC and rTPJ of each group member was assessed with fNIRS during the 4 min resting state and continuously during the subsequent 24-round intergroup contest. We used the wavelet transform coherence (WTC) index to identify the cross-correlation between two fNIRS time series of concentration changes in oxygenated haemoglobin (oxy-Hb) in pairs as a function of frequency and time (Fig. 2a). The contrast between the interactive task and the resting state (as the baseline) has been used in previous studies to identify inter-brain neural synchronization (INS) related to interactive tasks^{32,47}. We were interested in the neural responses specific to group interaction, hence we first compared coherence values during the intergroup contest and the 4 min resting state to index task-specific INS. This comparison allowed us to identify channels of interest (that is, channels 5, 6, 8 and 11 in the rDLPFC; Fig. 2b and Supplementary Table 3), with stronger neural synchronization during the intergroup contest than during the resting state. The rTPJ channels revealed no meaningful results and are subsequently ignored (Supplementary Table 3). Further analyses on neural data were focused on the frequency band of interest (FOI) (Methods and Extended Data Fig. 1) of the survived channels. We analysed data with mixed-model analysis of variance (ANOVA) designs, with role denoting whether the individual was nested in the attacker or defender group, and leader denoting whether the individual was elected leader or follower, or whether the interpersonal pair included leader (that is, leader–follower vs follower–follower pairs). Within the rDLPFC channels of interest that showed stronger neural synchronization during intergroup conflict than during resting state (that is, intergroup contest-specific channels 5, 6, 8 and 11), we considered inter-individual synchronization in neural activity alongside intra-individual neural activity.

We created pairs for each defender and attacker group and analysed interpersonal neural synchronization in rDLPFC activity between leaders and followers (L–F pairs, with averaged coherence values for the two L–F pairs) and between followers (F–F pairs) for each group (Fig. 2a). The role \times leader ANOVAs on the task-specific INS (that is, coherence value increases between intergroup contest and resting state) revealed stronger interaction-specific INS in the rDLPFC in L–F pairs than in F–F pairs (channel 11: $F_{1,78} = 6.566, P = 0.012, \eta^2_p = 0.078$ (90% CI: 0.009, 0.183)). Moreover, the stronger leader–follower INS was modulated by group position (leader \times role: channels 6 and 11 survived false discovery rate (FDR) correction for channels of interest, as well as FDR correction for all 7 channels in the rDLPFC, Supplementary Table 4; channel 11: $F_{1,78} = 7.312, P = 0.008, \eta^2_p = 0.086$ (90% CI: 0.013, 0.193), Fig. 2c; channel 6: $F_{1,78} = 6.613, P = 0.012, \eta^2_p = 0.078$ (90% CI: 0.010, 0.184)). In channel 11, the stronger neural synchronization in L–F (than in F–F) pairs was present in defender groups ($F_{1,78} = 14.905,$

Fig. 2 | Interpersonal neural synchronization between leaders and followers during defence and attack. a, Illustration of the WTC computation to assess neural synchronization of L–F pairs and F–F pairs. b, We calculated the coherence values for the resting state and the intergroup contest. The contrast between the intergroup contest and the resting state identified channels of interest (that is, channels 5, 6, 8 and 11 in the rDLPFC). c, Stronger neural synchronization in L–F than in F–F pairs, especially in defender but not in attacker groups. $n = 80$ 3-vs-3-person intergroup contest sessions. Data are shown as mean \pm s.e.m. with overlaid dot plots. ** $P < 0.01$, *** $P < 0.001$. d–i, Validation of the leader–role interaction and leader effect in the defender group. We generated pseudo groups by randomly grouping a real leader and two real followers from different original groups to a pseudo group (d) or generated within-group pseudo pairs for each

group by randomly assigning one of the two followers as a pseudo leader (g). The leader–role interaction (that is, stronger L–F (vs F–F) neural synchronization in defender than in attacker groups) was stronger in real interacting groups than in pseudo groups (e, defender-vs-attacker leader-increased effect: $P = 0.005$) or within-group pseudo pairs (h, $P = 0.013$). Moreover, we verified stronger L–F INS (that is, increased neural synchronization in L–F pairs than in F–F pairs) in real defender groups than permutation distributions based on pseudo groups (f, leader-increased effect in defender group: $P < 0.001$) or within-group pseudo pairs (i, $P = 0.001$). The upper 5% areas of the permutation distribution are highlighted by transparent blue rectangles. Red vertical lines indicate the position of true values of the original groups.

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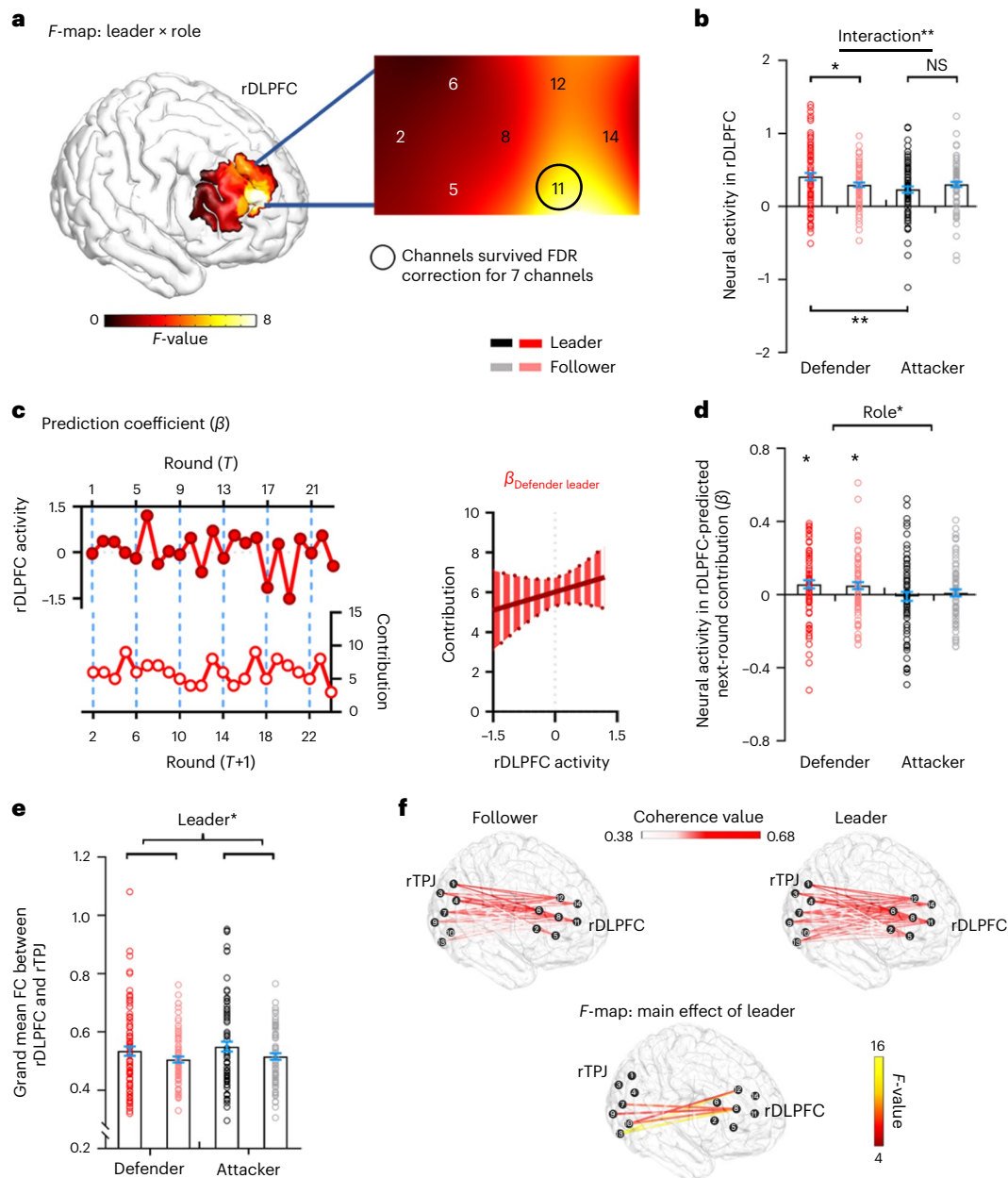


Fig. 3 | Intra-individual activity in the rDLPFC during intergroup conflict.

a, b, During contribution decisions, stronger rDLPFC activity in defender (vs attacker) groups was present in leaders but not in followers (**a** shows the leader-by-role interaction F -map for all the 7 channels in the rDLPFC and **b** illustrates the pattern at channel 11 in the rDLPFC). **c,** Illustration of the calculation of the prediction coefficient from rDLPFC activity at channel 11 (left, top graph) to round-by-round contributions (left, bottom graph). We built a linear regression of contribution on round T (with T ranging from 2 to 24) as a function of rDLPFC activity to outcome on the last round $T-1$ (that is, round 1 to 23) for each individual (right, for one example participant). **d,** Increased

rDLPFC activity was associated with increased contributions in defender groups (leader: $\beta = 0.056 \pm 0.022$; followers: $\beta = 0.049 \pm 0.019$) but not in attacker groups (leaders: $\beta = -0.010 \pm 0.025$; followers: $\beta = 0.010 \pm 0.019$). **e, f,** Leaders (vs followers) showed increased rDLPFC-rTPJ connectivity. Main effect of leader in the grand mean rDLPFC-rTPJ connectivity (**e**) (the averaged coherence value of 49 channel pairs among the 7 channels within rDLPFC and 7 channels within rTPJ) and channel-pairwise rDLPFC-rTPJ connectivity (**f**) (6 rDLPFC-rTPJ channel pairs survived FDR correction for 49 rDLPFC-rTPJ channel pairs). Data are shown as mean \pm s.e.m. with overlaid dot plots. $n = 80$ 3-vs-3-person intergroup contest sessions. * $P < 0.05$, ** $P < 0.01$.

$P = 2.318 \times 10^{-4}$, $\eta^2_p = 0.160$ (90% CI: 0.054, 0.279)) and absent in attacker groups ($F_{1,78} = 0.004$, $P = 0.950$, $\eta^2_p = 5.114 \times 10^{-5}$ (90% CI: 0, 1.375×10^{-4})). We replicated these effects when considering neural synchronization of the leader and a randomly selected follower, rather than across pair averages (leader \times role interaction, channel 11: $F_{1,78} = 9.230$, $P = 0.003$, $\eta^2_p = 0.106$ (90% CI: 0.022, 0.218); channel 6: $F_{1,78} = 9.219$, $P = 0.003$, $\eta^2_p = 0.106$ (90% CI: 0.022, 0.218), Extended Data Fig. 2).

Permutation tests revealed these effects to be present for actually interacting pairs rather than in pseudo groups (Fig. 2d–f, and

Extended Data Fig. 3 for each condition) or pseudo pairs (Fig. 2g–i, and Extended Data Fig. 4 for each condition). Specifically, the interaction effect of selectively enhanced leader–follower INS in defender (vs attacker) group and the stronger L–F INS (vs F–F INS) in the defender group were specific in real interacting pairs rather than in randomly grouped individuals within the same condition (that is, randomly grouping a group leader and two followers from different original, real groups under the same condition as a pseudo group, Fig. 2e, f) or randomly assigned leader and followers within the same group (that

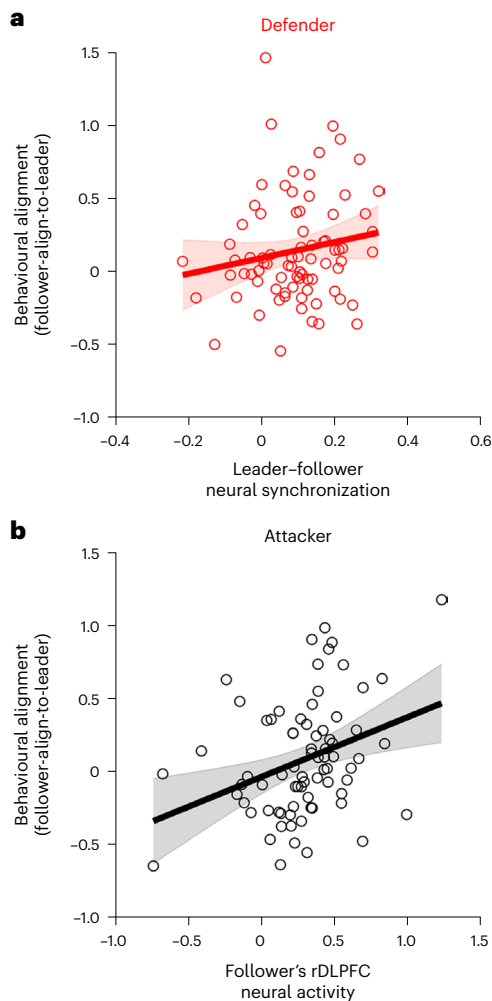


Fig. 4 | Prediction of behavioural alignment. **a**, In defender groups, stronger L-F neural synchronization predicted the extent to which followers aligned contributions to the leader's previous-round contribution. **b**, In attacker groups, the extent to which followers aligned contributions to their leader's previous-round contribution was predicted by stronger follower rDLPFC activity. The solid line represents the least-squares fit, and the shading represents the 95% CI of the linear fit.

is, randomly assigning the roles of group leader and followers for each original group, Fig. 2h,i).

We next examined intra-individual concentration changes in oxy-Hb for leaders and followers in defender and attacker groups (Methods). First, we found a significant role \times leader interaction on the intra-individual activity at channel 11 (Fig. 3a,b, $F_{1,78} = 7.883$, $P = 0.006$, $\eta^2_p = 0.092$ (90% CI: 0.015, 0.201)); channel 11 survived FDR correction for channels of interest, as well as FDR correction for all 7 channels in the rDLPFC, Supplementary Table 5), as leaders (vs follower) showed stronger rDLPFC activity, especially in defender groups ($F_{1,78} = 4.366$, $P = 0.040$, $\eta^2_p = 0.053$ (90% CI: 0.001, 0.150)) but not in attacker groups ($F_{1,78} = 1.933$, $P = 0.168$, $\eta^2_p = 0.024$ (90% CI: 0, 0.104)). This interaction also indicated that this defender-attacker difference in rDLPFC activity was present in leaders ($F_{1,78} = 8.397$, $P = 0.005$, $\eta^2_p = 0.097$ (90% CI: 0.018, 0.208)) but not in followers ($F_{1,78} = 0.025$, $P = 0.876$, $\eta^2_p = 3.156 \times 10^{-4}$ (90% CI: 0, 0.013)) (Fig. 3b). Second, the rDLPFC activity in channel 11 responding to the outcome of the last round was predictive of round-level contributions (Fig. 3c), especially in defender groups (main effect of role: $F_{1,72} = 6.405$, $P = 0.014$, $\eta^2_p = 0.082$ (90% CI: 0.009, 0.193), Fig. 3d). In defender groups, rDLPFC activity positively predicted next-round contributions for both leaders

($t_{77} = 2.546$, $P = 0.013$, Cohen's $d = 0.288$ (95% CI: 0.061, 0.514)) and followers ($t_{79} = 2.588$, $P = 0.011$, Cohen's $d = 0.289$ (95% CI: 0.062, 0.512), Fig. 3d) (Methods). In attacker groups, however, no such association between rDLPFC activity in channel 11 and contributions was apparent (leaders: $t_{75} = -0.392$, $P = 0.696$, Cohen's $d = -0.045$ (95% CI: -0.270, 0.180); followers: $t_{74} = 0.508$, $P = 0.613$, Cohen's $d = 0.059$ (95% CI: -0.168, 0.285), Fig. 3d).

We explored the functional connectivity between rDLPFC and rTPJ by performing coherence analyses between rDLPFC and rTPJ for leader and followers. The coherence values of the two followers were averaged to index follower functional connectivity. There was a significant main effect of leader, with leaders showing stronger rDLPFC-rTPJ functional connectivity than followers (grand mean rDLPFC-rTPJ connectivity: $F_{1,78} = 6.799$, $P = 0.011$, $\eta^2_p = 0.080$ (90% CI: 0.010, 0.186), Fig. 3e, and Fig. 3f for channel-pairwise rDLPFC-rTPJ connectivity, with 6 rDLPFC-rTPJ channel pairs surviving FDR correction for 49 rDLPFC-rTPJ channel pairs, Supplementary Table 6).

We concluded our analyses by analysing how leader and follower neural activity and synchronization at channel 11 in the rDLPFC in defender and attacker groups related to the degree to which leaders and followers aligned their behavioural contributions to in-group defence and out-group attacks, respectively. Interestingly, the degree to which leaders and followers aligned their contributions was associated with leader-follower rDLPFC neural synchronization (not their rDLPFC activity) in the defender groups, but was associated with rDLPFC activity in the attacker groups. Specifically, in defender groups, how much followers adjusted their contributions on the basis of their leader's previous contribution was predicted by stronger leader-follower neural synchronization in the rDLPFC activity ($r_{76} = 0.235$, $P = 0.038$, 95% CI: 0.013, 0.455, controlling for leader-track-follower, Fig. 4a) but not by follower's rDLPFC activity ($r_{76} = 0.192$, $P = 0.093$, 95% CI: -0.006, 0.382, controlling for leader-track-follower). Conversely, the degree to which leaders adapted to their follower's previous contribution was negatively associated with leader-follower rDLPFC synchronization ($r_{76} = -0.224$, $P = 0.048$, 95% CI: -0.458, -0.014, controlling for follower-track-leader) but not with leaders' rDLPFC activity ($r_{76} = -0.148$, $P = 0.195$, 95% CI: -0.339, 0.058, after controlling for follower-track-leader). In attacker groups, we observed less leader-follower synchronization, and no relations between leader-follower neural synchronization and how much followers adapted to their leaders ($r_{72} = 0.135$, $P = 0.250$, 95% CI: -0.072, 0.370, controlling for leader-track-follower), and how much leaders adapted to their followers ($r_{72} = -0.031$, $P = 0.795$, 95% CI: -0.301, 0.209, controlling for follower-track-leader). Interestingly, in attacker groups, followers' rDLPFC activity positively predicted to what extent they adapted their contribution to their leaders' contribution in the previous round ($r_{72} = 0.293$, $P = 0.011$, 95% CI: 0.068, 0.504, controlling for leader-track-follower, Fig. 4b), but leaders' rDLPFC activity was not associated with their adaptation of follower contribution ($r_{72} = -0.066$, $P = 0.578$, 95% CI: -0.285, 0.165, controlling for follower-track-leader).

Discussion and Conclusions

'The exigencies of war with outsiders are what makes peace inside'²⁶. The relationship between intergroup conflict and intragroup cohesion has long been discussed, proposing out-group threat as a prominent factor facilitating within-group coordination and cohesion⁴⁸⁻⁵⁰ and reinforcing social hierarchy^{6,31}. Here we show how group members coordinate their fighting capacity and neural activity to fight against outside rivals and resolve the conflict in their favour, and provide the neural mechanisms involved. Moreover, we dissociate the functional roles that leader (vs follower) and leader-follower (vs follower-follower) coordination played in the intergroup conflict, which are further modulated by the aim of the group. Defending the in-group (rather than launching out-group attacks) increased leaders' DLPFC activity and personally costly contributions to the in-group's ability to compete against the out-group, and enhanced leader-follower

(but not follower–follower) behavioural coordination and neural synchronization in the DLPFC.

Our results combined contribute to a neurobehavioral account of leader–follower coordination during intergroup conflict, and how leader initiatives and coordination with followers at both the behavioural and neural levels relate to successfully settling conflict in one's favour. As predicted, we find that groups with leaders successfully regulate intergroup conflict to the extent that both leader and followers align their contributions to conflict. Advancing beyond earlier work on leadership in intergroup conflict, and fitting work on within-group cohesion and coordination under collective threat^{20,24,33}, we observed stronger behavioural and neural alignment between leader and followers when groups defended against out-group threat, than when groups launched attacks on rival groups. During in-group defence in particular, we observed both leader and follower contributing behaviour to be associated with enhanced activity in the dorsolateral prefrontal cortex, a brain region linked to cost–benefit analyses^{51,52}, impulse inhibition^{24,53,54} and cognitive control, especially under threat^{55–57}. Leader initiatives were associated with increased prefrontal activation and the extent to which followers aligned with leader initiatives was linked to (1) followers' prefrontal activity and (2) the degree to which followers and leaders were synchronized in their prefrontal activity.

During in-group defence, leaders appear sacrificial, concerned with their group and disproportionately influenced defender survival from rival attack. In contrast, during out-group attack, leaders appear opportunistic and more extractive in their behaviour and concerned with themselves: they only contributed slightly more than their followers and, critically, contributed less the more their followers invested in conflict. Leader behaviour during out-group attack was also unrelated to prefrontal activity. Moreover, succeeding in intergroup conflict not only requires displays of and signalling sacrificial, group-serving behaviours in leaders but is also crucially determined by how leader initiatives are recognized and adapted by followers. Indeed, leaders and followers were strongly aligned at both the behavioural and neural levels during in-group defence, and coordination was far less during out-group attacks. In attacker groups, we observed no meaningful interpersonal synchronization in the prefrontal cortex between leaders and their followers. Partly because of these differences in leader behaviour and leader–follower coordination, groups disproportionately often survived out-group attacks, and out-group attacks regularly failed.

Before concluding, a few cautionary remarks are in order. First, leaders in our experimental groups were elected following a short online group discussion, but we have no insight into why some individuals and not others were elected as leader. There were no differences in key personality characteristics between elected leaders in defender and attacker groups, or between elected leaders and their followers. Therefore, we conjecture that the key differences between leaders in defender compared to attacker groups at both the behavioural and neural level are grounded in the very position during intergroup conflict and the stronger within-group interdependence present during in-group defence compared with out-group attack. Future research is needed to identify what makes a leader and a follower in intergroup conflict. Second, leaders in our experiments were strictly symbolic and could not sanction follower behaviour or communicate with them other than through signalling their own investments in the intergroup conflict contest. We need to be careful in generalizing conclusions to settings in which leaders have greater discretion, can communicate and consult with their group, or can be held accountable for their actions. Future research is needed to identify how different power bases for leadership⁵⁸ affect leader–follower coordination and the escalation of intergroup conflict. Finally, at the neural level, we observed an important role for neural synchronization between leader and follower (relative to that between followers) in the dorsolateral prefrontal cortex, especially during in-group defence but not during out-group attack. Protecting against outside threat is often taken as

a fast and intuitive response. The currently observed involvement of the dorsolateral prefrontal cortex suggests that organizing for in-group defence also involves cognitive control and cost–benefit computations. Future research could examine to which degree such cognitive control is functional for in-group defence and leader–follower coordination in particular.

Caveats and open questions notwithstanding, current findings show how leader–follower interactions make groups more or less successful competitors in intergroup conflict, and that the specific form and shape of such leader–follower interactions change at both the behavioural and neural level when groups defend against rather than attack out-groups. Whereas out-group attacks are difficult to organize and have leaders emerging as opportunistic and detached from their followers, in-group defence is characterized by group members coordinating well, aligning with their self-sacrificial leaders at both the behavioural and neural levels, and often disproportionately preventing defeat and surviving out-group hostility. We suggest that group structures not only shape leaders but also follower–leader coordination, and that both leader and leader–follower coordination in turn shape group success.

Methods

Participants and ethics

We recruited 558 healthy individuals as paid volunteers (252 males; age 18–30 yr, mean \pm s.e.m. = 22.070 \pm 0.111 yr) organized into 93 intergroup contest sessions. Five intergroup contest sessions that failed in the leader election section (3 sessions in which one or more participants failed the leadership manipulation check and/or were unable to correctly recall who was the elected leader) or did not complete the task (2 sessions) were excluded, leaving a total of 528 participants (240 males; 22.074 \pm 0.114 yr, Supplementary Table 1a) in 88 intergroup contest sessions for behavioural data analysis. Another 8 intergroup contest sessions were excluded because of technical failure with fNIRS measurements, leaving 480 participants (216 males; 21.998 \pm 0.134 yr, Supplementary Table 1a) in 80 intergroup contest sessions for neural data analysis.

All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. Those who majored in psychology or economics were excluded from participation. The experiment involved no deception. Participants were paid US\$12–16 compensation (a US\$10 show-up fee plus average earnings in two randomly selected contest rounds). The experimental protocols adhered to the standards set by the Declaration of Helsinki and were approved by a local research ethics committee at the State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, China (Protocol IORG0004944). All participants provided written informed consent to participate after the experimental procedures had been fully explained and acknowledged their right to withdraw at any time during the study.

Experimental procedures and tasks

Six same sex strangers were invited to the laboratory at the same time and randomly assigned to the 3-person attacker or 3-person defender group. Participants first played non-leader intergroup contests to get familiar with the game (the data for which were published in our previous work³³). Each 3-person group then completed a leader election section. Afterwards, participants performed the leader version of the intergroup contest game.

Leader election. After the non-leader intergroup contest, participants within each 3-person group were given 4 min to chat online with each other to determine the group leader for the next block of intergroup contests. The three participants were identified by different shapes and chatted via texting. Any group member could self-nominate or nominate other members to be the group leader. At the end of the

election section, participants informed the experimenter of the leader's shape for their group. While leaders in our experiment endogenously emerged during the leader election chat, we cannot exclude that some traits contributed to (or prohibited) leader emergence. To account for these possibilities, we measured traits related to social decision-making, justice and social hierarchy to statistically test post hoc whether (1) leaders and followers differed in any traits and (2) leaders/followers in the defender and attacker groups differed in any traits. Leaders and followers in defender and attacker groups did not differ in sex, age, education, social value orientation, pro-social personality, justice sensitivity, preference for social hierarchy, cultural orientation or life satisfaction (Supplementary Table 1).

Leader election validation. Ninety sessions correctly recognized and remembered their group leaders (in 3 sessions, one or more participants failed to correctly recall the elected leader). At the end of the experiment, participants reported their willingness to be the group leader (0, 5 and 10 for not willing at all, moderately willing and extremely willing, respectively). The analysis of these ratings revealed that the group leader was more willing to be the group leader in both defender and attacker groups (main effect of leader: $F_{1,83} = 67.276$, $P = 2.573 \times 10^{-12}$, $\eta^2_p = 0.448$ (90% CI: 0.314, 0.547); leader \times role interaction: $F_{1,83} = 0.204$, $P = 0.653$, $\eta^2_p = 0.002$ (90% CI: 0, 0.047)). Moreover, followers also reported that (1) they strongly approved and identified with their group leader (7.230 ± 0.144 on a scale of 0 (not approve at all) to 5 (moderately approve) to 10 (extremely approve)); (2) they perceived their group leader as more influential than themselves on the other fellows ($F_{1,86} = 9.211$, $P = 0.003$, $\eta^2_p = 0.097$ (90% CI: 0.020, 0.202)); and (3) the group leader performed better during the intergroup contest than they themselves ($F_{1,86} = 4.928$, $P = 0.029$, $\eta^2_p = 0.054$ (90% CI: 0.003, 0.146)) and the other follower ($F_{1,86} = 14.199$, $P = 3.006 \times 10^{-4}$, $\eta^2_p = 0.142$ (90% CI: 0.045, 0.254)).

The leader version of the intergroup contest game (leader-ICG).

The intergroup contest game is a dynamic, fully incentivized contest game with real-time feedback between a 3-person attacker group and a 3-person defender group, similar to our previous studies^{8,33}. The key difference between the non-leader ICG and the leader-ICG is the presentation of feedback. Specifically, the contributions made by group members in the non-leader ICG practice were indicated with black shape labels, whereas those in the leader-ICG were labelled with a red shape for the leader and black shapes for the followers.

In each leader-ICG round (Fig. 1b), participants decided the contribution they would make to the group pool within 12 s. If no decision was made within 12 s (0.216% of the leader-ICG rounds across all sessions), a random contribution would be generated by the computer. Participants then saw an 8 s waiting screen (jittered between 6–10 s), followed by a 10 s outcome screen presenting feedback. The feedback included: (1) the contribution of each in-group member; (2) the group-level contribution of own and rival groups (C_A and C_D); and (3) the pay-off of the current contest round. The outcome screen was followed by an 8 s interround interval (6–10 s). Each round lasted for 38 s (ref. 33).

fNIRS data acquisition

Two identical LABNIRS optical topography systems (52-channel high-speed LABNIRS, Shimadzu) were used to simultaneously collect neural data from each 6-person leader-ICG session, with 3 participants sharing the same role recorded by the same system. fNIRS signals were acquired at a sampling rate of 47.62 Hz and later downsampled to 9.52 Hz to decrease temporal autocorrelation^{33,59}. For each participant, we used two identical 3×2 optode probe sets, with each probe set measuring 7 channels (with 3 light emitters and 3 detectors, inter-optode distance of 30 mm). The probe sets were separately placed on the rTPJ and rDLPFC according to the positions of P6 and F4 in the international

10–10 system for electroencephalogram electrode placement⁶⁰ and the T1-weighted anatomical images³³.

The current study measured the relative changes in absorbed near-infrared light at wavelengths of 780 nm, 805 nm and 830 nm. These changes were transformed into the relative concentration changes of oxy-Hb, deoxygenated haemoglobin (deoxy-Hb) and total haemoglobin using a modified Beer–Lambert law⁶¹, allowing measurement of brain activity⁶². We focused on the concentration changes of oxy-Hb because it has been shown to be the most sensitive indicator of regional cerebral blood flow in fNIRS measures⁶³. Increases in oxy-Hb have been recognized as the consequence of brain activity and corresponding to the blood oxygenation level-dependent signal measured by fMRI^{64–66}.

Behavioural data analysis

We first averaged the two followers' behaviours and then performed ANOVAs with leader (leader vs follower) and role (attacker vs defender) as within-session factors and session-sex (male vs female session) as a between-session factor on: (1) contributions averaged across 24 rounds; (2) payment averaged across 24 rounds; (3) the influence of individual contribution on group success (that is, the regression parameter (β) of the logistic regression of group success (win = 1, lose = 0) as a function of leader's (or follower's) contributions across the 24 rounds); (4) within-group tracking parameter (that is, the behavioural alignment (Fisher's z -transformed α)). The leader-align-to-follower (follower-align-to-leader) behavioural alignment (α) was the regression parameter of linear regressions of leader's (follower's) contributions in a current round j as a function of follower's (leader's) contributions in the previous round ($j - 1$).

We further calculated two behavioural alignment patterns in leaders⁶⁷: (5) compensatory contribution pattern (that is, the proportion of rounds in which leaders increased or kept the same contributions when he contributed more than followers in the last round (equation 1)) and (6) free-riding behaviours (that is, the proportion of rounds in which leaders decreased or kept the same contributions when he contributed less than followers in the last round (equation 2)).

$$P_{\text{compensatory}} = P(\text{leader}_{r+1} - \text{leader}_r \geq 0 | \text{leader}_r - \text{follower}_r > 0) \quad (1)$$

$$P_{\text{free-ride}} = P(\text{leader}_{r+1} - \text{leader}_r \leq 0 | \text{leader}_r - \text{follower}_r < 0) \quad (2)$$

$P_{\text{compensatory}}$ and $P_{\text{free-ride}}$ indicate the proportion of rounds showing compensatory contribution pattern and free-riding contribution pattern; r indicates round, $r \in (1:23)$; leader_r and follower_r indicate the contributions made by the leader and his followers in the r th round.

fNIRS data analysis

The current study focused on INS between leader and follower or between followers (that is, interpersonal brain activities that co-vary along the time course), intra-individual neural activity and rDLPFC–rTPJ function connectivity. Pre-processing on the oxy-Hb data was conducted to remove systemic noise using MATLAB-based functions derived from the NIRS-SPM toolbox⁶⁸. Discrete cosine transforms with a cut-off period of 128 s and pre-colouring based on haemodynamic response function were applied to the oxy-Hb data to remove longitudinal signal drift, motion artefacts, and respiration and cardiac oscillations from the signal^{33,60}.

Identification of frequency bands and channels of interest. First, similar to a previous study³³, we identified an FOI according to the timeline of each intergroup contest round (that is, 0.0263 Hz to 0.0357 Hz, corresponding to the period between 28 s and 38 s, 38 s for one round and 28 s for one round without jitter). This frequency band also excluded high-frequency noise, including that related to respiration (around 0.2 to 0.3 Hz) and cardiac pulsation (around 1 Hz),

all of which may lead to artificial coherence. To validate that this FOI was indeed associated with the intergroup contest, we averaged coherence values across all 14 channels, and the averaged coherence value during the resting state was subtracted from that of the intergroup contest task. We then performed one sample *t*-tests on the coherence value difference for each of the 121 frequency bands (frequency range: 0.004–4.547 Hz). The frequency band from 0.0282 Hz to 0.0335 Hz (corresponding to the period between 29.82 s and 35.47 s) showed significantly increased coherence value for the intergroup contest (vs resting state, $P < 0.05$, FDR corrected for 121 frequency bands, Extended Data Fig. 1) and was overlapping with the chosen FOI. Moreover, the coherence value within the timeline-identified FOI also showed significant increase during the intergroup contest than during the resting state ($t_{79} = 2.963$, $P = 0.004$, Cohen's $d = 0.331$ (95% CI: 0.105, 0.555)).

Second, we identified channels of interest that showed stronger INS during the intergroup contest than during the resting state. Similar to previous studies⁶⁹, we averaged coherence values across the FOI identified in the first step and compared values between the intergroup contest and the resting state for each channel. We showed that the averaged INS was significantly higher during the intergroup contest than during the resting state in channels 5, 6, 8 and 11 in the rDLPFC (Fig. 2b, $P < 0.05$, corrected FDR for 14 channels, Supplementary Table 3 for full statistical reports). Taken together, further analyses of the increased INS of the above-identified frequency bands and channels of interest were conducted to reveal the effect of leader (L–F vs F–F pairs) and/or role on INS.

INS. Similar to our previous study³³, we employed WTC analysis (Wavelet Toolbox based on MATLAB R2019b) to assess the cross-correlation between two pre-processed oxy-Hb time series of pairs of participants as a function of frequency and time. We applied WTC analysis to each pair of 3 oxy-Hb time series and generated 3 time–frequency two-dimensional matrices of the coherence values for each 3-person group (leader and follower 1, leader and follower 2, followers 1 and 2, Fig. 2a). The coherence value for followers 1 and 2 indicated the INS for the F–F pair. We averaged 2 coherence values from leader–follower pairs as the INS for the L–F pair.

Similar to previous studies^{32,47}, INS during the resting state was used as a baseline and the coherence value increases during the intergroup contest (vs resting state) were used to index task-specific INS (Fig. 2a). The Fisher's *z*-transformed coherence value increases (intergroup contest minus resting state) were averaged across the FOI in each channel of interest. We then submitted the round-aggregated INS increase to leader (L–F vs F–F pairs) \times role (attacker vs defender) \times session-sex (male vs female) mixed-model ANOVAs, with significant effects threshold at $P < 0.05$ (Supplementary Table 4 for full statistical reports).

Individual brain activity. The pre-processed oxy-Hb time series of channels in the rDLPFC were segmented into three phases for each contest round: a decision-making phase (12 s), a waiting phase (6–10 s, 8 s on average) and an outcome phase (10 s). There was no event or trial that can be used to model activation during the resting state. Similar to previous work³³, we used the waiting phase as the baseline. The decision-making phase (outcome-processing phase) related activation was compared with the waiting phase (using a *z*-score transformation of the mean value and standard deviation of the waiting phase) and considered as oxy-Hb increases for decision-making (outcome-processing). First, individual brain activity was averaged across all intergroup contest rounds and submitted as the round-aggregated activity (Supplementary Table 5 for full statistical reports). Second, we built a linear regression of contributions of leader or followers on round *T* (with *T* ranging from 2 to 24) as a function of the leader's or followers' rDLPFC activity at channel 11 of the outcome phase on the last round *T* – 1 (round 1 to 23; with the standardized coefficient of the

regression θ indicating the prediction strength) for each 3-person group. The Fisher's *z*-transformed θ across conditions was compared against 0 to examine whether rDLPFC activity could predict a leader's or follower's contribution decisions. Similar to previous work³³, we performed coherence analyses (Wavelet Toolbox based on MATLAB R2022a) between rTPJ and rDLPFC to index functional connectivity (FC) of rDLPFC–rTPJ. We then analysed the rDLPFC–rTPJ FC at the channel-pairwise level (each of the seven channels in the rDLPFC with each of the seven channels in the rTPJ, that is, 49 channel pairs, Supplementary Table 6 for full statistical reports) and at the grand mean level (that is, averaged coherence value of 49 channel pairs). The two followers' neural indices were averaged³². The round-aggregated intra-individual activity, Fisher's *z*-transformed θ and FC were respectively subjected to leader \times role \times session-sex ANOVAs.

Validation analysis of neural synchronization. To validate that the effects on INS we observed were specific in real interacting pairs, we generated pseudo groups or pairs and compared INS between real interacting groups and pseudo groups. In the first set of analysis, we kept the hierarchy of each participant (leader or follower) and generated pseudo groups by randomly grouping a real leader and two real followers from different original groups as a pseudo group. In the second analysis, we kept each original group and generated within-group pseudo pairs for each group by randomly assigning one of the two followers as a pseudo leader. We then calculated INS of pseudo pairs using the same method as we did for real pairs. We repeated the generation of pseudo groups and recalculation of INS for 1,000 times. To test whether the INS and the role \times leader interaction on INS were specific to real interacting groups, we conducted non-parametric permutation tests^{70,71} to verify the null hypothesis of no difference between real and pseudo groups. Specifically, we tested (1) the INS of real groups against the permutation samples for each condition (that is, leader–follower INS in attacker or defender groups, follower–follower INS in attacker or defender groups) and the observed (2) main effect of leader and (3) role \times leader interaction on INS of real groups against that of the 1,000 permutation samples.

Additional analyses and results

Participants were either exposed or not exposed to a brief social bonding manipulation before the first 24-round block of the non-leader intergroup contest. We examined whether this bonding manipulation could have affected behaviour and neural responses in the second session by including bonding (in-group bonding vs no-bonding control) as a between-sessions factor in all the above models for behavioural and neural indices. We found that (1) all reported effects remained reliable after controlling for in-group bonding (Supplementary Tables 7a and 8a) and (2) in-group bonding did not interact with leadership or role in the current study (Supplementary Tables 7b and 8b). That in-group bonding had no effects on the behavioural and neural data may be because all groups went through the leader election group chat before the second 24-round block. Such chat might have already provided the chance for further social bonding among group members and have equalized the difference between the exposed and non-exposed groups.

To present the measured brain activity from different perspectives, the results based on deoxy-Hb signals were also analysed. We conducted the same analysis on the deoxy-Hb signals. For the index of INS, we did not find similar leader \times role interaction with deoxy-Hb signals. In addition, we found similar effects on intra-individual neural activity and functional connectivity for the analysis based on oxy-Hb and deoxy-Hb signals, but at different channels (channel pairs). Specifically, we found a similar leader \times role interaction effect on rDLPFC based on oxy-Hb signals (channel 11) and that based on deoxy-Hb signals (channel 2, leader \times role interaction: $F_{1,78} = 8.831$, $P = 0.004$, $\eta^2_p = 0.102$ (90% CI: 0.020, 0.213), but not at channel 11: $F_{1,78} = 0.044$, $P = 0.835$, $\eta^2_p = 0.001$

(90% CI: 0, 0.023)). The leader effect on the rDLPFC–rTPJ functional activity based on oxy-Hb was similarly observed in the deoxy-Hb analysis, but it was found between channel 13 in the rTPJ and channel 8 in the rDLPFC ($F_{1,78} = 9.591, P = 0.003, \eta^2_p = 0.109$ (90% CI: 0.024, 0.222)) and could not survive FDR correction for 49 channel pairs. The difference observed in INS and activity based on oxy-Hb and deoxy-Hb signals may be caused by different sensitivities of oxy-Hb and deoxy-Hb signals in reflecting task-induced changes in neural signals.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All behavioural data and materials have been made publicly available via the Open Science Framework and can be accessed at <https://osf.io/7grfu/>. The neural data supporting the main findings of this study are available from the corresponding author upon request.

Code availability

The custom routines for the main data analysis written in MATLAB are available in the Open Science Framework at <https://osf.io/7grfu/>.

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Author contributions

Y.M. and C.K.W.D.D. conceived the project and designed the experiment; H.Z., J.Y. and J.N. implemented the experiment and collected data; H.Z. and J.Y. analysed the data under the supervision of Y.M.; Y.M. and C.K.W.D.D. interpreted the results; Y.M. wrote the original and final version of the manuscript; J.Y. and C.K.W.D.D. provided critical revisions. All authors approved the final version of the manuscript for submission.

Competing interests

The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to Yina Ma.

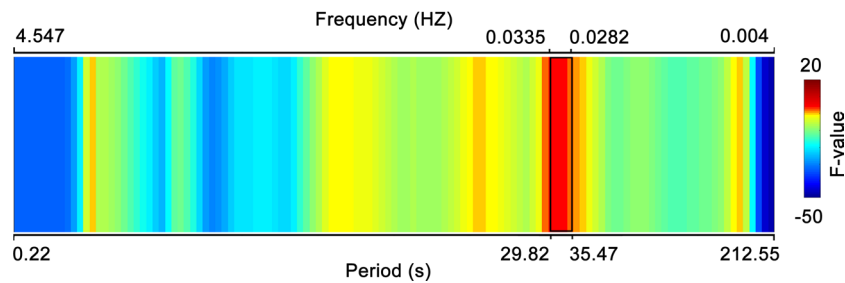
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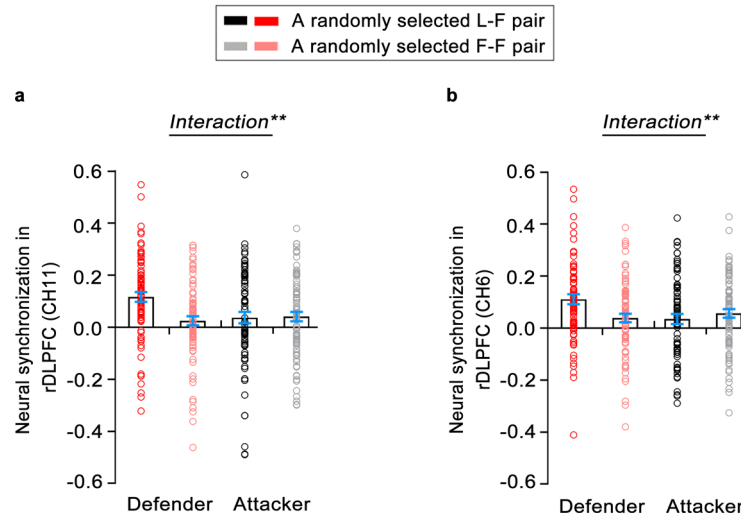
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T-map: intergroup contest vs. resting state

Extended Data Fig. 1 | Verify frequency band with increased neural synchronization to intergroup contest than resting-state. To validate that the timeline-based frequency band of interest, we averaged coherence values across all 14 channels and the averaged coherence value during the resting-state was subtracted from that of inter-group contest task. We performed one sample t-tests on the coherence value difference for each of the 121 frequency bands (frequency range: 0.004 to 4.547 Hz). Frequency band from 0.0282 Hz to 0.0335 Hz (corresponding to the period between 29.82s and 35.47s) showed

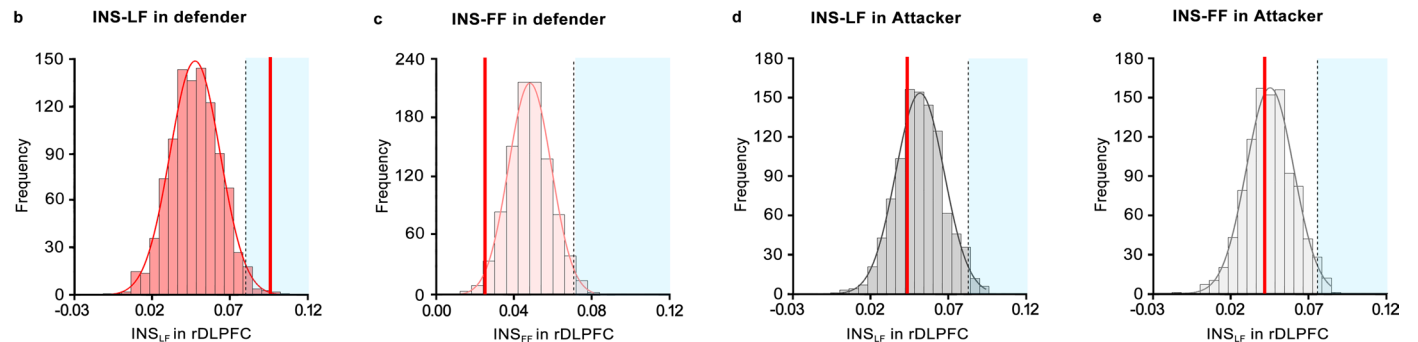
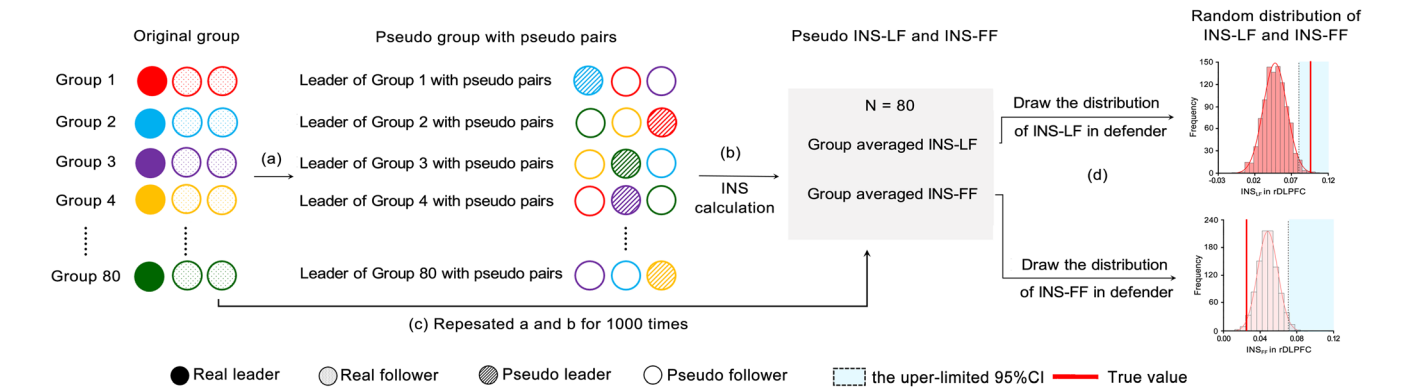
significantly increased coherence value of inter-group contest (*vs.* resting state, $p < 0.05$, corrected by False discovery rate (FDR) for 121 frequency bands), which was overlapping with the timeline-based frequency band of interest (that is, frequency band from 0.0263 Hz to 0.0357 Hz). Moreover, the coherence value within the timeline-identified frequency band of interest also showed significant increase during inter-group contest than the resting-state (Mean \pm SE = 0.011 ± 0.004 , $t_{79} = 2.963$, $p = 0.004$, Cohen's $d = 0.331$).



Extended Data Fig. 2 | Neural synchronization between the group leader and a randomly selected follower. There were significant leader-by-role interaction when considering neural synchronization of the leader and a randomly selected follower, rather than the across pair averages (a: channel 11, $F_{1,78} = 9.230$,

$p = 0.003$, $\eta^2 p = 0.106$; b: channel 6, $F_{1,78} = 9.219$, $p = 0.003$, $\eta^2 p = 0.106$). Data are shown as the mean \pm s.e. with overlaid dot plots. $n = 80$ three-versus-three-person intergroup contest sessions. ** $p < 0.01$.

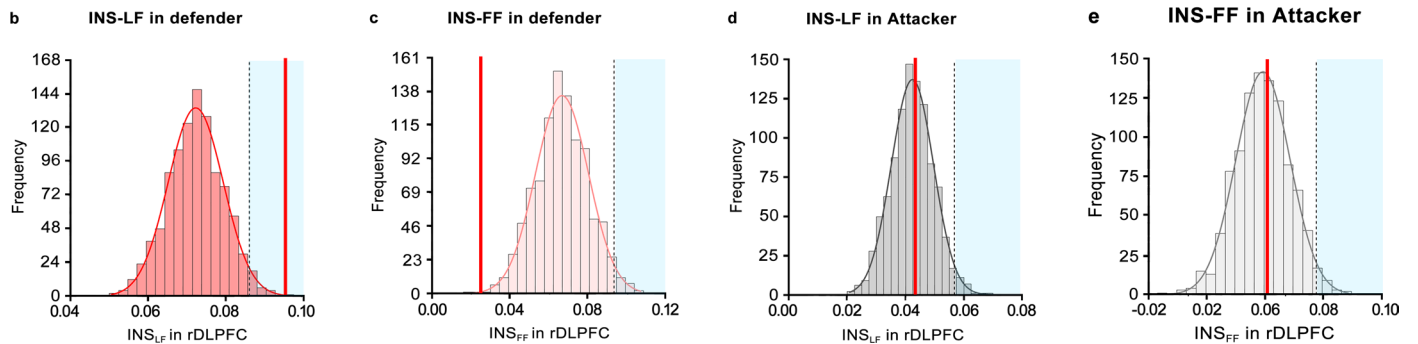
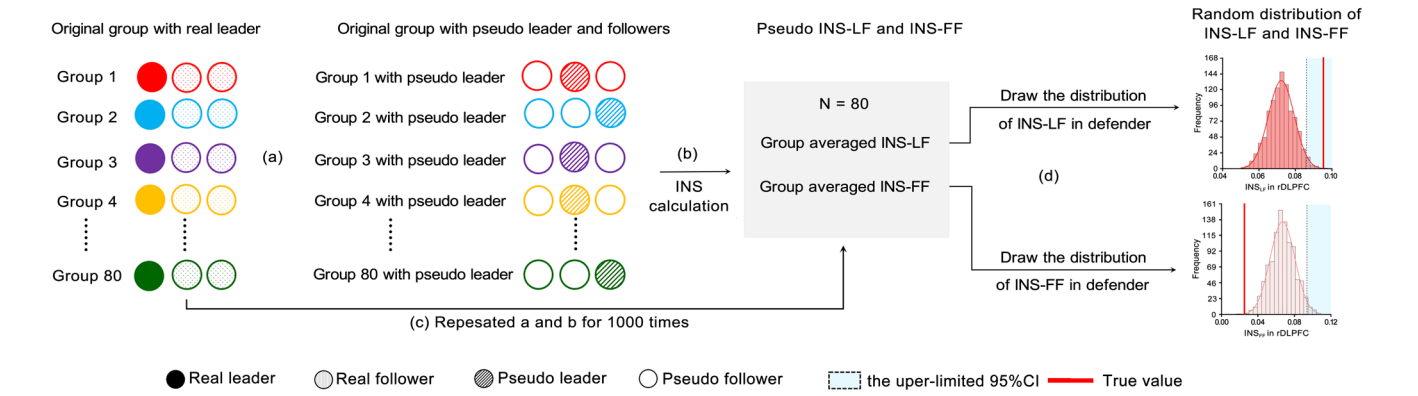
a Between-group permutation



Extended Data Fig. 3 | Validation of neural synchronization. (a) We generated pseudo groups by randomly grouping a real leader and two real followers from different original groups to a pseudo group. We then re-calculated neural synchronization of pseudo groups using the same method as we did for the real pairs. We repeated the generation of pseudo groups and recalculation of neural

synchronization for 1000 times. We verified stronger neural synchronization in real interacting leader-follower pairs of defender groups than pseudo groups (b, $p = 0.003$), but not for follower-follower pairs of defender groups (c, $p = 0.981$), nor leader-follower (d, $p = 0.711$), follower-follower (e, $p = 0.590$) pairs of attacker groups.

a Within-group permutation



Extended Data Fig. 4 | Validation of neural synchronization. (a) We kept each original group and generated within-group pseudo pairs for each group by randomly assigning one of the two followers as a pseudo leader. We then re-calculated neural synchronization of pseudo pairs using the same method as we did for the real pairs. We repeated the generation of pseudo pairs and

recalculation of neural synchronization for 1000 times. We verified stronger neural synchronization in real interacting leader-follower pairs of defender groups than pseudo groups (b, $p = 0.001$), but not for follower-follower pairs of defender groups (c, $p = 0.999$), nor leader-follower (d, $p = 0.450$), follower-follower (e, $p = 0.420$) pairs of attacker groups.

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Reporting on sex and gender	Six strangers of the same sex were invited to participate in one contest session at the same time and were randomly assigned to either the attacker or defender group. All participants provided written informed consent to participate after the experimental procedures had been fully explained and acknowledged their right to withdraw at any time during the study. Our study did not consider session-sex as a variable of interest, nor did we examine its main effect. However, to determine if session-sex influenced our primary findings, we conducted ANOVA analyses with gender as a between-session factor for both behavioral and neural indices. The results showed no modulation of session-sex, indicating that our findings are applicable to both male and female participants.
Population characteristics	558 healthy individuals (252 males, age 18-30 years, Mean \pm SE = 22.070 \pm 0.111 years) were invited as paid volunteers and organized in 93 6-person inter-group contest sessions. Five inter-group contest sessions who failed in the leader election section or did not complete the task were excluded, leaving a total of 528 participants (240 males, Mean \pm SE = 22.074 \pm 0.114 years) in 88 sessions for behavioral data analysis. Another 8 inter-group contest sessions were excluded because of technical failure with fNIRS measurements, leaving 480 participants (216 males, Mean \pm SE = 21.998 \pm 0.134 years) in 80 inter-group contest sessions for neural data analysis. The leaders and followers in defender and attacker group did not differ in gender, age, education, social value orientation, pro-social personality, justice sensitivity, preference for social hierarchy, cultural orientation or life satisfaction.
Recruitment	Healthy individuals were recruited in this study as paid volunteers through on campus flyer recruitment. No self-selection biases was involved in the participant recruitment.
Ethics oversight	The experimental protocols adhered to the standards set by the Declaration of Helsinki and was approved by a local Research Ethics Committee at the State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University Beijing, China (protocol number: IORG0004944).

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Sample size	Data from 528 participants organized in 88 6-person sessions was analyzed for the behavioral measurements. Neural signals from 480 participants organized in 80 6-person sessions were analyzed for the neural indices. The sample size was determined a priori using G*Power 3.1 to estimate the number of six-person sessions needed to detect significant effects with 80% statistical power. We originally considered conducting power analysis based on both behavioral and neural effects. However, most fNIRS studies have considered dyad-level interactions, and only a few have examined neural synchronization in single groups with group sizes $n \geq 3$, and we are unaware of fNIRS studies examining intergroup (economic) interaction. We thus calculated a priori sample size estimates on the basis of earlier behavioral studies using the intergroup contest that we also used here. This sample size was predetermined in our previous study (detailed in Yang et al., 2020, reference 33). Considering our study with a relatively large sample which is similar to or larger than the sample sizes of most hyper-scanning fNIRS studies, we think that our sample size is sufficient to investigate the effects we plan to examine and to draw robust conclusions.
Data exclusions	Five inter-group contest sessions who failed in the leader election section or did not complete the task were excluded from both behavioral and neural analyses. Another 8 inter-group contest sessions were excluded for neural sample because of technical failure with fNIRS measurements.
Replication	The experiment was performed once, and no replication experiments were conducted. The manuscript contains all information necessary to conduct replication experiment. The main analyses were performed on the populational level, in which case the variation in subject responses was incorporated into statistical testing. The variability in behavioral and neural responses is shown through the plotting of individual data or data range in all the figures. We conducted two permutation tests to confirm the findings in the current study to be present for actually interacting pairs rather than in pseudo groups (Fig. 2d-f, Extended Data Fig.3 for each condition) or pseudo pairs (Fig. 2g-i, Extended Data Fig.4 for each condition). The main effect of group role on behavioral measures (higher contribution and higher decision coordination for defender than attacker) replicated previous findings.
Randomization	Participants were recruited randomly, and randomly assigned with the role of attacker or defender.
Blinding	The Role (attacker vs. defender) was randomly assigned and blind to the experimenter during data collection. Because of the difference in

data organization between group leader and follower (e.g., the behavioral data from the two followers need to be averaged before comparison), data analysis was not performed blind to the conditions of the experiments.

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