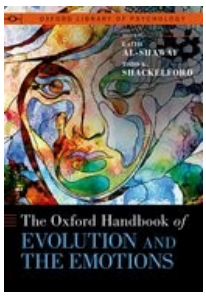


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CHAPTER

# 32 A Socio-functional Perspective on Emotion and Cooperation

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## Abstract

Humans sociality is inextricably linked to cooperation. The human life history required cooperation in the form of pair-bonding, alloparenting, intergenerational transfers of calories, and extensive food sharing among kin and non-kin. Cooperating to achieve mutual goals often led to better outcomes compared to uncoordinated individual efforts. However, avoiding exploitation was critical to managing the challenges of sociality. Building on a socio-functional perspective, this chapter summarizes evidence showcasing the role that emotion plays in guiding *proximate* mechanisms that facilitate cooperation or hinder competition through their effect on partner choice and relationship management. The authors further organize these emotions (e.g., compassion, sadness, gratitude, anger, shame, guilt) by their proposed interpersonal *ultimate* functions based on the ways in which they promote cooperation via (1) distinguishing high-value from low-value partners; (2) building and maintaining lasting cooperative relationships with valuable partners; and (3) identifying when to de-invest from or terminate existing relationships.

**Keywords:** social emotion, interpersonal function, fitness interdependence, cooperation, evolution

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Among human ancestors, cooperating to achieve mutual goals often led to better outcomes compared to individual efforts. While cooperation can be advantageous, cooperation also invites opportunities for exploitation. Throughout evolutionary history, humans have had to manage the challenges of sociality in order to enjoy the benefits. Ancestral humans had to cooperate with partners who were both willing and

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capable of generating benefits; avoid incapable or cost-inflicting partners; maintain long-lasting cooperative relationships; and decide when to terminate existing relationships.

We begin this chapter by summarizing theory and research on the human adaptive complex—the distinctly human collection of evolved physiological and behavioral traits linking life-span developmental trajectory, dietary needs, complex social living, and extensive cooperation with both kin and non-kin. We then discuss how emotions can function as social valuation regulatory mechanisms. Within this framework, emotions are thought to play an important role in guiding cooperative decisions, helping humans form and maintain strong interdependent relationships while managing the potential threats of social partners' cheating and/or defection. We then review the rich body of evidence about specific ways that emotions can support humans in building new positively interdependent relationships; investing in the ↳ maintenance of existing positively interdependent relationships; and terminating negatively interdependent or non-beneficial relationships. Table 32.1 shows a summary of the social emotions covered in this chapter, and their effects on relational valuation and cooperation, organized by their proposed interpersonal function.

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## Sources of Fitness Interdependence: The Human Adaptive Complex

Humans are highly interdependent organisms, relying on one another for survival and reproduction (Aktipis et al. 2018). Compared to nonhuman primates, humans reach reproductive maturity later, with far longer juvenile periods. During this juvenile period, children are dependent on others to subsidize their energy needs (Kaplan et al., 2000; Kaplan et al., 2007). In contrast, with the acquisition of knowledge and specialized skills, human adults eventually produce more calories than they consume, creating energy surpluses that are invested in juveniles.

The demands associated with the long period of juvenile dependency are managed in large part through cooperative resource provisioning and caregiving. Food production among hunter-gatherers is characterized by a division of labor by sex, with men primarily investing in hunting (and provisioning excess calories), and women primarily investing in gathering and high-quality childcare (Kaplan et al., 2000; Kaplan et al., 2007). Humans also engage in highly cooperative breeding, with juveniles receiving care from adults other than their mother, as well as older juveniles (Hrdy, 2007; Kramer, 2011), especially under harsher environments (Martin et al. 2020). Humans have remarkably long life spans as well, spending over one-third of their lives in the post-reproductive stage—a period in which they can continue to provide surplus food and caregiving support (Kaplan et al., 2000).

This unique human life history is thought to be an adaptation to the distinct ecological feeding niche exploited by humans (Del Giudice et al., 2016; Kaplan et al., 2000; Kaplan et al., 2007). The human diet consists of skill-intensive, nutrient-rich foods that demand extensive cooperation between kin and non-kin to forage effectively. On average, the hunter-gatherer diet consists of 60% hunted foods, 32% difficult to extract foods (e.g., food that is underground, or with hard shells), and only 8% easily collected foods (e.g., fruit) (Kaplan et al., 2000). A consequence of relying on nutrient-rich foods, such as large animals, is that the return rate is highly variable. For example, Hill and Hurtado (2009) observed that hunters can expect to be successful as little as 4% or as much as 60% of the time, depending on the ecology. In addition, illness and injuries often prevent individuals from foraging altogether.

A solution to this problem, observed across all hunter-gatherer groups, is to engage in cooperative food-sharing (Cronk et al., 2019). Food-sharing reduces variance in daily consumption, subsidizing caloric needs when one is sick, injured, or just unlucky (Kaplan et al., 2000). For example, Ache hunter-gatherers who share can consume up to 80% more calories than those who do not share (Kaplan et al., 1985; Kaplan & Hill, 1985). Similarly, Ache men who share larger amounts of food, in proportion to what they produce, typically receive more food from others when they are sick or injured (Gurven et al., 2000). Thus, humans pool

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calories by transferring to group members surpluses from large-game hunting and acquisition of other nutrient-rich foods—tasks that are themselves most effectively accomplished through cooperative efforts.

In addition to pooling calories, cooperation allows humans to mitigate a variety of other risks to fitness, such as injuries, illness, loss of valuable partners or objects, and conflicts such as aggression and exploitation. Among Tsimane horticulturalists, for example, people who experience these problems report receiving help in the form of food, medicine, money, or childcare—primarily from kin and spouses,
p. 624 although non-kin are also valuable sources of ↳

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support (Gurven et al., 2012). Beyond food-sharing, other forms of risk-pooling have also been observed across all types of subsistence groups. For example, Maasai herders transfer livestock to risk-pooling partners after droughts; Fijian fisher-horticulturalists provide aid after cyclones; and ranchers in the American Southwest help neighboring ranchers in response to unforeseeable labor challenges (Cronk et al., 2019). Whether it's in terms of calories, childcare, or labor, risk-pooling over time makes social partners intrinsically valuable, because partners share a stake in each other's fates (Aktipis et al., 2018; Ayers et al., 2023; Balliet et al., 2017; Roberts, 2005).

While they are crucial elements of the human adaptive complex, the cooperative behaviors above inherently involve social dilemmas, each with multiple potential solutions in which the best outcome for the *individual* is sometimes at odds with the most *mutually* beneficial outcome. One example involves the trade-off between investment in current offspring versus future reproduction (Del Giudice et al., 2016). The extended juvenile period during which children are calorically dependent requires heavy biparental investment. However, men may have the opportunity to increase their fitness by acquiring multiple mates (Courtiol et al., 2012), which can result in reduced investment in existing offspring and thereby imposes a cost on the mothers' fitness. Thus, men can increase their fitness by defecting on universally recognized rules of pair-bonded biparental investment (i.e., marriage).

Another example is in the domain of food-sharing. Hunting is risky, energetically costly, and presents opportunity costs (Kaplan et al., 2000). One could potentially maximize individual gains by exploiting others' generosity or defecting from the risk-sharing contract—if one can do so without suffering penalties. For example, experimental studies show that people are more likely to act greedy (i.e., request help when not in need), and stingy (i.e., refuse helping even when able to) when resources can be hidden, because people cannot know whether risk-pooling partners are faking need or are genuinely unable to help (Claessens et al., 2020).

Because the potential for "free-riding" invariably arises in cooperative relationships, humans have evolved cheater-detection mechanisms that help identify and sanction those who violate the rules of cooperation (Cosmides et al., 2010). While cheater-detection mechanisms are computationally complex, and punishing defectors can be individually costly, an alternative solution to the free-rider problem is to simply choose which partners to interact with (Noë & Hammerstein, 1994, 1995). Partner choice can involve selecting

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partners carefully, but also can simply be a matter of leaving uncooperative partners and groups (Aktipis 2004, 2011).

The need to differentiate high-quality cooperative partners from low-quality partners presented an important adaptive problem for ancestral humans. Individual variation in both ability and willingness to deliver benefits gave rise to biological markets for cooperators, in which high-quality individuals chose the best available partners, and individuals had to compete to be chosen by those with the most benefits to share (Barclay, 2016; Barclay & Willer, 2007). This competition for being chosen as a cooperative partner influenced our social evolution in myriad ways (Nesse, 2007). Humans who possessed psychological mechanisms that allowed them to both show that they were good partners and ascertain whether others were good partners would have an evolutionary advantage over those who didn't (Tooby & Cosmides 1996). This shaped selection pressures for the ability to identify high-quality prospective partners, sustain lasting, positive fitness-interdependent relationships, and decide when to de-invest from or terminate relationships that were costly or no longer beneficial.

## Emotions and the Problem of Cooperation: Theoretical Perspectives

If the need to differentiate high- from low-quality cooperative partners presents an adaptive problem, what
p. 631 is the solution? Emotions may have evolved to help humans (and our ↳ mammalian and primate relatives) navigate this complex terrain (e.g., Fischer & Manstead, 2016; Keltner & Haidt, 1999; Shiota et al., 2004). Emotions can be defined as complex responses to recurring, fitness-relevant situations, consisting of cognitive, physiological, motivational, and nonverbal expressive elements that, taken together, tend to orchestrate a behavioral response that proved adaptive more often than not for us and our mammalian ancestors (Adolphs & Andler, 2018; Cosmides & Tooby, 2000; Ekman, 1992; Hommel et al., 2017; Keltner & Gross, 1999; Tracy, 2014).

Twentieth-century research on emotions typically emphasized intrapersonal adaptive functions, in which emotionally motivated behavior directly enhances the organism's fitness. For example, fear can help an organism escape from a predator (Cosmides & Tooby, 2000; Ohman & Mineka, 2001); and emotions surrounding hunger, such as appetitive enthusiasm, support the organism's actions to acquire food (Levenson, 1999). In contrast, 21st-century research has more strongly emphasized interpersonal or social adaptive functions, in which emotions facilitate relationships with other conspecifics, with the relationships serving as the fitness-enhancing factor (Fischer & Manstead, 2008; Keltner et al., 2006; Keltner & Haidt, 1999). In the following sections we highlight examples of social/interpersonal functions, paying special attention to the proximal roles that emotional responses can play in supporting cooperative behavior.

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## Emotions as Valuation Regulatory Mechanisms

While most emotional responses likely include some elements that influence individual fitness by way of relationships with others, the "social emotions" are thought to have evolved specifically to solve distinct adaptive problems inherent in complex, cooperative social living. Social emotions are thought to track relationship partners' actual and probable impact on one's own fitness; to assign relational value to each partner corresponding to their expected fitness impact; and to update valuations based on partners' contributions to one's welfare (Al-Shawaf et al., 2016; Sznycer & Lukaszewski, 2019; Tooby et al., 2008). Expected fitness implications are evaluated in terms of conspecifics' attributes (e.g., skill) and behavior (e.g., sharing). All else being equal, one should assign higher value to conspecifics who possess benefit-generating attributes in relevant domains, such as skill in acquiring food. However, relationship partners with greater ability to generate benefits may also have greater ability to impose costs (e.g., strength), and partners who impose costs are assigned lower relational value. Thus, valuation is also calibrated by partners' *willingness* to deliver benefits and, to some extent, willingness to make sacrifices to avoid imposing costs.

Within this framework, social emotions serve a dual signaling function. First, emotions convey that one has the capacity to deliver or withhold benefits. For example, pride advertises one's status-elevating attributes and access to valuable resources. Second, emotions such as gratitude draw our attention to potential partners who appear willing to deliver benefits. Because pride can convey the ability to generate benefits, displays of pride can potentially influence others to value you more highly. Gratitude is thought to track others' willingness to sacrifice, and therefore elevates the valuation that the self assigns to benefactors (Sznycer & Lukaszewski, 2019).

## How Social Emotions Guide Cooperative Behavior

We begin this section by briefly describing how emotional expressivity supports cooperative action and allows people to differentiate cooperators from non-cooperators. The examples of cooperation that will follow include giving (i.e., unidirectional transfers of resources); direct, indirect, and generalized forms of reciprocity (i.e., bidirectional and third-party transfers of ↳ resources); negotiation (i.e., bidirectional demands and concessions of resources); punishment (i.e., unidirectional and third-party reductions in another's resources); as well as avoidance and exclusion (i.e., preventing others from gaining access to resources). We recognize that these examples reflect distinct ways in which people engage in and manage resources and resource transfers. However, we make use of the term *cooperation* throughout this chapter in reference to any one of the examples described above, with the unifying framework that these various types of cooperation are *proximately* guided by distinct emotional responses in the service of three basic *ultimate* interpersonal functions: promoting cooperation toward valuable partners, and defection toward low-value partners; shaping existing interdependent relationships to promote commitment to long-term cooperation; and allowing people to recognize when to de-invest from or terminate existing relationships. Wherever appropriate, we highlight the dual roles of emotions in conveying information regarding relational value: first, by conveying information to the self about a target's relational value; and second, by conveying one's own relational value to targets.

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## With Whom Should I Cooperate? Emotions' Role in Choosing Cooperative Partners

### Emotional Expressivity

Among mammals, nonverbal expressions of emotion generally help to coordinate behavior across individuals. For example, fear vocalizations communicate the presence of danger to other group members (e.g., Anderson et al. 2018), and crying evokes others' intent to provide support (e.g., Zickfeld et al., 2021). Laughter is particularly contagious, and shared amused laughter in particular has been found to promote cooperative behavior (Gervais & Wilson, 2005).

Emotional expressivity plays an important role in helping people distinguish likely cooperators from cheaters. People rate targets who smile as more likable and trustworthy, and consequently expect smiling targets to be more cooperative (Krumhuber et al., 2007). Emotional expressivity promotes cooperation in part because people believe that those who act on emotion, compared to people who act on reason, are more likely to make cooperative choices based on pro-social emotions such as guilt and empathy (Levine et al., 2018). This expectation is not unfounded. For example, cooperators tend to express more positive emotion prior to making fair offers; and more negative emotion after receiving unfair offers (Kaltwasser et al., 2017; Schug et al., 2010).

Although people can often distinguish real from feigned cooperative cues, such as smiles (Gunnery & Ruben, 2016) and laughter (Bryant & Aktipis, 2014; Bryant et al., 2018), these cues can be faked (Gunnery et al., 2013), and therefore have the potential to be false signals. For example, Danvers and Shiota (2018) found that partners who displayed dynamically engaged smiles—smiling that occurs in response to a partner's smiling—tended to evoke higher rates of partner cooperation in a subsequent prisoner's dilemma task, even though dynamically engaged smiles did not significantly predict one's own cooperative behavior. This suggests that smiling may sometimes be a manipulative cue rather than an honest signal of cooperative intent.

### Compassion and Empathy

Goetz and colleagues (2010) propose that states such as sympathy, pity, and empathy belong to a cluster of compassion-related states whose primary motivational and behavioral output is alleviating the distress of a target in need. People are more likely to experience empathy for kin and close others (de Waal & Preston, 2017; Preston & de Waal, 2002), but often experience empathy toward strangers as well (Depow et al., 2021; McAuliffe et al., 2018).

p. 633 Compassionate states motivate people to alleviate a target's distress, expending energy on in-the-moment cooperation. For example, trait affective empathy (i.e., feeling emotion in response to a target's emotions, as distinct from simply recognizing them) is associated with greater generosity (Edele et al., 2013). Inducing empathic concern increases cooperation in the prisoner's dilemma as well (Batson & Moran, 1999), even after learning that partners had previously defected (Batson & Ahmad, 2001), and sometimes even when partners defect more than once (Rumble et al., 2009).

Empathy is often manipulated by asking participants to take the emotional (i.e., affective) perspective of a distraught target. A meta-analysis on the effect of perspective-taking on empathy finds that people report similar levels of concern when they engage in affective perspective-taking and when no explicit instructions to empathize are given. In contrast, people report less concern when they engage in detached perspective-taking, relative to affective perspective-taking or no instructions to empathize. These findings suggest that empathic concern may be the default response to another's distress because taking a detached perspective dampens otherwise naturally emerging concern (McAuliffe et al., 2020).

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Compassion-related states reflect and are modulated by our expectations regarding a target's potential value as a relationship partner. Another study found that participants who empathized with a target in need perceived the target as a valuable partner, and in turn were more inclined to help the distressed target when need was the only available cue. However, empathic concern did *not* motivate helping if participants were told that the distressed target did not value the participant highly. Thus, while empathic concern is activated by need, empathic concern seems to only motivate helping partners who also value you, and therefore have high future potential as cooperative partners (Sznycer et al., 2019).

Highly empathetic people are more likely to provide assistance to others in need, and may therefore be better equipped to recruit new cooperative partners. For example, empathic concern predicts willingness to help when people perceive low interepdendence in their relationships, but not when they perceive high interdependence with others, presumably as a means to build new cooperative relationships (Guevara Beltran, Shiota & Aktipis, 2023). Empathetic people also benefit from greater network centrality among groups of friends, if those friends rely heavily on trust and sharing negative experiences (Morelli et al., 2017).

However, being highly empathetic can come with costs as well. For example, people who empathize with antagonizing groups are *less* liked and respected than those who reject those groups (Wang & Todd, 2021). Thus, while there are relational benefits to feeling empathy, doing so indiscriminately can be costly. This suggests that selection pressures likely pulled for emotional systems that could modulate empathy strategically, suppressing or enhancing it depending on the context and the potential costs or benefits associated with it (Ferguson et al. 2020; Zaki 2014).

## Sadness

People often feel sad after losing a valued partner or being unable to achieve a goal (Keller & Nesse, 2006). Sadness elicits compassion from others, and therefore social support (Bonanno et al., 2008). Notably, expressions of sadness met by chronically unresponsive partners may lead people to feel sustained lower moods (e.g., depression; Guerrero et al., 2008). This can lead people to value unresponsive partners less, ultimately increasing the likelihood of relationship dissolution (see section "Recognizing When to De-invest or Dissolve Existing Relationships").

p. 634 Sadness affects cooperation in experimental games. People in sad states are more likely to reject unfair offers in ultimatum games (Harlé & Sanfey, 2007), and to reciprocate (both positively and negatively) in trust games (Kirchsteiger et al., 2006). Sadness promotes cooperation especially when targets are empathetic. Dyads who engaged in a negotiation task in which one person was instructed to express sadness earned higher payoffs when the counterpart expressed other-oriented concern, and believed the opportunity for future cooperation was high (Sinaceur & Tiedens, 2006).

Sadness also tends to promote loss aversion (Andrews & Thomson, 2009). Sadness induces a cognitive state that enables people to analyze complex problems, allowing people to reflect on and understand the loss of valuable partners or goals (Andrews & Thomson, 2009). Loss aversion may, in turn, promote cooperative behavior. People in sad states make larger contributions to and take less from common pools. While yielding lower payoffs, taking too much or contributing too little could result in zero earnings. Presumably, sad participants make more conservative choices in order to ensure greater-than-zero payoffs (Polman & Kim, 2013).

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## Gratitude

People feel gratitude upon receiving a larger than expected benefit, and this feeling of gratitude makes people value the benefactor more (Sznycer & Lukaszewski, 2019). Gratitude is thought to be an important emotion in sustaining reciprocal altruism (Trivers, 1971)—a type of cooperation in which resource transfers flow back and forth in a tit-for-tat fashion. However, gratitude also promotes other types of cooperation that are not fully accounted for by reciprocal altruism. For example, Nowak and Roch (2007) argue that gratitude promotes indirect reciprocity—cooperation that occurs among three or more individuals, in which being the recipient of help motivates helping someone other than the benefactor. Employing agent-based modeling, they found that agents who engage in indirect reciprocity can outcompete cheaters over evolutionary time. Although Nowak and Roch (2007) did not directly model gratitude in their agent-based models, they argued that gratitude is a candidate proximate mechanism that allowed humans to sustain the evolution of indirect reciprocity.

Experimental work shows that gratitude toward a stranger motivates cooperation, even when individually costly, when the recipient is anonymous, when the target is dissimilar in moral values, and when the potential for future cooperation is low (DeSteno et al., 2010; Tsang & Martin, 2019). Gratitude also promotes pro-sociality and reduces antisociality. For example, in one study participants who were made to recall a time in which they felt gratitude subsequently helped a confederate more, and avoided assigning tasks that would have made it more difficult for the confederate to earn credits (Behler et al., 2020). Gratitude inhibits cheating as well. In one study, participants in a grateful state were less likely to lie about the result of a coin flip, even though lying would have allowed them to avoid an onerous task by having it assigned to another participant (DeSteno et al., 2019).

When people feel gratitude, they are more likely to assign higher valuation to those who gave to them, and to act more generously toward them in the future. In a cyberball game in which people could earn money by passing the ball to only one person (i.e., a "treasurer" who could pass the ball to multiple players), participants felt more gratitude when the treasurer excluded them from the first half of the game, but then passed the ball to participants in the second half. Presumably, participants who were excluded in the first half of the game perceived being included in the second half as an unexpected gesture of generosity. Participants who felt gratitude more strongly valued the treasurer more highly, and behaved more generously toward her (Smith et al., 2017).

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## Embarrassment

Showing embarrassment is thought to serve an appeasement function that leads to greater liking, trust, and overall greater affiliation (Feinberg et al., 2012; Keltner & Anderson, 2000). People experience embarrassment in response to trivial transgressions that are often humorous rather than derogating, and when the audience consists of distant rather than close others (Tangney et al., 1996). Embarrassment might signal cooperative intent. Feinberg and colleagues (2012) found that people who expressed stronger embarrassment tended to behave more generously. Moreover, people who express embarrassing stories are perceived as more pro-social (e.g., generous), and less antisocial (e.g., manipulative). Consequently, people are more trusting and cooperative toward targets who display high levels of embarrassment (Feinberg et al., 2012). Because people are more likely to experience embarrassment in the presence of distant rather than close others (Tangney et al., 1996), embarrassment might play a more prominent role earlier in relationships when people are signaling cooperative intent.

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## Pride

People feel authentic pride (i.e., pride that emerges from honest cues of capacity) when their ability to provide (or withhold) benefits from others is enhanced. Showing pride can elevate one's status, and prompt audiences to assign greater valuation toward the person exhibiting pride (Martens et al., 2012; Sznycer & Lukaszewski, 2019). Pride is thought to increase relational value through two routes. First, experiencing pride can motivate people to achieve relevant goals, increasing their ability to generate or withhold benefits in the future. Second, people who express pride are reliably perceived by others as possessing higher status (Martens et al., 2012; Sznycer & Lukaszewski, 2019).

Across several studies, participants who were shown targets displaying prototypical expressions of pride (i.e., raised chin, arms akimbo, expanded chest) were perceived to possess higher status than targets displaying no emotion (Shariff et al., 2012). Tracy et al. (2013) also found that both US undergraduates and Fijian villagers rate targets expressing nonverbal displays of pride as possessing higher status than targets expressing shame, happiness, or no affect. Thus, the nonverbal signals associated with feelings of pride are likely universally recognized. Similarly, people across industrialized countries and small-scale societies report that they would feel pride if others learned that they possess status-conferring attributes such as attractiveness and expertise (Sznycer, Al-Shawaf, et al., 2017; Sznycer, Xygalatas, Alami, et al., 2018; Durkee et al., 2019).

Because expressions of pride are reliably recognized as conveying skills, status, and expertise, pride expressions are expected to evoke cooperation from perceivers. Consistent with this idea, people are more likely to imitate those who convey nonverbal displays of genuine pride (Martens & Tracy, 2013). In another study, participants who received a pride-conveying message from their partner made more positive attributions about those partners (e.g., sympathetic), expected partners to take less from a common pool, and were themselves more cooperative (Wubben et al., 2012).

It appears that expression of pride can be perceived as a cue of cooperative intent. Perceived hubris, on the other hand, is associated with *lower* perceived cooperative intent. Hubris is defined as an inauthentic display of pride in that it does not emerge from honest cues of capacity. Because people anticipate less cooperation from hubristic partners, people who display inauthentic pride motivate defection from their partners (Wubben et al., 2012).

In addition, because expressions of pride signal greater ability to provide and withhold benefits, those
p. 636 expressions may also dampen perceived need. This may inhibit some forms ↳ of cooperation. A study examining donations toward start-ups in developing nations found that men who display pride in their profile pictures received less donations because they were perceived to be in less need than men who did not display pride (Tracy et al., 2018). Lastly, experiencing pride promotes goal attainment, and thus may promote cooperation when the goal to cooperate is salient (Martens et al., 2012). For example, participants who recalled a time when they felt pride agreed more strongly that cooperation was important, and were more cooperative in a common goods game (Dorfman et al., 2014).

## Anger

One proposed function of anger is to let others know they are not valuing you as highly as you expect them to. Thus, anger can be thought of as a tool for compelling others to raise the benefits they provide to you, and/or to reduce the costs they impose (Sell et al., 2017; Sznycer & Lukaszewski, 2019). In either case, anger tends to hinder in-the-moment cooperation. For example, in one study participants in an angry state took more money from, and contributed less to, a common resource pool (Polman & Kim, 2013). Similarly, people who feel anger after receiving negative feedback make smaller offers in ultimatum games (Fabiansson & Denson, 2012).

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Although anger may inhibit cooperation by the person feeling the anger, anger displays may *evoke* cooperative behavior from others. People make larger concessions to negotiation partners who express anger, therefore taking smaller gains (Sinaceur & Tiedens, 2006). In a related experiment, participants who learned that their partner was angry made larger offers in ultimatum games. These studies show that people are sensitive to displays of anger, and make larger offers/concessions to avoid retaliation (van Dijk et al., 2008). Anger also plays an important role in relationship resolution, relationship dissolution, and third-party punishment, which we discuss in later sections.

### Envy

People feel envy toward those who receive better treatment, or have something of value that the envier lacks. Feelings of envy can sometimes motivate people to spitefully harm others—the opposite of generosity. Ultimately, envy enhances one's relative standing by promoting behaviors that reduce the target's welfare (Sznycer, Lopez Seal et al., 2017). Reducing another's welfare decreases their ability to generate or impose costs, consequently lowering the valuation that others may assign to targets; and by extension, improving the relative valuation that others may assign to the self.

Work from behavioral economics shows that people high in dispositional envy are more likely to defect in prisoners' dilemmas when they receive smaller endowments than others, even when receiving additional resources later that would objectively attenuate inequality (Parks et al., 2002). In a related experiment, participants received unequal endowments and could see others' cumulative earnings. At the end of the study, 62% of participants chose to spend a portion of their money to reduce others' earnings, spending an average of 48% of their own funds to decrease other participants' accounts. Notably, people most frequently paid to reduce the funds of the highest-earning player (Zizzo & Oswald, 2001).

Incidental envy also inhibits cooperation more generally. In one series of studies participants instructed to feel envy picked up fewer pencils to help a confederate; reported greater intentions to harm a confederate; and assigned more onerous tasks to a confederate, making it more difficult for the confederate to earn research credits (Behler et al., 2020). A meta-analysis linking personality variables and cooperation found that dispositional envy is among the most reliable negative predictors of cooperation across social dilemmas (Thielmann et al., 2020).

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### Disgust

The model of disgust proposed by Tybur and colleagues (2013; Tybur & Lieberman, 2016), suggests that disgust serves three functions: pathogen avoidance, avoidance of fitness-jeopardizing mates, and coordinating disgust-evoking moral behavior. When people feel disgust, they value the targets of disgust less, and feel less positively interdependent towards them (Guevara Beltran, Whisner et al., 2023), in some cases hindering cooperation. In ultimatum games, participants are likely to experience disgust when receiving increasingly unfair offers (Chapman et al., 2009). People in experimentally evoked disgust states are also more likely to reject unfair offers in ultimatum games: participants who were shown disgust-inducing images (e.g., bodily waste) rejected 84% of unfair offers, whereas participants in sad and neutral states rejected 46% and 41% of unfair offers, respectively. In addition, participants made to feel disgust rated unfair offers as being more unfair, relative to participants in sad or neutral states (Moretti & di Pellegrino, 2010).

Beyond the effect of disgust on relational valuation, feeling disgust may also lead people to devalue other social groups. In some research, participants in a minimal group paradigm who were shown disgust-inducing images developed stronger prejudices toward out-groups, and disgust exacerbated existing prejudices against marginalized groups compared to the in-group (Dasgupta et al., 2009). In a related

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experiment, participants in an induced disgust state developed greater implicit dehumanization against out-groups relative to the in-group (Buckels & Trapnell, 2013).

Consistent with the view that disgust coordinates moral behavior, participants in one study who read vignettes of moral transgressions reported feeling angrier when they themselves were the victim, compared to when the victim was a third party. There was also suggestive evidence that people felt more disgust than anger when the victim was a third party. Lastly, while anger motivated willingness to engage in direct aggression (e.g., motivation to hit), disgust motivated willingness to engage in indirect aggression such as damaging the target's reputation, or ignoring the person (Molho et al., 2017).

## Building and Maintaining Cooperative Relationships

Beyond the initial stage of selecting partners for cooperative effort, emotions play important roles in coordinating, navigating, and strengthening ongoing cooperative relationships. We discuss several specific mechanisms in this section.

### Compassion, Empathy, and Capitalizing on Positive Experiences

Experiencing compassion motivates pro-sociality, which may give rise to gratitude and thereby promote future cooperation. However, a suffering target can also motivate an empathizer's avoidance (Grynberg & López-Pérez, 2018; López-Pérez et al., 2014). Although empathy toward individuals who are displaying distress can sometimes lead to avoidance, positive empathy—the process of understanding and vicariously sharing others' positive emotions—can strengthen bonds (Morelli et al., 2015). Positive empathy is correlated with social connectedness (Morelli et al., 2015). In addition, sharing positive events strengthens close relationships above and beyond the effect of the event itself. Among couples, talking about positive events in one's life, especially when met by an enthusiastic partner, predicts greater relationship satisfaction and lower relationship dissolution (Gable et al. 2004; Gable et al. 2006; Otto et al. 2015).

### Gratitude

As discussed earlier, gratitude promotes in-the-moment cooperation when people receive larger than
p. 638 expected benefits—often early in relationship initiation. Gratitude has bidirectional ↳ effects in developing relationships as well, helping to foster growing interdependence and strengthen bonds. In one study of a sorority initiation event, women reported feeling gratitude after receiving a series of gifts from more senior members. In turn, gratitude predicted greater closeness between junior and senior members, and a greater sense of community toward the sorority one month after the event (Algoe et al., 2008). In another study, participants instructed to recall a time in which they felt grateful toward a close other reported a greater sense of mutual responsibility for the target's welfare six weeks later (Lambert et al., 2010). Taken together, studies of the effects of gratitude on cooperation demonstrate that gratitude raises the valuation people place on benefactors, increases the probability of future cooperation, facilitates the formation of new relationships, and strengthens existing bonds.

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## Guilt

People experience guilt when they deliver lower than expected benefits to, or impose costs on, positively interdependent others. In response, guilt motivates people to make amends or repair losses of valuation (Sznycer & Lukaszewski, 2019). For example, people who were excluded because they were ostensibly caught free-riding reported more guilt than anger, and were willing to engage in greater cooperative behaviors to regain inclusion (Robertson et al., 2014). In iterated prisoner's dilemmas, people who were instructed to feel guilt acted more cooperatively if they had behaved uncooperatively during the first half of the study. In another study, people who made unfair offers in ultimatum games reported feeling guilt, and as hypothesized, this guilt predicted making more generous offers in the games one week later (Ketelaar & Tung Au, 2003).

The effect of guilt on cooperation appears to be moderated by a person's general tendency to cooperate. Pro-socials—people who seek to maximize joint outcomes—behave cooperatively whether or not they feel guilty. In contrast, pro-selfs—people who typically seek to maximize individual gains—are more cooperative only after remembering a time in which they felt guilt (Ketelaar & Tung Au, 2003). In another study, participants who recalled a previous time when they had felt guilt (e.g., breaking another's valuable objects) were more cooperative in a give some dilemma (i.e., giving to a common pool), but again the effects of guilt on cooperation were qualified by cooperative personality type. Whereas pro-socials were unaffected by the manipulation, guilt motivated pro-selfs to behave as cooperatively as pro-socials (de Hooge et al., 2007; Nelissen et al., 2007).

Guilt also promotes cooperation in negotiations. In a study where people performed a negotiation task, participants demanded larger concessions from partners who conveyed guilt (e.g., *I feel guilty for not having conceded more*; Van Kleef et al., 2006). These results highlight that people expect opponents who convey guilt to make amends. Lastly, a meta-analysis found that guilt-proneness was among the strongest trait-level predictors of cooperation across social dilemmas (Thielmann et al., 2020). In sum, guilt promotes cooperation because it allows people to amend wrongdoings in order to regain losses of valuation from interdependent others, thereby repairing existing valuable relationships.

## Shame

People typically feel shame if they have committed a transgression, such as violations of fairness, or show incompetence in a situation. Shame is activated in situations that might lead others to lower their valuation of you. In response, shame motivates withdrawal or avoidance to ameliorate or prevent further devaluation (Martens et al., 2012; Sznycer & Lukaszewski, 2019). People across subsistence groups report that they would feel the most shame if others learned that they possessed devaluing attributes such as being known
p. 639 as a thief (Durkee et al., ↳ 2019; Sznycer et al., 2016; Sznycer, Xygalatas, Agey, et al., 2018). Notably, people feel shame when they expect others to devalue them, even when *no* transgressions have been committed. For example, people experienced shame when they were ostensibly excluded from a public goods game because of their presumed low contributions, even when their contributions were actually high (Robertson et al., 2018). Shame can also influence cooperation more directly. In two studies, pro-selfs, but not pro-socials, in an experimentally induced shame state were more cooperative in a give some dilemma (i.e., giving to a shared pool); in another study, participants who experienced shame after receiving feedback that they were of low intelligence were more cooperative in a give some dilemma (de Hooge et al., 2008).

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## Anger

Although anger can hinder cooperation, people also recruit anger in service of re-balancing and resolving inequities in ongoing relationships. When one partner responds to a partner's anger appropriately, anger is diminished, allowing for reconciliation (Fischer & Giner-Sorolla, 2016). In negotiation tasks, participants who receive an anger-conveying message from partners make higher concessions in the following round, presumably in order to prevent further disagreement (Lelieveld et al. 2011). People expect more generous offers when negotiating with close friends than with acquaintances, and feel more anger when close friends, relative to acquaintances, make lower than expected offers. People who feel anger when receiving lower than expected offers from close friends are also less likely to accept such offers (Ramirez-Fernandez et al. 2018).

The function of increasing one's value to other relationship partners appears specific to anger, in contrast to other negative emotions. In recall studies, participants who remembered a time in which they felt anger reported less derogation and rejection, greater short-term verbal attacks, and higher reconciliation toward the target than those instructed to remember an experience of contempt. In addition, participants did not feel sustained anger after days (Fischer & Roseman, 2007). In another study, participants who were ostensibly excluded from a group because they posed a pathogen threat (a reason outside of their control) reported feeling more anger than guilt. Angrier participants were more likely to remind others of their existing interdependence to regain inclusion (Robertson et al., 2014).

Anger can deter others from taking advantage or exploiting you. People feel anger when others treat them unfairly, and consequently feel motivated to retaliate. In order for cooperation to be evolutionarily viable, individuals must be able to detect and deter free-riders (Cosmides et al. 2010; Fehr & Fischbacher 2004; Fehr & Gächter 2002). Across all types of subsistence groups, people punish unfair offers in ultimatum games (Henrich et al., 2006), and anger motivates third-party punishment in public goods tasks, even when it is individually costly (Fehr & Fischbacher, 2004; Fehr & Gächter, 2002). Those who punish are more generous in dictator games (Henrich et al., 2006), suggesting that punishment and generosity are mechanisms that go hand in hand in the long-term successful maintenance of cooperation. A review on the role of anger in ultimatum games shows that anger reliably predicts rejections of unfair offers (Van Kleef et al., 2008). Moreover, anger is actually a better predictor of rejecting unfair offers than the perceived unfairness of such offers (Pillutla & Murnighan, 1996).

Beyond in-the-moment effects, the threat of anger and punishment might also increase cooperation over the long term. Fehr and Gächter (2000) have demonstrated that people make more stable contributions in public goods tasks when others can punish. Moreover, third-party punishment results in higher collective earnings over longer periods of time, indicating that punishing free-riders, even though individually costly, is a viable strategy for sustaining long-term cooperation (Gächter et al., 2008).

p. 640 A prevailing view is that altruistic punishment is the primary mechanism via which defection is deterred, and thus cooperation maintained in groups over time. However, recent investigations challenge this view. In a study investigating over 300 formal and customary court cases of a horticultural society in Papua New Guinea, third-party individuals readily served as witnesses to provide information in service of restorative retributions. Conflicts arose primarily as a result of marital, land, or assault allegations. More often than not, third-party witnesses provided crucial information that helped to solve cases such that the wrongdoer was made to make amends toward the victim, instead of excluding or imposing a nonrestorative punishment on the wrongdoer. In this alternative to punishment, third-party witnesses gain standing in their community, victims see direct reparations, and wrongdoers are able to regain inclusion in the community if they make amends (Wiessner, 2020). Thus, restorative justice provides an alternative avenue through which defection can be managed, and cooperation sustained over time. However, whether or how social emotions differ in this context compared to punishment needs to be evaluated in future studies.

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## Recognizing When to De-invest or Dissolve Existing Relationships

Time and energy are limited, and thus investments toward one partner are accompanied by opportunity costs, such as reduced ability to invest in new and potentially more rewarding relationships (Tooby & Cosmides, 1996). Leaving relationships can be a viable strategy whenever better alternatives are available (Aktipis 2004, 2011). Failing to recognize when partners no longer provide benefits (i.e., absence of interdependence), or failing to recognize when others impose greater costs than benefits (i.e., negative interdependence) would have resulted in significant losses of fitness for ancestral humans. Social emotions play important roles in helping us navigate relationship dissolution.

### Anger and Sadness

What are the consequences of failing to respond appropriately to a valued partner's anger, or expressions of sadness? Work from industrial psychology shows that anger leads to de-investment toward organizations. Specifically, poor working conditions (e.g., low respect, unfairness) elicit feelings of anger toward employers, and anger in turn predicts lower work-related effort and higher intentions to quit (Kiefer, 2005).

Anger and sadness are also associated with de-investment within the context of close relationships. Married couples report more anger and sadness when they feel like they are getting less from the relationship than they are investing in it. People in under-benefiting relationships are more likely to experience sadness that promotes avoidant behaviors (e.g., spending time alone) than sadness that elicits social support (e.g., discussing problems). Similarly, people in under-benefiting relationships are more likely to experience anger that motivates disruptive behavior (e.g., criticizing), rather than relationship resolution. In turn, both sadness and anger between couples in under-benefiting relationships predict greater relationship dissatisfaction (Guerrero et al., 2008).

Relationship dissatisfaction was the strongest predictor of relationship dissolution among a large sample of European adults ($N > 18{,}000$). Specifically, women who reported the most relationship dissatisfaction were 3.26 times more likely to report divorce or separation than women reporting low relationship dissatisfaction. Moreover, men and women with depressive symptoms were 40%–50% more likely to report relationship dissolution than people reporting no depressive symptoms (Røsand et al., 2014). In a related study, Sweeney and Horwitz (2001) find that 20%–25% of people who initiate divorce report depressive symptoms, compared to only 10% for people who do not initiate divorce. Functional accounts of p. 641 depression ↳ propose that depression may lead to extensive rumination in order to allow people to arrive at the best solution to a complex problem (e.g., whether or not to divorce). An alternative functional account of depression is that it elicits support from people who have a stake in the depressed individual (e.g., a spouse; Hagen, 2011). Taken together, these studies highlight the role of sadness and anger as potential mediators between the perception of receiving lower than expected benefits over time (e.g., being in an under-benefiting relationship), to relationship dissatisfaction, and ultimately to relationship dissolution.

### Contempt

Contempt can be described as a sentiment consisting of basic emotions such as anger and disgust, as well as attitudes and cognitions toward specific people or groups (Fischer & Giner-Sorolla, 2016; Gervais & Fessler, 2017). People feel contempt when targets behave incompetently, or when targets are perceived to be incompetent, and therefore low in relational value. Consequently, contempt is accompanied by diminished pro-social emotions such as compassion, and motivates avoidance or exclusion rather than short-term aggression aimed at resolving the relationship (Fischer & Giner-Sorolla, 2016; Gervais & Fessler, 2017).

Experimental results support the idea that contempt tracks incompetency and low valuation. Participants who read vignettes of people behaving incompetently (e.g., a man tries to impress a woman by fixing her

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car, but makes it worse), or who were asked to recall a time in which another behaved incompetently, reported feeling more contempt than anger or disgust (Hutcherson & Gross, 2011). Participants also reported less motivation for reconciliation, more derogation, and greater rejection toward the target. In addition, people reported feeling sustained contempt after days, but not sustained anger. Because anger is thought to promote in-the-moment reparations, such as when people demand that others treat them more fairly, anger can promote reconciliation. In contrast, contempt is accompanied by a long-lasting devaluation of another and does not promote in-the-moment reparations. Thus, feeling sustained contempt indicates relationship dissolution rather than reparation (Fischer & Roseman, 2007). Contempt is also associated with relationship dissatisfaction and divorce. Married couples who made verbal and nonverbal displays of contempt during video-recorded interactions, accompanied by belligerence and defensiveness, were more likely to express relationship dissatisfaction and ultimately divorce compared to couples who did not show contempt (Gottman et al., 1998).

Although anger and sadness can be activated in service of relationship resolution, frequent, repeated feelings of these emotions toward a target may eventually lead to contempt. Repeated experiences of sadness in response to an interdependent partner's failure to provide support may translate into contempt for the partner. Similarly, repeated experiences of anger in response to an interdependent partner's failure to increase the benefits afforded toward the self may over time develop into feelings of contempt toward the partner. Unlike anger and sadness, which are typically short-lived, contempt is accompanied by long-lasting devaluation of the target (Fischer & Giner-Sorolla, 2016; Gervais & Fessler, 2017).

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**Table 32.1** Summary of the Impact of Emotion on Partner Valuation and Cooperation

| Interpersonal Function | Trigger | Emotion | Partner Valuation | Outcome (Direction) | Citation |
|---|---|---|---|---|---|
| Choosing partners to cooperate with | Distraught target | Compassion | Raises valuation assigned to target | Prisoner's Dilemma (+) | Batson & Moran, 1999; Batson & Ahmad, 2001; Rumble et al., 2009 |
| | | | | Dictator Game (+) | Edele et al., 2013 |
| | | | | Welfare Trade-off (+) | Sznycer et al., 2019 |
| | | | Lowers valuation third-parties assign the self when empathizing with negative groups | Like & respect (–) | Wang & Todd, 2021 |
| | Loss of valuable target, goal, or object | Sadness (loss aversion) | NA | Public & Common Good Game (+) | Polman & Kim, 2013 |
| | | | | Ultimatum Game (–) | Harlé & Sanfey, 2007 |
| | | | | Trust Game (mixed) | Kirchsteiger et al., 2006 |
| | | Sadness (elicit support) | Raises valuation others assign the self if they feel compassion | Negotiation (+) | Sinaceur & Tiedens, 2006 |
| | Receiving larger than expected benefits | Gratitude | Raises valuation assigned to target | Give Some Dilemma (+) | DeSteno et al., 2010 |
| | | | | Dictator Game (+) | Tsang & Martin, 2019 |
| | | | | | |
| | | | | Pick up pencils (+)<br><br>Allocate onerous tasks (–) | Behler et al., 2020 |
| | | | | Cheating (–) | DeSteno et al., 2019 |
| | | | | Dictator Game (+)<br><br>Welfare Trade-off (+) | Smith et al., 2017 |

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| | | | | | |
|---|---|---|---|---|---|
| | Trivial social transgression | Embarrassment | Raises valuation others assign the self | Dictator Game (+)<br><br>Trust Game (+)<br><br>Prisoner's Dilemma (+) | Feinberg et al., 2012 |
| | Information conveys capacity to provide/withhold benefits | Pride (status conferral) | Raises valuation others assign self | Common Goods Game (+) | Wubben et al., 2012 |
| | | | | Donations (–) | Tracy et al., 2018 |
| | | Pride (inauthentic) | Lowers valuation others assign the self | Common Goods Game (–) | Wubben et al., 2012 |
| | | Pride (goal pursuit) | NA | Common Goods Game (+) | Dorfman et al., 2014 |
| | Receiving lower than expected benefits | Anger (self expects amends) | Raises valuation others assign the self | Public & Common Goods Game (–) | Polman & Kim, 2013 |
| | | | | Ultimatum Game (–) | Fabiansson & Denson, 2012 |
| | Delivering lower than expected benefits | Target conveys anger (self makes amends) | Raises valuation assigned to target | Negotiation (+) | Sinaceur & Tiedens, 2006 |
| | | | | Ultimatum Game (+) | van Dijk et al., 2008 |
| | Target has something of value that one lacks<br><br>Receiving poorer treatment than target | Envy | Lowers valuation assigned to target | Prisoner's Dilemma (–) | Parks et al., 2002 |
| | | | | Betting Game (–) | Zizzo & Oswald, 2001 |
| | | | | Pick up pencils (–)<br><br>Allocate onerous tasks (+) | Behler et al., 2020 |
| | | | | Meta-analysis of trait envy & social dilemmas (–) | Thielmann et al., 2020 |
| | Moral transgression | Disgust | Lowers valuation assigned to target | Ultimatum Game (–) | Chapman et al., 2009 |
| | | | | Ultimatum Game (–) | Moretti & di Pellegrino, 2010 |

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| | | | | | |
|---|---|---|---|---|---|
| | | | | Damage reputation & avoidance (+) | Molho et al., 2017 |
| | | | | Prejudice (+) | Dasgupta et al., 2009 |
| | | | | | |
| | | | | Dehumanization (+) | Buckels & Trapnell, 2013 |
| Building and maintaining cooperative relationships | Sharing positive information | Positive empathy | Raises valuation assigned to target | Connectedness (+) | Morelli et al., 2015 |
| | | | | Relationship dissatisfaction & dissolution (–) | Gable et al., 2004; 2006; Otto et al., 2015 |
| | Receiving benefits from interdependent target | Gratitude | Raises valuation assigned to target | Closeness & belongingness (+) | Algoe et al., 2008 |
| | | | | Shared fate (+) | Lambert et al., 2010 |
| | Delivering lower than expected benefits to interdependent target | Guilt (self makes mends) | Repairs losses of valuation others assign the self | Intention to cooperate (+) | Robertson et al., 2014 |
| | | | | Prisoner's Dilemma & Ultimatum Game (+) | Ketelaar & Tung Au, 2003 |
| | | | | Give Some Dilemma (+) | de Hooge et al., 2007; Nelissen et al., 2007 |
| | | | | Meta-analysis of guilt-proneness in social dilemmas (+) | Thielmann et al., 2020 |
| | Receiving lower than expected benefits from interdependent target | Target conveys guilt (self expects amends) | Repairs losses of valuation assigned to target | Negotiation (–) | Van Kleef et al., 2006 |
| | Information conveys incompetency<br><br>Nontrivial social transgression | Shame | Attenuates losses of valuation others assign the self | Give Some Dilemma (+) | de Hooge et al., 2008 |

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| | | | | | |
|---|---|---|---|---|---|
| | Receiving lower than expected benefits from interdependent target | Anger (self expects amends) | Raises valuation target assigns the self | Aggression & reconciliation (+) | Fischer & Roseman, 2007 |
| | | | | Remind of interdependence (+) | Robertson et al., 2014 |
| | | | | Public Goods Game (+) | Fehr & Fischbacher, 2004; Fehr & Gächter, 2002; Gächter et al., 2008 |
| | | | | Ultimatum Game (–) | Henrich et al., 2006; Pillutla & Murnighan, 1996; Van Kleef et al., 2008 |
| | | | | Negotiation (–) | Ramirez-Fernandez et al. 2018 |
| | Delivering lower than expected benefits to interdependent target | Target conveys anger (self makes amends) | Raises valuation assigned to target | Negotiation (+) | Lelieveld et al. 2011 |
| | | | | | |
| Terminating costly relationships | Chronically receiving lower than expected benefits | Anger | Target fails to recalibrate valuation towards self | Work effort (–)<br><br>Intention to quit job (+) | Kiefer, 2005 |
| | | | | Relationship satisfaction (–)<br><br>Aggression (+) | Guerrero et al., 2008 |
| | | Sadness | Target fails to recalibrate valuation towards self | Avoidance (+)<br><br>Relationship satisfaction (–) | Guerrero et al., 2008 |
| | | | | Relationship satisfaction (–)<br><br>Relationship dissolution (+) | Røsand et al., 2014; Sweeney & Horwitz, 2001 |
| | Chronically receiving lower than expected benefits<br><br>Information conveys target is incompetent | Contempt | Long-lasting loss of valuation towards target | Reconciliation (–)<br><br>Derogation (+)<br><br>Exclusion (+) | Fischer & Roseman, 2007 |
| | | | | | |

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| | | |
|---|---|---|
| | Relationship satisfaction (–)<br><br>Relationship dissolution (+) | Gottman et al., 1998 |

*Note*: Except when specified (i.e., “Target conveys anger,” and “Target conveys guilt”), emotion always refers to the self experiencing/conveying the emotion, process, or sentiment.

## Conclusion

Drawing from the feeding-niche hypothesis (Kaplan et al., 2000), we have argued that the need to pool calories, and other sources of risks (Cronk et al., 2019), renders conspecifics intrinsically valuable because partners who pool risks share a stake in each other’s fates (Aktipis et al., 2018; Roberts, 2005). In turn, fitness interdependence facilitates the extensive cooperative behavior that is characteristic of the human life history. Cooperation often yields greater collective benefits than uncoordinated individual efforts, but
p. 642 the temptation ↳ to defect can undermine these cooperative relationships, and changing landscapes of costs and benefits can lead previously beneficial relationships to become costly. To reap the benefits of cooperation while avoiding exploitation, ancestral humans had to exert careful partner choice, giving preference to partners who were both able and willing to deliver benefits; build and maintain long-lasting relationships with valuable partners, and de-invest from or terminate relationships that were no longer beneficial. The social emotions, which are theorized to track expected contributions of fitness others will impose on the self (Al-Shawaf et al., 2016; Sznycer & Lukaszewski, 2019; Tooby et al., 2008), guide cooperation in service of these basic interpersonal functions.

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