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Review

Group Cooperation, Carrying-Capacity Stress, and Intergroup Conflict

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Peaceful intergroup relations deteriorate when individuals engage in parochial cooperation and parochial competition. To understand when and why intergroup relations change from peaceful to violent, we present a theoretical framework mapping out the different interdependence structures between groups. According to this framework, cooperation can lead to group expansion and ultimately to carrying-capacity stress. In such cases of endogenously created carrying-capacity stress, intergroup relations are more likely to become negatively interdependent, and parochial competition can emerge as a response. We discuss the cognitive, neural, and hormonal building blocks of parochial cooperation, and conclude that conflict between groups can be the inadvertent consequence of human preparedness – biological and cultural – to solve cooperation problems within groups.

Highlights

Human intergroup interactions can be peaceful, marked by mutually beneficial exchange and trade, but they often include an element of competition and can become violent.

To understand when and why intergroup relations change from peaceful to violent, we focus on the interdependence structures within and between groups, and on how individuals adapt to these interdependencies.

We identify carrying-capacity stress as a pivotal factor in transitioning intergroup relations from peaceful to conflictual, and discuss four neurocognitive building blocks of parochial cooperation and competition.

We suggest that parochialism may be best understood as an adaptation to group-living that can inadvertently lead to intergroup hostility and conflict.

Living in Groups

Humans are a gregarious, group-living species [1,2]. Many social interactions occur within **groups** (see Glossary) of familiar others with whom individuals share a past and a future. Groups exist next to other groups with whom interactions take place well – work teams operate in larger organizations, sports teams compete against each other, and companies and nation states operate in markets and alliances. Such intergroup interactions can be peaceful, marked by mutually beneficial exchange and trade [1–5]. Intergroup interactions often also include an element of competition and can become violent [1,6–10]. Examples include community feuds, tribal raids, hostile takeovers in industry, terrorist attacks, and interstate warfare.

Group-living and intergroup relations can be analyzed at four levels (Box 1). Across these levels of analysis, it is assumed that intergroup **conflict** emerges when individuals in at least one group contribute personal resources such as physical strength, money, skills, and knowledge to aggress out-groups and/or to respond to (anticipated) out-group threats with defensive action, pre-emptive strikes, and retaliation [7,11–14]. What remains puzzling is why groups of individuals initiate and escalate intergroup conflict. At the individual level, group members risk injury and loss of resources when they join and contribute to intergroup conflict. At the aggregate level, intergroup conflict is more wasteful than peaceful coexistence and **cooperation**.

To understand when and why intergroup relations change from peaceful to violent, we present a theoretical framework that maps out the different **interdependence** structures between groups. Groups are internally interdependent but can be (i) independent of other groups, allowing peaceful coexistence and the emergence of group-specific norms and practices, (ii) positively interdependent, allowing positive **(in)direct reciprocity** and cross-group cooperation to emerge, and (iii) negatively interdependent, increasing the likelihood of competition and conflict (Figure 1). Second, we review work in behavioral economics and cognitive neuroscience showing that humans often display parochial cooperation – people cooperate with in-group members more than with out-group members. We argue that sustained parochial cooperation can create

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Box 1. Group Living and Parochialism at Four Levels of Analysis

The functions of group living, and of parochialism in particular, can be analyzed and understood at four levels of analysis across different disciplines in the social and behavioral sciences (Figure I).

At the ultimate group level, natural selection may have favored groups (blue-fills for in-group; orange-fills for out-groups) that established stronger norms and habits of cooperation over those who cannot contain free-riding. Some scientists working from an evolutionary (group-selection) perspective have proposed that in-group cooperation evolved in the context of (presumably frequent) violent intergroup conflict, where groups that exhibit higher levels of in-group cooperation and between-group competition (red arrows) are more likely to prosper than groups that that have lower levels of such parochialism ([5,7,10]; also [4,9,27,29–31,45,132]). At the proximate group level, the interdependence structure within and between groups shapes the form and function of parochialism [6,8]. Scientists working from a social psychological or sociological perspective contrast parochialism to universal cooperation (blue arrows), and decompose parochialism into parochial cooperation and parochial competition (red arrows) [133]. Parochial competition imposes negative externalities on other groups that can ignite vengeance, retribution, and violent responses in otherwise peaceful out-groups (see also [12–14,19,22–26,32–42,47–61,63–67]. At this proximate group level, parochial competition and the underlying interdependence structure serve as an impetus for, rather than being a consequence of, the emergence and escalation of intergroup conflict [6,8,19]. At a proximate interindividual level, individuals cooperate and compete with other individuals, build cooperative and competitive reputations by reciprocating and exploiting each other's trust and cooperation, and select new interaction partners on the basis of reputation [15–18,20,21,51,63,64,67]. Through this mechanism of (in)direct reciprocity, interindividual interactions develop into groups of interdependent individuals with (in)formal norms and institutions that promote cooperation and deter free-riding [15,17,19,20,134,135]. At the proximate individual level, parochialism is related to group-bounded feelings of empathy and perspective-taking linked to specific brain areas and neuroendocrine systems. Cognitive neuroscientists have identified neural and neuroendocrine processes that shape parochialism and are shaped by parochialism displayed by out-groups [69,71,72,76–80,87,88,91,98,105,106,109–118,122–125,127–129]. Levels of analyses can interact bidirectionally. For example, evolutionary pressures favoring parochialism may have created a biobehavioral preparedness for individuals to display parochialism even when intergroup interdependencies would favor universal cooperation [5,8,85,110,133–135]. Along similar lines, group-level norms for parochialism shape emotional responses to norm violations within and between groups. Such emotions are related to specific patterns of neural and neuroendocrine activity, and can increase the likelihood to enforce and promote group-level norms [44,48,49,69,77–80,98,105,106,110].

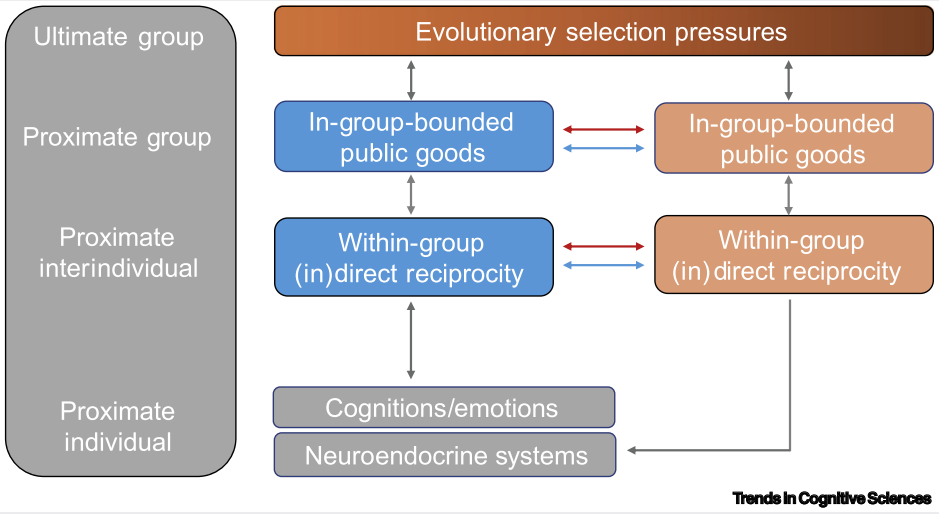


Figure I. Group-Living and Intergroup Relations at Four Levels of Analysis.

carrying-capacity stress and transform intergroup relations from independency or positive interdependency to negative interdependency. Through this (indirect) effect on intergroup interdependencies, parochial cooperation can inadvertently create the antecedents for parochial competition – competing instead of cooperating with out-group members. Third, to understand how intergroup relations change, we review the building blocks and emerging work on their associations with brain activity and hormonal modulation. We add to the well-known building blocks

Glossary

Anterior insula (AI): a cortical structure folded deep in the lateral frontal lobe that is involved in multiple (socio)cognitive and affective processes, such as empathy, interpersonal experience, and social exclusion.

Carrying-capacity stress: situations when a group needs more resources than the local environment can provide.

Conflict: situations in which there is an incompatibility between the values and goals of interdependent (groups of) individuals.

Cooperation: actions that create a benefit b to another agent (or agents) at a cost c, where $c < b$.

Dorsolateral prefrontal cortex (DLPFC): a functional area within the prefrontal cortex that has an important role in higher-order cognition, including working memory, cognitive flexibility, inhibition, and strategic planning.

Group: three or more positively interdependent individuals.

Hyperscanning: a method by which brain activity in two or more interacting individuals can be simultaneously recorded, thus permitting the study of inter-brain responses and neural coupling that underlie interactive decision-making.

(In)direct reciprocity: cooperating (versus competing) with those who (are assumed to) have a positive, cooperative (versus negative, competitive) reputation.

Interdependence: when agents (individuals or groups) positively or negatively impact on each other's (economic and/or psychological) states through individual and joint behavior.

Interpersonal neural synchronization: the degree to which the brain activities of two or more interacting individuals covary over time.

Perspective-taking: the capacity to process information from others' perspective (separate from one's own), typically to understand and predict others' emotions and behavioral intentions.

Social dilemma: a decision-making situation in which the individual is better off by not cooperating when others cooperate, but the group is better off when all members cooperate.

Temporoparietal junction (TPJ): a functional neural region at the border of the temporal and parietal lobes that integrates and processes information from the external environment and from

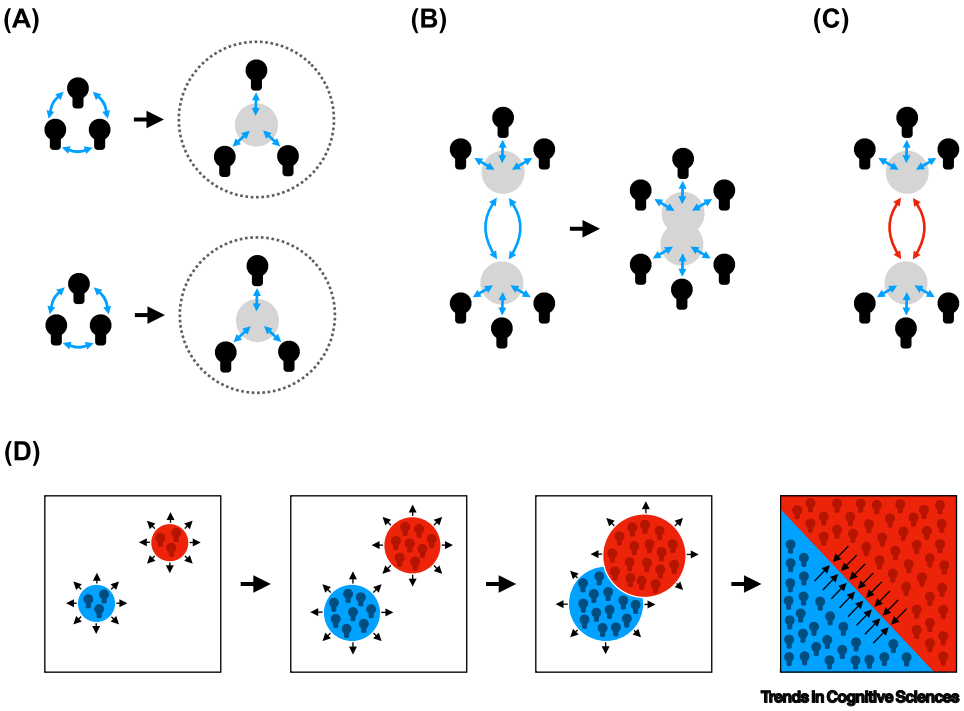


Figure 1. Topology of Intergroup Relations. (A) Cooperative reciprocal interactions (blue arrows) between individuals can lead to clusters of cooperative relationships that are upheld by shared expectations of reciprocity (norms of cooperation). Owing to boundaries in social contact and interaction frequency (e.g., through geographical or cultural separation), groups emerge that cooperate within their own group but not between groups. Cooperation may generalize beyond dyadic relations by establishing public goods (grey circles). In this case, costly contributions and benefits are not exchanged through interpersonal relationships, are but group-shared and group-bounded. (B) Positive interdependence between groups can allow cooperative norms or expectations of reciprocity to traverse group boundaries, ultimately allowing groups to merge and establish shared norms and act cooperatively. (C) By contrast, cooperative actions within groups that impose a negative externality on other groups (negative interdependence, red arrows) sharpen group boundaries and can lead to parochial competition. In the most extreme case, contributions to a public good do not create any benefits whatsoever but only impose an externality on another group ('spiteful' intergroup relations). (D). Through sustained parochial cooperation and public-good provision groups expand and increasingly require resources to sustain group-living; this can lead to carrying-capacity stress and negative interdependence in which groups compete for a shared resource in a zero-sum game.

within the body (also see perspective-taking).

Ventral striatum (VS): a cluster of neurons in the subcortical basal ganglia of the forebrain. A crucial component of the motor and reward systems, the VS is involved in the coordination of motivation, reinforcement, and reward processing.

of parochialism – social categorization, in-group biased preferences and beliefs, and (controlled) decision-making – a fourth mechanism: feedback-based learning and updating. We conclude that conflict between groups can be the inadvertent consequence of human preparedness – biological and cultural – to solve cooperation problems within groups.

Intergroup Relations as a Two-Level Game of Strategy

At the core of group-living is a fundamental **social dilemma**. If individuals maintain cooperative relationships, group-living provides levels of protection and prosperity that single individuals cannot achieve alone [15,16], but cooperation is exploitable. At the interindividual level, cooperation provides a net benefit to the partner that the partner can take advantage of by not reciprocating. At the group level, cooperation can provide and sustain public goods such as public security and social welfare systems from which all group members benefit. Public goods provision is fragile, however, because each group member has an incentive to withhold contributions and benefit from the public goods for free (i.e., free-riding) – the 'classic' dilemma of cooperation [15–17].

Cooperation and Intergroup Conflict

Groups with a large number of free-riders and concomitant cooperation failures face internal conflicts and may dissolve [18,19]. To avoid this, group members develop and enforce prosocial preferences, create and maintain social norms of reciprocity and fairness, trust that other group members hold these norms, and preferentially interact with members with a cooperative reputation but punish and disengage from those with a non-cooperative reputation [i.e., (in)direct reciprocity] [5,15–17]. Social norms and group regulations such as bonding rituals and formal laws promote (in)direct reciprocity and reduce free-riding. These norms and regulations also reinforce group boundaries by defining who is expected to contribute to and benefit from public goods, and who is not [20] (Figure 1A). In a nutshell, the mechanisms to suppress the free-rider problem are often tailored to particular groups and its members, reinforcing in-group-bounded, parochial cooperation (also see [21]).

When groups are embedded in networks of groups, individuals can contribute not only to group goods from which their own group benefits (parochial cooperation) but also to collective goods from which the entire network benefits (universal cooperation). Universal cooperation in, for example, coalitions of nation states, trade networks, city neighborhoods, and tribal communities within a nation state may develop to such an extent that it blurs between-group boundaries (Figure 1B). Universal cooperation is, however, more difficult to enforce than parochial cooperation. Norms, trust, and (in)direct reciprocity usually develop in and are confined to smaller collectives, and do not generalize to larger collectives or an entire network of groups [22–24]. In addition, the welfare of agents often depends more on socially close others with whom one has frequent and repeated interactions than on strangers and out-group members [5,16].

Although universal cooperation can, in principle, lead to the fusion of groups and the establishment of universal norms and practices of cooperation as seen in the history of nation states (Figure 1B), parochial cooperation can prevent this process by polarizing intergroup relations. Some groups may be better at enforcing (in-group-bounded) cooperation than others, and this creates between-group inequality. Individuals in 'inferior' groups may envy 'superior' groups, and individuals in superior groups may fear the envy from their inferior neighbors. Extant work in social psychology has shown that between-group inequalities and relative deprivations provide impetus for intergroup polarization and conflict [6,8,11,18,25,26]

Parochial cooperation can deteriorate intergroup relations for another reason that has received little attention in existing conflict theory. Parochial cooperation can lead to group growth and expansion that increasingly tax the group's environment and its finite resources to the point where the group experiences carrying-capacity stress [2,27]. Carrying-capacity stress can be relaxed not only through innovations in, for example, production technology and agricultural practices [2,27,28], but also by capturing resources from neighboring groups. Resonating with this perspective are studies in political geography and climate research that have linked environmental degradation to political conflict and intergroup violence [8,27,29–31]. Thus, through successful and sustained parochial cooperation, groups inadvertently create negative interdependencies between groups (Figure 1C), where parochial competition and intergroup conflict are a possible result (Figure 1D).

Revealing Parochial Cooperation through Nested Social Dilemma Games

Nested social dilemmas model multilayered group relations to study parochial cooperation [15,32,33] (Figure 2A). Typically, research participants are divided into two groups of equal size and can contribute resources to a group-exclusive public good (parochial cooperation) from which they receive a share that is independent of their contributions (creating the classic dilemma

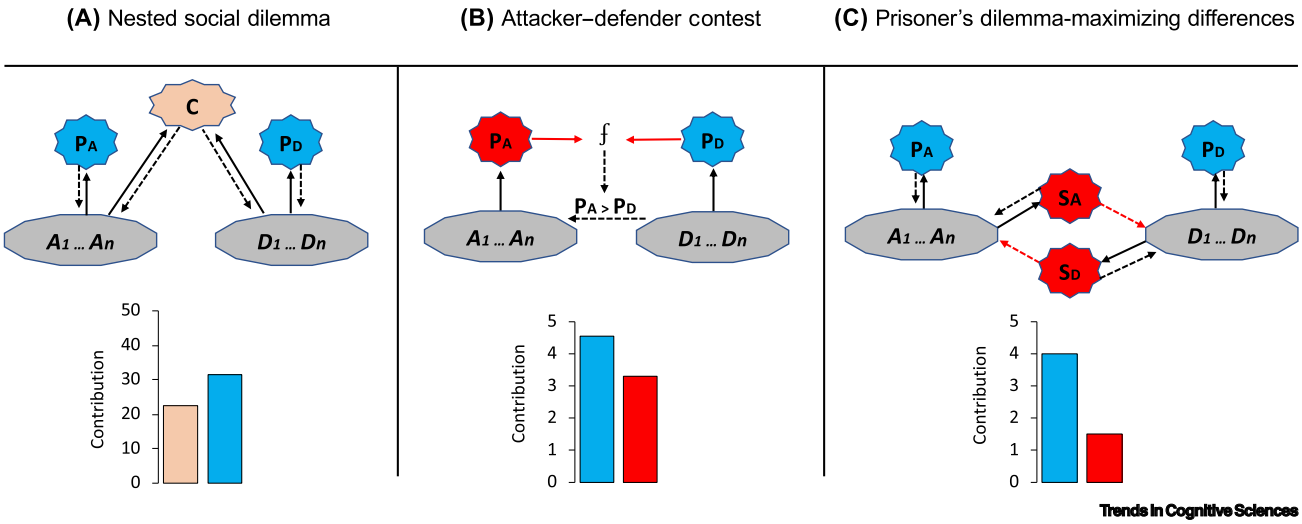


Figure 2. Experimental Models of Inter-Group Relations in which Individuals Are Assigned to Two Groups A and D of Usually Equal Size $N_A = N_D$. (A). In the nested social dilemma, individuals can contribute (unbroken black arrow) to a group-exclusive public good P (blue). Contributions gain in value with factor k (where $1 < k < N$) and are redistributed equally among group members (broken black arrow). Individuals in both groups can also contribute resources to a universal pool C (beige). Contributions are likewise multiplied by k' (typically $k = k'$) and are redistributed equally among in- and out-group members. The bar-chart shows sample-size weighted levels of parochial (blue) and universal (beige) cooperation (expressed as mean percentages from the total endowment) from 11 independent experiments (N = 882 in total) reported in [32–36]). (B) In the intergroup attacker–defender contest (IADC), individuals can contribute resources to their own group's pool P (red, attackers; blue, defenders). Contributions are wasted, but group A wins the non-invested resources of D when pool P_A > pool P_D. When $P_A \leq P_D$, individuals on both sides earn whatever resources they have not invested. The bar-chart shows sample-size weighted average contributions (of e = 10) to out-group attack (red) or in-group defense (blue) (N = 1.608 in 268 three-person groups from five independent experiments reported in [14,47–49]). (C) In the intergroup prisoner's dilemma-maximizing differences game, IPD-MD), each individual in groups A and D can contribute to an in-group P (blue) or a between-group pool S (red). Contributions to P and S are multiplied by k and redistributed equally among the members of groups A and D. Contributions to S additionally impose a cost on each member of the opposite group (red broken arrow). The bar-chart shows sample-size weighted average contributions (of e = 10) to parochial cooperation (P, blue bar) and competition (S, red bar) (N = 960 from 13 independent experiments reported in [34,39,52–59]).

of cooperation). Individuals in both groups can also contribute resources to a universal pool (universal cooperation) from which both in-group and out-group members receive a share regardless their contributions.

Experiments using nested social dilemmas typically find more parochial than universal cooperation (Figure 2A) [15,32–36]. This resonates with meta-analyses showing that individuals cooperate more with members of their own group than with strangers or out-groups [37,38]. In fact, even when groups are constructed randomly, people treat others differently depending on their group membership, displaying in-group biases in prosocial preferences and cooperative beliefs – people value and trust in-group members more than out-group members [33,34,37,39–42]. One explanation for this 'mere membership' effect [43] is that people assume, rightly or not, that interactions with in-group members are cooperative to a greater extent than interactions with strangers and out-groups [37,42]. Indeed, when individuals can punish other participants, they promote a norm of parochial cooperation by punishing free-riding within one's group more harshly than free-riding within or towards out-groups [42,44,45]. Group members also more readily reward parochial individuals and elect them to leadership positions, rather than those who free-ride or display universal cooperation [34,46].

Revealing Parochial Competition through Intergroup Contest Games

Groups under carrying-capacity stress (Figure 1D) may try to take over their neighbors' resources [26,27,29–31,47], and groups that fear such out-group attacks may feel justified to pre-empt out-group threat by initiating a conflict [8,12,13]. Such parochial attack and defense have been

modeled in the intergroup attacker–defender contest (IADC) and investigated experimentally [14] (Figure 2B). Individuals allocated to an attacker or an (opposing) defender group can contribute personal resources to their group's pool. Contributions are wasted, but when the attacker group's contributions exceed those of the defender group, attackers win the non-invested resources of the defenders (who thus leave empty-handed). When attackers invest equal or less than the defender, individuals on both sides earn whatever resources they have not invested.

Experiments show that contributions to in-group defense outrank those to out-group attack [14,47–49] (Figure 2B). Contributions to out-group attack (i.e., out-group aggression) are, however, non-trivial – individuals frequently spend personal resources to exploit (members of) the out-group. Moreover, people enforce a norm of parochial competition through punishment of group members who do not contribute to out-group attack [14,50,51], and elect individuals who display hawkish behavior towards out-groups into leadership positions [34].

Parochial competition sometimes emerges even if it provides no material benefits to one's own group. This is the case in the intergroup prisoner's dilemma-maximizing differences game (IPD-MD) [26,34] (Figure 2C). Individuals are divided in two groups and can contribute to an in-group (parochial cooperation) or a between-group pool. From both pools individuals and their own group earn a share regardless of their contributions. However, contributions to the between-group pool also impose a cost on each out-group member at no material benefit to the in-group. Experiments show that individuals typically contribute more resources to the in-group pool (parochial cooperation), but contributions to the between-group pool also occur (i.e., out-group spite) [26,34,40,52–59] (Figure 2C).

Synthesis

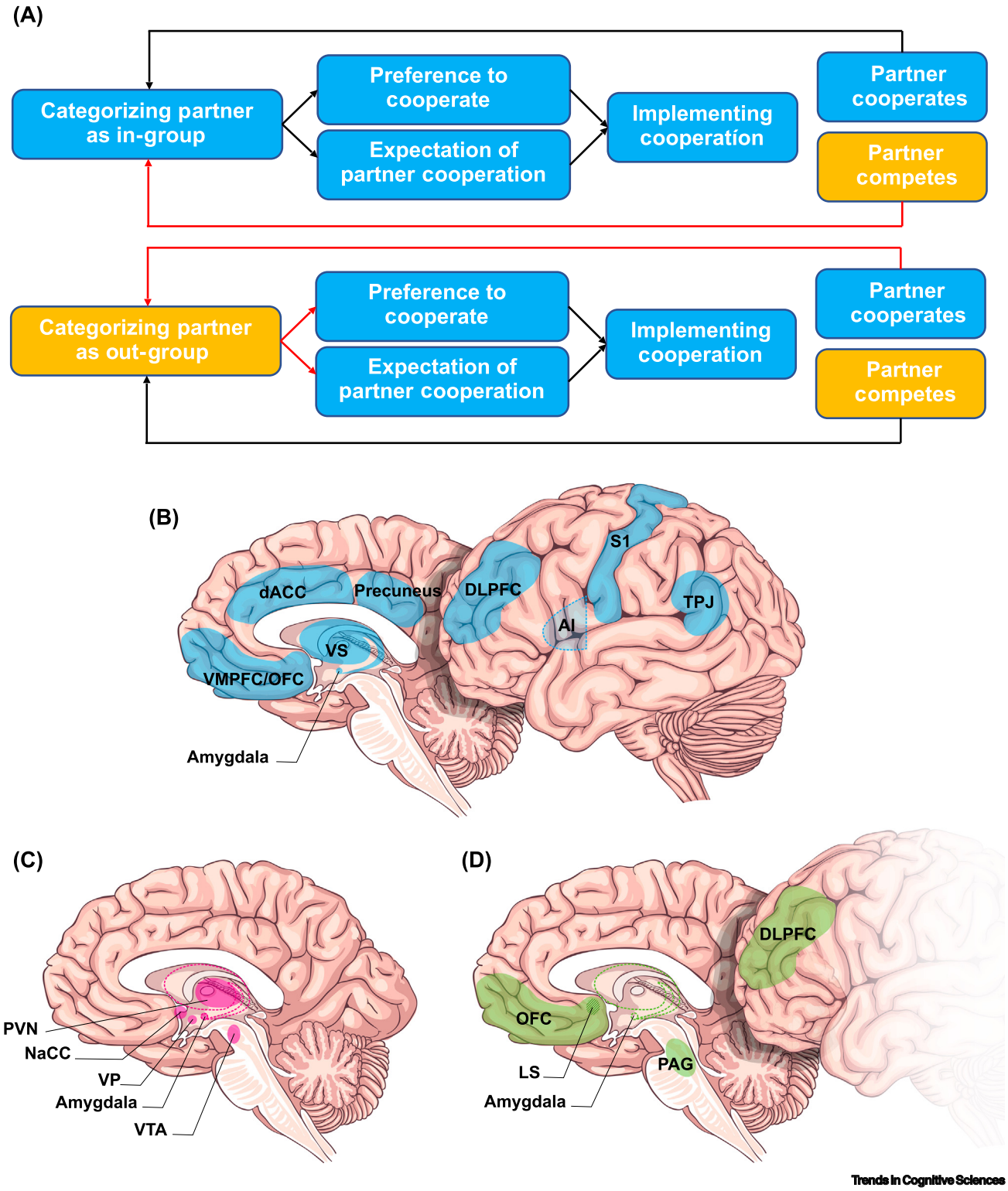
The experimental data from two-level games of conflict fit the dynamics proposed in Figure 1. Parochial cooperation already emerges in the absence of interdependencies with other groups [60–62]. Parochial cooperation is stronger following in-group bonding [48,63,64], when within-group similarity is emphasized [36,65,66], and when group members have strong friendship ties [11,67]. Possibly, groups use bonding rituals and highlight similarity to emphasize and reaffirm their members of their mutual interdependence. Parochial competition, by contrast, emerges when intergroup relations are marked by negative interdependencies. Parochial competition is largely – but perhaps not exclusively – confined to situations in which groups compete for finite resources. Parochial competition brings in-group benefits ('spoils of war'), deters and neutralizes out-group threat [12,13,68], improves personal reputation within one's group [34,46], and perhaps relieves envy towards wealthier out-groups [18,25,26,69].

Building Blocks of Parochial Cooperation and Competition

For parochialism to emerge, humans need to (i) (quickly) identify and categorize who is and who is not part of one's own group, (ii) form preferences and beliefs about the cooperativeness of the interaction partner(s), (iii) make decisions based on these preferences and beliefs, and (iv) update social categorization and concomitant (in-group biased) preferences and beliefs based on feedback from interaction outcomes. Although they are psychologically and neurobiologically distinct, as we discuss later, these building blocks of parochialism have recursive elements and dynamically adapt as interactions unfold (Figure 3A).

Social Categorization

People structure and represent the world by quickly classifying objects into categories based on basic features such as similarity in shape and color, as well as physical proximity. In the case of other people, categorization also follows cues of familiarity, shared habits and values inferred



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from observed behavior, and common fate such as shared exposure to threat and opportunities [44,47,65,70,71]. For example, others' contributions to the provision of public goods may be a powerful cue for categorizing others as 'in-group' or 'out-group' [21,36,42,72]. However, even arbitrary partner characteristics, such as ethnicity and language spoken, can become associated with beliefs and expectations of who can be trusted or not, and who is deemed to be a cooperator or defector [43]. For example, infants ~1 year of age selectively imitate and adopt the preferences of someone speaking their own (in-group) language rather than those of someone speaking a foreign (out-group) language [73], and they prefer individuals who treat similar others well and treat dissimilar others poorly [74]; children of preschool age already display in-group bias and parochial cooperation [75]. Such generalized cue-based heuristics (i.e., group stereotypes) can explain when and why cooperation remains parochial even when interdependency between groups is or becomes positive. Cue-based decision making may prohibit or slow down the development of cross-group cooperation and generalized trust.

Forming (Parochial) Preferences and Beliefs

Once interaction partners are identified as part of the individual's group or as out-group members, different behavioral scripts for treating in-group members and out-group members emerge. Such scripts rest, first, on in-group biased prosocial preferences and empathy [37]. There is good evidence that prosocial preferences impact more on parochial cooperation when people interact with in-group than with out-group members [3,33,39,41,52,53], and that empathy is higher for people identified as part of the in-group rather than the out-group. At the neurobiological level, empathy has been related to activity in the ventromedial prefrontal cortex (VMPFC), somatosensory cortex (S1), and the **anterior insula** (AI) (Figure 3B); neural activity in these areas is higher when participants see in-group rather than out-group members experiencing painful treatment [76–80]. Such in-group biased 'empathy for pain' in turn has been linked to parochial cooperation and competition. For example, in [79], Jewish-Israeli and Arab-Palestinian adolescents witnessed painful treatment of in-group and out-group members. Imaging results showed more brain activity in the somatosensory cortex when targets were in-group rather than out-group members, and this in-group biased neural response predicted subsequent hostility towards out-group members.

Differential treatments of in-group versus out-group members also rest on in-group biased expectations of partner cooperation. There is good evidence that individuals readily expect more cooperation from in-group than from out-group partners [33,37,39,40]. To some extent, such expectations are preference-based, in that individuals tend to rely on their own preferences when predicting the actions of similar others and use group stereotypes when predicting the actions of dissimilar others [81]. In addition, beliefs and expectations involve **perspective-taking** and 'theory-of-mind' [82–86], which has been related, at the neurobiological level, to activation in the precuneus and the **temporoparietal junction** (TPJ) (Figure 3B) [83–86]. Activity in these neural structures may be engaged more when dealing with in-group than with out-group

Figure 3. Neurocognitive Building Blocks of Parochial Cooperation and Competition. (A) Categorizing the interaction partner as in-group (blue, top panel) feeds cooperative preferences and expectations that promote the implementation of cooperative decisions (black arrows). In-group partner cooperation reinforces (black feedback arrow) categorizing the partner as in-group, whereas partner competition undermines (red feedback arrow) categorizing the partner as in-group. Categorizing the interaction partner as out-group (orange; bottom panel) inhibits cooperative preferences and expectations (red arrows). Partner cooperation undermines categorizing partner as out-group (red feedback arrow), whereas partner competition reinforces (black feedback arrow) categorizing partner as out-group. (B) Cortical and subcortical regions that have been linked to (in-group bias in) social preferences and cooperative beliefs include VMPFC, AI, S1, precuneus, and TPJ; regions implicated in implementing decision-making include OFC, dACC, and DLPFC; regions involved in feedback processing and in updating preferences and beliefs include VS and AMY. (C) Neural regions modulated by oxytocin include NaCC, AMY, PVN, VP, and VTA. (D) Neural regions modulated by the release of testosterone include DLPFC, OFC, AMY, LS, and PAG. Abbreviations: AI, anterior insula; dACC, dorsal anterior cingulate cortex; AMY, amygdala; DLPFC, dorsolateral prefrontal cortex; LS, lateral septum; NaCC, nucleus accumbens; OFC, orbitofrontal cortex; PAG, periaqueductal grey; PVN, paraventricular nucleus of the thalamus; S1, somatosensory cortex; TPJ, temporoparietal junction; VMPFC, ventromedial prefrontal cortex; VP, ventral pallidum; VS, ventral striatum; VTA, ventrotegmental area.

members. For example, decisions to trust in-group members more than out-group members were observed when TPJ functionality was intact, but not when TPJ functionality was temporarily disrupted [87].

Implementing (Parochial) Decisions

Because extending trust, cooperating, and enforcing norms of cooperation or competition all involve personal costs and risks, implementation may depend on some strategic deliberation about such costs and potential future benefits. Although we lack good understanding of how social categorization influences such cost–benefit calculations, there is some evidence that parochial decision-making emerges especially when strategic deliberation about costs and benefits is reduced [88]. Indeed, some studies have shown that individuals under cognitive load, which is associated with reduced top-down control and strategic deliberation [89], display more parochialism ([39,57,90,91]; but see [33]).

At the neurobiological level, calculating the costs and benefits of decision options has been related to activity in the **dorsolateral prefrontal cortex** (DLPFC) and dorsal anterior cingulate cortex (dACC) (Figure 3B) [92–97], and there is emerging evidence that reduced activity in these regions associates with stronger parochialism [48,88]. For example, in a multi-round IADC game [48], reduced neural activity in the right DLPFC predicted stronger contributions to out-group attacks that favor the in-group at the expense of the out-group.

Learning and (Biased) Updating from Feedback

Decisions to cooperate or trust, and subsequent observations of reciprocity, can reinforce parochial cooperation and competition (Figure 3A). When people engage in social decision-making they may use (learned) partner cues to guide their decision to cooperate or defect [19–21,51]. This paves the way for stereotypical views – people with feature X cannot be trusted – and further corroborate categorizations of 'us' and 'them' [21,72,98,99]. It can also lead to selective sampling (i.e., not taking a risk to cooperate with 'them' in the first place) and a self-fulfilling prophecy of parochialism when groups share the same (wrong) stereotypes about each other. This not only prevents universal cooperation but also reinforces biased beliefs, group boundaries, and parochialism, and can polarize intergroup relations [5,19–21,98,99].

That interaction dynamics shape parochialism raises the important question of how partner cues are (un)learned. In general, learning can take place through direct experience (e.g., Pavlovian and instrumental learning [100,101]), from (observing) others' choices, or from gossip in combination with simple heuristics such as 'a friend of a friend is a friend,' and 'an enemy of a friend is an enemy' [19]). When in-group members reciprocate trust and cooperation, individuals not only learn the long-term benefits of trust and cooperation with in-group members [98] but also update expectations about in-group trustworthiness. A similar process may apply to parochial competition, which can lead to positive reputation benefits within one's in-group [34,46], and concomitant updating of expectations about what parochial competition brings.

At the neurobiological level, learning has been, in particular, linked to the neural responses in the **ventral striatum** (VS) and AI (Figure 3B) [102,103]. VS activity modulates learning in non-social environments [102,103], and learning from cooperation and competition [21,72,93,96,104]. Importantly, VS activity tracks not only the benefits others receive from cooperation [93] but also the benefits people experience from out-competing their rivals [72,104]. For example, winning an intergroup competition was associated with VS activity which, in turn, predicted willingness to aggress out-group targets ([72]; also [69,80,104–106]). Accordingly, VS activity may play an important role in the reinforcement of both parochial cooperation and competition.

Synthesis and Future Research

Parochial cooperation and competition rest on (i) social categorization of others as in-group versus out-group, and (ii) behavioral scripts for cooperation based on in-group biased prosocial preferences and beliefs. We have added (iii) feedback-based learning from decision consequences and partner behavior as a mechanism that can (iv) reinforce (or weaken) the tendency to categorize partners as in-group versus out-group, and strengthen (biased) beliefs about the cooperativeness of interaction partners based on their group membership.

Neuroimaging studies have begun to link specific neural activity to these building blocks of parochialism, but more principled research is needed. First, the evidence is mostly correlational and largely ignores the fact that social categorization and in-group biased preferences and beliefs are continuously updated as interactions within and between groups develop. Second, associating neural responses in particular brain structures to specific cognitive building blocks, of course, rests on oversimplified assumptions, and the field increasingly moves towards uncovering the computational mechanisms and interactions between brain regions [107]. This should help to go beyond reverse inference and simplified brain region-to-function associations. In addition, many other regions, not discussed here, may well be involved in the processes underlying parochialism. For example, the amygdala – a subcortical structure involved in threat detection and emotion processing (Figure 3B) – has been linked to both social categorization and belief formation and updating [108]. Third, existing work is mostly limited to individual (neural) responses in relation to individual decisions to cooperate and/or compete with in-group versus out-group members, often in one-shot decisions. How feedback and learning reinforce group membership biases at the behavioral, cognitive, and neurobiological levels, is still poorly understood (see Outstanding Questions).

Although we know how individuals within groups coordinate decision making and organize collective action [15], we understand less well how individual neural activity is modulated by other group-member displays of parochial cooperation and competition. This is unfortunate because within-group coordination of collective action is important for public good provision [15–17] and has been related to group victory and success in IADCs [8,14,47–49]. Research needs to study dynamic situations in which the actors act, react, and reinforce each other's beliefs and behavior. Recent work using **hyperscanning** has provided the first evidence that individual brain activity during IADCs synchronizes across members of one's own group [48]. The degree of such **interpersonal neural synchronization** within groups predicts how much group members contribute to intergroup conflict, and to out-group attack in particular (Figure I in Box 2).

Hormonal Modulators of Parochial Cooperation and Competition

Several of the building blocks of parochialism have been linked to modulation by hormones with established social functionalities: oxytocin and testosterone. Oxytocin is a 9 amino acid peptide synthesized primarily in the hypothalamus and pituitary that functions as both a hormone and neurotransmitter. It modulates the functionality of different brain regions, including the amygdala, hippocampus, striatum, and brainstem [109]. Oxytocin also interacts with neural circuitries associated with (social) reward computation [110–112] (Figure 3C). Testosterone, a steroid hormone secreted primarily by the male testicles and female ovaries, acts on androgen and estrogen receptors that are widely distributed throughout the neural circuitry underlying reactive aggression (amygdala, hypothalamus, periaqueductal grey; Figure 3D), and reduces the functional connectivity of the amygdala with prefrontal regions including the orbitofrontal cortex (OFC) and DLPFC [112–114].

Oxytocin

In several mammalian species, oxytocin has been implicated in kin recognition, reduced fear-responding, feedback-based learning, and promoting social approach in the context

of pair-bonding, affiliation, and the nurturing and protection of offspring [110–112]. There is evidence that these processes emerge especially during intergroup competitions and conflict [79–81,110,115–117].

Oxytocin contributes to parochialism through, first, an enhanced ability to categorize interaction partners as part of one's own group. In non-human mammals, oxytocin release during pair-bond formation forges an olfactory memory that helps to later recognize the partner as familiar [111]. In humans, some studies likewise show that increased levels of oxytocin link to faster and more accurate recognition of others as 'familiar' (versus unfamiliar) and as belonging to one's in-group (versus not belonging) [118,119]. Second, oxytocin contributes to parochialism by facilitating the development of in-group biased preferences and beliefs ([120,121] for meta-analyses). Intranasal administration of oxytocin increases the liking of in-group members [122], parochial cooperation [35,53,56,80,123,124], and the behavioral coordination of attacks on out-groups that benefit the in-group [49]. There is some evidence that these effects of oxytocin on parochial cooperation are mediated by TPJ activity and perspective-taking [80,125], and that oxytocin facilitates learning from positive, cooperative feedback [126].

There is reason to assume that oxytocin modulates parochial cooperation in particular. Although oxytocin has been associated with aggressive responding to outsiders, there is no evidence that oxytocin modulates the (dis)liking of out-groups [122] or (spiteful) parochial competition [53,56,127]. Possibly, oxytocin-induced aggression, when observed, is aimed at defending and protecting one's own group (in particular offspring) [109–111]. Indeed, oxytocin-induced aggression of out-groups is observed especially when out-groups threaten in-group survival and prosperity (i.e., reactive aggression [53,56,80]).

Testosterone

At the behavioral level, testosterone has been associated with enhanced competition for territory and (aggressively) seeking and protecting status-ranking [112–114]. A few studies have examined the role of testosterone in parochial cooperation and competition. In an experiment using the IPD-MD, endogenous levels of testosterone were associated with more contributions to the within-group pool (i.e., parochial cooperation) and with more contributions to the between-group pool (i.e., parochial competition) [57]. In another study, male soccer fans were confronted with (un)fair offers either from a fan of their own team (in-group) or from a fan of a rival team

Box 2. Inter-Brain Neural Synchronization as a Proximate Mechanism Underlying Intergroup Attacker–Defender Contests

Inter-brain neural synchronization (also termed inter-brain neural coupling) refers to the cross-time covariation in brain activities between two or more people. In group interactions, inter-brain neural synchronization can emerge when interacting group members' actions or intentions are shared, and this has been suggested to mediate social contagion in which individuals mimic and align with each other's vocalizations, postures, or movements [85,86]. Simultaneous recordings from two or more interacting individuals using brain imaging techniques [hyperscanning using fMRI, electroencephalography (EEG), or functional near-IR spectroscopy (fNRIS)] have been employed to reveal how neural responses align across individuals that engage in social interaction. Recent studies have examined the role of inter-brain neural synchronization in (inter)group interactions (Figure I). For example, Yang and colleagues [48] assigned 546 individuals to 91 three-versus-three-person attacker–defender contests and used fNIRS – a non-invasive form of optical imaging that uses arrays of lasers and detectors to measure changes in oxygenated hemoglobin and deoxygenated hemoglobin concentrations in cortical brain regions – to simultaneously record brain activity while group members made contribution decisions (Figure IA). In-group bonding before the contest increased contributions to out-group attack and in-group defense, decreased neural activity in the right dorsolateral prefrontal cortex (DLPFC), and increased functional connectivity of the right (r) DLPFC and temporoparietal junction (TPJ). Crucially, in-group bonding during out-group attack (but not defense) increased within-group synchronization (WG-Sync) in the rDLPFC and rTPJ (Figure IB), and this increased alignment of prefrontal activity among in-group members predicted out-group attack (Figure IC). The shared within-group reduction in rDLPFC activity may be a potential neural mechanism of parochial competition that explains how in-group bonding leads to collective hostility towards out-groups.

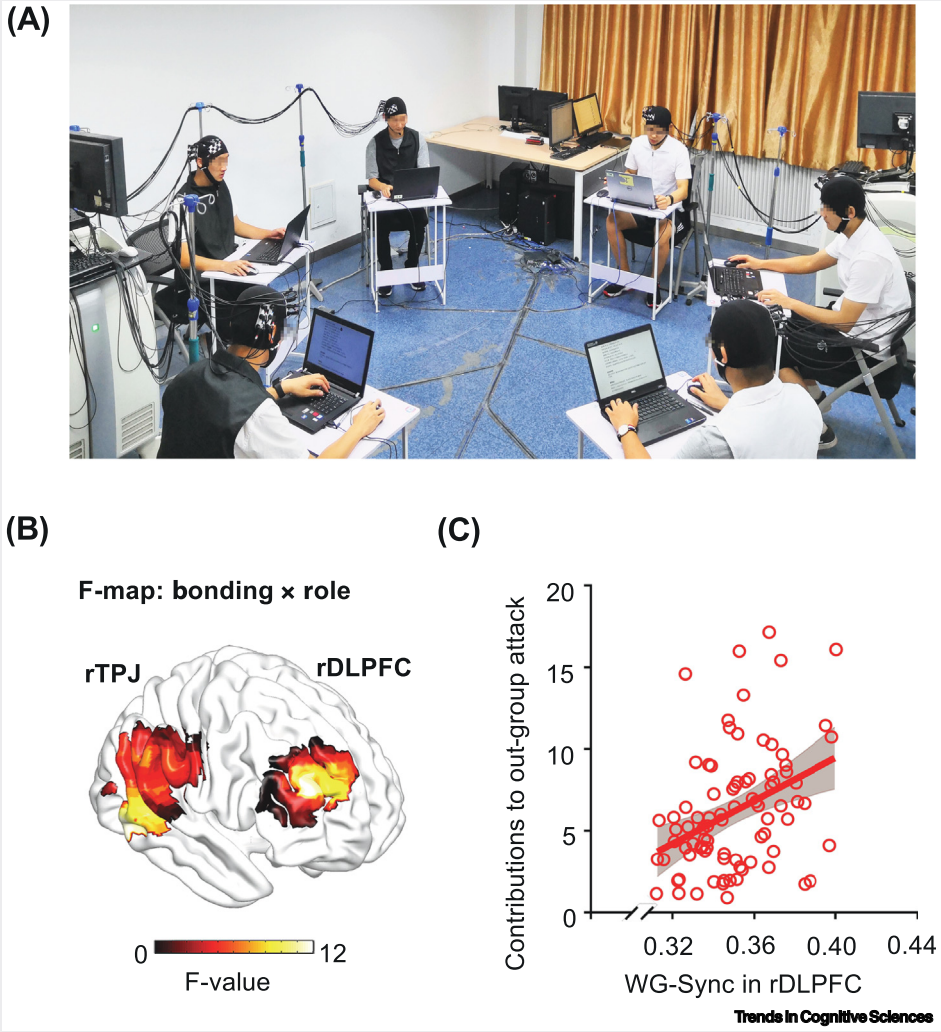

Figure I. Hyperscanning Within-Group Neural Synchronization during Intergroup Conflict

(out-group). Higher levels of testosterone predicted soccer fans' generosity towards in-group members (i.e., parochial cooperation) and the rejection of both fair and unfair offers from the antagonistic out-group, revealing a tendency to punish the out-group at a personal cost (i.e., parochial competition) [128,129]. Possibly, testosterone is related to parochialism because of the positive within-group reputation and/or status benefits that individuals earn when displaying parochial cooperation and competition. Such an explanation would fit the finding that testosterone promotes, in both human and non-human primates, risk-taking [130] and the aggressive pursuit of within-group status-ranking [112–114].

Synthesis and Future Research

Both primary and meta-analytic studies reveal that oxytocin facilitates parochial cooperation, but not competition, through its influence on social categorization and the development of in-group biased preferences and beliefs. Testosterone, by contrast, facilitates both parochial cooperation and competition, possibly because parochialism is related to within-group reputation and status-ranking. Hostility

towards an out-group should lead to positive reputation and status, especially when groups are negatively interdependent and competing with the out-group can benefit the own group. The evidence for this possibility is, however, limited, and more research is needed (see Outstanding Questions).

Regarding brain-imaging research, most evidence for hormonal modulation of parochialism is based on individual decisions, and little is known about hormonal modulation of parochialism in interacting groups. An exception is a study on oxytocin in which individuals engaged in a real-time dyadic coordination game while brain activity was tracked using electroencephalography (EEG) [131]. Greater inter-brain synchrony during coordination was related to better behavioral coordination, and intranasal oxytocin (versus placebo) improved both α-band interbrain neural oscillations and behavioral coordination. Similarly, oxytocin (versus placebo) has been shown to promote the coordination of successful out-group attacks in IADCs [49].

Concluding Remarks

Gordon Allport, a pioneer in social and personality psychology, once remarked that 'humans live in groups and, sometimes, for their group' [1]. The development of group-bounded indirect reciprocity, and its supporting institutions, can be best understood as an adaptive response to the fundamental problem of group-living – the social dilemma between personal and group interests. Indeed, cooperation is easier to maintain when groups are confined, agents can easily track the past actions of interaction partners, the benefits of cooperation are transparent, and people have long-term relationships. We have identified four building blocks, and their neuroendocrine correlates, that underpin parochialism – (i) the ability to recognize whether interaction partners belong to the in-group or not, (ii) the development of in-group biased preferences and cooperative beliefs, (iii) the implementation of decisions, and (iv) the reinforcement of parochial cooperation and competition through learning and updating (Figure 4).

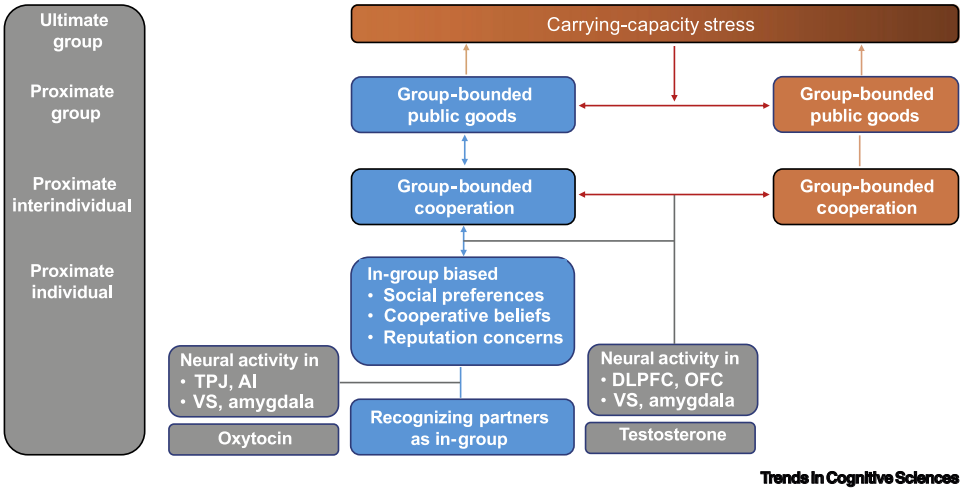

Figure 4. Biobehavioral Mechanisms for Parochial Cooperation and Competition. At the proximate interindividual and group level, within-group (in)direct reciprocity and in-group public-good provision reinforce each other (blue arrows) and can lead to group growth and expansion (orange arrows) with, at the ultimate level, carrying-capacity stress and between-group competition (red arrows) as a consequence. At the proximate individual level, parochialism emerges with the recognition and categorization of interaction partners as (not) belonging to the in-group, and the development of in-group biased preferences, beliefs, and reputation concerns (possibly associated with the release of oxytocin and neural activity in the TPJ, amygdala, VS, and AI). In-group biased preferences, beliefs and reputation concerns facilitate within-group (in)direct reciprocity and biased updating of beliefs that in-group members are cooperative and out-group members cannot be trusted (possibly modulated by testosterone and neural activity in the DLPFC, OFC, amygdala, and VS). Abbreviations: AI, anterior insula; DLPFC, dorsolateral prefrontal cortex; OFC, orbitofrontal cortex; TPJ, temporoparietal junction; VS, ventral striatum.

Outstanding Questions

Why do people react differently to reward and punishment by in-group members versus out-group members? How is such in-group reward and out-group punishment weighted and incorporated into the decision-making process?

When do carrying-capacity stress and resource scarcity lead to group innovation or instead to out-group aggression; how do (groups of) humans trade-off the cost of investing in innovation against the costs of intergroup conflict?

How do cultural factors, including culture-specific norms and institutions, shape in-group biased preferences and beliefs, and influence transitions from parochial cooperation to competition in intergroup relations?

How does neural activity associated with executive control interact with emotional responses, empathy, and perspective-taking in producing parochial cooperation and competition?

How is parochial cooperation related to group-based emotions (e.g., feelings of belonging and closeness)? What are the functions of feelings such as anger, envy, and revenge versus guilt, shame, and regret in the development and change of parochial cooperation and competition?

What neurocomputational mechanisms support the reinforcement and extinction of parochial cooperation and competition?

How does winning or losing intergroup conflict influence in-group dynamics, including its underlying neurocognitive mechanisms? When would losing or winning an intergroup conflict promote stronger parochialism (revenge) or universal cooperation (reconciliation)?

What is the function of testosterone in the emergence of parochial cooperation and competition? How do related hormones, such as cortisol and noradrenaline, modulate parochial cooperation and competition? Are the modulations independent, or do hormonal levels coemerge and interactively shape parochial cooperation and competition?

Scientists working from an evolutionary (group-selection) perspective have proposed that parochialism evolved because of frequent and violent intergroup conflicts [7,10] (Box 1). Whether intergroup conflicts were sufficiently frequent and violent to create such evolutionary selection pressures is contested [4,9,132]. Our analysis and review suggest that parochialism may not only be created by intergroup competitions and conflict [7,10] but also serve as its root cause. Sustained and successful parochial cooperation over time increases group wealth and size, but inequality and carrying-capacity stress are possible consequences. In such cases of (endogenously created) carrying-capacity stress, intergroup relations are more likely to become negatively interdependent, and parochial competition can emerge as a response [8,14,29–31,133].

How can neurocognitive mechanisms for parochialism be redirected to promote peaceful intergroup interactions?

How do people navigate a social environment that is marked by multiple group memberships embedded in a complex network of interdependency structures?

Parochial cooperation and competition are often assumed to co-occur and to have coevolved (i.e., parochial altruism) [7,10,45,53,133]. Our analysis shows that such co-occurrence depends on the nature of between-group interdependencies. For example, parochial cooperation may emerge when groups are non-dependent, but parochial competition should not. When groups manage to create cooperative relationships across group boundaries (e.g., through trade and division of labor), the resulting positive interdependence between groups can blur group boundaries and lead to group fusion [24]. Our review also suggests that parochial cooperation and competition rest on distinct neuroendocrine systems (i.e., oxytocin and testosterone, respectively). Parochial cooperation seems to be functionally, behaviorally, and biologically distinct from parochial competition.

Individuals contribute resources to their in-group when (and because) it protects and benefits themselves and the group upon which they depend [1,133]. Because of this high interdependence between the individual and the group, parochial sentiments may emerge and over time become habitual, a process that may be biologically prepared and can be seen as an adaptive response to solve social dilemmas in groups [42,110,134,135]. When groups exist next to other groups, the mechanisms for group-living – norms, reputation, and trust – can reinforce group boundaries, carrying-capacity stress, and lead to negative interdependencies with neighboring groups. Intergroup relations oscillate between peace and conflict depending on the changing or endogenously created interdependencies between groups. From this perspective, intergroup conflict, in ancestral and modern times, can be the inadvertent outcome of individual preparedness for living in groups.

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