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[−] **Abstract and Keywords**

Evolutionary psychologists seek to understand prosocial behavior at four complementary levels of analysis: psychological mechanisms, development of those mechanisms (ontogeny), their adaptive or evolutionary function, and their evolutionary history (phylogeny). In terms of adaptive function, prosocial behavior is often costly to perform, so it is an evolutionary enigma. To evolve and be maintained, prosocial sentiment needs to bring corresponding fitness benefits. The authors outline a number of such evolutionary functions of prosocial behavior. Adaptive functions include direct benefits, mutualisms, stake or vested interests, kinship, reciprocity (direct and indirect), and costly signaling. Nonadaptive functions include mistakes, byproducts, and cultural learning. They provide a diagnostic tool for determining the likely function of any particular prosocial act and discuss three emerging perspectives in the study of prosocial behavior: scale of competition, multilevel selection, and biological markets. We conclude with future directions in evolutionary research on prosocial behavior.

Keywords: altruism, cooperation, reciprocity, costly signaling, evolutionary psychology, levels of analysis

Introduction

Humans are a prosocial species. People make substantial sacrifices to help their kin and support their friends, rescue complete strangers in bystander emergencies, make large financial donations to charities, and defend their in-groups against outsiders (Dovidio, Pilliavin, Schroeder, & Penner, 2006). Yet human prosociality is an evolutionary puzzle because over time natural selection will ruthlessly winnow out any traits that reduce an individual's fitness (i.e., someone's relative reproductive success). Thus, for any costly trait to evolve and persist, there need to be some corresponding ultimate benefits in terms of spreading the actor's genes. A first-pass glance at natural selection would suggest that prosocial sentiments should have been selected against because they cause us to perform behaviors that may be costly. Nevertheless, prosocial sentiments persist such that prosocial behavior is ubiquitous in human interactions and in many nonhuman interactions, too. Why? This is the question that this chapter addresses.

In this chapter, we start by clarifying two major sources of confusion over evolutionary explanations: differences in (1) definitions and (2) the types of questions that are being addressed. We then introduce a flowchart outlining a number of potential factors that could cause prosocial sentiment to emerge, either because they have been directly selected for through natural selection or because they are byproducts of other adaptations. We briefly discuss some new perspectives that researchers are investigating and present some conclusions and questions for future research.

Definitions

Prosocial behavior is defined as behavior "intended to benefit one or more people other than oneself" (Batson & Powell, 2003, p. 463). This is a very broad term that includes many subcomponents, such as cooperation, mutualism, altruism, helping, and so on. Because different scientific disciplines use these terms differently, we will simply provide the definitions we are using and invite readers to substitute their preferred terms for these phenomena. That way, the focus is on the phenomena, not the semantics. We will use the term "prosocial behavior" to refer to any actions that are intended to benefit others, regardless of whether the actor also benefits in the process. We will use the more popular word "helping" synonymously with "prosocial behavior." We will use the term "prosocial sentiment" to refer to any emotions or psychological mechanisms that trigger this helping. Some types of prosocial behavior are costly to the actor, at least temporarily ("costly cooperation"), whereas other types of prosocial behavior carry no costs or provide return benefits to the actor almost immediately ("noncostly cooperation"). Biologists use the term "altruism" to refer to actions which decrease one's lifetime reproductive success, and it is one form of costly cooperation (West, El Moulden, & Gardner, 2011). A mutualism is a form of (noncostly) cooperation when the actor and another agent both benefit from something the actor does. This could include active coordination between the two of them but does not need to. Those who disagree with our terminology should simply substitute their own where appropriate.

Levels of Analysis: What Question(s) Are We Addressing?

Evolutionary psychology draws from many disciplines, including but not limited to evolutionary biology, experimental economics, mathematical game theory, anthropology, and of course psychology (social, developmental, cognitive, etc.). It uses tools and methods from all of these to investigate behavior. As such, evolutionary psychology is not a field or subdiscipline in the traditional sense. Instead, it is a meta-theoretical stance which can be applied to any field, subdiscipline, or topic (Daly, 2011; Van Vugt & Schaller, 2008). What often differentiates evolutionary researchers from nonevolutionary researchers is the types of questions they ask, and how those questions are interconnected.

Researchers often get into unnecessary quarrels over the "causes" of prosocial behavior, without realizing that they may be providing valid answers to different questions (Barclay, 2011a; West et al., 2011). For example, one researcher may say "people help each other because they feel empathy." A second researcher may say "people help each other because they learn to help." A third researcher will say "people help each other because those who help tend to receive help." A fourth research may say "people help each other because we share this trait with other apes and it evolved out of kin altruism." What these researchers may not realize is that they could all be right—or could all be wrong—because they are answering questions at different levels of analysis. Nobel prize-winning ethologist Niko Tinbergen (e.g., 1968) introduced his four levels of analysis to clarify the different types of questions and avoid unproductive debates over explanations at different levels.

In our example, the first researcher is talking about proximate psychological *mechanisms*, that is, what is going on within the individual at the time he or she helps. The second research is talking about *development*, that is, how that psychological mechanism (whatever it happens to be) develops within the life span of an individual and how genes and environments interact. The third researcher is asking about ultimate *function*, that is, why an individual would develop in such a way as to have that psychological mechanism, what the benefits of having it are, and what selective pressures cause it to persist. The fourth research is addressing *phylogeny* or evolutionary history, that is, how and when the mechanism evolved in our evolutionary history, and what prior trait(s) it evolved from.

Our example shows how these four levels of analysis are complementary, not mutually exclusive: all behaviors require an explanation at all four of these levels of analysis to be fully understood. The only fruitful scientific discussion is between explanations within the same level. For example, researchers can debate whether the psychological mechanism that triggers helping behavior is empathy versus "oneness with others" (e.g., Batson et al., 1997, versus Cialdini et al., 1997). They can also debate development by asking whether that psychological mechanism is learned versus innate (though this is actually a false dichotomy, see Ridley, 2003). When debating adaptive function, researchers can argue over whether prosocial behavior serves to invite reciprocation or serves to signal desirable qualities. For phylogeny, we can discuss whether our prosocial sentiments are unique to the human lineage versus evolutionarily ancient, and we can debate which other sentiments they evolved from. However, we cannot, for example, say that because prosociality is learned, it therefore does not function to invite reciprocation, because these are explanations at different levels (e.g., the reciprocation could be the reinforcer

that causes prosociality to be learned). Much of the controversy over evolutionary explanations of prosociality is because researchers mix up these levels of analysis, for example by assuming that people are consciously concerned with receiving benefits for helping or that all acts of helping are based on selfish personal motivations (Barclay, 2011a, 2012b; Van Vugt & Van Lange, 2006; West et al., 2011). We agree with evolutionary biologist Richard Dawkins who argued that "selfish genes" can produce genuinely selfless organisms (Dawkins, 1976/2006) —these are two different levels of analysis!

All four levels of analysis are important to study and can inform each other. Different researchers focus on different levels, depending on their scientific discipline. For example, this volume includes several chapters on proximate psychological mechanisms and their proximate neural underpinnings, such as empathy (Batson et al.; Davis), mood (Clark), mortality salience (Hirschberger), and the neuroscience underlying these (Grijalva and colleagues). Some chapters focus on the development of prosociality (Eisenberg), culture (Piliavin & Siegl), and we are happy to even see a chapter on the phylogeny of prosociality (de Waal). In this chapter, we will primarily address the question of evolutionary function. If we can understand the evolutionary functions of prosociality, then we can make better predictions about how to change social situations to foster prosociality. Paraphrasing the great evolutionary biologist George Williams (1966, p. 6) we believe that our understanding of human prosociality would be aided greatly by knowing the purpose for which it was designed.

Evolutionary Functions of Prosociality

What selective pressures have caused prosocial sentiment in the human lineage? While the answer is not yet completely certain, there are several intriguing possibilities as to the evolutionary origins of prosocial behavior. We can roughly divide these evolutionary accounts into two categories: adaptive explanations versus nonadaptive explanations. Adaptive explanations are those that find some benefit to prosocial behavior, such that being prosocial increases one's inclusive fitness (i.e., spread of one's genes). Nonadaptive explanations are ways in which prosocial behavior could spread even if they do not increase one's fitness: for example, the behavior could be a byproduct of some other adaptive mechanism or it could be a mistake produced by a prosocial psychology that is adaptive on average (or once was). Some of these explanations have received more attention than others, but it does not mean that they are more important, more interesting theoretically, or even more common in nature (Clutton-Brock, 2009; West et al., 2011).
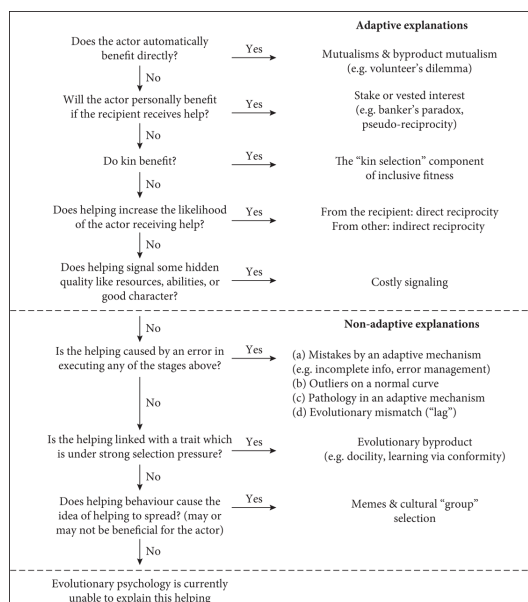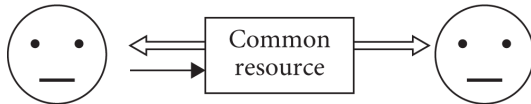

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Figure 1 . Diagnostic flowchart of the functional causes of prosocial behavior. For any instance of prosocial behavior, one should start at the top and determine whether the benefits at that stage are sufficient to outweigh the costs of helping. If not, one should investigate lower stages. These explanations are ordered in an estimated order of parsimony (e.g., direct benefits are easiest to explain); we are not committed to the exact order, and some changes in order are expected with more research on each of these areas.

Figure 1 outlines these different explanations in a flow chart. This figure is designed to roughly move from prosociality with obvious and well-studied adaptive benefits to the less obvious or less-studied types of benefits associated with prosociality. The flowchart could be used as a diagnostic tool for discovering the origins and functions of different types of helping in the real-world. For similar charts that distinguish between functions of helping behavior, see Bshary and Bergmüller (2008) or West et al. (2011).
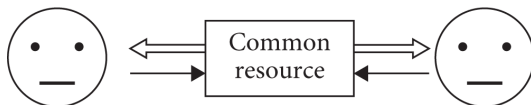
Adaptive Explanations

(a) Volunteer's dilemma

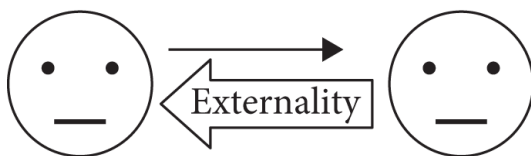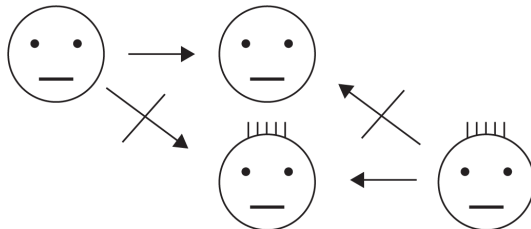*Click to view larger*

(b) Mutualism

Click to view larger

(c) Stake or vested interest

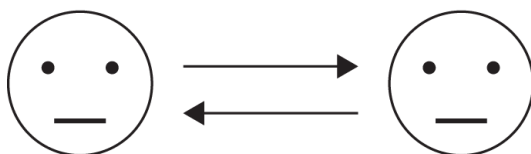*Click to view larger*

(d) Kinship

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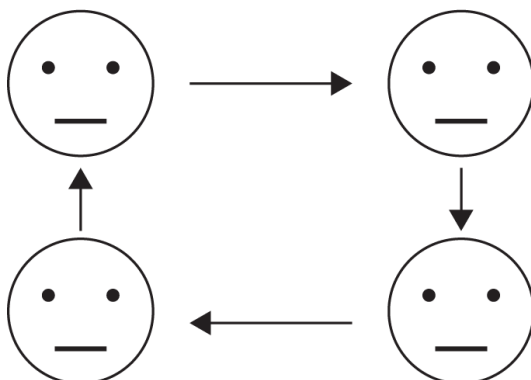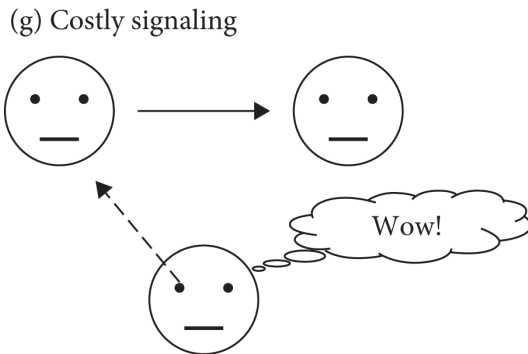
(e) Direct reciprocity

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(f) Indirect reciprocity

Click to view larger

(g) Costly signaling

Click to view larger

Figure 2 . Adaptive explanations for prosocial behavior (a) Volunteer's Dilemma, where one individual produces a resource that others happen to also benefit from (byproduct mutualism); (b) mutualisms (including coordination) where multiple individuals benefit from working toward a common goal; (c) one individual has a vested interest of the well-being of someone else who produces positive externalities; (d) individuals behave nicer to kin than to nonkin, because the former are more likely to carry copies of the same gene(s); (e) two individuals directly reciprocate prosocial acts, possibly with some time lag or in different currencies; (f) prosociality is reciprocated indirectly (i.e., by someone other than the recipient); and (g) costly signaling, where prosociality allows audiences to infer some difficult-to-observe trait about the actor. Solid arrows indicate direction of helping, dashed arrows indicate observation, hollow arrows indicate positive externalities flowing from one individual or resource to someone else, and arrows that are crossed out indicate an absence of helping (or at least less helping than with solid arrows).

Adaptive explanations are cases where the eventual benefits of helping outweigh the costs, either for the individual (direct fitness) or for copies of his/her genes residing in other bodies (indirect fitness)—together referred to as inclusive fitness (Hamilton, 1964). To help differentiate between them, we will illustrate each with the example of hunting. Hunting is a common practice in the societies in which humans evolved, and hunted meat is often shared. As such, hunting is very common topic in evolutionary studies of cooperation, and the underlying principles can generalize to other forms of prosocial behavior. Please see Figure 2 for a visual depiction of each kind of explanation. Each of these listed explanations for prosocial behavior could warrant an article unto itself, so we can give only a quick overview of each and refer the reader to the relevant literatures.

Direct Benefits and Byproduct Mutualism

Imagine a hunter who catches a large mammal which ends up getting shared with others, even the nonhunters who scrounge from his kill. Many would consider this hunting to be prosocial behavior because others benefit, even though the actor may not have intended for them to benefit—he may have simply been concerned with filling his own empty belly (Harpending, 1998). Hunting provides a direct benefit to the hunter because he gets to eat. Even if there is a cost to hunting, hunting is better than starving. Importantly, even sharing the meat may be directly beneficial if it stops others from pestering the hunter for meat. Any benefits to others are a byproduct of the hunter doing what is in his best interest. In this sort of situation, prosocial behavior is selected for, yet primarily because of the direct benefits to the actor (think of a wealthy person purchasing a golf course to play on from which other golfers could profit too).

Volunteering. A special case of direct benefit prosociality is when a lone hunter volunteers to catch food that others can scrounge. Everyone is better off if someone hunts but they are personally best off if it is someone *else* who expends that effort. This sort of situation has received extensive theoretical work, but under different names, such as a Volunteer's Dilemma (Diekmann, 1985; Murnighan et al., 1993; Myatt & Wallace, 2008); producer/scrounger game (Barnard & Sibly, 1981; Vickery et al., 1991), Dragon-Slayer game (Bliss & Nalebuff, 1984), Snowdrift Game (Doebeli & Hauert, 2005; Kümmerli et al., 2007), and Brave Leader game (Shen et al., 2010). The names may differ, but the logic of the game[1] is the same: for each person, the worst situation is if no one pays the cost of volunteering to produce the food, slay the dragon, or clear the snowdrift, and the best situation is if someone else (not oneself) does so. *If others are unlikely to volunteer, then one is best off to volunteer oneself.* Others will happen to benefit from this, but that is a byproduct of an individual following his/her best interests. This type of scenario has been used to explain to all sorts of situations including bystander helping, food production, vigilance against enemies, voting, and so on (Komorita & Parks, 1994). It has even been applied to the enforcement of group cooperation, in that people might take on the cost of punishing noncooperation if no one else

does (O'Gorman, Henrich, & Van Vugt, 2009; Raihani & Bshary, 2011).

There have been many theoretical and empirical studies of Volunteer's Dilemmas in humans and other animals. For example, Kümmerli and colleagues (2007) show that people are much more likely to cooperate with each other in this sort of situation than in the traditional Prisoner's Dilemma game (where free-riding is the strategy that maximizes individual payoff in any given round). This result matches game theoretical predictions by Doebeli and Hauert (2005). If only one (or a few) individual(s) need to volunteer in such situations, then people will be less likely to volunteer in larger groups because it is more likely that someone else can do so (e.g., Archetti, 2009). This prediction integrates evolutionary biology with the vast literature on "diffusion of responsibility" in bystander helping, which shows that group size inhibits helping (for a meta-analysis, see Fischer et al., 2011). Individual characteristics of group members are also relevant. For example, Diekmann (1993) has empirically shown that if one person has greater ability to provide a public good because he/she pays lower costs for doing so, then that person is more likely to "volunteer" and others are more likely to refrain. Finally, the costs of failure are also relevant: Archetti (2009) has mathematically shown that people are actually better off when there is a high cost of no one volunteering, because people are more likely to volunteer in such cases. Such counterintuitive predictions show how taking an evolutionary approach can lead to novel predictions about prosocial behavior.

Mutualisms. Sometimes hunting requires coordination: Individuals working together can accomplish something that they could not accomplish alone. Each individual benefits from working with others, and this is the basis of mutualisms. Mutualisms are ubiquitous in nature (Clutton-Brock, 2009; Sachs et al., 2004), and are also ubiquitous among humans, as exemplified in the classic Adam Smith quote that "it is not from the benevolence of the butcher, the brewer, or the baker that we expect our dinner, but from regard to their own interest." Some researchers do not find mutualisms as "theoretically interesting" as other forms of cooperation, but they are arguably the most common kind of cooperation in nature (Clutton-Brock, 2009; West et al., 2011). One party in a mutualism may benefit more than the other, but it is better for both parties to keep the mutually beneficial relationship than to break it (e.g., Bergstrom & Lachmann, 2003).

A special form of prosocial behavior through mutualistic cooperation is leadership (Van Vugt, 2006). Two hunters might benefit from coordinating their efforts to hunt down prey. Yet one hunter might get hungrier quicker or he has a more impulsive or dominating personality so that he will always lead the hunt. Given the risks associated with leading a hunt, he might be slightly worse off than to be the follower yet he still profits from the presence of another hunter (King, Johnson, & Van Vugt, 2009).

Coercion and punishment. Not all help is willingly provided. Researchers in many disciplines have noted that people are nicer to each other when they could be punished or harassed for not being nice (e.g., Blurton-Jones, 1984; Fehr & Gächter, 2002; O'Gorman et al., 2009; Ostrom, 1990; Yamagishi, 1986). When such coercion is present, there are direct benefits for helping others in order to avoid the costs of punishment. We will not elaborate on this here, because many readers will not consider coerced helping to be "prosocial," but we mention briefly it because it fits the definition of prosocial behavior and seems to be relatively common – think of a hunter being ostracized for not sharing his meat.

Stake or Vested Interests

In television show *Survivor*, the point is to vote people out of a group until one person remains, while gathering food and surviving a hostile environment (maybe much like the environment in which humans evolved). In the show's first season, the candidate Richard Hatch became irreplaceable to his group by becoming a good hunter. Although others may have wanted to vote him out, they also relied on the food he provided, such that they had a vested interest in keeping him in the group and ensuring his "survival." Reality television may border on fiction, but the principle here is general: one person can have some stake or vested interest in the welfare of another, such that the former person directly benefits from helping the latter. This principle carries many names, including pseudoreciprocity (Connor, 1986, 1995), stake (Roberts, 2005), the Banker's Paradox (Tooby & Cosmides, 1996), and interdependence or Selective Investment Theory (Brown & Brown, 2006). Studies in hunter-gatherers support the anecdote with Richard Hatch: those who provide meat for their groups tend to receive more food from others when they themselves are sick (Gurven et al., 2000, see also indirect reciprocity, later).

When people have a vested interest in the well-being of their friends and social partners, they benefit from helping

those friends, even if the friend is unaware of the help. People benefit from being part of groups, such that they directly benefit from helping those groups survive (Barclay & Benard, 2013; Kokko et al., 2001; Lahti & Weinstein, 2005; Reeve & Hölldobler, 2007). These vested interests in others' welfare can explain much helping toward individuals and even groups: if you will eventually benefit from the survival and well-being of your allies and in-group members, then you have a vested interest in helping them (De Cremer & Van Vugt, 1999; West et al., 2007).

Little empirical work has been done on the psychological mechanisms that trigger vested interests prosocial behavior (though see Brown & Brown, 2006). We would predict that they will be related to genuine concern of some sort toward the recipients; after all, you do not want someone to be incapacitated if you depend on them, and your concern will motivate you to ensure that they keep benefitting you. Tooby and Comides (1996) have suggested that from the actor's perspective such situations will also be associated with a desire to be irreplaceable to others, because this gives those people a stake in your welfare, and thus increases their likelihood of helping you.

Kinship

The vast majority of the more costly forms of helping in both humans and nonhumans are directed toward kin. Why is this? Imagine that you are a gene trying to propagate copies of yourself. The great evolutionary theorist William Hamilton (1964) noted that there are at least two ways you can do this: by increasing the reproduction of your current body (direct fitness), or by increasing the reproduction of other bodies that carry a copy of yourself (indirect fitness). *Inclusive fitness* is the sum of these effects—direct fitness plus indirect fitness—and is what organisms have evolved to maximize.[2] For any given gene, close kin are statistically likely to carry identical copies. Any gene that causes an individual to help close kin will often cause help to be targeted toward copies of itself. Thus, we should predict that psychological mechanisms that cause nepotism will evolve in many species, and that this nepotism should depend in part on the closeness of kinship (as well as the fitness costs and benefits). This prediction has been abundantly confirmed in many species (for a review, see Alcock, 1993); the fact that it has even been studied in plants (e.g., Dudley & File, 2007) suggests that inclusive fitness is a powerful idea that applies across all of life.

Much research has shown that—all else being equal—people are nicer to kin than nonkin: they are more likely to help kin, less likely to harm kin, and more willing to tolerate injustices from kin (e.g., Burnstein, Crandall, & Kitayama, 1994; Daly & Wilson, 1988; DeBruine, 2002; Grayson, 1993; Hames, 1987; Krupp et al., 2008; Stewart-Williams, 2007). Of course, all else is never equal, but even when people are in competition with others, they will compete less sharply with kin than with nonkin in the same situations (Daly & Wilson, 1988; Gardner & West, 2004). Kinship is a major form of grouping in many pre-industrial societies, and appears to be a major factor affecting who shares food with whom in many societies (Gurven, 2004). In fact, the most persistent, long-term, selfless, and unreciprocated help that we see people perform—namely parental care—is actually just a special case of kinship because offspring carry copies of parental genes (Daly & Wilson, 1988; Dawkins, 1976/2006). Natural selection has crafted a psychology that includes such powerful sentiments as parental love, filial attachment, fraternal and sororal solidarity, and other such nepotistic emotions. These emotions are the proximate psychological mechanisms that function to promote nepotism toward kin. All told, kinship appears to be one of the most powerful causes of prosocial behavior for most humans on the planet.

Reciprocity

Hunting food is difficult, and hunters often come home empty-handed. This means that each hunter is at risk of going hungry some days and having a bonanza of food on others days when he catches something. To resolve the problem of being hungry on some days, two or more hunters could agree to help each other. Each hunter will share with the other(s) when he has plenty, and gets a share when he is hungry. This way, each has fewer hungry days and is more likely to survive.

There is a risk associated with this type of prosociality because sharing is costly: Sharing involves giving up meat (or time, effort, money, etc.). If one person received meat from others without giving anything in return, then he would be better off than someone who paid the cost of sharing. This strategy of "free-riding" on others would be beneficial if people are willing to give to anyone. One solution is for people to preferentially help those who have provided help in return: this is the basis of reciprocity (Axelrod, 1984; Trivers, 1971; Van Vugt & Van Lange,

2006). In this way, the helpers tend to receive help and the nonhelpers tend to not receive anything. Reciprocity comes in two basic forms—direct and indirect reciprocity—which differ in whether the help is repaid by the recipient or by others in the community.

Direct reciprocity. People often get involved in exchange relationships where they take turns helping each other. In our meat example, two hunters might share with each other as long as each of them has given in the past. Colloquially, we have such expressions as "you scratch my back and I'll scratch yours," which carry the implicit condition that "I will not scratch your back *unless* you scratch mine."

Is this kind of prosocial behavior beneficial for the actor? Most readers of this chapter will be familiar with Axelrod's computer simulations of the Prisoner's Dilemma Game (Axelrod, 1984). A Prisoner's Dilemma is a two-person game where each player has the binary choice either "cooperating" or "defecting" in each of a number of rounds (iterations). Axelrod conducted computer simulated tournaments with different strategies for playing iterated Prisoner's Dilemmas, and the strategy that consistently survived the best was Tit-for-Tat. Tit-for-Tat is a simple strategy of initially cooperating with one's partner, and thereafter simply imitating the partner's action on the previous interaction. Tit-for-Tat is a remarkably good strategy because it cooperates with other cooperators and does not get "suckered" for long by those who do not cooperate. As such, it tends to do better than many other strategies (Axelrod, 1984; Boyd & Lorberbaum, 1987; Dawkins, 1976/2006; Wilson, 1971).

There are conditions that limit the effectiveness of Tit-for-Tat, of course. Tit-for-Tat only works if the "shadow of the future" is long enough such that the future benefits of one's partner's reciprocation will outweigh the cost of immediate helping (much subsequent work shows decreased cooperation in the last round of a cooperative task, a.k.a., "endgame effects"). Tit-for-Tat requires enough other reciprocators around to make it worth initiating a reciprocal relationship. Also, Tit-for-Tat must not be directly competing against its partners, because this decreases the benefits of prosocial behavior (West et al., 2006; see "Scale of Competition", later). Under some conditions, Tit-for-Tat can be beaten by more forgiving strategies that overlook accidental failures to cooperate, or by strategies that exploit unconditional cooperators (e.g., Brembs, 1996; Klapwijk & Van Lange, 2009; Nowak & Sigmund, 1992, 1993). Although Tit-for-Tat is not always the best reciprocal strategy to follow, the net sum of years of theory is that *some* willingness to reciprocally exchange help can be a highly successful strategy.

Recent work has moved beyond the simple Prisoner's Dilemma by allowing people to use graded levels of prosociality instead of a binary choice. Roberts and Sherratt (1998; Sherratt & Roberts, 1999) have mathematically shown that the best strategy in such situations is "Raise-the-Stakes," which means starting out moderately prosocial and getting increasingly prosocial when one's partner reciprocates. This accurately models what people actually do in experimental games (Roberts & Renwick, 2003; Van den Bergh & Dewitte, 2006), especially with strangers with whom they have not yet built up a trusting relationship (Majolo et al., 2006).

Contrary to popular belief, the existence of reciprocity does not require calculations or strict bookkeeping of past acts (recall from the introduction to this chapter that an act may be selfish at the gene level but genuinely selfless at the level of the individual actor). Instead, reciprocity explains why people are capable of possessing genuine warmth toward others like friends. If I genuinely value your welfare, it will cause me to help you, which can cause you to genuinely help me when I need it, which causes me to value your welfare more, and so on. In other words, reciprocity is the adaptive evolutionary cause of prosocial behavior, whereas empathy and feelings of warmth are potential proximate psychological causes (e.g., Barclay, 2012b; de Waal, 2000; de Waal & Suchak, 2010; Frank, 1988; West et al., 2011). What reciprocity does require are the cognitive abilities to detect when others might fail to reciprocate (Cosmides et al., 2010), remember who has and has not reciprocated (Barclay, 2008; Mealey et al., 1996), and delay gratification in order to reap the long-term gains of reciprocation (Harris & Madden, 2002; Stevens & Hauser, 2004; Van Vugt & Van Lange, 2006).

Indirect reciprocity. People do not only help their immediate friends and reciprocal partners. Human prosociality is much broader than that. People regularly help those who will not have the opportunity to reciprocate. Imagine one hunter who is known to regularly share with others, and a second hunter who is known for stinginess. When the generous hunter gets sick and is unable to hunt for himself, others are likely to give him meat, whereas the stingy hunter is much less likely to receive meat when sick (Gurven et al., 2000). This is an example of indirect reciprocity, which is when prosocial acts are reciprocated by someone other than the recipient (Alexander, 1987; for a review see Nowak & Sigmund, 2005). Under indirect reciprocity, people acquire a good reputation when they

help others, and this makes them more likely to receive help when they themselves need it. People who refuse to help good people get a bad reputation, which reduces their likelihood of receiving help.

Wedekind and Milinski (2000) had participants play an experimental game where they could give money to other participants and could gain a reputation for giving or refusing. The experimenters ensured that there was no possibility of direct reciprocation from the recipient because participants would never be paired with the same person again. Despite this, participants tended to give money to others who had given in the past, such that people with a good reputation were more likely to receive money. This result has been replicated in several other similar experiments (Milinski et al., 2001; Semmann et al., 2004; Seinen & Schram, 2006; Wedekind & Braithwaite, 2002). People seem to use a combination of personal experience and social information about others when deciding whether to help them (Roberts, 2008; Sommerfeld et al., 2007). Evolutionary game theorists are currently investigating what types of acts will result in obtaining a good versus bad reputation, and how a refusal to help a "bad" person might or might not harm one's own reputation (Bolton et al., 2005; Milinski et al., 2001; Ohtsuki & Iwasa, 2004, 2007). This research has implications for the genetic or cultural evolution of moral systems (Alexander, 1987).

Indirect reciprocity can also be used to support large-scale cooperation. People who provide public goods that benefit the whole group tend to receive more help from others (Milinski et al., 2002; Panchanathan & Boyd, 2004). As a result, reputational forces like indirect reciprocity can be harnessed to support prosocial actions like the fight against climate change, because people who work against climate change tend to benefit in terms of indirect reciprocity (Milinski et al., 2006; Van Vugt, 2009).

Costly Signaling

Hunting big game is challenging, and hunters regularly come home empty-handed. It takes a lot of skill to catch big game with any regularity. If you see someone who is often sharing meat from big game that he has caught, what do you conclude about him? Probably that he has resources and skills. These can include talents such as athletic ability, physical strength, coordination, intelligence, perseverance, leadership, and commitment—all of which are desirable traits in a sexual mate or in a coalitional partner and undesirable traits in an enemy. As such, hunting (and sharing) large game may be a way of signaling qualities about oneself that may otherwise be difficult to observe directly (Hawkes, 1991; Smith & Bliege Bird, 2000; Smith, 2004). This is an example of costly signaling, which is a way to broadcast information about oneself in a way which constrains it to be honest (Searcy & Nowicki, 2007; Zahavi & Zahavi, 1997).

Individual A benefits from sending signals to convince Individual B that A has certain qualities (e.g., abilities, resources, cooperative intent), and B benefits from determining whether A honestly does possess those qualities. How does B know if A's signals are honest or if A is bluffing? Signals can be constrained to be honest if they carry a potential fitness cost which is only worthwhile for someone who honestly possesses the quality (Gintis et al., 2001; Searcy & Nowicki, 2007). For example, it is fairly easy for Bill Gates to donate $1 billion to charity. As such, Bill Gates pay a relatively low *fitness* cost for such large donations, and this can be outweighed by any reputational benefits he receives. For most other folks, the reputational benefits would not outweigh the crippling cost of sacrificing that much money, so the fitness cost is too high and therefore not worth it. As a result of these differing fitness costs, audiences can infer that Bill Gates is very rich because he has over a billion dollars *to spare*. Bill Gates thus receives status, respect, mating opportunities (if he were so inclined), and a host of other social benefits.

Costly signaling theory has explained many forms of prosociality like philanthropy (Harbaugh, 1998), large public feasts and potlatches (e.g., Boone, 1998; Smith & Bliege Bird, 2000; Van Vugt & Hardy, 2010; reviewed by Barclay, 2010a), peer-to-peer file-sharing (Lyle & Sullivan, 2007), blood donations (Lyle et al., 2009, volunteering (Van Vugt & Iredale, 2012), and even organizational citizenship behavior (Engelhardt & Van Vugt, unpublished data).

In addition to signaling talents, abilities and resources, prosocial behavior also signals cooperative intent: "You know that I am unlikely to cheat you because any short-term benefits I would gain are not enough to outweigh the cost of the signal" (André, 2010; Barclay, 2010a). This principle has successfully predicted various forms of prosocial activities such as apologies (Ohtsubo & Watanabe, 2009), commitment to relationships (Seymour & Sozou, 2009), contributions to charities and public goods (Iredale et al., 2008; Van Vugt & Iredale, 2012), and

religious rituals (Sosis, 2004) by looking at them as types of costly signals of cooperative intent. Much laboratory research shows that people treat prosocial behavior as though it signaled future cooperative intent (reviewed by Barclay, 2010a).

In animal behavior, costly signaling theory has been particularly useful in investigating sexual selection and mate choice. Given that people have a vested interest in choosing prosocial mates, and helping behavior can be one way of signaling that trait, costly signaling may also be involved in sexual selection for prosociality (Barclay, 2010; Van Vugt & Iredale, 2012) and moral virtue (Miller, 2007).

Summary of Adaptive Explanations

The previous section gives several ways in which individuals may benefit from prosocial behavior (direct benefits from an outcome, stake or vested interests in the recipient, direct or indirect reciprocity, and costly signaling of hidden traits). In addition, any genes influencing prosociality could spread if they cause an organism to help kin who are statistically most likely to carry copies of those genes. These benefits would result in the evolution and maintenance of prosocial sentiment. However, not all instances of prosocial behavior bring benefits, so the next section deals with such instances.

Nonadaptive Explanations

Contrary to popular belief, evolutionary theory does not predict that every instance of prosocial behavior will bring benefits and increase inclusive fitness. For example, prey species sometimes get eaten because they mistake where predators are (e.g., a zebra running toward a hidden lion) and several bird species are tricked into raising cuckoo chicks. These animals clearly produce a benefit to the other animals, such that these behaviors fit some definitions of prosociality. Clearly, such mistakes and manipulations frequently occur in nature but they are not adaptive. What evolutionary theory can do is make predictions about when such nonadaptive outcomes might result, and why.

Mistakes

No one would suggest that all behavior is perfectly executed or that all consequences are intended. Or at least, no one with any experience of the world should suggest this. Humans have imperfect information, limited time, and many other such constraints (Todd, 2001). Mechanisms break down. There are at least four types of mistakes that are worth mentioning regarding prosociality (a) mistakes from mechanisms that are "adaptive on average," (b) outliers on a normal curve, (c) pathologies or breakdowns of adaptive mechanisms, and (d) mismatched environments due to evolutionary lag. Each of these could cause instances of prosocial behavior that do not yield benefits.

Adaptive on Average. Suppose that one day you have successfully hunted meat, but you would prefer not to share with the rest of the group because you and your family are hungry. You could try to smuggle it back to your family or consume it on the spot, but what if others catch you? You would risk losing your reputation, getting punished, and having others not share with you in the future. That would be really bad. It *looks* like you would get away with it and you could defect on your group anonymously, but is it really worth the risk? It is easy to say with hindsight whether you could have gotten away with it, but you cannot tell this in advance. Perhaps it is safer to share, just in case someone comes along. That way, you are guaranteed to keep your reputation and avoid punishment. Sure, you will sometimes end up helping others when you did not strictly *need* to, but that may be a small cost compared with the risk of reputational loss. Natural selection might even favor a psychology that makes people *want* to share, because someone who genuinely wants to share will be guaranteed to keep their reputation (Delton et al., 2011; Frank, 1988; Simpson & Willer, 2008).

Our psychological mechanisms have evolved to be *adaptive on average*, in that they bring more benefits than costs when averaged across all situations. All mechanisms occasionally make mistakes because errors are inevitable in any decision-making process (Haselton & Buss, 2000; Nesse, 2005). Prosocial sentiments, like empathy, cause us to help others (Batson et al., 1997; de Waal & Suchak, 2010). In a world with reciprocity and reputation, this usually results in prosocial people receiving benefits for helping, even if those people do not intend

to receive such benefits. As long as those benefits outweigh the costs of occasionally helping the "wrong" people (e.g., those who will not reciprocate) or in the "wrong" situations (e.g., when we are anonymous) then it would still be adaptive to have prosocial sentiments (Barclay, 2011a; Delton et al., 2011; Frank, 1988).

What predictions does this nonadaptive hypothesis allow us to make? Firstly, we would explicitly predict that possession of prosocial sentiments tends to bring benefits on average. Secondly, we can use evolutionary principles to predict when people will err on the side of helping versus err on the side of not-helping. This is a classic example of signal detection, also known as the "smoke-detector principle" (Nesse, 2005) or "error management" theory (Haselton & Buss, 2000). Basically, we really want to avoid making the more costly or more frequent errors, like having our smoke detector fail to detect a real fire. In this context, the optimal decision rule depends on the costs and benefits of helping versus not helping, in situations when one "should help" (i.e., when there are benefits) versus in situations where one "need not help" (i.e., when there are no benefits) (Delton et al., 2011).

All else being equal, biases toward helping will be strong (1) when there are large benefits for helping when one "should help" (e.g., if audiences respond very favorably to helpers); (2) when there are high costs of not-helping when one "should have helped" (e.g., if audiences react unfavorably to nonhelpers); and (3) if the most common situations are ones where one "should help" (e.g., truly anonymous situations are rare, and interactions that appear anonymous are usually not actually anonymous). By helping in such situations, one receives high social benefits and avoids high social costs, so it is worthwhile to "err on the side of helping." Conversely, all else being equal, people should be biased against helping (1) when there are high costs for helping when one "need not" do so (e.g., embarrassment, unnecessary exposure to risk); (2) when there are large benefits for avoiding unnecessary helping (e.g., avoiding helping when it is costly relative to the potential gains); and (3) if one is most likely to encounter situations where one "need not" actually help (e.g., if most interactions that appear anonymous actually are anonymous). By avoiding helping in such situations, one avoids paying the costs of helping when it is unnecessary to do so. The overall bias toward helping—and the frequency of "unnecessary" help—will depend on the relative magnitude of these average costs and benefits and the frequency of each type of situation.

We can also predict that people will be more cooperative when presented with cues that they might benefit from helping. In other words, we can design experiments to cause participants to make "mistakes" by helping when they receive no benefits for doing so, as long as we trigger cues that would normally indicate the presence of benefits. For example, the presence of eyes is normally a cue that one is being observed, and many experiments have shown that people are more generous with their money when they can observe eye-like stimuli on a computer or on a poster (Bateson et al., 2006; Burnham & Hare, 2007; Haley & Fessler, 2005; Mifune et al., 2010; Rigdon et al., 2009; but see Sparks, 2011). As another example, facial resemblance is one cue that people use to detect kinship (DeBruine, 2005), and participants in experimental games are more cooperative when they are playing with people whose faces have been morphed to slightly resemble the participant's own face (DeBruine, 2002, 2005; Krupp et al., 2008). In both of these examples, an adaptive psychological mechanism is being "tricked" to produce a prosocial response even when the participant does not benefit from being helpful to others. This mistake hypothesis has some interesting implications for how societies can encourage prosocial behavior, for instance, providing cues of being watched in anonymous public spaces.

Outliers. Imagine that in any selection environment, there is an "optimal" level of helping behavior where one receives the most inclusive fitness benefits per unit of cost. The optimum will inevitably vary with social and ecological circumstances, including the local norms, the cooperation of others, the possibilities for reputation, proximity to kin, the "shadow of the future," and so on. Ideally, if one wants to maximize inclusive fitness, one would help exactly that much, but no more. Helping less than the optimum would result in reaping fewer benefits, and helping more would result in needlessly incurring costs (e.g., Barclay, 2011b; Baumard et al., 2013).

Of course, almost no one will ever hit this optimum exactly. Individuals will differ in their combinations of genes, their developmental histories, their past learning experiences, their accuracies in assessing the situation, and so on. This will all cause deviations around the optimum, such that some people help others less than would be optimal for them to do, and other people help more than would be optimal. This is inevitable, because all traits are expected to have some deviations around the optimum (Tooby & Cosmides, 1990). We can imagine a bell-curve, with most people being somewhat close to the optimum, some people being further away from optimality in either direction, and a few rare people deviating so far from optimality that their helping seriously oversteps (or

understeps) the bounds of utility.[3]

It is interesting to ask what maintains such variation, but lengthy discussion of this is beyond the scope of this chapter (see Buss & Greiling, 1999; Tooby & Cosmides, 1990). For present purposes, we need only know that variation exists, and sometimes, when prosociality carries no benefits, it might just be because the person is at the tail end of the optimality bell curve. For instance, people might be on the extreme tail of the empathizing trait and as a result they might be more prone to help across a wide range of situations even when there are no adaptive benefits—the extreme female brain hypothesis (Baron-Cohen, 2003).

Pathologies. When Phineas Gage had a metal bar accidentally driven through his skull in 1848, it radically changed his personality and he became more irreverent, profane, and impulsive. One would never ask, "What is the function of his impulsiveness?," because it is obvious that something had gone seriously wrong with Gage's brain, namely that part of it had been blasted outside of his skull. On a less severe note, developmental accidents can easily happen when building or maintaining any organ as complex as a brain. Any slight perturbations during development can cause deviations from optimality. With modern machines, some car or computer owners discover this upon purchasing a "lemon." In human development, pathologies can be caused by physical trauma, pathogens, senescence, genetic mutations, or chemicals and other teratogens. If there is evidence that something has gone "wrong" in someone's development or that something is "broken," then we should not expect all of their behavior to be adaptive. All bets are off in such cases.

Some pathologies will result in less prosocial behavior rather than more. For example, it is well known that head trauma can cause antisocial behavior (e.g., Andrews et al., 1998). However, it is at least theoretically possible that some breakdowns could result in heightened prosocial behavior. For example, a breakdown in the brain areas responsible for self-interested behavior could possibly result in more decision weight being placed on the interests of others. If a developmental perturbation caused someone to feel less hunger, then that person would be more willing to share food because he or she would not want it as much. We know of no research on whether heightened prosociality can be caused by pathologies, but such studies would be very interesting if found. Perhaps people have not investigated this topic because excessive generosity is seen as "nice" rather than pathological, and therefore not in need of "fixing."

Mismatches and evolutionary lag. Natural selection does not plan ahead. Our current adaptations are "designed" to work well in past environments: Those who had more offspring in past environments tended to pass their traits on to current generations. If the environment stays relatively constant, then those traits will function well in the current environment. However, if the environment has changed recently, then traits which were once adaptive may no longer be adaptive. In other words, the "old" adaptations might not yet have been selected out of a population if the selection pressures have recently changed. This idea is known as "evolutionary lag" or "mismatch," because the changes in genes lag slightly behind the changes in environments (Laland & Brown, 2006; Van Vugt & Ahuja, 2010). The classic example of evolutionary lag is our preferences for sweets, salts, and fats: it was adaptive to crave these when they were rare, because they were valuable sources of energy and nutrients. People still crave them even though they are overabundant in modern environments and lead to obesity and other health problems.

Social environments have changed dramatically in the last several centuries and millennia. As such, some prosocial sentiments that were once adaptive might no longer be adaptive. For example, we have gone from living in small kin-based groups to much larger groups of mostly nonkin. In the former circumstances, a psychology with the decision rules such as "feel warmth toward all group members" and "help someone who needs aid" would result in prosocial behavior mostly targeted toward kin or to reciprocal partners, whereas in modern circumstances it would not. Thus, prosocial sentiments that once increased inclusive fitness may no longer do so.

In addition to changes in the scale and kin composition of groups, we now also have many more opportunities for anonymity and movement *between groups*. This means that people can now get away with more selfish behavior than they could have in small bands, and it is now easier to move to a new group and run from one's bad reputation. Accordingly, reputation may be less important in modern environments than in past environments— though this requires empirical testing. If so, then it would not be as beneficial as it once was to possess social emotions like guilt and shame. Such emotions help people maintain their reputations and make amends for any damage they have done to cooperative relationships (Frank, 1988; Ketelaar & Au, 2003).

When people can simply run from a bad reputation or simply gain new partners to replace any partners they have estranged then these emotions are no longer functional. This situation may be changing with the advent of the internet and social media technologies such as Facebook and Twitter as people are now able to spread information about others' reputation—for good or for ill—quickly and efficiently. As it stands now, it is currently unknown whether evolutionary lag is a major factor in explaining human prosociality. Yet it is worth investigating prosocial behavior in smaller and largely kin-based social networks that were the norm until fairly recently to see if humans still apply the same decision rules in large, modern and complex societies (Dunbar et al., 2012; West et al., 2011).

Evolutionary byproducts

Not every trait we see was specifically selected for in evolution. Some traits exist as incidental byproducts of other traits (spandrels; Gould & Lewontin, 1979). For example, we should not ask "What is the advantage of birds' bones being so brittle?" because brittleness is a necessary consequence of being light, and lightness has presumably been selected for because of its importance in flight. Thus, brittleness is a byproduct of selection for lightness. To what extent could prosocial behavior be a nonadaptive byproduct of other traits that are adaptive themselves?

Developmental byproducts. Natural selection is a very blunt instrument. It is very hard to select for one single trait without accidentally selecting for other traits. Different traits can be correlated if they are caused by the same gene ("pleiotropy"), if they are caused by genes that share the same region of a chromosome ("linkage"), or if the same brain regions or pathways are involved in multiple behavioral traits. In such cases, strong selection for one feature will result in any correlated features "piggybacking" along and also increasing in frequency. These correlated features are not selected for directly, but their existence is a byproduct of something that was selected for.

The best examples of byproducts come from animal breeding. For example, the poultry industry intensively breeds their chickens for things like fast growth, but sometimes other correlated traits end up increasing in frequency also. This has resulted in what Temple Grandin calls "rapist roosters" who attempt to forcefully mate with the hens, and often end killing them in the process (Grandin & Johnson, 2005). Because of the intense selection pressure that is being applied for fast growth, other traits that would normally be maladaptive can increase in frequency if they happen to be genetically correlated with genes controlling growth—there is little selection pressure against them if the selection for fast growth is so strong.

On a more positive note, some types of prosociality may be developmentally linked with each other. Over 40 years ago, Dmitri Belyaev began breeding foxes for one single trait: tameness. This has resulted in a number of other changes in his breeding population, including floppy ears, shorter tails and legs, light patches of fur, altered fear and corticosteroid responses, "feminized" head shape, and altered reproductive patterns (Trut, 1999). These are all developmentally linked with tameness, such that they increase in frequency when tameness is selected for. Most interesting are the behavioral changes regarding sociability, which have resulted in foxes who "seek out human contact and lick experimenters' hands and faces" (Trut, 1999, p. 169).

How does this apply to human prosociality? Humans have likely been under strong selection for the ability to get along with fellow group members, because some degree of mutual tolerance pays better than constant hostility. This "self-domestication" of humans could have had other effects on human evolution, because the ability to get along is developmentally linked with other traits (Ridley, 2003). As such, prosocial sentiment could have arisen as a byproduct of natural selection for "tameness" or tolerance in humans (Hare et al., 2007). Just like the foxes who were bred for tameness toward humans and now behave very nicely toward their handlers, natural selection for mutual tolerance in humans could have resulted in humans who now actively behave very nicely toward each other and show strong affiliative needs (Baumeister & Leary, 1995).

Byproducts of other adaptations. Some types of prosocial behavior may be byproducts of other adaptive mechanisms. For example, Richerson and Boyd (2005) argue that people could learn cooperative behavior through "conformist transmission," which means copying whatever behaviors are most common within a population. Copying common behaviors is normally an adaptive way of learning how to do things because others may have already figured out the best way of doing things. However, it can also cause people to make systematic errors when they also copy behaviors that turn out to not be optimal—an effect that has been triggered in dozens of articles on conformity (for a review, see Cialdini & Goldstein, 2004). Given that humans rely so much on socially

learned behaviors, this bias toward conformist transmission is probably adaptive on average, even if it occasionally causes us to learn maladaptive behaviors. Thus, it is possible that our tendency to copy prosocial behavior could be a maladaptive byproduct of our adaptive tendency to copy common behaviors. Herbert Simon (1990, 1993) has made a similar argument about our disposition to learn from others, which he calls "docility." This is a highly advantageous trait yet it allows other people to occasionally manipulate us into learning altruistic behaviors which do not benefit us.

On a much more speculative note, social emotions like empathy may be evolutionary byproducts of selection for our ability to copy others. Humans are extraordinarily good at imitation and other forms of social learning (Herrmann et al., 2007), and we rely on these abilities in order to survive (Bandura, 1962). The ability to imitate seems to involve specialized neurons called "mirror neurons." These mirror neurons allow us to form an internal representation of others' actions in order to replicate those actions ourselves (Keysers, 2006). These mirror neurons may also be involved in empathy, which is the ability to share others' emotional states, and may possibly be involved in Theory-of-Mind (Keysers & Gazzola, 2006). It is highly likely that imitation and Theory-of-Mind are adaptive traits which have been under strong selection pressure. This would cause an increase in mirror neurons (or whatever else happen to be the neurological mechanisms), which could possibly have side effects like causing the presence of empathy. Under this hypothesis, empathy—and the prosocial behavior it triggers—is not adaptive itself, but exists because of strong selection for imitative abilities and theory-of-mind.

Evolutionary byproduct hypotheses can explain how costly behaviors arise if they happen to be incidentally caused by other adaptations or if they piggyback on selection for other traits. Byproducts can only explain prosocial behavior with relatively low costs because the selection against the "prosocial byproduct" would have to be weaker than the selection pressures favoring the correlated trait. For example, if conformist transmission caused too many people to imitate suicidal self-sacrifice, then conformist transmission would be selected against unless the benefits for imitation were so large as to outweigh the cost of suicidal self-sacrifice (Mesoudi, 2009). Furthermore, given enough generations, natural selection should tend to sever any genetic or developmental links that cause costly byproducts, so that organisms could get the benefits of one adaptation without any of the costly byproducts. For these reasons, it is unwise to simply assume that costly forms of prosociality are byproducts of something else, unless we can demonstrate that there has been recent strong selection for a correlated trait. And of course, any byproduct explanations must be subjected to empirical testing of their predictions, just as we would do for adaptive explanations.

Propagation of Ideas: Memes and Cultural Group Selection

Most people think of evolution as dealing mostly with genes, but cultural traits can also evolve. If a cultural trait is better at propagating itself and attracting new bearers, then it will spread in a population at the expense of alternative cultural traits. The study of such transmission is known as "memetics" after Richard Dawkins' concept of "memes"—units of culture which jump from one mind to the next (Dawkins, 1976/2006), or Dual-Inheritance Theory, because of the fact that humans inherit traits both genetically and culturally (Boyd & Richerson, 2002; Richerson & Boyd, 2005).[4]

One trick for a cultural trait to spread is to be good for the bearer: others will see that the bearer is doing well and will imitate that cultural trait (Richerson & Boyd, 2005). In such cases, the cultural trait and the genetic trait are in a symbiotic mutualism; both benefit from such arrangements. However, a cultural trait need not necessarily be good for its bearer to spread. If a cultural trait is exceptionally good at getting itself copied by new minds, then it will spread even if it has no net effect—or even a negative effect—on its bearer's fitness (Dawkins, 1976/2006). Thus, cultural traits can also be like parasites in that they can manipulate their hosts to increase their own propagation at the expense of their bearer's fitness (Dennett, 2006).

When it comes to prosocial behavior, public acts of generosity attract attention, not least because others want to receive a share of that generosity (Blackmore, 2000). As such, public generosity is likely to be observed by many people. All else being equal, this visibility increases the likelihood that those behaviors will be imitated. After all, an act needs to be noticed to be imitated. In this way, the meme of "go out and help others" turns its bearer into what Susan Blackmore has called a "meme fountain"—someone who broadcasts memes that others can then pick up (Blackmore, 2000). This may or may not be good for the bearer, but it does aid the propagation of the meme for helping.

By definition, prosocial behavior benefits others in one's group, so members of a prosocial group are better off than members of less prosocial groups. This means that there are advantages of being part of a prosocial group, even if helping others is personally costly. This can lead to cultural change as more prosocial (and thus more successful) groups replace less prosocial groups and bring their cultural norms with them, or by less-successful groups imitating the prosocial norms of more successful groups (Boyd & Richerson, 2002). People may also "vote with their feet" by joining groups with norms fostering prosocial behavior (Gürerk et al., 2006). For example, this may have been a factor in the spread of early Christianity because there were large benefits for joining a group which had strong norms about helping others (Wilson, 2002). This process of cultural change has been called "cultural group selection" (Richerson & Boyd, 2005), as successful cultural norms spread at the expense of less successful norms. In previous writing, one of us has noted that a better name is simply "cultural selection," because groups are neither necessary nor sufficient for this process to happen (Barclay, 2010a). Regardless of the name, it is clear that culture evolves, and that norms about prosociality can spread through cultural evolution.

Summary of Nonadaptive Explanations

These examples demonstrate that in addition to explaining adaptive instances of prosociality, evolution can also explain the existence of nonadaptive prosocial behavior. Such behavior could be a mistake by an adaptive mechanism, a breakdown of an adaptive mechanism, an outlier on a normal curve, a case of evolutionary lag, an evolutionary or developmental byproduct, or an idea spreading at the expense of its bearer. Importantly, evolutionary theory makes novel predictions in each of these cases. In the next section, we discuss some new perspectives that may (or may not) prove useful.

Emerging Evolutionary Perspectives on Prosocial Behavior

Scale of Competition

Suppose that you and another candidate are interviewing for a job at a company. If this other candidate makes a mistake that you can easily correct for him, do you help him out? Your willingness to do so will probably be affected by whether you are both interviewing for the same job. If you are, and if there is only one position, then any help you give to him will directly harm you because it increases the likelihood that he will get the job instead of you. All of your competition is against this one person, and this "local" competition undermines your incentives to cooperate with each other. If you are interviewing for different jobs, then you are not in competition, and you could both benefit from helping each other to compete against your respective competitors. In this case, you have no local competition, because you are both competing against separate pools. How about an intermediate situation? If you are both competing for a position, but there are many positions, then you could still benefit from helping each other because this puts you both in a better position to compete with the larger pool of candidates. You would still be partly in competition with each other, and this would somewhat suppress your incentives to cooperate, but most of the competition is with others.

This example illustrates the principle of "scale of competition," which evolutionary biologists have started to apply to cooperative interactions among kin and nonkin alike (West et al., 2002, 2006). Competition is said to be "local" when people are in direct competition with their partners, such that they are in a zero-sum relationship. Competition is "global" when this local competition does not exist. Local competition will tend to suppress cooperation, and may even cause spite because people will have an incentive to harm their partners (Gardner & West, 2004).

West and colleagues (2006) demonstrated this principle in an elegant experiment using an iterated Prisoner's Dilemma game. Participants were divided into groups of three from within a larger class. They would play separate Prisoner's Dilemmas games with each of their two partners, and would earn points from each set of games. Prizes were either given to the highest earners in the class (global competition) or to the highest earner in each group of three (local competition). When prizes went to the highest earners in the class, there was an incentive to cooperate with one's partners in order to earn a higher score than others in the class, and people cooperated about 45% of the time. When prizes went to the highest earner in each group of three, cooperating with one's partners would help them win against oneself, so cooperation rates plummeted to less than 20%. This experiment shows how the scale of competition affects prosocial behavior and how changes in this structural factor can

enhance or inhibit cooperation (e.g., in workplaces). This research group has also demonstrated the importance of scale of competition on prosocial behavior in other species such as fig wasps (West et al., 2001) and bacteria (Griffin et al., 2004), demonstrating that scale of competition is an important factor across all taxa of life.

Multilevel Selection

In this chapter, we have largely focused on how prosocial behavior can increase inclusive fitness. Inclusive fitness theory examines how one's behavior affects one's own reproduction and one's kin's reproduction (Hamilton, 1964). However, this is not the only perspective one can take when seeking adaptive explanations for behavior. Inclusive fitness theory is simply one method of counting fitness, and alternative methods exist. For example, one can use "neighbor-modulated fitness." Instead of examining one's effects on oneself and on kin (as in inclusive fitness theory), neighbor-modulated fitness examines only one's own reproduction and includes kin's effects on oneself (Queller, 2011; West et al., 2011). These two methods are mathematically equivalent; they only differ in whether kin effects are counted when going from oneself toward kin or when coming from kin to oneself.

Another common—though more controversial—alternative is multilevel selection (e.g., Boyd et al., 2003; O'Gorman et al., 2008; Sober & Wilson, 1998; Wilson, 1979, 1990, 1998, 2004). Some types of cooperation will decrease one's fitness relative to one's group but will increase the fitness of that group relative to other groups. Multilevel selection looks at how one's actions affect group fitness versus individual fitness, and whether between-group selection for cooperation is stronger than the within-group selection against costly cooperation; cooperation will arise when the latter is stronger than the former.

It is important to stress that multilevel selection and inclusive fitness theory are mathematically equivalent (e.g., Foster et al., 2006; Queller, 2011; Reeve, 2000; Sober & Wilson, 1998; West et al., 2007, 2011).[5] This is no longer under any serious debate. All multilevel selection models can be translated into inclusive fitness models and vice versa. Rather than being a "new selective force," multilevel selection is simply another way of looking at fitness, much like a different way of looking at a Necker cube (Sober & Wilson, 1998; Reeve, 2000). This involves defining some words like "altruism" differently, which has caused much of the confusion over multilevel selection. Multilevel selectionists define "altruism" as behavior that decreases one's fitness *relative to the local group*, whereas inclusive fitness theorists define "altruism" as behavior that decreases one's fitness *relative to the global population* or relative to what one would have gotten if one had not taken action (Kerr et al., 2004; Reeve, 2000; West et al., 2007, 2011). By the former definition, "a positive effect on self … can be *altruistic* if the effects on others are even greater" (Wilson, 1990, p. 135, emphasis added). This means that a hunter would be defined as "altruistic" if he catches big game solely because he is hungry but others happen to receive an equal share of his meat (Harpending, 1998).

The big question is: Is it useful to look at group fitness when looking at prosocial behavior? Evolutionary researchers disagree on this, as do the two authors of this chapter. Some researchers (including one of us) have written about how human groups can function as single reproductive units, much like beehives, and have arguably done so for much of human evolutionary history (Wilson, Van Vugt, & O'Gorman, 2008). This would involve heritable group-level adaptations for promoting altruism and cooperation within groups as well as suppressing intragroup aggression and competition, fostering coordination, making group decisions, and dealing with intergroup conflict. These heritable group-level adaptations may include means of inculcating others with a set of moral rules (e.g., religion, the practice of monogamy), punishing norm violators and noncooperators, creating roles of leadership and followership, and creating symbolic social identities (e.g., Bowles, 2006; Wilson et al., 2008). Through these mechanisms, within-group selection forces have significantly weakened compared with between-group selection forces, allowing for these group adaptations to spread. One conducive factor to this kind of group selection is the rate and scale of deadly intergroup conflict among ancestral hunter-gatherer societies (Bowles, 2009), which allowed for the emergence of prosocial traits such as altruism, bravery, and heroism toward in-groups as well as aggression and prejudice toward out-groups (the male warrior hypothesis; Van Vugt et al., 2007).

Other researchers (including the other one of us) emphasize that all alleged examples of group selection can be viewed much more effectively from an inclusive fitness perspective (e.g., Barclay, 2010a; Reeve, 2000; West et al., 2011). Group selection is invoked when an act increases the group's fitness but decreases one's reproduction *relative to that group average*. Some things are called "group selection" but are actually directly beneficial because an individual receives a share of whatever public good he/she provides for others (see the different

definitions of "altruism" earlier; see also the section on volunteering); groups are neither necessary nor sufficient for prosocial behavior in such situations. Other situations are called "group selection" when an organism has a stake in the well-being of fellow group members, for example because it benefits from being part of large groups (see "Stake or vested interests" earlier). Finally, other things are called "group selection," which are actually a disguised form of kin altruism because the group members are all descended from recent common ancestors. Because it is often unclear which of these situations is being referred to whenever someone says "group selection," it creates great confusion to lump them together under that banner (Barclay, 2010a; see also West et al., 2011). These three situations involve distinct selective pressures and psychological mechanisms and should thus be kept distinct. Furthermore, these situations usually do not involve group-level adaptations, that is, the adaptation is a heritable property of individuals instead of the group (Gardner & Grafen, 2009). This is not to say that these situations are not interesting; they are all extremely interesting, though for different reasons. Indeed, some of these situations (e.g., stake) have unfortunately been under-researched by inclusive fitness theorists until recently.

Ultimately, the question will be whether it is useful to look at groups as single units when investigating prosocial behavior. This will be decided by whether this perspective tends to generate enough testable and accurate predictions about prosocial behavior that researchers using standard inclusive fitness theory do not generate, and whether it can do so without creating semantic confusion over redefinitions of altruism.

Biological Markets and Competitive Altruism

Humans can choose many of their social partners and leave uncooperative partners if there are better options available (comparison level of alternatives; Kelley & Thibaut, 1978). The presence of partner choice creates a market for social partners (Noë & Hammerstein, 2004, 2005). In such markets, people choose the best partners they can obtain, given their own value in this market. This perspective has implications for the evolution and development of prosocial behavior because it creates a selection pressure for fairness and cooperation. If you are not receiving a "fair" deal then you can simply find someone else who will offer that deal (André & Baumard, 2011; Baumard et al., 2013). In a biological market, the best way to get a good partner is to be a good partner. As long as there are enough opportunities for reputation building or there are costs for being abandoned then this will cause an escalation of prosocial behavior, in a process known as "runaway social selection" (Nesse, 2007) or "competitive altruism" (Barclay, 2004, 2011b; Barclay & Willer, 2007; Hardy & Van Vugt, 2006; Roberts, 1998; Van Vugt & Hardy, 2010).).

The theory of biological markets combines aspects of mutualisms, reciprocity and costly signaling in explaining prosociality. For example, traditional evolutionary perspectives predict that people will be more prosocial when they are being observed, but biological markets go further by predicting that people will be even more generous when competing over access to partners (Barclay & Willer, 2007; Sylwester & Roberts, 2011; Van Vugt & Iredale, 2012); similar results are found in cleaner fish (Bshary & Grutter, 2005). Such competition pays off because high contributors gain status for helping others (Hardy & Van Vugt, 2006), and are more likely to be chosen as partners (Barclay & Willer, 2007) and mates (Barclay, 2010b). In biological markets, prosociality is affected by factors like the supply and demand of different currencies of help, and one's market value and outside options (Barclay & Reeve, 2012; Noë & Hammerstein, 1994, 1995).

Conclusions and Future Directions

Evolutionary psychology is inherently interdisciplinary and draws from all of the behavioral sciences. In addition, by investigating the evolutionary function (this chapter) and phylogenetic history of behavior (e.g., de Waal, this volume), evolutionary approaches help link the behavioral sciences with the natural sciences. By investigating prosocial behavior from all four levels of analysis—proximate psychological mechanisms, individual development, ultimate function, and evolutionary history (phylogeny)—we can get a more complete understanding of the causes of prosocial behavior, and we can use explanations at one level to inform our research on the other levels (Daly, 2011; Van Vugt & Schaller, 2008). Different fields and subdisciplines will simply address different levels. In this chapter, we have focused largely on ultimate function because other authors in this volume have covered the other three levels.

By investigating prosocial behavior at all four levels of analysis, evolutionary psychology is thus a useful framework for uniting all the work on prosocial behavior found in this volume. Rather than being seen as a specific discipline or subdiscipline unto itself, evolutionary psychology should thus been seen as a perspective that can be applied to *any* field or subdiscipline (e.g., Daly, in press). Thus, there can, and should be, evolutionary *social* psychology, evolutionary *cognitive* psychology, evolutionary economics, evolutionary sociology, and so on. We would encourage researchers in all of these areas to incorporate evolutionary thinking into their current disciplines.

Where do we go from here? Evolutionary psychology shows the potential functions of different forms of prosocial behavior and helps to elaborate what neurological, cognitive and emotional mechanisms will underlie them. Nevertheless, there are many remaining questions about how exactly these selection pressures work, how they interact, and how they have shaped our psychology. Here is a list of questions which could shape the future research agenda on prosocial behavior.

1) What is the relative importance of different selective pressures? How do we know if a prosocial act is adaptive? We have presented a number of factors that could select for prosocial sentiment (see Figure 1). No single one of them will explain all prosocial behavior, because different situations call for different behaviors (e.g., helping kin versus friends). Prosocial behavior is not a unitary phenomenon and should not be treated as such (Barclay & Reeve, 2012). Because of this, we need to investigate different situations to see what types of prosocial behavior are best explained by each of the pressures listed. Furthermore, the importance of each selective pressure may vary with time and with socioecological environment (e.g., reputation may be less important in today's large groups, see "Evolutionary Lag"); this variation requires investigation.

2) How do these different selective pressures interact with each other? These pressures are not necessarily mutually exclusive, and more than one may apply in any particular case (e.g., Barclay, 2010a). Some may counteract each other. For example, strict reciprocity is not needed among close kin (Hames, 1987), and it is harder to infer people's cooperative intent from their prosocial behavior if they receive direct benefits from being prosocial (Barclay & Willer, 2007; Mulder et al., 2006). Other pressures may enhance each other, such as when moralistic punishers benefit from raising their group's cooperation and as a result they receive reputational benefits for punishing (Barclay, 2006). We need more theoretical and empirical work on integrating these different selective pressures.

3) What psychological mechanisms would be selected for by each selection force? Throughout this chapter, we have made some comments about the psychologies that each pressure would likely select for (e.g., a vested interest in someone resulting in a genuine concern for their welfare). Some of this work has already been done, but some is still just hypothesized (e.g., empathy as adaption or byproduct of cultural learning). By examining the psychological mechanisms, and their development, we can better integrate across the four levels of analysis.

4) How do the dynamics of reputation-based prosociality work? There are a number of questions here that are still unknown. How do people come to believe that certain acts are prosocial and are thus worthy of reward (Barclay, 2011a; Panchanathan & Boyd, 2004)? How does prosocial behavior come to signal certain traits such as honesty, intelligence, resources, and commitment (Jensen-Campbell et al., 1995; Van Vugt & Iredale, 2012)? What exact traits are being signaled, and when? By answering such questions, it can help us to create reputational systems to support prosocial goals (Barclay, 2011a).

5) Why (and when) is prosocial behavior an honest cue of future cooperative intent? People have an incentive to present themselves as more cooperative than they actually are. Nevertheless, prosocial behavior at time A does appear to predict prosocial behavior at time B, at least under some conditions—this is the basis of an agreeable personality (Graziano et al., 1996). Why and when is there such consistency of behavior across situations, and why are not more people deceptive about their future intent (e.g., Barclay & Willer, 2007)? How is the honesty of such prosocial signals maintained? If honesty is maintained by the cost of being prosocial, then how could it pay off for honestly prosocial people but not pay off for deceptive Machiavellians who are just trying to appear nice? How do other extrinsic incentives undermine the validity of cues of prosociality (e.g., Mulder et al., 2006)? Answering these questions is important for predicting others' behavior and for any reputational system that relies on predicting others' cooperative intent.

6) To what extent is prosociality an in-group phenomenon (shaped by intergroup conflict)? Intergroup conflict gives people a stake in the well-being of group members and changes the scale of

competition. Given the presence of intergroup competition in human history (Bowles, 2009), how has this shaped our prosociality and morality through both genetic and cultural evolution?

7) Why are there individual differences in prosocial behavior? If prosocial behavior is so adaptive, why are not all people prosocial to the same degree? Do these individual differences represent different strategies (e.g., Mealey, 1995), or adaptive responses to differences in costs and benefits for prosociality (Barclay & Reeve, 2012; Diekmann, 1993, Takahashi et al., 2006)? Why and when are there sex differences in prosocial behavior (Balliet et al., 2011)? Evolutionary theory can inform the study of individual differences and their development (e.g., Buss & Greiling, 1990; Sih et al., 2004; Tooby & Cosmides, 1990).

8) Why are there cultural differences in prosocial behavior? How do differences in social and ecological environments result in cultural differences in prosociality? How and why are cultures affected by factors such as market integration (Henrich et al., 2006), group size (Marlowe & Berbesque, 2008), and partner mobility (Barclay, 2011b)? The evolutionary study of cultural differences is a new and exciting field.

Such questions can open up many new lines of research and help clarify why different prosocial sentiments exist, when each one acts, and how and why they are triggered by different situations. Such an understanding would help us understand how to structure situations to increase prosocial behavior (Barclay, 2012a). As such, we look forward to this and other research in the future. Finally, we hope that this outline of evolutionary approaches will inspire other researchers to use evolutionary thinking to inform their understanding of prosociality at all four levels of analysis.

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Notes:

([1]) The term "game" refers to an interaction between multiple parties ("players"), each of whose behaviors affect each other's payoffs. Such "games" are used as simplified models for more complex situations, and are amenable to mathematical and empirical analysis by designating payoffs for different actions and outcomes.

([2]) Inclusive fitness theory is sometimes erroneously called "kin selection." This latter term is potentially misleading because it can cause researchers to forget that inclusive fitness includes benefits to self. Inclusive fitness is the broader term because it equals kin selection (indirect benefits) plus individual selection (direct benefits).

([3]) Instead of a single bell-curve, there may actually be a bimodal distribution with two optima, one for cooperators and one for cheaters (e.g., psychopaths) who persist in low frequencies (Mealey, 1995; Harris et al., 1994). This does not change our basic logic, because there will be deviations from either optimum.

([4]) Proponents of Dual-Inheritance Theory appear to want to distance themselves from any associations with the idea of memes (Richerson & Boyd, 2005; Henrich et al., 2008). We see these theories as having many underlying philosophical similarities despite the superficial differences. Rather than engage in this debate or speculate on its root causes, we will merely state that both theories agree that cultural norms can evolve and can spread even if they do not increase the genetic fitness of their bearers.

([5]) For interested readers, Reeve (2000) gives a very simple mathematical demonstration of why these perspectives are mathematical equivalent.

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