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*“Empathy may be uniquely well suited for bridging the gap between egoism and altruism, since it has the property of transforming another person’s misfortune into one’s own feeling of distress.”*

— (Hoffman, 1981, p. 133)

### Abstract

This chapter reviews the ultimate and proximate levels of analysis on altruism in humans, hoping to create an overarching framework that places each within a larger context that can stimulate human research informed by extensive empirical research in animals. The available neuroscientific evidence will be reviewed at the end, demonstrating consistently that decisions to help are mediated through overlapping decision and reward circuits that integrate emotional and contextual information into a unified somatic state that guides decisions to help. The chapter first defines the important terms, reviews in brief the most common and widely used biological models of altruism, and then provides evidence for these models. After this, the proximate mechanism will be explicated, largely through indirect evidence regarding the motivational and neural circuits thought to underlie decisions to help. The chapter ends with recommendations for future research to provide more direct evidence for the proximate mechanism, using more ecological tasks that elicit altruistic tendencies while being amenable to concurrent recording with neuroscientific tools.

**Keywords:** altruism, empathy, reciprocity, consolation, prosocial behavior, sympathy, cooperation

### Introduction

There has been persistent and intense debate about the nature and even existence of altruism throughout the history of formal academic discourse. For the past half-century, a theoretical tug of war has existed between those who take an ultimate perspective (i.e., focused on function and evolution) and those who view altruism from a proximate perspective (i.e., focused on motivation and intention). The first school focuses on why a behavior evolved over thousands of generations, which depends on its fitness consequences (Dugatkin & Mesterton-Gibbons, 1996;

Koenig, 1988; Trivers, 1971; Wilson, 1997). As such, they have studied the adaptive significance of individuals helping other individuals and assume that all behaviors evolved to serve the performer’s long-term genetic interests, not worrying about whether the behaviors are motivationally altruistic. Even on occasions when personal, genetic interests are not served, biologists construe the behavior as the evolutionary product of self-interest, rendering its performance a “big mistake” or the product of genetic “misfiring.” The second school focuses on the immediate situation that triggers behavior, and



1 the role of learning, physiology, and neural processes—  
2 typically the domain of psychologists. As such, they  
3 have studied emotional-motivation states that  
4 underlie acts of helping, situational and trait factors  
5 that mediate the response, and the development of  
6 prosocial tendencies (Batson, 1998; Eisenberg &  
7 Strayer, 1987; Hoffman, 1981; Zahn-Waxler &  
8 Radke-Yarrow, 1982). Within this school, a large  
9 body of research has examined whether humans are  
10 truly capable of altruism, focusing their efforts on  
11 the plight of the other in the absence of personal  
12 gain or a perception of the self in the other (e.g.,  
13 Batson et al., 1989; Cialdini, Brown, Lewis, Luce,  
14 & Neuberg, 1997).

15 The biological and psychological literatures  
16 appear to study the same topic from conflicting  
17 points of view. In point of fact, there is virtually no  
18 formal discourse between these two literatures; they  
19 represent different interpretations of the term “altru-  
20 ism,” and they investigate different types of prob-  
21 lems. But because they divide along proximate and  
22 ultimate levels of analysis, we view them as largely  
23 complementary. They can and should be used to  
24 inform one another (Mayr, 1961; Tinbergen, 1963).  
25 Indeed, the empirical evidence points to a contin-  
26 uum between nonhuman and human acts of altru-  
27 ism, with similar findings in each. For example,  
28 across mammals, acts of altruistic giving are directed  
29 most often to relatives, friends, and helpless others  
30 in need, particularly in response to a salient cue of  
31 need and in the context of a positive social bond. To  
32 demonstrate this continuity across species, consider  
33 the following examples:

34 A juvenile vampire bat, not yet experienced at  
35 foraging, is starving and without help will not survive  
36 until the next day. The juvenile approaches a  
37 successful adult forager who is familiar to the juvenile  
38 through a social bond with his mother. The juvenile  
39 grooms the unrelated adult on the stomach and licks  
40 her face. In turn, she regurgitates a meal of blood for  
41 the young individual in need, enough for it to survive  
42 until the next day (Wilkinson, 1990).

43 Rhesus monkeys trained to pull chains for differential  
44 rewards discover that pulling the more rewarding  
45 chain causes another monkey to be shocked. After  
46 witnessing this shock, two-thirds of the subjects  
47 prefer the nonshock chain, receiving half as many  
48 rewards. Of the remaining third, one stops pulling  
49 the chains altogether for 5 days and another for 12  
50 days, starving themselves to avoid shocking another  
51 monkey (Masserman, Wechkin, & Terris, 1964).

52 A 3-year old boy, walking along the edge of the  
53 gorilla enclosure at the Brookfield Zoo, falls 18 feet  
54 onto the concrete enclosure floor. Binti Jua, a female  
55 gorilla caring for her baby, picks up the unconscious  
56 boy in her arms and rocks him as she carries him to  
57 and places him next to an access door where he is  
58 retrieved by zookeepers and paramedics (BBC h2g2  
59 contributors, December 30, 2005).

60 Michael Keenan is celebrating Christmas Eve with  
61 a friend at a San Francisco yacht club when he  
62 witnesses a car plunge into the Bay. He grabs a  
63 wrench, dives into the cold water, breaks the back  
64 window and pulls one woman to safety. Six years  
65 later, he dies after returning to a burning building to  
66 save a dog for whom he was pet sitting (Allday, 2007).

67 The altruism literature holds many such striking  
68 similarities across cases, from widely varying taxa,  
69 looking at both anecdotal and experimental evi-  
70 dence. For obvious reasons, there exists hardly any  
71 systematic research on costly altruism in both  
72 humans and other animals but, increasingly, stud-  
73 ies address and report striking examples of low-  
74 cost altruism. Prominent similarities include the  
75 role of visible distress or need, a social bond, favors  
76 exchanged for other favors, and a requirement that  
77 the giver understand the appropriate response to the  
78 other’s state or situation. Thus, although little work  
79 has directly investigated the proximate mechanisms  
80 of altruism in humans, cross-species similarities  
81 offer a window into the mechanism.

82 This volume is dedicated to the social neurosci-  
83 ences, and thus deals largely with proximate mecha-  
84 nisms; however, the neuroscientific literature on  
85 altruism per se in humans is limited (excluding stud-  
86 ies of empathy, covered in other chapters in this  
87 volume). As such, this chapter will review the ulti-  
88 mate and proximate levels of analysis equally, hoping  
89 to create an overarching framework that places each  
90 within a larger context that can spur human research  
91 that is informed by extensive empirical research in  
92 animals. The available neuroscientific evidence will  
93 be reviewed at the end, demonstrating consistently  
94 that decisions to help are mediated through overlap-  
95 ping decision and reward circuits that integrate emo-  
96 tional and contextual information into a unified  
97 somatic state that guides decisions to help.

98 We first define the important terms, review in  
99 brief the most common and widely-used biological  
100 models of altruism and then provide evidence for  
101 these models. After this, the proximate mechanism  
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3 with recommendations for future research to pro-  
4 vide more direct evidence for the proximate mecha-  
5 nism, using more ecological tasks that elicit altruistic  
6 tendencies while being amenable to concurrent  
7 recording with neuroscientific tools.

## 8 Terminology

9 Some have claimed that humans are the only truly  
10 altruistic species (e.g., Dawkins, 1976/2006; Fehr  
11 & Fischbacher, 2003; Kagan, 2000; Silk et al.,  
12 2005), while on the other hand, the vast majority of  
13 empirical work on altruism examines the behavior  
14 of animals, particularly nonmammals such as euso-  
15 cial insects and birds, but also mammals (reviewed  
16 by Dugatkin, 1997; Gadagkar, 1997). Underlying  
17 this paradox is a differential focus on the level of  
18 analysis. These perspectives can be united by separ-  
19 ating the term altruism into three overlapping types  
20 (cf. Sober & Wilson, 1998).

21 *Evolutionary altruism* makes no assumptions  
22 about motivations or intentions, and considers only  
23 effects; it refers to behavior that benefits the recipi-  
24 ent at a cost to the actor. This kind of altruism is  
25 widespread, including honeybee attacks of intruders  
26 to the hive and alarm calls by birds and ground  
27 squirrels that alert conspecifics to danger. The vast  
28 majority of animal research on altruism refers to this  
29 level of analysis, which focuses on the *function* of  
30 behavior. These studies are aimed at answering the  
31 question: “How did this behavior evolve, assuming  
32 that evolution favors behavior that benefits the indi-  
33 vidual and its close kin, promoting replication of  
34 the genes responsible for the behavior?”

35 On the other hand, *psychological altruism* is a  
36 reaction to the signals and situation of another indi-  
37 vidual and involves an attempt to alleviate the oth-  
38 er’s negative state. It is motivated by other-directed  
39 emotions, such as nurturance or empathy, without  
40 necessarily requiring a full awareness of the effect  
41 on the other. This kind of altruism is common in  
42 mammalian species, such as monkeys who cease  
43 to pull food chains to avoid shocking a conspecific  
44 (Masserman et al., 1964), and chimpanzees who  
45 approach and console a distressed friend with an  
46 embrace (de Waal & Aureli, 1996). Most of the  
47 human work on empathy and altruism is aimed at  
48 this middle level of analysis, which focuses on the  
49 *motivation* or *causation* of the act of giving. These  
50 studies typically aim to answer the question: “What  
51 is the psychological state of an individual that  
52 reaches out to help? Are they stressed and annoyed,

53 seeking simply to terminate the other’s display or  
54 do they truly feel compassion and sympathy for the  
55 other?” Thus, when one asks if an act is either “truly  
56 altruistic” or “selfish” it is the motivation that is  
57 at issue. Those who study evolutionary altruism do  
58 not need to know what is in the mind of the giver;  
59 they simply want to demonstrate that the behav-  
60 ior has potential benefits to the giver’s reproductive  
61 success.

62 One kind of psychological altruism that goes  
63 beyond other-directed motivation is *intentional*  
64 *altruism*. This is a rare form that rests on an appre-  
65 ciation of how one’s behavior benefits the other and  
66 requires knowledge of one’s behavioral impact upon  
67 others. Intentional altruism is tailored to the other’s  
68 specific situation, such as when dolphins save com-  
69 panions by biting through harpoon lines or hauling  
70 them out of nets in which they got entangled  
71 (Caldwell & Caldwell, 1966). Such so-called “tar-  
72 geted helping” requires perspective-taking, which  
73 may be limited to a few large-brained animals  
74 (de Waal, 2008). Most human research assumes  
75 intentional altruism, but rarely demonstrates this  
76 level, having simply measured whether helping  
77 occurred or the extent of helping, not the type  
78 or the degree to which it is tailored to the other’s  
79 situation.

80 With a framework that separates altruism into its  
81 component levels of analysis, we assume that altru-  
82 ism evolved because acts of helping, on average and  
83 in the long run, return benefits to the giver or its  
84 close relatives. Therefore, we do not require that an  
85 act has no possible benefits to the self in order to be  
86 construed as altruism. We thus define altruism as  
87 *any instance where one individual helps another, in*  
88 *the absence of any clear, immediate benefit to the self,*  
89 *even though such behavior may ultimately be to the*  
90 *giver’s evolutionary advantage.*

91 *Empathy.* In human research, empathy and altru-  
92 ism overlap considerably in their usage and concep-  
93 tualization. This makes sense, given a multi-level  
94 model where the observer’s resonating state moti-  
95 vates them to give. For example, the most extensive  
96 work investigating empathy and altruism in humans  
97 proposes that we are indeed capable of true altru-  
98 ism, because witnessing the distress of a relatable  
99 target elicits an emotional state called “empathic  
100 concern” (akin to sympathetic, softhearted compas-  
101 sion for the other), which is focused on the other  
102 and predisposes helping (Batson, 1986; Batson &  
103 Coke, 1981).

104 The definition of empathy is itself a topic of  
105 debate that has been covered in other treatments

1 (Preston & de Waal, 2002; Wispé, 1986) and will  
2 be addressed elsewhere in this volume. According  
3 to most researchers, *empathy* (sometimes called  
4 “*emotional empathy*”) occurs when the emotional  
5 state of the observer results from perceiving the state  
6 of the object, and generates a state in the subject  
7 more applicable to the object’s situation than the  
8 subject’s own prior state or situation (cf. Hoffman,  
9 2000). More cognitive forms of empathy, where the  
10 subject actively imagines him or herself in the posi-  
11 tion of the other, is usually referred to as *cognitive*  
12 *empathy* or *perspective taking*, while feeling sorry for  
13 the subject and wanting to alleviate their distress is  
14 usually referred to as *sympathy*. People disagree as to  
15 whether empathy or sympathy can exist without a  
16 concurrent desire to help the other. In this chapter,  
17 we assume that empathy and sympathy are emo-  
18 tional and motivational states that predispose help-  
19 ing, but reserve the terms *altruism* or *prosocial*  
20 *behavior* to refer specifically to acts of helping.

### 21 **Biological Models of Altruism**

22 According to *kin selection theory* one helps another  
23 in accordance with shared genetic relatedness; that  
24 is, by helping an individual who is related to you,  
25 you in turn increase the success of your own genes  
26 insofar as they are represented in the other, also  
27 known as *inclusive fitness* (Hamilton, 1964). This  
28 theory predicts that helping scales with the degree  
29 of relatedness, with more risky and costly aid being  
30 administered to closer relatives.

31 According to *reciprocal altruism theory* (Trivers,  
32 1971), helping even non-kin is adaptive if it results  
33 in a future reciprocation of help by the original  
34 recipient. Reciprocal altruism predicts, in distinc-  
35 tion to kin selection, that help will be given even  
36 to unrelated individuals who are likely to return  
37 the favor in the future, such as close friends, group  
38 members, and trusted individuals. Using game-the-  
39 oretic models, reciprocal benefit has been demon-  
40 strated to be an evolutionary stable strategy (ESS;  
41 Maynard Smith, 1964) even in relatively asocial  
42 environments (Axelrod, 1984).

43 *Group selection* takes direct advantage of the nat-  
44 ural division of social species into separate popula-  
45 tions and colonies, postulating that it is adaptive to  
46 help individuals from one’s own population, because  
47 the success of group members raises the success of  
48 the entire group relative to other groups, conferring  
49 genetic success to all members (Darwin, 1871/1982;  
50 Wilson, 1975, 1997; Wilson & Sober, 1994;  
51 Wilson, 2005). Most biologists, however, regard  
52 group selection as a variant of kin selection that

only applies to genetically isolated populations, 53  
which is a rare condition in our close relatives, the 54  
primates (Lehmann, Keller, West, & Roze, 2007). 55

### Origins of Altruism 56

Emotional states such as empathy and sympathy 57  
may have evolved because of the selection pres- 58  
sure to evolve rapid emotional connectedness in 59  
the context of parental care, long before our species 60  
appeared (Eibl-Eibesfeldt, 1971/1974; MacLean, 61  
1985). During mammalian evolution, females alert 62  
to and affected by their offspring’s needs likely 63  
out-reproduced those who remained indifferent. 64  
Signaling their state through smiling and crying, 65  
human infants urge their caregiver to pay attention 66  
and come into action (Acebo & Thoman, 1995; 67  
Bowlby, 1958). Essentially the same mechanisms 68  
operate in all mammals. Having descended from a 69  
long line of mothers who nursed, fed, cleaned, car- 70  
ried, comforted, and defended their young, we 71  
should not be surprised by gender differences in 72  
human empathy, which appear well before socializa- 73  
tion (Hoffman, 1978). The same sex difference is 74  
found in the second year of life, with girls showing 75  
more concern for others than boys (Zahn-Waxler, 76  
Radke-Yarrow, Wagner, & Chapman, 1992). The 77  
literature on adult gender differences is more equiv- 78  
ocal, but women are better readers of subtle affec- 79  
tive cues than men (Hall, 1978) and report stronger 80  
empathic reactions (Eisenberg & Fabes, 1998). 81  
Moreover, a recent neuroimaging study found that 82  
females were more cooperative than males, associ- 83  
ated with greater grey matter volume in multiple 84  
regions involved in social cognition including pos- 85  
terior inferior frontal and left anterior medial pre- 86  
frontal cortices (Yamasue et al., 2008). 87

88 The complexity and variety of needs a mamma- 88  
lian mother must accommodate would make a 89  
genetically encapsulated, reflex-like system for 90  
caring difficult. Conversely, a system where mothers 91  
are directly affected by offspring distress, and are 92  
subsequently motivated to help, is adaptive and can 93  
be built upon pre-existing perception-action mech- 94  
anisms in the nervous system. Thus, infants and off- 95  
spring in need cry, whine, and scream, which in 96  
turn creates empathic distress or sympathy in the 97  
mother, who becomes motivated to both terminate 98  
the distress and provide the necessary care to soothe 99  
the offspring. While some aspects of this model are 100  
specific to a “perception-action model” (PAM) of 101  
empathy (Preston & de Waal, 2002), most of 102  
the primary elements are shared across models. For 103  
example, mirror-neuron theories of empathy also 104

1 emphasize the fact that the nervous system is  
2 designed to automatically activate the other's state  
3 in the perceiver (Gallese, 2001) and developmental  
4 theories of attachment, bonding, and social behav-  
5 ior (e.g., Sroufe, 1988; Ungerer, 1990; Zahn-Waxler,  
6 Radke-Yarrow, & King, 1979) as well as biological  
7 theories of altruism (e.g., de Waal, 2008; Eibl-  
8 Eibesfeldt, 1971/1974; Hirata, 2009) emphasize  
9 the importance of the mother-offspring bond in  
10 developing compassionate, prosocial behavior.  
11 Thus, models of empathy and altruism generally  
12 agree that helping is motivated by positive, other-  
13 regarding emotional states that evolved in the con-  
14 text of the mother-offspring bond (for an extensive  
15 treatment see Hrdy, 2009).

16 Once the empathic capacity evolved, it could of  
17 course be applied outside of the parental-care con-  
18 text and play a role in the wider network of social  
19 relationships typical of group-living animals. Here  
20 too, caring responses have high survival value. For  
21 example, primates often lick and clean each other's  
22 wounds. This form of allogrooming is so critical for  
23 healing that adult male macaques often temporarily  
24 return to their native group to receive the service  
25 (Dittus & Ratnayeke, 1989). Empathy and altruism  
26 are not necessarily bound by the original context in  
27 which they evolved, however, because the tendency  
28 to help has gained "motivational autonomy" in that  
29 one can experience empathy and want to help in  
30 cases far removed from the original context, inde-  
31 pendent from the ultimate goal of increasing fitness  
32 (de Waal, 2008).

### 33 **Animal Evidence for Altruism**

34 Altruistic behavior is found across the animal king-  
35 dom, including insects, fish, birds, and mammals.  
36 Most research has been directed at investigating the  
37 extent to which kin selection and/or reciprocal  
38 altruism can explain the existence of altruistic or  
39 cooperative behavior. The vast majority of such  
40 examples involve predator detection and defense,  
41 offspring care, foraging, and grooming, demonstrat-  
42 ing that altruistic giving most often evolves to sub-  
43 serve behaviors that are advantageous, but difficult  
44 for a single individual to achieve.

45 For example, Belding's ground squirrels give  
46 alarm calls which are costly to the individual who  
47 attracts attention to himself, but beneficial to neigh-  
48 boring animals, who receive advance notice of the  
49 approaching predator. Supporting the role of kin  
50 selection, such calls occur more often when the sur-  
51 rounding animals are related than when they are not  
52 (e.g., Sherman, 1977). Subordinate individuals in

53 naked mole-rat colonies contribute greatly to the  
54 maintenance and defense of the colony even though  
55 they do not themselves reproduce (e.g., Lacey &  
56 Sherman, 1991). This feature of the colony increases  
57 the reproductive success of queens and the survival  
58 of the colony, and is thought to be due to an extremely  
59 high average relatedness among colony members  
60 (Jarvis, O'Riain, Bennett, & Sherman, 1994; Reeve,  
61 Westneat, Noon, Sherman, & Aquadro, 1990),  
62 again indicating a role for kin selection. There are  
63 many examples of inclusive fitness in birds, in which  
64 "helpers at the nest" are common, with female off-  
65 spring helping to care for siblings rather than them-  
66 selves mating (Stacey & Koenig, 1990).

67 Evidence for reciprocal altruism also tends to  
68 focus on two forms, defense and food procurement.  
69 For example, Pied wagtail birds allow intruder con-  
70 specific to forage in their territories in exchange for  
71 cooperation in defense of the region (Davies &  
72 Houston, 1981). Guppies cooperatively engage in  
73 "predator inspection," alternating turns to move  
74 closer to a potentially dangerous source (Pitcher,  
75 1992) and multiple unrelated queens in colonies of  
76 seed harvester ants (*Messor pergandei*) cooperate,  
77 which in turn increases the success of brood raiding  
78 (Pollock & Rissing, 1989; Rissing & Pollock,  
79 1987).

80 In primates, support during aggressive encoun-  
81 ters is the most common form of collaboration, often  
82 performed on behalf of close kin, but also distrib-  
83 uted reciprocally among nonrelatives. Chimpanzees  
84 show evidence for so-called calculated reciprocity,  
85 that is, reciprocal exchange of favors based on  
86 mental record keeping of previous events. For exam-  
87 ple, chimpanzees have been shown to support each  
88 other reciprocally in fights (de Waal & Luttrell,  
89 1988) and to exchange services even after delays in  
90 time (de Waal, 1997b; Koyama, Caws, & Aureli,  
91 2006b). In contrast to claims in the literature that  
92 humans are the only primates to extensively cooper-  
93 ate with nonrelatives, recent testing of DNA sam-  
94 ples from wild chimpanzees has confirmed a high  
95 frequency of collaborative partnerships between  
96 unrelated individuals (Langergraber, Mitani, &  
97 Vigilant, 2007). Reciprocity is a rapidly growing  
98 topic in and of itself, particularly in animal cogni-  
99 tion, and has been extensively studied in primates in  
100 particular (Brosnan & de Waal, 2002; de Waal &  
101 Brosnan, 2006; de Waal & Berger, 2000; Hauser,  
102 McAuliffe, & Blake, 2009).

103 It is widely agreed that kin selection and reciproc-  
104 al altruism can, and likely do, act in concert with  
105 each other, with maximal reinforcement in small

1 groups where one tends to be surrounded by indi- 53  
2 viduals who are either related or close friends with 54  
3 multiple, long-term opportunities for giving and 55  
4 receiving (e.g., Brown & Brown, 2006; Preston 56  
5 & de Waal, 2002). A recent study set out to deter- 57  
6 mine if chimpanzee helping occurs outside of recip- 58  
7 rocal altruism by creating situations with unfamiliar 59  
8 individuals and in the absence of return rewards. 60  
9 Chimpanzees spontaneously assisted humans regard- 61  
10 less of whether doing so yielded a reward, or not, 62  
11 and were also willing to help fellow chimpanzees 63  
12 reach a room with food. One would assume that 64  
13 rewards, even if not strictly necessary, would at least 65  
14 stimulate helping; but in fact, rewards seemed to 66  
15 have no impact on the giving in this study. Since the 67  
16 decision to help did not seem to be based on a self- 68  
17 focused cost/benefit calculation, it may have been 69  
18 genuinely other-oriented at the motivational level 70  
19 (Warneken, Hare, Melis, Hanus, & Tomasello, 71  
20 2007).

21 Recent studies further demonstrated spontane- 72  
22 ous helping in marmosets (Burkart, Fehr, Efferson, 73  
23 & van Schaik, 2007) and capuchin monkeys. In the 74  
24 latter study, two monkeys were placed side by side 75  
25 in separate enclosures in full view of one another. 76  
26 One monkey could barter with small plastic tokens, 77  
27 exchanging them for food. Two differently colored 78  
28 tokens were used, with different consequences: one 79  
29 was “selfish,” the other “prosocial.” If the bartering 80  
30 monkey picked the selfish token, it could receive 81  
31 a small piece of apple upon exchange, but the part- 82  
32 ner got nothing. The prosocial token rewarded 83  
33 both monkeys equally. The bartering monkey was 84  
34 rewarded either way, so the only difference was in 85  
35 the partner’s receipt of a reward. The stronger the 86  
36 social tie between partners, the more the bartering 87  
37 monkey would select the prosocial token. The pro- 88  
38 cedures were repeated many times with differ- 89  
39 ent social combinations and sets of tokens, and the 90  
40 prosocial behavior persisted. Their choices could 91  
41 not be explained by fear of punishment, because the 92  
42 dominant monkey consistently proved to be the 93  
43 most prosocial (de Waal, Luttrell, & Canfield, 94  
44 1993). Similar results on capuchin monkeys have 95  
45 been obtained by Lakshminarayanan and Santos 96  
46 (2008).

### 47 **Exchanges Involving Food** 48 **Sharing and Grooming**

49 One of the most common ways to investigate altru- 100  
50 ism and reciprocity in animals is to study food-sharing 101  
51 among non-kin. There is an extensive literature on 102  
52 food sharing and its relation to altruism, which is 103

beyond the scope of this paper (Brosnan & de Waal, 53  
2002; de Waal, 1989; de Waal, 1997b; Kaplan & 54  
Hill, 1985; Moore, 1984). Importantly, food shar- 55  
ing with non-kin has been observed in many mam- 56  
mals including vampire bats (Wilkinson, 1988), 57  
lions (Pusey & Packer, 1997), chimpanzees (e.g., de 58  
Waal, 1989; Goodall, 1963; Teleki, 1973), bonobos 59  
(Hohmann & Fruth, 1993), and New World capu- 60  
chin monkeys (e.g., de Waal, 1997a; Perry & Rose, 61  
1994). Such food sharing has been specifically found 62  
to be reciprocal (with individuals sharing with those 63  
who have shared with them in the recent past) 64  
in vampire bats (Wilkinson, 1984), chimpanzees 65  
(de Waal, 1989; de Waal, 1997b), and capuchin 66  
monkeys (de Waal, 2000a). 67

Allogrooming is also considered an altruistic act 68  
since grooming another is risky for the giver, who is 69  
necessarily rendered less vigilant (Maestriperi, 70  
1993; Mooring & Hart, 1995). Conversely, groom- 71  
ing is highly beneficial for the recipient, reducing 72  
many key physiological variables including stress 73  
and tension (Schino, Scucchi, Maestriperi, & 74  
Turillazzi, 1988), allostatic load (Liu et al., 1997), 75  
damaging ticks (Hart, 1990; Mooring, McKenzie, 76  
& Hart, 1996), heart rate (Aureli, Preston, & de 77  
Waal, 1999; Boccia, Reite, & Laudenslager, 1989; 78  
Feh & de Mazières, 1993; Smith, Astley, Chesney, 79  
Taylor, & Spelman, 1986), and increasing beta-en- 80  
dorphins (Keveme, Martensz, & Tuite, 1989). 81  
Allogrooming is reciprocally distributed, with indi- 82  
viduals grooming those who previously groomed 83  
them (even among non-kin), in mice (Stopka & 84  
Graciasova, 2001), impala (Hart & Hart, 1992; 85  
Mooring & Hart, 1997), macaques (Manson, David 86  
Navarrete, Silk, & Perry, 2004) capuchin monkeys 87  
(Manson et al., 2004), and baboons (Henzi & 88  
Barrett, 1999; Silk, Seyfarth, & Cheney, 1999). 89

Allogrooming in particular seems to be a useful 90  
biological economy for animals (Henzi & Barrett, 91  
1999), as it has been proven not only to increase the 92  
receipt of grooming, but to influence the future 93  
likelihood of agonistic support (Hemelrijk, 1994; 94  
Koyama, Caws, & Aureli, 2006a; Seyfarth & 95  
Cheney, 1984), food sharing (de Waal, 1982; de 96  
Waal, 1997b; Koyama et al., 2006a), and sex (Stopka 97  
& Graciasova, 2001; Stopka & Macdonald, 1999). 98

Importantly, descriptions of food sharing bear a 99  
remarkable similarity to each other, with data from 100  
vampire bats (Wilkinson, 1984, 1990), capuchin 101  
monkeys, and chimpanzees (Brosnan & de Waal, 102  
2002; de Waal, 1997b) all involving a particular 103  
form of exchange whereby individuals share food 104  
with others who have previously groomed them. 105

1 For example, in a study with captive chimpan-  
2 zees, with a sample of 200 food trials and 6,972  
3 approaches to the individual endowed with a shar-  
4 able leafy branch, previous grooming increased the  
5 probability of sharing and the few examples of hos-  
6 tile reactions to requests were directed at beggars that  
7 had not previously groomed the food possessor. In  
8 this sample, grooming was separated from food shar-  
9 ing by at least two hours and was specific to the indi-  
10 vidual who did the grooming, not being explainable  
11 by a general positive mood effect (de Waal, 1997b).

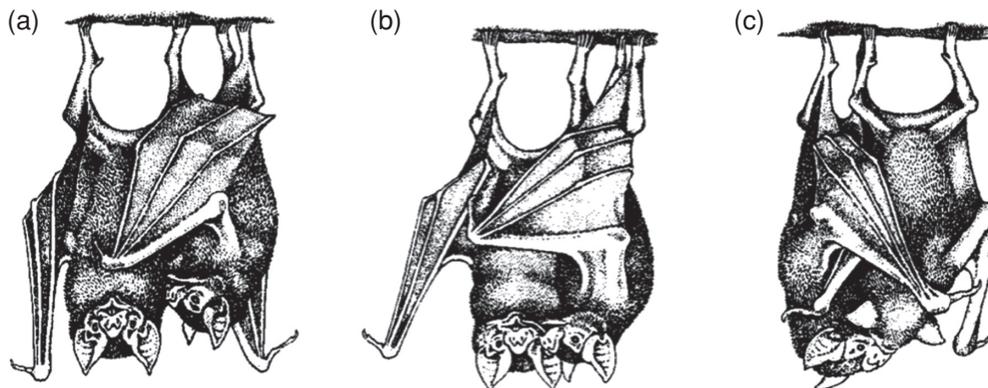
12 In studies with vampire bats, the probability of  
13 sharing can be more strictly tied to the costs and  
14 benefits of the act, with giving being greater for kin  
15 and familiar individuals, but also demonstrating  
16 reciprocity and being scaled, in a cost-benefit fash-  
17 ion, to the level of need of the recipient and the  
18 food supply of the giver. As with the descriptions  
19 of food sharing in chimpanzees and capuchin mon-  
20 keys, food sharing in vampire bats almost always  
21 involves an older, more experienced forager shar-  
22 ing food with a younger, less-experienced forager,  
23 after the young individual has approached and  
24 groomed the older (Wilkinson, 1984, 1986, 1990;  
25 Figure 38.1).

## 26 Consolation Behavior

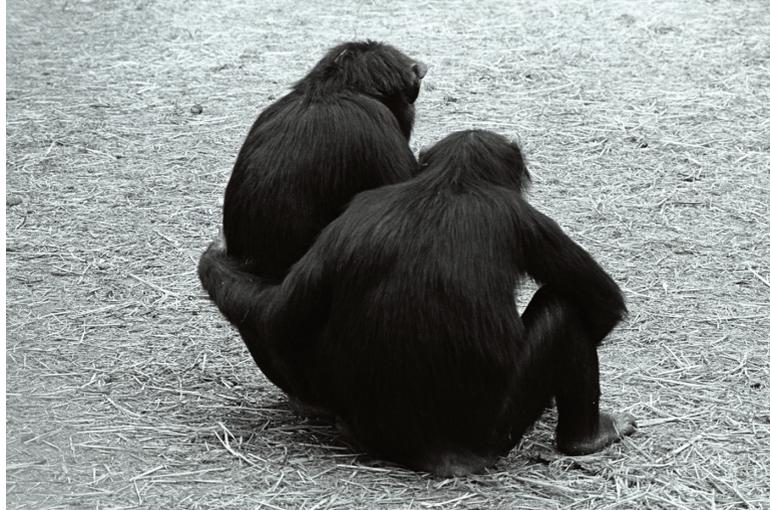
27 When one individual is distressed, the most common  
28 and oftentimes most necessary act of helping is to  
29 simply approach the distressed other and provide  
30 emotional support and soothing; this in turn reduces  
31 the other's distress as well as the associated negative  
32 attention. The development of concern and consola-  
33 tion was extensively studied in humans, looking at

34 children's reactions to distressed family members  
35 in the home, through direct recording of behavior  
36 and indirectly through questionnaires (Zahn-Waxler  
37 et al., 1992). In these studies, they found that  
38 almost all children exhibited some form of prosocial  
39 responding to another's distress as early as one  
40 year (hugging, patting), by 18 months most showed  
41 a full repertoire of prosocial actions, and by two years  
42 nearly all children responded prosocially. Empathy  
43 and helping differed for caused than observed dis-  
44 tress in expected ways, with caused distress involving  
45 more aggression, positive affect, and less hypothesis-  
46 testing. Supporting presumed gender differences,  
47 girls showed more empathic concern than boys, but  
48 only for naturally occurring observed distress, and  
49 they also showed more self-referential behavior (e.g.,  
50 patting one's own arm when the other's arm is hurt)  
51 at 18 months. Interestingly, within individuals,  
52 prosocial behavior at 18 months was more associ-  
53 ated with hypothesis testing than empathic concern  
54 and empathic concern with self-referential behavior,  
55 likely reflecting the different demands of helping  
56 and feeling with another; by two years, the four  
57 measures were all highly intercorrelated, supporting  
58 empathy-altruism models more generally (Batson &  
59 Coke, 1981; Hoffman, 2000).

60 In animal research, similar behavior has become  
61 known as "consolation," defined as a reassuring behav-  
62 ior by an uninvolved bystander towards one of the  
63 combatants in a previous aggressive incident (de  
64 Waal & van Roosmalen, 1979). For example, a third  
65 party approaches the loser of a fight and gently puts  
66 an arm around his or her shoulders (Figure 38.2).  
67 De Waal and van Roosmalen (1979) analyzed



**Fig. 38.1** Depiction of food-sharing between roost-mate vampire bats, a form of reciprocal altruism. During a typical sequence of events, the hungry bat would solicit a meal of regurgitated blood from a more successful roost-mate by first licking the potential donor under her wing (a) and then by licking the donor's lips (b). In turn, the receptive donor (most likely a close relative or social affiliate) would regurgitate blood into the recipient's mouth (c), greatly increasing their likelihood of survival until the next day. Reproduced from Wilkinson, 1990, with permission of Scientific American and www.patriciawynne.com.



**Fig. 38.2** There has been a tendency in the literature to emphasize the competitive and aggressive side of chimpanzees, but our close relatives also often show altruistic and affectionate behavior, such as here a female with her daughter apprehensively watching a fight among others.

Photograph by Frans de Waal.

1 hundreds of post-conflict observations of consolation  
 2 tion in chimpanzees, and a replication by de Waal  
 3 and Aureli (de Waal & Aureli, 1996) included an  
 4 even larger sample, strongly suggesting that consolation  
 5 is indeed distress alleviating.

6 Subsequent studies have confirmed consolation in  
 7 chimpanzees, gorillas, and bonobos (Cordoni, Palagi,  
 8 & Tarli, 2006; Fuentes, Malone, Sanz, Matheson, &  
 9 Vaughan, 2002; Palagi, Cordoni, & Borgognini,  
 10 2006; Palagi, Paoli, & Borgognini, 2004; Mallavarapu,  
 11 Stoinski, Bloomsmith, & Maple, 2006), but it has  
 12 not been found in monkeys despite extensive attempts  
 13 using the same procedures (de Waal & Aureli, 1996;  
 14 Watts, Colmenares, & Arnold, 2000). This is surprising  
 15 as species after species of monkey does exhibit  
 16 reconciliation (i.e., friendly reunions between former  
 17 opponents) (de Waal, 2000b). The consolation gap  
 18 between monkeys and the Hominoidea extends even  
 19 to the one situation where consolation is most  
 20 expected: Macaque mothers fail to reassure their  
 21 offspring who have lost a fight (Schino, Geminiani,  
 22 Rosati, & Aureli, 2004). O'Connell's (1995) content  
 23 analysis of over 2,000 anecdotal reports of non-  
 24 human primate empathy confirmed that comforting  
 25 responses to the emotional state of others are typical  
 26 of apes but rare in monkeys. Thus, the evidence suggests  
 27 that apes are affected by the emotions of others and  
 28 take action to reduce the target's distress. The data  
 29 on consolation suggest that apes evaluate the emotions  
 30 and situations of others with a greater understanding  
 31 than most other nonhuman animals,

but more research is needed to determine the extent  
 to which ape consolation is actually similar to  
 human consolation.

Recent studies have also investigated the physiological  
 effects of consolation. An initial report documented  
 no stress-reducing effect of consolation (Koski &  
 Sterck, 2007), but a more detailed follow-up study  
 found that recipients reduced self-directed behavior  
 (e.g., self-scratching), a behavioral response  
 commonly associated with anxiety (Maestripieri,  
 Schino, Aureli, & Troisi, 1992), leaving the authors  
 to conclude that consolation is beneficial to the  
 other (Fraser, Stahl, & Aureli, 2008). Since this  
 behavior also occurs mostly in reaction to distress  
 signals, it most closely resembles empathy-induced  
 altruism in humans.

### Proximate Mechanisms

The above review of the animal literature reveals  
 that examples of altruism from across the animal  
 kingdom support the ultimate-level models, such  
 as kin selection and reciprocal altruism. But can  
 these examples inform the proximate mechanisms  
 of altruism? Some of the aforementioned forms  
 of altruism appear to be relatively specific to the  
 species and its ecology and, thus, are more likely  
 to involve specific adaptations that are restricted  
 to *evolutionary altruism* and not homologous with  
 human giving, empathy, or sympathy.

For example, extensive research on allogrooming  
 in impala suggests that this cooperative behavior

1 does not reflect a general economy of exchange, but  
2 rather is a specific adaptation for removing ticks,  
3 which exists across dyads, is dependent on season,  
4 body size, and habitat, is always traded for groom-  
5 ing, and is visible from the first days of life (Mooring,  
6 Blumstein, & Stoner, 2004). Research on coopera-  
7 tion among colony members in eusocial species such  
8 as hymenoptera and the naked mole-rat suggests  
9 that their particular form of cooperation is restricted  
10 to colony members with a high degree of interrelat-  
11 edness, owing to their haplo-diploid genetic struc-  
12 ture. Such examples likely reflect an independent  
13 evolution of cooperative behavior within species, to  
14 solve particular ecological problems.

15 At a functional and neuroanatomic level, it is not  
16 expected that neural mechanisms underlying altru-  
17 ism in solitary fish and eusocial insects will bear much  
18 resemblance to that of social, diploid mammals, such  
19 as rodents, nonhuman primates, and humans. In  
20 addition, it seems that the types of altruistic giving  
21 that receive the most attention in primate and  
22 human behavior are those that are flexible, inter-  
23 changeable across various forms of giving, socially  
24 embedded, and the result of a decision to help  
25 (implicit or explicit), rather than a biological desti-  
26 ny. Thus, in explicating the proximate mechanism  
27 of altruism in humans, we will focus on data from  
28 social mammals that depict flexible, interchange-  
29 able giving at the level of *psychological altruism*.

### 30 Emotions Guide Decisions to Help

31 Traditional models of altruism, similar to classical  
32 models of decision making, assumed that decisions  
33 are made through rational comparative processes  
34 that explicitly integrate pros and cons, taking into  
35 account remembered past events and projections of  
36 future outcomes. When computed explicitly, this  
37 process is relatively inefficient and slow, but does  
38 accord with the common belief that true decision  
39 making is restricted to intentional choice and  
40 restricted to humans. The overt weighting of costs  
41 and benefits surely does occur, but its contribution  
42 to behavior is probably overstated due to its dispro-  
43 portional availability in consciousness (Nisbett &  
44 Wilson, 1977).

45 The research reviewed above and current models  
46 of decision making highlight an alternative to the  
47 explicit, comparative approach. Consider the exam-  
48 ples of animal altruism given above. Almost all  
49 involve a conspecific recipient with greater need  
50 (due to age, rank, foraging skill) given access to a  
51 valued resource (food, grooming, coalitionary sup-  
52 port) from a group member that is socially bonded

and previously groomed or supported the potential  
53 giver. The important role of kin and friends, social  
54 bonding, and prior acts of social support and  
55 grooming imply a role for affectively driven cues  
56 that do not require explicit calculation. For exam-  
57 ple, we know that grooming and interpersonal  
58 touch are positive, relaxing experiences for the  
59 recipient (Aureli et al., 1999; Feh & de Mazières,  
60 1993; Kalin, Shelton, & Lynn, 1995) that predis-  
61 pose future giving, even in a different modality (e.g.,  
62 food). We also know from work on empathic emo-  
63 tion that similarity, familiarity, social closeness, and  
64 positive experience with the other strengthen the  
65 empathic response across species, which is known to  
66 increase the likelihood of helping (vide Table 1 in  
67 Preston & de Waal, 2002). This is consistent with  
68 the social relationships in which biologists expect  
69 altruism to occur, which are those between close  
70 relatives and potential reciprocators. Negative social  
71 relationships or competitive situations, on the other  
72 hand, can produce counter-empathy, or *schaden-*  
73 *freude* (e.g., Smith et al., 1996; Takahashi et al.,  
74 2009). The empathy mechanism is therefore biased  
75 precisely the way that one would expect from an  
76 evolutionary perspective (de Waal, 2008). Thus,  
77 decisions to help must at least be influenced by posi-  
78 tive associations with the target. While this affect-  
79 ive information could be represented explicitly at  
80 the time of the decision in the mind of the giver, all  
81 of the data on decision processes in neuroscience  
82 and human decision-making indicate that it need  
83 not be.  
84

85 For example, the “risk as feelings” model from  
86 judgment and decision making (Loewenstein,  
87 Weber, Hsee, & Welch, 2001), the “mood as infor-  
88 mation” model from social psychology (Schwarz &  
89 Clore, 2003), and the “somatic marker hypothesis”  
90 (Damasio, 1994) from cognitive neuroscience all  
91 assume and provide evidence that internal states are  
92 implicitly used to guide decisions, either by being  
93 directly and unconsciously accessed at the time of  
94 judgment (Schwarz & Clore, 2003) or by generat-  
95 ing affective signals during conscious deliberation  
96 that are neurally integrated to bias choice on the  
97 basis of past experience. A similar argument has  
98 been proposed to specifically explain primate giving  
99 as reciprocity, called the “emotional mediation”  
100 hypothesis (Aureli & Schaffner, 2002; Aureli &  
101 Schino, 2004; Aureli & Whiten, 2003; see also,  
102 Pryce, 1996; Whiten, 1996). In this model, current  
103 physiological emotional states that reflect prior out-  
104 comes from social interaction serve as the bridge  
105 between neural processes and behavior. As evidence,

1 heart rate (Aureli et al., 1999) and self-scratching—  
2 both indicators of anxiety—increase in the presence  
3 of a dominant individual (Castles & Aureli, 1999;  
4 Maestripieri, 1993; Pavani, Maestripieri, Schino,  
5 Turillazzi, & Scucchi, 1991; Troisi & Schino, 1987)  
6 and the frequency of post-conflict reconciliation is  
7 moderated by friendship quality (reviewed by Aureli,  
8 Cords, & van Schaik, 2002; de Waal, 2000b). Thus,  
9 the anxiety of the victim or target individual is  
10 thought to indirectly indicate the status of the rela-  
11 tionship between individuals, which in turn predicts  
12 avoidance or a friendly reunion.

13 At the neural level, affective and declarative infor-  
14 mation from many subsystems are thought to con-  
15 verge in the orbital frontal cortex (OFC) where they  
16 are integrated to influence choice (Bechara et al.,  
17 2000; Kringelbach & Rolls, 2004). The amygdala is  
18 thought to generate the initial emotional response to  
19 rewards and punishments (Bechara, Damasio, &  
20 Damasio, 2003) while the hippocampus and associ-  
21 ated cortical representations feed forward contextual  
22 information from past experience that can moderate  
23 the effect. In the other direction, the OFC is known  
24 to also send signals back to the amygdala (basolateral  
25 nucleus; BLA) to track expected outcomes during  
26 delays, in the absence of the cue, and in probabilistic  
27 settings (O'Doherty, 2003; Schoenbaum, Chiba, &  
28 Gallagher, 1998; Schoenbaum, Setlow, Saddoris, &  
29 Gallagher, 2003). This is important as it allows ani-  
30 mals and people to represent situations and out-  
31 comes that are not strictly locked to the presence of  
32 the stimulus, which can be used to anticipate and  
33 plan actions. Similarly, the dorsolateral prefrontal  
34 cortex (DLPFC) is expected to be necessary for  
35 more explicit, cost-benefit tradeoffs and tracking of  
36 favors given and received, as well as for maximizing  
37 learning and performance by the more medial and  
38 emotional system (Krain et al., 2006). For example,  
39 in gambling tasks, the DLPFC is needed to develop  
40 conscious, explicit knowledge about the contingen-  
41 cies of the different decks of cards, even if subjects  
42 can chose advantageously without it (Bechara,  
43 Damasio, Tranel, & Anderson, 1998; Krain et al.,  
44 2006).

45 Both the amygdala and the OFC are highly inter-  
46 connected with the ventral striatum, in particular  
47 the nucleus accumbens (NAcc), which is thought to  
48 be involved in many different, overlapping processes  
49 related to decisions about reward that should play  
50 a role in altruistic giving. The largest literature on  
51 the dopaminergic reward system focuses on addic-  
52 tion (for reviews, see Berridge & Robinson, 2003;  
53 Robinson & Berridge, 2003). Dopaminergic signals

54 in the NAcc are thought to mediate the motivation  
55 to attain rewards (“wanting”) (Wyvell & Berridge,  
56 2000) while opioid processes underlie the *hedonic*  
57 *pleasure* (i.e., “liking”) of consuming those rewards  
58 (Peciña & Berridge, 2005). Dopamine signals in the  
59 NAcc are also thought to track the *expectation* of  
60 rewards (Berns, McClure, Pagnoni, & Montague,  
61 2001; Fiorillo, Tobler, & Schultz, 2003; Schultz,  
62 2002) while the neuropeptide action of oxytocin  
63 and vasopressin in the NAcc is necessary for the for-  
64 mation of long-term social bonds in animals (Insel  
65 & Young, 2001) and is implicated in multiple  
66 models to underlie social bonding, trust, and giving  
67 in primates and humans (Carter et al., 2008;  
68 Churchland, 2008; Hrdy, 2009; Kosfeld, Heinrichs,  
69 Zak, Fischbacher, & Fehr, 2005; Preston & Brown,  
70 submitted; Zak, 2008).

71 Given these findings in the decision literature,  
72 one would predict particular involvement of the  
73 NAcc, amygdala, and hippocampus to initially  
74 encode, as important and emotional, the fact that  
75 your new neighbor either called the police or  
76 brought over a bottle of wine to your first party. The  
77 OFC, acting in concert with the DLPFC, would be  
78 needed to recall these facts when your neighbor later  
79 comes over to borrow a cup of sugar. The NAcc-  
80 driven motivational systems would also be expected  
81 to motivate you to approach the neighbor who ini-  
82 tially brought you wine when you later see him in  
83 the adjacent driveway, and as the relationship grows  
84 may even motivate you to help him bring in the  
85 groceries or shovel ice from the driveway. The  
86 DLPFC would be necessary in particular to boost  
87 explicit comparisons of past outcomes, such as may  
88 occur in a case where your neighbor of many years  
89 (with whom you had experienced both ups and  
90 downs) comes to ask you for a relatively costly  
91 favor—one that you want to really consider and be  
92 able to justify. Most substantial acts of helping prob-  
93 ably take this form, containing an amalgam of  
94 unconscious, affective feelings associated with the  
95 other and explicit memories and analyses.

96 These existing models provide an excellent start-  
97 ing point for understanding the embodiment of  
98 decision process; however, it is hard to generalize  
99 from experimental tests of decision making to real-  
100 world empathic altruism. Decision-making experi-  
101 ments typically use highly constrained numbers of  
102 variables and provide relatively precise information  
103 on the expected utility of various options. In con-  
104 trast, real-world decisions that have a large impact  
105 on reproductive success usually involve many con-  
106 ceivable options, each with multiple positive and

1 negative consequences, all of which must be esti-  
2 mated from very noisy, indirect, or nonexistent past  
3 data. For example, when deciding to marry, you  
4 must estimate your intended partner's commitment  
5 to a long-term monogamous relationship; when you  
6 leave your young child with a babysitter, nanny, or  
7 relative, you must estimate the likelihood that they  
8 will vigilantly and lovingly care for your offspring;  
9 when you allow your young adult child to go to  
10 school abroad, you must estimate the likelihood  
11 that they can succeed in a large city thousands of  
12 miles from home. Such decisions require great infer-  
13 ential leaps from individual events that may have  
14 distant relevance to the issue at hand. It is precisely  
15 this complexity and uncertainty that supports the  
16 adaptiveness of an implicit, affectively driven deci-  
17 sion process. Next we review the existing data on the  
18 neural substrates of altruistic giving. These studies,  
19 while consistent in their emphasis on the role of the  
20 aforementioned mesolimbocortical system, are also  
21 limited in that they refer only to very constrained  
22 forms of giving, most of which are financial. There  
23 is a large and still growing literature on the neural  
24 substrates of empathic emotion and perspective-  
25 taking, which are presumed to play an important  
26 role as the mediating psychologically felt emotion  
27 that intervenes between the perception of another's  
28 need and the decision to help. However, as other  
29 chapters in this volume are dedicated to empathy  
30 and its substrates (e.g., chapter 41), we will focus  
31 our evidence on studies that actually require giving.

### 32 Evidence for Human 33 Altruism in Neuroimaging

34 The role for decision and reward circuits in interper-  
35 sonal giving has been demonstrated in two recent lines  
36 of research in cognitive and affective neuroscience—  
37 trust and cooperation in behavioral economics, and  
38 the neural substrates of charitable giving. While  
39 these studies are convergent with the neuroanatom-  
40 ical circuits explicated above because they consis-  
41 tently find engagement of the same regions (OFC,  
42 NAcc, insula, amygdala), the function of each  
43 region in context with the specific task or behavior  
44 is largely speculative at this point, with the same  
45 region being implicated in opposing processes or  
46 the same process being located to different regions  
47 across studies. A detailed analysis of these data is  
48 beyond the scope of this chapter, but we provide the  
49 authors' interpretations of the activation after each  
50 finding as a guide.

51 A growing body of research has investigated pat-  
52 terns of neural activation while people play economic

53 games designed to solicit trade-offs between keep- 53  
54 ing monetary rewards for oneself, versus giving to 54  
55 another, or trusting another with one's investment 55  
56 in order to secure a larger reward (see Camerer & 56  
57 Fehr, 2006; Fehr & Camerer, 2007; Walter, Abler, 57  
58 Ciaramidaro, & Erk, 2005; Zak, 2004 for reviews). 58  
59 In a study of women doing the iterated prisoner's 59  
60 dilemma game, both the OFC and NAcc were activa- 60  
61 ted when both partners cooperated, interpreted 61  
62 as representing the rewards of cooperation, which 62  
63 enhanced and sustained cooperation over selfish 63  
64 decisions (Rilling et al., 2002). In a subsequent 64  
65 study, reciprocated cooperation was associated with 65  
66 activation in the ventromedial prefrontal cortex 66  
67 (vmPFC) while unreciprocated cooperation was 67  
68 associated with activation in the ventral striatum, 68  
69 suggesting that the striatum provided an error signal 69  
70 when the partner failed to reciprocate, which could 70  
71 inform future decisions (presumably to punish 71  
72 defection) (Rilling, Sanfey, Aronson, Nystrom, & 72  
73 Cohen, 2004). In another study, subjects played 73  
74 the same game outside of the scanner and subse- 74  
75 quently viewed pictures of the hypothetical part- 75  
76 ners in the scanner (Singer et al., 2006). Pictures 76  
77 of former cooperators elicited activation in the 77  
78 amygdala, NAcc, lateral OFC, insula, fusiform 78  
79 gyrus, and superior temporal sulcus (STS), activat- 79  
80 ing a large network associated with social cognition, 80  
81 memory, and associated memories. Importantly, 81  
82 partners classified as intentionally cooperative par- 82  
83 ticularly activated the ventral striatum and lateral 83  
84 OFC. In contrast, activation to defectors was lower 84  
85 overall and only increased relative activation in the 85  
86 medial OFC, perhaps activating stronger represen- 86  
87 tations for expected loss similar to effects in the ven- 87  
88 tromedial prefrontal cortex (VMPFC) for learning 88  
89 to avoid risky gambling decks (Bechara, Damasio, 89  
90 Tranel, & Damasio, 1997).

91 When the Ultimatum Game was played in the 91  
92 scanner against partners believed to be humans or 92  
93 computers, unfair offers produced higher activation 93  
94 in the insula, ACC, and DLPFC (Sanfey, Rilling, 94  
95 Aronson, Nystrom, & Cohen, 2003). Insula and 95  
96 ACC activity are presumed to result from the nega- 96  
97 tive reaction to unfairness, motivating a change 97  
98 in subsequent behavior. DLPFC activation is pre- 98  
99 sumed to reflect the cognitive control brought 99  
100 online to accept fair offers (the optimal choice) 100  
101 despite such negative emotional signals. As evidence 101  
102 for a role for the lateral frontal cortex, temporary 102  
103 disruption of the right DLPFC using transcran- 103  
104 ial magnetic stimulation (TMS) reduces the rejec- 104  
105 tion rate of unfair offers (Knoch & Fehr, 2007; 105

1 Knoch et al., 2008; Knoch, Pascual-Leone, Meyer,  
2 Treyer, & Fehr, 2006). Conversely, patients with  
3 damage to the VMPFC reject more unfair offers  
4 than comparison groups (Koenigs & Tranel, 2007).

5 In the trust and reciprocity game, only subjects  
6 who cooperated with a human partner showed  
7 increased activation in the prefrontal cortex while  
8 waiting to learn the outcome of their choices, an  
9 effect not seen in noncooperators or against com-  
10 puter partners (McCabe, Houser, Ryan, Smith, &  
11 Trouard, 2001). This effect is similar to the effect  
12 seen in rats (above), where the OFC is needed to  
13 maintain outcome representations in the absence of  
14 the stimulus (Schoenbaum et al., 2003). In another  
15 version of the trust game, intentional and real pun-  
16 ishment (as opposed to symbolic) was associated  
17 with activation in the dorsal striatum while punish-  
18 ment that was intentional and costly (as opposed  
19 to free) specifically activated the medial orbital fron-  
20 tal and VMPFC (de Quervain et al., 2004). In a  
21 recent reciprocal trust game where both players were  
22 scanned simultaneously (hyperscanning), condi-  
23 tional trust behavior increased relative activation in  
24 the VTA while unconditional trust increased activa-  
25 tion in the septal region (Krueger et al., 2007).

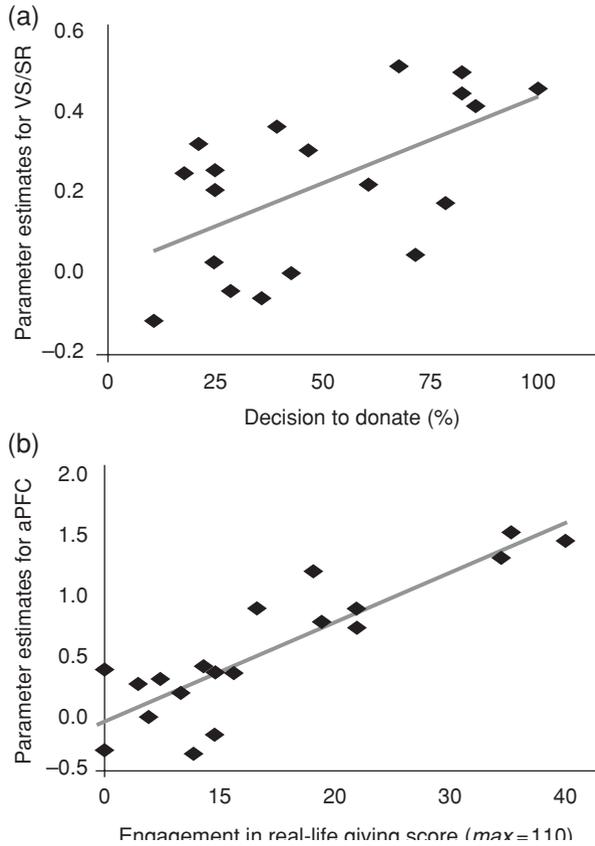
26 Effects of agency during behavioral economic  
27 games are mirrored in two other functional imaging  
28 studies of altruism. In the first, subjects performed  
29 or watched a reaction-time task that delivered earn-  
30 ings to themselves and a charity. Trait altruism posi-  
31 tively correlated with the tendency to recruit the  
32 right posterior superior temporal sulcus ( $r$  pSTS) as  
33 well as the OFC for watching more than playing  
34 (Tankersley, Stowe, & Huettel, 2007). The authors  
35 suggest that pSTS activation is associated with altru-  
36 ism because it encodes low-level actions, which can  
37 feed into more general empathic processes when  
38 observing the actions or state of another. These data  
39 are consistent with a perception-action model of  
40 empathy that places a bottleneck on empathic pro-  
41 cesses on the observer's attention to the other's state,  
42 necessary for downstream activation of resonating,  
43 self-related representations (Preston & de Waal,  
44 2002). In addition, they confirm the importance of  
45 observing the others' need and being able to model  
46 the appropriate action, which has been found to  
47 play a role in helping across species and contexts.

48 Another study that more directly studied deci-  
49 sions to give to others also found an important role  
50 for agency by pitting charitable donations against  
51 money for one's self, under a condition of voluntary  
52 or mandatory transfer (resembling taxation for  
53 public goods) (Harbaugh, Mayr, & Burghart, 2007).

Supporting common neural mechanisms for rewards 54  
to the self and to others, monetary gains to both 55  
parties activated a common network in the ventral 56  
striatum. Individuals did make cost-benefit trade- 57  
offs, giving more when it cost them less, but sup- 58  
porting an altruistic motivation to give to the 59  
charity, individuals with higher activity in the ven- 60  
tral striatum during giving donated almost twice as 61  
much voluntarily. Also supporting the "warm glow" 62  
motivation for giving (for the positive affect that 63  
ensues), activation in the caudate and right NAcc, 64  
as well as satisfaction with the donation, increased 65  
when donations were made voluntarily, even after 66  
controlling for the fact that subjects earned more by 67  
rejecting proposals to give voluntarily. 68

69 A similar study had participants allocate earnings  
70 either to themselves or a variety of real causes that  
71 had differential political appeal across subjects,  
72 allowing them to differentiate giving to valued and  
73 disliked recipients (Moll et al., 2006; Figure 38.3).  
74 As in the prior study, both personal rewards and  
75 charitable donations activated a common network  
76 in the mesolimbocortical system including the VTA,  
77 and dorsal and ventral striatum. In particular, the  
78 degree of costly charitable donation was correlated  
79 with activation in the ventral striatum. The more  
80 selfless the decision, or the more costly the dona-  
81 tion, the more anterior the activation, including  
82 frontopolar and medial frontal cortex (also correlat-  
83 ing with real-world charitable giving). Activity in  
84 the sgACC was particularly associated with donat-  
85 ing when contrasted with monetary reward. In an  
86 fMRI study by the same group, the subgenual region  
87 of the ACC (sgACC; BA 25) was also associated  
88 with guilt from having imagined actions against  
89 another that violated social norms while pride and  
90 gratitude were associated with additional activation  
91 in mesolimbic and basal forebrain regions (Zahn  
92 et al., 2008).

93 These pertinent studies by Moll and colleagues,  
94 as well as additional evidence from research on emo-  
95 tion and psychopathology, may suggest a particu-  
96 larly important role for the sgACC in mediating  
97 altruistic acts in the context of empathic concern  
98 because of its ability to mediate emotional responses  
99 and associated effects on motivation, learning, and  
100 memory. This region has extensive interconnections  
101 with the OFC, lateral hypothalamus, amygdala,  
102 nucleus accumbens, subiculum, VTA, raphe locus  
103 coeruleus, PAG, and the nucleus tractus solitarius  
104 (NTS) (reviewed in (Freedman, Insel, & Smith,  
105 2000; Ongür & Price, 2000; Ongür & Price, 2003).  
106 Projections from the sgACC to the hypothalamic



**Fig. 38.3** Positive correlations between charitable giving and brain activation in the mesolimbocortical system. In the top panel (a), the frequency of costly donation (how often each participant made costly donations) increases with parameter estimates in the ventral striatum/septal region (VS/SR;  $x = -6, y = 11, z = 4; r = 0.58; p < 0.01$ ). In the bottom panel (b), the level of self-reported engagement in real-life voluntary activities increases with the degree of aPFC activation during costly donation (peak:  $x = -6, y = 25, z = -14; r = 0.87; p < 0.0001$ ).

Graphs reproduced from Figures 3d and 4e in: 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 U S A*, 103(42), 15623–15628.

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1 and brainstem autonomic regions are presumed to  
 2 regulate emotional arousal (reviewed in Freedman,  
 3 Insel, & Smith, 2000; Barbas, Saha, Rempel-Clower,  
 4 & Ghashghaei, 2003), particularly parasympa-  
 5 thetic control (Critchley, 2004; O'Connor, Gundel,  
 6 McRae, & Lane, 2007), which would be particu-  
 7 larly germane for both a role in responding to others'  
 8 distress and in the normal experience of negative  
 9 emotions (Kross, Davidson, Weber, & Ochsner,  
 10 2008; van den Bos, McClure, Harris, Fiske, &  
 11 Cohen, 2007), such as sadness (Damasio et al.,  
 12 2000; Liotti et al., 2000; Talbot & Cooper, 2006)  
 13 major depression, and bipolar disorder (reviewed by  
 14 Charney & Nestler, 2005; Drevets, Savitz, &  
 15 Trimble, 2008). Displays of need typically involve  
 16 some form of expressed sadness or distress, which  
 17 would be expected to activate the parasympathetic

system and sgACC. As evidence, this region is spe- 18  
 cifically activated when mothers listen to infant cries 19  
 (Lorberbaum et al., 2002; Lorberbaum et al., 1999) 20  
 and experiments consistently find an orienting 21  
 response (a reduction in heart rate presumed to 22  
 result from increased parasympathetic tone) when 23  
 subjects attend to and are concerned about the 24  
 plight of another and offer to help (Eisenberg & 25  
 Fabes, 1990; Eisenberg et al., 1989). Taken together, 26  
 the subgenual region may be best thought of as a 27  
 region that normally mediates the ability to redirect 28  
 cognitive and physiological resources (attention, 29  
 metabolism, motivation, memorial processes) in 30  
 response to biologically important stimuli in con- 31  
 text. This makes it a good candidate for mediat- 32  
 ing acts of helping, which depend both on an 33  
 emotionally salient distress signal, the relationship 34

1 of the distressed other to the observer, and the  
2 ability/knowledge of the observer to respond  
3 appropriately. It also allows for a neural link between  
4 the assumption that empathy and altruism origi-  
5 nated in the mother-offspring bond, which causes  
6 caregivers to respond to the cues of distress in  
7 offspring.

8 Thus, extensive evidence from neuroimaging  
9 supports the view that the ventral striatum and  
10 orbital frontal regions in particular are necessary  
11 for making cost-benefit trade-offs during social  
12 decisions such as cooperative investment games.  
13 However, despite being “social,” compared to gam-  
14 bling with known or fixed probabilities, these situa-  
15 tions are still heavily biased towards cost-benefit  
16 processes, which may not underlie typical forms of  
17 giving in the real world. For example, when some-  
18 one retrieves and cuddles a distressed infant, runs to  
19 the rescue of a fallen child, or gives up their seat on  
20 the bus to an older passenger, a trade-off between  
21 helping and monetary reward is not involved. Even  
22 implicit trade-offs between the needs of the giver  
23 and the receiver may not be practically important in  
24 situations where the motivational inputs to respond  
25 are sufficiently strong that they clearly dominate  
26 processing. The involvement with monetary rewards  
27 and the explicitness of the tradeoff indicate that  
28 frontal-striatal systems may be particularly involved  
29 when giving involves a clear trade-off, such as when  
30 deciding whether to use a windfall of earning to buy  
31 an expensive accessory or donate to a charity, or  
32 when deciding to help one individual or charity  
33 over another. Activation is expected to be more  
34 anterior and involve interactions between medial  
35 and lateral portions of the frontal cortex the more  
36 abstract and cogitated the decisions, while more  
37 immediate stimuli/situations should activate more  
38 posterior, medial structures such as the amygdala,  
39 NAcc, and sgACC.

#### 40 **Putting it All Together**

41 More than three decades ago, biologists deliberately  
42 removed the altruism from altruism. Now, there is  
43 increasing evidence that the brain is hard-wired for  
44 social connection, and that individuals often have  
45 an emotional stake in the emotions of others. The  
46 brain may have evolved to maximize personal fit-  
47 ness, but did so by running a genuine reach-out  
48 program that is at least as old as the mammals.

49 Mechanisms designed to subserve mating, pair  
50 bonding, offspring care, and food procurement affect  
51 and mediate our propensities towards others, predis-  
52 posing us to act towards others who are socially

53 bonded, loved, positively regarded, or sexually desired.  
54 At a proximate level, such decisions rely on the  
55 neural and physiological systems involved in reward  
56 processing and decision making, elucidated in  
57 animal and human models of bonding, maternal  
58 care, food reward, drug addiction, and economic  
59 choice. These basic mesolimbocortical mechanisms  
60 are shared across species and likely explain the vast  
61 majority of implicit behavioral investment choices,  
62 but also explain how giving does not act in a vacuum,  
63 but is highly sensitive to cost-benefit factors that  
64 make giving more or less valuable or desired. Thus,  
65 while the motivation for reward-based giving  
66 is largely implicit, it is also sensitive to context:  
67 1) information from past experience with the indi-  
68 vidual and situation feeds into the system from  
69 association cortex and the hippocampus, 2) giving  
70 is suppressed by feelings of uncertainty, risk, fear,  
71 and vulnerability, through inputs from amygdala to  
72 ventral striatum, and 3) giving is sensitive to cost-  
73 benefit effects on resource allocation such as have  
74 been documented for food availability, group size,  
75 and relationship quality.

76 Indeed, as pointed out by many skeptics of a  
77 seemingly “automatic” mechanism for empathy and  
78 altruism, sometimes empathy seems wholly absent.  
79 On the opposite end of the spectrum, people can  
80 brutally hurt others in the service of personal pro-  
81 tection or gain and even revel in another’s misfor-  
82 tune in artificial laboratory experiments. However,  
83 consistent with the model, *schadenfreude* occurs par-  
84 ticularly for nonbonded, nonrelatives who directly  
85 compete for resources and may be surpassing the  
86 subjects. Chimpanzees are also capable of brutally  
87 killing each other (de Waal, 1982; Wrangham &  
88 Peterson, 1996) and, hence, must be able to elimi-  
89 nate empathic activation in relation to conspecifics  
90 (Jane Goodall, 1986, p. 532 refers to chimpanzee  
91 victims as “dechimpized”).

92 Originally, the mechanisms of reward and deci-  
93 sion making were likely designed to facilitate con-  
94 summatory behaviors (sex, eating, pup retrieval,  
95 allogrooming) where the incentive salience of a  
96 stimulus draws the individual toward the target, to  
97 obtain an expected reward. With increased involve-  
98 ment of the interconnected mesolimbocortical  
99 system and bidirectional connections between the  
100 ventral striatum and prefrontal cortex, primates can  
101 extend this act of consumption over time, such  
102 that the initial act of opening oneself up for another  
103 can occur in more abstract contexts and before  
104 any expected reward is salient. Such decisions likely  
105 rely on these interactions between expected reward

1 as processed by the ventral striatum and control  
2 functions subserved by interconnections with the  
3 amygdala, hippocampus, anterior cingulate and  
4 orbital frontal cortex. Emotional associations with  
5 the other generate the motivation to help, with a  
6 particular moderating influence from relationship  
7 quality and situational variables (such as food supply  
8 or the presence of a dominant individual), produc-  
9 ing behavior that maximizes inclusive fitness and  
10 reciprocal altruism with minimal demands on  
11 explicit calculation.

12 In cases where the recipient is a truly loved and  
13 bonded individual, reward mechanisms associated  
14 with the bond and past experience generate an  
15 incentive salience-like state to approach and com-  
16 fort the other, which still need not be compulsory.  
17 For example, giving can be inhibited if fear is associ-  
18 ated with the situation or the other or there are  
19 overriding personal needs.

20 In humans, even giving that is not mediated by  
21 a high-quality social relationship can occur as cog-  
22 nitive capacities allow individuals to override imme-  
23 diately obvious risks and model less immediate  
24 potential rewards. In so doing, potential givers can  
25 take control of situations in myriad ways. Individuals  
26 can actively inhibit options that are compelling, but  
27 non-optimal (such as helping individuals who are  
28 liked, but nonetheless unlikely to reciprocate), or  
29 highlight options that are not compelling, but opti-  
30 mal (such as helping someone unliked, but likely to  
31 reciprocate), planning long-term cooperative ven-  
32 tures that require multiple stages and long-term  
33 payoffs, and enacting rules or strategies that avoid  
34 manipulation while maximizing the potential for  
35 return (like stop-loss rules for social investments or  
36 tit-for-tat strategies).

37 Choices are likely to reflect maximization of  
38 salient variables, which were generally adaptive in  
39 our evolutionary history, but may or may not be  
40 beneficial in the individual case. For example, when  
41 your friend is standing at your doorstep, it would be  
42 all but impossible to turn them away and you will  
43 offer more than if their plight was presented indi-  
44 rectly. However, the friend at the door may be a  
45 freeloader (something you knew, but could not use  
46 to override the immediate salience), while the sin-  
47 cere friend across town harbors resentment that  
48 you did not rush to her aid (which you also knew,  
49 but which was insufficiently salient to get you out  
50 of the house). This variability in the salience of  
51 variables that are immediately or more distantly  
52 perceived is known as the “hot-cold empathy gap,”  
53 and has been applied to myriad discounting

54 problems including drug addiction and financial  
55 investments (Loewenstein, 2000). Choices are also  
56 sensitive to costs and benefits, such that even when  
57 the person is standing at the door, a mother of  
58 five may turn them away while a single person may  
59 drive across town to comfort their friend. Adding a  
60 decision-making perspective to prosocial giving  
61 allows us to defeat misgivings about the role of  
62 empathic emotion in mediating truly altruistic  
63 giving. In this view, empathic and sympathetic emo-  
64 tions surely do predispose giving, but must be inte-  
65 grated with many simultaneous motivational and  
66 situational cues that may bias behavior in different  
67 directions.

68 As exemplified by this review, the vast majority  
69 of empirical evidence for altruism exists in animals,  
70 even nonprimates. The existing evidence in humans  
71 has relied on financial decisions because of our con-  
72 current interest in financial decisions as well as the  
73 ease of demonstrating them in the lab. However,  
74 this approach biases our knowledge in favor of cost-  
75 benefit approaches and implies necessarily a trade-  
76 off between self and other rewards. In the real world,  
77 many decisions to help do not take this structure.  
78 For example, when you rush out of your home to  
79 help the boy who has fallen off of his bike, spend an  
80 evening at work to help a distressed colleague, or  
81 pick up the phone after a particularly moving plea  
82 for help on the television, the conflict between  
83 personal and other goals is minor while the compul-  
84 sion to act is strong. In reality, everyone in our envi-  
85 ronment could use help and, thus, the decision is  
86 not *whether* to help, but *who* and *how much* (making  
87 an evolutionary perspective particularly produc-  
88 tive). People even persist in giving to their detriment  
89 or reveal unfettered self-interest, demonstrating  
90 trait-like tendencies that are robust to cost-benefit  
91 information. Thus, while genetic contribution to  
92 future generations is the bottom line in evolution,  
93 the proximate mechanism is dynamic, imprecise,  
94 and highly affected by temperament and past expe-  
95 rience. Successful models of altruism must capture  
96 this inherent complexity and variability better while  
97 being grounded in the known neural and physiolog-  
98 ical mechanisms of decision making. Creativity is  
99 needed to develop paradigms that elicit active help-  
100 ing in noneconomic settings in ways that are feasi-  
101 ble during neuroscientific recording such as with  
102 PET, fMRI, ERP, and TMS. Only by taking a  
103 broader view can we understand the complexity of  
104 a behavior that can be observed in our most dis-  
105 tant relatives and hard to demonstrate in our own  
106 species.

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