

# The Sociocultural Appraisals, Values, and Emotions (SAVE) Framework of Prosociality: Core Processes from Gene to Meme

Dacher Keltner,<sup>1</sup> Aleksandr Kogan,<sup>2</sup> Paul K. Piff,<sup>3</sup> and Sarina R. Saturn<sup>4</sup>

<sup>1</sup>Department of Psychology, University of California, Berkeley, California 94720; email: keltner@socrates.berkeley.edu

<sup>2</sup>Department of Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, United Kingdom; email: ak823@cam.ac.uk

<sup>3</sup>Department of Psychology, University of California, Berkeley, California 94720; email: ppiff@berkeley.edu

<sup>4</sup>School of Psychological Science, Oregon State University, Corvallis, Oregon 97331; email: sarina.saturn@oregonstate.edu

Annu. Rev. Psychol. 2014. 65:425–60

The *Annual Review of Psychology* is online at <http://psych.annualreviews.org>

This article's doi: 10.1146/annurev-psych-010213-115054

Copyright © 2014 by Annual Reviews. All rights reserved

## Keywords

prosociality, altruism, cooperation, trust, elevation, compassion, empathy

## Abstract

The study of prosocial behavior—altruism, cooperation, trust, and the related moral emotions—has matured enough to produce general scholarly consensus that prosociality is widespread, intuitive, and rooted deeply within our biological makeup. Several evolutionary frameworks model the conditions under which prosocial behavior is evolutionarily viable, yet no unifying treatment exists of the psychological decision-making processes that result in prosociality. Here, we provide such a perspective in the form of the sociocultural appraisals, values, and emotions (SAVE) framework of prosociality. We review evidence for the components of our framework at four levels of analysis: intrapsychic, dyadic, group, and cultural. Within these levels, we consider how phenomena such as altruistic punishment, prosocial contagion, self–other similarity, and numerous others give rise to prosocial behavior. We then extend our reasoning to chart the biological underpinnings of prosociality and apply our framework to understand the role of social class in prosociality.

## Contents

INTRODUCTION.....	426
THE SOCIOCULTURAL APPRAISALS, VALUES, AND EMOTIONS	
FRAMEWORK OF PROSOCIALITY.....	427
INTRAPERSONAL PROCESSES AND PROSOCIALITY.....	430
The Kindness Instinct: Intuitive Bias Toward Prosociality ( <i>D</i> ).....	430
Individual Factors Shaping the Propensity to Act Prosocially ( <i>D</i> ).....	431
Giving Feels Good: Intrinsic Personal Benefits of Prosocial Action ( <i>B<sub>self</sub></i> ).....	431
Guilt as Deterrent: Intrapyschic Costs of Inaction ( <i>C<sub>inaction</sub></i> ).....	432
INTERPERSONAL PROCESSES AND PROSOCIALITY.....	432
Selective Prosociality: Dyadic Processes that Shape the Propensity to Help	
a Particular Recipient ( <i>K</i> ).....	433
Give to Receive: Dyadic Benefits of Prosociality ( <i>B<sub>self</sub></i> ).....	435
GROUP PROCESSES AND PROSOCIALITY.....	436
Prosocial Contagion: Prosocial Behavior Within the Group Induces	
Bias Toward Prosociality ( <i>D</i> ).....	436
Rewarding the Kind: Reputation as a Group Benefit to Self	
for Acting Prosocially ( <i>B<sub>self</sub></i> ).....	437
Gossip and Altruistic Punishment: Group Mechanisms to Guard	
Against Inaction ( <i>C<sub>inaction</sub></i> ).....	439
CULTURAL VALUES, NORMS, AND PROSOCIALITY.....	441
The Prosocial Force of Numbers: Norms, Values, and Others'	
Actions Shape Social Momentum ( <i>M</i> ).....	441
Faith and Kindness: Prosociality Is a Universal Religious Virtue ( <i>M</i> ).....	442
TOWARD THE STUDY OF THE PROSOCIAL NERVOUS SYSTEM.....	443
Neurophysiological Underpinnings of the Kindness Instinct:	
Oxytocin and Vasopressin.....	445
Benefits of Prosociality: Dopamine and the Reward Pathways of the Brain.....	447
Attunement to Others and Emotion Regulation: Serotonin.....	448
THE POOR GIVE MORE: THE CASE OF SOCIAL CLASS	
AND PROSOCIAL BEHAVIOR.....	449
CONCLUSION.....	450

## INTRODUCTION

[Sympathy] will have been increased through natural selection; for those communities, which included the greatest number of the most sympathetic members, would flourish best, and rear the greatest number of offspring. [Darwin 2005 (1871), p. 130]

How selfish soever man may be supposed, there are evidently some principles in his nature, which interest him in the fortune of others, and render their happiness necessary to him, though he derives nothing from it except the pleasure of seeing it. [Smith 2006 (1759), p. 3]

All the world faiths insist that true spirituality must be expressed consistently in practical compassion, the ability to feel with the other. (Armstrong 2009, p. 8)

Prosocial behavior—when people act in ways that benefit others—has many forms: altruism, cooperation, caregiving, mutual coordination, and the experience of moral emotions, such as compassion, elevation, and gratitude (de Waal 2008, Penner et al. 2005). Understanding prosocial behavior has long been the provenance of controversy and scientific advance. Evolutionary theorists have sought explanations for why people would behave in ways costly to the self, with treatments of the distal mechanisms, such as inclusive fitness and reciprocal altruism, and proximal forces, including tit-for-tat, altruistic punishment, and status seeking (Axelrod 1984; Fehr & Fischbacher 2003; Hamilton 1964; Hardy & Van Vugt 2006; Henrich 2004; Nowak & Sigmund 2005; Rand et al. 2009; Sober & Wilson 1998; Trivers 1971, 1972). Some of social psychology's most enduring studies are counterintuitive demonstrations of why people fail to act on behalf of those who suffer (e.g., Darley & Batson 1973). Studies within developmental psychology have long grappled with the ontogenetic development and individual variation in prosociality (e.g., Fehr et al. 2008, Warneken & Tomasello 2006). Recent modeling of cooperative behavior suggests that prosociality is evident throughout nature and at many levels of analysis, from genes to multicellular organisms to societies (Nowak 2006). Indeed, cooperation may very well be necessary for complex biological systems to emerge from genomes to the global community.

These lines of inquiry converge on a question that we seek to answer in this article: Why are people good to others? Twenty years ago, social scientists sought to demonstrate rigorously the existence of what might be thought of as selfless prosociality—that is, that people do indeed act on behalf of others independent of the benefits to the self. Batson and colleagues' elegant work demonstrated that even when the most obvious forms of self-interest (social rewards, distress reduction) cannot be gratified, people still help others in need, owing to a state of empathic concern or sympathy (Batson & Shaw 1991). Here, we build on this work, synthesizing different discoveries to home in on a set of core processes—from inside the mind to those distributed across social collectives—that enable prosocial action.

Our review is organized into four parts. We first present briefly an equation for modeling the psychological decision to engage in prosocial behavior. Broadly, our framework encapsulates the sociocultural appraisals, values, and emotions that guide prosocial behavior; as such, we refer to our framework as the SAVE framework of prosociality. After outlining the theoretical components of our framework, we consider how proximal forces at four levels of analysis shape the components of our equation, reviewing intrapsychic, dyadic, group, and sociocultural factors that influence prosociality. Third, we rely on certain components of our framework to review the new science of the neurophysiology of prosociality. We then conclude by summarizing the emerging literature on social class and prosociality as a case study of our framework.

## **THE SOCIOCULTURAL APPRAISALS, VALUES, AND EMOTIONS FRAMEWORK OF PROSOCIALITY**

Evolutionary theorists have proposed several mechanisms by which cooperation and altruism could have evolved, including inclusive fitness, direct reciprocal altruism, indirect reciprocal altruism, genetic group selection, and cultural group selection (Bshary & Bergmüller 2008, Hamilton 1964, Henrich 2004, Nowak 2006, Seyfarth & Cheney 2012, Sober & Wilson 1998, Trivers 1971). Within this scholarship, theorists have developed mathematical frameworks for understanding under which conditions cooperation is evolutionarily advantageous. These models focus primarily on extrapsychic mechanisms—i.e., those outside the individual—that render prosocial behavior biologically sensible and evolutionarily stable over time. Underspecified in such models are the intrapsychic processes—i.e., those inside the mind—that shape the individual's decision to act in

prosocial fashion. For instance, why do certain psychological states but not others enable prosocial responding? Why are individuals more likely to behave prosocially when they see that others have done the same? How do social collectives encourage prosocial behavior?

Here, we turn to this task: developing a framework of the core psychological processes that give rise to prosocial behavior. Several theories posit that prosocial behavior follows from cost-benefit analyses in which the individual takes stock of the person in need, the costs of helping, and the immediate or delayed rewards for the self to be derived from prosocial action (e.g., Darley & Batson 1973, Hamilton 1964, Nesse 1990, Nowak 2006, Sober & Wilson 1998, Trivers 1971). Our analysis builds on and extends this foundation, introducing new processes that investigators have discovered over the past 20 years of research to be critical determinants of prosocial behavior.

Our framework focuses on individual-level appraisal processes that give rise to prosocial action, but we model how this intrapsychic cost-benefit analysis is further shaped by dyadic, group, and cultural factors. All components of our equation are conceptualized as perceptions of the giver—the person who acts in prosocial fashion. As such, the components of our equation need not be accurate or rational. Indeed, our equation may yield decisions to act prosocially that contrast with different kinds of rationality: psychological rationality (e.g., is the perception founded on reasonable appraisals of the situation?), economic (e.g., is the cost-benefit analysis appropriate?), and evolutionary (e.g., will the behavior maximize fitness?). Although each component in our framework can be subdivided into subprocesses, to balance parsimony with completeness, we provide an equation whose components capture the complexities of the intrapsychic processes that lead to prosocial behavior:

$$\mathbf{M} \times (\mathbf{D} \times (\mathbf{1} + \mathbf{B}_{\text{self}}) + \mathbf{K} \times \mathbf{B}_{\text{recipient}} - \mathbf{C}_{\text{inaction}}) > \mathbf{C}_{\text{action}}$$

In our framework,  $\mathbf{M}$  is what we call the social momentum for acting prosocially (ranging from 0 to infinity). This term represents the degree to which the individual's sociocultural milieu encourages or discourages prosocial action. Social momentum is largely affected at the cultural level in the form of representations of social norms and values relating to prosocial behavior. Values of  $\mathbf{M}$  ranging from 0 to 1 represent social resistance: a dampening of prosocial behavior. Values of  $\mathbf{M}$  exactly at 1 capture an absence of social influence. Finally, values ranging from 1 to infinity capture positive social momentum, where social norms and group behavior catalyze prosocial behavior.

The terms within the parentheses build on previous attempts to model the cost-benefit analyses that give rise to prosocial behavior. Two of our components deal first with the giver. A first determinant is  $\mathbf{B}_{\text{self}}$ , the perceived benefit to the self of acting prosocially. Numerous discoveries have emerged regarding the benefits to self for acting prosocially. These benefits come in many forms, as we consider later: positive emotions carrying short- and long-term benefits for the individual; dyadic rewards of reciprocity; and group-based experiences of respect, status, and prestige, reflecting indirect reciprocity (Nowak 2006). Our second term is  $\mathbf{D}$ , or default, which captures the biases and perceptions a person carries that are independent of the particular person who is in need that make prosocial behavior more or less likely. Most broadly,  $\mathbf{D}$  captures (a) individual differences in prosociality, and (b) situational factors that characterize the immediate social context (e.g., features of the physical environment), which shape people's default proclivities to act prosocially independent of the potential recipient of prosocial action. In our formulation,  $\mathbf{D}$  multiplies by  $(1 + \mathbf{B}_{\text{self}})$ , allowing for  $\mathbf{D}$  to both act independent of benefits to the self (e.g., love of humanity) and also magnify the benefits to self (e.g., highly prosocial people reap greater personal benefits from acting kindly).

**Table 1** Prosociality constructs at four levels of analysis

Level	Construct
Intrapsychic	Intuitive bias ( <i>D</i> )
	Individual differences ( <i>D</i> )
	Giving feels good ( <i>B<sub>self</sub></i> )
	Guilt ( <i>C<sub>inaction</sub></i> )
Dyadic	Reciprocity ( <i>B<sub>self</sub></i> )
	Prosocial detection ( <i>K</i> )
	Self-other similarity ( <i>K</i> )
Group	Prosocial contagion ( <i>D</i> )
	Reputation ( <i>B<sub>self</sub></i> )
	Gossip ( <i>C<sub>inaction</sub></i> )
	Altruistic punishment ( <i>C<sub>inaction</sub></i> )
Cultural	Norms and values ( <i>M</i> )
	Religion ( <i>M</i> )

Two of our components explicitly address the recipient.  $B_{recipient}$  is the perceived benefit to the recipient of a particular prosocial act: It captures changes in the state of the recipient of prosocial action (e.g., enhanced ability to cope, reductions in distress when suffering, increased pleasure of mutual gain through cooperation).  $K$  captures the giver's biases and perceptions of the specific recipient, which range from positively valenced preferences (e.g., in-group members) to negative values that reflect adversarial stances toward others (e.g., competition, intergroup biases). We conceptualize  $K$  as a modifying factor: It directly influences  $B_{recipient}$ , which captures the benefit another person can receive from the prosocial action. Processes such as perceptions of self–other overlap, and the recipient's prosocial intentions can amplify the perceived connectedness to the recipient.

Finally, we include two terms to conceptualize the costs that figure into prosocial behavior.  $C_{action}$  has received extensive theoretical treatment (e.g., Nowak 2006, Sober & Wilson 1998) and refers to the cost to the self for acting prosocially. For example, prosocial behavior can involve the giving up of a valued resource (e.g., money) to benefit another.  $C_{inaction}$  captures distinct sets of cost altogether ignored by past mathematical models of prosocial behavior: the perceived consequences of not acting. This can take the form of guilt at the intrapsychic level. Furthermore, groups and cultures have developed numerous forms of sanctions against noncooperators to promote prosocial norms. These include reputation loss, gossip, altruistic punishment, and legal norms that punish antisocial behavior.

The components of our equation set the stage for the next sections of our review (see **Table 1**). Below, we examine how processes that arise across four levels of analysis—from the intrapersonal and the dyadic to the group and the cultural—inform the terms of our equation. Intrapersonal processes represent individual-level characteristics that can vary from one person to the next (e.g., temperament, personality traits) and are largely independent of the specific context and situation. Dyadic processes capture shifts in the prosocial calculus as a result of interacting with specific targets; they are inherently interpersonal. At the group level, we examine how events occurring within one's immediate social network—that is, others with whom a person interacts—can affect a person's prosocial behavior within the network. Finally, we examine how prosociality is affected by mechanisms at the cultural level, which refers to the broader social context one lives in and identifies with and that includes a group far larger than those any one person can expect to encounter (i.e., not within one's immediate social network).

## INTRAPERSONAL PROCESSES AND PROSOCIALITY

### The Kindness Instinct: Intuitive Bias Toward Prosociality (*D*)

The past 20 years have seen startling discoveries that support the supposition that humans have an intuitive, default tendency toward some degree of prosociality. Here is but a sampling. Studies of nonhuman primates yield compelling evidence of altruism and generosity (de Waal 2009, 2012). For example, both chimpanzees and bonobos maintain long-term partnerships with nonkin, routinely sharing resources and the provision of care (de Waal & Lanting 1997, Langergraber et al. 2007). High levels of prosociality are observed cross-culturally. For instance, across numerous studies, when people are asked to split a resource between themselves and a stranger, people typically choose to give between 40% and 50%—high levels of generosity considering that in many of these studies, (*a*) the recipient was anonymous and (*b*) there were no repercussions for keeping the entire resource for oneself (Camerer 2003). Even within small-scale societies, the most common offer is 50%, and the average offer in many societies is above 40% (Henrich et al. 2005). Infants as young as three months show a preference for geometric shapes depicted as helping another (Hamlin et al. 2007, 2010, 2011), and children as young as 14 months and 18 months old actively help others and cooperate in joint tasks (Warneken & Tomasello 2006, 2007). In the United States, more than 30% of the population reported volunteering in 2005–2006 (Omoto et al. 2010), and in 2008, Americans donated on average 4.7% of their income to charity (Gipple & Gose 2012), showing the pervasiveness of prosociality even within societies that emphasize individuality and competition. These empirical examples illustrate that prosociality is likely (*a*) intuitive, (*b*) widespread, and (*c*) deeply engrained in human behavioral tendencies. Kindness, it seems, may very well be a basic instinct.

Recent studies on the prevalence of prosociality align with earlier analyses of the tendency for humans to respond to harm, need, vulnerability, and weakness in others—a response that many have been attributed to the emergence of the need to care for hypervulnerable human offspring (Bowlby 1969, Keltner 2009, Mikulincer & Shaver 2009). More specifically, distress vocalizations, facial displays of sadness, baby-faced facial morphology, submissive posture, and the blush and display of embarrassment increase the likelihood of prosocial response (Goetz et al. 2010, Penner et al. 2005). In fact, a recent fMRI study found that images of suffering and need (e.g., images of physical malnutrition in children) activated a midbrain region known as the periaqueductal gray, which when stimulated in mammalian species triggers caregiving behavior (Simon-Thomas et al. 2012). Within the social psychological literature, cues related to need, harm, vulnerability, and weakness trigger more prosocial tendencies (Penner et al. 2005, Piff et al. 2010).

This intuitive tendency toward prosociality is most clearly brought into focus in recent work by Rand and colleagues (2012). In a series of experiments, participants took part in the public goods game in groups of four. Each participant was given 40¢ and allowed to give some amount, between 0¢ and 40¢, to the group, which was doubled and then split between the four members. In such a game, the best outcome for the group is if everyone contributes everything they started with—in that case, each person will end the game with 80¢. However, for each individual, the best strategy is to keep one's own endowment and free ride—receive the group benefits without incurring any cost. People who made their allocation decisions in ten seconds or less contributed about 65% of their endowment; people who deliberated for longer than ten seconds contributed closer to 50%. Follow-up experiments yielded similar evidence of a default tendency toward prosociality: Causing individuals to make their decisions quickly prompted them to cooperate more with others (by allocating ~67% to the group) than did individuals instructed to deliberate and reflect on their decision (these individuals allocated 50% to the group). These findings indicate that cooperation is

a relatively intuitive snap judgment, whereas self-interest may be the product of more deliberative and calculative cognitive processes.

### **Individual Factors Shaping the Propensity to Act Prosocially (*D*)**

Prosociality is one of many basic tendencies humans show toward one another. Yet not all people are equally cooperative and prosocial. Any treatment of prosociality, then, must consider the striking individual differences in prosocial behavior (*D* within our framework). In studies of economic games and social values, some individuals are strongly disposed to cooperate, others to compete (Van Lange 1999), some to give to public goods, others to exploit such resources (Frank 1988). In the literature on adult personality, highly agreeable individuals show high levels of cooperation across different tasks (Graziano et al. 2007), and individuals who are high in openness to experience display greater perspective taking (McCrae & Sutin 2009). Studies find that individuals with other personality profiles, such as Machiavellians, are very likely to exploit others and abandon cooperation in favor of self-interest (Gunnthorsdottir et al. 2002). Fairly novel with respect to formal modeling of prosocial behavior, the *D* component of our framework captures these meaningful, default variations in the individual and how she or he responds to opportunities for prosocial responding.

Where do these individual differences come from? One part of the answer is biologically based temperament. Recent studies highlight several neurotransmitters and their underlying genetics as being related to prosocial behavior, including oxytocin (e.g., Kogan et al. 2011, Kosfeld et al. 2005, Rodrigues et al. 2009b), serotonin (e.g., Crockett et al. 2008, 2010), and dopamine (e.g., Bachner-Melman et al. 2005, Reuter et al. 2011). Other work has linked individual differences in vagus nerve activity to prosociality (e.g., Eisenberg et al. 1995; A. Kogan, C. Oveis, J. Gruber, I.B. Mauss, A. Shallcross, E. Impett, I. Van der Löwe, B. Hui, C. Cheng, and D. Keltner, manuscript under review; Oveis et al. 2009).

### **Giving Feels Good: Intrinsic Personal Benefits of Prosocial Action (*B<sub>self</sub>*)**

Previous formulations of prosocial behavior have focused primarily on the costs to the giver and the benefits to the recipient, with little emphasis on the immediate benefits of prosocial acts for the giver. Yet emerging evidence suggests that acting with kindness yields many kinds of benefits for the giver. For example, research has documented that caring for others is linked to greater self-esteem and self-efficacy (Crocker 2008, Piferi & Lawler 2006). In other work, Dunn and colleagues (2008) investigated how spending money on oneself versus others affects happiness. Results from a nationally representative US sample demonstrated a positive link between prosocial spending (e.g., gifts for others, charities) and self-reported happiness. In an experimental follow-up, participants were given \$5 or \$20 and told to spend the money either on themselves or on someone else by the end of the day. Participants who spent the money on others reported higher levels of happiness than did participants who spent money on themselves. These findings have since been replicated in 136 cultures (Aknin et al. 2013). Kindness and prosociality, it seems, are universally rewarding. In our framework, these sorts of intrinsic rewards associated with prosociality are a central component of the benefits enjoyed by the self (*B<sub>self</sub>*) and point to novel hypotheses to guide future research. For instance, given recent evidence suggesting that individuals' desired levels of positive emotion vary (e.g., Diener et al. 2006), future work should explore how this individual difference modulates inclinations toward prosociality.

In still other work on the personal benefits of prosociality, researchers have shown that prosocially disposed people tend to be happier and healthier. Within organizations, employees who

are more prosocially inclined tend to be more creative and engage in enhanced problem solving (Grant & Berry 2011). In our own work, we have documented that people with increased tendencies toward prosociality report greater levels of life satisfaction, positive emotions, self-esteem, happier relationships, and more love experiences with close others and even with humanity in their daily lives (Le et al. 2013). People especially motivated to care for their partners experience greater positive emotions and relationship satisfaction when they engage in daily sacrifices for their partners (Kogan et al. 2010)—these findings illustrate the importance of studying the interactions among framework components. In this instance, individual differences toward prosociality ( $D$ ) appear to amplify the rewards for prosocial action ( $B_{self}$ ); giving feels good, but particularly for those who are prosocially inclined.

More generally, there appear to be strong emotional benefits to acting prosocially and being prosocially inclined. Prosocial emotions such as compassion (Fredrickson 2001, Goetz et al. 2010, McCullough et al. 2004) may give rise to numerous social and personal benefits, including greater social support and purpose in life (Fredrickson et al. 2008), feelings of being close to friends (Waugh & Fredrickson 2006), relationship satisfaction (Harker & Keltner 2001, Impett et al. 2010), personal success (Lyubomirsky et al. 2005), and life expectancy (Danner et al. 2001). Prosocial behavior also tends to trigger affective responses, such as gratitude, that engage neurophysiological processes known to have beneficial regulatory effects on basic systems such as the immune and cortisol systems, a point to which we return below.

### **Guilt as Deterrent: Intrapyschic Costs of Inaction ( $C_{inaction}$ )**

Alongside the individual benefits derived from prosocial acts, failures to act prosocially can yield intrapsychic costs. Given that prosociality is a valued group norm, failures to behave prosocially can result in negative self-evaluation and distress that accompany failures to adhere to internal standards (Tangney et al. 2007). Under such circumstances, a particularly significant negative emotion likely to arise is guilt.

Feeling guilt is costly in several ways. It threatens the self and is thus aversive. Guilt is associated with elevated sympathetic autonomic arousal (Strauman 1989) and is metabolically costly. People are motivated to avoid this distress by behaving prosocially and avoiding transgressions. In this way, guilt helps maintain prosocial and other-oriented behavior.

Empirical evidence corroborates this claim. Guilt-prone individuals—who anticipate negative feelings about personal wrongdoing—report greater empathy and perspective taking, and they engage in more communal, ethical, and prosocial patterns of behavior (Cohen et al. 2011, 2013). In situations that are private and confidential, absent pressures to conform to social norms or risks of punishment, the anticipation of guilt promotes prosocial behavior (Cohen et al. 2013). Even when one has not personally transgressed, guilt is a powerful motivator of prosocial behavior. For instance, vicarious feelings of guilt—that is, guilt felt on behalf of another’s misdeeds—can motivate prosocial reparative behavior (Brown et al. 2008). These findings converge on the notion that the motivation to avoid feeling guilt can maintain prosocial responding even absent other costs to the self (e.g., punishment).

## **INTERPERSONAL PROCESSES AND PROSOCIALITY**

Thus far, we have seen how the default tendency toward prosociality, the rewards of prosocial action, and the costs of inaction all increase the likelihood of prosocial behavior. In the following section, we focus on the dyadic, face-to-face processes that encourage prosocial responses.



## Selective Prosociality: Dyadic Processes that Shape the Propensity to Help a Particular Recipient (*K*)

Opportunities for prosocial action often arise in the context of face-to-face, dyadic interactions: helping someone in obvious distress, cooperating with a colleague, giving care to someone who is ill, intervening during an emergency. Previous studies focused on how recipient characteristics, such as gender and ethnicity, influence rates of prosocial response (Penner et al. 2005). Building on this prior work, here we consider recent advances in the study of dyadic processes that influence tendencies toward prosociality.

**Identifying prosocial recipients.** Many analyses of the emergence of prosocial behavior center on what is known as the trust problem (Axelrod 1984, Frank 1988, Nesse 1990, Nowak 2006, Sober & Wilson 1998): How do people selectively engage in relationships with others who are going to cooperate rather than exploit? The costs of prosocial behavior are self-evident—directing resources to others—and the risks are just as clear, from harm to self to varying forms of exploitation.

Given the potential risks of prosocial action, rates of cooperation and altruism are highest when individuals can systematically detect the individuals who are prosocially inclined (e.g., Frank 1988, Nowak 2006). The capacity to detect prosocial tendencies in others allows individuals to strategically enter into cooperative, mutually beneficial relations, and avoid the costs of being exploited. For example, Wedekind & Milinski (2000) and others have found using iterative economic games that once individuals know others' predilection to cooperate or defect, they will preferentially allocate resources to more cooperative group members. Within our framework, we conceptualize this bias toward helping prosocial others as a dyadic process that affects the biases and perceptions toward the specific recipient (*K*) component of our equation.

A critical step in the process of preferentially helping those who are prosocially inclined is to identify who is likely to be prosocial. Mounting evidence suggests that humans can infer the traits and states of others from thin slices, or brief segments, of behavior (Ambady et al. 2000). For instance, seeing someone for less than one minute is enough to reliably detect at better-than-chance levels people's sexual orientation (Ambady et al. 1999), personality (Borkenau 2004, Oltmanns et al. 2004), and socioeconomic status (Kraus & Keltner 2009). People are also strikingly adept at detecting the prosocial tendencies of others. In one study, interpersonal tendencies associated with psychopathy were detectable from as little as five seconds of facial behavior (Fowler et al. 2009). In our own work, we have shown that naïve perceptions of the prosociality of targets of observers who had viewed 20-second silent video clips mapped onto differences in the rs53576 single-nucleotide polymorphism (SNP) of the target's oxytocin receptor gene (Kogan et al. 2011)—a gene that is related to individual differences in prosocial behavior (Rodrigues et al. 2009b, Tost et al. 2010). Perhaps most strikingly, Albrechtsen and colleagues (2009) showed naïve observers 15-second video clips taken from confession statements of inmates. Some of these confessions were honest and others were lies. On the basis of these brief videos, naïve observers could detect at better-than-chance levels who was lying and who was honest.

Such quick and reliable detection of a target's prosocial motivations depends on the reliable signaling and recognition of behavioral displays of prosocial intention. This issue of whether there are telltale nonverbal signals of prosociality has been investigated in studies we present in **Table 2**. Indeed, evidence suggests that prosociality is signaled through a combination of head tilts, gaze, smiling, head nods, blush, embarrassment displays, oblique eyebrows, and laughter (Bachorowski & Owren 2001; Eisenberg et al. 1989; Feinberg et al. 2012b; Gonzaga et al. 2001, 2006; Kogan et al. 2011). In a related literature, researchers have investigated which behaviors

**Table 2** Nonverbal signs of prosocial character

Nonverbal behavior	Significance
Head tilts, gaze, smile <sup>a</sup>	Social engagement
Head nods <sup>b</sup>	Deference, submissiveness
Blush <sup>c</sup>	Concern over social evaluation
Embarrassment display <sup>c</sup>	Desire to appease, reconcile
Oblique eyebrows <sup>d</sup>	Concern for other
Laughter <sup>e</sup>	Warmth, cooperativeness

<sup>a</sup>Gonzaga et al. 2001, 2006; <sup>b</sup>Kogan et al. 2011; <sup>c</sup>Feinberg et al. 2012a; <sup>d</sup>Eisenberg et al. 1989; <sup>e</sup>Bachorowski & Owren 2001.

people use to detect prosocial intent. This literature reveals that observers rely on many of the signals of prosociality to detect those who are more prosocially inclined (Goetz et al. 2010).

These studies establish that the likelihood of a target acting in prosocial fashion—and eliciting such action from another—is reliably signaled in specific patterns of nonverbal behavior. This signaling component is an important dyadic process of prosociality and informs the **K** of our framework by motivating prosocial behavior (in the presence of prosocial cues) or constraining it (absent such cues). It is important to note there is no single signal of prosocial intention. And the nonverbal displays of prosociality will no doubt have context-specific meaning and will likely signal different dimensions of prosociality. For example, head nods signal respect and an interest in the other's welfare. Embarrassment displays—defined by their gaze aversion, controlled smile, head movements down and away, and occasional face touching—signal a concern over social norms and fear of negative evaluation. As novelists have long known and psychologists are beginning to document, there is a rich nonverbal vocabulary of prosocial intention.

**Perceived self–other similarity.** Perceived self–other similarity is a second dyadic process that informs the **K** component, acting as a motivator of prosocial behavior (in the case of perceived similarity) or constraint (in the case of perceived dissimilarity). Perhaps one of the most dramatic demonstrations of this principle comes from reports of people who helped save Jewish members of their community during the Holocaust; they consistently report a sense of shared humanity and commonality as a powerful motivator for their behavior (Monroe 1996, 2004).

Direct manipulations of similarity between self and other also increase the likelihood of prosocial response. One recent demonstration capitalized on people's tendency to mimic, often unconsciously, the nonverbal behaviors of others. Valdesolo & DeSteno (2011) had participants and confederates sit across from one another and listen with earphones to rhythmic patterns of tones while tapping their fingers to the tones. The participant and confederate either (*a*) listened to the same pattern of tones, and therefore mimicked one another in synchronous tapping, or (*b*) listened to different patterns of tones, and therefore tapped their fingers at different times. Participants whose tapping was mimicked by the confederate later reported feeling more similar to the confederate, had higher levels of compassion, and were more likely to help that person complete a long and uninteresting task later in the study. Much like acts of behavioral synchrony used to induce social cohesion and cooperation among groups in the real world (e.g., coordinated marching in the military), even subtle acts of mimicry in the lab can induce feelings of self–other similarity and enhance prosocial responding.

## Give to Receive: Dyadic Benefits of Prosociality ( $B_{self}$ )

An enduring contribution to the study of prosocial behavior is the notion of reciprocal altruism—that exchanges of generosity and the ensuing rewards for the self outweigh the immediate costs of prosocial behavior, leading altruism to be an evolutionarily viable strategy (Axelrod 1984, Nowak 2006, Trivers 1971). Implied by reciprocal altruism is the notion that individuals are more likely to behave favorably toward others when they expect their favors to be returned. Reciprocity amplifies the perceived benefits of prosocial action ( $B_{self}$ ) and promotes more prosocial relations. The mutual sharing of resources is a foundation of cooperative bonds among both nonhuman primates (de Waal 2012) and humans (Sussman & Cloninger 2011). In humans, reciprocation in nonverbal behavior—when one person reciprocates a dominance display of another with submissive posture—tends to produce greater interpersonal liking (Tiedens & Fragale 2003). Flynn and colleagues have found that the exchange of favors at work is a powerful mechanism by which individuals build alliances and rise in respect and status (Flynn et al. 2006). In negotiations between counterparts, reciprocated concessions are a pathway to more integrative outcomes that benefit both sides and, by implication, more prosocial outcomes (Thompson 2006). More broadly, in a meta-analysis of more than 180 effect sizes, Balliet and colleagues (2011) found that rewards promoted cooperation across a number of different paradigms and cultures.

Guided by theoretical claims about reciprocal altruism, gratitude brings into focus the benefits to the self for acting in prosocial fashion in at least two ways (McCullough et al. 2004, Nesse 1990, Nesse & Ellsworth 2009). First, the expression of gratitude, in the form of linguistic acts or gifts, rewards the generous acts of others. Algoe and her colleagues (2008) have documented that expressions of gratitude predict increased closeness among group members over time. Within romantic couples, longitudinal data have revealed that feelings of gratitude at time 1 predict greater responsiveness to the partner's needs at time 2 (Gordon et al. 2012). In work settings, managerial expressions of gratitude can enhance feelings of social worth among employees (i.e., causing them to view themselves as viable members of the community) and subsequently increase their prosocial behavior (Grant & Gino 2010).

The manner in which expressions of gratitude by the recipient serve as rewards to the giver is brought into sharp focus by recent discoveries concerning the prosocial functions of touch. The tactile system of hand, skin, and parts of the cortex plays an important role in rewarding prosocial behavior within dyadic interactions. The right kind of touch can trigger activation in reward regions of the frontal lobes (Rolls et al. 2003), as well as oxytocin release (Holt-Lunstad et al. 2008) and activation in the vagus nerve, which is associated with social connection, as we discuss below (Porges 2007). Touch is a primary reinforcer. And recent studies by Hertenstein and colleagues have found that strangers can communicate gratitude (and other prosocial emotions such as sympathy and love) with brief touches to a stranger's arm (Hertenstein et al. 2006, Piff et al. 2012a). Follow-up studies have found that touch can increase cooperation in economic games and in team activities (Kraus et al. 2010, Kurzban 2001). When recipients of prosocial behavior express gratitude to their benefactor through touch, they are providing a powerful reward for prosocial action.

Beyond serving as a reward for acts of kindness, gratitude also influences the default tendency toward prosocial action ( $D$ ). It produces increased tendencies toward generosity, favors, sacrifices, and expressions of appreciation, which are critical to prosocial relations. As an illustration, participants in studies by DeSteno and colleagues (Bartlett & DeSteno 2006, DeSteno et al. 2010) were helped unexpectedly by a confederate (to fix a computer problem). Being the recipient of generosity led participants to feel gratitude, and in this state, they then proved to be more generous in allocating their time and resources to other strangers. For these and other reasons, gratitude has

been considered a moral emotion and a primary determinant of prosocial behavior (McCullough et al. 2001), as it reinforces the self and rewards prosocial action ( $B_{self}$ ).

## GROUP PROCESSES AND PROSOCIALITY

Cooperation has many advantages within groups (e.g., Sober & Wilson 1998). In the most immediate sense, highly adversarial, self-focused individuals—for instance, free riders and hyper-competitive types—undermine group functioning (Felps et al. 2006). By contrast, other-focused individuals, who are relatively more attuned to the needs of others, actually make for more effective problem solving in collective tasks (e.g., Woolley et al. 2010). Cast within an evolutionary framework, groups likewise are invested in more prosocial members, in light of the dependence humans experience vis-à-vis others to accomplish basic tasks of survival and reproduction. These converging lines of reasoning suggest that group-based processes should increase the prosociality of members within a group or social network. Here we focus on recent discoveries related to several group processes and how they alter the terms of our SAVE framework.

### Prosocial Contagion: Prosocial Behavior Within the Group Induces Bias Toward Prosociality ( $D$ )

From laughter, blushing, and voting patterns to destructive health habits, feelings of anxiety, and expressions of gratitude, nearly all manner of social behavior is potentially contagious, spreading to others in rapid, involuntary fashion (for reviews, see Christakis & Fowler 2009, Hatfield et al. 1993). Humans are a highly mimetic species, disposed to imitate and take on the tendencies of others in their surroundings and social networks.

Contagious prosociality—the spreading of altruistic, cooperative intention and action to others—is one means by which members of groups avoid the risks of mutual exploitation and foster cooperation (e.g., Goetz et al. 2010). More specifically, prosocial contagion should bias people toward prosocial behavior in general and thus is a group-level dynamic affecting the bias and perceptions independent of the recipient term ( $D$ ) in our equation.

There is intriguing evidence for contagious prosociality (Nowak & Roch 2007). For example, in a study of charity in organizations, when individuals were transferred to sections of an organization that had higher levels of charity, their levels of charity rose in volume (Christakis & Fowler 2009). Of course, this finding can be interpreted in multiple ways—explicit social norms or pressures may have led to the documented increase in charity—but it is intriguing nonetheless that the degree to which generosity is part of a social milieu can influence in contagious fashion others' generosity. Other studies further bolster the notion of contagious prosociality. In one study, participants who played a dictator game after observing other participants behaving prosocially exhibited more generosity compared with those participants in a baseline condition (Krupka & Weber 2009). In other work, witnessing one person helping another caused participants to engage in more helping behavior in a subsequent task (Jonas et al. 2008). Thus, prosocial actions of others can elicit altruistic tendencies in oneself.

In experimental work, Fowler & Christakis (2010) have demonstrated with greater rigor how prosocial behavior spreads through social networks. In this important study, participants played several rounds of the public goods game (described above) in groups of four, but in this version, each round was played with an entirely new set of participants. In each round of the game, the participant was given 20 money units (MUs) and allowed to give some amount, between 0 and 20, to the group. Each MU the participant gave to the group was translated to an increase of 0.4 MU for each of the four group members; a gift of 1 MU would ultimately cost the giver

0.6 MU personally but benefit each other group member, translating into a collective gain of 1 MU. If participants kept all their MUs, they would end the game with 20 MUs; if they each gave all their MUs to the group, each member would end the game with 32 MUs. In this study, results revealed that for every MU a player gave, his or her partners would give 0.19 MUs more on average to a new set of players in the next round and 0.07 MUs on average to yet another new set of players.

One potential mechanism behind contagious altruism comes in the form of elevation: moral emotion elicited by witnessing the virtuous behavior of others (Algoe & Haidt 2009). In a series of studies, Schnall and colleagues (2010) documented that participants who were induced to feel elevation after seeing another person acting prosocially were more likely to volunteer for another unpaid study and spent double the time helping on a tedious task than did participants who were not induced to feel elevation. In follow-up work, Schnall & Roper (2012) showed that elevation is especially effective in promoting prosocial behavior after people reminded themselves of previous prosocial behavior, suggesting that elevation boosts people's propensity to act on their moral values. Elevation, then, can act as a powerful group-level force that shapes the *D* component of our framework—boosting the propensity to act prosocially independent of the specific needs and characteristics of the benefactor.

### **Rewarding the Kind: Reputation as a Group Benefit to Self for Acting Prosocially ( $B_{self}$ )**

Reputation refers to the beliefs, evaluations, and impressions about an individual's character held by group members within a social network (Emler 1994). Reputations differ from impressions of an individual's personality, the temperament-like idiosyncrasies of the individual (Craik 2009). Theoretical analyses of the emergence of prosociality posit that reputation is critically important for the development and sustainability of indirect reciprocity: a system in which people receive reciprocal benefits for their kindness not from the person they helped but from another member of the same group (Fu et al. 2008, Nowak 2006, Nowak et al. 2000). Empirical evidence from numerous domains has documented the pervasiveness of reputation and the benefits people can gain in the form of reputation for their prosocial behavior, which result in group-level benefits for the person acting kindly ( $B_{self}$ ).

Studies of organizations and residence halls have documented the alacrity with which reputations form and are distributed across group members (Craik 2009). In studies of social networks that arise in financial advising firms, individuals gain reputations for the quality of the work they do and the degree to which they are good team players (Burt et al. 2013). Perhaps more impressively, those reputations travel with the individual as they move to different units in the organization: If one moves to a new unit within an organization, the members of that new group will know his/her reputation. Dovetailing with these observations, in studies of residence hall members and MBA students in working groups, individuals came to acquire a distributed reputation (for example, as someone who is collaborative or someone who routinely free rides) within a week of the group's formation (Anderson et al. 2001, Anderson & Shirako 2008). Group members also reach considerable consensus in their judgments of other group members' reputations, suggesting that individuals within a group share reputational information reliably. For example, the average correlation between two dorm members' judgments of a third dorm member's reputation for influence and status was about  $r = 0.70$ , a high degree of reliability.

What is the content of a person's reputation? Presently, empirical data are sparse—this is an area in need of empirical inquiry and could be guided by recent formulations of the basic dimensions of person perception, which state that impressions of others, for example, emphasize perceptions

of competence and warmth (Fiske et al. 2007). However, some suggestive evidence does exist. For example, the reputation an individual earns within a social network is based on that individual's tendency to cooperate and to be a good community member (Keltner et al. 2008). In this research, members of a residence hall wrote about the reputations of two other members in their residence hall. The reputation stories centered on whether the person was a good member of the community—the degree to which she or he was believed to be considerate, kind, sharing, agreeable.

Recent work has documented that reputation-related processes increase prosocial tendencies within social groups. Computer simulations (Nowak & Sigmund 1998) have repeatedly demonstrated that cooperation can be a viable evolutionary strategy because of the reputational benefits that it affords the cooperator. In effect, cooperating confers the reputation of a valuable community member to the cooperating individual and increases the likelihood that they will be cooperated with in the future. Reputation, in this way, functions in the same way as prosocial detecting at the dyadic level: It solves the commitment problem. In a direct test of the hypothesis, Wedekind & Milinski (2000) provided players knowledge of the other players' past history of cooperation, mirroring the reputation-related conversations about an individual's predilection for prosociality that emerge naturally in groups. They found that participants will readily cooperate and give resources to an interaction partner whom they know to have a history of cooperation, but they will compete and choose not to give resources to interaction partners known to be greedy or competitive (see also Milinski et al. 2001). In a compelling follow-up, Milinski et al. (2002) conducted a laboratory test of whether public displays of prosociality (donations to the relief fund UNICEF) conferred important advantages to the individual. Participants played 16 successive rounds of an economic game in groups in which, for each round, participants decided whether to donate money to a group member and thereafter to charity. During the game, information about each participant's allocation decisions was displayed to the other group members. At the end of the sixteenth round, participants also cast their vote for one group member to represent their group as a potential delegate in the student council. Results revealed that the more money participants gave away in general, the more they received from others. More importantly, the more participants donated to charity, the more money they also received from others, and the more votes they received to represent the group in the student council; thus it appears that individuals are rewarded for prosocial acts even when others did not directly benefit from those acts. These findings indicate that prosocial behavior is rewarded by others via indirect reciprocity and enhanced reputation, and they underscore the very clear benefits ( $B_{self}$ ) associated with prosociality in social networks and collectives.

The evaluative dimension to a person's reputation captures the esteem that person enjoys within the eyes of group members. Analysis of reputation and the status benefits associated with acting prosocially has led to the competitive altruism hypothesis: Given the rewards associated with reputation and status, social collectives can encourage individuals to act in prosocial fashion in exchange for social status afforded to them by group members (e.g., Milinski et al. 2002). Group members trade resources for social esteem.

Two kinds of empirical study support the competitive altruism thesis. A first concerns who rises in the ranks of social hierarchies. Judge et al. (2002) brought together nearly 75 studies that determined which social traits predict who enjoys elevated status and who emerges as leaders in organizations, schools, and military units. In these studies, prosociality—as captured in self-reports of the trait agreeableness—predicted rises in social standing in school settings (the correlation across studies between social standing and agreeableness in organizations and the military was near zero). In this same meta-analysis, Judge et al. observed that agreeableness predicted the ability to remain in positions of elevated rank across group contexts. Here one might infer that once in positions of power, individuals are indeed trading prosociality for elevated esteem.

Experimental evidence provides a second line of support for the competitive altruism thesis. For example, van Vugt and his colleagues have found that group members will give greater social status and power to other group members who act altruistically (Hardy & Van Vugt 2006). In other research, Willer (2009) asked participants to rank the status of individuals who gave to a public good or did not, and the study found that participants ranked the generous as being of higher status. More recent work suggests that motivations to gain status can cause individuals to behave in costly proenvironmental fashion, but only in situations where such acts are public and observable by others (Griskevicius et al. 2010). Groups conspire to give status and esteem to those who act in prosocial fashion, which in turn motivates prosocial behavior.

### **Gossip and Altruistic Punishment: Group Mechanisms to Guard Against Inaction ( $C_{inaction}$ )**

**Gossip.** Gossip is a form of evaluative commentary between two people about the character of a third individual who is not present (Craik 2009; Wert & Salovey 2004a,b). The information spread in gossip is most typically plausible, unverifiable, and potentially damning to the person's reputation. Thus gossip, like teasing, employs many of the linguistic features of off-record communication—forms of exaggeration, humor, indirectness—that suggest that the communicative act is as much hypothetical as rooted in truth. Craik (2009) refers to gossip as a primary form of reputational discourse: It is how group members investigate and arrive at consensus about the reputations of other members of social networks. We suggest that concern over gossip is a powerful check against free riding—that is, gossip is a form of cost for not acting prosocially ( $C_{inaction}$ ) and thereby motivates others to prosocial action.

In keeping with this thesis, new studies using innovative methods are beginning to document how gossip promotes cooperation within social networks. For example, in more ethologically oriented work, Kniffin & Wilson (2005) found that in the banter and badinage of a college rowing crew, the crew members systematically focused their gossip on one member who was not making practices or being a good team member. Our own research focused on how acts of gossip were distributed among members of a sorority house at a Californian university (Keltner et al. 2008). Surveys of the members of the group allowed us to identify who were frequent targets of gossip and to whom the gossip flowed. The frequent targets of gossip in the sorority were well-known and highly visible but not well-liked, and they themselves, in separate surveys, reported that they were cold, aggressive, and highly Machiavellian, willing to backstab and take others down to rise in power. It would seem that gossip targets those individuals who pose the most threat to the cooperative fabric of social groups.

Several recent studies have documented more systematic associations between gossip and increases in prosociality in groups. For example, Beersma & van Kleef (2011) have found that if individuals play an economic game with a person identified as a gossip, they behave in more cooperative fashion. And in still other research, Feinberg and colleagues (2012b) have found that the most prosocial individuals, as captured in the social values inventory, are the most likely to resort to gossip to warn others about free riders in social networks, again attesting to the notion advanced here that gossip is a group-level process that helps increase prosociality.

**Altruistic punishment.** In addition to gossip, researchers have identified a second group-level process that guards against free riding by increasing the cost of not acting prosocially ( $C_{inaction}$ ): altruistic punishment. Empirical studies suggest that altruistic punishment—that is, punishing free riders at a cost to oneself—is an effective method of preventing free riders from spreading and

prevailing within social collectives, and it is also extremely widespread. Within our framework, altruistic punishment serves as both a dyadic and a group-level mechanism to increase the cost of inaction.

At the dyadic level, people with whom one interacts can directly sanction the individual for not acting prosocially. Fehr and colleagues have conducted numerous studies using the ultimatum game to model dyadic altruistic punishment (Fehr & Fischbacher 2003). In the ultimatum game, participant A is given an allotment of MUs (e.g., 10 MUs) and must make a decision of how many of the MUs to share with participant B. Participant B then must decide whether to accept or reject the offer from participant A, in which case both participants get nothing. If participant B is being rationally selfish, he/she will accept any offer greater than 0; however, numerous studies show that people would rather get nothing at all than accept an unfair offer (Fehr & Fischbacher 2003, Güth et al. 1982, Henrich 2001). In fact, most people regularly reject offers that are less than 25% of the total MUs. These findings illustrate that people are more than willing to engage in altruistic punishment—and punish those who take more than their fair share—in the name of upholding fairness and equality, even at a cost to the self. Furthermore, multiple evolutionary analyses of altruistic punishment suggest that punishment is a stable strategy, even with one-time anonymous interactions and within large groups (Boyd et al. 2003, Fehr & Fischbacher 2003, Fowler 2005).

At the group level, people are perhaps even more willing to assume costs to punish free riders for not acting fairly, even with complete strangers. In one telling study, Fehr & Fischbacher (2004) gave participant A 100 MUs, which he/she could share with participant B, who had no ability to reject the offer. Additionally, the game involved a third participant C, who was given 50 MUs and had the ability to punish participant A at a cost—specifically, participant C had to give up 3 MUs for every 1 MU they removed from participant A. Nearly two-thirds of all participant Cs chose to punish participant As for acting unfairly, and the level of punishment increased as a function of how unfair participant A behaved. In another demonstration of group-level altruistic punishment, participants in a study by Fehr & Gächter (2002) played the public goods game (described above). In the key punishment condition in the study, participants were informed of each other's decisions and then allowed to spend between 0 and 10 MUs to punish each specific member of the group—for every 1 MU spent to punish, 3 MUs would be subtracted from the punished participant. Fehr & Gächter found that not only did participants regularly punish other participants who were acting selfishly, but cooperation in fact increased over successive rounds of the game when punishment was allowed. These studies suggest that the threat of punishment from the group is a powerful force to promote prosocial behavior—and is thus a core aspect of the cost of the inaction ( $C_{inaction}$ ) component of our equation.

Recent findings suggest that punishment is not the only route—or even the best route—toward promoting prosocial behavior within groups. Rand and colleagues (2009) had participants partake in an iterative public goods game, playing with the same three others for a series of rounds. After each round, participants could either punish the free riders who had not contributed to the public investment or reward the virtuous others who acted cooperatively and contributed heavily into the public investment. They found that when participants could both punish and reward, only rewarding led to greater payoffs for the group and higher levels of cooperation; punishment became unrelated to cooperation and actually resulted in lower overall group payoffs. However, this study examined punishment of not acting prosocially; presently, no studies have examined the relative effects of punishment or reward as deterrents for antisocial action (e.g., stealing from the group resource)—an intriguing area for future research. It thus remains to be seen whether altruistic punishment can truly be supplanted by group rewarding or, alternatively, if punishment plays an important role in guarding against antisocial behavior.



## CULTURAL VALUES, NORMS, AND PROSOCIALITY

No human societies exist without social norms and values that guide social behavior. In fact, the ability to develop and enforce normative standards of behavior has been argued to be among the most distinguishing features of the human species (e.g., Fehr & Fischbacher 2004). Ethnographies of various cultures around the world provide vivid descriptions of the powerful values and norms that shape behavior in collectives—from norms about participation in group rituals to food sharing to cooperation (e.g., Gurven 2004, Henrich et al. 2004, Sober & Wilson 1998). Given the importance of prosociality to stable human societies, it is not surprising that values about prosociality and altruism are found cross-culturally (Schwartz & Bilsky 1990). A rich literature documents the extent to which prosocial behavior can be influenced by social norms: a person's beliefs about the rules and standards that guide or constrain social behavior in a given situation without the force of laws (Cialdini & Trost 1998). Dozens of studies have documented the extent to which prosocial norms are important impetuses to prosocial behavior (or the lack thereof). With regard to our SAVE framework, prosocial norms can increase or decrease what we have called in our framework the social momentum (*M*) of prosocial behavior—that is, multiplying the benefits of prosocial behavior in the positive case or potentially nullifying them in the negative case.

### The Prosocial Force of Numbers: Norms, Values, and Others' Actions Shape Social Momentum (*M*)

Empirical studies inevitably document striking variations in levels of prosociality across cultures. Perhaps the most rigorous demonstration of such variation is Henrich and colleagues' study of ultimatum game behavior in 15 different small societies (Henrich et al. 2001, 2005, 2006). In the study, the participants were foragers, slash-and-burn farmers, nomadic herding groups, and individuals in settled, agriculturalist societies in Africa, South America, and Indonesia. On average, across the 15 cultures, participants gave 39% of the good to anonymous strangers. Yet there was significant cultural variation—in particular, according to the extent to which individuals within a culture needed to collaborate with others to gather resources to survive. The more the members of a culture depended on one another to gather food and see to others' survival needs, the more they offered to a stranger when they were allocators in the ultimatum game. For example, the Machiguenga people of Peru rarely collaborate with group members outside their family to produce food. Their average allocation in the ultimatum game was 26% of the resource. The Lamerala of Indonesia, by contrast, fish in highly collaborative groups of individuals from different families. The average gift in this culture, so dependent on cooperation for survival, was 58%.

Cultural values concerning individualism (an orientation toward self-interest and one's own goals) versus collectivism (an orientation toward collective goals and others' interests) can also underlie different patterns of prosociality, both across cultures as well as within them. Cultures vary profoundly in terms of relational style, cooperation, and reciprocity as a function of culturally upheld values of collectivism (for instance, in China) versus individualism (for instance, in the United States; for a review, see Oyserman et al. 2002). Collective versus individual norms also predict important variations in cooperative tendencies within cultures. In one study, individuals who reported more collectivistic values in an organization were more likely to engage in a variety of prosocial acts, including increased helping, to benefit their organization as a whole (Moorman & Blakely 1995). Using an experimental approach, Utz (2004) found that supraliminal primes of collectivistic values using words such as “group” and “together” caused individuals to behave more prosocially in an economic game relative to participants who unscrambled sentences with individualistic-related words such as “individual” and “independent.” These studies highlight

how culturally upheld values concerning individualism versus collectivism underpin prosocial tendencies (see also Oyserman & Lee 2008).

The activation of social norms—or beliefs about how one should behave in a given context—can also influence prosocial tendencies, including generosity and helping behavior (Cohen et al. 2010, Effron & Miller 2011, Gailliot et al. 2008, Jonas et al. 2008, Schindler et al. 2012). For instance, simply priming participants with prosocial norm-related words such as “equality” and “helping” can cause individuals to help more (Jonas et al. 2008). The effects of prosocial norms are malleable and context specific. In one study, participants were less generous in tasks that were framed as “economic”—which presumably activated beliefs that one should behave in self-interested fashion—compared with participants in tasks framed as noneconomic (Pillutla & Chen 1999). Situation-specific norms and values can significantly influence the extent to which prosocial behavior is perceived to be endorsed by others and, as a consequence, either dampen or accentuate prosocial responding.

Beyond norms concerning how one should behave, beliefs about how others do behave in a given situation can also significantly enhance prosociality. In one illustrative study, Goldstein and colleagues (2008) studied the effects of social norms on proenvironmental behavior among hotel patrons. They randomly assigned patrons of a particular hotel to receive in their rooms a towel reuse card that employed either a descriptive social norm (which stated that the majority of guests reuse their towels at least once) or a standard proenvironmental message (“Help save the environment”). The rate of towel reuse was 9% higher when patrons were exposed to the descriptive norm compared with the plea to save the environment. This evidence indicates that perceptions of what the majority of others do in a given situation can be a driving force in an individual’s decision to behave prosocially. The more people there are perceived as exhibiting a particular prosocial act, the more momentum there is perceived to underlie that act (*M*), which, in turn, increases one’s own likelihood of behaving in that fashion.

### **Faith and Kindness: Prosociality Is a Universal Religious Virtue (*M*)**

People the world over define themselves in terms of religion—as Muslims, Protestants, Methodists, Unitarians, Jews, Catholics, Mormons, Buddhists, Hindus, or Sikhs (Diener et al. 2011). Religions are a powerful kind of culture (Cohen 2009). The world’s major religions are similar in the esteem they attach to compassion, altruism, and treating others, even strangers and adversaries, with kindness (Armstrong 2009). This conduct is seen in such practices as tithing and tending to those who suffer. It is seen in moral codes such as the Golden Rule—that people treat others as they themselves would like to be treated (see **Table 3**).

Survey studies repeatedly find associations between self-reports of increased religious conviction and practice and prosocial tendencies. For instance, a recent survey of charitable giving in the United States found that individuals in religious regions of the country (e.g., the Bible Belt) gave significantly more of their incomes to charity than did individuals in less religious regions (i.e., the Northeast; Gipple & Gose 2012). Religious individuals report that their religious convictions help them to be ethical, fair, helpful, and kind toward others (Woods & Ironson 1999). Religious participants also exhibit increased feelings of “compassionate love” for close others and strangers (Sprecher & Fehr 2005). Moreover, two recent meta-analyses indicate that increased religiosity is associated with increased agreeableness (a trait defined by cooperativeness; Saroglou 2002) and benevolence (a value rooted in desires to help others; Saroglou et al. 2004).

Experimental research yields a similar conclusion: Exposure to religious concepts increases people’s tendency to act in more prosocial fashion (Norenzayan & Shariff 2008, Shariff & Norenzayan 2007). In a first study in this research, participants were presented with sequences

**Table 3 The Golden Rule across cultures and religions**

Source	Statement
Matthew 7:12	“In everything, therefore, treat people the same way you want them to treat you, for this is the Law and the Prophets” ( <i>New American Standard Bible</i> 1995).
Sextus the Pythagorean	“What you wish your neighbors to be to you, you will also be to them.”
Buddhism	“Putting oneself in the place of another, one should not kill nor cause another to kill.”
Hinduism (Mahabharata)	“One should never do that to another which one regards as injurious to one’s own self.”
Muhammad	“Hurt no one so that no one may hurt you.”
Taoism	“He is kind to the kind; he is also kind to the unkind.”
Dalai Lama	“If you want others to be happy, practice compassion. If you want to be happy, practice compassion.”

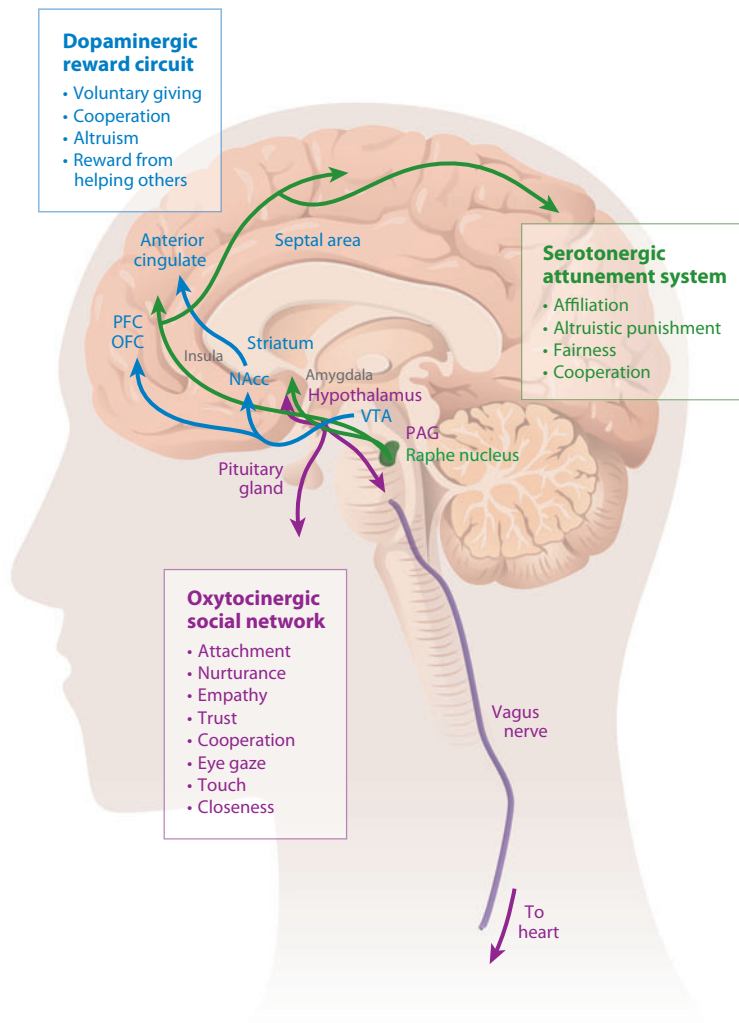
of five words, randomly arranged, and asked to generate sentences using four of those words. In the religion prime condition, the five words always included at least one word with religious meaning, such as Spirit, divine, God, sacred, and prophet. In a neutral prime condition, participants did the same task of unscrambling sentences, but none of the words had religious meaning. Participants then received ten Canadian dollars and were asked to give some amount away to a stranger. Participants in the neutral prime condition were more than twice as likely to give nothing to a stranger as compared with those in the religion prime condition (36% versus 16%). By contrast, people who were primed with religious concepts were more than four times as likely to treat a stranger as an equal by giving half of the money to the stranger (52% in religious prime versus 12% in control condition). This same line of research documented that secular, nonreligious concepts related to ethical behavior—words such as civic, jury, court, police, and contract—generated similar levels of generosity as the religious words prompted. Social institutions that value prosocial behavior—be they religious or civic—significantly enhance prosocial behavior within collections.

Our conceptual review and the findings we have summarized are in keeping with a broader theme in the literature on the cultural triggers of prosociality: Making prosociality more salient in narratives, stories, conversations, and concepts, as religious practice often does, increases prosociality. Cast within the SAVE framework, we would suggest that such practices, ranging from religious doctrine to family dinner-time conversation, contribute to *M*, the cultural milieu, which influences the proclivity toward prosociality.

## TOWARD THE STUDY OF THE PROSOCIAL NERVOUS SYSTEM

In our review, we have highlighted several processes that enable prosocial behavior. Given the many evolutionary arguments for the functions of prosociality, we presuppose that there should be genetically encoded neurophysiological processes, from peripheral nerves to molecules in the brain, which underlie the core mechanisms of prosocial behavior identified in this review.

In the abstract, one might think of these multiple interacting processes as the prosocial nervous system in humans, with parallels in the rudimentary neurobiological architecture of many other mammalian species. This thinking finds theoretical precursors in earlier formulations: claims about the role of the vagus nerve (Porges 2003) and the neuropeptide oxytocin (Carter et al. 2008) in attachment and love, and recent attempts to map empathy networks in the brain (Bernhardt



**Figure 1**

The circuitry underlying the prosocial nervous system. PFC, prefrontal cortex; OFC, orbitofrontal cortex; NAcc, nucleus accumbens; VTA, ventral tegmental area; PAG, periaqueductal gray.

& Singer 2012). Select studies have begun to explore neurophysiological correlates of specific prosocial processes outlined in our SAVE framework (see **Figure 1**).

Here we review evidence concerning biological correlates of prosociality that broadly fall into three classes. A first concerns the systems that promote affiliation, closeness, and ultimately nurturance toward others. We would expect these systems to be active in many acts of prosociality—a thesis garnering increasing support—and to covary with several components of our SAVE framework, most notably the individual's default propensity for prosocial behavior (*D*) and perceptions of specific others (*K*). Second, we would expect specific neurophysiological systems to enable experiences of personal reward for acting prosocially, thus carrying the intrinsic benefits of selflessness (*B<sub>self</sub>*). Third, we posit that a global system related to behavioral inhibition and the coordination of affective states with actual behavior would also be recruited to guide prosociality. This system is

likely to affect several components, including **D** and  $C_{inaction}$ , as we discuss below. Three families of neurotransmitters map onto these functions: oxytocin/vasopressin, dopamine, and serotonin.

At the outset, we note that virtually every biological system implicated in prosociality has been linked to numerous other social and nonsocial processes. For instance, oxytocin was originally identified in its role in uterine contractions during birth and lactation (Donaldson & Young 2008). The vagus nerve, in addition to being linked to prosociality, is also involved in attention (Hansen et al. 2003), self-regulation (Bornstein & Suess 2000), exercise (Dixon et al. 1992), respiration (Grossman & Kollai 1993), and sleep (Vanoli et al. 1995). Likewise, serotonin has broad influences on mood, sleep, appetite, and memory (Roth 1994). Furthermore, the dopaminergic system plays roles in addiction (Belin & Everitt 2008) and numerous psychopathologies (Pritchard et al. 2009). These findings underscore that many biological systems are intimately involved in promoting prosociality, but no biological system exclusively exists to promote prosociality.

### **Neurophysiological Underpinnings of the Kindness Instinct: Oxytocin and Vasopressin**

Concern for others—the motivation that guides prosociality—arises from neurophysiological processes that promote attachment and caregiving (Decety & Svetlova 2012, Panksepp 2007) and includes the hypothalamus and its release of the neuropeptides oxytocin and vasopressin. Homologs of oxytocin and vasopressin are seen across the animal kingdom, in species as diverse as worms, hydra, insects, and vertebrates. Oxytocin and vasopressin are thus, not surprisingly, ancient systems, dating back to at least 700 mya (Donaldson & Young 2008). Traditionally known for their roles in reproduction and homeostasis in a variety of species (Carter et al. 2008), more recent studies have shown their pivotal roles in different manifestations of human prosocial behavior (Bartz et al. 2011, Domes et al. 2007b, Kosfeld et al. 2005). Oxytocin and vasopressin double as neurotransmitters and hormones and are projected to various brain areas, as well as ferried to the pituitary gland for peripheral release (Donaldson & Young 2008). Centrally, these neuropeptides exert social influences by targeting key emotional processing areas in the brain, including the amygdala, septal area, and reward circuitry described shortly (Young et al. 2001, Zink & Meyer-Lindenberg 2012). They both also have a strong presence in the periaqueductal gray (Jenkins et al. 1984), which is a key processing area for pain of the self and others, as well as for nurturance (Bartels & Zeki 2004, Simon-Thomas et al. 2012). A link between the prosocial and pain systems also involves other neurochemical players, including prolactin and opioids (Panksepp 2007).

A growing body of work has linked oxytocin to affiliation and closeness, critical processes in prosociality. For example, the strength of romantic ties, as measured by nonverbal displays of romantic love (Gonzaga et al. 2006) and interactive reciprocity (Schneiderman et al. 2012), directly relates to the amount of oxytocin released during dyadic interactions. Oxytocin's involvement in different attachments, including romantic, parental, and filial, have the same underlying mechanisms by promoting biobehavioral synchrony (Feldman 2012). Furthermore, empathy toward strangers relates to natural oxytocin release and more generosity toward strangers in the ultimatum game (Barraza & Zak 2009). Likewise, oxytocin administration promotes trust and cooperation (Kosfeld et al. 2005). These findings converge on the role of oxytocin in influencing the bias and perceptions of specific others (**K**) component of our framework—that is, the shifts in the oxytocin system in response to specific others promotes prosocial behavior toward them. This specificity is perhaps best seen in work by De Dreu and colleagues (De Dreu et al. 2010, 2011), who have found that intranasal oxytocin promotes prosocial behavior only toward in-group members.

Further supporting this claim, levels of oxytocin also strongly reflect the strength of the mother–infant bond, including eye gaze, affectionate touch, vocalizations, and bonding behaviors.

Moreover, mothers who display more synchronicity of behaviors with their infants' signals show more nucleus accumbens activation and this neural region's correlation with oxytocin release (Atzil et al. 2011). Both maternal and paternal touch and play trigger oxytocin release in parents and activate caregiving circuitry, which includes the prefrontal cortex and nucleus accumbens (Feldman 2012). Interestingly, giving fathers oxytocin artificially induces natural oxytocin increases in their infants (Weisman et al. 2012). Additionally, nonfamilial relationships later in life are related to parenting styles and oxytocin such that more synchronous parenting in infancy influences reciprocity of offspring with their future best friends (Feldman et al. 2013).

Oxytocin and vasopressin are also involved in default, individual differences in prosociality (*D*). In particular, genetic variations of the oxytocin and vasopressin systems, by way of naturally occurring polymorphisms, have also been associated with individual differences in prosociality. For example, variations of the vasopressin receptor AVPR1a are associated with individual differences in the allocation of funds in the dictator game (Knafo et al. 2008) and civic duty (Poulin et al. 2012). Furthermore, an SNP of the oxytocin receptor (OXTR) has been related to a variety of prosocial behaviors, such as compassionate displays toward one's romantic partner (Kogan et al. 2011), trait empathy and empathic accuracy (Rodrigues et al. 2009b), prosocial temperament (Tost et al. 2010), and engagement in charitable activities (Poulin et al. 2012). OXTR SNPs have also been connected to prosocial behaviors in the dictator game and social value orientation (Israel et al. 2009). OXTR variations influence affiliative behavior via neural structure and activation (Tost et al. 2010), as well as through physiological influences on the hypothalamic-pituitary-adrenal (HPA) stress system (Norman et al. 2012, Rodrigues et al. 2009b).

A second pathway for the oxytocin system to affect *D* is through the vagus nerve, a primary branch of the autonomic nervous system. Central release of oxytocin regulates the output of the dorsal motor nucleus of the vagus nerve. Peripherally, the vagus nerve exits the brain stem and contains branches that are involved in modulating the muscles behind behavioral displays of social engagement, including eye gaze, facial expressions, vocal communication (prosody), orientation, and social gestures (Porges 2001, 2007). These branches communicate with the nucleus ambiguus, which interacts with the myelinated vagus and oxytocin to promote calm states via parasympathetic-mediated heart rate decreases (Norman et al. 2012). Therefore, prosociality can be intertwined with powerful calming and soothing experiences via oxytocin and the myelinated vagus (Carter 1998, Porges 2003).

Psychological evidence suggests that greater baseline activity of the vagus nerve—as indexed by respiratory sinus arrhythmia—is associated with numerous processes linked to prosociality, including positive emotions, social connection, emotion regulation, and emotion expressivity (Beauchaine 2001, Butler et al. 2006, Côté et al. 2011, Eisenberg et al. 1995, Fabes & Eisenberg 1997, Kok & Fredrickson 2010, Oveis et al. 2009, Porges 2001). More recently, we have shown that vagus nerve activity is related to self-reports and peer reports of prosociality (A. Kogan, C. Oveis, J. Gruber, I.B. Mauss, A. Shallcross, E. Impett, I. Van der Löwe, B. Hui, C. Cheng, and D. Keltner, manuscript under review). Differences in baseline vagus nerve activity are thought to be relatively stable, reflecting individual differences in the vagus system. Within the SAVE framework, the vagus nerve then affects the individual difference component of prosociality: the default tendency toward prosociality (*D*).

The relationship between vagus nerve activation and prosocial behavior is driven, in part, by a reduction in arousal, which enables a shift in attention to the person in need (A. Kogan, C. Oveis, J. Gruber, I.B. Mauss, A. Shallcross, E. Impett, I. Van der Löwe, B. Hui, C. Cheng, and D. Keltner, manuscript under review). The same appears to be true of oxytocin: Oxytocin can dampen stress reactivity in both the brain and the body (Carter et al. 2008, Gimpl & Fahrenholz 2001, Meyer-Lindenberg 2008) via interactions with the HPA axis and sympathetic nervous system

(Rodrigues et al. 2009a). Circulating levels of oxytocin are associated with lower cardiovascular and sympathetic stress reactivity (Grewen & Light 2011). Oxytocin also robustly decreases amygdala activation and coupling to brain stem regions involved in the coordination of fearful responses (Domes et al. 2007a).

## Benefits of Prosociality: Dopamine and the Reward Pathways of the Brain

One of the key components of our SAVE framework is the benefit to self ( $B_{self}$ ) for acting prosocially. Recent neurological studies support this part of our framework, that giving feels good. Indeed, the dopaminergic reward pathway is central to prosociality owing to reward-pathway inhibition of threat-related responding and the intrinsic rewards that become associated with prosocial acts (Eisenberger & Cole 2012). The reward circuitry includes cortical regions, such as the anterior cingulate cortex and the orbitofrontal cortex of the prefrontal cortex, as well as sub-cortical structures including the ventral tegmental area and the ventral striatum, which includes the nucleus accumbens. The nearby caudate nucleus, which is part of the dorsal striatum, is important for feedback processing related to social learning associated with rewards, punishments, and cooperation (Delgado 2007; Delgado et al. 2005; Rilling et al. 2002, 2004).

Patterns of activation in this reward circuit provide motivations and incentives for acting on behalf of strangers. Important neuroimaging evidence suggests that both voluntary and mandatory transfers of funds to a charity activate regions of the ventral striatum and nucleus accumbens, which are implicated in the processing of self-relevant rewards, from the prospects of winning money to consuming sweet foods (Harbaugh et al. 2007). The reward system also guides decisions to donate (Moll et al. 2006). Furthermore, a number of studies have illustrated how cooperation and fairness activate reward regions of the brain, as well (Tabibnia & Lieberman 2007). In addition, the prefrontal cortex is involved when altruistic choices prevail over selfish ones (Moll et al. 2006). Decety et al. (2004) also showed that cooperation is socially rewarding and involves the orbitofrontal cortex. Additionally, mutual cooperative outcomes in the prisoner's dilemma are associated with increased activity in the anterior cingulate cortex, striatum, prefrontal cortex, and ventral striatum (Rilling et al. 2002, 2004).

Other studies have examined the activation of the reward circuit when caring for close others. Giving support to a romantic partner by holding their arm while receiving a shock activates reward circuitry, specifically the ventral striatum and septal area. Furthermore, activity in these areas correlates with self-reports of support-giving effectiveness and social connection, as well as reduced amygdala activity. Additionally, septal activity is associated with reduced bilateral amygdala activity (Inagaki & Eisenberger 2012). Dopaminergic reward areas are also activated when mothers view their own infant's face compared with that of an unknown's, implicating a role in perceiving relationship strength ( $K$ ) (Strathearn et al. 2008). These regions, including ventral tegmental area and caudate nucleus, are also activated during feelings of romantic love (Bartels & Zeki 2004, Fisher et al. 2005). Collectively, these findings demonstrate the powerful role the dopamine-rich reward circuit of the brain plays in prosociality—in particular, by creating the “feeling good” effect of acting kindly ( $B_{self}$ ).

Individual differences in prosocial tendencies also map onto differential sensitivity within the reward circuitry when acting prosocially. For example, there are distinct neural correlates in social value orientation (SVO), one measure of prosociality, such that in individuals who display more prosocial behavior, the anterior cingulate cortex is more active when reciprocating than when defecting and vice versa for individualistic individuals. Furthermore, insula activation relates to going against one's SVO tendencies. This study also illustrates that those in the prosocial group

of SVO have more activity in the ventral striatum and prefrontal cortex than activity in baseline states, whereas those in the individualistic group experience the opposite (Van den Bos et al. 2009).

Spitzer et al. (2007) offer one more example of how differences in proclivities manifest themselves in the brain: Orbitofrontal cortex activity is strongly related to Machiavellian personality characteristics and norm compliance in the dictator game. Moreover, dopaminergic polymorphisms have also been associated with both self-reported and behavioral altruism (Bachner-Melman et al. 2005, Reuter et al. 2011). These findings highlight an interaction between  $D$  and  $B_{self}$ : Individual differences (captured by  $D$ ) in sensitivity of the reward circuit boost or dampen the benefit of acting prosocially for the individual ( $B_{self}$ ), thus shifting people's propensity to act prosocially in general.

### Attunement to Others and Emotion Regulation: Serotonin

Prosocial actions require tuning to the needs of others and regulating self-relevant actions. Serotonin (5-HT) is a monoamine neurotransmitter with widespread functions throughout the entire nervous system; these core processes give rise to prosocial behavior. Much like the other neurotransmitters tied to prosociality, the serotonin system is extremely multifunctional and highly conserved among mammals. The serotonin system is active throughout the forebrain and has at least 14 known receptors (by comparison, oxytocin has only one known receptor), making it likely the most complex of the neurotransmitter systems involved in prosociality (Crockett 2009). It helps regulate mood, appetite, libido, sleep, and many cognitive processes. One of serotonin's theorized roles is as a behavioral inhibitor; such a role in orchestrating social cognition and emotional responses (Lesch & Waider 2012) allows it to modulate prosocial behaviors as well. And indeed, empirical data have broadly linked serotonin to a wide variety of prosocial (and antisocial) behaviors.

Serotonin is synthesized from the amino acid tryptophan and many studies have shown that acute tryptophan depletion, an experimental procedure for lowering central serotonin levels, robustly influences neural responses for key brain areas, including the amygdala, prefrontal cortex, and anterior cingulate, involved in social and emotional processes (Evers et al. 2010). Tryptophan depletion reduces the level of cooperation in participants playing an iterated prisoner's dilemma game (Wood et al. 2006). Moreover, lowering serotonin levels also increases altruistic punishment and impulsive choice in the ultimatum game (Crockett et al. 2010). In addition, depletion reduces ventral striatal responses to fairness and increases dorsal striatal responses to punishment, which is accompanied by an increase in the likelihood to punish unfair behavior in the ultimatum game (Crockett et al. 2013).

Likewise, increasing serotonin levels through selective serotonin reuptake inhibitors (SSRI), commonly used as antidepressants, also influences prosociality in "healthy" participants. For instance, SSRI administration increases a behavioral index of social affiliation (Knutson et al. 1998). In addition, enhancing serotonin causes individuals to reduce the points awarded to the self and increases cooperative messages, thereby increasing affiliative behavior and social status in a mixed-motive prisoner's dilemma game (Tse & Bond 2002). Increasing the level of this neurotransmitter also makes participants less likely to reject unfair offers in the ultimatum game. In this same study, Crockett et al. (2010) showed that individuals with high trait empathy displayed stronger effects of SSRI on moral judgment and behavior compared with those low in trait empathy.

Serotonergic polymorphisms have been associated with individual differences in amygdala activity, vagal control of the heart, and the propensity to develop depressive and anxious symptoms (Caspi et al. 2010). This heightened stress reactivity can influence one's ability to regulate personal distress and tend to others. Indeed, genetic variation in the serotonin system relates to social learning, economic decision making, and attachment anxiety, suggesting that this association would expand to prosocial tendencies (Crisan et al. 2009).



Our SAVE framework of prosociality allows us to contextualize these findings within the broader prosociality literature. First, serotonin is clearly an important factor in shaping  $D$ , people's default proclivity toward prosociality. Those with genetic polymorphisms that promote greater levels of serotonin within their systems appear poised to act more prosocially toward people in general, showing greater restraint from aggression. Serotonin also plays an indirect role in affecting  $C_{inaction}$ . When people experience reductions in serotonin levels, they engage in greater altruistic punishment (Crockett et al. 2008), which suggests that those with low baseline serotonin levels act at least in part as “prosociality enforcers” within society—punishing violators of the fairness norm.

## THE POOR GIVE MORE: THE CASE OF SOCIAL CLASS AND PROSOCIAL BEHAVIOR

Our SAVE framework points to several promising lines of inquiry in the study of cultural variations in prosociality. For example, in accounting for cultural variation in prosociality across 15 societies, Henrich and colleagues theorize that it is economic interdependence that gives rise to increased prosociality. We suggest that such interdependence alters the  $D$  component of our framework, the local default tendency toward different forms of prosociality. The emergence of certain memes—units of cultural information—such as the Golden Rule (Armstrong 2009) during certain historical periods quite sensibly would alter the  $M$  component. Historical changes in privacy, and the extent to which one's behavior is publicly monitored, would change the role of reputation and, in turn, the benefits of acting prosocially ( $B_{self}$ ) and the costs of inaction ( $C_{inaction}$ ). Technological innovation and trends toward globalization have given rise to increased connections and contact among individuals from different groups and nations, in turn boosting  $K$  by increasing people's sense of self–other similarity with an ever-expanding and diverse community of individuals.

Perhaps the most developed literature that fits within our analysis of cultural variations is that on social class. Defined in terms of a person's wealth, education, and prestige of work relative to others in society (Adler et al. 2000, Oakes & Rossi 2003), social class exerts a pervasive influence on people's social cognitive tendencies (for review, see Kraus et al. 2012). In our own research, we have investigated how social class influences prosocial behavior.

In several different studies, we found that upper-class individuals are less altruistic than lower-class individuals. They endorse fewer contributions to charity, share less in economic games, and are less inclined to help those who are in need (Piff et al. 2010). They even behave more unethically—for instance, by cheating in a game—to maximize self-interest (Piff et al. 2012b).

The finding that those with more tend to give less may seem inherently paradoxical. However, a more detailed consideration of the person- and situation-level factors that vary by social class yields deeper insight into the class–prosociality link. Upper-class individuals tend to have more independence and control over others (Adler et al. 2000), and they value their independence over social connection (Piff et al. 2012b, Stephens et al. 2007). By contrast, individuals from lower-class backgrounds are more interdependent: They spend more time taking care of others (Argyle 1994), have stronger extended family ties (Lareau 2002), and are more embedded in social networks that depend on reciprocal aid (Lamont 2000). These findings suggest that among lower-class individuals there exist norms and values that specifically reinforce prosocial behavior and communal relationships ( $D$ ), and the frequency at which lower-class individuals observe instances of prosocial behavior and helping may be relatively high (the  $M$  component of our framework). By contrast, the norms and values of upper-class individuals may be oriented more toward individual achievement and self-interest, and the perceived rates of helping behavior in their social networks and environments may be relatively low.

Individuals from different social class groups also diverge in their perceptions of others ( $K$ ). Recent studies suggest that lower-class individuals are more empathic and compassionate than their upper-class counterparts across self-report, physiological, and neurological measures of these constructs (Kraus et al. 2010, Stellar et al. 2012). Class differences in perceptions of and sensitivity to others should drive differential levels of prosociality (e.g., Batson & Shaw 1991). Indeed, when individuals from upper-class backgrounds were made to feel compassion via an experimental manipulation, class-based differences in prosocial helping behavior—which were otherwise observable in a control condition—virtually disappeared (Piff et al. 2010).

The perceived costs and benefits of prosocial behavior are also likely to vary as a function of social class. Upper-class individuals have more privacy and freedom from observation, which may reduce the cost of inaction ( $C_{inaction}$ ). Upper-class individuals are also less likely to rely on others for assistance (Piff et al. 2012c), which could undermine the perceived benefits of prosocial behavior ( $B_{self}$ ). By contrast, selfishness may be more costly for lower-class individuals, who reside in communities in which decency and kindness are central to one's reputation (Lamont 2000). Lower-class individuals also rely more on their relationships to cope (in contrast with upper-class individuals, who prioritize individual forms of coping; Piff et al. 2012c), which should heighten the perceived personal benefits of prosocial action.

$$M*(D*(1 + B_{self}) + K*B_{recipient} - C_{inaction}) > C_{action}$$

Let us now return to our SAVE framework to synthesize the above insights. Lower-class people exist within more prosocial communities, leading to altruistic contagion and other mechanisms that boost  $D$  (bias and perceptions independent of the recipient) as well as  $M$  (the social momentum for prosocial action). Lower-class people also rely more on others and reputation is more centrally important, making the benefit to self ( $B_{self}$ ) of prosocial behavior higher than it is for upper-class individuals. Findings also suggest that lower-class individuals experience greater compassion, thus boosting the  $K$  component (perceived need and self-other similarity). Thus, although the cost of action ( $C_{action}$ ) is higher among lower-class people, the factors that promote prosocial behavior on the left side of the equation are higher as well. Given that lower-class individuals have proven to be more prosocial than higher-class individuals across a variety of contexts, the increases on the left side of the equation are likely to be greater—and potentially much greater—than those on the right side for lower-class individuals as compared with upper-class people.

## CONCLUSION

Since at least the time of Darwin, scientists have grappled with the question of how, and why, behavior that is costly to the self but beneficial to others can emerge. In our review, we have aimed to synthesize the confluence of psychological factors that shape the individual's inclinations toward prosociality. We have focused our efforts on encapsulating these varied factors within our SAVE framework, capturing the default bias toward prosociality, perceptions of recipients, emotional and reputation benefits to the self for acting prosocially, the potential costs of not acting prosocially, and the social momentum of a prosocial action—all factors that are central to prosocial responding. We have focused our review on emergent studies at four levels of analysis: the individual, dyad, group, and culture. In offering our synthetic SAVE framework, and casting our net broadly across levels of analysis, we hope new studies will continue to examine the proposition that sympathy is one of humanity's strongest instincts.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## LITERATURE CITED

- Adler NE, Epel ES, Castellazzo G, Ickovics JR. 2000. Relationship of subjective and objective social status with psychological and physiological functioning: preliminary data in healthy white women. *Health Psychol.* 19(6):586–92
- Aknin LB, Barrington-Leigh CP, Dunn EW, Helliwell JF, Burns J, et al. 2013. Prosocial spending and well-being: cross-cultural evidence for a psychological universal. *J. Personal. Soc. Psychol.* 104(4):635–52
- Albrechtsen JS, Meissner CA, Susa KJ. 2009. Can intuition improve deception detection performance? *J. Exp. Soc. Psychol.* 45(4):1052–55
- Algoe SB, Haidt J. 2009. Witnessing excellence in action: the “other-praising” emotions of elevation, gratitude, and admiration. *J. Posit. Psychol.* 4(2):105–27
- Algoe SB, Haidt J, Gable SL. 2008. Beyond reciprocity: gratitude and relationships in everyday life. *Emotion* 8(3):425–29
- Ambady N, Bernieri FJ, Richeson JA. 2000. Toward a histology of social behavior: judgmental accuracy from thin slices of the behavioral stream. *Adv. Exp. Soc. Psychol.* 32:201–71
- Ambady N, Hallahan M, Conner B. 1999. Accuracy of judgments of sexual orientation from thin slices of behavior. *J. Personal. Soc. Psychol.* 77(3):538–47
- Anderson C, John OP, Keltner D, Kring AM. 2001. Who attains social status? Effects of personality and physical attractiveness in social groups. *J. Personal. Soc. Psychol.* 81(1):116–32
- Anderson C, Shirako A. 2008. Are individuals’ reputations related to their history of behavior? *J. Personal. Soc. Psychol.* 94(2):320–33
- Argyle M. 1994. *The Psychology of Social Class*. London: Routledge
- Armstrong K. 2009. *The Case for God: What Religion Really Means*. New York: Knopf
- Atzil S, Hendler T, Feldman R. 2011. Specifying the neurobiological basis of human attachment: brain, hormones, and behavior in synchronous and intrusive mothers. *Neuropsychopharmacology* 36(13):2603–15
- Axelrod R. 1984. *The Evolution of Cooperation*. New York: Basic Books
- Bachner-Melman R, Gritsenko I, Nemanov L, Zohar AH, Dina C, Ebstein RP. 2005. Dopaminergic polymorphisms associated with self-report measures of human altruism: a fresh phenotype for the dopamine D4 receptor. *Mol. Psychiatry* 10(4):333–35
- Bachorowski JA, Owren MJ. 2001. Not all laughs are alike: Voiced but not unvoiced laughter readily elicits positive affect. *Psychol. Sci.* 12(3):252–57
- Balliet D, Mulder LB, Van Lange PM. 2011. Reward, punishment, and cooperation: a meta-analysis. *Psychol. Bull.* 137(4):594–615
- Barraza JA, Zak PJ. 2009. Empathy toward strangers triggers oxytocin release and subsequent generosity. *Ann. N.Y. Acad. Sci.* 1167:182–89
- Bartels A, Zeki S. 2004. The neural correlates of maternal and romantic love. *NeuroImage* 21(3):1155–66
- Bartlett MY, DeSteno D. 2006. Gratitude and prosocial behavior: helping when it costs you. *Psychol. Sci.* 17(4):319–25
- Bartz JA, Zaki J, Bolger N, Ochsner KN. 2011. Social effects of oxytocin in humans: Context and person matter. *Trends Cogn. Sci.* 15(7):301–9
- Batson CD, Shaw LL. 1991. Evidence for altruism: toward a pluralism of prosocial motives. *Psychol. Inq.* 2(2):107–22
- Beauchaine T. 2001. Vagal tone, development, and Gray’s motivational theory: toward an integrated model of autonomic nervous system functioning in psychopathology. *Dev. Psychopathol.* 13(2):183–214
- Beersma B, Van Kleef GA. 2011. How the grapevine keeps you in line: Gossip increases contributions to the group. *Soc. Psychol. Personal. Sci.* 2(6):642–49
- Belin D, Everitt BJ. 2008. Cocaine seeking habits depend upon dopamine-dependent serial connectivity linking the ventral with the dorsal striatum. *Neuron* 57(3):432–41

- Bernhardt BC, Singer T. 2012. The neural basis of empathy. *Annu. Rev. Neurosci.* 35:1–23
- Borkenau P, Mauer N, Riemann R, Spinath FM, Angleitner A. 2004. Thin slices of behavior as cues of personality and intelligence. *J. Personal. Soc. Psychol.* 86(4):599–614
- Bornstein MH, Suess PE. 2000. Physiological self-regulation and information processing in infancy: cardiac vagal tone and habituation. *Child Dev.* 71(2):273–87
- Bowlby J. 1969. *Attachment*. New York: Basic Books
- Boyd R, Gintis H, Bowles S, Richerson PJ. 2003. The evolution of altruistic punishment. *Proc. Natl. Acad. Sci. USA* 100(6):3531–35
- Brown R, González R, Zagefka H, Manzi J, Cehajic S. 2008. Nuestra culpa: collective guilt and shame as predictors of reparation for historical wrongdoing. *J. Personal. Soc. Psychol.* 94(1):75–90
- Bshary R, Bergmüller R. 2008. Distinguishing four fundamental approaches to the evolution of helping. *J. Evol. Biol.* 21(2):405–20
- Burt RS, Kilduff M, Tasselli S. 2013. Social network analysis: foundations and frontiers on advantage. *Annu. Rev. Psychol.* 64:527–47
- Butler EA, Wilhelm FH, Gross JJ. 2006. Respiratory sinus arrhythmia, emotion, and emotion regulation during social interaction. *Psychophysiology* 43(6):612–22
- Camerer CF. 2003. *Behavioral Game Theory: Experiments in Strategic Interaction*. Princeton, NJ: Princeton Univ. Press
- Carter CS. 1998. Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology* 23(8):779–818
- Carter CS, Grippo AJ, Pournajafi-Nazarloo H, Ruscio MG, Porges SW. 2008. Oxytocin, vasopressin and sociality. *Prog. Brain Res.* 170(8):331–36
- Caspi A, Hariri AR, Holmes A, Uher R, Moffitt TE. 2010. Genetic sensitivity to the environment: the case of the serotonin transporter gene and its implications for studying complex diseases and traits. *Am. J. Psychiatry* 167(5):509–27
- Christakis NA, Fowler JH. 2009. *Connected: The Surprising Power of Our Social Networks and How They Shape Our Lives*. New York: Little, Brown
- Cialdini RB, Trost MR. 1998. Social influence: social norms, conformity, and compliance. In *The Handbook of Social Psychology*, ed. DT Gilbert, ST Fiske, G Lindzey, pp. 151–92. New York: McGraw-Hill. 4th ed.
- Cohen AB. 2009. Many forms of culture. *Am. Psychol.* 64(3):194–204
- Cohen TR, Panter AT, Turan N. 2013. Predicting counterproductive work behavior from guilt proneness. *J. Bus. Ethics.* 114:45–53
- Cohen TR, Wildschut T, Insko CA. 2010. How communication increases interpersonal cooperation in mixed-motive situations. *J. Exp. Soc. Psychol.* 46(1):39–50
- Cohen TR, Wolf ST, Panter AT, Insko CA. 2011. Introducing the GASP scale: a new measure of guilt and shame proneness. *J. Personal. Soc. Psychol.* 100(5):947–66
- Côté S, Kraus MW, Cheng BH, Oveis C, Van der Löwe I, et al. 2011. Social power facilitates the effect of prosocial orientation on empathic accuracy. *J. Personal. Soc. Psychol.* 101(2):217–32
- Craik KH. 2009. *Reputation: A Network Interpretation*. New York: Oxford Univ. Press
- Crişan LG, Pana S, Vulturar R, Heilman RM, Szekely R, et al. 2009. Genetic contributions of the serotonin transporter to social learning of fear and economic decision making. *Soc. Cogn. Affect. Neurosci.* 4(4):399–408
- Crocker J. 2008. From egosystem to ecosystem: implications for relationships, learning, and well-being. In *Transcending Self-Interest: Psychological Explorations of the Quiet Ego*, ed. HA Wayment, JJ Bauer, pp. 63–72. Washington, DC: Am. Psychol. Assoc.
- Crockett MJ. 2009. The neurochemistry of fairness: clarifying the link between serotonin and prosocial behavior. *Ann. N. Y. Acad. Sci.* 1167:76–86
- Crockett MJ, Apergis-Schoute A, Herrmann B, Lieberman M, Müller U, et al. 2013. Serotonin modulates striatal responses to fairness and retaliation in humans. *J. Neurosci.* 33(8):3505–13
- Crockett MJ, Clark L, Hauser MD, Robbins TW. 2010. Serotonin selectively influences moral judgment and behavior through effects on harm aversion. *Proc. Natl. Acad. Sci. USA* 107(40):17433–38
- Crockett MJ, Clark L, Tabibnia G, Lieberman MD, Robbins TW. 2008. Serotonin modulates behavioral reactions to unfairness. *Science* 320:1739

- Danner DD, Snowdon DA, Friesen WV. 2001. Positive emotions in early life and longevity: findings from the nun study. *J. Personal. Soc. Psychol.* 80(5):804–13
- Darley JM, Batson CD. 1973. “From Jerusalem to Jericho”: a study of situational and dispositional variables in helping behavior. *J. Personal. Soc. Psychol.* 27:100–8
- Darwin C. 1871. *The Origin of the Species and the Descent of Man*. Chestnut Hill, MA: Adamant Media Corp.
- De Dreu CKW, Greer LL, Handgraaf MJJ, Shalvi S, Van Kleef GA, et al. 2010. The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science* 328:1408–11
- De Dreu CKW, Greer LL, Van Kleef GA, Shalvi S, Handgraaf MJJ. 2011. Oxytocin promotes human ethnocentrism. *Proc. Natl. Acad. Sci. USA* 108(4):1262–66
- De Waal FBM. 2008. Putting the altruism back into altruism: the evolution of empathy. *Annu. Rev. Psychol.* 59:279–300
- De Waal FBM. 2009. *Primates and Philosophers: How Morality Evolved*. Princeton, NJ: Princeton Univ. Press
- De Waal FBM. 2012. The antiquity of empathy. *Science* 336:874–76
- De Waal FBM, Lanting F. 1997. *Bonobo: The Forgotten Ape*. Berkeley/Los Angeles: Univ. Calif. Press
- Decety J, Jackson PL, Sommerville JA, Chaminade T, Meltzoff AN. 2004. The neural bases of cooperation and competition: an fMRI investigation. *NeuroImage* 23(2):744–51
- Decety J, Svetlova M. 2012. Putting together phylogenetic and ontogenetic perspectives on empathy. *Dev. Cogn. Neurosci.* 2(1):1–24
- Delgado MR. 2007. Reward-related responses in the human striatum. *Ann. N.Y. Acad. Sci.* 1104:70–88
- Delgado MR, Frank RH, Phelps EA. 2005. Perceptions of moral character modulate the neural systems of reward during the trust game. *Nat. Neurosci.* 8(11):1611–18
- DeSteno D, Bartlett MY, Baumann J, Williams LA, Dickens L. 2010. Gratitude as moral sentiment: emotion-guided cooperation in economic exchange. *Emotion* 10(2):289–93
- Diener E, Lucas R, Scollon CN. 2006. Beyond the hedonic treadmill: revising the adaptation theory of well-being. *Am. Psychol.* 61:305–14
- Diener E, Tay L, Myers DG. 2011. The religion paradox: If religion makes people happy, why are so many dropping out? *J. Personal. Soc. Psychol.* 101(6):1278–90
- Dixon EM, Kamath MV, McCartney N, Fallen EL. 1992. Neural regulation of heart rate variability in endurance athletes and sedentary controls. *Cardiovasc. Res.* 26(7):713–19
- Domes G, Heinrichs M, Gläscher J, Büchel C, Braus DF, Herpertz SC. 2007a. Oxytocin attenuates amygdala responses to emotional faces regardless of valence. *Biol. Psychiatry* 62(10):1187–90
- Domes G, Heinrichs M, Michel A, Berger C, Herpertz SC. 2007b. Oxytocin improves “mind-reading” in humans. *Biol. Psychiatry* 61(6):731–33
- Donaldson ZR, Young LJ. 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 322:900–4
- Dunn EW, Aknin LB, Norton MI. 2008. Spending money on others promotes happiness. *Science* 319:1687–88
- Effron DA, Miller DT. 2011. Diffusion of entitlement: an inhibitory effect of scarcity on consumption. *J. Exp. Soc. Psychol.* 47(2):378–83
- Eisenberg N, Fabes RA, Miller PA, Fultz J. 1989. Relation of sympathy and personal distress to prosocial behavior: a multimethod study. *J. Personal. Soc. Psychol.* 57(1):55–66
- Eisenberg N, Fabes RA, Murphy B, Maszk P, Smith M, Karbon M. 1995. The role of emotionality and regulation in children’s social functioning: a longitudinal study. *Child Dev.* 66(5):1360–84
- Eisenberger NI, Cole SW. 2012. Social neuroscience and health: neurophysiological mechanisms linking social ties with physical health. *Nat. Neurosci.* 15(5):669–74
- Emler N. 1994. Gossip, reputation, and social adaptation. In *Good Gossip*, ed. R Goodman, A Ben-Ze’ev, pp. 117–33. Lawrence: Univ. Kans. Press
- Evers EAT, Sambeth A, Ramaekers JG, Riedel WJ, Van der Veen FM. 2010. The effects of acute tryptophan depletion on brain activation during cognition and emotional processing in healthy volunteers. *Curr. Pharm. Des.* 16(18):1998–2011
- Fabes RA, Eisenberg N. 1997. Regulatory control and adults’ stress-related responses to daily life events. *J. Personal. Soc. Psychol.* 73(5):1107–17
- Fehr E, Bernhard H, Rockenbach B. 2008. Egalitarianism in young children. *Nature* 454:1079–83
- Fehr E, Fischbacher U. 2003. The nature of human altruism. *Nature* 425:785–91

- Fehr E, Fischbacher U. 2004. Social norms and human cooperation. *Trends Cogn. Sci.* 8(4):185–90
- Fehr E, Gächter S. 2002. Altruistic punishment in humans. *Nature* 415:137–40
- Feinberg M, Willer R, Keltner D. 2012a. Flustered and faithful: embarrassment as a signal of prosociality. *J. Personal. Soc. Psychol.* 102(1):81–97
- Feinberg M, Willer R, Stellar J, Keltner D. 2012b. The virtues of gossip: reputational information sharing as prosocial behavior. *J. Personal. Soc. Psychol.* 102(5):1015–30
- Feldman R. 2012. Oxytocin and social affiliation in humans. *Horm. Behav.* 61(3):380–91
- Feldman R, Gordon I, Influss M, Gutbir T, Ebstein RP. 2013. Parental oxytocin and early caregiving jointly shape children's oxytocin response and social reciprocity. *Neuropsychopharmacology* 38:1154–62
- Felps W, Mitchell TR, Byington E. 2006. How, when, and why bad apples spoil the barrel: negative group members and dysfunctional groups. *Res. Organ. Behav.* 27:175–222
- Fisher H, Aron A, Brown LL. 2005. Romantic love: an fMRI study of a neural mechanism for mate choice. *J. Comp. Neurol.* 493(1):58–62
- Fiske ST, Cuddy AJC, Glick P. 2007. Universal dimensions of social cognition: warmth and competence. *Trends Cogn. Sci.* 11(2):77–83
- Flynn FJ, Reagans RE, Amanatullah ET, Ames DR. 2006. Helping one's way to the top: Self-monitors achieve status by helping others and knowing who helps whom. *J. Personal. Soc. Psychol.* 91(6):1123–37
- Fowler JH. 2005. Altruistic punishment and the origin of cooperation. *Proc. Natl. Acad. Sci. USA* 102(19):7047–49
- Fowler JH, Christakis NA. 2010. Cooperative behavior cascades in human social networks. *Proc. Natl. Acad. Sci. USA* 107(12):5334–38
- Fowler KA, Lilienfeld SO, Patrick CJ. 2009. Detecting psychopathy from thin slices of behavior. *Psychol. Assess.* 21(1):68–78
- Frank R. 1988. *Passions Within Reason: The Strategic Role of the Emotions*. New York: Norton
- Fredrickson BL. 2001. The role of positive emotions in positive psychology. The broaden-and-build theory of positive emotions. *Am. Psychol.* 56(3):218–26
- Fredrickson BL, Cohn MA, Coffey KA, Pek J, Finkel SM. 2008. Open hearts build lives: Positive emotions, induced through loving-kindness meditation, build consequential personal resources. *J. Personal. Soc. Psychol.* 95(5):1045–62
- Fu F, Hauert C, Nowak M, Wang L. 2008. Reputation-based partner choice promotes cooperation in social networks. *Phys. Rev. E* 78(2):026117
- Gailliot MT, Stillman TF, Schmeichel BJ, Maner JK, Plant EA. 2008. Mortality salience increases adherence to salient norms and values. *Personal. Soc. Psychol. Bull.* 34(7):993–1003
- Gimpl G, Fahrenholz F. 2001. The oxytocin receptor system: structure, function, and regulation. *Physiol. Rev.* 81(2):629–83
- Gipple E, Gose B. 2012. America's generosity divide. *Chron. Philanthr.* Aug. 19. <http://philanthropy.com/article/America-s-Generosity-Divide/133775/>
- Goetz JL, Keltner D, Simon-Thomas E. 2010. Compassion: an evolutionary analysis and empirical review. *Psychol. Bull.* 136(3):351–74
- Goldstein NJ, Cialdini RB, Griskevicius V. 2008. A room with a viewpoint: using social norms to motivate environmental conservation in hotels. *J. Consum. Res.* 35(3):472–82
- Gonzaga GC, Keltner D, Londahl EA, Smith MD. 2001. Love and the commitment problem in romantic relations and friendship. *J. Personal. Soc. Psychol.* 81(2):247–62
- Gonzaga GC, Turner RA, Keltner D, Campos B, Altemus M. 2006. Romantic love and sexual desire in close relationships. *Emotion* 6(2):163–79
- Gordon AM, Impett EA, Kogan A, Oveis C, Keltner D. 2012. To have and to hold: Gratitude promotes relationship maintenance in intimate bonds. *J. Personal. Soc. Psychol.* 103(2):257–74
- Grant AM, Berry J. 2011. The necessity of others is the mother of invention: intrinsic and prosocial motivations, perspective taking, and creativity. *Acad. Manag. J.* 54(1):73–96
- Grant AM, Gino F. 2010. A little thanks goes a long way: explaining why gratitude expressions motivate prosocial behavior. *J. Personal. Soc. Psychol.* 98(6):946–55
- Graziano WG, Habashi MM, Sheese BE, Tobin RM. 2007. Agreeableness, empathy, and helping: a person x situation perspective. *J. Personal. Soc. Psychol.* 93(4):583–99

- Grewen KM, Light KC. 2011. Plasma oxytocin is related to lower cardiovascular and sympathetic reactivity to stress. *Biol. Psychiatry* 87(3):340–49
- Griskevicius V, Tybur JM, Van den Bergh B. 2010. Going green to be seen: status, reputation, and conspicuous conservation. *J. Personal. Soc. Psychol.* 98(3):392–404
- Grossman P, Kollai M. 1993. Respiratory sinus arrhythmia, cardiac vagal tone, and respiration: within- and between-individual relations. *Psychophysiology* 30(5):486–95
- Gunthorsdottir A, McCabe K, Smith V. 2002. Using the Machiavellianism instrument to predict trustworthiness in a bargaining game. *J. Econ. Psychol.* 23(1):49–66
- Gurven M. 2004. Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter/gatherers. *Behav. Ecol. Sociobiol.* 56(4):366–80
- Güth W, Schmittberger R, Schwarze B. 1982. An experimental analysis of ultimatum bargaining. *J. Econ. Behav. Organ.* 3(4):367–88
- Hamilton WD. 1964. The genetical evolution of social behaviour. *J. Theoret. Biol.* 7(1):1–52
- Hamlin JK, Wynn K, Bloom P. 2007. Social evaluation by preverbal infants. *Nature* 450:557–59
- Hamlin JK, Wynn K, Bloom P. 2010. Three-month-olds show a negativity bias in their social evaluations. *Dev. Sci.* 13(6):923–29
- Hamlin JK, Wynn K, Bloom P, Mahajan N. 2011. How infants and toddlers react to antisocial others. *Proc. Natl. Acad. Sci. USA* 108(50):19931–36
- Hansen AL, Johnsen BH, Thayer JF. 2003. Vagal influence on working memory and attention. *Int. J. Psychophysiol.* 48(3):263–74
- Harbaugh WT, Mayr U, Burghart DR. 2007. Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science* 316:1622–25
- Hardy CL, Van Vugt M. 2006. Nice guys finish first: the competitive altruism hypothesis. *Personal. Soc. Psychol. Bull.* 32(10):1402–13
- Harker L, Keltner D. 2001. Expressions of positive emotion in women’s college yearbook pictures and their relationship to personality and life outcomes across adulthood. *J. Personal. Soc. Psychol.* 80(1):112–24
- Hatfield E, Cacioppo JT, Rapson RL. 1993. Emotional contagion. *Curr. Dir. Psychol. Sci.* 2(3):96–99
- Henrich J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. *J. Econ. Behav. Organ.* 53(1):3–35
- Henrich J, Boyd R, Bowles S, Camerer C. 2001. In search of homo economicus: behavioral experiments in 15 small-scale societies. *Am. Econ. Rev.* 91(2):73–79
- Henrich J, Boyd R, Bowles S, Camerer C, Fehr E, et al. 2005. “Economic man” in cross-cultural perspective: behavioral experiments in 15 small-scale societies. *Behav. Brain Sci.* 28(6):795–815
- Henrich J, Boyd R, Bowles S, Camerer CF, Fehr E, Gintis H. 2004. *Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies*. Oxford, UK: Oxford Univ. Press
- Henrich J, McElreath R, Barr A, Ensminger J, Barrett C, et al. 2006. Costly punishment across human societies. *Science* 312:1767–70
- Hertenstein MJ, Keltner D, App B, Bulleit BA, Jaskolka AR. 2006. Touch communicates distinct emotions. *Emotion* 6(3):528–33
- Holt-Lunstad J, Birmingham WA, Light KC. 2008. Influence of a “warm touch” support enhancement intervention among married couples on ambulatory blood pressure, oxytocin, alpha amylase, and cortisol. *Psychosom. Med.* 70(9):976–85
- Impett EA, Gordon AM, Kogan A, Oveis C, Gable SL, Keltner D. 2010. Moving toward more perfect unions: daily and long-term consequences of approach and avoidance goals in romantic relationships. *J. Personal. Soc. Psychol.* 99(6):948–63
- Inagaki TK, Eisenberger NI. 2012. Neural correlates of giving support to a loved one. *Psychosom. Med.* 74(1):3–7
- Israel S, Lerer E, Shalev I, Uzefovsky F, Riebold M, et al. 2009. The oxytocin receptor (OXTR) contributes to prosocial fund allocations in the dictator game and the social value orientations task. *PLoS ONE* 4(5):e5535
- Jenkins JS, Ang VTY, Hawthorn J, Rossor MN, Iversen LL. 1984. Vasopressin, oxytocin and neurophysins in the human brain and spinal cord. *Brain Res.* 291(1):111–17

- Jonas E, Martens A, Kayser DN, Fritsche I, Sullivan D, Greenberg J. 2008. Focus theory of normative conduct and Terror-Management Theory: the interactive impact of mortality salience and norm salience on social judgment. *J. Personal. Soc. Psychol.* 95(6):1239–51
- Judge TA, Bono JE, Ilies R, Gerhardt MW. 2002. Personality and leadership: a qualitative and quantitative review. *J. Appl. Psychol.* 87(4):765–80
- Keltner D. 2009. *Born to Be Good: The Science of a Meaningful Life*. New York: Norton
- Keltner D, Van Kleef GA, Chen S, Kraus MW. 2008. A reciprocal influence model of social power: emerging principles and lines of inquiry. *Adv. Exp. Soc. Psychol.* 40:151–92
- Knafo A, Israel S, Darvasi A, Bachner-Melman R, Uzefovsky F, et al. 2008. Individual differences in allocation of funds in the dictator game associated with length of the arginine vasopressin 1a receptor RS3 promoter region and correlation between RS3 length and hippocampal mRNA. *Genes Brain Behav.* 7(3):266–75
- Kniffin KM, Wilson DS. 2005. Utilities of gossip across organizational levels. *Hum. Nat.* 16(3):278–92
- Knutson B, Wolkowitz OM, Cole SW, Chan T, Moore EA, et al. 1998. Selective alteration of personality and social behavior by serotonergic intervention. *Am. J. Psychiatry* 155(3):373–79
- Kogan A, Impett EA, Oveis C, Hui B, Gordon AM, Keltner D. 2010. When giving feels good: the intrinsic benefits of sacrifice in romantic relationships for the communally motivated. *Psychol. Sci.* 21(12):1918–24
- Kogan A, Saslow LR, Impett EA, Oveis C, Keltner D, et al. 2011. Thin-slicing study of the oxytocin receptor (OXTR) gene and the evaluation and expression of the prosocial disposition. *Proc. Natl. Acad. Sci. USA* 108(48):19189–92
- Kok BE, Fredrickson BL. 2010. Upward spirals of the heart: Autonomic flexibility, as indexed by vagal tone, reciprocally and prospectively predicts positive emotions and social connectedness. *Biol. Psychol.* 85(3):432–36
- Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, Fehr E. 2005. Oxytocin increases trust in humans. *Nature* 435:673–76
- Kraus MW, Côté S, Keltner D. 2010. Social class, contextualism, and empathic accuracy. *Psychol. Sci.* 21:1716–23
- Kraus MW, Huang C, Keltner D. 2010. Tactile communication, cooperation, and performance: an ethological study of the NBA. *Emotion* 10(5):745–49
- Kraus MW, Keltner D. 2009. Signs of socioeconomic status: a thin-slicing approach. *Psychol. Sci.* 20(1):99–106
- Kraus MW, Piff PK, Mendoza-Denton R, Rheinschmidt ML, Keltner D. 2012. Social class, solipsism, and contextualism: how the rich are different from the poor. *Psychol. Rev.* 119(3):546–72
- Krupka E, Weber RA. 2009. The focusing and informational effects of norms on pro-social behavior. *J. Econ. Psychol.* 30(3):307–20
- Kurzban R. 2001. The social psychophysics of cooperation: nonverbal communication in a public goods game. *J. Nonverbal Behav.* 25(4):241–59
- Lamont M. 2000. *The Dignity of Working Men: Morality and the Boundaries of Race, Class, and Immigration*. New York: Russell Sage Found.
- Langergraber KE, Mitani JC, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proc. Natl. Acad. Sci. USA* 104(19):7786–90
- Lareau A. 2002. Invisible inequality: social class and childrearing in black families and white families. *Am. Sociol. Rev.* 67(5):747–76
- Le BM, Impett EA, Kogan A, Webster GD, Cheng C. 2013. The personal and interpersonal rewards of communal orientation. *J. Soc. Personal Relatsh.* 30:694–710
- Lesch K-P, Waider J. 2012. Serotonin in the modulation of neural plasticity and networks: implications for neurodevelopmental disorders. *Neuron* 76(1):175–91
- Lyubomirsky S, King L, Diener E. 2005. The benefits of frequent positive affect: Does happiness lead to success? *Psychol. Bull.* 131(6):803–55
- McCrae RR, Sutin AR. 2009. Openness to experience and its social consequences. In *Handbook of Individual Differences in Social Behavior*, ed. MR Leary, H Hoyle, pp. 257–73. New York: Guilford
- McCullough ME, Kilpatrick SD, Emmons RA, Larson DB. 2001. Is gratitude a moral affect? *Psychol. Bull.* 127(2):249–66
- McCullough ME, Tsang J-A, Emmons RA. 2004. Gratitude in intermediate affective terrain: links of grateful moods to individual differences and daily emotional experience. *J. Personal. Soc. Psychol.* 86(2):295–309



- Meyer-Lindenberg A. 2008. Impact of prosocial neuropeptides on human brain function. *Prog. Brain Res.* 170:463–70
- Mikulincer M, Shaver PR, eds. 2009. *Prosocial Motives, Emotions, and Behavior: The Better Angels of Our Nature*. Washington, DC: Am. Psychol. Assoc.
- Milinski M, Semmann D, Bakker TC, Krambeck H-J. 2001. Cooperation through indirect reciprocity: image scoring or standing strategy? *Proc. R. Soc. B* 268(1484):2495–501
- Milinski M, Semmann D, Krambeck H-J. 2002. Reputation helps solve the “tragedy of the commons.” *Nature* 415:424–26
- Moll J, Krueger F, Zahn R, Pardini M, De Oliveira-Souza R, Grafman J. 2006. Human fronto-mesolimbic networks guide decisions about charitable donation. *Proc. Natl. Acad. Sci. USA* 103(42):15623–28
- Monroe K. 1996. *The Heart of Altruism: Perceptions of a Common Humanity*. Princeton, NJ: Princeton Univ. Press
- Monroe K. 2004. *The Hand of Compassion: Portraits of Moral Choice During the Holocaust*. Princeton, NJ: Princeton Univ. Press
- Moorman RH, Blakely GL. 1995. Individualism-collectivism as an individual difference predictor of organizational citizenship behavior. *J. Organ. Behav.* 16(2):127–42
- Nesse RM. 1990. Evolutionary explanations of emotions. *Hum. Nat.* 1(3):261–89
- Nesse RM, Ellsworth PC. 2009. Evolution, emotions, and emotional disorders. *Am. Psychol.* 64(2):129–39
- Norenzayan A, Shariff AF. 2008. The origin and evolution of religious prosociality. *Science* 322:58–62
- Norman GJ, Hawkey L, Luhmann M, Ball AB, Cole SW, et al. 2012. Variation in the oxytocin receptor gene influences neurocardiac reactivity to social stress and HPA function: a population based study. *Horm. Behav.* 61(1):134–39
- Nowak MA. 2006. Five rules for the evolution of cooperation. *Science* 314:1560–63
- Nowak MA, Page KM, Sigmund K. 2000. Fairness versus reason in the ultimatum game. *Science* 289:1773–75
- Nowak MA, Roch S. 2007. Upstream reciprocity and the evolution of gratitude. *Proc. R. Soc. B* 274(1610):605–9
- Nowak MA, Sigmund K. 1998. Evolution of indirect reciprocity by image scoring. *Nature* 393:573–77
- Nowak MA, Sigmund K. 2005. Evolution of indirect reciprocity. *Nature* 437:1291–98
- Oakes JM, Rossi PH. 2003. The measurement of SES in health research: current practice and steps toward a new approach. *Soc. Sci. Med.* 56(4):769–84
- Oltmanns TF, Friedman JN, Fiedler ER, Turkheimer E. 2004. Perceptions of people with personality disorders based on thin slices of behavior. *J. Res. Personal.* 38(3):216–29
- Omoto AM, Snyder M, Hackett JD. 2010. Personality and motivational antecedents of activism and civic engagement. *J. Personal.* 78(6):1703–34
- Oveis C, Cohen AB, Gruber J, Shiota MN, Haidt J, Keltner D. 2009. Resting respiratory sinus arrhythmia is associated with tonic positive emotionality. *Emotion* 9(2):265–70
- Oyserman D, Coon HM, Kimmelmeier M. 2002. Rethinking individualism and collectivism: evaluation of theoretical assumptions and meta-analyses. *Psychol. Bull.* 128(1):3–72
- Oyserman D, Lee SWS. 2008. Does culture influence what and how we think? Effects of priming individualism and collectivism. *Psychol. Bull.* 134(2):311–42
- Panksepp J. 2007. The neuroevolutionary and neuroaffective psychobiology of the prosocial brain. In *The Oxford Handbook of Evolutionary Psychology*, ed. RIM Dunbar, L Barrett, pp. 145–62. Oxford, UK: Oxford Univ. Press
- Penner LA, Dovidio JF, Piliavin JA, Schroeder DA. 2005. Prosocial behavior: multilevel perspectives. *Annu. Rev. Psychol.* 56(1):365–92
- Piferi RL, Lawler KA. 2006. Social support and ambulatory blood pressure: an examination of both receiving and giving. *Int. J. Psychophysiol.* 62(2):328–36
- Piff PK, Kraus MW, Côté S, Cheng BH, Keltner D. 2010. Having less, giving more: the influence of social class on prosocial behavior. *J. Personal. Soc. Psychol.* 99(5):771–84
- Piff PK, Purcell A, Gruber J, Hertenstein MJ, Keltner D. 2012a. Contact high: mania proneness and positive perception of emotional touches. *Cogn. Emot.* 26(6):1116–23

- Piff PK, Stancato D, Côté S, Mendoza-Dentona R, Keltner D. 2012b. Higher social class predicts increased unethical behavior. *Proc. Natl. Acad. Sci. USA* 109(11):4086–91
- Piff PK, Stancato DM, Martinez AG, Kraus MW, Keltner D. 2012c. Class, chaos, and the construction of community. *J. Personal. Soc. Psychol.* 103(6):949–62
- Pillutla M, Chen X. 1999. Social norms and cooperation in social dilemmas: the effects of context and feedback. *Organ. Behav. Hum. Decis. Proc.* 78(2):81–103
- Porges SW. 2001. The polyvagal theory: phylogenetic substrates of a social nervous system. *Int. J. Psychophysiol.* 42(2):123–46
- Porges SW. 2003. The polyvagal theory: phylogenetic contributions to social behavior. *Physiol. Behav.* 79(3):503–13
- Porges SW. 2007. The polyvagal perspective. *Biol. Psychol.* 74(2):116–43
- Poulin MJ, Holman EA, Buffone A. 2012. The neurogenetics of nice: receptor genes for oxytocin and vasopressin interact with threat to predict prosocial behavior. *Psychol. Sci.* 23(5):446–52
- Pritchard AL, Ratcliffe L, Sorour E, Haque S, Holder R, et al. 2009. Investigation of dopamine receptors in susceptibility to behavioural and psychological symptoms in Alzheimer's disease. *Int. J. Geriatr. Psychiatry* 24(9):1020–25
- Rand DG, Dreber A, Ellingsen T, Fudenberg D, Nowak MA. 2009. Positive interactions promote public cooperation. *Science* 325:1272–75
- Rand DG, Greene JD, Nowak MA. 2012. Spontaneous giving and calculated greed. *Nature* 489:427–30
- Reuter M, Frenzel C, Walter NT, Markett S, Montag C. 2011. Investigating the genetic basis of altruism: the role of the COMT Val158Met polymorphism. *Soc. Cogn. Affect. Neurosci.* 6(5):662–68
- Rilling JK, Gutman DA, Zeh TR, Pagnoni G, Berns GS, Kilts CD. 2002. A neural basis for social cooperation. *Neuron* 35(2):395–405
- Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, Cohen JD. 2004. Opposing BOLD responses to reciprocated and unreciprocated altruism in putative reward pathways. *NeuroReport* 15(16):2539–43
- Rodrigues SM, LeDoux JE, Sapolsky RM. 2009a. The influence of stress hormones on fear circuitry. *Annu. Rev. Neurosci.* 32:289–313
- Rodrigues SM, Saslow LR, Garcia N, John OP, Keltner D. 2009b. Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *Proc. Natl. Acad. Sci. USA* 106(50):21437–41
- Rolls ET, O'Doherty J, Kringelbach ML, Francis S, Bowtell R, McGlone F. 2003. Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cereb. Cortex* 13(3):308–17
- Roth BL. 1994. Multiple serotonin receptors: clinical and experimental aspects. *Ann. Clin. Psychiatry* 6:67–78
- Saroglou V. 2002. Religion and the five factors of personality: a meta-analytic review. *Personal. Individ. Differ.* 32(1):15–25
- Saroglou V, Delpierre V, Dernelle R. 2004. Values and religiosity: A meta-analysis of studies using Schwartz's model. *Personal. Individ. Differ.* 37(4):721–34
- Schindler S, Reinhard M-A, Stahlberg D. 2012. Mortality salience increases personal relevance of the norm of reciprocity. *Psychol. Rep.* 111(2):565–74
- Schnall S, Roper J. 2012. Elevation puts moral values into action. *Soc. Psychol. Personal. Sci.* 3(3):373–78
- Schnall S, Roper J, Fessler DM. 2010. Elevation leads to altruistic behavior. *Psychol. Sci.* 21(3):315–20
- Schneiderman I, Zagoory-Sharon O, Leckman JF, Feldman R. 2012. Oxytocin during the initial stages of romantic attachment: relations to couples' interactive reciprocity. *Psychoneuroendocrinology* 37(8):1277–85
- Schwartz SH, Bilsky W. 1990. Toward a theory of the universal content and structure of values: extensions and cross-cultural replications. *J. Personal. Soc. Psychol.* 58(5):878–91
- Seyfarth RM, Cheney DL. 2012. The evolutionary origins of friendship. *Annu. Rev. Psychol.* 63:153–77
- Shariff AF, Norenzayan A. 2007. God is watching you: Priming God concepts increases prosocial behavior in an anonymous economic game. *Psychol. Sci.* 18(9):803–9
- Simon-Thomas ER, Godzik J, Castle E, Antonenko O, Ponz A, et al. 2012. An fMRI study of caring versus self-focus during induced compassion and pride. *Soc. Cogn. Affect. Neurosci.* 7(6):635–48
- Smith A. 2006 (1759). *The Theory of Moral Sentiments*. Mineola, NY: Dover
- Sober E, Wilson DS. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard Univ. Press

- Spitzer M, Fischbacher U, Herrnberger B, Grön G, Fehr E. 2007. The neural signature of social norm compliance. *Neuron* 56(1):185–96
- Sprecher S, Fehr B. 2005. Compassionate love for close others and humanity. *J. Soc. Personal Relatsh.* 22(5):629–51
- Stellar JE, Manzo VM, Kraus MW, Keltner D. 2012. Class and compassion: Socioeconomic factors predict responses to suffering. *Emotion* 12:449–59
- Stephens NM, Markus HR, Townsend SSM. 2007. Choice as an act of meaning: the case of social class. *J. Personal. Soc. Psychol.* 93(5):814–30
- Strathearn L, Li J, Fonagy P, Montague PR. 2008. What's in a smile? Maternal brain responses to infant facial cues. *Pediatrics* 122(1):40–51
- Strauman TJ. 1989. Self-discrepancies in clinical depression and social phobia: cognitive structures that underlie emotional disorders? *J. Abnorm. Psychol.* 98(1):14–22
- Sussman RW, Cloninger CR, eds. 2011. *Origins of Altruism and Cooperation*. New York: Springer
- Tabibnia G, Lieberman MD. 2007. Fairness and cooperation are rewarding: evidence from social cognitive neuroscience. *Ann. N. Y. Acad. Sci.* 1118:90–101
- Tangney JP, Stuewig J, Mashek DJ. 2007. Moral emotions and moral behavior. *Annu. Rev. Psychol.* 58:345–72
- Thompson LL, ed. 2006. *Negotiation Theory and Research*. New York: Psychol. Press
- Tiedens LZ, Fragale AR. 2003. Power moves: complementarity in dominant and submissive nonverbal behavior. *J. Personal. Soc. Psychol.* 84(3):558–68
- Tost H, Kolachana B, Hakimi S, Lemaitre H, Verchinski BA, et al. 2010. A common allele in the oxytocin receptor gene (OXTR) impacts prosocial temperament and human hypothalamic-limbic structure and function. *Proc. Natl. Acad. Sci. USA* 107(31):13936–41
- Trivers RL. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46(1):35–57
- Trivers RL. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man*, ed. B Campbell, pp. 136–79. Chicago: Aldine
- Tse WS, Bond AJ. 2002. Serotonergic intervention affects both social dominance and affiliative behaviour. *Psychopharmacology* 161(3):324–30
- Utz S. 2004. Self-activation is a two-edged sword: the effects of I primes on cooperation. *J. Exp. Soc. Psychol.* 40(6):769–76
- Valdesolo P, Desteno D. 2011. Synchrony and the social tuning of compassion. *Emotion* 11(2):262–66
- Van den Bos W, Van Dijk E, Westenberg M, Rombouts SARB, Crone EA. 2009. What motivates repayment? Neural correlates of reciprocity in the Trust Game. *Soc. Cogn. Affect. Neurosci.* 4(3):294–304
- Van Lange PAM. 1999. The pursuit of joint outcomes and equality in outcomes: an integrative model of social value orientation. *J. Personal. Soc. Psychol.* 77(2):337–49
- Vanoli E, Adamson PB, Pinna GD, Lazzara R, Orr WC. 1995. Heart rate variability during specific sleep stages: a comparison of healthy subjects with patients after myocardial infarction. *Circulation* 91(7):1918–22
- Warneken F, Tomasello M. 2006. Altruistic helping in human infants and young chimpanzees. *Science* 311:1301–3
- Warneken F, Tomasello M. 2007. Helping and cooperation at 14 months of age. *Infancy* 11(3):271–94
- Waugh CE, Fredrickson BL. 2006. Nice to know you: positive emotions, self-other overlap, and complex understanding in the formation of a new relationship. *J. Posit. Psychol.* 1(2):93–106
- Wedekind C, Milinski M. 2000. Cooperation through image scoring in humans. *Science* 288:850–52
- Weisman O, Zagoory-Sharon O, Feldman R. 2012. Oxytocin administration to parent enhances infant physiological and behavioral readiness for social engagement. *Biol. Psychiatry* 72(12):982–89
- Wert SR, Salovey P. 2004a. A social comparison account of gossip. *Rev. Gen. Psychol.* 8(2):122–37
- Wert SR, Salovey P. 2004b. Introduction to the special issue on gossip. *Rev. Gen. Psychol.* 8(2):76–77
- Willer R. 2009. Groups reward individual sacrifice: the status solution to the collective action problem. *Am. Sociol. Rev.* 73:23–43
- Wood RM, Rilling JK, Sanfey AG, Bhagwagar Z, Rogers RD. 2006. Effects of tryptophan depletion on the performance of an iterated Prisoner's Dilemma game in healthy adults. *Neuropsychopharmacology* 31(5):1075–84
- Woods TE, Ironson GH. 1999. Religion and spirituality in the face of illness: how cancer, cardiac, and HIV patients describe their spirituality/religiosity. *J. Health Psychol.* 4(3):393–412

- Woolley AW, Chabris CF, Pentland A, Hashmi N, Malone TW. 2010. Evidence for a collective intelligence factor in the performance of human groups. *Science* 330:686–88
- Young LJ, Lim MM, Gingrich B, Insel TR. 2001. Cellular mechanisms of social attachment. *Horm. Behav.* 40(2):133–38
- Zink CF, Meyer-Lindenberg A. 2012. Human neuroimaging of oxytocin and vasopressin in social cognition. *Horm. Behav.* 61(3):400–9



# Contents

## Prefatory

I Study What I Stink At: Lessons Learned from a Career in Psychology  
*Robert J. Sternberg* ..... 1

## Stress and Neuroendocrinology

Oxytocin Pathways and the Evolution of Human Behavior  
*C. Sue Carter* ..... 17

## Genetics of Behavior

Gene-Environment Interaction  
*Stephen B. Manuck and Jeanne M. McCaffery* ..... 41

## Cognitive Neuroscience

The Cognitive Neuroscience of Insight  
*John Kounios and Mark Beeman* ..... 71

## Color Perception

Color Psychology: Effects of Perceiving Color on Psychological  
Functioning in Humans  
*Andrew J. Elliot and Markus A. Maier* ..... 95

## Infancy

Human Infancy... and the Rest of the Lifespan  
*Marc H. Bornstein* ..... 121

## Adolescence and Emerging Adulthood

Bullying in Schools: The Power of Bullies and the Plight of Victims  
*Jaana Juvonen and Sandra Graham* ..... 159

Is Adolescence a Sensitive Period for Sociocultural Processing?  
*Sarah-Jayne Blakemore and Kathryn L. Mills* ..... 187

## Adulthood and Aging

Psychological Research on Retirement  
*Mo Wang and Junqi Shi* ..... 209

## Development in the Family

Adoption: Biological and Social Processes Linked to Adaptation  
*Harold D. Grotevant and Jennifer M. McDermott* ..... 235

## Individual Treatment

- Combination Psychotherapy and Antidepressant Medication Treatment  
for Depression: For Whom, When, and How  
*W. Edward Craighead and Boadie W. Dunlop* ..... 267

## Adult Clinical Neuropsychology

- Sport and Nonsport Etiologies of Mild Traumatic Brain Injury:  
Similarities and Differences  
*Amanda R. Rabinowitz, Xiaoqi Li, and Harvey S. Levin* ..... 301

## Self and Identity

- The Psychology of Change: Self-Affirmation and Social  
Psychological Intervention  
*Geoffrey L. Cohen and David K. Sherman* ..... 333

## Gender

- Gender Similarities and Differences  
*Janet Shibley Hyde* ..... 373

## Altruism and Aggression

- Dehumanization and Infrahumanization  
*Nick Haslam and Steve Loughnan* ..... 399
- The Sociocultural Appraisals, Values, and Emotions (SAVE) Framework  
of Prosociality: Core Processes from Gene to Meme  
*Dacher Keltner, Aleksandr Kogan, Paul K. Piff, and Sarina R. Saturn* ..... 425

## Small Groups

- Deviance and Dissent in Groups  
*Jolanda Jetten and Matthew J. Hornsey* ..... 461

## Social Neuroscience

- Cultural Neuroscience: Biology of the Mind in Cultural Contexts  
*Heejung S. Kim and Joni Y. Sasaki* ..... 487

## Genes and Personality

- A Phenotypic Null Hypothesis for the Genetics of Personality  
*Eric Turkheimer, Erik Pettersson, and Erin E. Horn* ..... 515

## Environmental Psychology

- Environmental Psychology Matters  
*Robert Gifford* ..... 541

## **Community Psychology**

Socioecological Psychology <i>Shigehiro Oishi</i> .....	581
--	-----

## **Subcultures Within Countries**

Social Class Culture Cycles: How Three Gateway Contexts Shape Selves and Fuel Inequality <i>Nicole M. Stephens Hazel Rose Markus, and L. Taylor Phillips</i> .....	611
--	-----

## **Organizational Climate/Culture**

(Un)Ethical Behavior in Organizations <i>Linda Klebe Treviño, Niki A. den Nieuwenboer, and Jennifer J. Kish-Gephart</i> .....	635
--	-----

## **Job/Work Design**

Beyond Motivation: Job and Work Design for Development, Health, Ambidexterity, and More <i>Sharon K. Parker</i> .....	661
---	-----

## **Selection and Placement**

A Century of Selection <i>Ann Marie Ryan and Robert E. Ployhart</i> .....	693
--	-----

## **Personality and Coping Styles**

Personality, Well-Being, and Health <i>Howard S. Friedman and Margaret L. Kern</i> .....	719
---	-----

## **Timely Topics**

Properties of the Internal Clock: First- and Second-Order Principles of Subjective Time <i>Melissa J. Allman, Sundeep Teki, Timothy D. Griffiths, and Warren H. Meck</i> .....	743
--	-----

## **Indexes**

Cumulative Index of Contributing Authors, Volumes 55–65 .....	773
Cumulative Index of Article Titles, Volumes 55–65 .....	778

## **Errata**

An online log of corrections to *Annual Review of Psychology* articles may be found at <http://psych.annualreviews.org/errata.shtml>