The thing he wanted to do seemed like a natural choice to him—almost inevitable, “Like dominoes falling,” he said. And yet it could not have seemed more unnatural to everyone else. “Lunatic” they called people like him (Henderson et al., 2003). His wife intimated they might be right. It would certainly be painful. It might make him sick. There was a slim chance it could kill him—although, fortunately, it did not. Today, years later, he still thinks about the day it finally happened when he wakes up every morning. It brought him, as he sees it, only positive outcomes. But the practice was only permitted in the United States beginning in 1999, and it is still forbidden in many countries. This is despite the fact that it is proven to save lives. What is this natural but unnatural, painful but positive, beneficent but banned act? It is the nondirected, or altruistic, donation of a kidney to a stranger. And this man is one of roughly 1,400 people in the United States who have ever chosen to undertake it.

Nondirected altruistic kidney donors request that one of their own working kidneys be surgically removed and implanted into a stranger. Whether that stranger is male or female, young or old, compassionate or callous they may never know. Some donors meet their recipient before the surgery, but more often they do not. They may never meet, either because the recipient prefers to remain anonymous, or, in some cases, because the recipient dies. Recovery from donation can be painful—sometimes excruciatingly so—and results in weeks of lost work. Debates continue about its long-term effects on health and longevity (Leichtman et al., 2011; Massey et al., 2010). In rare cases, donors have lost their health insurance when their insurer declared the removal of a kidney to be a preexisting condition (Rabin, 2012; Yang, Thiessen-Philbrook,
Klarenbach, Vlaicu, & Garg, 2007). If there is such a thing as altruism, altruistic kidney donation surely qualifies.

Altruism—behavior intended to benefit another person instead of the self—is among the most mysterious and controversial behaviors in the human repertoire. Longstanding questions persist about what qualifies as altruism, what drives it, and what neurocognitive processes support it. This chapter will explore these questions and consider how a better understanding of extraordinary altruists like altruistic kidney donors may help to answer them. Answering these questions may provide us with not only a deeper understanding of extraordinary altruism, but of ordinary altruism as well, and the basic social and affective capacities of the human brain that support it.

WHAT IS ALTRUISM?

A dominant belief among many contemporary scientists, philosophers, and policymakers is that human altruism does not exist (Miller, 1999). For most of Western history, the prevailing view has been that every human action is ultimately motivated by self-serving goals—and that this is as it should be. It is both a descriptive and a prescriptive belief (Batson, 1991). Arguments in favor of the existence of genuine altruism are generally based on some form of the empathy-altruism hypothesis, which holds that an other-oriented motivational state, termed empathy, can drive us to act on behalf of others even at cost (or at least at no benefit) to ourselves (Batson & Shaw, 1991). Understanding altruism, according to this hypothesis, requires understanding empathy.

Efforts to understand empathy and altruism are often hampered by the use of these two terms to describe a variety of distinct processes (de Waal, 2008). To begin with, it is essential to distinguish among three distinct phenomena to which the term empathy may refer: emotional empathy, cognitive empathy, and empathic concern. Emotional empathy usually refers to a low-level emotional response to another person's distress. This form of empathy is sometimes termed “emotional contagion,” in reference to the idea that emotional information may be transmitted from sender to receiver via low-level or unconscious processes (de Waal, 2008). This form of empathy can be identified using any method that can detect an emotional response, including measurements of brain activation, peripheral physiology, facial movements, or self-reported emotion. Correctly identifying another person’s emotional state is also considered an index of emotional empathy (Nichols, 2001). So if, for example, witnessing another person’s distress causes the viewer to show increased physiological arousal (e.g., increased heart rate or sweating), to exhibit facial
behavior similar to the distressed person’s (e.g., knitting the brows together), or to correctly identify the distressed person’s distress, we can infer that emotional empathy has occurred.

At the neural level, accumulating evidence supports the idea that emotional empathy represents the activation of shared representations for personal and vicarious experiences of emotion (Bernhardt & Singer, 2012). For example, a large body of research demonstrates that viewing or inferring another person to be experiencing pain results in the activation of cortical and subcortical structures, such as the anterior insula and dorsal anterior cingulate cortex, that also respond during personally experienced pain, a phenomenon that may enable the viewer to generate a representation of the social and affective components of another person’s pain by mapping it onto his or her own experiences (Lamm, Decety, & Singer, 2011). Parallel processes may also underlie emotional empathy for fear, disgust, and perhaps anger (Goldman & Sripada, 2005; Marsh, 2011). Critically, theories of shared neural representations require that empathizing with distinct emotional states relies upon distinct neural processes, such that a person can be skilled in empathizing with some emotions but not others. Emotional empathy can be contrasted with cognitive empathy, which refers to the understanding of others’ cognitive states, such as beliefs and intentions (Baron-Cohen, 1997). The brain regions that subserve cognitive empathy overlap minimally, if at all, with those that subserve emotional empathy, underscoring the importance of resisting the tendency to conflate the two phenomena (Blair, 2008; Gallagher & Frith, 2003).

Cognitive and emotional empathy index how well the empathizer interprets the internal state of another person. The third form of empathy, empathic concern, departs from this emphasis. This form of empathy entails caring about the other person’s internal state. Beyond simply understanding another person’s internal state, empathic concern entails feeling for them—wishing, in the case of another’s distressed emotional state, that it were better and desiring to make it so (Eisenberg, 2007). Whereas both cognitive and emotional empathy apply to a variety of internal states, empathic concern generally occurs in response to distress (Nichols, 2001). There have been suggestions that empathic concern constitutes a distinct emotional state with distinct physiological signatures (Eisenberg et al., 1989), but the primary means of assessing this form of empathy is via self-report. Empathic concern appears not to be closely tied to cognitive empathy (Blair, 1999a). By contrast, emotional empathy, at least some forms of it, appears to be critical for experiencing empathic concern (Nichols, 2001). Empathic concern—an other-oriented motivational state associated with wanting to improve another’s welfare—is the form of empathy thought to drive altruism (Batson, 1991, 2010), at least, when altruism is defined psychologically, in terms of its motivation.
Some of the best evidence for the existence of empathic concern-driven altruism derives, paradoxically, from psychopaths. Psychopathy is a condition characterized by persistent antisocial behaviors like aggression, theft, and deceit, and by personality traits like a lack of remorse, guilt, or empathic concern, which are termed callous-unemotional traits (Blair, Peschar, Budhani, Mitchell, & Pine, 2006; Hare & Neumann, 2008). Psychopathic traits vary continuously in the population, such that a given person can be minimally, moderately, or highly psychopathic, and these are differences of degree, not kind (Edens, Marcus, Lilienfeld, & Poythress, 2006; Guay, Ruscio, Knight, & Hare, 2007). Highly psychopathic individuals consider the needs and rights of others minimally or not at all and fill the ranks of the world’s notorious serial murderers, con artists, and repeat offenders (Hare, 2006). How can such a population support the possibility of altruism? Because, very simply, they are unlike everybody else. That psychopaths exist requires that other people exist who are not psychopaths—who have some capacity for empathic concern.

These facts also support the possibility of extraordinary altruists. If psychopaths occupy the low end of an empathic concern spectrum, it stands to reason others would exist who are the mirror image of psychopaths: “anti-psychopaths”, who experience more empathic concern than average. Altruistic kidney donors seem, potentially, like excellent representatives of this population. Rather than being set apart by their antisocial behavior, they are set apart by their prosocial behavior, often engaging in a variety of other prosocial acts, such as donating blood or registering as marrow donors (Henderson et al., 2003). Their behavior is clearly altruistic in the biological sense. Donors are forbidden from benefitting materially (e.g., being paid), and it is debatable whether donation results in more abstract gains like increased social esteem (Massey et al., 2010). And when queried about their motivations for donating, most altruistic donors cite the desire to help another person as their foremost consideration (Lennerling, Forsberg, Meyer, & Nyberg, 2004; Massey et al., 2010). Even stronger evidence that donors are driven by empathic concern would be evidence that donors possess qualities that experimental research paradigms have previously linked to psychological altruism.

Studies of human altruism in the laboratory show that it is primarily elicited by the distress of a victim, and the more sensitive to distress participants are, the more likely they are to behave altruistically (Eisenberg & Miller,
Extensive research conducted by Batson and colleagues shows that sensitivity to distress can be experimentally manipulated (Batson & Shaw, 1991), prompting altruism in even the unlikeliest of circumstances. In one study, Batson and Ahmad (2001) stacked the deck solidly in favor of selfish behavior: University student participants played a one-trial prisoner’s dilemma against an anonymous partner they would never meet. Payoffs were made concrete and real in the form of raffle tickets for a $30 gift certificate at a store of the winner’s choice. Ostensibly by chance, the partner was always selected to play first, and she always defected. Participants could either defect in return, earning 5 tickets (the partner would also earn 5 tickets), or cooperate, whereby the participant would win 0 tickets and the partner 25. Why would any player cooperate in response to defection from an anonymous stranger? Most theoretical frameworks predict defection, which maximizes personal gain and satisfies norms of reciprocity, fairness, and distributive justice (Batson, 2010). Defection was in fact universal (20/20 participants) when participants received no communication from their partner. But responses changed dramatically when participants read a short note from the partner describing her distress about recent events in her life. This prompt induced an altruistic response in nearly half (9/20) of the participants who read it following instructions to imagine how the partner was feeling.

The results of this and similar studies demonstrate the effectiveness with which distress-induced empathy produces altruism. It also shows than any given distress cue will be more effective in eliciting altruism from some people than others, since even in the empathy condition of this experiment more than half the participants still defected. This, together with a long tradition of research on bystander intervention showing that the clarity or interpretability of a target’s distress predicts helping in bystanders (Clark & Word, 1974; Shotland & Huston, 1979), suggests that individual differences in the ability to correctly interpret others’ distress cues will predict individual differences in altruism.

Studies conducted by my colleagues and I have confirmed this to be the case. We have measured altruistic behavior in the laboratory and found that the ability to recognize emotional expressions that convey distress, particularly fear, predicts altruism in the laboratory (Marsh, Kozak, & Ambady, 2007). Individual differences in fear recognition predicted altruism more accurately than gender, mood, and self-reported empathic concern. These findings support the contention that the ability to simply recognize when others are experiencing distress (a low-level form of emotional empathy) is the most important requirement for experiencing empathic concern (Nichols, 2001). Together with abundant evidence that psychopathy impairs the recognition of fearful expressions (Dawel, O’Kearney, McKone, & Palermo, 2012; Marsh & Blair, 2008),
these findings suggest that the ability to recognize others’ fear is a strong indicator of where an individual falls on the empathic concern spectrum.

Predicting Extraordinary Altruism

In light of this prior evidence, we developed a paradigm aimed at assessing neural and behavioral responses to others’ distress in altruistic kidney donors to test the hypothesis that their altruistic behavior may result from increased sensitivity to others’ distress (Marsh et al., 2014). We recruited 19 altruistic kidney donors and 20 matched controls who all underwent brain scanning while viewing fearful, neutral, and angry facial expressions. Later, participants were asked to identify these expressions in a separate task conducted outside the scanner and then completed a large number of self-report scales and measures such as self-reported empathy and psychopathy. Our first hypothesis was that altruists would exhibit enhanced amygdala activation in response to fearful facial expressions during brain scanning. This hypothesis was based on abundant evidence that, in healthy adults, activity in the amygdala, a subcortical structure in the temporal lobes, is greater when participants view fearful facial expressions relative to any other type of emotional expression (Fusar-Poli et al., 2009; Murphy, Nimmo-Smith, & Lawrence, 2003), and that this response is attenuated in individuals with psychopathic traits (Blair, 1999b; Dolan & Fullam, 2009; Jones, Laurens, Herba, Barker, & Viding, 2009; Marsh et al., 2008; White et al., 2012). Because the amygdala is a structure that is critical to generating the experience of fear (Davis, 1992; Feinstein, Adolphs, Damasio, & Tranel, 2011; LaBar, LeDoux, Spencer, & Phelps, 1995), heightened amygdala responses to others’ fearful expressions may represent manifestations of the emotional empathy upon which empathic concern depends (Goldman & Sripada, 2005; Marsh, 2011). We also hypothesized that altruists’ heightened amygdala activation would correspond to heightened accuracy for recognizing these expressions. Finally, we hypothesized that altruistic kidney donors would be less psychopathic than healthy controls.

All three hypotheses were confirmed: the amygdalae of altruistic kidney donors were more active in response to fearful expressions, a pattern that corresponded to improved recognition of these expressions, and they reported reduced psychopathic traits. These findings support the idea of altruists exhibiting enhanced empathic responses to others’ distress, and therefore their donations reflect genuinely heightened concern for others’ well-being, a conclusion of considerable importance to the transplantation community (Levey, Danovitch, & Hou, 2011). Even today, some transplantation centers will not perform transplants using non-directed donors (Woodle et al., 2010), in part
due to concerns that these decisions reflect psychological disorders or irrational expectations of self-benefit rather than genuine altruism (Henderson et al., 2003). The finding that, neurocognitively, altruistic donors fit the profile of individuals who experience unusually high levels of empathic concern and psychological altruism may mitigate these concerns. This is of particular importance given the critical and growing need for donor kidneys in the United States (Coresh et al., 2007).

More generally, an exploration of what sets extraordinary altruists apart from other individuals may also help to answer basic psychological and neuroscientific questions about the nature of altruism. That altruistic kidney donors exhibit hallmarks of altruism as determined by laboratory work provides support for the possibility that empathic processes do in fact underlie acts of extraordinary altruism, and this may help to illuminate the fundamental neurocognitive processes that support these behaviors.

UNANSWERED QUESTIONS

A number of questions about altruism remain, however, that are unlikely to be addressed from a study of extraordinary altruists without further development of the theoretical understanding of altruism and its origins. Among the central remaining questions about altruism is the question of what drives the leap from emotional empathy to empathic concern. A historically favored explanation (MacDougall, 1908) that has seen a recent resurgence (e.g., Batson, 2010; Bell, 2001; de Waal, 2008; Marsh, Adams, & Kleck, 2005; Preston, 2014) is that empathic concern is a more generalized form of the parental nurturing response. Parental nurturing requires an organism to place the needs of another organism before its own, sometimes at great expense and for protracted periods, and its emergence marked an extraordinary development in the evolution of vertebrate behavior (Eibl-Eibesfeldt, 1996). Parental nurturing is primarily a mammalian behavior—indeed, the word “mammal” is a reminder of the resources mammals expend nurturing and raising their young relative to their evolutionary progenitors. This development was facilitated by the emergence of the oxytocin system. Oxytocin is a mammalian hormone produced in the hypothalamus that, via dedicated receptors in the brain and body, promotes a variety of essential parental behaviors (Carter & Altemus, 1997).

The oxytocin system may be especially critical to the emergence of a mammalian behavior closely linked to altruism, which is alloparenting (Keebaugh & Young, 2011; Ross et al., 2009). Alloparenting is the provision of care and protection to unrelated young within the social group, and it has been observed in
over 100 mammalian species, including elephants, dolphins, wolves, and many species of primate, including humans (Riedman, 1982). Characteristics of species in which alloparenting occurs include organization into small, close-knit, and cooperative groups and infants being born relatively helpless and dependent on care from adults. Among alloparenting species, adults provide parental care not only for their own offspring but for offspring in general, and they possess strong mechanisms to prevent aggression in response to infantile cues.

It is hypothesized that because alloparenting mammals respond to generalized offspring cues with parental nurturing and the inhibition of aggression, fear and submission cues in these species evolved to mimic infantile cues, exploiting the parental nurturing response to inhibit aggression toward vulnerable adults (Lorenz, 1966). For example, wolves’ stereotyped fear and submission behaviors include rolling on the back, pinning back the ears, and tucking in the tail, all of which mimic appearance cues of pups and are thought to serve an appeasement function (Schenkel, 1967). Similar processes may occur in humans. Like other alloparenting species, humans respond to a variety of infant-like cues with parental nurturance. Abundant evidence demonstrates that nurturing responses are elicited by many stimuli that resemble infants, including adults with babyish facial features (Zebrowitz, 1997). Human fear and submission behaviors may also exploit this tendency by mimicking infantile cues. Fearful expressions are perceived to be morphologically similar to infantile faces, sharing with them features like wide eyes, high brows, a flat brow ridge, and a generally rounded appearance, and eliciting attributions of dependence, weakness, submissiveness, and babyishness (Marsh et al., 2005). This may explain why fearful expressions are perceived as highly affiliative (Hess, Blairy, & Kleck, 2000), elicit behavioral approach (Marsh, Ambady, & Kleck, 2005; Hammer & Marsh, 2014), and promote empathic concern (Marsh & Ambady, 2007). These findings support the idea that humans’ tendency to care for distressed infants is the progenitor of their tendency to experience empathic concern toward adults who display distress cues like fearful expressions that mimic the appearance of infants.

Considering how parenting and alloparenting responses relate to psychological altruism may help guide the development of future questions about the neurocognitive basis of human altruism. The role of primitive subcortical structures like the hypothalamus and periaqueductal gray should be investigated, given the important role these structures play in parental nurturance (Bartels & Zeki, 2004; Champagne, Diorio, Sharma, & Meaney, 2001; Francis, Young, Meaney, & Insel, 2002; Sheehan, Paul, Amaral, Numan, & Numan, 2001). Recent findings support the possibility that these structures’ role in human altruism and empathic concern can be assessed using current technologies (Moll et al., 2012; Simon-Thomas et al., 2012). Whether responses in
these regions mediate altruistic responses to distress cues like fearful expressions merits investigation. Another potentially fruitful avenue of investigation may be oxytocinergic function in altruists, given the importance of the oxytocin system for alloparenting. Differences in the oxytocin receptor gene have been shown to influence responses to novel human infant faces, especially following the inhalation of intranasal oxytocin (Marsh et al., 2012).

**CONCLUSION**

Whether humans possess the capacity to genuinely care about others’ welfare affects not only our beliefs about ourselves and others, but how we construct our societies. A normative belief that humans can only ever be driven by self-interest leads to the creation of social institutions that reflect that belief (Miller, 1999). The existence of transplant centers that refuse organs from altruistic donors due to doubts that these donations reflect genuine altruism is only one such example. Undoubtedly, many patients in need of a donor kidney have died as a result. An improved understanding of extraordinary altruism has the potential, then, to change the lives of those whose health depends on the altruism of others, and perhaps in the process to transform humans’ understanding of ourselves and the evolutionary forces and neural processes that undergird our most profound and mysterious social behaviors.

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