

The Origins of Altruism in Offspring Care

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The current review aims to unify existing views of altruism through an examination of the biological bases of a fundamental form of giving: *altruistic responding*. Altruistic responding is most salient during heroic acts of helping but is also observed any time one perceives another's distress or need, which in turn motivates one to help at a current cost to the self. Such aid is simple, observable across species, and rooted in the instincts and circuits that evolved to maximize inclusive fitness through the care of helpless offspring. By design, the system already biases aid to both kin and nonkin under conditions that are largely adaptive. These inherent benefits are also buttressed in primates and humans by known, later-arriving benefits to helping in group-living animals. Evidence for the proposed homology between altruistic responding and offspring retrieval is presented through 10 key shared factors. Conceptually, both require (a) participation by nonmothers, (b) motor competence and expertise, (c) an adaptive opponency between avoidance and approach, and a facilitating role of (d) neonatal vulnerability, (e) salient distress, and (f) rewarding close contact. Physiologically, they also share neurohormonal support from (g) oxytocin, (h) the domain-general mesolimbocortical system, (i) the cingulate cortex, and (j) the orbitofrontal cortex. The framework intermixes ultimate and proximate levels of analysis and unifies existing views by assuming that even complex human behaviors reflect ancient mammalian neural systems that evolved to solve key problems in adaptive ways, with far-reaching consequences for even our most venerated human traits.

Keywords: altruism, empathy, prosocial behavior, caregiving, decision making

Organisms are thought to be hardwired to selfishly promote their own genes, yet many mammals display acts of kindness and care in situations we are only beginning to understand. Broadly, such behaviors are considered “altruistic” when an organism issues a behavior that appears to benefit another at a current cost to the self. To resolve the paradox of such seemingly selfless behaviors, researchers have identified ways that altruism can benefit the fitness of a giver's genes (reviewed in Batson, 2011; de Waal, 2008; Fehr & Rockenbach, 2004; McAndrew, 2002; Preston & de Waal, 2011; J. M. Wang, Seidler, Hall, & Preston, 2012), such as through inclusive fitness (Dugatkin, 2007; Hamilton, 1964), reciprocity (Axelrod, 1984; Trivers, 1971), and later, indirect advantages in competition for resources at the individual, family, and group level (e.g., see Alexander, 1987; Fehr & Rockenbach, 2004; Gintis, Bowles, Boyd, & Fehr, 2003; McAndrew, 2002; Sober &

Wilson, 1998; Wilson & Wilson, 2007; Wilson, 2012). Human altruism is also known to be suppressed by the presence of capable others and promoted by motivational states such as feeling sorry for the plight of another (i.e., sympathy) or resonating with the emotions of another (i.e., empathy), both of which are assumed to have evolved from the mother–offspring bond (e.g., see reviews in Batson, 2011; S. L. Brown, Brown, & Penner, 2011a; de Waal, 2008; Dovidio, Piliavin, Schroeder, & Penner, 2006; Eisenberg & Strayer, 1987; Hoffman, 2000; Hrdy, 2009; Preston & de Waal, 2002b).

Despite such extensive work on altruism and empathy—across fields, species, and levels of analysis—a unified understanding of human altruism remains out of reach. The different disciplines that study altruism do not interact, and we still do not have a comprehensive idea of how altruism is instantiated in the brain and body. One way to address these problems is to focus on the neural bases of a conserved mammalian system that underlies the simple behavioral assistance of another in need, hereafter referred to as “altruistic responding.” Altruistic responding is most salient in cases of heroic responding but can be observed any time one perceives another's distress or need, which in turn motivates one to act in the moment, at a current cost to oneself. This form of aid is simple, is observable across mammalian species, and appears to have early roots in the instincts and neural system that evolved to care for helpless newborn offspring—a system that is already adaptively designed to promote care when it most benefits recipients while minimizing the costs to givers.

The potential homology between retrieving a helpless newborn and altruistic retrieval can be demonstrated across species through some salient examples drawn from both the academic and popular press:

A rat pup is separated from his mother and siblings nursing a meter away. The distressed infant makes ultrasonic vocalizations

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that the mother hears, causing her to leave the nest to retrieve and return him to the nest to nurse with the others (Hofer, 2000; see Figure 1, left panel).

A rat dam is placed in an operant conditioning box in which barpresses allow her to access and retrieve a series of unrelated, isolated, neonate pups. The highly motivated dam presses the bar for hours, retrieving hundreds of pups before the session is finally terminated by the exhausted experimenters (Wilsoncroft, 1969; see Figure 2).

A 3-year-old boy falls 18 feet into a gorilla enclosure at the Brookfield Zoo. Binti Jua, a female gorilla caring for her baby, picks up the unconscious boy and rocks him as she carries him to safety, protecting him from an elder female (BBC h2g2 Contributors, 2005; see Figure 1, right panel).

A man in Trinidad is saved from a house fire by his dog, barking and tugging at the leg of his pants until he awakens. After safely exiting the home, the dog dies after running back into the burning home, possibly to retrieve the parrot (Associated Press, 2007).

A young man recovering from a seizure falls onto the subway track. Wesley Autrey, who was waiting for the train with his two daughters, jumps down into the track to retrieve him but, without time to pull him out, instead lies on top of him between the rails as the train drives over them both, missing them by mere centimeters (Buckley, 2007).

Offspring retrieval surely evolved to protect the helpless newborn, ensuring the reproductive success of the mother who shares half of her genes with the endangered pup. However, the subsequent examples involve an unrelated or even heterospecific target that the observer incurs great personal risk to rescue (see Trivers, 1971). While all species do not retrieve pups in their mouths like rodent dams, all caregiving species show some analogous and costly behavior to retrieve and maintain contact with vulnerable, dependent, altricial offspring (e.g., Noren,

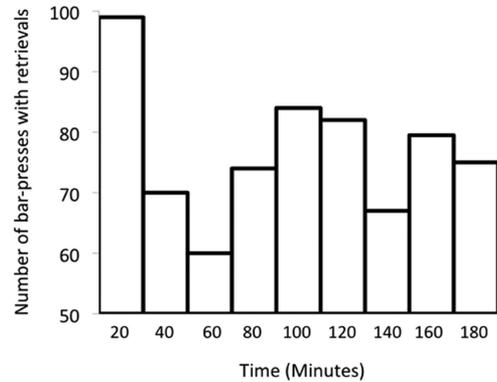


Figure 2. From Wilsoncroft (1969), displaying the number of barpresses with retrievals of neonate pups by a parturient female in the day following parturition. The first six trials were rewarded with food, the next six were rewarded with the dam's own six pups, and the remainder were rewarded with foster (unrelated) pups from nonexperimental mothers. Note that the level of retrieval remains high throughout the experiment, with almost four per minute even after 3 hr of continuous retrieval trials. The experiment was eventually terminated by the experimenters, tired of administering the procedure that did not appear to be reaching an asymptote in performance in the highly motivated dams. From "Babies by Bar-Press: Maternal Behavior in the Rat," by W. E. Wilsoncroft, 1969, *Behavior Research Methods, Instruments & Computers*, 1, p. 229. Copyright 1969 by Springer Science and Business Media. Reprinted with permission.

2008). Even some ants appear selected to rescue and retrieve conspecifics who have become trapped under sand or debris during foraging (Nowbahari & Hollis, 2010; Vasconcelos, Hollis, Nowbahari, & Kacelnik, 2012). Such behavioral similarities across species suggest that altruistic retrieval may be a neces-



Figure 1. Images of retrieval. The panel on the left depicts a typical rodent mother retrieving her offspring that became separated from the group or nesting site. Adapted from *An Introduction to Behavioral Endocrinology* (2nd ed., p. 356), by R. J. Nelson, 2000, Sunderland, MA: Sinauer Associates. Copyright 2000 by Sinauer Associates. Adapted with permission. The panel on the right depicts the rescue and care from mother gorilla Binti Jua of a 3-year-old boy who had fallen into her compound. Binti picked up the unconscious boy and carried him to a log adjacent to the enclosure door, holding him gently while waiting for the technicians to arrive. Drawings by Stephanie D. Preston.

sary primitive behavior in caregiving and social species, which needs to be examined across levels of analysis if we are to determine the extent to which these similarities impact the development of human giving.

At the surface, all of the aforementioned examples involve a *distressed target who is vulnerable, hurt, or in danger, and whose need is salient to the observer, who responds by approaching and/or retrieving them to relieve their distress or spare them from harm*. Intuitively, many situations of need take this form, and thus, the known mechanisms for simple offspring retrieval appear to offer a promising starting point for an integrated ultimate and proximate model of altruistic responding. Moreover, the neurobiological evidence available to date in mammals suggests that the similarities do not just reflect an analogy, in which similar behaviors evolved in distinct species in response to similar problems across time, but actually represent a homology, in which the behaviors are thought to have evolved from a common source, sharing genes that were passed directly from individual to individual. According to this view, human altruism—and most clearly altruistic responding—directly evolved from the neural and behavioral systems for caring for and retrieving offspring. As such, altruistic responding and offspring retrieval are presumed to not only share common goals or surface features but also neurobiological substrates and genetic influences. Such a homology is not only parsimonious, it can contribute to our broader understanding of altruism by providing a primitive building block upon which more complex forms of human helping can be placed. For example, even abstract cases of cooperation or donating money to strangers may be driven by the releasing stimuli of a vulnerable target in immediate distress even if they also involve more significant deliberation or top-down cognitive processes that are not possible for some other species.

The current review summarizes the ultimate and proximate argument for a homology between altruistic responding and offspring retrieval, presenting the strongest evidence for their relationship through 10 key shared factors: Conceptually, both require (a) participation by nonmothers, (b) motor competence and expertise, (c) an adaptive opponency between avoidance and approach, and a facilitating role of (d) neonatal vulnerability, (e) salient distress and (f) rewarding close contact. Physiologically, they also share neurohormonal support from (g) oxytocin, (h) the domain-general mesolimbocortical system, (i) the cingulate cortex, and (j) the orbitofrontal cortex. This review intentionally intermixes ultimate and proximate levels of analysis under the principle that complex human behaviors are best understood as extensions of ancient behaviors that rely upon highly conserved neural mechanisms, which in turn influence even complex human phenomena in adaptive and predictable ways. Before diving in to the key arguments, a few definitional and conceptual issues are addressed, including the operational definition of altruistic responding and how it relates to other known types of giving, both active and passive.

Defining Altruistic Responding

Altruistic responding is defined as any form of helping that applies when the giver is motivated to assist a specific target after perceiving their distress or need (see Figures 3 and 4). Altruistic responding implies an active behavioral response initiated by the

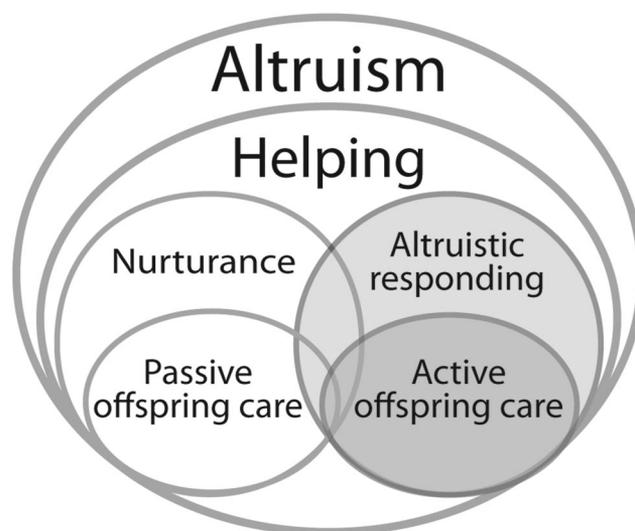


Figure 3. Schematic of the relationship between offspring care and altruism. Mechanisms of active offspring care, particularly retrieval, heavily influence the nature of altruistic responding—the focus of this review. Active offspring care usually results in passive care (e.g., huddling, close body contact, nursing); analogously, altruistic responding often results in nurturance (e.g., consolation or comforting) once the target is removed from danger. Passive care and nurturance occur during development and social relationships as part of the normal mechanisms of nervous system development and bonding. Active and passive care are then behavioral primitives upon which many forms of helping derive, even those that are more abstract or removed from the context of offspring. In turn, helping is a subclass of the broader category of altruism, which includes diverse types of giving, not all of which are influenced by offspring care (e.g., strategic helping, bacterial altruism). Even abstract or complex forms of human altruism that appear complex may have roots in offspring care when facilitated by the perceived distress, need, and vulnerability of the target (see Figure 4).

perception of need, which is differentiated from cooperative, diffuse, or unintentional forms of altruism that likely derive from other evolutionary and mechanistic origins. Altruistic responding can be considered a subtype of Warneken and Tomasello's (2009b) "helping," which exists in even young children and social mammals like apes, dogs, and dolphins (de Waal, 2009; Masson & McCarthy, 1995; Warneken & Tomasello, 2009b). It is also a subtype of de Waal's "directed altruism," which is directed at a specific individual, rather than broadly, as with alarm calls (de Waal, 2008).

Because these existing subclassifications were not created to group types of altruism by their motivations or evolutionary origins, they aggregate cases with different mechanistic properties (e.g., high and low explicit cognitive processing). Altruistic responding further narrows these classifications to only include cases where the motivation to respond is fomented by direct or indirect perception of the other's distress or need (see Figure 4). This excludes cases that emerged later in time or include diverse processes, such as cooperation or helping influenced by strategic goals, social norms, display rules, or mate signaling. Such causes surely participate in the human altruistic response, but they are not considered early or key drivers in primitive care-based aid, which

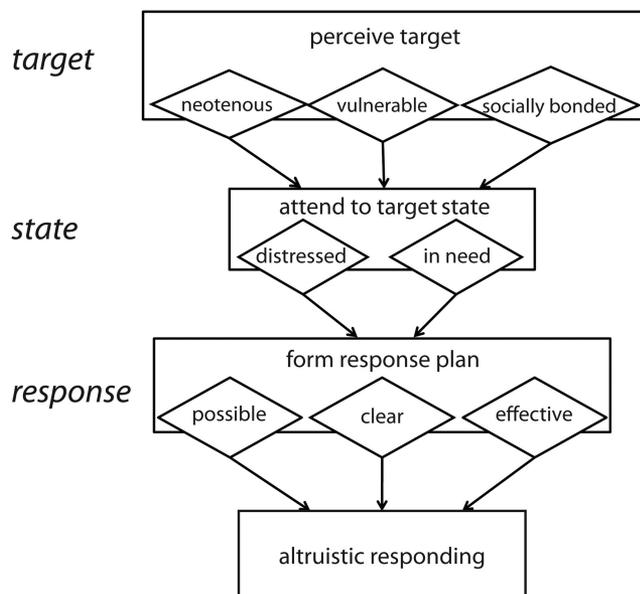


Figure 4. Drivers of the altruistic response. This is based on the fixed-action pattern (FAP) quality of offspring retrieval and altruistic responses. Certain qualities in the target, the target's state, and the observer's ability to help predispose action, like situational "releasers" of care that need not require extensive cognition, deliberation, or perspective taking. Each quality (in diamonds) is theoretically distinct and additive, though they typically co-occur in neonatal and compelling need situations.

can be observed across caregiving mammals such as rodents, who have minimal capacities for explicit deliberation and little selective pressure to appear beneficent. Multiple benefits are achieved by carving nature at its joints in this way, from the bottom-up. By identifying a type of altruism that is defined by its common form, function, mechanism, and evolutionary origin, we can finally merge motivational and evolutionary explanations into a coherent framework, we can comprehend the essential interrelationship between ultimate and proximate levels of analysis, and we can shed light on multiple remaining paradoxes in the literature of giving (the distinction between motivational and evolutionary explanations for altruism is provided in [Batson, 2011](#); [de Waal, 2008](#); [Krebs, 2011](#); [Preston & de Waal, 2011](#); [Sober & Wilson, 1998](#)).

The Relationship Between Altruistic Responding and Abstract or Passive Care

Of course, modern human life abounds with examples of altruistic responding that are probably motivated by the instinct to care for a distressed other but are more abstract or less active than rushing to save a stranger from a burning building or icy waters. For example, people altruistically write checks to feed starving children on the other side of the world and arrange for people in the community to deliver meals to ailing neighbors. In addition, forms of aid like comforting and soothing—known as "consolation" in apes—are surely also forms of caregiving, but ones that are much less active than the heroic cases provided above ([Cordoni, Palagi, & Tarli, 2006](#); [de Waal & Aureli, 1996](#); [de Waal & van Roosmalen, 1979](#); [Palagi, Cordoni, & Borgognini, 2006](#);

[Palagi, Paoli, & Borgognini, 2004](#)). According to animal models of offspring care, consolation is a "passive" and consummatory form of caregiving, while approaching and retrieving helpless newborns is "active" and appetitive; however, both share significant conceptual, mechanistic, and evolutionary origins (see [Figure 3](#)).

Active, abstract, and passive giving are all evolutionarily altruistic, as they benefit another at a current cost to the giver. Monetary donations carry a literal cost and consolation carries an energetic cost ([Noren, 2008](#)); both entail opportunity costs for more self-serving goals like mating and foraging. Consolation additionally entails an increased risk of predation ([Maestripieri, 1993](#)) and conflict from opposing alliances ([de Waal, 1982, 1989](#)). All three types of helping are also motivationally altruistic when they emanate from apprehension of the target's distress or need (see [Figure 4](#)). Thus, active human helping shares evolutionary and motivational origins with the more abstract and passive cases when they are also based in the mechanisms for offspring care.

In addition, the neural mechanisms of all three overlap as part of a suite of social behaviors like sexual behavior, social bonding, and protective aggression ([Mason & Mendoza, 1998](#); [Newman, 1999](#); [Numan, 2011](#); [Panksepp, 1986](#)). For example, the neuropeptides required for active care (e.g., oxytocin [OT] and vasopressin) also subserv other social processes ([Carter, Grippo, Pournajafi-Nazarool, Ruscio, & Porges, 2008](#); [Insel, 1997](#); [Numan, 2011](#); [Panksepp, 1986](#)), producing theories about the role of social bonding mechanisms in human morality and prosociality more generally (e.g., see [Barraza & Zak, 2009](#); [S. L. Brown, Brown, & Penner, 2011](#); [S. L. Brown, Brown, & Preston, 2011](#); [Churchland, 2008](#); [Fehr, Fischbacher, & Kosfeld, 2005](#); [Heinrichs, von Dawans, & Domes, 2009](#); [Hrdy, 2009](#); [Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005](#); [Morhenn, Park, Piper, & Zak, 2008](#); [Numan, 2011](#); [Panksepp, 1986](#); [Singer et al., 2008](#); [Taylor et al., 2000](#); [Zak, 2008](#)). All of these behaviors require approaching an unfamiliar target that would normally be avoided, indicating a key need for approach-avoidance opponent processes (see below and [Insel, 1997](#); [Insel & Young, 2001](#); [Mason & Mendoza, 1998](#); [Moll, de Oliveira-Souza, & Zahn, 2008](#); [Moll & Schulkin, 2009](#); [Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005](#); [Skuse & Gallagher, 2009](#)). Thus, conceptually, evolutionarily, and mechanistically, abstract and passive caregiving overlap considerably with active altruistic responding (see [Figure 3](#)).

Despite this clear overlap, the current article focuses on overt, active, altruistic responding per se, because this type of aid requires additional features that are not required for abstract or passive cases and have yet to be explicated (see [Figure 4](#)). For example, rodent offspring retrieval and human altruistic responding appear to require a unique role for the medial preoptic region of the hypothalamus (MPOA), motor systems, autonomic tone, and the knowledge/ability to enact the appropriate response—features that are less germane to abstract or passive giving. Motor-motivational and expertise processes are particularly underappreciated in current models of altruism, which may be key to unlocking existing paradoxes in the literature, such as the fact that empathy and altruism do not always co-occur (e.g., see [Buchanan, Bagley, Stansfield, & Preston, 2012](#); [Preston & Hofelich, 2012](#); [Prinz, 2011](#)) and the fact that helping can be predicted both by contagious distress and physiological arousal as well as by concerned attention and physiological deceleration (see reviews of physiological effects in [Batson, 2011](#); [Eisenberg, Wentzel, &](#)

Harris, 1998). Thus, the current article focuses upon active altruistic responding, but it is assumed that most of the described mechanisms also apply to abstract and passive cases, particularly when they share motivational processes associated with the drive toward young or distressed individuals who are vulnerable or in danger.

Article Summary

The following review summarizes the argument for a proposed homology between rodent offspring retrieval and human altruistic responding. First, ultimate arguments for altruism are reviewed and integrated by framing altruistic responding as a rudimentary and evolutionarily conserved neurobehavioral mechanism for responding to others' needs. The bulk of the review supports the homology between rodent offspring retrieval and altruistic responding by highlighting 10 key factors shared between them. Conceptually, both require (a) participation by nonmothers, (b) motor competence and expertise, (c) an adaptive opponency between avoidance and approach, and a facilitating role of (d) neonatal vulnerability, (e) salient distress, and (f) rewarding close contact. Physiologically, both behaviors also share neurohormonal support from (g) oxytocin, (h) the domain-general mesolimbocortical system, (i) the cingulate cortex, and (j) the orbitofrontal cortex (see Table 1).

Each of the 10 key factors focuses on data from the neurobiology of rodent offspring retrieval, because this provides the clearest functional and proximate homology to human altruistic responding and extensive data on this behavior already exist at a fairly specific level. Diverse data from other species and domains are included wherever possible to support the assumption that these data generalize to other contexts and species, particularly human helping. A brief overview of the neurobiology of rodent offspring retrieval

is included first. More detailed information can be found in existing reviews on the mechanisms of maternal care (see J. B. Becker & Taylor, 2008; Lonstein & Morrell, 2007; Maestripieri, 1999; Numan, 2007; Numan & Insel, 2003; Rosenblatt, 1992) or reward and decision processes (see Bechara, Damasio, & Damasio, 2000; Damasio, 1994; Kringelbach & Rolls, 2004; Robinson & Berridge, 2003; van den Bos, McClure, Harris, Fiske, & Cohen, 2007; Zak, 2004).

The Ultimate Origins of Altruism in Offspring Care

Existing Ultimate Views From Biology and Economics

Ultimate theories for why altruism is adaptive and how it evolved largely come from biology and economics, which combine behavioral demonstrations of giving, helping, or cooperation with mathematical models that demonstrate the optimality of doing so. Models in nonhuman biology focus on cooperation in eusocial animals or microorganisms, which can be explained by inclusive fitness and direct reciprocity between the highly interrelated and interdependent organisms (e.g., see reviews in Dugatkin, 2007; Strassmann, Zhu, & Queller, 2000; West, Griffin, & Gardner, 2007; Wilson & Hölldobler, 2005). Those addressing human altruism usually assume a modified version of Trivers's (1971) reciprocity model, which focuses upon later, more indirect return rewards to givers (e.g., see reviews in Fehr & Rockenbach, 2004; Gintis et al., 2003; McAndrew, 2002), including "indirect reciprocity" (Alexander, 1987; M. A. Nowak, 2005; M. A. Nowak & Sigmund, 1998; Wedekind, 1998), "costly signaling theory" (CST; Grafen, 1990; Johnstone, 1995; Zahavi & Zahavi, 1997), "competitive altruism" (Roberts, 1998), and "strong reciprocity" (Bowles & Gintis, 2004; Fehr, 2004; Gintis, 2000). These "multilevel fitness" models largely assume that altruism is adaptive toward relatives, direct reciprocators, and other group members because it affords later success in competition for critical resources such as mates, coalition partners, and food. These models are also supported by human anthropological data from the Ache foragers of Eastern Paraguay (Hawkes, 1991) and the Meriam of Torres Strait, Australia (Bliege Bird, Smith, & Bird, 2001; Smith & Bird, 2000), that show that those who share are benefitted later through increased mating success, social standing, and support to their family during resource bottlenecks (Boone, 1998).

Theoretical limitations of biological and economic views.

The aforementioned models surely support the evolution of prosocial behavior, but virtually none attempt to explain active or heroic aid to endangered or distressed targets, except when they include such salient acts in the introduction to demonstrate humans' vast potential for altruism. Moreover, these models do not attempt to address how such motivations or decisions are proximately conveyed, except when assuming that cooperation is hardwired (as in bacteria) or is explicitly mediated through an accounting of favors (in humans). For example, models of strong reciprocity and human cooperation assume a high level of cognition and awareness (e.g., Bowles & Gintis, 2004; Fehr, Fischbacher, & Gächter, 2002; Gintis, 2000), which cannot explain why altruistic responding also occurs in mammalian species like rodents and dogs that lack significant abilities to deliberate. Altruistic responding is also commonly described as a compulsion rather than a decision, albeit one that is context-sensitive. For example, heroes in the Holocaust

Table 1

The 10 Key Factors in Common Between Altruistic Responding and Active Offspring Care

Number	Key factors
1	Care Must Be Extended Beyond Parturient Mothers
2	The Requirement for Motor Competence and Expertise
3	The Adaptive Opponency Between Avoiding and Approaching
4	Attraction Toward Cues of Neonatal Vulnerability
5	The Salience of Neonatal Distress
6	Rewarding, Close Contact Augments the Motivation to Assist
7	Oxytocin Critically Reduces Avoidance and Increases Passive Care
8	The NAcc and DA Motivate Approach and Mediate Conditioned Social Rewards
9	Increasing the Emphasis of the ACC in Caregiving and Altruism
10	The PFC Integrates Multisensory Cues to Promote Adaptive Responding

Note. The proximate review is organized around these ten factors. Other factors surely exist, but these are the most salient contributors to a proposed homology for which extensive evidence already exists. NAcc = nucleus accumbens; DA = dopamine; ACC = anterior cingulate cortex; PFC = prefrontal cortex.

who rescued and hid victims in their own homes reported helping when directly confronted with the other's distress, which produced feelings of empathy, love, compassion, and a personal responsibility that simply compelled action, without "considering risk or thinking about being either lauded or maligned" (Oliner, 2002, p. 127; see also S. W. Becker & Eagly, 2004). Similarly, even bystander apathy studies find that nearly every subject who faced the target alone helped, the vast majority in fewer than 10 s, with few reporting any accompanying thoughts when they did (Darley & Latané, 1968).

Humans may minimize the extent to which they contemplate decisions, and they can surely calculate decisions implicitly, but even young children and chimpanzees exhibit altruistic responding and show limitations in their capacity for helping only when it requires inhibiting personal rewards or significant theory of mind processes (Warneken & Tomasello, 2009b). Moreover, there is no evidence that chimpanzees can anticipate return favors, which further undermines the assumption that helping requires an explicit accounting of favors (de Waal, 2008). Many human economic models also emphasize the rewards that are bestowed upon heroes to support the adaptiveness of such startling acts (e.g., see Macaulay & Berkowitz, 1970; Wong, 2000); however, a focus upon return rewards is also inconsistent with the fact that altruistic responding can be observed across species. For example, rodents retrieve unrelated pups despite the fact that they do not engage in social signaling of beneficence or receive concrete rewards for helping.

Biological and economic ultimate models are also unlikely to capture altruistic responding *per se* because they make at least implicit predictions about who should help the most, which are not consistent with human data. For example, because their models are largely based upon the role of sexual display and male–male cooperation in shaping the evolution of altruism, they at least implicitly favor the expression of altruism in males. Males are more likely to engage in the most heroic forms of altruism, likely because of a more general selection pressure for sexual dimorphism and display. However, the costs of injury or death in the most heroic cases surely surpass the benefits of publicity, medals, or even increased mating success, and females are actually more likely to respond in almost every other prosocial setting, including risky contexts (S. W. Becker & Eagly, 2004). Moreover, human helping is known to shift with hormone status, pregnancy, and exposure to offspring (reviewed below), which is also not consistent with existing multilevel fitness views but is predicted by a caregiving view of altruism (see also Hrdy, 2009). The current review aims to integrate these inconsistencies by building more complex forms of altruism from the primitive form of altruistic responding described herein.

Empirical limitations of biological and economic views.

Extensive laboratory research on cooperation in economics and biology is also not aimed at capturing altruistic responding *per se*, because the paradigms do not entail overt aid to targets in real need—a key precondition for care-based aid. This applies to game-theoretic models (e.g., Gintis, Smith, & Bowles, 2001; M. A. Nowak, 2005; Panchanathan & Boyd, 2004), behavioral economics experiments (e.g., Fehr et al., 2002; Hardy & Van Vugt, 2006; Jerdee & Rosen, 1974; Milinski, Semmann, & Krambeck, 2002; Milinski, Semmann, Bakker, & Krambeck, 2001), and mate preference experiments (e.g., P. Barclay, 2010; Jensen-Campbell, Gra-

ziano, & West, 1995; Roney, Hanson, Durante, & Maestripieri, 2006). Some food-sharing research involves real risk to targets who could starve without the shared resource, but apart from a few anthropological studies (e.g., Bliege Bird, et al., 2001; Hawkes, 1991; Kaplan & Hill, 1985; Smith & Bird, 2000), most of this work is performed in nonhumans (e.g., birds, vampire bats, monkeys, and apes, see Dugatkin, 1997; Preston & de Waal, 2011; Wilkinson, 1990) and almost never in the context of risky deprivation where giving is most expected. The fact that real and immediate need is a key motivator of offspring care, which is rarely included in experimental protocols, could partly explain perplexing null results, such as those of ape food-sharing studies (Brosnan et al., 2009; Hrdy, 2009; Silk et al., 2005; Silk, Paul, Colin, Ernst, & Russell, 2009; Warneken & Tomasello, 2009b). As evidence, when food sharing does occur in social groups of apes it is most often in direct response to begging (Hrdy, 2009; Preston & de Waal, 2011). Moreover, recent experiments revealed greater prosocial behavior in apes when the experimental context was changed to be more naturalistic (Horner, Carter, Suchak, & de Waal, 2011). Neuroimaging studies of charity donation are more directly relevant to altruistic responding because they use targets in real need and positive rewards for giving; in accordance, these studies also find the most pervasive activation of all neuroeconomic paradigms in the neural regions involved in offspring care (Harbaugh, Mayr, & Burghart, 2007; Moll et al., 2006; Tankersley, Stowe, & Huettel, 2007).

Even when neuroeconomic studies do use targets in need such as charities, the results cannot necessarily be extended to explain altruistic responding because the paradigms virtually always entail highly deliberated cost–benefit decisions made with money (for extensive reviews of these studies, see Camerer & Fehr, 2006; Fehr & Camerer, 2007; Moll et al., 2008; Preston & de Waal, 2011; Walter, Abler, Ciaramidaro, & Erk, 2005; Zak, 2004). These studies do find a key role for the domain-general portions of the caregiving system including the orbitofrontal cortex (OFC), nucleus accumbens (NAcc), insula, and amygdala, which supports the idea that primitive affect-regulating structures also subserve complex and explicit decisions to give (Bechara et al., 2000; Damasio, 1994; Preston & de Waal, 2011; Preston & Hofelich, 2012). For example, subjects viewing pictures of former cooperators showed increased activation in the amygdala, NAcc, OFC, insula, fusiform gyrus, and superior temporal sulcus (STS). Despite this overlap, caution is warranted because studying altruism in an explicit, financial context can render decisions more controlled, explicit, calculated, and planned than nonmonetary decisions (J. M. Wang et al., 2012), which may not generalize to the processes required for simple behaviors like retrieval.

Phenomenologically, every-day acts of helping—such as helping a lost toddler at the mall, picking up a neighborhood child who fell off his bike, or surrendering your seat on the bus—do not necessitate a trade-off between helping and monetary reward and may not involve any explicit decision whatever. Such acts are decisions in the nominal sense that all motor acts are decisions, because there were multiple possible options and one was selected through an implicit, cost–benefit calculation. However, as with action selection in motor behavior (Grèzes, Tucker, Armony, Ellis, & Passingham, 2003; Tucker & Ellis, 2001), the existence of other alternatives is characteristic of the situation and not the mind of the

actor—a critical distinction that is greatly underappreciated by models of morality and altruism.

The controlled, cognitive processes required for neuroeconomic tasks may even inhibit the helping impulse by disengaging the emotional-motivational state from the current context (S. L. Brown, Brown, & Preston, 2011). For example, even indirect priming with the concept of money has been shown to make subjects less prosocial and more goal-directed (Vohs, Mead, & Goode, 2006). Moreover, money is a hedonic, incentivizing stimulus like an addictive drug (Lea & Webley, 2006), which can compete against reward-based motivations to help. As evidence, in altruism studies of children and chimpanzees, subjects do not help more when they are clearly offered rewards for helping; 20-month old children actually help *less* in the presence of concrete rewards (Warneken, Hare, Melis, Hanus, & Tomasello, 2007). Moreover, temporal neural regions associated with explicit theory of mind processes are actually deactivated when subjects view rewarding pictures of offspring or romantic partners (Bartels & Zeki, 2000, 2004). Thus, while the offspring care system combines a primitive system for action with cortical modulatory inputs, these inputs can both initiate and inhibit action. Studies are needed that specifically examine the neural correlates of active responding and measure the effect of explicit processes or monetary incentives on the response.

Existing Caregiving Ultimate Views

In contrast to the work described above, psychology has often studied the direct response to another's immediate need (e.g., Batson et al., 1997; Darley & Latané, 1968; Eisenberg & Strayer, 1987; Latané & Rodin, 1969; Warneken & Tomasello, 2009b; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992) and typically does so through a framework that assumes helping evolved from the need for mammals to care for helpless offspring (e.g., Batson, Lishner, Cook, & Sawyer, 2005; S. L. Brown, Brown, & Preston, 2011; de Waal, 2008; Eisenberg & Strayer, 1987; Hrdy, 2009; MacLean, 1985; Marsh, Adams, & Kleck, 2005; Preston & de Waal, 2011). Most of these existing evolutionary theories are not detailed, but a few are more comprehensive, such as Bowlby's (1958) work on the mother-infant attachment system, McDougall's (1908/1923) writing on the parental instinct and tender emotions that propel caregivers to protect vulnerable targets, and Eibl-Eibesfeldt's (1971/1974) views on the behavioral ecology of responding to offspring across species. MacLean (1985) also proposed that key developments in the mammalian brain corresponded with the shift toward altricial care of offspring, including the development of nursing, play, and the separation call. More recently, comparative views have argued that empathy, altruism, and morality exist as extensions of the need for mammals to care for offspring (de Waal, 1996, 2008, 2009) or perhaps particularly the need to provide them with cooperative care (Hrdy, 2009).

Despite general agreement that caregiving pressures influenced the evolution of helping, there is significant controversy over whether these phenomena extend to nonhumans. For example de Waal proposes a "Russian doll" model that assumes gradually increasing prosocial competency across species (de Waal, 2008), while Tomasello and Warneken restrict most

moral behaviors to humans and possibly apes because of their larger emphasis on complex perspective-taking skills (Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2009a, 2009b). Batson holds a caregiving view that is similar to de Waal's but that is even more human-centric than Tomasello's; Batson assumes that motivational altruism is only possible in humans and does not derive from inclusive fitness, reciprocity, or genetic success (see Batson, 2010, 2011). Thus, most theorists make a connection between offspring care and human prosociality, but they vary widely on whether such phenomena are assumed to exist across species and entail higher level cognitive capacities. Moreover, none of these views explicitly address offspring retrieval or its neural bases (but see S. L. Brown, Brown, & Preston, 2011; MacLean, 1985; Preston & de Waal, 2011). Thus, the current review is focused upon the neurobiology of altruistic responding per se, as an encapsulated starting point for the altruistic urge, which can be augmented to address more complex forms of giving that vary more widely across species.

The Current Ultimate View

The maternal instinct, which impels the mother to protect and cherish her young, is common to almost all the higher species of animals. . . . Its impulse is primarily to afford physical protection to the child, especially by throwing the arms about it; and that fundamental impulse persists in spite of the immense extension of the range of application of the impulse and its incorporation in many ideal sentiments. (McDougall, 1908/1923, pp. 69, 74)

An integrated caregiving framework presumes that altruistic responding accommodates direct, inclusive, and reciprocal fitness pressures by assuming that altruistic responding persists as the byproduct of a strong, necessary predisposition to assist one's own offspring. Behaviors designed to care for altricial offspring—particularly nursing and emitting and responding to separation calls—are considered fundamental to the emergence of early mammals from reptiles, who provide virtually no care for their young after hatching (MacLean, 1985; Preston & Hofelich, 2012). In contrast, mammals as distant from humans as rodents clearly respond to the distress of conspecifics with affective empathy and reactive altruism (e.g., Bartal, Decety, & Mason, 2011; Chen, Panksepp, & Lahvis, 2009; Church, 1959; Langford et al., 2006; Masserman, Wechkin, & Terris, 1964; Rice & Gainer, 1962). Some even suggest that ants exhibit a highly similar rescue behavior, as they retrieve trapped conspecifics from under sand or debris (Nowbahari & Hollis, 2010; Vasconcelos et al., 2012). Ant rescue is at least analogous to offspring retrieval in mammals. It may also be homologous because the behavior is thought to derive from perception-action processes similar to mammalian empathy (Buchanan et al., 2012) whereby olfactory stress from the victim is perceived by the giver, who then also becomes hormonally stressed and helps. Without inferring any intentionality, these behaviors at least serve the same function across species, they are adaptive for similar reasons (i.e., kin selection), and they share some rudimentary aspects of the proximate mechanism. Of course, ant brains are different from rodent or human brains, and the ant form of rescue need not operate through maternal care circuits. However, the core commonalities in function, behavior, and mechanism could still represent a homology across taxa to facilitate the

interindividual transfer of emotion or aid, but it could also represent an analogy in which similar mechanisms spontaneously and efficiently emerged to support such behaviors when necessary in social species.

Retrieval as a fixed action pattern (FAP). In this model, offspring retrieval behavior is assumed to represent a sort of “fixed action pattern” (FAP; Lorenz & Tinbergen, 1939) that can be released toward nonoffspring when the conditions are similar to those of offspring need (similar to the “misplaced parental care hypothesis” for avian cooperative breeding, e.g., Hrdy, 2009; Ligon & Burt, 2004). In an often-described FAP, geese sit upon and retrieve eggs that roll out of the nest. The geese do not only retrieve their own eggs but will also retrieve any similar stimuli under maternal conditions. Moreover, “supernormal” stimuli, such as the large eggs of other species, are retrieved even more quickly than their own eggs. This seemingly odd behavior can be taken as an indication that the behavior is proximately encoded with reference to the perceptual features of eggs, rather than through direct reference to their genetic relatedness. Similarly, altruistic responding is assumed to represent a flexible FAP that can be released toward offspring and nonoffspring alike when the situation shares features in common with offspring in need. These features include vulnerability, distress, and immediate need, all of which are not only direct markers of need but also indirect markers of relatedness. Through evolution, these features were shaped to adaptively elicit care toward related or interdependent individuals; however, because they are indirect markers, the releasers can also elicit need toward unrelated individuals and adults (see Figure 4).

As early as 1908, McDougall similarly argued,

when we see, or hear of, the ill-treatment of any weak, defenceless creature (especially, of course, if the creature be a child) tender emotion and the protective impulse are aroused on its behalf. The response is as direct and instantaneous as the mother’s emotion at the cry of her child or her impulse to fly to its defence, and it is essentially the same process. (McDougall, 1908/1923, p. 77)

Importantly, modern biologists do not define FAPs as encapsulated, innate, unalterable or uncontrollable but rather define them as spontaneous, stereotyped behaviors that are hard to control once enacted, are expressed by all typically developing members of the species, and are subject to contextual and epigenetic effects (e.g., see Dewsbury, 1978; Eibl-Eibesfeldt, 1975; Moltz, 1965). Thus, a few decades after McDougall, Slotnick (1967) directly applied Tinbergen’s stickleback FAP to explain maternal care sequences in rodents, carefully specifying that rodent sequences would not be as fixed and hierarchical as in fish, but instead employing a flexible response that was organized by frontal, cingulate, and septal areas. Mammalian neural systems are inherently goal-directed and context-sensitive; therefore, even behaviors assumed to be “innate” are not inflexible or noncognitive; they reflect an implicit decision that maximizes the *goal* of helping, while integrating contextual cues and reflecting the unique developmental history of the giver.

Is altruism an error? The instantiation of an FAP, and interindividual variation in the mechanism for offspring care, would naturally produce “accidental” acts of helping even if altruism were not specifically selected for. For example, one may instinctively reach for an unfamiliar toddler falling when the bus accelerates, and some individuals would be more or less prone to do so, for example, because they are less sensitive to novelty or more sensitive to need. Such accidental giving could also be extended to

total strangers without negatively affecting fitness when the aid is very rare or low cost (like a few dollars or minutes; Neuberger et al., 1997). In addition, it would be very difficult in neural evolution to modify a powerful and necessary motivation to rescue endangered offspring in a way that prevented such accidental extensions to nonkin, without also impeding the primary goal of ensuring offspring survival.

Does this mean that altruism, as an FAP, is a simple tolerated error? Other reasons for the persistence of altruism positively support the behavior, which adaptively balances the needs of self and other. For example, costly, heroic, and dangerous help is already limited by the offspring care mechanism, which is only released toward vulnerable and signaling targets when the observer does not fear for his or her own safety and knows how to respond. The mechanism also produces aid only when the target is in clear need, minimizing the extent to which help is falsely solicited or manipulated (see S. L. Brown, Brown, & Preston, 2011). In addition to these costs that are not actually that costly, altruistic responding also produces positive benefits to givers through the return rewards that were already suggested by prior ultimate-level models (described above), such as inclusive fitness, reciprocity, group fitness, and social signaling. The caregiving system can even provide the mechanism for “strong reciprocity,” without requiring any explicit record keeping (S. L. Brown & Brown, 2006; de Waal, 2008; Preston & de Waal, 2002b). Helping nonkin in one’s own group additionally helps givers by ameliorating the negative effects of displays of distress on health, group harmony, and predation (e.g., see Acebo & Thoman, 1992; Bowlby, 1958; Buchanan et al., 2012; Eimon & Potegal, 1994; Hendriks, 2005; Hoffman, 1981; Murray, 1979; Zeifman, 2001).

Thus, altruistic responding is not simply a mistake. It is necessary for one’s own reproductive success, which makes it difficult to constrain, and it is already balanced by the mechanisms of caregiving in a way that benefits both the receiver and the giver. These conditions render a caregiving-based view adaptive according to all of the conditions outlined by Hoffman (1981). They also accommodate other ultimate-level views by assuming a key role for one’s own inclusive fitness when helping offspring, and by scaffolding later-arriving benefits to helping in cooperative groups upon the key releasers that already existed.

Blurring Proximate and Ultimate Levels of Analysis

In the complex organization of the phylogenetically old and new structures . . . we presumably have neural ladders . . . for ascending from the most primitive sexual feeling to the highest level of altruistic sentiments. (MacLean, 1967, p. 380)

Researchers from different domains typically avoid conflict by theorizing that research on evolution, adaptation, development, and proximate causes represent different but compatible explanations for behavior (Mayr, 1961; Tinbergen, 1963). However, bottom-up views like this one inherently cut across levels of analysis, while avoiding just-so-stories, by focusing upon the evolution and conservation of the nervous system itself (Finlay & Darlington, 1995; Krubitzer, 1995), particularly for mammalian systems that subserve attachment, bonding, and maternal care (Insel & Young, 2001). This biobehavioral continuity constrains the ability of the nervous system to produce novel human adaptations, requiring complex human behaviors to be

built upon preexisting systems (Gould & Lewontin, 1979). This approach efficiently explains not only typical and clearly adaptive behaviors but also unusual propensities that often confound researchers who fail to link the brains and behaviors of humans to those of other species. By analogy, only by knowing how imprinting is encoded at the proximate level could biologists explain why Greylag geese imprint not only to their mothers but also to humans, stuffed animal heads, and even swinging balls (Blumberg, 2005; Lorenz, 1937). Only by understanding the proximate mechanism of offspring care across species can we explain why mammals adaptively retrieve not only their own endangered offspring but also complete strangers and pets in extreme danger. The subsequent major section describes the proximate homology between human altruistic responding and rodent offspring retrieval through 10 key features that are shared between them.

The Proximate Homology Between Offspring Care and Altruism: 10 Key Factors

Overview of the Rodent Neural System for Offspring Retrieval

Much research on the neuroscience of offspring care examines behavioral and neurobiological changes associated with a particularly important behavior—the retrieval of distressed and separated newborns (see reviews in J. B. Becker & Taylor, 2008; Lonstein & Morrell, 2007; Numan, 2007; Numan & Insel, 2003; Rosenblatt, 1992). In a typical pup retrieval scenario, the pup makes ultrasonic vocalizations after becoming separated from his mother and siblings, causing the mother to leave the nest, retrieve the pup, and carry him in her mouth back to the nest where he can resume nursing and huddling (Hofer, 2000; see Figure 1, left panel). Efficient retrieval not only prevents offspring from being located by predators but also ensures that pups have access to the mother's food, as well as her associated close bodily contact and sensory stimulation (Gubernick, 1981; Hrdy, 2009; Mason & Mendoza, 1998)—all of which are critical for proper development of the nervous system in altricial mammals (F. A. Champagne, Francis, Mar, & Meaney, 2003; Meaney, 2001). This arrangement bears striking resemblance to other salient acts of altruism, particularly in active and heroic cases where individuals risk their lives to retrieve a distressed, endangered, and vulnerable stranger in immediate distress or need.

Active offspring retrieval, in contrast to more passive forms of care like nursing and licking, has been shown to rely upon interactions among the prefrontal cortex, amygdala, medial preoptic region of the hypothalamus (MPOA), ventral bed of the stria terminalis (vBST), and ventral striatum (e.g., Numan & Insel, 2003, see Figure 5, acronyms in Table 2). The system can be ostensibly divided into avoidance and approach routes, which are selected when processing a potential target of need depending on the experience and hormonal condition of the observing individual. The avoidance route proceeds from activation of the amygdala to the anterior hypothalamus (AHN) and periaqueductal gray (PAG; bottom of Figure 5) while the approach circuit inhibits the avoidance system through inhibitory connection from the amygdala to the AHN while also motivating approach through

connections from the amygdala to the MPOA/vBST and then to the dopaminergic ventral striatal system.

To extend offspring care to human altruism, the neural regions depicted in the rodent offspring care system (placed on the right of Figure 6) have to be augmented with more recently expanded domain-general cortical processes that are more prominent in human emotional and behavioral systems, permitting developmental and behavioral flexibility and control (on the left of Figure 6; addressed in greater detail below). Human domain-general reward-based decision processes particularly involve connections between the prefrontal cortex (PFC), amygdala, hypothalamus, anterior cingulate cortex (ACC and its subgenual region [sgACC]), and the ventral and dorsal striatum. Anterior cortico-limbic regions (amygdala, OFC, sgACC) output to regions in the brainstem that organize autonomic and motor outputs to the periphery (e.g., through the PAG) and to regions in the hypothalamus that organize offspring care motivation (MPOA) and generate the necessary adrenocortical tone for responding (originating in the paraventricular nucleus). In parallel, efferent projections from the OFC and MPOA activate motor-motivational circuits in the ventral and dorsal striatum, potentiating the approach and retrieval of the distressed other.

While the evidence provided in the below review supports a key role for an avoidance and approach opponency in offspring care, as

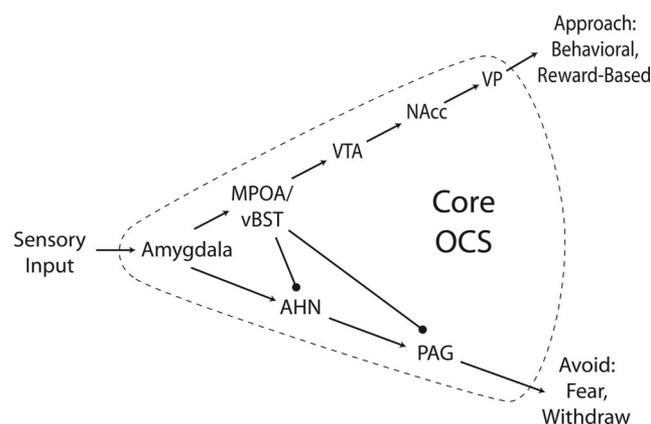


Figure 5. Major elements of the offspring care system (OCS), as described by Numan (2006), Lonstein and Morrell (2007), and others. Initially, for rats that have not been primed by maternal hormones (males, virgin females), the olfactory cues of neonates produce a withdraw response that is mediated by the AHN and PAG. Once the system has been primed by the hormones of pregnancy and parturition, projections from the MPOA/vBST inhibit the avoidance system (AHN and PAG) while activating dopamine-dependent approach responses in the ventral striatum (VTA, NAcc, VP). Note that many of these subregions can participate in both excitatory and inhibitory actions, and in both approach and withdraw, so the current formulation is a generalization based upon existing empirical work for this system per se (e.g., in rodents, the amygdala is involved in both approach and avoidance, e.g., see Lai, Ramiro, Yu, & Johnston, 2005; separable subregions of the PAG are involved in both predator avoidance and prey approach, Comoli, et al., 2012; and glutamatergic dopamine signals can produce both reward and fearlike responses, Faure, Reynolds, Richard, & Berridge, 2008). AHN = anterior hypothalamus; PAG = periaqueductal gray; MPOA = medial preoptic area of the hypothalamus; vBST = ventral bed of the stria terminalis; VTA = ventral tegmental area; NAcc = nucleus accumbens; VP = ventral pallidum.

Table 2

Acronyms for Neuroanatomical Regions, Neuropeptides, and Neurotransmitters Used Throughout the Text

Region	Acronym
Anterior cingulate cortex	ACC
Basolateral amygdala	BLA
Dopamine	DA
Dorsolateral prefrontal cortex	DLPFC
Hippocampus	HPP
Medial amygdala	MeA
Medial prefrontal cortex	mPFC
Medial preoptic area of the hypothalamus	MPOA
Nucleus accumbens	NAcc
Orbital frontal cortex	OFC
Oxytocin	OT
Prefrontal cortex	PFC
Paraventricular nucleus	PVN
Periaqueductal gray	PAG
Prefrontal cortex	PFC
Subgenual region of the anterior cingulate cortex	sgACC
Ventral pallidum	VP
Ventral tegmental area	VTA
Ventrolateral prefrontal cortex	VLPFC
Ventromedial prefrontal cortex	VMPCF

well as the aforementioned neural regions in both offspring care and human altruism, there are notable exceptions in the search for common mechanisms. Evidence is almost completely lacking for the role of the MPOA in human altruism due to the poor spatial resolution in neuroimaging methods to date and the fact that no one was previously looking for this region to participate in altruism. Some evidence even undermines the potential role for the MPOA outside of species-specific behaviors involving perioral sensory cues (Insel & Young, 2001; Numan, Corodimas, Numan, Factor, & Piers, 1988). However, the MPOA does play a more general role in maternal motivation (e.g., in bar pressing for pups; for a discussion see Numan & Insel, 2003), so it may still participate in altruistic responding, particularly for active retrieval. Human neuroscience has investigated the role of the striatum in altruism and cooperation, but the specific role of the ventral pallidum (VP) also still needs to be confirmed with high-resolution scanning techniques.

Because of these caveats, the review below focuses on the more extensive evidence for the role of the dopaminergic nucleus accumbens, anterior cingulate, and orbitofrontal cortex in caregiving and altruism. Of course, terms like “caregiving system” do not imply a fixed system utilized solely for this context. Indeed, most of the caregiving system is part of a larger social behavior network (Newman, 1999), which is also implicated across domains for decision-making and reward processes involving food, drugs, romantic love, and even material goods (e.g., see review in Preston, 2011). It is assumed that the regions that participate in offspring retrieval also perform similar functions in other processes and collaborate whenever one approaches a desired or valued target. In addition, the term “rewards” herein does not refer to concrete compensation for good deeds but rather refers to the reinforcing quality of items that motivate one to approach, which need not be subjectively experienced (e.g., see Berridge & Winkielman, 2003; Damasio, 2000). The factors that are shared between offspring

retrieval and altruistic responding, as evidence for their homology, are presented next.

Factor 1: Care Must Be Extended Beyond Parturient Mothers

For an offspring-care based model to be explanatory, the proposed mechanisms must first explain why both offspring care and altruism are exhibited by males and females, as well as by mothers and nonmothers. Indeed, offspring retrieval in rodents is not only possible for parturient rodent females but also occurs in males and virgin females under the right conditions, and in mothers of other species. For example, virgin female rats do eventually care for pups left in their chamber following a habituation process that can take up to a week, which gradually downregulates the avoidance system (Rosenblatt, 1967). Male rats can also be induced to care for pups through similar exposure techniques or by application of estradiol (Rosenblatt & Ceus, 1998; Rosenblatt, Hazelwood, & Poole, 1996). Evidence also supports the role of the MPOA in directing paternal care in biparental species, such as the California mouse, in which lesions of the MPOA reduce parental care in both males and females (Gubernick, Sengelaub, & Kurz, 1993; Lee & Brown, 2002). In prairie voles, male parental behavior is associated with the release of vasopressin in the lateral septum (Z. Wang, Ferris, & De Vries, 1994), which may be tied to the sexually dimorphic behavior of these males, who defend and protect the female and pups from intruders in the nest (Insel, 1997).

Multiple features of the rodent offspring care system have also been demonstrated in nonrodents including sheep, birds, and non-human primates (Insel & Young, 2001; Maestripieri & Zehr, 1998). For example, the mechanisms that induce postpartum cleaning and kin recognition in sheep are largely similar to those in rodents, relying upon the combined influence of peripartum hormones, the birthing process, and olfactory cues from the offspring (Kendrick et al., 1997; R. Nowak, Keller, Val-Laillet, & Lévy, 2007). The specific role for the MPOA in the response of mothers to separated offspring has also been demonstrated in sheep and is particularly strong in primiparous (first time) mothers (Perrin, Meurisse, & Lévy, 2007; Poindron, Lévy, & Keller, 2007). Primates are often thought to have a reduced requirement for maternal hormones for infant care, because juveniles, nonmaternal female relatives, and males often provide care in these species; however, there are still significant effects of maternal hormones on the interest, care, protection, and treatment of infants (Hrdy, 2009; Maestripieri, 1999; Maestripieri & Zehr, 1998). For example, even though nonperinatal pigtail macaques care for infants, pregnant females increase infant interest and care before giving birth; moreover, experimental application of estrogen increases infant contact (Maestripieri & Zehr, 1998). Even species that are highly divergent from mammals, such as squid, crocodiles, clownfish, and rattlesnakes demonstrate functionally similar behaviors to sequester and protect young from predators during their most vulnerable developmental stage, shortly after birth (Hrdy, 2009). Comparative research has also shown that even humans as young as 14 months and chimpanzees will help another person in discrete need, for example by picking up a dropped item (Warneken & Tomasello, 2009b). Even among Old World langur monkeys, females of all ages—even those too young to give birth—show an intense interest in newborns, responding to their calls and attempting to hold

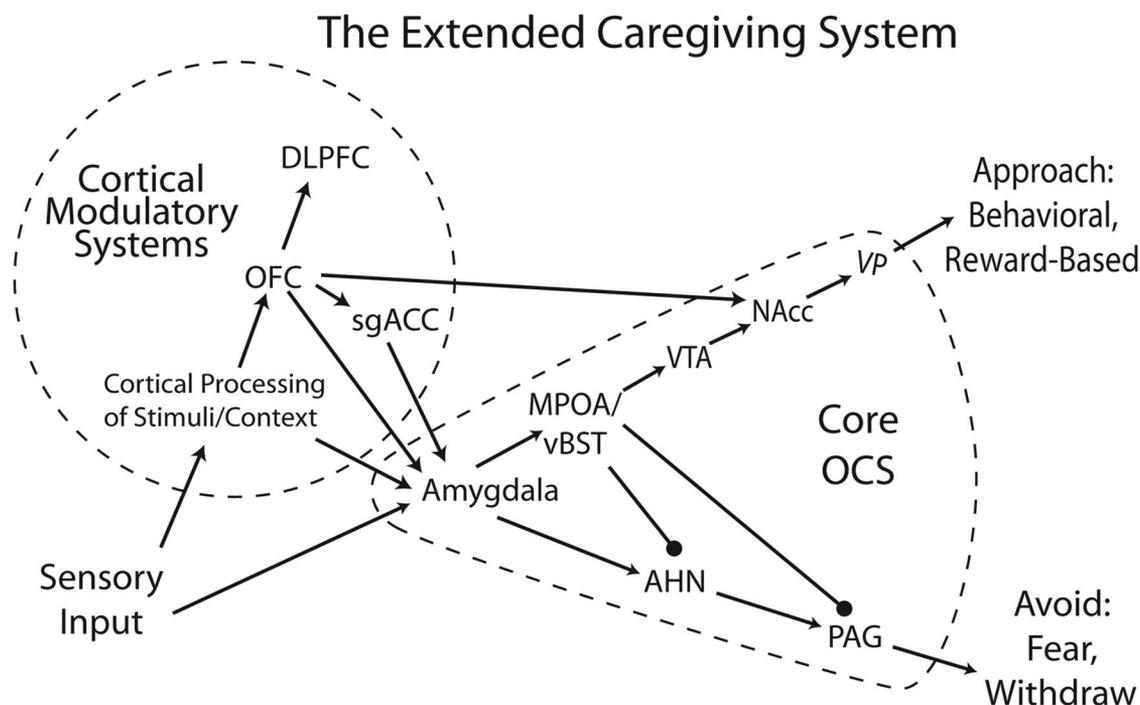


Figure 6. Major elements of the extended caregiving system. The major elements of the rodent offspring care system (OCS) are retained in the more general caregiving system in humans as core neural processes. The sensory input in the human caregiving system is expected to be biased toward visual and auditory cues of distress, but the core rodent OCS still exists in this expanded model, and olfactory inputs likely still play an important role in maternal care, offspring recognition, and bonding between kin and mates. The caregiving system augments the rodent OCS with domain-general reward and decision processes in the neocortex (particularly the PFC), which augment caregiving to account for the complexity of human altruistic responding. Note that only the most important functional connections described in the text are included in the figure; known connections among these areas and to other areas are not shown for simplicity. PFC = prefrontal cortex; DLPFC = dorsolateral prefrontal cortex; OFC = orbital frontal cortex; sgACC = subgenual region of the anterior cingulate cortex; AHN = anterior hypothalamus; PAG = periaqueductal gray; MPOA = medial preoptic area of the hypothalamus; vBST = ventral bed of the stria terminalis; VTA = ventral tegmental area; NAcc = nucleus accumbens; VP = ventral pallidum.

and carry them (Hrdy, 2009). Thus, offspring interest and altruistic helping may be primitive responses that are available across species, breeding conditions, and age, which nonetheless unfold in different ways depending upon the species and their breeding arrangement (Hrdy, 2009; Warneken & Tomasello, 2009b). For example, rodents are particularly likely to respond to unrelated pups because their offspring are normally raised in underground nests in which unrelated newborns are unlikely. In contrast, sheep are born able to walk in large, mobile herds in close proximity with unrelated offspring; thus, mechanisms are required in sheep to ensure that care is quickly directed toward one's own specific offspring. Humans recognize their own kin but also live in interdependent social groups and engage in cooperative breeding with care that is often provided by fathers, siblings, relatives, and friends—conditions that may additionally promote the response to nonkin (Hrdy, 2009).

Specific formulations of the rodent offspring care model are also expected to extend to human mothers and even fathers, though the above evidence suggests that male responses may have a different and more overtly physical quality, may require longer exposure

times to compensate for lacking pregnancy hormones, and may include a larger role for vasopressin. Evidence across monogamous bird, rodent, and primate species (particularly tamarins) does find increases in vasopressin, oxytocin, and prolactin and decreases in testosterone in fathers; the substantial role for prolactin is dependent on combined cues from the mate, pups, and past experience with offspring (Wynne-Edwards & Timonin, 2007; Ziegler, 2000; Ziegler, Washabaugh, & Snowdon, 2004). Human fathers show similar patterns as human mothers in their hormonal and emotional responses to infant cues. Specifically, fathers show higher levels of cortisol in the late, prepartum period and higher levels of prolactin and lower testosterone after birth (Storey, Walsh, Quinton, & Wynne-Edwards, 2000). In that same study, fathers who held a doll for longer and were more concerned during infant crying also had higher levels of prolactin and decreased testosterone. In a similar study, the level of sympathy and desire to help was higher in fathers than nonfathers and correlated positively with prolactin and negatively with testosterone (although fathers increased testosterone during baby cries; Fleming, Corter, Stallings, & Steiner, 2002). In mothers, sympathy, concern, and feel-

ings of attachment during infant distress were associated with higher heart-rate responses to the cries and higher baseline cortisol but larger decreases in cortisol in response to the cries; experienced mothers also showed increased sympathy for cries of pain than hunger (Stallings, Fleming, Corter, Worthman, & Steiner, 2001). Thus, there is growing evidence that some of the mechanisms that have been confirmed in rodents during offspring care also exist in humans, including mothers and fathers.

Despite some assumptions of similarity across species, and between females and males, differences are expected. For example, human females are assumed to be more likely to provide nurturant care, but males, young individuals, and those without children certainly also feel empathy and offer help (see reviews in Batson, 2011; S. W. Becker & Eagly, 2004; de Waal, 2009; Eisenberg & Lennon, 1983; Klein & Hodges, 2001). Life-threatening, discrete, and heroic forms of altruistic responding may occur more often in males, exemplified by the fact that none of the newspaper articles of heroes researched for this article described females. Moreover only 9% of the first 9,000 Carnegie Hero Medals, most of which were for rescuing others from fire or drowning, went to women (S. W. Becker & Eagly, 2004). However, males have also been shown to require more intense cues of distress before responding (Hrdy, 2009), and females are actually favored in all other prosocial behaviors for which a gender difference exists. Females more often care for nonrelatives, have higher rates of volunteering and protective nurturance, and are equally or *more* likely than males to exhibit even risky aid, such as rescuing Holocaust victims, donating kidneys, and volunteering for Doctors of the World (S. W. Becker & Eagly, 2004).

Thus, both altruistic responding and offspring retrieval occur across gender and age, but the quality and ontogeny of these responses differ in important ways that are not fully understood. Perhaps sexual signaling, testosterone, vasopressin, physical strength, and expertise effects render males more likely to respond in discrete moments of highly physical (and public) need, while human female aid is more likely when targets require sustained provisioning, typified by cases like Mother Theresa or Florence Nightingale. For example, in an extensive survey, the vast majority of hospice and high-level volunteers were distinguished by being religious older females whose mothers also volunteered (more so than their fathers; Oliner, 2002). However, one should avoid an oversimplified view of mothers or women as necessarily or uniformly gentle or nurturing. For example, the same mechanisms that support succorant care of offspring also support increased maternal aggression toward intruders (e.g., oxytocin, vasopressin, the central amygdala, and the bed nucleus of the stria terminalis, Bosch & Neumann, 2012). Hrdy (2009) similarly describes the extremely physical and active responses of grandmother nonhuman primates to the attack of grandchildren. Thus, properly motivated females can be extremely active in both nurturing as well as protecting young (see also Mason & Mendoza, 1998), responses that would both be useful in responding to the urgent needs of nonkin. Future work needs to specifically investigate relationships between sex hormones, expertise, and the *quality* of help offered to fully characterize the nature of gender differences in altruistic responding.

Taken together, there is evidence for shared mechanisms of helping kin and nonkin across species and stages of life, which warrants the extension of a caregiving mechanism beyond the mother–offspring context. Thus, a caregiving view is not inconsistent with the fact that males and nonparents often also help. However, there are also known

and likely differences in the precise way that the caregiving mechanism is implemented across species, development, and gender. These differences do not compromise the overall utility of the homology, which does not require, for example, that the exact same receptors be employed in every situation. The homology simply requires evolutionary continuity in the genes and neural arrangements that support such behaviors over time and across species. In a way, this is an ideal situation for a growing science, because we have sufficient evidence that existing neurobiological knowledge can be applied to altruism, but there is still significant work to be done to document the precise mechanisms.

Factor 2: The Requirement for Motor Competence and Expertise

Now that evidence has been provided that a caregiving view does not only apply to mothers, at least one additional important concern should be addressed. Whenever a behavior is suggested to rely upon an ancient or instinctual response that predates humans, the assumption is that the behavior is then “stupid” and uncontrolled, issued without any sensitivity for the context, and at odds with the fact that people actually do *not* always show the instinctual response. Indeed, our many embarrassing cultural and national failures to help others in need attest to the capriciousness of our good nature (cf. Darley & Latané, 1968; Dovidio et al., 2006; Latané & Rodin, 1969). However, highly conserved neural mechanisms are not “stupid.” Rather, they have been refined over hundreds of millions of years to facilitate rapid responses to important events without requiring extensive cognitive deliberation, while preventing overgeneralizations that are damaging to the individual. No exception, the extended caregiving system includes at least two features that ensure that aid is directed when it is needed most and when it will not place the giver at a serious disadvantage: the need for motor competence or expertise and the inclusion of an approach-avoidance opponency. Motor expertise is explained first since it is the most unique component of the current model, which has been overlooked in research on altruism to date and potentially provides substantial power for explaining when people exhibit the compulsion to act.

Active altruistic responding requires a *behavior*, encoded not only by the releasing stimulus but also by the specific and appropriate motor response. Simple and spontaneous acts like pulling a child from danger could rely upon motor programs that are directly encoded in the offspring care system—such as to pull someone away from danger and toward safety. Such a motor response could even be innate. However, more complex situations often require exceptional strength, skill, knowledge, and mediation among competing responses, especially in emergency and heroic scenarios (S. W. Becker & Eagly, 2004). This complexity requires greater expertise and decision making than the simple retrieval of offspring in rodents, which may in turn help explain gender differences in heroism as well as the fact that people often fail to help in complex or dangerous conditions.

For example, human bystanders who fail to help self-report that they did not know “what do to” (reviewed in Dovidio et al., 2006) while expert firefighters report an intuitive understanding of the safety of the conditions, which allows them to respond quickly and adaptively to changing conditions under risk (Zsombok & Klein, 1997). The father from the opening example who jumped onto the

subway tracks was also a construction worker who credited his fast, life-saving response to the oncoming subway car to his work in confined spaces for the Local 79 union (*Laborer's Health and Safety Fund of North America*, 2007). Similarly, Good Samaritans who intervened during crimes were physically larger than matched comparison individuals, had more training to deal with crimes and emergencies, and described themselves as “strong, aggressive, principled, and emotional”; they also reported feeling inspired to act by their “sense of capability founded on training experiences and rooted in personal strength” (Huston, Ruggiero, Conner, & Geis, as cited in *S. W. Becker & Eagly*, 2004, p. 168). Thus, just as the soccer player implicitly determines how hard to kick the ball by integrating the distance to the goal, to the nearest defender, and the condition of an old ankle injury, the presumed altruist implicitly integrates situational factors to determine the mode and likelihood of approaching, even if they are not explicitly deliberated or subjectively available (e.g., How far away is the train? How heavy is the boy? Can I get him out in time?).

Because of this emphasis on procedural knowledge, the dopaminergic striatal pathway is regarded herein as a system that motivates physical approach toward desirable and adaptive targets, such as food and social partners (*Preston*, 2011). As evidence, the MPOA is also involved in locomotion, projecting directly to brainstem locomotor regions (*Swanson, Mogenson, Simerly, & Wu*, 1987). In addition, the dorsal striatum—usually considered the “motor” counterpart to the “reward” function of the ventral striatum—is involved in upregulating maternal care in rodents (*Lonstein, Dominguez, Putnam, De Vries, & Hull*, 2003) and is activated when humans consider loved ones (*Bartels & Zeki*, 2004) or help strangers by giving money (*de Quervain, et al.*, 2004). However, much more empirical research is needed to directly investigate the role of expertise in altruistic responding, as is already being systematically done for other motor behaviors.

Factor 3: The Adaptive Opponency Between Avoiding and Approaching

The second major factor that explains why people do not always help, despite possessing an evolved capacity for responding to need, is the natural avoidance-approach opponency in the offspring care mechanism. As described in the overview of the offspring care model (see *Figure 5*), the rodent model includes a natural opponency between the “default” avoidance response that prevents individuals from approaching novel and unfamiliar stimuli, while facilitating approach for targets that are familiar and under conditions that are adaptive. This arrangement makes it rare for observers to respond when they are scared or when conditions are dangerous, while still facilitating responses when the observer is confident in his or her ability to help and when the target is bonded, familiar, or related—conditions that are consistent with the *a priori* requirements for an adaptive giving instinct (*Hoffman*, 1981).

In rodents, extensive evidence supports a momentous shift in mothers from an avoidance to an approach motivation toward pups, as first posited by *Rosenblatt and Mayer* (1995). Under nonmaternal conditions, the avoidance response adaptively prevents rats from caring for unrelated offspring and more generally from approaching novel and potentially dangerous stimuli (lower portion of *Figure 5*). Normally, an active avoidance system is in

place in males and virgin, nulliparous (never given birth) females who initially avoid pups, sometimes even attacking and cannibalizing the novel stimuli (*Rosenblatt*, 1967). This avoidance has been shown through extensive work to be subserved by serial connections between the accessory olfactory bulb (AOB), medial amygdala (MeA), anterior hypothalamic nucleus (AHN) and lateral periaqueductal gray (PAG) of the brainstem (*Fleming & Luebke*, 1981; *Lonstein*, 2005; *Numan*, 2006; *Numan & Numan*, 1996). In fact, the delay to respond can be directly increased by stimulating the MeA (*H. D. Morgan, Watchus, Milgram, & Fleming*, 1999) or can be decreased by ablating it (*Fleming, Vaccarino, & Luebke*, 1980; *Numan, Numan, & English*, 1993), inducing anosmia (*Fleming & Rosenblatt*, 1974), or applying maternal hormones (*Siegel & Rosenblatt*, 1975).

During normal rodent pregnancy and parturition, the “default” avoidance of novel pups is shifted to a motivated approach response through a series of neurohormonal processes that render neonatal pups highly attractive and rewarding, causing the parturient dam to retrieve and huddle even unrelated, isolated, or separated pups (upper portion of *Figure 5*). During pregnancy, estradiol and prolactin increase (*Rosenblatt*, 1994) and estrogen receptors in the MPOA and MeA are upregulated (*Giordano, Siegel, & Rosenblatt*, 1991), decreasing the aversion to pups while increasing the attraction toward them (*Kinsley & Bridges*, 1990). After delivery of the litter, this primed system is additionally affected by high levels of oxytocin (OT) and low progesterone, which further prime the MPOA to fully inhibit the avoidance system (by inhibiting the AHN and PAG) and to activate the approach system through connections to the ventral tegmental area (VTA). Similar transitions from avoidance to approach can also be demonstrated in virgin females and males through a process of habituation, in which the nonmaternal rodent gradually comes to care for pups left in their chamber over the course of a week (*Rosenblatt*, 1967; *Rosenblatt & Ceus*, 1998; *Rosenblatt, Hazelwood, & Poole*, 1996).

According to *Numan's* model of active maternal care in rodents (e.g., see *Numan*, 2006; *Numan & Insel*, 2003; *Numan, Numan, Schwarz, et al.*, 2005; *Numan & Stolzenberg*, 2009; *Stolzenberg & Numan*, 2011), the expression of behaviors like pup retrieval and nest building are causally linked to the MPOA, which both inhibits the avoidance system and activates the reward-based approach system. Activity in the MPOA projects through dorsolateral ascending fibers to the VTA, which causes dopamine (DA) release. The DA inhibits activity in the nucleus accumbens (NAcc), which releases the downstream ventral pallidum (VP) from tonic inhibition via GABAergic projections from the NAcc. The inhibition of the NAcc releases the downstream VP and motor output regions and adds to prevailing signals from the basolateral amygdala (BLA) and prefrontal cortex (PFC), which acted on both the NAcc and VP (associated with the presence of pups), producing the active response to pups. (Note that DA effects on the NAcc are complex and diverse, not only including inhibition of the NAcc but also activation and modulation of voltage-dependent conductances, e.g., see *Nicola, Surmeier, & Malenka*, 2000.) Lesions of this system specifically affect retrieval, leaving intact the passive maternal behaviors such as nursing and huddling, as well as the motivation to approach pups and the motor skills necessary to retrieve and carry food (*Numan & Insel*, 2003; *Numan, Numan, Schwarz, et al.*, 2005). The MPOA also mediates more appetitive

features of maternal care, being necessary for the conditioned preference to be in the same place as the pups and the operant barpressing response to obtain access to them.

Data on this avoidance-approach bifurcation in the human motivation to help is more scant and must be inferred from a wide variety of indirectly related sources (see Moll & Schulkin, 2009). For decades, psychologists have assumed bifurcating neural and behavioral systems for appetitive versus aversive motivation, which have been particularly applied to individual differences in personality and psychopathology. Gray initially associated the septohippocampal system, its monoaminergic projections from the brainstem, and its efferent projections to the frontal cortex with a behavioral inhibition system (BIS) and catecholaminergic and dopaminergic pathways with a behavioral activation system (BAS; Carver & White, 1994; Gray, 1970). These two systems (BIS and BAS) are now also associated with asymmetrical activation in the right and left hemispheres, respectively (Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Sutton & Davidson, 1997). Regarding the specific regions of Numan's active offspring care system, human neurobiology does support the role of the amygdala in processing avoidance responses to novelty as in the offspring care system. For example, a patient with bilateral damage to the amygdala is specifically impaired at processing facial expressions of fear, does not perceive others as "untrustworthy," and is extremely approachable in social situations (Adolphs, 2004). This area is also activated in healthy control subjects who view extremely untrustworthy or extremely trustworthy faces in the scanner (Engell, Haxby, & Todorov, 2007; Said, Baron, & Todorov, 2009; Winston, Strange, O'Doherty, & Dolan, 2002). There is also a demonstrated inverse relationship between OT and amygdala activity during empathy and altruism paradigms (below). However, the role of the amygdala must not be oversimplified as it is required for both avoidance and approach motivation in the offspring care system (Numan, 2011) and for processing positive and negative information in humans (e.g., see Everitt, Cardinal, Parkinson, & Robbins, 2003; Everitt, Morris, O'Brien, & Robbins, 1991; Hamann & Mao, 2002; Said et al., 2009).

In human parents, the appropriate response to offspring cries also seems to rely upon prior caregiving experience, as was demonstrated for the parturient females or habituated males and virgin female rodents (e.g., Fleming et al., 2002; Stallings et al., 2001). The simple behavior of retrieving neonates as described for rodents actually occurs quite often in humans (via the hands instead of the mouth), as children are routinely retrieved and nurtured after a fall or grabbed from potential dangers like cars, steps, or strange dogs. However, no known studies have specifically examined these overt retrieval responses in humans, despite their great frequency and importance for survival. Research on bystander apathy, in which observers fail to respond to the immediate need of a stranger (Darley & Latané, 1968; Dovidio et al., 2006; Latané & Rodin, 1969; Zahn-Waxler, Radke-Yarrow, & King, 1979), do support an underlying opponency, as people fail to respond to strangers in the presence of high uncertainty, more capable responders, or when they fear retribution—conditions that pervade culturally salient and embarrassing cases of inaction, such as during domestic abuse or genocide. While there are many instances in which our fear prevented us from acting when we should have, this natural opponency also prevents the instinct to help from getting us into trouble. Knowing how this balance is achieved, we

can perhaps help to encourage aid for targets who genuinely need assistance but whom people may naturally tend to avoid.

Factor 4: Attraction Toward Cues of Neonatal Vulnerability

Related or not, infants can be powerful sensory traps. (Hrdy, 2009, p. 211)

Mammals, due to their altricial developmental system, are particularly attuned to signals associated with neonatal immaturity and distress, which is thought to facilitate the motivation to respond to one's own offspring, while promoting aid toward similarly distressed, vulnerable, and helpless nonrelatives in need (e.g., see Batson, 2010; Hrdy, 2009; Preston & de Waal, 2002b). Organisms in general direct attention and aid toward neotenus young—individuals who are young and immature but also older individuals who are similarly rendered vulnerable by advanced age or disability. For example, the often-quoted case of the man leaping onto the subway tracks to save someone from an oncoming car involved a teenage boy who had just suffered an epileptic seizure (Buckley, 2007). Multiple of the most cited cases of altruism involve apes rescuing young children or injured animals (de Waal, 1996, 2008, 2009; O'Connell, 1995), animals saving or adopting the offspring of a relative, group member, or other species (Hrdy, 2009), or people hiding children from soldiers during the Holocaust (Oliner, 2002). The rodent offspring care literature suggests that these are not just reporting biases but reflections of a propensity to attend and respond to neotenus targets that share features with babies who are immature, cute, bonded, and vulnerable (see also Batson, 2010, 2011).

Evolutionary models have long assumed that the positively attractive features of dependent offspring adaptively increase attention toward these biologically salient stimuli (Brosch, Sander, & Scherer, 2007; Kringelbach et al., 2008), providing the incentive for observers to approach and care for them, known as "*Kindchenschema*" in German (Lorenz, 1943, 1971, see Figure 7), or "infant appeal" in English (e.g., Zeanah, Boris, & Larrieu, 1997). Similarly, the Epio culture in Micronesia has a specific word ("*bico*") to refer to creatures like babies and small mammals that are cute, sweet, and need protection and that motivate us to approach and cuddle them (Schiefenhövel, 1988). Newborn human infants are not only diminutive in size but also have distinct facial features such as disproportionately large eyes and heads that have been increasingly exploited to make animated characters and toys more attractive (Hinde & Barden, 1985). Zebrowitz and colleagues have argued for an ecological Gibsonian affordance in face perception that causes "babyface overgeneralization," in which even adults with baby-like attributes are rated and responded to as if they are more submissive, warm, honest, and weaker (Zebrowitz & Montepare, 2008). Demonstrating some universality, these ratings are somewhat similar between Americans and culturally isolated Tsimane' individuals in the remote Bolivian rainforest (Zebrowitz et al., 2012). Fear expressions have also been posited to attract aid and attention because features of the expression are similar to those of immature, baby faces (Marsh & Kleck, 2005; Marsh, Kozak, & Ambady, 2007). Thus, the attractive qualities of others, particularly dependent offspring, are thought to contribute to the

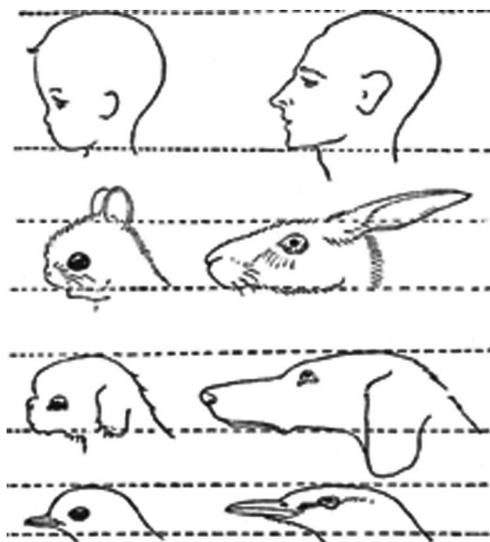


Figure 7. The original figure from Konrad Lorenz depicting *Kindchenschema* or infant appeal. Lorenz stated in his Figure 4 caption that the image represents, “The releasing schema for human parental care responses. Left: Head proportions perceived as ‘loveable’ (child, jerboa, Pekinese dog, robin). Right: Related heads that do not elicit the parental drive (man, hare, hound, golden oriole).” From *Studies in Animal and Human Behaviour: II* (p. 155), by K. Lorenz, 1971, Cambridge, MA: Harvard University Press. Copyright 1950 by Springer.

motivation to sacrifice for them, as is needed for continuous provisioning in humans.

This positive attraction toward neonates is not specific to humans. Even rodent dams appear not to be simply enacting innate and “cold” motor programs when they retrieve pups (as assumed by [Batson, 2010](#)); they are motivated toward and rewarded by the pups, even when they are unrelated (see also [Insel & Young, 2001](#)). Indicating the strength of this drive toward neonates, hormonally primed dams do not just cease to avoid pups, they actually prefer them, seeking the soiled bedding of litters over clean bedding ([Bauer, 1983](#); [Fleming, Cheung, Myhal, & Kessler, 1989](#)), working to gain access to pups in an operant chamber ([Lee, Clancy, & Fleming, 2000](#)) and even preferring pups to cocaine the week after parturition ([Mattson, Williams, Rosenblatt, & Morrell, 2001, 2003](#)) as long as they were permitted full contact with the pup ([Magnusson & Fleming, 1995](#)). This preference for pups over hedonically stimulating drugs is associated with interactions between the amygdala, paraventricular nucleus (PVN), and ventral striatum. Nonhuman primates also show such appetitive responses, as virgin marmosets will bar-press to gain access to infant stimuli if late-pregnancy hormones are applied ([Pryce, Dobeli, & Martin, 1993](#)).

Supporting the role of the offspring care system in this incentive salience process, multiple components of the system have been identified through human neuroimaging to be activated during social attraction. The most relevant data examine the neural basis for *Kindchenschema* in nulliparous women, finding that “baby schema” images, which are also rated “cuter” and elicit a stronger caregiving motivation ([Glocker, Langleben, Ruparel, Loughead, Gur, & Sachser, 2009](#)), activate the NAcc more than control

images, leading the authors to posit that the reward-based, appetitive mesolimbocortical system can support altruism beyond kin ([Glocker, Langleben, Ruparel, Loughead, Valdez, et al., 2009](#)). The domain-general mesolimbocortical components of the system (VTA, striatum, medial PFC, ACC, insula, plus dorsolateral prefrontal cortex [DLPFC] and primary motor area) were all more strongly activated in first-time mothers by pictures of their own versus unfamiliar infants; activation in nigrostriatal regions was even stronger when those faces were happy ([Strathearn, Li, Fonagy, & Montague, 2008](#)). The medial OFC is also rapidly activated in response to pictures of newborns, even those who are unrelated and compared to attractive adult faces ([Kringelbach et al., 2008](#)). The NAcc is activated when people work to maintain visual access to attractive faces ([Aharon et al., 2001](#)) and the VTA, caudate, putamen, and insula are activated when people view targets of intense, passionate love ([Aron et al., 2005](#); [Bartels & Zeki, 2000](#); [Fisher, Aron, & Brown, 2005](#)). The caudate, putamen, insula, and anterior cingulate (both dorsal and sgACC) are commonly activated by intense romantic and maternal love, while the OFC and PAG are specifically activated by maternal love, perhaps placing a more important role for OT-dependent processes in the maternal context ([Bartels & Zeki, 2004](#)). Supporting the avoidance-approach framework (above), the amygdala, posterior cingulate, and multiple temporal regions associated with emotion and social cognition are actually deactivated when subjects view pictures of offspring or romantic partners ([Bartels & Zeki, 2000, 2004](#)). Note that multiple of these neural regions are located in the dorsal rather than ventral striatum, perhaps reflecting the highly active urge to approach the targets in these tasks (e.g., your crying baby or new love).

Thus, neonates appear to be naturally rewarding and motivating, ensuring that they are natural targets of affection and help. Despite this, care can also be provided through stimulus-driven, habitual, or planful means, particularly after the bond is established. For example, female rodents begin to prefer cocaine to the pups after a few weeks but provide equally good care of the pups even after the intense motivation subsides. Human fathers report requiring extensive time to bond with their offspring, even when they provide care throughout the early neonatal period (e.g., see [L. Barclay & Lupton, 1999](#)). Thus, care appears to be positively directed toward neotenous young, particularly for maternal or bonded individuals, but not all natural provisioning is empathically driven, and even motivated caregivers may withhold care under conditions that tip the scales toward avoidance (e.g., when a parent is near).

Factor 5: The Salience of Distress

Evidence across taxa suggests that offspring care is strongly motivated not only by the presence of neotenous cues but also by the specific indication of distress, particularly in vulnerable and bonded targets. Even crocodiles and alligators have a graded “distress call” that can elicit maternal protection (see [Gordon, 1977](#); [Staton, 1978](#)). Mother birds are also highly motivated by the begging calls of their hungry young, which prompt them to find and deliver food ([Kilner & Johnstone, 1997](#)). Some avian species exploit this sensitivity by placing their eggs into the nests of other species (brood parasitism), which then hatch and make particularly loud and aversive begging calls to ensure feeding ([Zahavi, 1979](#)).

Common Cuckoo chicks can mimic the begging calls of up to eight host young (Kilner, Noble, & Davies, 1999), while the “screaming” cowbird gives more intense calls when experiencing similar hunger to the host’s own offspring (Lichtenstein, 2001). These cues of distress must be particularly hard to ignore if they can trigger giving that directly diminishes the success of the mother’s own offspring.

MacLean argued that the separation call, along with nursing and play, were critical social developments in early mammals that ensured contact between mothers and their altricial offspring, driving changes in the thalamocingulate in the taxonomic split from reptiles (MacLean, 1985). The specific separation calls have been extensively studied in rodents and promote the maternal retrieval and huddling response (Panksepp, 1986, 1998). In primates, ape mothers are described as being extremely sensitive to cues of need in their young, constantly shifting the babies’ clutching bodies as they walk to ensure the offspring are comfortable and attached (Hrdy, 2009). Carel van Schaik describes orangutan mothers as responding to infant cues of need “with the attentiveness of a private nurse and the patience of an angel” (quoted in Hrdy, 2009, p. 70).

In humans, cues of distress are largely perceived through auditory and visual channels (in contrast to the olfactory and very high-pitched auditory cues in the rodent system; Broad, Curley, & Keverne, 2006; Insel, 1997). Perceived distress that is rapidly detected by fast perceptual routes through the amygdala can orient observers toward the target, while slower routes proceeding from primary sensory to prefrontal regions can provide specific, contextualized information about the target and situation (LeDoux, 1996). Auditory cues are known to be particularly salient in the peak range of detection (approximately 2–5kHz, Fletcher & Munson, 1933), which is thought to be adaptively tuned to the most distressing elements of human baby cries (3–4 kHz range; Gustafson & Green, 1989). This same spectral region corresponds to the singer formant region, characteristic of vocalizations that convey and evoke the most emotion in songs (Beeman, 2005), suggesting that adult cries may also contain compelling features that motivate aid. The extended offspring care system has been shown to be also implicated in the human response to distress, as the OFC, hypothalamus, dorsal and ventral striatum, lateral septum, and sgACC are all activated when human mothers hear infant cries (Lorberbaum et al., 1999, 2002).

Despite widespread agreement that distress cues do motivate aid, there appear to be multiple motivational and subjective responses to distress, perhaps reflecting differential activation of the avoidance and approach routes described above. For example, research on the empathy-altruism hypothesis emphasizes positive sympathetic, compassionate, and tender feelings for distressed targets—particularly vulnerable and needy ones—which are associated with a parasympathetic heart rate deceleration or “orienting response” (e.g., see Batson, 2010, 2011; Eisenberg & Miller, 1987). However, perception of another’s distress has also been associated empirically (Acebo & Thoman, 1992, 1995; Buchanan et al., 2012; Krebs, 1975; Levenson & Ruef, 1992) and theoretically (Bowlby, 1958; Preston & de Waal, 2002b) with a contagious and personally distressing response that motivates care because the observer wants to terminate the cue; this response produces a divergent physiological response that includes sympathetic or heart rate *increases* while also predicting aid (see review in Bat-

son, 2011). The aversive properties of distress are also supported by the fact that cries can be used as experimental stressors (V. Morgan, Pickens, Gautam, Kessler, & Mertz, 2005) and often produce very negative responses including anger, horror (Preston, Hofelich, & Stansfield, 2012), and even physical abuse (Potegal & Knutson, 1994). Adding to the complexity, sympathetic and aversive responses to others’ distress are statistically highly intercorrelated and usually co-occur (see Preston & Hofelich, 2012). Evidence for the complicated affect elicited by crying, a recent Japanese DVD is filled with clips of young women weeping as they relay traumatic events to elicit feelings of masculinity and power in men who come to view themselves as their protectors (Haworth, 2010).

Paradoxical effects of perceiving another’s distress can be resolved through careful consideration of the proximate mechanism and the ecological factors that dictate when attention, arousal, and action are warranted. According to the perception-action model, all interpersonal understanding requires activation of the observer’s own personal neural representations for the state of the target (Preston & de Waal, 2002b), but this resonance only needs to occur at a neural level and does not have to produce subjective distress or self-focus in the observer; in fact, positive and compassionate states should occur during caregiving in the presence of neonatal cues of vulnerability and need (see Batson, 2010; Preston & Hofelich, 2012). Truly neonatal cries may evoke particularly tender states, as they are softer in amplitude and more “pathetic” or “cute” than the cries of juveniles or adults. From the perspective of competing demands to avoid or approach targets, neonates are helpless and thus unlikely to frighten or endanger the observer.

Further reflecting the need for expertise and competence to respond, altruistic responding likely requires a sense of dominance and agency that allows the observer to feel in control enough to respond (Penner, Fritzsche, Craiger, & Freifeld, 1995; Preston & Hofelich, 2012). Such a state is consistent with the demonstrated physiological upregulation in testosterone, cortisol, or autonomic tone in observers of distress (see also Buchanan et al., 2012; Shirtcliff et al., 2009). In accordance, observers watching emotional videos who felt more empathic concern and less personal distress also had greater OT increases, but actual donations were higher in women and more associated with increased plasma cortisol (Barraza & Zak, 2009). Observers of a stressful speech also had increased sympathetic nervous system responses that correlated with their trait empathic concern for the speakers (Buchanan et al., 2012). Mothers also reported sympathy, concern, and attachment toward crying babies when their baseline cortisol was higher and heart-rate increased (but cortisol decreased) in response to the cries (Stallings et al., 2001). Mothers responded to the cries of their own baby with an increased heart rate and skin conductance, but responded with a decelerating orienting response to the cries of strange infants (Wiesenfeld & Klorman, 1978). More research is needed to parse these physiological correlates of empathy and helping, but perhaps OT is associated with tender and sympathetic feelings that predispose nurturant care, while autonomic and glucocorticoid systems are additionally necessary to upregulate active aid.

Ecologically, more aversive and negative responses are most likely when the observer does not believe the need is genuine or does believe it is but cannot channel the mobilized energy into help (e.g., because they are a bystander, cannot control the situation, do

not know how to help, or cannot). For example, new world cooperative breeders such as marmosets and tamarins share food with helpless and begging babies but offer less to juveniles who begin begging in increasingly aversive ways and eventually start stealing the food (Hrdy, 2009). Also, child abuse largely occurs when dependent offspring signal distress that cannot be terminated to caregivers who are frustrated and stressed (Potegal & Knutson, 1994). Over a hundred years ago McDougall associated vulnerable offspring with a fundamental tender emotion but went on to say that,

the distress of any child will evoke [the tender emotion and protective response] in a very intense degree . . . [some] cannot sit still, or pursue any occupation, within sound of the distressed cry of a child; if circumstances compel them to restrain their impulse to run to its relief, they yet cannot withdraw their attention from the sound, but continue to listen in painful agitation. (McDougall, 1908/1923, p. 76)

Thus, distress cues adaptively motivate positive care toward genuine need in offspring who can be helped. Conversely, these cues become aversive and prevent action when the need is disingenuous, exploitative, costly or when the observer's actions are unlikely to help. Future work needs to examine the qualitative perception of cries from individuals across ages and types of need, including the "damsel in distress," while segregating the influence of attractive versus aversive qualities. Research also needs to directly compare the effects of social bonding, immediacy of need, and ability to help on the perception of distress cues to provide a more complete picture of the response to distress, which can be both compassionate and aversive. In addition, neuroimaging work can determine whether the substrates already identified as belonging to the approach versus the avoidance motivation toward pups is similarly implicated in the positive versus the negative responses to cues of need.

Factor 6: Rewarding, Close Contact Augments the Motivation to Assist

They did not ask any questions, and I did not think that they thought of themselves as doing anything heroic when they saved my life. They did it out of love. (rescued Holocaust survivor, quoted in Oliner, 2002, p. 123)

Both active and passive responding in the offspring care system requires close contact between the giver and target to create and reinforce the social bond, along with the likelihood of approaching and retrieving. Touch is necessary between rodent pups and dams to motivate and sustain maternal care, including retrieval, licking, and quiescent nursing (Lonstein & Morrell, 2007). The feedback system between touch, social bonding, and social motivation is likely mediated by opioid systems, positive interactions among the OFC, sgACC, and ventrolateral PFC, and decreases in the amygdala and temporal pole (e.g., Broad et al., 2006; Francis et al., 1999; Ochsner & Gross, 2005; Phelps, 2004). Opiate effects associated with pleasant affective experiences are also implicated in maintaining social bonds, as they reinforce the rewards of interacting with and giving to others (Broad et al., 2006; Panksepp, 1998; Taylor et al., 2000). Activation of the opiate system during parturition and nursing is thought responsible for the positive affect associated with caregiving. As evidence, application of opioid agonists across species increases passive and active mater-

nal behaviors, while opiate-antagonists reduce caregiving, protection, retrieval, and grooming, and generally eliminate the "focused preoccupation" of primate mothers with their infant (reviewed by Broad et al., 2006, p. 2203, see also Panksepp, 1986). In recent phylogenetic history, the strict dependence on maternal hormones associated with pregnancy and parturition is thought to have declined while the dependence on more domain-general, reward-based DA and opioid systems for caregiving increased, as the expanded neocortex allows for more flexible provisioning across a longer period of time (Broad et al., 2006).

In primate social behavior, distressed individuals are consoled by social partners who approach, touch, and groom them, which alleviates the victims' distress, soothes the consoler (Fraser, Stahl, & Aureli, 2008; Romero, Colmenares, & Aureli, 2009), and limits the effects of prolonged distress on the nervous system and group harmony (Sapolsky, 2006; Sapolsky, Romero, & Munck, 2000). For example, social grooming in monkeys significantly reduces heart rate above and beyond the effects of simply lying still (Aureli, Preston, & de Waal, 1999). Under crowded conditions, when tensions run high, primates appear to use grooming, close contact, and self-touching to reduce tension and curtail social conflict (de Waal, Aureli, & Judge, 2000). Directly implicating neurophysiological rewards, female macaques given an opiate antagonist have poor maternal care and allogroom less (Martel, Nevison, Rayment, Simpson, & Keverne, 1993). Peripherally, dedicated afferent fibers have been identified on human hairy skin that convey the affective sensations of pleasant touch, presumably to signal these important tactile cues during affiliative social behaviors (Löken, Wessberg, Morrison, McGlone, & Olausson, 2009).

Research with humans has also demonstrated positive effects from nursing, such as a calmer mood, better stress regulation, decreases in sympathetic arousal, and increases in sociability and maternal responsiveness (reviewed in Taylor et al., 2000). These effects are presumed to result from the physiological release of OT as well as the close physical contact required by the behavior. In addition, touch has been used effectively to ameliorate the symptoms of multiple psychopathologies including autism, attention-deficit/hyperactivity disorder, depression, and anxiety, and touch improves the responses of hospital patients (Field, 1996; Khilnani, Field, Hernandez-Reif, & Schanberg, 2003). Pleasant touch has been identified using functional magnetic resonance imaging (fMRI) as being specifically represented by elements of the offspring care system that code for the context-dependent rewards of stimuli (i.e., the OFC and ACC; Francis et al., 1999; Rolls et al., 2003). Similar to the aforementioned results in nonhuman studies, human women who are given an opioid receptor antagonist withdrew from social interaction and enjoyed it less while the pleasant touch associated with massage increased OT, even in women who had not given birth (see Taylor et al., 2000), in groups of mixed gender (Rapaport, Schettler, & Bresee, 2012) and in groups consisting only of men (Carter et al., 2007).

One drawback of the underlying mechanism for the empathic transfer of emotion, and the benefits of subsequent interpersonal touch, is that seemingly altruistic responses like approaching and contacting a distressed target are sometimes generated more for the benefit of the contagiously distressed giver than for the target. For example, juvenile monkeys can be observed piling on top of one another when one is distressed, seeking reassurance from one

another as the negative affect spreads (de Waal, 2008). A study of human children enduring cancer treatment found that *less* empathic parents made more close body contact with their sick children, which in turn increased their children's subjective pain (Penner, Harper, & Albrecht, 2011). Most research assumes that poor social development causes observers to fail to respond to need or to even respond with aggression (e.g., see Maestripieri, 1999; Numan, 2011); however, individuals with preoccupied attachment styles may actually do the opposite, clinging to others for their own benefit because of their hypervigilance to distress (Brennan & Shaver, 1995; Pistole, 1994). Thus, seemingly empathic but misdirected acts of helping can also arise from the natural arrangement of our intersubjective nervous system. Moreover, because touch is reinforcing to the giver, these unhelpful responses can actually end up making the giver feel better, reinforcing their desire to respond that way in the future, despite the negative consequences for the recipient.

Taken together, close contact and touch are soothing to both distressed targets and approaching observers, which reduces the stress of both participants, promotes bonding, and increases the likelihood of a future approach. This is an important ontogenetic component of both active and passive care, in which individuals learn positive, reinforcing physiological consequences of approaching and contacting others that can be either fostered or compromised in early development. The neurohormonal processes that help shift the system toward approaching the target and that promote the social bond are addressed next.

Factor 7: Oxytocin Critically Reduces Avoidance and Increases Passive Care

The most examined proximate mediator of prosocial behavior to date is oxytocin (OT), a hormone and neuropeptide that facilitates maternal care and social bonding across taxa (Insel, Young, & Wang, 1997). During pregnancy, particularly at parturition when mothers give birth, OT increases not only in rats (Landgraf, Neumann, Russell, & Pittman, 1992) but also in sheep (Kendrick, Keverne, Baldwin, & Sharman, 1986) and humans (Chibbar, Wong, Miller, & Mitchell, 1995).

The rodent literature includes strong evidence that OT is involved in maternal motivation and bonding, including in supporting offspring retrieval per se, at least initially. OT in rodents is thought to reduce avoidance while fostering passive maternal behaviors such as crouching, kyphosis, licking, and nursing through processes mediated by the central nervous system (J. B. Becker & Taylor, 2008; Lonstein & Morrell, 2007; Pedersen, Vadlamudi, Boccia, & Amico, 2006). There are receptors for OT in multiple regions of the rodent offspring care system including the VTA, MPOA, NAcc, and amygdala (de Kloet, Voorhuis, Boschma, & Elands, 1986; Pedersen, Caldwell, Walker, Ayers, & Mason, 1994). In addition, OT infusion can directly activate the mesolimbocortical DA system presynaptically (Schulz, Kovács, & Telegdy, 1979).

As evidence that OT is required for proper care of offspring, lesions of the OT-rich paraventricular nucleus (PVN) can produce avoidance and even cannibalism in postpartum females (Insel & Harbaugh, 1989). While these lesions more typically affect passive maternal behaviors (F. Champagne, Diorio, Sharma, & Meaney, 2001; Pedersen & Boccia, 2003), OT or vasopressin V1a receptor

antagonists infused into the MPOA during parturition can also impair pup retrieval per se (Pedersen et al., 1994) as can kainic acid-induced lesions of the PVN (Olazabal & Ferreira, 1997). However, effects on retrieval are more pronounced in the first few days after parturition and appear to stabilize once the dam has had extensive contact with the pups (Insel & Harbaugh, 1989; Numan & Corodimas, 1985; Olazabal & Ferreira, 1997; Pedersen, Caldwell, Peterson, Walker, & Mason, 1992).

Genetically mediated effects of oxytocin have also been demonstrated. For example, rapid changes in behavior toward pups may be facilitated by fosB, an immediate early gene that is thought to potentiate care through OT-related processes in the preoptic area and broader offspring care system (e.g., striatum, amygdala, olfactory bulbs). As evidence for the role of fosB, genetic knock-out mice who lack this gene have severe deficits in postpartum maternal behavior, with significantly reduced crouching and pup retrieval, long retrieval latencies, and few if any surviving pups (J. R. Brown, Ye, Bronson, Dikkes, & Greenberg, 1996). In mice altered to lack oxytocin (oxytocin knockout or OTKO mice), the mothers demonstrate a normal latency to approach, lick, or crouch over foster pups, but they pick up the pups significantly less often and are less likely to move them from the center of the cage to a safer corner (Pedersen et al., 2006). Thus, OT appears to act during retrieval to reduce the avoidance response, promoting the early approaches and subsequently facilitating the memory for the social bond, which in turn promotes subsequent responses to the target (McCarthy, Kow, & Pfaff, 1992).

In humans, OT has been clearly linked to hormonal changes during parturition and infant care, being particularly necessary for stimulating the birth process and subsequent nursing (Insel et al., 1997). OT levels in early pregnancy and the postpartum period predict maternal behaviors like gaze, vocalizations, positive affect, and affectionate infant touch, as well as attachment-related thoughts and frequent checking (Feldman, Weller, Zagoory-Sharon, & Levine, 2007). Another study found high variability in the extent to which OT levels increased, decreased, or remained the same throughout the pregnancy, but the mothers who increased over time had greater maternal bonding (Levine, Zagoory-Sharon, Feldman, & Weller, 2007). A study that examined both mothers and fathers found increased OT in both parents after infant contact, but only for parents who had displayed a lot of affection (Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010). Mothers with secure attachment styles have shown greater neural activation in the ventral striatum and oxytocin-associated region of the hypothalamus while viewing pictures of their child, and this activation predicted OT increases to infant contact at 7 months (Strathearn, Fonagy, Amico, & Montague, 2009). Moreover, intranasal administration of OT appears to increase the attractiveness of infant (but not adult) faces, an effect that was only present in individuals with the homozygous rs53576G allele of the oxytocin receptor (OXTR) gene (Marsh et al., 2012).

OT effects on human prosocial behavior have been demonstrated, but it is unclear whether the effects are centrally or peripherally mediated. During human behavioral economic games, subjects in the trust game who receive allocations from their giving partners have increased plasma OT correlated with the amount of money they receive, presumably because the recipient feels trusted by the giver, who assumes that some of their investment will be voluntarily returned to them at a profit. Moreover, recipients with

higher OT responses to the initial allocation from their investing partner also return more of the tripled sum back to the initial giver (Zak, Kurzban, & Matzner, 2004, 2005). The initial monetary allocation in this game can also be increased with pretreatment of intranasal OT (Kosfeld et al., 2005; Zak, Stanton, & Ahmadi, 2007), an effect that is augmented by a prior massage (Morhenn et al., 2008), presumably because it primes the OT system. (But note questions about the reliability of these findings summarized in Conlisk, 2011.) Three of the single nucleotide polymorphisms in the oxytocin receptor (OXTR) gene region, which constitute part of the genetic basis for monogamy and are associated with autism spectrum disorder (ASD), are also associated with giving in the human dictator game and social values orientation task (Israel et al., 2008). These effects of OT on neuroeconomic trust appear to be specific to social trust and do not reflect general changes in risk-aversion (Kosfeld et al., 2005). Subjects given OT during neuroimaging experiments have also shown reduced activation in the offspring care system, including in the amygdala, midbrain, and dorsal striatum (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008), paralleling the rodent maternal transition from avoidance to approach. Pretreatment with OT can also eliminate conditioned aversion to human faces designed to be threatening, which usually activates the amygdala and fusiform gyrus (Petrovic, Kalisch, Singer, & Dolan, 2008). Another study found decreased amygdala responses to pain after OT administration but did not find an association between empathic pain, oxytocin, and monetary donation (Singer et al., 2008), perhaps pointing to a need for ecological tasks that dissociate empathy and altruism.

Taken together, social bonding processes associated with oxytocin appear to increase helping by decreasing fear and uncertainty while increasing the motivation to approach vulnerable others. This is particularly important early on to help establish a memory for the target and the association between giving and its rewards. As stated above, the effects of OT on social bonding still require downstream engagement of the dopaminergic mesolimbocortical system, forming the conceptual and neurobiological overlap between felt rewards and the motivation to approach that are addressed next.

Factor 8: The NAcc and DA Motivate Approach and Mediate Conditioned Social Rewards

Normal rodent maternal responsiveness, particularly for active behaviors like retrieval, clearly involves dopaminergic inputs from the VTA to the NAcc. However, the precise role of this system is complex and likely centers upon incentive learning and the drive to approach and care for pups once the initial contact has been made. For example, one study did not find any disruptions in maternal behavior after lesions of just the medial NAcc (Numan, Numan, Pliakou, et al., 2005). However, demonstrating a clear need for dopamine (DA) in offspring care, maternal behavior is impaired by lesions of the VTA (Gaffori & Le Moal, 1979; Hansen, Hartho, Wallin, Löfberg L, & Svensson, 1991b; Numan & Smith, 1984) or the NAcc (Hansen et al., 1991b; Lee et al., 2000; Numan, Numan, Pliakou, et al., 2005) or by antagonism (Hansen, Hartho, Wallin, Lofberg, & Svensson, 1991a; Keer & Stern, 1999; Silva, Bernardi, Cruz-Casallas, & Felicio, 2003) or depletion (Hansen, 1994) of dopamine in the NAcc. Moreover, normal maternal behavior releases DA (F. A. Champagne et al., 2004; Hansen, Bergvall, &

Nyiredi, 1993) and increases c-Fos expression in the NAcc (Lonestein, Simmons, Swann, & Stern, 1997; Stack, Balakrishnan, Numan, & Numan, 2002). In addition, circulating estrogens increase DA neurotransmission in the striatum (J. B. Becker & Taylor, 2008). The conditioned place preference for chambers associated with pups is also mediated by dopamine (Fleming, Korsmit, & Deller, 1994). Thus, dopaminergic processes in the ventral striatum are clearly needed for the normal expression of maternal behavior. What precisely is their role?

In the Numan (2007) model, the NAcc is necessary for offspring retrieval to convey DA effects from the VTA that release maternal care through the VP and downstream motor outputs. The NAcc is unlikely to be necessary for pup retrieval per se, at least not immediately, in the same way that the MPOA is. For example, lesions of the shell and core do not affect licking, nest building, or nursing, but lesions of the shell alone can disrupt retrieval; however, even this effect takes at least two trials to establish, being normal on the first trial postlesion (Li & Fleming, 2003). Similarly, NAcc lesions in another study impaired multiple dimensions of maternal care, but only after a day postlesion, while MPOA effects were immediate (Lee et al., 2000). In this same study, operant barpressing to obtain pups was never affected by NAcc lesions, perhaps because of the low motor demands of the task. Thus, DA may support the motivation to approach, at least in part, by providing a rewarding signal from the close contact of successful retrieval, which builds over time and sustains behavior in intact females.

Research specifically on the role of DA in retrieval indicates that it is particularly necessary to motivate and sustain offspring retrieval, more so than nursing or other active behaviors like nest building, maternal aggression, or sexual behavior. But the relationship between DA and retrieval is graded and complex. Even animals given bilateral VTA-DA lesions with bilateral 6-hydroxydopamine (6-OHDA) sometimes exhibit completely normal retrieval behavior (which could be caused by missed injections in some cases; e.g., see Hansen, 1994; Hansen et al., 1991b). Regardless, even among the clearly affected dams, there is a great variability in the response to DA depletion; most dams sometimes retrieve offspring but do it more slowly and less often (Hansen et al., 1991a) and in a manner that depends upon the degree of DA antagonism (Hansen et al., 1991b). In a more qualitative examination, DA-depleted dams did usually approach the separated pups and provide some care (even leaving other pups in the nest to do so), but their behavior was less directed, more disorganized, and ineffective (Hansen et al., 1991a). Moreover, another study found more retrieval on initial than on later trials (Hansen et al., 1991b), further indicating that the effects of DA on retrieval are not necessary for the act itself but for the heightened motivation and subsequent reinforcing properties of the contact that results from successfully completed actions.

Important support for this presumed role for DA in maternal motivation is that the rats in the aforementioned study who were given bilateral VTA-DA lesions could still retrieve normally if they were temporarily separated from the pups (Hansen, 1994); presumably, the separation increased maternal motivation to the point where it compensated for the support lacking from the VTA. This effect was so strong that after 3 or more hours of separation, the dams' retrieval patterns returned to normal and persisted over time, creating a lasting compensatory mechanism. Moreover, after

separation, being reunited with the pup released DA in the mother, measurable through in vivo microdialysis (Hansen et al., 1993). After 1 day of separation, being reunited with a clean pup raised DA by 123% over baseline; if the pups were presented covered in soil in order to instigate more active care, DA release increased to 154%. Using similar methods, DA release was demonstrated in the substantia nigra and olfactory bulb in sheep mothers during suckling, which decreased during separation (Kendrick, Keverne, Chapman, & Baldwin, 1988). These data are particularly relevant to the analogy with altruistic responding because they suggest that the need state and vulnerability of neonous targets directly enhance the motivation to approach, which can then augment the motivation already provided by the offspring's babylike features.

Thus, perhaps under normal circumstances, the pregnant female is primed with the appropriate hormones, gives birth, and is motivated by processes subserved in the MPOA, amygdala, and striatum to approach, clean, stimulate, huddle, and nurse the pup. These behaviors, in turn, provide opioid-dependent rewards to the mother, which feed back onto the NAcc, increasing the dopamine-dependent motivation to approach and retrieve on subsequent occasions. In addition, glutamatergic connections between the PFC and NAcc likely facilitate context-dependent increases in the stimulus salience of the pup, which boost activation in the NAcc by the MPOA, adaptively ensuring that attention, motivation, and effort match the needs of the situation.

This parsing of effects into different subregions of the mesolimbocortical system, which occur in an unfolding sequence over time, is also consistent with research that segregates the hedonic pleasure derived from consuming rewarding substances (opioid-dependent in the medioventral shell of the NAcc; Pecina & Berridge, 2005) from the subsequent motivation to obtain them (DA-dependent in the core; Wyvell & Berridge, 2000). (See reviews in Berridge & Robinson, 2003; Robinson & Berridge, 2003.) In addition, it is consistent with a presumed role for the dopaminergic NAcc in adaptively tracking important and changing reward contingencies (Berns, McClure, Pagnoni, & Montague, 2001; Fiorillo, Tobler, & Schultz, 2003; Schultz, 2002). Thus, the specific role for DA and the NAcc in maternal care and altruistic responding is presumed to be similar to that for decisions to obtain rewards more generally, but the specific circuits that mediate maternal retrieval may be more ingrained and predictable in sequence and ontogeny than for other types of rewards.

There is also some support already that these neural regions are involved during altruistic giving in humans. Functional neuroimaging studies of human altruism, even when they use monetary donations as the dependent measure, reliably engage the domain-general decision and reward system, with consistent activation of the VTA, NAcc, and subgenual cingulate (sgACC) when people give to others. Using behavioral economic tasks, the ventral striatum is engaged by cooperation (Rilling et al., 2002; Singer et al., 2006) and trust (Krueger et al., 2007), but it is also activated by *unreciprocated* cooperation (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004), cautioning against assumptions that the region only mediates positive affective drive states.

The ventral striatum is also associated in the economic literature with a "warm glow" motivation to help, fueled by the good feelings one experiences from helping (Andreoni, 1990). One study found that monetary gains to both subjects and charities activated a common network in the ventral striatum; moreover, the

more pronounced this "warm glow" activity, the larger the subject's voluntary donation (Harbaugh et al., 2007). Further supporting the warm glow motivation, activation in the caudate and right NAcc, as well as donation satisfaction, increased when donations were voluntary. A similar study found common activation for rewards to the self and the charity in the mesolimbocortical system including the VTA and dorsal and ventral striatum; more selfless or costly choices produced more anterior activation that included the frontopolar and medial frontal cortex—areas that correlated with subjects' real-world charitable giving (Moll et al., 2006, see Figure 8) and are part of the extended caregiving system. Future work needs to more carefully determine whether activation in the dopaminergic ventral striatum in these tasks is more associated with the subject's motivation to approach a pitied target (even if only conceptually) or is more associated with the subject's perception of the potential monetary or emotional rewards that should ensue.

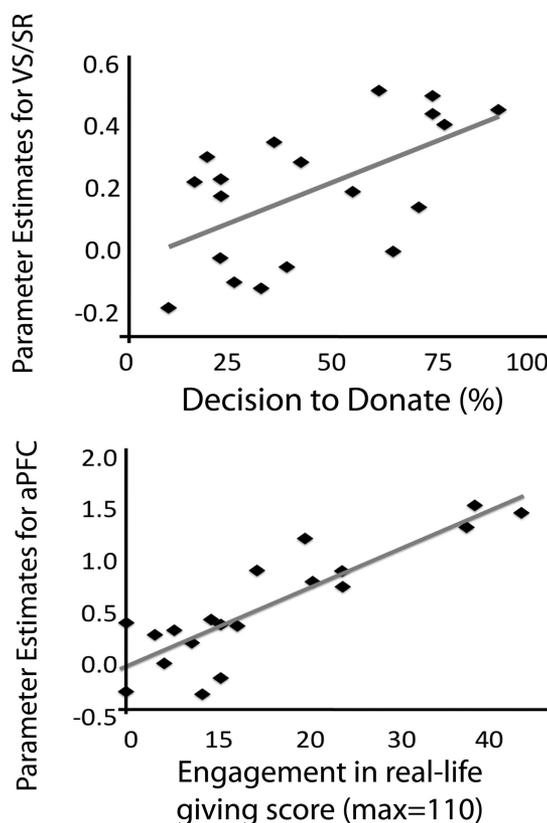


Figure 8. Positive correlations between charitable giving and brain activation in the mesolimbocortical system. Top: The frequency of costly donation (how often each participant made costly donations) increases with parameter estimates in the ventral striatum/septal region (VS/SR; $x = -6$, $y = 11$, $z = 4$; $r = 0.58$; $p < 0.01$). Bottom: The level of self-reported engagement in real-life voluntary activities increases with the degree of prefrontal cortex (PFC) activation during costly donation (peak: $x = -6$, $y = 25$, $z = -14$; $r = 0.87$; $p < 0.0001$). Adapted from "Human Fronto-Mesolimbic Networks Guide Decisions About Charitable Donation," by J. Moll, F. Krueger, R. Zahn, M. Pardini, R. de Oliveira-Souza, and J. Grafman, 2006, *PNAS: Proceedings of the National Academy of Sciences of the United States of America*, 103, pp. 15623–15628. Copyright 2006 by National Academy of Sciences, U.S.A. Adapted with permission.

Factor 9: Increasing the Emphasis of the ACC in Caregiving and Altruism

Modern descriptions of the rodent maternal care system do not emphasize the cingulate cortex because they focus upon subcortical interactions (e.g., see Numan, 2006, 2007). However, early work on the maternal care system extensively investigated the effect of cingulate lesions on maternal care in rodents (e.g., see Slotnick, 1967; Slotnick & Nigrosh, 1975; Stamm, 1955; Wilsoncroft, 1963), following early observations that maternal care was profoundly disrupted by large cortical lesions that included the cingulate (e.g., Beach, 1937, 1938). Across these early studies, cingulate lesions usually produced a spared motivation to retrieve pups and the motor ability to do so, but through efforts that were highly disorganized and ineffective. For example, cingulate-lesioned females (and males induced to retrieve through castration, Slotnick, 1967) carried pups around the cage aimlessly without immediately depositing them into the nest, picked them up and dropped them again, and even retrieved pups out of the nest into open space and retrieved their own tail (Slotnick, 1967; Slotnick & Nigrosh, 1975; Stamm, 1955; Wilsoncroft, 1963). Such effects clearly interacted with the learning and reinforcing processes that were described above for OT and the striatum, as retrieval did improve substantially across days in these animals (Slotnick, 1967; Slotnick & Nigrosh, 1975; Stamm, 1955; Wilsoncroft, 1963). The practice and ensuing lactation that occurred after successful retrieval was thought to be enough to upregulate and organize the behavior (see especially Stamm, 1955). Learning processes that compensated for the lost cingulate functioning were further implicated because the recovered retrieval behavior could be abolished by changing the testing context, such as moving it to a cage with unusually bright lighting (Slotnick, 1967). The researchers concluded by supporting MacLean's (1959) view of the cingulate as a region that organizes species-specific behaviors in context, particularly for behaviors like maternal care, which are critical for survival in caregiving mammals.

This view of the cingulate from over a half-century ago does largely accord with more modern views of the human cingulate as an area needed during advanced cognitive and emotional processes to promote “emotional self-control, focused problem solving, error recognition, and adaptive response to changing conditions” (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001, p. 107). Consequent to functional neuroimaging and event-related potential experiments in humans, the functions of the ACC have been segregated into medio-dorsal and ventro-medial regions that, respectively, handle more cognitive and affective functions. The medio-dorsal region is thought to signal problems in the environment or conflict associated with competing responses (see reviews in Carter et al., 1998; Gehring & Fencsik, 2001; Luu, Don, Derryberry, Reed, & Poulsen, 2003). The ventro-medial portion is thought to process emotionally salient signals and, in turn, modulate physiological responses during stress in a way that is sensitive to the context and available prepotent responses.

The cingulate and hippocampus (HPP) are also particularly sensitive to epigenetic and plastic effects, as these areas develop differently when individuals are raised without a father (Ovtscharoff, Helmeke, & Braun, 2006) and respond differentially to stress depending on the degree of postpartum maternal stimulation (D. L. Champagne et al., 2008). The cingulate and HPP also

work together with the PFC and DA to modulate memory and the motivation to approach (Chudasama, Wright, & Murray, 2008; Jay et al., 2004; Lewis, Critchley, Smith, & Dolan, 2005; Markowitz, Vandekerckhove, Lanfermann, & Russ, 2003; Nelson et al., 2003; Pochon et al., 2002). With respect to altruistic responding, these features of the cingulate, in tandem with the rest of the extended caregiving system, render observers of another's need additionally sensitive to cues about their relationship to the target, the target's need, and their own experiences of stress and fear. These contextual modulations further augment the requirement for expertise, and the approach-avoidance opponency described above, to prevent “knee-jerk” or maladaptive responses that could be incorrectly associated with an innate predisposition to respond.

The subgenual region of the anterior cingulate (sgACC; BA 25) may play a particularly important role in the homology between offspring care and altruism (for a review of the sgACC in empathy and altruism, see Preston and de Waal, 2011). Anatomically, it is interconnected with the dopaminergic reward system (Drevets, Öngür, & Price, 1998) and most of the offspring care system including the OFC, lateral hypothalamus, amygdala, NAcc, VTA, and PAG (Freedman, Insel, & Smith, 2000; Öngür, Ferry, & Price, 2003; Öngür & Price, 2000). The sgACC is thought to mediate vigilance and emotion regulation through downstream projections to the hypothalamus and brainstem (Barbas, Saha, Rempel-Clower, & Ghashghaei, 2003; Freedman et al., 2000), which activate the adrenocortical negative feedback loop and parasympathetic nervous system (Critchley, 2004; O'Connor, Gundel, McRae, & Lane, 2007). The parasympathetic nervous system is postulated to play a particularly important role in social bonding and empathy because it is activated during face-to-face bonding (Porges, Doussard-Roosevelt, & Maiti, 1994) and is associated with the orienting response (characterized by an increase in attention and decrease in heart rate) that occurs in humans (Fabes, Eisenberg, Karbon, Troyer, & Switzer, 1994) and mice (Chen et al., 2009) during the concerned attention of another's distress (reviewed by Beauchaine, 2001).

Taken together, the sgACC is positioned to redirect cognitive and physiological resources in response to important events—like the salient distress of another—while producing adaptive responses that regulate emotion and promote helping. As evidence for the key role of the sgACC in responding to need, this region (as well as the larger anterior and posterior cingulate cortices and most of the rodent maternal care circuit) is activated when human mothers listen to infant cries (Lorberbaum et al., 1999, 2002). The sgACC was also the only region in an fMRI study to correlate with the amount of money donated to charities, above and beyond what was produced from the “warm glow” of receiving money for one's self (Moll et al., 2006). The sgACC was also uniquely associated with the presumed guilt from imagining taking an action against another person (Zahn et al., 2009). Studies of charitable giving are particularly relevant to altruistic responding because they are the only ones in neuroeconomics that involve a target in actual need, as well as the warm-glow motivation to give (e.g., see Andreoni, 1990; Harbaugh, 1998; Harbaugh et al., 2007)—features that are required for care-based aid in the current framework. Thus, while research has not heretofore focused upon the role of the sgACC in altruistic responding, its role in maternal care, social bonding, and organizing affective responses suggests that it should be more intensely studied.

Factor 10: The PFC Integrates Multisensory Cues to Promote Adaptive Responding

Through the higher reaches of the brain . . . it would appear that a parental concern for the young may generalize to other members of the species, a psychologic development that amounts to an evolution from a sense of responsibility to what we call conscience. (MacLean, 1985, p. 416)

The orbitofrontal cortex (OFC) is a key part of the domain-general mesolimbocortical system, which is assumed to be necessary for myriad types of mammalian decision processes, particularly when multiple types of cues or options must be weighed or integrated. The earliest neuroanatomical work on maternal care in rodents initially established that the cortex in general was necessary for effective maternal care (Beach, 1937, 1938). This research was later extended to demonstrate that the more medial portion of the rodent cortex was particularly essential for effective maternal care (Stamm, 1955). More recently, two specific studies also found a role for the more narrowly defined medial prefrontal cortex (mPFC) in offspring retrieval per se, which is proposed herein to be homologous to altruistic responding. In one study, chemical inactivation of the mPFC, or inhibition of the region via GABA, after a week postpartum almost eliminated retrieval without affecting other maternal behaviors or nonmaternal locomotion (Febo, Felix-Ortiz, & Johnson, 2010). In the other study, electroencephalography (EEG) recording from the left and right mPFC and VTA showed increased power in one band of the EEG signal during pup retrieval compared to walking and in all three bands of the signal during pup licking compared to control forepaw licking (Hernández-González, Navarro-Meza, Prieto-Beracochea, & Guevara, 2005).

In the rodent offspring care system described above, the OFC is generally thought to modulate processes that occur in subcortical regions of the system (e.g., see Numan & Stolzenberg, 2009). More specifically, glutamatergic connections between the OFC and multiple regions of the rodent offspring care system (NAcc, VTA, BLA, and MPOA) are assumed to allow the OFC to adaptively influence dopaminergic reward and motivational processes (Grace, Floresco, Goto, & Lodge, 2007; McFarland, Lapish, & Kalivas, 2003). Numan's model further assumes that the rodent BLA and PFC project back to the VP to enhance mesolimbic processes in the presence of infant cues—a connection that strengthens with caregiving experience (Numan & Stolzenberg, 2009). Proper functioning of the BLA is known to be necessary for active, goal-directed retrieval behavior (Numan et al., 2010), potentially because it mediates the fear response that motivates adults to attend to separated and vulnerable pups (Martel, Nishi, & Shumyatsky, 2008). Again, the fact that these projections from the BLA and PFC require infant cues, and are modulated by experience with newborns, indicates that even in rodents an “innate” response is intrinsically designed to be sensitive to the observer's context and life experience.

This view of the OFC in the rodent offspring care literature is largely consistent with the view of the OFC from human functional neuroanatomy. The human OFC is best described as a “convergence-divergence” zone that integrates perceptual, cognitive, and affective information from diverse structures (e.g., ventral and dorsal streams, insula, brainstem, amygdala, NAcc, hip-

pocampus) and outputs to autonomic and motor regions to generate adaptive responses to salient external cues (Bechara et al., 2000; Damasio et al., 2000; Krangelbach & Rolls, 2004). Evidence from rodents, monkeys, and humans implicates the OFC particularly when decisions are made indirectly, in the abstract, or through an explicit weighting of ambivalent, somatic, and hedonic cues (Bechara, Damasio, Damasio, & Lee, 1999; Krangelbach, 2005; Krangelbach & Rolls, 2004; O'Doherty, 2003; Schoenbaum, Chiba, & Gallagher, 1998; Schoenbaum, Setlow, Saddoris, & Gallagher, 2003). Some believe that the OFC can be further divided into subregions with different functional properties. For example, the more medial and caudal portions of the OFC are heavily interconnected with subcortical and brainstem autonomic regions in the caregiving and domain-general reward system that encode affective components of decisions, while the more anterior, rostral, and polar portions are thought to be involved in more abstract decision processes (Krangelbach & Rolls, 2004). More medial regions are also thought to monitor reward values while more lateral regions appear to evaluate punishments (Krangelbach & Rolls, 2004; O'Doherty, Krangelbach, Rolls, Hornak, & Andrews, 2001). Research is needed to extend these proposed subdivisions to altruistic contexts.

Based on these functions of the OFC, the region is expected to be most necessary for altruistic decisions that require explicit deliberation, comparing multiple possible options, or contemplating possible future outcomes. For example, such conditions occur when one must consider whether helping a stranger on the street will be dangerous and lead to regret or will be innocuous and lead to the “warm glow” of giving. The OFC is also expected to be necessary to attribute someone's distress or need from indirect cues of their plight, such as associating smoke from a window with people trapped inside, associating wet spring ice with danger to skaters, or associating the insult you plan to deliver with the hurt that will ensue. Efferent signals from the OFC back to the subcortical portions of the caregiving system can also enhance processing for targets or situations that are anticipated or important. For example, OFC signals can help observers detect the need of bonded offspring more quickly than for unfamiliar targets; it can also help observers notice a hurt individual more quickly when they are looking for them, especially in the absence of other rewarding activities that compete for access to the motivational system. As evidence, a magnetoencephalography (MEG) study found activation in the medial OFC within a seventh of a second when subjects viewed unrelated infant faces but not matched adult faces (Krangelbach et al., 2008).

Existing evidence from human functional neuroimaging does support the presumed role for the OFC and the larger ventromedial prefrontal cortex (VMPFC) during prosocial behavior (see review in Preston & de Waal, 2011). This role is fairly broad and occurs during tasks that involve cooperation (Rilling et al., 2002, 2004; Singer et al., 2006), as well as games that measure trust and reciprocity (McCabe, Houser, Ryan, Smith, & Trouard, 2001). The OFC is also more active when subjects observe (over played) a game that delivered money to themselves or a charity (Tankersley et al., 2007). However, as with the fact that the NAcc mediates both positive (Krueger et al., 2007; Rilling et al., 2002; Singer et al., 2006) and negative (Rilling et al., 2004) prosocial outcomes, one cannot conclude that the OFC is required to implement *any* affective decision or that it tracks the amount of prosocial reward

per se. For example, the OFC responds more to defectors than to cooperators (Singer et al., 2006) and responds to intentional, costly punishment of defectors in a trust game (de Quervain, et al., 2004). Moreover, patients with VMPFC damage actually *reject more* very unfair offers than comparison groups (Koenigs & Tranel, 2007), demonstrating that they are capable of responding affectively to the slight and may even be disinhibited in doing so because of an inability to modulate the subcortical signals.

Taken together, it appears that subcortical and cortical affective signals can generate affectively influenced responses, with or without the OFC, particularly toward incentive-salient options that can be either positive or negative. The OFC is particularly involved when the decision requires the observer to integrate conflicting or complex signals during deliberated choice or to make an indirect association. Supporting this view, the OFC was particularly implicated in the human altruism studies reviewed above that included multiple possible responses or when multiple predicted outcomes biased the decision to help.

OFC Interacts With the DLPFC

Early research with rodents using the lesion method did not assume that the dorsolateral prefrontal cortex (DLPFC) was necessary for offspring care, because dorsolateral cortical lesions produced less noticeable deficits than medial lesions. However, when more than 30% of the dorsolateral cortex was lesioned (an extensive area that ran the full length of the cortex), all maternal behavior ceased, which suggests that it does at least play some supporting role (Stamm, 1955). Human functional neuroanatomy research assumes that the OFC and DLPFC cooperate during explicit decision making, with the DLPFC supporting executive and working-memory processes that sustain the contemplation of cues or options being integrated in the OFC (Bechara, Damasio, Tranel, & Anderson, 1998; Hinson, Jameson, & Whitney, 2002; Jameson, Hinson, & Whitney, 2004). Based on this research, the interaction between the DLPFC and OFC should be most important during altruistic responses that require abstract or strategic processing. For example, people routinely make highly planned decisions to determine how to help a sick coworker or how to spread their paycheck across personal and philanthropic needs. Some neuroeconomic games that assess prosociality also require such explicit processing. For example, decisions to reject unfair offers in the Ultimatum Game—which are altruistic because the subject relinquishes their payment to punish an uncooperative player—increases activation in the DLPFC, ACC, and insula (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Some believe that the DLPFC is necessary to *resist accepting* unfair offers to punish the proposer, because disruption of the right DLPFC with transcranial magnetic stimulation (TMS) reduces the altruistic rejection of unfair offers (Knoch & Fehr, 2007; Knoch et al., 2008; Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006). However, these interpretations are premature and need to be followed with more definitive contrasts. The DLPFC could just as well be needed to compare the multiple possible options (to gain or to punish) or to maintain thoughts about unfair proposers in working memory that fuel rejection (e.g., “Hey! How could he do that to me?!”). Future research needs to demonstrate functional connectivity between the DLPFC and OFC during decisions to help, which should be more pronounced when options must be explicitly compared.

For example, when the neighbor comes to borrow your lawnmower, you may first sympathize with his plight but then feel less inclined after remembering that he previously returned something in bad condition. While planning to say “no,” you could additionally anticipate the embarrassment of saying this to his face and instead try to conjure polite ways to reject his request. Without being able to think of one, you might instead settle upon a tempered “yes,” aimed at simply preventing such inquiries in the future. Such a decision can be made in mere seconds but likely requires the coordinated efforts of the OFC and DLPFC to contemplate and integrate the possible responses and their likely outcomes.

The ACC, OFC, and DLPFC were among the first regions to be examined for the neural bases of maternal care, using incredibly brute-force lesion methods in species that are not particularly known for their complex cortical processing. However, these regions clearly do participate—across species—in offspring care and even in offspring retrieval per se. These regions are also expected to be important for the development of more complex forms of giving that probably emerged only later in the primate and hominid lines, including particularly strategic, multistage, or longer-term cooperation, sharing, and aid to nonkin. The current framework suggests that while we may divide the brain into reptilian, limbic, and neocortical regions (cf. MacLean, 1990), we should not assume that only the limbic portion is needed for rodent offspring care and only the cortex is needed for human, rational giving. Rather, all three subsystems appear to have existed and cooperated for at least two hundred millions years to allow primitive mammals to care for offspring in simple but adaptive ways. Subsequently, all three subsystems have evolved together, allowing for the more concrete assistive behaviors to be adapted to each species’ ecology. In humans, these systems further evolved to allow assistance to be extended over time, space, and individuals, in such complex ways that it is hard to even comprehend how the beautiful flower of human compassion sprouted from such a small but elegant motivational seed.

Summary of the Model for Altruistic Responding

Previously, extensive research on altruism and altruistic responding existed but was not integrated across species, fields, or levels of analysis. Researchers in theoretical biology and economics mainly studied the costs and benefits of cooperation, without addressing the human motivation to help others in need (e.g., see Axelrod, 1984; Axelrod & Hamilton, 1981; Bowles & Gintis, 2004; Crowley et al., 1996; Dugatkin, 1997; Fehr & Fischbacher, 2003; Gintis et al., 2001; McCabe et al., 2001; M. A. Nowak, 2005; Roberts, 1998; West et al., 2007). In contrast, psychologists did examine the motivation to help (e.g., Batson, 2011; Darley & Latané, 1968; Dovidio et al., 2006; Eisenberg & Miller, 1987; Latané & Rodin, 1969; Zahn-Waxler et al., 1979) and even assumed that prosocial behavior evolved from the mother–offspring bond (e.g., see Ainsworth, 1969; Batson, 2010; Batson et al., 2005; Bowlby, 1969; S. L. Brown & Brown, 2006; S. L. Brown, Brown, & Penner, 2011; S. L. Brown, Brown, & Preston, 2011; de Waal, 2008; Eibl-Eibesfeldt, 1971/1974; Hrdy, 2009; MacLean, 1985; Marsh et al., 2005; Murray, 1979; Preston & de Waal, 2002b; Tronick, 1989; Zahn-Waxler, Hollenbeck, & Radke-Yarrow, 1984). However, the work in psychology did not clarify the evo-

lution or neural bases of active giving or make significant contact with the biological and economic approaches (but see S. L. Brown, Brown, & Preston, 2011; de Waal, 2008; Hrdy, 2009; Preston & de Waal, 2011). Further complicating the patchwork of existing work on altruism, there has been neural work on economic altruism (see review above and in Fehr & Camerer, 2007; Preston & de Waal, 2011; Walter et al., 2005; Zak, 2004) and empathy (i.e., the role of personal representations of pain and emotion in the perception of others' similar states; see reviews in Decety & Ickes, 2009; Decety & Jackson, 2006; Singer, 2006); however, these studies also may not necessarily capture the neurobiology of altruistic responding, which is so simple, available across species, and not necessarily preceded by deliberation or subjective empathy (aka the "empathy-altruism gap," see Buchanan et al., 2012; Preston & Hofelich, 2012; Prinz, 2011).

The current caregiving view of altruism attempts to integrate these prior theories by assuming that *offspring care was the primary, initial driver for a mammalian instinct to retrieve and huddle vulnerable and endangered targets, especially when one knows and can safely enact the proper response*. This instinct may exist across taxa (i.e., in ants, birds, or even some protective reptiles), but it at least existed across altricial mammals whose offspring needed significant protection after birth. Subsequent to this, virgin females, males, and juveniles in cooperatively breeding species evolved to issue such protective responses toward kin and sometimes nonkin group members. Even later in primate and human evolution, these active altruistic responses were likely further augmented and extended to include strategic forms of helping, sharing, and cooperation in larger group contexts where there existed additional pressures to maintain a reputation and compete for resources. Through such a stepwise process, all existing views on the evolution of altruism can be accommodated into one larger picture, which builds later forms of altruism upon the primitive base.

The current emphasis on the neural development of altruistic responding was necessary to link human altruism to its natural origin, but it also provides a building block upon which future research can be built, particularly in the neurosciences. Through the 10 key factors, it was demonstrated that similar biobehavioral processes—across species and targets—promote the approach, retrieval, and succorant care of both kin and nonkin. These responses are facilitated by cues of target vulnerability, neoteny, distress, and a social bond—features that are all characteristic of contexts that involve caregiving and targets in genuine need. These features are supported at the neurohormonal level by the presence of pregnancy hormones and involve interconnections between OT, DA, the ventral striatum, cingulate cortex, and prefrontal cortex (see Table 1). Focusing on these bottom-up features of altruistic responding allows us to explain some paradoxical findings in the literature, such as the fact that many species appear to sometimes exhibit a costly compulsion to assist complete strangers, but even humans often fail to respond in scary or uncertain situations that seem to warrant help.

To build this foundation for an interdisciplinary study of altruism, the review had to focus upon the basic homology between offspring retrieval and primitive altruistic responding. Of course, humans are capable of more abstract and strategic decision processes, owing to their increased executive and mnemonic capacities, long periods of developmental immaturity, and longer life

spans. The 10 key factors for active responding are assumed to also participate in passive and abstract cases to the extent that the situation involves the motivation to care for a sympathetic target (refer back to Figure 4). Moreover, because the altruistic response system is derived from such a powerful and conserved circuit, its role can explain large effect-size differences in the propensity to respond across types of tasks or conditions, even for deliberated decisions to give. Despite a lot of overlap in the mechanism across types of altruism, it is important to keep in mind that active altruistic responding has some unique entailments that need to be emphasized, including the need for the observer to know and be able to enact the appropriate response without fearing for their own safety. A prepared motor response downregulates the adaptive tendency to avoid situations of novelty or danger; it also prepares the approach response without requiring explicit decision processes. These features must be understood if we are to understand when people do and do not act, and why there are differences in helping between males and females, experts and novices, caregivers and noncaregivers.

Importantly, the "caregiving circuit" is not specific to offspring care, apart from maybe the MPOA. As with all decision making or information-processing, each region in the caregiving system is expected to be recruited proportionally to the extent that a task requires that region's presumed function (see Table 3). For example, the amygdala, striatum, and sgACC should respond when the distress and approachability of the target are salient and the response is clear. The MPOA, sgACC, and downstream autonomic regions should be *less* necessary for help driven by purely strategic motives like enhancing prestige, except when necessary to imagine desired rewards or unwanted punishments. The OFC, HPP, and DLPFC should be increasingly engaged when the observer must compare options or integrate key contextual cues to select a response.

Supporting the neural extended caregiving model presented herein, functional imaging studies of altruism do find extensive participation of the system in explicit and deliberated decisions to help, excepting the MPOA and VP, which have yet to be targeted in humans. These regions should be more necessary for tasks that use targets in real need or require active responses; moreover, discovering their participation requires researchers to acquire and analyze regions of interest that are very small. Moreover, the controlled cognitive processes required for behavioral economic tasks may directly inhibit the immediate responding associated with the MPOA and VP. Studies of fairness that currently predominate the altruism neuroscience literature are particularly different from altruistic responding because they require additional executive capacities to calculate equitable splits and monitor possible outcomes (e.g., DLPFC, OFC, ACC); they also usually require theory-of-mind to predict the partner's response (e.g., temporo-parietal junction).

Of course, all decision processes require some reference to likely positive and negative cues or potential outcomes, making it unsurprising that the domain-general mesolimbocortical system is implicated in both offspring care and financial altruism. To determine which patterns of activation simply reflect the need to make affectively relevant decisions, versus a specific predisposition to care for vulnerable others, requires more research. Future work should directly contrast different types of giving, including active responses like those studied in the behavioral bystander apathy

Table 3
General Description of the Role of Each of the Major Areas in the Caregiving Model of Altruistic Responding

Region	Proposed role in altruistic responding
ACC	Mediates prepared responses to targets of need; indicates the potential for an error or a mismatch between the situation and response; arbitrates between executive control processes and instinctual responses to the other's immediate need.
DLPFC	Necessary for more explicit, top-down decisions to help by augmenting comparison process through interactions with the OFC.
HPP	Provides contextual information from long-term memory that mediates the response to the other's need based on stored representations of the person and situation.
MeA	Subserves novelty/vigilance responses to unfamiliar individuals and situations that produce downstream avoidance responses in individuals who are not hormonally primed.
MPOA	Provides the basic impetus for active care such as retrieval. Is presumed necessary for instinctual responding to vulnerable others in immediate need as occurs during pup retrieval in rats.
NAcc	Subserves both learned associations between the subject and socially bonded targets and, in turn, increases the motor-affective motivation to approach bonded others.
OFC	Integrates affective, homeostatic, and sensory information to facilitate adaptive, rewarding responses. Increasingly involved during explicit decisions to help, but also mediates basic behavioral responses through interconnections with the NAcc and brainstem autonomic areas.
sgACC	Integrates contextual information from the HPP with reward inputs from NAcc; responsible for increases in parasympathetic tone and glucocorticoid responses to another's distress.

Note. Each role is consistent with the presumed function of the region across fields and in the rodent offspring care system, while including the expected role in active human altruism given the evidence available. ACC = anterior cingulate cortex; DLPFC = dorsolateral prefrontal cortex; HPP = hippocampus; MeA = medial amygdala; MPOA = medial preoptic area of the hypothalamus; NAcc = nucleus accumbens; OFC = orbital frontal cortex; sgACC = subgenual region of the anterior cingulate cortex.

studies. Methods used to study altruism in other species (reviewed in Preston & de Waal, 2002a, 2002b) may be particularly useful for developing paradigms for studying the human altruistic response, because those paradigms were already developed to demonstrate giving within confined spaces and without self-report or extensive cognitive requirements (e.g., Bartal et al., 2011; Chen et al., 2009; Church, 1959; Langford et al., 2006; Masserman et al., 1964; Rice & Gainer, 1962).

Final Remarks

Despite extensive research and theory, a unified view of human helping has eluded us. Most work has avoided crossing research boundaries that need to be integrated in order to understand a behavior that is both ancient and complex. By focusing upon a primitive form of human giving—the instinct to care for distressed and vulnerable others—we can apply existing data on the neuroscience of maternal care to explain active aid across evolutionary time, species, and forms of altruism. This bottom-up approach parsimoniously explains many common and troubling findings in the prosocial literature, while integrating existing views of altruism into a larger evolutionary picture. In a literature that is increasingly influenced by biology and economics, such a bridge also provides a strong theoretical and empirical foundation upon which to build future work in the neurosciences.

Humans often strive to see themselves as special and distinct from other species, particularly when discussing behaviors as

lauded as human kindness. But the mammalian nervous system—particularly those systems that regulate social behaviors—are highly conserved across evolutionary time. Because of this, even the most complex human behaviors are built upon a rather strong and powerful foundation, which produces notable similarities between offspring care and altruistic responding across species. Thus, like the rodent mother who works for hours to retrieve unrelated and isolated neonate pups, people rush to the aid of strangers in immediate danger, making the difference between death and survival. Both are motivated by similar contextual cues, require specific action sequences that are only effective when performed in an organized and efficient manner and are subserved by mesolimbocortical processes that potentiate action when it is adaptive.

Extensive research is still needed. We need to clarify differences between rodent and human caregiving and among active, abstract, and nurturant aid—each of which may be differentially organized in males and females. Additional work can examine caregiving impairments that occur during sociopathy, psychopathy, and developmental neglect. The caregiving instinct should also be examined as a possible mediator of opposing drives to amass material goods and to save the Earth's natural resources and species (Preston, 2011; J. M. Wang et al., 2012). Much work is needed to test specific hypotheses generated by this view, particularly in contexts that include genuine, active aid. But with this solid foundation in place, informed by research across levels of analysis, future work

can be more theoretically grounded and empirically relevant. Perhaps we can come a little closer to integrating our most primitive and most celebrated human characteristics into a coherent view of our “good nature.”

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