CHAPTER ONE

Parochial Cooperation in Humans: Forms and Functions of Self-Sacrifice in Intergroup Conflict

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Abstract

Although cooperation between groups is not unusual, most forms of human cooperation are in-group bounded and, sometimes, motivated by the desire to ward-off and subordinate rivaling out-groups. Building on evolutionary perspectives and models, we propose that humans evolved a capacity for parochial cooperation, which entails (1) in-group love: the tendency to cooperate with and extend trust toward those others who are similar, familiar rather than unfamiliar, and belong to one’s own group; and (2) out-group hate: a willingness to fight against rivaling out-groups. This chapter reviews our own work, and that of others, showing that parochial cooperation (1) emerges especially when it benefits individuals’ within-group reputation, (2) affects one’s within-group status, (3) is more prominent among individuals with chronic prosocial rather than proself value orientation, and (4) is sustained and motivated by oxytocin, an evolutionary ancient hypothalamic neuropeptide pivotal in social bonding, pair-bond formation, and empathic responding. Across the board, findings resonate well with relatively recent evolutionary theory on (inter)group relations and add to classic theory in social psychology.

1. INTRODUCTION

May 1940, World War II is raging through Europe and after 10 days of resistance, the Dutch army surrenders and German forces occupy the Netherlands. During the first year, the Germans impose their increasingly severe anti-Jewish regulations. In Amsterdam, and elsewhere, signs that read “Jews Prohibited” appear at entrances to cafés, theaters, parks, and other public places. Jews are dismissed from government jobs and their children are sent home from school. In the summer of 1942, deportations begin. Those without a place to hide do not stand a chance and, eventually, over 80% of all Jewish men, women, and children living in Amsterdam are transported to concentration camps in Eastern Europe, where they are murdered.

One of these people was Walter Süskind, a refugee from Germany and member of the Jewish Council in Amsterdam. He lived with his family close to a nursery where the Nazis put young Jewish children before deportation. In utmost secrecy and risking their lives every day, Süskind and a small group of confidents rescued children through the backyard of the nursery, from where they went, in a backpack or laundry basket, to rural areas in the Netherlands. Estimates are that they saved about 600 children. Süskind and his family, however, were captured, deported, and killed in late 1944, just a few months before World War II ended.
October 1991, Chechnya, a mostly rural region in the North Caucasus declares independence from Russia and thousands of people of non-Chech ethnicity leave the newly established republic amidst reports of discrimination and violence. In the following 10 years, the country is crippled by two separatist wars against Russian army forces, leaving families, households, farms, and factories destroyed. By early 2000, Moscow enforces full control over Chechnya and its neighboring states in the North Caucasus, including Ossetia and Dagestan.

It is against this background that Dmitry Sokolov, a student in Moscow with roots in Chechnya, carefully takes the explosive belt with 500 g of TNT equivalent and filled with sharp metal objects and dowel pins. He straps the belt to Naida Asiyalova, the women he fell in love with less than three years ago and who recruited him to join the rebels in her native Dagestan. In those past three years, Dmitry and Naida converted into Muslim faith and became increasingly fanatic. And on October 23, 2013, with rush hour just setting in, Naida blew herself up in a bus near the Russian town of Volgorad, killing herself along with five others, and injuring another thirty.1

Different as they are, the stories about Süsskind and Asiyalova share three elements that are at the core of the current chapter. Both Walter Süsskind and Naida Asiyalova operated in a small group of people sharing a common purpose and fate, and working together to achieve that purpose. Both these individuals, and their groups, operated in an intergroup setting marked by competition, conflict, and extreme violence. And both Süsskind and Asiyalova risked and sacrificed their lives to bring their group’s goal closer—to save Jewish children from the gas chambers, to prevent the Nazis from achieving their goals, to bring closer an independent North Caucasus, and to hurt Russians for past war cruelty and oppression.

Here we try to understand this set of observations: That humans self-sacrifice to promote the survival, cause, and prosperity of the groups they belong to, and that such self-sacrifice may take benign and prosocial, but also utterly hateful and destructive forms. We wonder whether the self-sacrificial “in-group love” by Süsskind and the self-sacrificial “out-group hate” by Asiyalova are confined to a handful of heroes and fanatics, or whether milder traces of such tendencies rest within each of us, and affect

1 The narrative about Walter Süsskind is based on Wikipedia (retrieved February 10, 2014); the narrative on Sokolov and Asiyalova is derived from a newspaper article (retrieved February 10, 2014 from http://www.news.com.au).
our day-to-day behavior. We surmise that these prosocial and antisocial ten-
dencies may not be as distinct as they seem, and may be, in fact, brighter and
darker sides of the same coin. We explore the possibility that prosocial
martyrdom and spiteful terror share motivational and neurobiological roots,
and we identify chronic predispositions, and social psychological conditions
that amplify or restrain human willingness to self-sacrifice in intergroup
conflicts.

We proceed as follows. Section 2 reviews game-theoretic, social psycho-
logical, and evolutionary models’ assertions about self-sacrifice in intergroup
competition and conflict. Although these perspectives make sometimes
competing predictions, they converge on the core proposition that in inter-
group settings, self-sacrifice and cooperation is parochial (in-group oriented
and bounded), with its ultimate function to increase inclusive fitness
(Alexander, 1990; Bowles & Gintis, 2011). Accordingly, parochial cooper-
ation is motivated by, and manifested in (1) protecting and promoting the
in-group (henceforth in-group love), and (2) derogating and fighting
more or less rivaling out-groups (henceforth out-group hate).

In Section 3 we consider in-group love and out-group hate in more
detail, and review our experimental and meta-analytic studies suggesting
that in-group love is primary to out-group hate in motivating parochial
cooperation. Section 4 asks whether, when, and how displays of parochial
cooperation depend on reputation concerns, and influences within-group
reputation and status. Section 5 relates parochial cooperation, and in-
group love and out-group hate, to individual differences in social value
orientation—the chronic tendency to value personal outcomes only
(individualistic), or instead personal and others’ outcomes alike (prosocial).
Section 6 traces parochial cooperation back to oxytocin—a neurohormonal
modulator of social bonding, pair–bond formation, and empathy. In Section
7 we summarize the main conclusions and implications for contemporary
theory on human cooperation in intergroup competition and conflict.
We conclude with avenues for future research.

2. ORIGINS AND ORCHESTRATION OF PAROCHIAL
COOPERATION

Humans are group-living, social animals and much of their evolu-
tionary success has been attributed to their strong capacity for cooperation
and collective action (Wilson, 2012). Humans create cohesive groups and,
more than any other species, engage in complex forms of cooperative
exchange with unfamiliar and genetically unrelated others (Nowak, Tarnita, & Wilson, 2010). It is within such groups that negotiation and trade evolved (Horan, Bulte, & Shoran, 2005); social and technological innovations were designed, disseminated, and implemented (Wynn, Coolidge, & Bright, 2009; Flinn, Ponzy, & Muehlenbein, 2012); artistic expressions and cultural rituals developed (Zilhao, 2007); and ways to disseminate knowledge, insights, values, and preferences were perfected (Baumeister, Masicampo, & Vohs, 2011; Nijstad & De Dreu, 2012).

2.1 (Inter)Group Life as a Multilevel Social Dilemma

One core reason that humans evolved into such social animals is that creating and promoting group life increases individual survival and prosperity probabilities well beyond what individuals could achieve in isolation. It is because humans work hard, contribute accurate information and solid insights to the group, adequately process others’ contributions, and stick to agreed-upon rules and regulations; so that the group avoids disaster, reaches high quality decisions, and prospers (De Dreu, Nijstad & Van Knippenberg, 2008). And being part of such strong, well-functioning, and innovative groups provides fitness functionality to its individual members, who thus are more likely to survive, prosper, and reproduce than individuals living in groups where most members lack such cooperative inclinations. In short, individuals in cooperative groups function relatively well and herein lies a strong motivation for individuals, and their offspring, to contribute to their group, and to cooperate with its members (Darwin, 1873).

Darwin’s insight suggests that humans may have evolved a “group psychology” that includes a propensity to (1) identify with groups and its members, (2) empathize with the needs and interests of fellow group members, (3) self-sacrifice, trust, and cooperate with other group members, and (5) loyal commit and contribute to the functioning of one’s group. Indeed, evidence is accumulating that even preverbal infants selectively imitate in-group members over out-group members (Buttelmann, Zmyj, Daum, & Carpenter, 2013) and use self-other similarity as the basis of social categorization and discrimination (Hamlin, Mahajan, Liberman, & Wynn, 2013; Mahajan & Wynn, 2012), and that in-group favoritism emerges early in development (Fehr et al., 2008). Moreover, adult humans quickly and automatically assign themselves and others to social categories (Amodio, 2008; Cikara & Van Bavel, 2014); form a self-concept that is partly determined by group membership (Brown, 2000; Turner, Oakes, Haslam, & McGarty, 1994); experience greater empathy for in-group members in need (Hein,
Silani, Preuschoff, Batson, & Singer, 2010), and engage in costly cooperation with in-group members (Balliet, Wu, & De Dreu, 2014). Additionally, these cognitive and motivational processes that result in behavioral discrimination in favor of in-groups recruit the evolutionary ancient, subcortical circuitry involved in reward processing (Lamm, Decety, & Singer, 2011; Rilling & Sanfey, 2011; Shamay–Tsoory, 2011) and appear in cultures around the world (LeVine & Campbell, 1972; Hruschka & Henrich, 2013). Not surprisingly, across the globe, adults teach their children the virtue of prosocial behavior and generosity, while simultaneously emphasizing the vice of greedy selfishness (Boyd & Richerson, 1982; Campbell, 1975; De Dreu & Nauta, 2009; Keltner, Kogan, Piff, & Saturn, 2014).

Of course, there are a number of critical issues with this evolutionary analysis. First and foremost, group efficiency—the surplus generated by the combination of individual contributions (Bowles, 2006)—typically benefits each individual group member regardless of how hard they worked toward group goals, how much they processed and integrated information, and how well they conformed to and enforced group norms, rules, and regulations (Hardin, 1968; Olson, 1972). All group members benefit from the group shelter, from high quality decisions and innovations, and from economic gains generated by the group. In each case, however, the noncontributing, free-riding individuals benefit relatively more—they reap the benefits of collective effort without making substantial contributions. Accordingly, group life is marked by a fundamental and perpetuating social dilemma in which each individual (1) serves personal interests best by opting for non-cooperation and (2) is worse off when all members opt for non-cooperation compared to cooperation (Dawes, 1980; Van Lange, Balliet, Parks, & Van Vugt, 2014).

In formal terms an N-person social dilemma can be modeled as follows. Each individual member has a personal endowment $e$ (e.g., money, physical strength, time, information) from which they can contribute $c$ (with $0 \leq c \leq e$) to group efficiency (e.g., public health care, a strong army, a high quality decision); $e$ is multiplied by $r$ (with $1 < r < N$) and each group member obtains an equal share (i.e., $(re)/n$). Because $e > (re)/n$,
contributions are personally costly, each individual is best off personally if she keeps \( e \) (i.e., \( c = 0 \)). In fact, when all group members except one free rider contribute their maximum amount (\( c = e \)), the free-riding individual receives \( [e + (n - 1)(\bar{r})/n] \) while cooperators receive \( [(n - 1)(\bar{r})/n] \). This reveals that individuals in groups may decide not to contribute anything because of greed (to obtain the “temptation payoff” \( e + c(N - 1/N) \)) and/or because they fear their cooperation is exploited by free-riding others (i.e., they wish to avoid the “sucker payoff” \( c(N - 1/N) \)) (Coombs, 1973; Komorita & Parks, 1995).

Some have argued that it is precisely because of greed and fear that it is hard to see how evolution produced a biological preparedness for cooperation, unless we assume that groups exist over time and encounter \( N \)-person social dilemma decisions not just once, but many times (Ostrom, 1998; Rilling & Sanfey, 2011; Kollock, 1998). In fact, such “repeated games” where group members share past and future, and interact with each other repeatedly and in various configurations, are rule rather than exception in ancestral as well as contemporary times (Delton, Krasnow, Cosmides, & Tooby, 2011). In such “repeated games” low group efficiency threatens group survival and future prosperity (i.e., group efficiency increases from \( Ne \) if no one contributes, to \( N(\bar{r}) \) if all contribute their maximum amount), and this explains the human readiness to cooperate and contribute (Komorita, 1976; Komorita, Sweeney, & Kravitz, 1980), the motivation to prevent free riding in others through targeted reward and punishment systems (Price, Tooby & Cosmides, 2002; Fehr & Gächter, 2002; Yamagishi, 1986), and the development and (inter-generational) transmission of norms for generosity and cooperation through cultural practices, rites, and socialization (Balliet & Van Lange, 2013; Bowles & Gintis, 2011; Boyd & Richerson, 1982; Keltner et al., 2014).3

The evolutionary analysis of human cooperation and group living raises another issue, namely, that groups do not exist in a social vacuum. Instead, groups exist next to other groups with whom they cooperate, compare, and compete. In such intergroup settings, group efficiency is relative—groups that generate greater surplus than other groups become relatively stronger and prosperous, achieve a relatively favorable social status position, and may be better able to exert power and influence over other groups, and their

3 We note that, especially in larger groups and social categories, the “shadow of the future” facilitates reciprocal strategies, but without punishment or other enforcement mechanisms in place cooperation typically unravels and dwindles over time (Takezawa & Price, 2010).
members. It is Darwin himself who observed that “groups with a greater number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other … would spread and be victorious over other tribes” (1873; p. 156). It suggests that evolution prepared humans to cooperate not only with others, but especially with those they rely upon, are interdependent with, and expect interactions within the future, that is, with those others who are perceived to be part of one’s group. Put differently, humans may be biologically and culturally prepared to be in-group bounded, parochial cooperators (Bernard, Fishbacher, & Fehr, 2006; Campbell, 1975; LeVine & Campbell, 1972).

If in-group bounded, parochial cooperation partly evolved in, and functions to regulate intergroup comparison and competition, it should be particularly prominent in such intergroup settings. Indeed, there is solid evidence from studies involving both humans, and nonhuman animals, that intergroup competition motivates parochial cooperation (Bornstein, 2003; Reeve & Holldobler, 2007; Manson & Wrangham, 1991; Wildschut, Pinter, Vivea, Insko, & Schopler, 2003). Bornstein (2003) modeled this in his so-called team games, two-level games involving simultaneous outcome interdependence within as well as between groups. To demonstrate the role of intergroup competition in boosting parochial cooperation, Bornstein and Ben-Yosef (1994) compared behavior in the single-group (N-person) social dilemma with behavior in the structurally equivalent intergroup prisoner’s dilemma (IPD) game. Results showed that embedding the N-person social dilemma game in an intergroup competition doubled cooperation rates among group members. Other studies similarly found that intergroup competition increases coordination among group members (e.g., in the minimal-effort game: Bornstein, Gneezy, & Nagel, 2002) and eliminates social loafing in group tasks (e.g., joint orange-picking: Erev, Bornstein, & Galili, 1993).

In intergroup competition, both greed and fear operate to mobilize parochial cooperation during intergroup conflict (e.g., Bornstein & Gilula, 2003). Groups motivated by the “temptation payoff” compete against their rivaling out-group, hoping to win from them and acquire its resources (viz. offensive, or territorial aggression). To be successful, groups should mobilize more cooperators within their group than are mobilized within the out-group: Intergroup greed motivates and mobilizes cooperation within each group. Similarly, groups motivated to avoid the “sucker payoff” (i.e., cooperating with an out-group that competes back) should mobilize at least as much cooperators as are mobilized in the out-group so as to properly defend and protect itself against out-group threat (viz. defensive, or reactive
aggression). Put differently, intergroup fear and distrust motivates and mobilizes cooperation within each group.

2.2 Forms and Functions of Parochial Cooperation

In both single-group $N$-person social dilemmas and in intergroup competition games (e.g., IPD), cooperation creates strong in-groups, and this may explain not only why people self-sacrifice and cooperate, but also condemn and punish free-riding behavior and reward—materially or symbolically—cooperation by fellow group members. Such in-group love thus emerges in the absence of rivaling out-groups, yet probably is stronger in the presence of intergroup competition and conflict where in-group survival and prosperity is contingent upon the cooperativeness of in-group members relative to the cooperativeness of out-group members. Importantly, however, in intergroup competition, parochial cooperation may be motivated also by out-group hate—the desire to harm out-group members, which is manifested in a willingness to make personal sacrifices in order to reject, derogate, and aggress against rivaling out-groups, and tendencies to perceive in-group members’ displays of out-group hate as heroic and patriotic (De Dreu, Aaldering, & Saygi, 2014; also see Boyd & Richerson, 1982). After all, when competing for relative standing, increasing in-group efficiency through in-group love or reducing out-group efficiency through out-group hate are two means toward the same end—in-group survival and prosperity (Brewer, 1979, 1999; also see Bowles, 2009; De Dreu et al., 2014; Dovidio & Gaertner, 2010; Fiske, 2002; Messick & Mackie, 1989; Tajfel & Turner, 1979).

In-group love and out-group hate as manifestations of parochial cooperation figure prominently in social identity and self-categorization theory (Ellemers & Haslam, 2012; Tajfel & Turner, 1979; Turner & Reynolds, 2012). According to the social identity approach, humans categorize themselves and others as belonging to a specific group in the presence of an out-group and derive part of their self-concept from the knowledge of their membership of a social group (or groups) together with the emotional significance attached to that membership (Tajfel, 1974). Because humans strive to develop and maintain a positive self-concept, mere categorization into in-group and out-group initiates thoughts, feelings, and behaviors that attempt to positively differentiate the in-group from the out-group (Ellemers & Haslam, 2012; Hewstone, Rubin, & Willis, 2002; Tajfel & Turner, 1979). Indeed, there is abundant evidence that humans are prone to both in-group favoritism—emphasizing positive in-group’s attributes and characteristics and ignoring or downplaying its negative attributes and
characteristics—and out-group derogation—emphasizing negative out-group’s attributes and characteristics and ignoring or downplaying its positive attributes and characteristics (Fiske, 2002; Hewstone et al., 2002; Mummendey & Otten, 1998).

In the social identity approach, in-group love and out-group hate function to maintain and increase a positive social identity. The evolutionary approach to human cooperation (e.g., Axelrod, 1984; Bowles & Gintis, 2011; Darwin, 1873; Heinrich & Heinrich, 2007; Trivers, 1971; Wilson, 2012; Wilson & Wilson, 2007) assumes the functions of in-group love and out-group hate to be quite different. These alternative functions are well articulated in the theory of bounded generalized reciprocity (BGR; Yamagishi, Jin, & Kiyonari, 1999; Yamagishi & Mifune, 2009). BGR assumes that human groups provide a container for a generalized exchange network of indirect reciprocity whereby individuals behave in ways to maintain a positive reputation, because people cooperate with others who have a cooperative reputation and exclude others who lack such a reputation (Feinberg, Willer, & Schultz, 2014; Yamagishi et al., 1999). Accordingly, people must maintain the reputation of a reliable cooperator to avoid the cost of exclusion from the group, and to gain the benefits of cooperative exchange in future interactions with other in-group members. BGR specifies that humans evolved to (1) have depersonalized and generalized trust that other in-group members will cooperate, (2) be motivated to establish and maintain a cooperative reputation among in-group members, and (3) expect to receive benefits from other in-group members, but not necessarily from the same in-group member they cooperated with or helped (Kiyonari & Yamagishi, 2004; Yamagishi et al., 1999). Thus, BGR argues that because of generalized trust in in-group members and the need to build a positive reputation among in-group members, people display in-group love (Mifune, Hashimoto, & Yamagishi, 2010; Yamagishi et al., 1999) and, sometimes, out-group hate.

Taken together, our analysis suggests that when and because human groups exist and operate in intergroup settings, individuals may have a propensity toward in-group bounded, parochial cooperation, and that such parochial cooperation manifests itself in in-group love as well as out-group hate. In-group love and out-group hate function to render the in-group relatively more efficient and successful than comparison groups, and thus increase the likelihood of the in-group coming out ahead and of not falling behind (De Dreu et al., 2014; Halevy, Chou, Cohen, & Bornstein, 2010; Jervis, 1976; Simunovic, Mifune, & Yamagishi, 2013). The ultimate function of parochial cooperation thus is to increase inclusive fitness; the
proximal functions of in-group love and out-group hate are to (1) provide
the individual with a positive social identity and (2) provide the individual
with a positive reputation of being a reliable and trustworthy cooperator,
and a loyal and committed group member. Returning to Walter Süskind
and Nadia Asiyalova, these perspectives essentially propose that their
self-sacrificial displays of in-group love and out-group hate, respectively,
were motivated by social identity striving, by reputation concerns, or
some combination of both.

3. PAROCHIAL COOPERATION RESTS ON IN-GROUP
LOVE MORE THAN ON OUT-GROUP HATE

Both biological and social scientists have claimed that in-groups are
primary relative to out-groups—people live in them, and sometimes, for
them—and that in-group favoritism has strong adaptive value because it fa-
cilitates within-group coordination and the survival of individuals and
groups (Allport, 1954; Brewer, 1979, 2007; Darwin, 1871; Fu et al.,
2012; Greenwald & Pettigrew, 2014; Halevy, Bornstein, & Sagiv, 2008;
Hammond & Axelrod, 2006; Masuda, 2012; Mummendey & Otten,
1998). In addition, developmental research has shown that in-group love
develops earlier in childhood as compared with out-group hate (Buttelmann
& Böhm, 2014); that parochial and altruistic motives gain prominence in
parallel during adolescence (Fehr, Glätzle-Rüttler, & Sutter, 2013); and
that greater exposure to war produces a lasting increase in egalitarian motives
toward fellow in-group members only for children and adolescents and not
in adults (Bauer, Cassar, Chytílová, & Henrich, 2014). These findings sup-
port evolutionary claims about the co-evolution of parochial altruism and
intergroup conflict—enhanced intergroup competition may have posed se-
lective pressure on psychological adaptations promoting parochial altruism
(Choi & Bowles, 2007).4

3.1 Intergroup Discrimination in Cooperative
Decision-Making

The evidence for in-group favoritism and out-group derogation pertains
to attitudes and beliefs, and much less to intergroup discrimination in
self-sacrifice and (parochial) cooperation. Accordingly, we set out to

4 Population biology models of parochial altruism suggest it may be possible that parochial altruism
may be selected for in the absence of intergroup competition. We return to this in Section 7.
meta-analyze over four decades of game-experimental studies on human cooperation with in-group versus out-group partners conducted in social psychology, (experimental and behavioral) economics, and sociology (see Balliet et al., 2014). Our goal was to establish whether humans discriminate between in-group and out-group when deciding to cooperate, how strong such intergroup discrimination is, and what conditions moderate its existence.

By September 2013, the data set included a total of 78 retained articles and 214 eligible studies. While the majority of the work included in the meta-analysis involved (variants of) the $N$-person social dilemma shown in Figure 1(a), some studies employed the Dictator Game (Forsythe, Horowitz, Savin, & Sefton, 1994). It involves a participant in the role of “dictator” deciding how much of endowment $X$ he or she donates to a recipient. The recipient does not have a say in the decision and cannot affect the dictator’s outcomes—donations thus reflect reduced greed and/or positive other-concern. Another subset of studies employed the Trust Game (Berg, Dickhaut, & McCabe, 1995), where the participants act as investors who decide how much of endowment $X$ to transfer to a trustee. Transfer $Y$ (with $0 \leq Y \leq X$) is tripled and the trustee is given the possibility to back-transfer $Z$ (with $0 \leq Z \leq 3Y$). Because trustees have a selfish temptation to keep the entire transfer $3Y$ for themselves, making any transfer by investors involve the risk of exploitation by their trustee. Put differently, transfer $Y$ reflects trust and concern for other’s outcomes among investors, and back-transfer $Z$ reflects among

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**Figure 1** Effects size (Cohen’s $d$) for cooperation with in-group versus out-group partners (In/Out), for cooperation with in-group versus unknown partners (In/Unknown), and for cooperation with out-group vs. unknown partners (Out/Unknown) (based on Balliet et al., 2014).
trustees positive other-concern/reduced greed, along with a compliance with a norm of reciprocity.

Across these different games of cooperation, Balliet et al., 2014 observed a small to medium effect size indicating that people are more cooperative with in-group, compared to out-group members (Cohen’s $d = 0.32$). Second, intergroup discrimination in cooperation appeared to be motivated by in-group love rather than by out-group hate. This followed from three comparisons—one in which cooperation with in-group members was contrasted with cooperation with out-group members; another in which cooperation with in-group members was contrasted with cooperation with unclassified strangers; and, finally, one in which cooperation with out-group members was contrasted with cooperation with unclassified strangers. In-group love dictates more cooperation with in-group members, than with both out-group members and unclassified strangers. Out-group hate, in contrast, dictates more cooperation with in-group rather than out-group members, and less cooperation with out-group members compared to unclassified strangers. Figure 1 shows that effect sizes patterned conducive to in-group love; because (the low level of) cooperation with out-group members was equal to that with unclassified strangers; out-group hate as a core motivation underlying intergroup discrimination in cooperative decision-making seems less tenable.

3.2 Social Identity Striving and Group Interdependence

The work summarized in Balliet et al., 2014 fits evidence gathered in the context of social identity theory suggesting that in-group favoritism is a stronger and more dominant mechanism underlying positive social identity formation and maintenance than out-group derogation (Dovidio & Gaertner, 2010; Mummendey & Otten, 1998). This should not be taken as evidence that social identity formation and striving explains why people engage in in-group love (and sometimes out-group hate as well). For one, the social identity approach implies that social identity striving comes about even when decision makers are not interdependent with others—simply categorizing others as in-group or out-group should be sufficient to elicit intergroup discrimination, in-group favoritism and, for that matter, in-group love. Additionally, a social identity approach claims that a salient out-group must exist for individuals to self-categorize as a group member and to discriminate based on group membership (Turner & Reynolds, 2012). However, whether social categorization and an explicit out-group are necessary and sufficient for intergroup discrimination to emerge has been
disputed by a number of scholars arguing that intergroup discrimination comes about when and because individuals are interdependent with in-group and out-group members (Gaertner & Insko, 2000; Gaertner & Schopler, 1998; Rabbie & Horwitz, 1969; Rabbie, Schot, & Visser, 1989; Yamagishi et al., 1999; Yamagishi & Kiyonari, 2000), even when there is no salient out-group present (Gaertner, Iuzzini, Witt, & Orina, 2006). Yet, there exists conflicting evidence on these issues (e.g., Gaertner & Insko, 2000; Gagnon & Bourhis, 1996; Rabbie et al., 1989; for reviews see Balliet et al., submitted for publication; Scheepers, Spears, Doosje, & Manstead, 2006; Yamagishi et al., 1999).

To examine whether and how interdependence affect in-group favoritism, Balliet et al., 2014 compared the amount of in-group favoritism in generosity in the dictator game, a situation that contains no interdependence, with the amount of in-group favoritism during cooperation in social dilemmas (e.g., prisoner’s dilemma), a situation in which people are interdependent. The results clearly showed that people more strongly discriminated in favor of in-group members compared to out-group members in social dilemmas ($d = 0.46$), and people displayed much less discrimination in favor of in-group members in dictator games ($d = 0.19$). While these findings do provide some support that mere categorization may affect discrimination in the absence of any meaningful interdependence, these findings also clearly support a position that outcome interdependence is an important condition for the emergence of parochial cooperation. Only 1% of variation in behavior in dictator games was explained by partner group membership, while about 5% variation in behavior in social dilemmas is explained by partner group membership.

Most, if not all, of this work, however, examined individuals making cooperative decisions in direct interaction with either an in-group member or an out-group member and, therefore, does not directly speak to parochial cooperation and its underlying motivations when people operate in groups that compete with rivaling out-groups. To examine this, Halevy et al. (2008) and Halevy, Weisel, and Bornstein (2012) conducted a series of studies using the IPD game (see Figure 1(b)), and a variant to it, the intergroup prisoner’s dilemma—maximizing differences (IPD-MD) game. In the IPD game, intragroup cooperation simultaneously benefits in-group members and harms out-group members. In its variant, the IPD-MD game, individual group members can choose whether they wish their contributions to benefit in-group members without affecting out-group members in any way, or simultaneously benefit in-group members and harm out-group members.
Allowing group members to express in-group love independently of out-group hate through their cooperative choices disambiguates group members’ motivations for participation in intergroup conflict.

Experiments using both one-shot and repeated-game versions of the IPD and IPD-MD games found in-group love to be much more common than out-group hate. Within-group communication in the IPD-MD game increased in-group love, but not out-group hate (Halevy et al., 2008). In addition, introducing the option to cooperate with in-group members without harming out-group members half way through a 60-round repeated game significantly reduced intergroup conflict: Group members quickly and efficiently modified their contribution behavior without any verbal communication, thereby increasing the payoffs to members of both groups (Halevy, Weisel, et al., 2012). These findings indicate that the desire to benefit fellow in-group members trumps the desire to harm out-group members in intergroup interactions, and that the confounding of in-group love and out-group hate increases participation in harmful intergroup conflict.

Taken together, evolutionary and cultural pressures molded humans into a species that has strong motivation and ability to provide for the groups within which they operate, on which they depend, and with which they identify. In intergroup settings marked by competition and conflict, such parochial cooperation is primarily motivated by, and revealed in, displays of in-group love and to a lesser extent by out-group hate (Balliet et al., 2014; Halevy, Weisel, et al., 2012; also see Dovidio & Gaertner, 2010; Fiske, 2002; Yzerbyt & Demoulin, 2010). In support of the theory of BGR, parochial cooperation is primarily displayed in situations when people are interdependent with in-group members. In contrast to a social identity approach, but consistent with BGR, humans discriminate in their cooperative decision-making between in-group and out-group partners especially in N-person social dilemmas (compared to dictator and trust games). This fits the idea that parochial cooperation rests, in part at least, on expectations of indirect reciprocity. We review empirical evidence that lends support to this idea in the next section.

4. INDIRECT RECIPROCITY AND REPUTATION

In the previous section we saw that humans are parochial cooperators and that parochial cooperation manifests itself primarily in in-group love and to a lesser extent in out-group hate. These tendencies have several functions,
including social identity striving, reputation building, and maintaining indirect reciprocity. Whereas reputation and indirect reciprocity are not included in social identity approaches, these are pivotal in general evolutionary theory and the theory of BGR in particular. Some first indication that parochial cooperation serves reputation and indirect reciprocity followed from the finding that parochialism was stronger when decision makers were interdependent, and especially when such interdependence allowed for indirect reciprocity. Here we review more direct evidence, from our laboratory and from others’, showing that parochial cooperation (1) rests on reputation concerns and (2) benefits one’s reputation among in-group members.

4.1 Reputation Concerns and Indirect Reciprocity Motivate Parochial Cooperation

If (parochial) cooperation is partly motivated by reputation concerns and the expectation that costly cooperation recruits cooperation from others in future exchanges, intergroup discrimination in cooperative decision-making should be stronger when decisions have implications for one’s reputation and in the presence of potential indirect reciprocity. Reputation concerns are certainly present in situations that contain common knowledge of group membership (i.e., when everyone is knowledgeable of each person’s group membership), but reputational concerns should be weak when interaction partners are unaware of the decision maker’s group membership (Kiyonari & Yamagishi, 2004; Yamagishi et al., 1999; Yamagishi & Mifune, 2009).

The meta-analysis by Balliet et al., 2014 identified a number of studies that manipulated whether the decision maker knew that the interaction partner did or did not know about the decision maker’s group membership. Parochial cooperation was strong and present when others knew the decision maker’s group membership ($d = 0.32$); it disappeared completely when the decision maker’s group membership was unknown to the interaction partner ($d = 0.04$). In addition to lending support to the prediction that parochial cooperation rests on reputation concerns, this finding also is difficult to reconcile with a social identity approach. After all, this perspective would suggest that people should display similar amounts of parochial cooperation regardless of whether one’s partner(s) know that one is, or is not, part of the in-group.

The theory of BGR suggests that people are parochial cooperators because it creates a positive reputation in a social network contained in a
group. In such social networks, people decide to cooperate with others based on the other’s reputation, expect that others in their group will cooperate to maintain their reputation, and expect to receive benefits from others based on their own cooperation (and enhanced reputation), but not necessarily from the person they have directly helped themselves. This is different from situations that allow for direct reciprocity, in which people expect others to directly reciprocate their cooperation and thus are motivated to cooperate. For example, the trust game affords direct reciprocity—people can send money to their partner (or not) and expect them to return some of that money. Such direct reciprocity is absent in N-person social dilemmas where people simultaneously make their decisions; because decisions are made simultaneously rather than sequentially, decision makers cannot expect others to respond directly to their own decisions. In N-person social dilemmas, indirect reciprocity is present, and cooperation in these contexts may afford an opportunity to increase one’s own reputation and the expectation that others will similarly behave in ways to enhance their reputation.

Focusing on social dilemma studies where only indirect reciprocity matters, Balliet et al., 2014 found that people do indeed expect greater amounts of cooperation from in-group members, compared to out-group members \( (d = 0.41) \). Such expectations of cooperation can be considered a measure of generalized trust (Balliet & Van Lange, 2013b), and this greater trust that in-group members will cooperate can lead people to cooperate more themselves (Yamagishi et al., 1999). Second, Balliet et al., 2014 observed some parochialism in the trust games \( (d = 0.25) \) and much stronger parochial cooperation in N-person social dilemmas \( (d = 0.46) \). This pattern suggests that opportunities for direct reciprocity may inhibit parochial cooperation, while opportunities for indirect reciprocity enable parochial cooperation. Not only do these findings lend support to the theory of BGR, they also are difficult to reconcile with a social identity approach, which has no place for (in)direct reciprocity in predicting and explaining parochial cooperation among humans.

Taken together, the previous section concluded that parochial cooperation is driven more by, and manifests itself more readily in, in-group love than out-group hate, and that parochial cooperation is stronger when group members are interdependent. Here parochial cooperation strongly rests on expectations of indirect reciprocity. Within such systems of indirect reciprocity, maintaining a positive reputation as a reliable but not gullible cooperator is important, and consistent with BGR; we observed
that parochial cooperation is stronger in situations where reputation matters than in situations where reputation cannot be affected by (withholding) cooperation.

4.2 Reputation and Social Standing Benefits from Parochial Cooperation

If parochial cooperation is motivated by reputations and opportunities for indirect reciprocity, we should see also that displays of parochial cooperation, and in-group love and out-group hate, benefit one’s reputation and social standing within one’s group. From the meta-analytic findings (Balliet et al., submitted for publication), and the work summarized therein, it appears that reputation concerns motivate parochial cooperation, and that displays of in-group love in particular seem to provide the individual with reputation benefits such as rewards from fellow in-group members, a greater probability of being included in rather than excluded from potentially beneficial social exchange, and an increase in social status within the in-group. Indeed, Hardy and Van Vugt (2006) and Willer (2009) found that making information about contributions public, thus boosting reputation concerns, increases cooperation in N-person social dilemmas, with the most cooperative group members being rewarded with social status and material benefits.

Because individuals have a strong need to belong (Baumeister & Leary, 1995), and social status represents the culmination of social approval, acceptance, and liking (Leary, 2010), reputation benefits from displays of in-group love and, perhaps, out-group hate, may show up also in fellow in-group members’ social approval, liking and, ultimately, status conferrals. In fact, status conferral is less costly than other solidarity and enforcement mechanisms designed to increase and sustain cooperation in groups (e.g., punishments: Balliet et al., 2011; Chudek & Henrich, 2011; Henrich et al., 2006), which make gossip and other forms of social transmission of reputation particularly effective in boosting cooperation in groups.

Recent research investigated status conferral in the context of inter-group interactions (Halevy, Chou, Cohen, & Livingston, 2012), distinguishing between two types of social standing in a group: Prestige, reflecting respect-and-admiration-based deference to those making costly contributions (e.g., knowledge, resources) to the group, and dominance, reflecting fear-and-force-based deference to those using coercion and intimidation to ascertain social influence (Cheng et al., 2013; Henrich & Gil-White, 2001). In the Halevy, Weisel, et al. (2012) study, participants
first played the IPD-MD game in which they could withhold contribution, show in-group love by making costly contributions to benefit in-group members without affecting out-group members in any way, or show out-group hate by simultaneously benefiting in-group members and harming out-group members through their contributions. They then rated the prestige and dominance of social targets, indicated who they would like to lead the group in a subsequent round of the IPD-MD game, as well as who they would like to exclude from the group for that subsequent round. Behavioral displays of in-group love were rewarded with higher levels of prestige, leadership support, and protection against exclusion from the group as compared with displays of selfishness or out-group hate. In addition, displays of in-group love led to lower perceptions of dominance as compared with either selfishness or out-group hate.

A subsequent study employed a nested social dilemma game in which participants could withhold contribution, show in-group love by making costly contributions to benefit in-group members without affecting out-group members in any way, or show universalistic concern by simultaneously benefitting in-group members and out-group members to the same degree through their contributions. Displays of in-group love in this intergroup context led to higher ratings of prestige and dominance as compared with displays of universalistic concern for both in-group and out-group members. Displays of in-group love received more leadership support and protection against exclusion from the group as compared with both selfishness and universalistic concern. Taken together, these findings highlight the parochial nature of status conferral: prestige is conferred to in-group members who benefit “us” rather than harm “them” or benefit “everyone.”

4.3 Summary and Conclusions

This section reviewed evidence suggesting that reputation concerns, which enable indirect reciprocity, motivate parochial cooperation in groups. Three requirements have to be met for reputation concerns to fuel parochial cooperation: (1) information about others’ group membership, (2) costly contributions to the group must be available, and (3) social benefits must be conditional on displays of group-serving behavior by in-group members. Consistent with these requirements, three main findings support the conclusion that reputation concerns drive parochial cooperation. First, making information about decision makers’ available shared group membership increases cooperative behavior. Second,
parochial cooperation is stronger in decision tasks that involve simultaneous rather than sequential choices; thus, group-BGR motivates greater cooperation than direct reciprocity. Third, displaying in-group love increases actors’ social standing more than displays of selfishness, out-group hate, or universalistic concern. Taken together, these findings highlight that parochial cooperation rests on social monitoring and rewarding of costly contributions made by in-group members with the purpose of benefitting in-group members.

5. PAROCHIALISM IS MORE PROMINENT AMONG PROSOCIAL INDIVIDUALS

At the outset, we noted that individual willingness to self-sacrifice and cooperate depends on the individual’s positive other-concern paired with the trust that others will reciprocate (Pruitt & Kimmel, 1977). There are important individual differences in the tendency to have high other-concern and trust, and thus to cooperate. Whereas some individuals are predisposed to be concerned with their personal welfare, and disregard or even negatively value others’ welfare (henceforth individualists), a substantial portion of the human population is prosocial in its orientation and value the welfare of others, as well as themselves (henceforth prosocials) (McClintock, 1972; Van Lange, 1999; Van Lange & Kuhlman, 1994). Decades of research in social psychology has shown such social value orientations not only to be relatively stable but also to predict cooperation in a variety of situations. For example, prosocial individuals are more likely to make concessions and to value fairness in bargaining and negotiation (De Dreu & Boles, 1998; De Dreu & Van Lange, 1995; Handgraaf, Van Dijk, & De Cremer, 2004); they opt for more constructive conflict resolution in organizational disputes (Nauta, De Dreu & Van der Vaart, 2002) and, most relevant here, contribute to group efficiency in both two-person and N-person social dilemmas (e.g., Balliet, Parks, & Joireman, 2009; De Dreu & McCusker, 1997; McClintock & Liebrand, 1988).

5.1 Prosocial Individuals Escalate Intergroup Conflict

Because of its heavy focus on interpersonal and single-group dilemmas, past work on social value orientation leaves unclear how prosocial individuals operate in intergroup settings more or less marked by intergroup competition. In fact, two markedly different possibilities exist. First, if prosocial individuals are primarily motivated to contribute to collective efficiency, then
we should see reduced intragroup cooperation in intergroup competition because such cooperation implies collective inefficiency (i.e., cooperation is “wasted” on competing against the out-group and destroying each other’s resources). Alternatively, however, if prosocial individuals are primarily motivated to contribute to in-group efficiency, then we should see increased cooperation in intergroup competition in the form of in-group love and, perhaps, out-group hate (Arrow, 2007). If this were true, it would follow that prosocial values are parochial and reminiscent of an evolved capacity to contribute to relatively confined and well-defined in-groups.

First evidence that prosocial individuals are parochial rather than universal cooperators derives from a study by Abbink, Brandts, Herrmann, and Orzen (2012). These authors classified individuals on the basis of decisions in one-shot prisoner’s dilemma games, as cooperators (viz., prosocials) or non-cooperators (viz., proselfs), created groups of prosocials and proselfs, and pitted these groups against one another in an intergroup competition game. Individuals within each group contributed out of a personal endowment, and group totals were compared. The group with the greatest overall investment from its members won the contest and acquired a prize. Results showed that groups invested more than the value of the prize to be won and, critically, groups composed of prosocials invested more than groups composed of proselfs. Thus, intergroup competition was much fiercer between groups of prosocials, rather than between groups of proselfs.

The Abbink et al. study was not designed to decompose parochial cooperation into in-group love and out-group hate. This issue was, however, addressed in De Dreu (2010a). Participants in that study were invited to the laboratory for two independent sessions. In the first, their social value orientation was assessed using a well-established decomposed game measure (De Dreu & McCusker, 1997; Van Lange, 1999; Van Lange & Kuhlman, 1994). Most participants could be reliably classified as prosocial or individualist, and moved on to the second session in which they engaged in the IPD-MD game (Halevy et al., 2008; also see Section 1.3). Following decision-making in the IPD-MD game, a short questionnaire assessed in-group trust and out-group distrust, and the extent to which allocation decisions were motivated by egoism, fairness, or spite.

Figure 2 shows in-group love and out-group hate as a function of social value orientation in De Dreu (2010a). Compared to individualists, prosocial participants contributed significantly more to in-group love, and not more or less to out-group hate. This implies that prosocial individuals are parochial cooperators more than universal cooperators because in the latter case, we
should have seen increased in-group love as well as reduced out-group hate. Follow-up analyses revealed that prosocial individuals, more than individualists, expected greater in-group love from fellow in-group members (but not more or less out-group hate), and these positive expectations accounted for their own contributions to in-group love. Put differently, prosocials not only display strong levels of in-group love, but also trust such in-group love to be reciprocated by fellow in-group members.

5.2 Prosocial Representatives are Parochial in Intergroup Bargaining

Especially when groups are relatively large, intergroup competition is regulated by delegates who represent their in-group, for example, in negotiating settlement with the rivaling out-group (De Dreu et al., 2014). Economic theory identified the principal-agent problem, which includes the possibility that delegates’ self-interests may not be aligned with those of the in-groups they represent. Put differently, delegates may be motivated to negotiate settlements that serve themselves more than their in-group. For example, paying a divorce attorney by the hour will incentivize the attorney to proceed slowly, even when quick settlement is in the best interest of the partner she is representing.

Situations in which delegates’ self-interests are misaligned with those of their in–groups allow for parochial cooperation. From the above studies showing that prosocial individuals tend to be parochial cooperators more than individualists, it follows that delegates with a prosocial value orientation would be more inclined to self-sacrifice to benefit their in-group than
individualistic delegates. To test this possibility, Aaldering, Greer, Van Kleef, and De Dreu (2013), developed an intergroup conflict game in which individuals negotiated on behalf of their in-group with the out-group representative. The negotiation was structured so that the individual’s self-interest was either opposed to, or aligned with the interests of their in-group, and always opposed to the out-group. Concessions always hurt the delegate’s self-interest and always benefited the out-group. Depending on condition, however, concessions either benefited or hurt in-group interests. Aaldering et al. predicted that individualists would be relatively immune to such interest (mis)alignment, and that prosocial delegates would be more cooperative with the out-group, but only when this would benefit their in-group as well.

In Experiment 1, delegates were randomly assigned to the conditions of a $2 \times 2$ factorial design that orthogonally crossed structure of the negotiation task (personal interests opposed to out-group only or to both in-group and out-group) and social value orientation of the delegate (prosocial or individualistic). Results showed that prosocials made more generous first offers and needed fewer rounds to settle than individualistic representatives. Crucially, however, prosocials were more cooperative toward the out-group only when their self-interests opposed those of the in-group (and conceding to the out-group thus benefitted their in-group too); when cooperation benefitted the out-group and hurt the in-group (and the delegate’s self-interest as well), prosocials were as tough in negotiating as individualists.

Experiment 2 replicated and extended these results. Participants were randomly assigned to the conditions of a $3 \times 2$ factorial design crossing negotiation structure (self-interests opposed to out-group only, self-interests opposed to both in-group and out-group, or self-interests opposed to in-group only) with social value orientation (prosocial or individualistic). Replicating the findings from the first experiment, when delegates’ self-interests opposed those of both their in-group and the out-group, prosocials were more self-sacrificial than individualists (i.e., more cooperative offers, faster settlement rates, and better deals); no such stronger self-sacrifice among prosocials was observed when their self-interests were aligned with their in-group and opposed to their out-group. Critically, when delegates’ self-interests were opposed to those of their in-group (and aligned with the out-group’s), prosocials again were more self-sacrificial than individualists.

Much in line with the idea that prosocial individuals are essentially parochial cooperators, the results from Aaldering et al. thus showed that
prosocials sacrificed themselves more when it benefitted their in-group only compared to when self-sacrifice benefitted both in-group and out-group. Individualists, in contrast, sacrificed their in-group to benefit themselves: When their self-interests were opposed to the in-group only rather than to both in-group and out-group, they negotiated fewer rounds and reached more self-benefitting agreements.

5.3 Summary and Conclusions
Decades of research on social motives focused exclusively on interpersonal and intragroup interactions. Recent investigations explored two competing hypotheses concerning prosociality’s consequences in intergroup settings. The first hypothesis suggests that prosociality is manifested in greater concern for others’ well-being, disregarding others’ group membership. The competing hypothesis suggests that prosociality is manifested in greater concern for others’ well-being, conditional on others’ in-group membership. Consistent with the theory of BGR, we found support for the latter hypothesis over the former. These findings shed light on an important person–situation interaction in intergroup interaction, and uncover the parochial nature of prosocial motivation.

6. PAROCHIALISM IS SUSTAINED BY HYPOTHALAMIC OXYTOCIN
That both reputational concerns and prosocial values underlie parochialism is consistent with evolutionary perspectives on human cooperation. Such findings support the position that humans have evolved adaptations designed to encourage individuals to be concerned about group outcomes and to maintain a positive standing in the group in order to reap the indirect benefits from a system of indirect reciprocity that is bounded by group membership. While such reputational concerns and prosocial values may be conditioned by culture, socioeconomic situations, and institutional specificities, an evolutionary perspective proposes an adaptation to process information from the social context and output motivational responses relevant to promoting cooperation (Tooby & Cosmides, 1992). Put differently, if parochialism promoted individual and group survival in the ancestral environment (Darwin, 1871), then it may have its ultimate cause in evolved psychological adaptations that are designed to process information relevant to the problem of detecting when to engage in parochial cooperation and that operate via neurobiological circuitries
(Rilling & Sanfey, 2011). Indeed, recent evidence finds that parochial cooperation rests on neurobiological circuitries that are evolutionary ancient and transcend species.

One possible candidate is oxytocin, a nine-amino-acid, cyclic neuropeptide that is produced in the hypothalamus and targets the amygdala, hippocampus, and regions of the spinal cord that regulate the parasympathetic branch of the autonomic nervous system (Bos et al., 2012; Donaldson & Young, 2008; Ludwig & Leng, 2006; Neumann, 2008). Oxytocin interacts with the hypothalamic–pituitary–adrenal axis to attenuate stress responses—it reduces cortisol levels after exposure to stressors, inhibits cardiovascular stress responses, and modulates brain areas and neural circuitries involved in the processing of fear-related information (Heinrichs, Von Dawans, & Domes, 2009; Kirsch et al., 2005; Petrovic et al., 2008).

In addition to these anxiolitic effects, oxytocin up-regulates social approach and reward processing and plays a key role in pair–bond formation and maintenance. Accordingly, oxytocin sustains the ability, in humans and nonhuman animals, to quickly recognize others as familiar and in-group versus unfamiliar and out-group (Brennan & Kendrick, 2006; Ferguson et al., 2000; Rimmelle et al., 2009). Oxytocin also enables the individual to experience affective reactions to the observed or anticipated experiences of others, and to take another person’s perspective, and increases tendencies to extend trust to others, and to cooperate with them (Kosfeld et al., 2005), especially those that people have met before (DeClerck et al., 2010) and those that appear trustworthy (Mikolajzak et al., 2010).

In short, oxytocin targets two core motives underlying (parochial) cooperation—it reduces anxiety and fear of betrayal, and it up-regulates positive other-concern. Importantly, these two functions transcend mammalian species, and have been documented in voles, rats, sheep, and (non)human primates (Carter, 2014; De Dreu, 2012; Donaldson & Young, 2008). It makes oxytocin a strong candidate for providing the neurohormonal underpinnings of parochial cooperation. Here we review the evidence for this possibility.

### 6.1 Oxytocin Enables Parochial Cooperation

That parochial cooperation is rooted in, and sustained by oxytocin follows from a study by Ten Velden, Baas, Shalvi, Kret & De Dreu, 2014. Male participants received 24IU oxytocin or matching placebo, and played four rounds of an incentivized two-player poker game with either an in-group or out-group antagonist. On each round participants received either low
or high value cards to create differences in competitive strength, and then responded to a (pre-programmed) bet placed by their in-group or out-group antagonist. The three possible responses were (1) withdrawing (i.e., pass), (2) settling (i.e., calling), or (3) aggressing (i.e., raising). Results shown in Figure 3 revealed that under placebo, participants withdrew and competed depending on their own (low vs high) competitive strength, regardless of their antagonist’s group membership. Under oxytocin, however, participants settled more and competed less with an in-group as compared to an out-group antagonist; withdrawal was unaffected by group membership. This result suggests that oxytocin sensitizes humans to the group membership of their interaction partner, rendering them relatively more benevolent toward in-group, compared to out-group partners.

Perhaps the most direct evidence for the notion that parochial cooperation is modulated by oxytocin was provided in De Dreu et al. (2010). Experiments 1 and 2 relied on the IPD-MD to examine whether oxytocin motivates in-group love, out-group hate, or both. In a double-blind, randomized between-subjects design, male participants self-administered oxytocin or placebo and were given an endowment of €10 to keep, to invest in in-group love, or to invest in out-group hate. Across both experiments, participants given oxytocin kept less for themselves, contributed more to in-group love, and contributed equally to out-group hate, than those given placebo. Clearly, oxytocin motivated parochial cooperation, and in-group love in particular.

Figure 3 Average settlement (calling) and aggression (raising) in a simplified poker game with in-group or out-group antagonists for individuals given placebo or oxytocin (based on Ten Velden et al., 2014).
6.2 Oxytocin Motivates Defensive Aggression

In the IPD-MD, investing in out-group hate is essentially spiteful—it does not, in any way, benefit the in-group more than investing in in-group love, nor does it protect the in-group against possible harm inflicted by the rivaling out-group more than investing in in-group love. Put differently, the IPD-MD does not allow expression of defensive aggression against the out-group (e.g., Simunovic et al., 2013). Experiment 3 by De Dreu et al. (2010) was designed to examine whether oxytocin could, in principle, motivate group members to aggress against the out-group to (1) protect and defend the in-group against out-group threat, (2) subordinate the out-group and increase the (relative) wealth of the in-group, or (3) some combination of these two goals. Participants in Experiment 3 were given oxytocin or placebo, and made a series of decisions to cooperate or compete in a two-person social dilemma. Participants represented their in-group knowing that revenues from the decision making task would be split evenly across all three in-group members, the participant included, and the antagonist represented his out-group, knowing that revenues from the decision making task would be split evenly across all three out-group members, the out-group antagonist included. Cardinal payoffs from the game were manipulated between-subjects so that (1) competing yielded relatively high or low gains when the out-group antagonist would cooperate and/or (2) cooperating yielded relatively high or low losses when the out-group antagonist would compete. Thus, the game structure was altered to make greed either stronger or weaker as a motive for competing, and to make fear either stronger or weaker as a motive for withholding cooperation.

Results from Experiment 3 revealed, first of all, that oxytocin compared to placebo neither strengthened nor weakened the greedy motivation to compete against out-groups. Second, as shown in Figure 4, participants given oxytocin did compete more against the out-group when fear of possible exploitation was high rather than low, whereas participants given placebo were not affected by the fear manipulation. Whereas oxytocin does not (de)motivate territorial, offensive aggression against rivaling out-groups, it does seem to motivate defense-oriented aggression against out-groups that pose a strong threat to the in-group (Figure 5).

The conclusion that oxytocin motivates defensive aggression fits results from several other studies. Hahn-Holbrook et al. (2011), for example, observed that breastfeeding mothers (compared to bottle-feeding mothers) were more aggressive against intruding strangers and that such heightened
aggression was mediated by peripheral (i.e., blood plasma) oxytocin levels. Madden and Clutton-Brock (2011) studied free-living meerkats and observed that peripheral administration of oxytocin rather than placebo increased not only tending behavior such as associating with pups, but also defending behavior such as time spent on guard; in rats oxytocin can motivate aggression against threatening intruders (Bosch et al., 2005).

Without exception, in all of these studies, personal and in-group interests were perfectly aligned and aggressing against threatening out-group rivals served both personal and in-group interests simultaneously. Accordingly, these studies left unanswered whether defensive responses were motivated by increased desire to care for and protect (1) in-group members, and vulnerable members in particular, (2) personal interests, or (3) some

**Figure 4** Mean contributions to in-group love and out-group hate by individuals given placebo or oxytocin (based on De Dreu et al., 2010).

**Figure 5** Competitiveness (out of three possible choices between cooperation or competition) among individuals given placebo or oxytocin when their out-group antagonist is low versus high threat to in-group outcomes (based on De Dreu et al., 2010).
combination of personal and in-group interests. To disentangle these possibilities, De Dreu, Shalvi, Greer, Van Kleef, and Handgraaf (2012) conducted an experiment modeled after Experiment 3 in De Dreu et al. (2010). Male participants represented their three-person in-group and made decisions to compete or cooperate in a prisoner’s dilemma with an out-group antagonist who represented the three-person out-group. The game structure was manipulated to create four different conditions. In the high (low) personal fear conditions, cooperating with the out-group yielded relatively high (low) losses to oneself when the out-group antagonist would compete. In the high (low) in-group fear conditions, cooperating with the out-group yielded relatively high (low) losses to one’s fellow in-group members when the out-group antagonist would compete. Thus, personal vulnerability and in-group vulnerability were manipulated independently of each other, which allowed seeing whether oxytocin (compared to placebo) would motivate competition toward the out-group when personal and/or in-group vulnerability was high.

Results revealed that when personal vulnerability was high, participants competed against the out-group rival and this competition was not influenced by oxytocin or whether in-group vulnerability was high or low. When personal vulnerability was low, participants relaxed their competitiveness and more often made cooperative choices. Importantly, however, this was not the case when in-group vulnerability was high and participants received oxytocin rather than placebo. Put differently, oxytocin motivated a defensively aggressive response when out-group rivals threatened fellow in-group members even when personal interests were not at stake.

6.3 Oxytocin Motivates In-Group Serving Dishonesty

Whereas De Dreu et al. (2012) focused on understanding better oxytocin-motivated competition against out-group rivals, Shalvi and De Dreu (2014) examined whether oxytocin-motived in-group love can be understood in terms of increased motivation to serve self-interest, in-group interests, or some combination thereof. Grounded in the idea that humans tradeoff universal morals (e.g., “thou shall not lie”) and self-interests, they examined cheating in a setting where cheating would be profitable and undetectable. Participants were asked 20 times to predict the outcome of a coin toss, keep their prediction in mind while the coin was tossed, and after they saw the outcome, indicate whether they did or did not correctly predict the outcome. Correct predictions were rewarded with 0.10 each; incorrect predictions were not rewarded. In one condition, participants’
earnings from the prediction task would be split evenly amongst themselves and two other in-group members who also made predictions. In another condition, participants’ earning would be awarded to themselves only and not affect the outcomes of the two other in-group members who also made predictions. Thus, by cheating (i.e., indicating they correctly predicted the coin toss more often than 50% of the time) participants could earn money for themselves only, or for themselves and two other in-group members.

Half of the participants in Shalvi and De Dreu (2014) received oxytocin; the other half received a matching placebo (double-blind, randomized between-subjects). Results showed that when earnings went to oneself only, participants cheated moderately and their cheating was not influenced by oxytocin. When earnings went to oneself and the two other in-group members, however, cheating was more prevalent and especially when participants received oxytocin rather than placebo. Put differently, oxytocin motivates humans to bend the truth but only when this serves their in-group and not when it exclusively serves their personal self-interest.

6.4 Summary and Conclusions

Research on the neurobiological circuitries underlying parochial cooperation consistently identified oxytocin as a catalyst of self-sacrificial behavior in intergroup conflict situations. Oxytocin dampens self-interested behavior and increases costly displays of in-group love (but not out-group hate). Oxytocin has been shown to increase defensive aggression in intergroup interactions, as well as cheating on behalf of an in-group. These findings are consistent with the evolutionary perspective on parochial cooperation; they also advance knowledge about the group-level (rather than interpersonal) functions of oxytocin by showing that it regulates important inter-group behaviors.

7. DISCUSSION AND RESEARCH AGENDA

We began our chapter with short narratives of Walter Süskind, a Jewish refugee who risked and sacrificed his life to save Jewish children from the Nazis, and Nadia Asyalova, a women from the North Caucasus who blew herself up to kill and wound civilians from enemy Russia. We wondered whether the benign and prosocial “in-group love” by Süskind and the utterly destructive and violent “out-group hate” by Asyalova are, perhaps, extreme manifestations of some basic motives within each of us, and we
wondered whether these prosocial and antisocial tendencies may not be brighter and darker sides of the same coin, sharing neurobiological roots and chronic predispositions.

We approached these possibilities by reviewing work on parochial, in-group bounded cooperation that helps groups avoid disasters and generate surplus from which all individual group members benefit, in their proximal well-being and prosperity as well as in their long-term inclusive fitness. Our review documented that (1) in intergroup comparisons and conflict, parochial cooperation can take the form of in-group love and out-group hate; (2) in-group love is both the primary motive and manifestation (Balliet et al., 2014; Halevy et al., 2008; Halevy, Weisel, et al., 2012); (3) self-sacrifice and parochial cooperation emerges when opportunities for indirect reciprocity are present, so that (4) parochial cooperation benefits the individual’s reputation as a reliable and trustworthy cooperator who should be included in, rather than excluded from the group. Indeed, parochial cooperation, and in-group love in particular (5) creates a positive reputation and affords the individual with social standing and status within one’s group. Finally, we showed that (6) parochial cooperation is enabled and modulated by oxytocin.

The work reviewed here, and the emerging insights just reviewed, is consistent with the idea that evolution and culture pressured humans into parochial cooperators, willing and able to self-sacrifice for the benefit of fellow in-group members, to care for and identify with their group as a whole and, if necessary, to lash out against rivaling out-groups and threatening intruders. As such, bothSuskind and Asiyalova were extreme exemplars of the prototypical parochial cooperator, with their extreme forms of in-group love and out-group hate leading to, and perhaps being motivated by, the same ultimate goal—providing for the relative survival and prosperity of their own group. We surmise that their socialization, religious background, or peer pressures added the reputation benefits and prosocial values that strengthened their biologically prepared inclination to care for their group and enabled them to make the ultimate self-sacrifice.

### 7.1 Evolutionary Perspectives versus Social Identity Perspectives

That human “group psychology” evolved in, is motivated by, and functions to deal with intergroup relations fits two important strands of theory and research, and the research we reviewed here speaks to both. The social
identity approach essentially argues that humans categorize themselves and others into in-groups and out-groups, and base part of their self-view on the social categories and groups they belong to. To achieve and maintain a positive self-view, humans seek to develop a positive social identity by developing and protecting benevolent views of their in-group, and sometimes also by developing and enacting more negative views of out-groups (e.g., Dovidio & Gaertner, 2010; Ellemers, 2012; Hewstone et al., 2002; Tajfel & Turner, 1979). Positive social identity striving should, according to this social identity approach, be the primary function of and reason for parochial cooperation in general, and in-group love and out-group hate in particular (Brewer, 1979, 2007).

Evolutionary perspectives on human cooperation offer a radically different view on the functions of in-group love and out-group hate. Articulated well in the theory of BGR, the idea is that because groups provide for survival and prosperity, individuals are biologically and culturally prepared to contribute to their group, and if necessary to fight rivaling out-groups (Yamagishi et al., 1999). Groups provide opportunities for indirect reciprocity, and interdependent individuals within groups are thus concerned about their reputation of being a reliable, loyal, and trustworthy cooperator. Developing and maintaining such a reputation should, according to these evolutionary perspectives, be a primary function of and reason for parochial cooperation in general, and in-group love and out-group hate in particular.

The evolutionary perspective most directly deals with costly cooperation. In contrast, most of the work inspired by the social identity approach provides solid evidence for the existence of social identity striving, and for the consequences of having a strong (versus weak or absent) positive social identity for individuals’ self-esteem (Rubin & Hewstone, 1998), their attitudes and behavior in organizational contexts (Riketta, 2005), or the tendency to display less costly and consequential forms of intergroup bias, which Mummendey and Otten (2001, pp. 112–132) labeled “mindless in-group favoritism.” The evidence that social identity is related to self-sacrificial cooperation is less abundant, typically gathered in N-person social dilemmas (e.g., Brewer & Kramer, 1986; Wit & Kerr, 2002) and can, accordingly, be explained also by implicitly activated reputation concerns and expectations of partner cooperation (Yamagishi & Mifune, 2008). In fact, we showed here that when mutual interdependence increases, cooperation becomes more parochial, and with reputation concerns rendered moot, individuals no longer discriminate in the costly cooperation
between in-group and out-group members (Balliet et al., 2014; Kiyonari & Yamagishi, 2004; Yamagishi et al., 1999; Yamagishi & Mifune, 2009).

An admittedly bold and provocative implication that follows from the present analysis is that social identity striving is largely distinct from parochial cooperation in general, and does little to motivate behavioral displays of in-group love and out-group hate in particular. While targeted research is needed to confirm this, downplaying the role of social identity striving in parochial cooperation not only allows for a more parsimonious perspective—opportunities for indirect reciprocity are all we need—but also allows theory to generalize to other group living animals that clearly have no room for social identity striving, yet do display parochial cooperation, such as ants (Wilson, 2012) and nonhuman primates (Manson and Wrangham, 1991). Interestingly, in different group-living mammals, parochial cooperation has been traced back to oxytocin—the neuropeptide we discussed here for its crucial role in creating a tend-and-defend response in humans. Possibly, oxytocin reduces the fear of betrayal and increases the concern and empathy for familiar others, that is, it enables group living animals, including humans, to recognize, adapt to, and act upon opportunities for indirect reciprocity.

Some people more readily recognize, adapt to, and act upon opportunities for indirect reciprocity, and individual differences therein may reside in their biological make-up, in their socialization, or in some combination of both. The traditional distinction between individualistic and prosocial value orientation was invoked to see whether those with prosocial values, who are more likely to have positive other-concern and more strongly focus on joint welfare and group prosperity, would either be more or less inclined toward parochial cooperation. Indeed, as recent studies showed, prosocial individuals are parochial cooperators more than their individualistic counterparts. New research is needed to examine whether prosocial individual’s tendency toward parochialism rests on their greater sensitivity to opportunities for indirect reciprocity, and the concomitant reputation concern to be seen as reliable and trustworthy cooperator. If true, we should see, for example, that prosocials’ display of parochial cooperation weakens or disappears when reputation is not at stake and opportunities for indirect reciprocity are absent.

The work reviewed here requires rethinking of the role and relevance of social identity striving in parochial cooperation and self-sacrifice in intergroup conflict. It requires some rethinking also of the mere concept of prosocial values, which may be less about benefitting all and more about
benefitting close and similar others. Clearly, new research is needed to further explore and formalize these possibilities. Such new research should also consider including additional manifestations of in-group love and out-group hate, including (implicit) attitudes and beliefs, pressures to conform and adherence to group norms, and tendencies to punish free-riders and reward cooperators from one’s in-group and herald those who derogate and aggress out-groups. Social psychological science has studied many of these components in sophisticated research designs, and these early works provide an excellent starting point for further understanding and documenting the root causes of parochial cooperation, its distinct forms, along with its distal and proximal functions.

### 7.2 Hypotheses Inspired by Biological Models

One thriving area of research on human cooperation is testing population biology models of the evolution of human cooperation (Axelrod & Hamilton, 1981; Rand & Nowak, 2013). This approach begins with various well-established assumptions about evolutionary dynamics and then uses computer simulations to test hypotheses about how different social structures can facilitate the evolution of specific strategies that promote cooperation. One consistent finding of this literature is that evolution tends to select for conditional cooperators—that is, strategies to cooperate only under specific circumstances, such as with kin, with other’s whom we share extended future interactions, and when we know another’s reputation (Nowak, 2006). More recently, these biological models have provided some support for an additional form of conditional cooperation, parochial cooperation, which can be a successful strategy to promote cooperation (Choi & Bowles, 2007; Efferson, Lalive, & Fehr, 2008; Fu et al., 2012; Garcia & van den Bergh, 2011; Hammond & Axelrod, 2006; Jansson, 2013; Konrad & Morath, 2012; Masuda, 2012). Yet, such findings need to be extended to formulating and testing specific information processing procedures that evolved as the adaptations promoting such behavioral strategies (see Tooby & Cosmides, 2005).

These models can prove to be an inspiration to social and behavioral scientists seeking to generate testable hypotheses about the conditions that affect parochial cooperation. For example, the models can imply that it is plausible that a specific strategy evolved to promote cooperation and these strategies may provide insight into potential psychological processes that enable that behavioral strategy. To illustrate, one difference amongst models of parochial cooperation is the extent that inter-group
competition is necessary to fuel the evolution of parochial cooperation. While some models emphasize that inter-group competition is important for parochial cooperation to evolve (e.g., Choi & Bowles, 2007) other models imply that parochial cooperation may evolve in the absence of inter-group competition (e.g., Fu et al., 2012; Masuda, 2012). While there is work that does suggest that people cooperate more with the in-group in the presence of inter-group competition (Bornstein & Ben-Yossef, 1994), there has not been a systematic program of research that outlines the different forms of input from the social context that would promote parochial cooperation and the extent that the input relies on information about out-groups.

Other models outline how different aspects of the social structure could promote that evolution of strategies for parochial cooperation, such as the type of interdependence and group size. Jansson (2013) discovered that parochial cooperation was a successful strategy for solving coordination games, but not necessarily a situation that contains a conflict of interests, such as a social dilemma. Certainly, there is an abundance of research that does suggest people cooperate more with in-group, compared to out-group, members, in social dilemma situations (Balliet et al., 2014). Yet, research has not considered if people perceive the social dilemma as an actual dilemma when interacting with either in-group versus out-group members, and future work could compare decisions to cooperate with in-group and out-group members in situations with corresponding versus conflicting outcomes. Additionally, Konrad and Morath (2012) discovered that parochial cooperation is an evolutionary successful strategy especially in smaller group sizes. This would suggest that humans may employ parochial cooperation under smaller, compared to larger, group sizes—a hypothesis that has not yet been tested. As we illustrate here, evolutionary models of parochial cooperation may provide a rich source of inspiration for generating and testing hypotheses.

### 7.3 The Role of Emotions in Parochial Cooperation

One particularly relevant issue awaiting new research concerns the emotions associated with, and giving rise to displays of in-group love and out-group hate. Research on intergroup emotions from an evolutionary perspective (Cottrell & Neuberg, 2005) suggested that out-groups that pose threats to different desired ends (e.g., physical safety vs purity) trigger different emotional reactions (e.g., anger vs. disgust) aimed at promoting adaptive behavioral reactions (e.g., aggressing vs avoiding). Future research may
investigate how different types of threats and the ensuing emotional reactions relate to parochial cooperation within groups. Another interesting direction for future research concerns the relationship between prosociality, in-group love, and the experience of moral collective emotions (e.g., collective guilt; Branscombe & Doosje, 2004; Roccas, Klar, & Liviatan, 2006). The research we reviewed earlier suggests that prosociality and in-group love motivate participation in intergroup conflict, which causes much harm to out-group members. Future research may investigate whether heightened concern for the welfare of fellow in-group members diminishes sensitivity for wrongdoing by in-group members and for the suffering of out-group members.

Finally, future research should explore antecedents of human cooperation across group boundaries. Although much cooperation takes place within groups, there are notable exceptions of cross-group cooperation. Recent investigations emphasized the ability of global identities to motivate large-scale, cross-group cooperation (Buchan et al., 2009, 2011). One theoretical possibility is that such cooperation, while collectively beneficial, is nonetheless driven by individuals’ desire to benefit fellow in-group members rather than by a universalistic concern. Parochialism is not without bounds, and future research should address the environmental and psychological conditions that curb the robust tendency to cooperate primarily within groups.

7.4 Reinvigorating Experimental Games and Expanding Its Base

Much of the research reviewed in the preceding sections relied on experimental games to model and study behavior in single-group and intergroup interactions. Nearly four decades ago, in a paper titled “Twenty years of experimental gaming”, Pruitt and Kimmel (1977) characterized research using experimental games as “popular”, yet critiqued it for “lacking theory” and having “little concern for external validity” (p. 363). Considerable progress has been made since that landmark paper on both fronts, with new research testing competing theoretical hypotheses (e.g., about the role of self- and social-categorization versus outcome interdependence in shaping allocation behavior, Balliet et al., 2014; about the effects of prosociality in intergroup interactions: Aaldering et al., 2013; De Dreu 2010b), and researchers complementing laboratory experiments with field studies (e.g., Gneezy & Fessler, 2012; Henrich et al., 2001). In addition, experimental games provided a spring-board for understanding the neurobiological and endocrine bases of human motivation in general, and parochial cooperation
in particular (De Dreu, 2012). And, they have been successfully used to document the ontogeny and developmental course of in-group love and out-group hate (Bauer et al., 2014; Buttelmann & Böhm, 2014; Hamlin et al., 2013).

Although experimental games can be, and have been, crucial in understanding parochial cooperation, and testing targeted hypotheses, they are limiting in some respects. First, the game-experimental tradition has a strong focus on human decision making when humans have two options—to cooperate (contribute) at a cost to oneself, versus to withhold cooperation (contributions) at a cost to others and one’s group. Quite often, however, social animals have a third option to withdraw from the situation—they leave the scene, hide, or refuse to take part in the game (Miller & Holmes, 1975; Shalvi, De Dreu, & Handgraaf, 2011). Future research using experimental games as a tool to understand the neurobiological and motivational underpinnings of parochial cooperation in intergroup conflict would benefit from incorporating opportunities for withdrawal and opting out.

7.5 Parochialism and Intergroup Cooperation

Parochial cooperation is motivated and mobilized by intergroup competition and conflict (Bowles, 2009), yet because parochialism creates strong in-groups that may induce envy and fear in out-groups, parochial cooperation may indirectly fuel conflict between groups (De Dreu et al., 2014). One way to regulating (escalated) intergroup conflict is through negotiation, in which parties communicate about what to give and take in an attempt to settle their (perceived) conflicts of interest and restore feelings of deprivation (Carnevale & Pruitt, 1992; De Dreu, 2010a). Intergroup negotiation is often delegated to individuals or small teams that represent their larger constituencies, and such representatives need to strike a balance between their in-group interests on the one hand, and those of the rivaling out-group on the other—they need to satisfy parochialism within both their in-group and their out-group. Shown here, and elsewhere, in-group love is primary to out-group hate, and herein lies a possible solution for regulating intergroup conflict through negotiation. When intergroup conflict involves several issues, as they often do, and when some issues are less and other issues are more important to one group than to the other, these conflicts have so-called integrative potential. They allow opposing groups to negotiate agreements and settlement that meet the interests and aspirations of both sides, rather than one group in particular (Pruitt, 1981; Raiffa, 1982).
There is a rich literature on integrative negotiation, highlighting a broad range of individual dispositions and situational factors that lead individuals away from or toward exploring and exploiting integrative potential, and settlements that satisfy both sides. However, this literature is heavily focused on interpersonal and within-group negotiations (for reviews see, Bazerman, Curhan, Moore & Valley, 2000; De Dreu, Beersma, Steinel, & Van Kleef, 2007). The (older) literature on intergroup negotiation engaged experimental simulations without integrative potential (for a review, see Druckman, 1994), and only recently work has started to examine intergroup negotiations with integrative potential (e.g., Aaldering & De Dreu, 2012; Halevy, 2008). Thus, the experimental simulations being available together with the sound theoretical base about the origins, functions, and forms of parochial cooperation in intergroup competition provides input for new studies examining when and how intergroup conflict and competition can be meaningfully regulated and settled through (representative) negotiation. Such new research would not only integrate currently disconnected lines of inquiry, but also provide practical insights in how into create and maintain communities, organizations, and societies where strong groups operate next to each other and do not waste resources on protecting themselves against putatively greedy and potentially aggressive out-groups.

8. CODA

We will never know what motivated Walter Süskind to rescue Jewish children from the Nazis and Naida Asiyalova to blow up herself amidst Russian commuters. But their stories triggered some pertinent questions about the root causes and consequences of parochial cooperation in general, and in-group love and out-group hate in particular. Our work, and that of others, strongly suggests that Süskind’s prosocial martyrdom and Asiyalova’s spiteful terror were extreme reflections of the in-group love and out-group hate that resides within each of us, tendencies that are modulated by the oxytocinergic circuitry, that are more prominent among individuals with stronger prosocial value orientations, and that emerge especially in group settings where reputation matters and cooperation is rewarded. Possibly, Walter Süskind and Naida Asiyalova were, like all of us, the products of evolutionary and cultural pressures that molded them into being typically human—a social animal that is prepared to sacrifice self-interest in order to tend-and-defend the group, preferably through in-group love but, if necessary, through out-group aggression.
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