

A Model of Human Caregiving Motivation

The tendency to provide care to others, over a long period of time, and even in the absence of reciprocity attracted our attention as psychologists trained to consider how behavior is shaped by reinforcement. How is it that individuals come to pair the costs of helping another person with reward for the self? We viewed actions that involve the sustained allocation of resources to someone other than the self as a scientific mystery. As a father-daughter team—developmental psychologist and social psychologist, respectively—S. Brown & R. Brown became interested in using evolutionary theory to explain the motivation to help others. We (Brown & Brown) were unable to reconcile insights generated from evolutionary biology with models used in psychology and economics to describe human motivation. After considerable reflection and analysis, we decided to abandon an assumption that is pervasive in the social sciences—that all social behavior can be reduced to the pursuit of rewards and benefits for the self, and to general impulses that compel individuals to seek pleasure and avoid pain (S. Brown & R. Brown, 2006; R. Brown & S. Brown, 2006; R. Brown & S. Brown, 2005). As an alternative, we entertained the hypothesis that a dedicated neurobiological system, independent of but interacting with pleasure-pain systems, drives individuals to prioritize and promote the well-being of others—under certain, well-specified conditions. In this essay, we have teamed up with Stephanie Preston, a biological psychologist, to delineate what this dedicated neurobiological system might look like.

What do we mean by sacrifice and altruism?

As an example of the type of behavior that we are hoping to explain, we start with the case of parenting. Motivational accounts of parenting that invoke self-interest—the standard maximize rewards-minimize costs calculus—are, at the very least, strained. Although parents may experience pleasurable states generally and feelings of love specifically (Swain, this volume), these emotions are not always revealed in surveys of parent mood or in reports of parent marital satisfaction—For example, some studies show that there is no elevation of mood for parents when they are taking care of their children (Kahneman, et al., 2004). And considerable data from

studies of marital happiness show that the early years of marriage, and in particular the transition to parenting, are characterized by declining relationship satisfaction (Linville, et al., 2010).

On the contrary, these data suggest that parenting, however rewarding, generates significant cost. Indeed, as parents of young children, many of us (but not all) give up sleep, sex, and freedom to become vigilant protectors and promoters of someone other than ourselves. And, for some of us, this heavy investment continues for a lifetime. This level of sacrifice may explain why our children do not always elevate our mood, or why marital satisfaction can be elusive. If anticipation-of-reward explanations (or other self-interest accounts) are to explain the motivation to parent, they must demonstrate the ways in which the significant costs of parenting are outweighed by its benefits. So far, this has not happened.

Even if one could make a case that parenting occurs in anticipation of the rewards it generates, what about other examples of caregiving? For instance, if a loved one becomes ill or gets injured, some of us give up career, social life, mating opportunities, and/or financial security to spend months or years taking care of the person in need. What are the underlying rewards that motivate this level of sacrifice?

Perhaps the most challenging examples of sacrificial behaviors for reward-based models are found outside the realms of parenting and caring for sick family members or loved ones.

Dramatic instances of self-sacrifice include so-called altruistic suicides (Durkheim, 1951), in which individuals intentionally end their lives, ostensibly (at least in some cases) to relieve the burden they perceive they place on others (deCatanzaro, 1986; R. Brown, et al., 2009; Joiner, 2005). And we are all familiar with instances of heroic sacrifice in combat (Wong, 2003), in which soldiers risk injury or death to save their comrades. From our perspective, the motivation for such behavior is difficult to explain in terms of the pursuit of benefits, pleasure, or preferences. On the contrary, these behaviors require individuals to forgo immediate and future pleasure and reward in favor of certain pain, injury, and perhaps even death.

We developed selective investment theory (SIT) as an alternative way to explain the motivational basis for instances of sacrifice and costly, long-term investment in others (CLI). According to the theory, social bonds—the glue of close relationships—provide access to a motivational architecture that enables individuals to suppress their own self-preservation goals and preferences when necessary in order to prioritize and promote the well-being of another person. This view of social bonds represents a departure from traditional reward-based, learning models of close relationships, which emphasize the importance of using relationship partners to meet individual needs (e.g., attachment theory, learning theory).

Considering the significant costs of helping others on a sustained basis (Krebs; Shultz & Monin; Penner, Harper, & Albrecht—this volume), our theory also suggests that social bonds are formed selectively, under conditions referred to as positive “fitness interdependence.” In essence, positive fitness interdependence is a state of linked reproductive success between two or more individuals in which increases in one person’s fitness result in increases in the fitness of the other. As we discuss in our elaboration of selective investment theory (S. Brown & R. Brown, 2006), individuals can be interdependent if they share genes, as in the case of blood relatives, or if they are linked to one another for outcomes and resources that affect survival and reproduction. Cues for positive fitness interdependence include, for example, perceptions of phenotypic similarity, familiarity, common threat, and shared emotions, as well as circumstances such as sexual intercourse (mating behavior) that create a positive linkage in fitness-related outcomes.

States of positive fitness interdependence are an appealing pre-requisite for forming social bonds and behaving altruistically because attempts to exploit or otherwise decrease the fitness of one individual result in a comparable decrease in the fitness of the other. In ancestral conditions that were likely marked by high degrees of fitness interdependence, exploitation of a common resource would have been lethal not only to the altruist, but also to the cheater. Thus, we have argued that exploitation could not have been selected for under states of positive fitness

interdependence, which provides a genetic safety net for behaving altruistically. From the vantage point of our theory, social bonds, based on positive fitness interdependence, are viewed as proximate (motivational) causes of costly, long-term investment in others.

In our first published presentation of selective investment theory (Brown & Brown, 2006), we did not flesh out the motivational system that mediates between social bonds and caring for and helping others, other than to hypothesize that it is rooted in the evolution of parental care. We now address this omission, turning attention to what we (and others) have referred to as a “caregiving system”—the neurophysiological circuitry that allows cues for interdependence and social bonds (and other selected stimuli) to drive cognitions, emotions, and behaviors that propel us beyond self-interest.

The Caregiving System: A Theoretical Framework

We propose that a dedicated neurobiological system, shaped by evolution to direct maternal care (Brown & Brown, 2006; Numan, 2006), is selectively recruited to motivate many forms of helping behavior (both human and non-human), including costly long-term investment in others. Below we describe our caregiving system framework, including functional and evolutionary requirements of such a system, as well as potential candidate brain regions, hormones, and neural circuits that may be capable of directing the motivation to provide help to others.

Our model proposes that perceptions of another’s need for help interact with relationship variables and available resources to influence both caregiving motivation and behavior (Figure 1). The medial preoptic area of the hypothalamus is responsible for activating caregiving motivation in response to these need, relationship, and resource inputs. This other-related and resource related information also outputs to other motivational centers, including those that generate reward-based and avoidance-driven impulses that can conflict with caregiving motivation. Helping behavior is released through inhibition of these competing impulses.

Sensitivity to Need

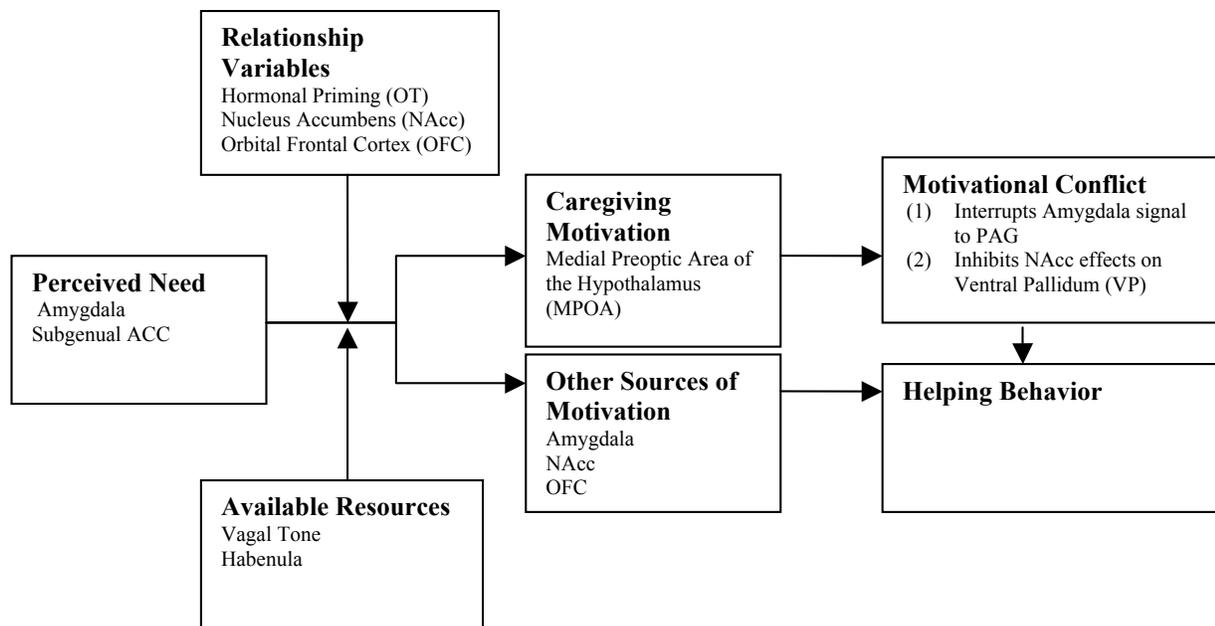
At a minimum, a caregiving system must be sensitive to the needs of others. Although overt distress, solicitation, or other cues for need may not be necessary for activating caregiving motivation, helping behavior that is not attuned to the needs of the recipient risks compromising the inclusive fitness of the helper. Accordingly, an effective and evolutionarily adaptive caregiving system must be sensitive to cues for distress or need in others (Preston and Brown, under review). For example, a mother who sees a lion approaching her toddler must register the threat to her child in addition to the threat to herself. This sensitivity component is a common sense requirement for any caregiving system, and was a centerpiece of Bowlby's (1969) ideas. Indeed, attachment researchers, beginning with Ainsworth (1972), have highlighted caregiver sensitivity, but mainly in terms of its effects on the security of infant attachments. Until recently, there has been little theoretical or empirical emphasis on determinants of such sensitivity in humans (but see Collins, Guichard, Ford, & Feeney, 2006).

Animal research, on the other hand, has documented not only the importance of need detection in provisioning offspring, but also suggested mechanisms by which this happens. Species studied include insect (Kolliker, Chuckalovcak, Haynes, & Brodie, 2006), avian (Kilner & Johnstone 1997; Budden & Wright 2001; Wright & Leonard 2002), and nonhuman primate (Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Ueno & Matsuzawa, 2004), but the most detailed and extensive neurophysiological data come from rodents {for extensive reviews see Numan, 2003; Numan, 2006; Numan, 2007; Numan, this volume; Lonstein & Morrell, 2007; Rosenblatt, 1992}.

The rodent data suggest that caregiving motivation is directed within the hypothalamus, which is generally known to regulate homeostatic states such as body temperature, weight, blood pressure, and fluid and electrolyte balance (Molavi, 1997). In the context of maternal care, the medial preoptic area (MPOA) of the hypothalamus, and the surrounding ventral bed nucleus of the stria terminalis (vBST), are thought to act as a "switch" (p.164) that turns on maternal

motivation, *influencing* sensory-motor integration to facilitate active, voluntary maternal responses such as pup retrieval, protection, and nest-building (Numan, 2006). Evidence that the hypothalamus may become active in response to cues for need in others comes from studies of the amygdala and the subgenual anterior cingulate cortex (sgACC), both of which have been implicated in helping behavior (Moll et al., 2006; Marsh, in preparation; Numan, 2006), perceiving need in others (Loderbaum et al., 1999; Lorderbaum et al., 2002), and influencing hypothalamic processes, including activation of the MPOA (Diorio, Viau, & Meaney, 1993; Numan, 2006).

Figure 1. A Biological Framework for Studying the Caregiving System¹



The Motivation to Help

Data from rodent studies indicate that the MPOA/vBST directs maternal behavior in two ways, by increasing approach motivation and by inhibiting avoidance motivation that would interfere with providing help to another. As evidence for its role in maternal care, the MPOA/vBST must be intact for normal maternal behavior to occur (Numan, 2003). For example,

¹ Brain regions, hormones, and circuits are described under each variable in the model.

damage to the MPOA/vBST interferes with *active* maternal responses to the pup, such as pup retrieval, but does not interfere with passive maternal responses such as huddling and nursing (e.g., Jacobson, 1980, Terkel, 1979). Moreover, damage to the MPOA/vBST does not impair motor behavior, sexual behavior, hoarding, activity levels, body weight, or temperature regulation, which are also under the control of the hypothalamus (reviewed in Numan, 2006). These data suggest that the MPOA/vBST is specialized for active maternal care, and that the motivation for maternal care can be disassociated from the motivation to engage in other types of motor behaviors, including those that are reward-based such as sexual activity.

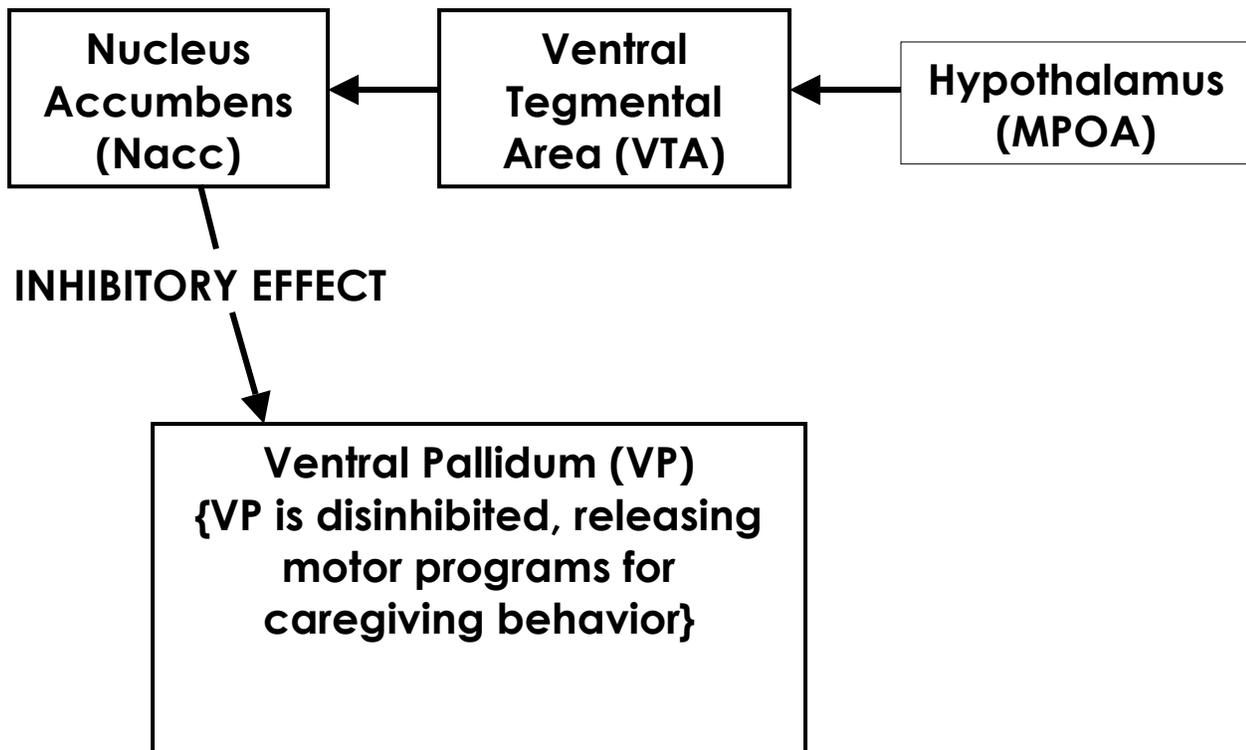
Inhibiting Impulses that Compete with Providing Care

An effective caregiving system must be capable of resolving motivational conflict that undermines the allocation of valuable resources to those in need (S. Brown & R. Brown, 2006; R. Brown & S. Brown, 2006). There are at least two ways in which the caregiving system we have proposed can deal with such conflicts. First, it could directly inhibit the *motivation* to seek rewards for the self, as originally hypothesized by Brown & Brown, 2006. Studies of the interaction of maternal motivation and reward processes support this possibility.

Inhibition of Reward-Seeking Motivation?

A closer look at the rodent model of maternal care reveals that MPOA-directed caregiving motivation might be accomplished via inhibitory processes in the nucleus accumbens (NAcc), a group of subcortical, dopaminergic neurons located near the septum, with inputs from and outputs to components of the limbic system. The NAcc plays a critical role in mediating reward-based behavior across species, including the development and expression of food preferences, sexual behavior, and drug and chemical addiction (Swain, this volume). The NAcc receives inputs from the prefrontal cortex via the Ventral Tegmental Area (VTA—the origin of dopaminergic neurons), and from limbic structures, including the hypothalamus (MPOA). The NAcc outputs to the Ventral Pallidum (VP), which, in turn, plays a role in orchestrating motor programs involved in caregiving (Figure 2).

Figure 2. MPOA-Directed Inhibition of Reward Motivation



There are both inhibitory (D1) and excitatory (D2) receptors in the NAcc, and there is evidence that dopamine activation of D1-like (inhibitory) receptors is important in facilitating maternal behavior (Numan, 2005a) and, interestingly, in maintaining (but not forming) monogamous pair bonds in prairie voles (Aragona, et al., 2006; Aragona, et al., 2009). If NAcc –VP reward circuits are *inhibited* at the same time maternal behavior is facilitated (via input from the MPOA region of the hypothalamus), then it raises the intriguing possibility that NAcc-mediated reward processes are not driving maternal behavior.²

If human caregiving can be characterized by MPOA inhibition of the NAcc, then perhaps this inhibitory process is experienced as a shift in motivation—away from addictive or consumptive types of motivation (e.g., drugs, sex, food, money, alcohol), toward the behavior of allocating resources to others in need. Indeed, the importance of inhibiting the nucleus accumbens for other goal-directed behaviors has been shown across a variety of studies (e.g., Stratford and Kelley 1999; reviewed in Numan 2006). And some studies (but not others) demonstrate that maternal behavior can still occur despite lesions to the NAcc (e.g., Numan, Numan, Schwarz, et al., 2005b). This work indicates that the NAcc is not always necessary for active, voluntary types of maternal behavior such as pup retrieval.

The second way that engagement of a caregiving system may lead to suppression of competing (self-maximizing) motives is by minimizing the projected costs to the self of helping behavior. As we review below, there is clear evidence to suggest that the caregiving system suppresses avoidance motivation (i.e., the fight-or-flight stress response).

Avoiding Avoidance

² S. Brown and Preston interpret this data differently (see Preston & Brown, under review). Whereas Brown suggests that animal models of maternal care can be used to hypothesize the inhibition of reward-seeking motives in the case of humans, Preston considers the involvement of the NAcc in the caregiving circuit to be evidence that helping behavior in humans is mediated by reward processes in the NAcc.

To go back to our earlier example, a lion that approaches a mother who is some distance from her toddler would likely trigger competing impulses in the mother—behaviors aimed at saving the child may be in opposition to behaviors triggered by the mother’s own fight-or-flight response. In this situation, an effective caregiving system would function to inhibit the behavioral response to the threat to mother’s survival while facilitating protection of her child.

Data from rodents are entirely consistent with this possibility. That is, in the animal model, the hypothalamus (MPOA) appears to motivate helping behavior in part by inhibiting the fear-based (avoidance) response to the novel pup stimuli. After the threat/need stimulus is perceived and activates the amygdala, inhibition of the avoidance response by the MPOA is theorized to occur by suppressing projections from the amygdala to the periaqueductal grey (PAG), the command center for mobilizing sympathetic activation (Numan, 2006).

There is support for the possibility that caregiving behavior occurs via inhibition of the competing avoidance response—namely: damage to either the medial amygdala or PAG, which would interfere with the avoidance response, facilitates caregiving behavior in virgin females (e.g. Fleming, et al., 1980). Furthermore, there are substantial interconnections between the MPOA and PAG, which are thought to be inhibitory in nature (Lonstein & Stern, 1997), and some parts of the PAG express Fos protein synthesis (indicating inhibition) during maternal behavior. Together, this work is consistent with the possibility that caregiving motivation depends on inhibition of the competing avoidance (stress) response.

Further evidence in favor of a linkage between helping behavior and inhibition of the stress response comes from studies of the hormonal correlates of helping behavior. For example, oxytocin, which has been shown to stimulate altruistic behavior in humans and non-humans (including maternal behavior, reviewed in Brown & Brown, 2006), decreases activity in the hypothalamic-pituitary-adrenal (HPA) axis (Carter 1998), blood-pressure and cortisol, and delays the withdrawal from heat and mechanical stimuli (Uvnas-Moberg 1997; Uvnas-Moberg 1998; Uvnas-Moberg 1998).

In humans, evidence indicates that helping behavior is indeed associated with reduced stress or accelerated recovery from stress. Specifically, helping behavior predicts faster recovery from depressive symptoms that accompany spousal loss (Brown, Brown et al. 2008), accelerates cardiovascular recovery from a stress induction (Brown, Johnson et al. under review), and buffers the effect of exposure to stressful life events on mortality (Poulin et al., under review).

In summary, this body of research is consistent with the possibility that a motivational system that responds selectively to the needs of others must compete with the system or systems that help individuals seek rewards and respond to threats to self-preservation. In humans, resolution of this motivational conflict may be accomplished by inhibiting addictive or consumptive reward-seeking motivation, and by inhibiting fear/avoidance motivation (Brown & Brown, 2006; Numan, 2006). Importantly, an intimate connection between helping behavior and stress-regulation may explain why helping behavior has been shown repeatedly to be associated with better health and longevity (Post 2007).

Responding Selectively to Bonded Targets

Another critical requirement for an effective caregiving system is to provide some degree of protection against exploitation. This assumption is fundamental to virtually all contemporary accounts of the evolution of altruism that focus on implications of selection at the level of the gene as opposed to selection at the level of the group (e.g., Alexander 1987); Brown & Brown, 2006; Hamilton 1964; Trivers 1971; Zahavi 1995 1997). Accordingly, any evolved mammalian caregiving system should be particularly responsive not only to cues for need, but also to cues that indicate the risk of exploitation. We hypothesize that to limit the threat of exploitation, caregiving neural circuitry is modulated by cues for fitness interdependence, social bonds based on fitness interdependence, and cues that signal another person's vulnerability (indicating to the potential giver that the person in need is in no position to exploit). Below we describe how oxytocin (a hormonal correlate of helping behavior), interdependence, and social bonds may modulate access to caregiving neural circuitry.

Hormonal modulation of the caregiving system

Oxytocin (OT) is causally related to helping behavior and stress-regulation (Brown & Brown, 2006, Carter, 1998), and has receptors throughout the maternal caregiving circuit (Brunton & Russel, 2008). OT is selectively released in non-humans and humans under circumstances that suggest fitness interdependence—for example, birth, breast-feeding, sexual behavior (Carter, 1998); among humans OT has been associated with trust. (Zak, Kurzban et al. 2004).

Oxytocin has been hypothesized to be the hormonal basis of social bonds, love and affiliation (Carter, 1998) because it can facilitate bonding behaviors such as grooming, the formation of partner preferences, and the exploration of novel environments. Despite its apparent role in establishing social bonds and the onset of maternal behavior, OT is not essential for the *maintenance* of maternal behavior. The evidence shows that OT antagonists, antibodies to oxytocin, or lesions of oxytocin-producing neurons can interfere with maternal care only *before* it has been established (Carter, 1998; Numan and Corodimas 1985). This implies that postpartum maternal behavior is not directly mediated by OT (e.g., Numan 1990), but rather that it may be needed to prime the MPOA in order to inhibit the typical fear-based avoidance response of virgin rat females to pups, and facilitate the release of caregiving behaviors (Numan 2006).

Recognizing Bonded Partners

The fact that OT is not essential for sustaining maternal responses suggests that it may produce changes in brain regions that activate caregiving neural circuitry, possibly through pairing the recognition of a bonded partner with activation of maternal care neural circuitry. We are intrigued by the possibility that connections³ between the orbital frontal cortex (OFC) and hypothalamus allow the OFC to modulate access to subcortical hypothalamic circuitry. Below

³ There are heavy interconnections between the hypothalamus and the anterior cingulate cortex (especially the subgenual area of the ACC) and the medial OFC. These interconnections become less dense as projections originate from more lateral areas, with the fewest interconnections to the hypothalamus in the lateral prefrontal cortex (Kringelbach & Rolls 2004).

we describe the basis for this hypothesis in which we consider how properties of the OFC make it a candidate brain region for facilitating bond-formation, maintenance, and dissolution.

The medial OFC stores emotional and visceral experiences of social memories (Ongür and Price 2000), a function that is essential for the formation and maintenance of social bonds (Brown and Brown 2006). The OFC is also important for odor discrimination (Tanabe, Lino et al. 1975; Zatorre and Jones-Gotman 1991), which is well established as important in triggering maternal responsiveness in nonhuman mammals (Numan 2006). The ability of the OFC to code for stimulus specificity (Zald and Kim 1996) derives from its bimodal cells that respond to multiple sensory inputs from a single stimulus. These neurons make the OFC an ideal mechanism for helping individuals code, recognize, and discriminate trustworthy, bonded, or interdependent partners.

Cells in the OFC are also noteworthy because they alter their firing with changes in motivational state. For example, some cells in the OFC will fire in response to food when an animal is hungry, but not when it is satiated (Rolls, Sienkiewicz et al. 1989). Although the OFC is not essential for many reinforcement tasks, “the OFC appears to be essential in situations where the affective value of a stimulus changes” (p. 252, Zald & Kim 1996). This characteristic of the OFC could help individuals navigate new relationships, altering patterns of neuronal firing as strangers become acquaintances, friends, and loved ones, or former relationship partners become estranged. Thus, the OFC could detect important changes in the status of social bonds (and the likelihood of exploitation), and help mediate the caregiving system’s responses to such changes.

Lesions to the ventromedial OFC in human patients provide evidence for its role in coordinating the establishment and dissolution of social bonds. If the OFC can alter social bonds, then damage to this area should disrupt social behavior. Indeed, patients with damage to the ventromedial OFC show reduced autonomic activity with exposure to socially meaningful stimuli (Damasio, Tranel et al. 1990).

To summarize, there is sufficient evidence that social bonds and helping behavior share neurohormonal features, and some evidence that the underlying neural circuitry is also similar. The OFC may code for specific individuals and memories, coordinate different responses to the same social stimuli, and trigger the release of oxytocin. Although the research is not reviewed here, the OFC has been implicated in rational thought and decision-making processes, including decisions about whether to help another person (Preston & de Waal, in press). Because of this, we hypothesize that activation in the OFC may determine whether helping behavior is motivated by the caregiving system, or whether it is motivated by a deliberate cost-benefit analysis (Figure 1). Eisler and Levine (2002) offer a similar proposal, suggesting that the OFC releases caring capacities and prevents their inhibition by emotional stress, stimuli, and beliefs (Eisler and Levine 2002).

Selective Engagement as a function of Resource Availability

As discussed above, providing care for others can be inherently costly, risking exploitation, resource depletion, or even death. Given these threats, the caregiving system should be sensitive to the resource-providing potential of the helper, and access to the system should be limited to instances in which helpers have sufficient resources to invest. Cues that enable individuals to track their own resource-providing potential may include early developmental experiences that alter the landscape of the caregiving system. Studies show, for example, that variability in the adequacy of maternal care in infancy influences individual differences in the development of neuroendocrine responses to stress (Liu et al., 1997). Early exposure to stress in the form of maternal separation, loss, abuse, or neglect results in changes to brain morphology and neurochemistry, and may alter the expression of genes that influence anxiety and mood disorders (Sanchez et al., 2001). These findings are consistent with the possibility that unpredictable parental investment may dysregulate the stress response in infants, which could interfere with the normal development of their caregiving neural circuitry. Consequently, as adolescents and adults, such individuals may turn out to be hypersensitive to cues for danger or exploitation, and

reluctant to invest heavily in others unless there is good evidence that the situation is safe and resources are adequate.

Conclusions

The evidence we have reviewed is compatible with the existence of a dedicated neurobiological system for giving care to others, not readily reducible (at a neurological level) to anticipation of reward or avoidance of pain. The existence of such a system poses a critical challenge to dominant views in psychology and the behavioral sciences that rely on concepts such as rational self-interest or psychological hedonism to explain social behavior. We believe that our framework has implications for a wide variety of phenomena, including providing a mechanism to explain the health benefits of helping others (e.g., Brown, Nesse, Vinokur, & Smith, 2003; Brown et al., 2009a). Hormones involved in caregiving, such as oxytocin and progesterone, can be neuroprotective (e.g., progesterone, Brown et al., 2009b), and restorative in terms of physical health (Heaphy and Dutton 2006). Moreover, the ability of caregiving system motivation to enhance stress-regulation may decrease individuals' exposure to harmful levels of stress hormones such as cortisol.

We are only beginning to understand the neurobiological substrates of helping behavior and interpersonal relationships. However, even a glimpse into these systems illuminates a critical divide between assumptions of human behavior that we use to construct social policy (rational self-interest), and the neural architecture that was shaped by evolution to ensure the organism's role in promoting the survival and reproductive success of others. It is our hope that by advancing a biological framework for the study of the caregiving system, we can take steps towards bridging this divide.

References

- Ainsworth, M. D. S., Bell, S. M., & Stayton, D. J. (1972). Individual differences in the development of some attachment behaviors. *Merrill-Palmer Quarterly*, 18, 123-143
- Alexander, R. D. (1987). *Biology of moral systems*. Seattle, WA, University of Washington Press.
- Aragona, B. J., & Wang, Z. (2009). Dopamine regulation of social choice in a monogamous rodent species. *Frontiers in Behavioral Neuroscience*, 3, 1-11.
- Aragona, B. J., Liu, Y., Yu, Y. J., Curtis, J. T., Detwiler, J. M., Insel, T. R., & Wang, Z. (2006). Nucleus accumbens dopamine differentially mediates the formation and maintenance of monogamous pair bonds. *Nature Neuroscience*, 9, 133-139.
- Bowlby, J. (1969). Disruption of affectional bonds and its effects on behavior. *Journal of Contemporary Psychotherapy*, 2, 75-86.
- Brown, R. M., & Brown, S. L. (2007). Towards uniting the behavioral sciences with a gene-centered approach to altruism. *Behavioral and Brain Sciences*, 30, 19-20.
- Brown, R. M. & Brown, S. L. (2006). SIT Stands and Delivers: A Reply to the Commentaries. *Psychological Inquiry*, 17, 60-74.
- Brown, S. L., R. L. Brown, et al. (2008). "Coping with spousal loss: The potential buffering effects of self-reported helping behavior." *Personality & Social Psychology Bulletin* 34: 849-861.
- Brown, S. L. and R. M. Brown (2006). "Selective Investment Theory: Recasting the functional significance of close relationships." *Psychological Inquiry* 17(1): 1-29.
- Brown, S. L., Fredrickson, B. L., Wirth, M., Poulin, M., Meirer, E., Heaphy, E., Cohen, M., & Schultheiss, O., (2009). Closeness Increases Salivary Progesterone in Humans. *Hormones and Behavior*, 56, 108-111.

- Brown, S. L., K. Johnson, et al. (under review). "Helping behavior accelerates recovery from cardiovascular stress."
- Brown, S. L., R. M. Nesse, et al. (2003). "Providing social support may be more beneficial than receiving it: results from a prospective study of mortality." *Psychological Science* 14(4): 320-327.
- Brown, S. L. Smith, D. M., Schulz, R. Kabeto, M., Ubel, P., Yee, J., Kim, C. & Langa, K. (2009). Caregiving and Decreased Mortality in a National Sample of Older Adults, *Psychological Science*, 20, 488-494.
- Brown, W. M., N. S. Consedine, et al. (2005). "Altruism relates to health in an ethnically diverse sample of older adults." *Journals of Gerontology: Series B: Psychological Sciences & Social Sciences* 60B: 143-152.
- Brunton, P. & Russell, J. (2008). The expectant brain: adapting for motherhood. *Nature Reviews Neuroscience* 9, 11-25.
- Budden, A. E. and J. Wright. (2001). Begging in nestling birds. In V. Nolan, Jr. & C. F. Thompson (Eds.), *Current Ornithology*, vol. 16 (pp. 83-118). New York: Plenum Press.
- Carter, C. S. (1998). "Neuroendocrine perspectives on social attachment and love." *Psychoneuroendocrinology* 23: 779-818.
- Cialdini, R. B., D. K. Darby, et al. (1973). "Transgression and altruism: A case for hedonism. ." *Journal of Experimental Social Psychology* 9: 502-516.
- Christoph, G., Leonzio, R., & Wilcox, K. (1986). Stimulation of the lateral habenula inhibits dopamine-containing neurons in the substantia nigra and the ventral tegmental area of the rat. *The Journal of Neuroscience*, 6, 613-619.
- Collins, N. L., Guichard, A. C., Ford, M. B., & Feeney, B. C. (2006). Responding to need in intimate relationships: Normative processes and individual differences. In M. Mikulincer & G. S. Goodman (Eds.), *Dynamics of romantic love: Attachment, caregiving, and sex* (pp. 149-189). New York: Guilford Press.

- Damasio, A. R., D. Tranel, et al. (1990). "Individuals with sociopathic behavior caused by frontal damage fail to respond autonomically to social stimuli." *Behavioural Brain Research* 41(2): 81-94.
- deCatanzaro, D. (1986). A mathematical model of evolutionary pressures regulating self-preservation and self-destruction. *Suicide and Life-Threatening Behavior*, 16, 166-181.
- Diorio, D., Viau, V., & Meaney, M. J. (1993). The role of the medial prefrontal cortex (cingulate gyrus) in the regulation of hypothalamic-pituitary-adrenal responses to stress. *Journal of Neuroscience*, 13, 3839-3847.
- Drevets, W. C., Öngür, D., & Price, J. L. (1998). Neuroimaging abnormalities in the subgenual prefrontal cortex: implications for the pathophysiology of familial mood disorders. *Molecular psychiatry*, 3(3), 220-226.
- Durkheim E. (1951). *Suicide: A study in sociology*. New York: The Free Press
- Eisler, R. and D. S. Levine (2002). "Nurture, nature, and caring: We are not prisoners of our genes." *Brain and Mind* 3: 9-52.
- Hamilton, W. D. (1964). "The genetic evolution of social behavior: I and II." *Journal of Theoretical Biology* 7: 1-52.
- Heaphy, E. D. and J. E. Dutton (2006). *Embodying Social Interactions: Integrating Physiology into the Study of Positive Connections and Relationships at Work*.
- Jacobson, C. D., Terkel, J., Gorski, R. A., & Sawyer, C. H. (1980). Effects of small medial preoptic area lesions on maternal behavior: Retrieving and nest building in the rat. *Brain Research*, 194, 471-478.
- Kahneman, D., A. B. Krueger, et al. (2004). "A survey method for characterizing daily life experience: the day reconstruction method." *Science* 306 (5702): 1776-80.
- Kölliker, M. J., Chuckalovcak, J. P., Haynes, K.F., & Brodie III, E. D. (2006). Maternal food provisioning in relation to condition-dependent offspring odours in burrower bugs

- (*Sehirus cinctus*). *Proceedings of the Royal Society of London, Series B* 273, 1523-1528
- Joiner, T. (2005). *Why people die by suicide*. Cambridge: Harvard University Press.
- Kilner, R. and R. A. Johnstone. (1997). Begging the question: Are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*, 12, 11–15.
- Kringelbach, M. L. and E. T. Rolls (2004). "The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology." *Progress in Neurobiology* 72(5): 341-372.
- Linville, D., Chronister, K., Dishion, T., Todahl, J., Miller, J., Shaw, D., Gardner, F., & Wilson, M. (2010). Longitudinal analysis of parenting practices, couple satisfaction, and child behavior problems. *Journal of Marital Family Therapy*, 36, 244–255.
- Liu, D., Diorio, J., Tannenbaum, B., Caldji, C., Francis, D., Freedman, A., et al., (1997). Maternal Care, Hippocampal Glucocorticoid Receptors, and Hypothalamic-Pituitary-Adrenal Response to Stress. *Science*, 277, 1659 – 1662.
- Lonstein, J. S., & Morrell, J. I. (2007). Neuroendocrinology and neurochemistry of maternal motivation and behavior. In A. Lajtha & J. D. Blaustein (Eds.), *Handbook of Neurochemistry and Molecular Neurobiology* (3rd ed., pp. 195-245). Berlin: Springer-Verlag.
- Lonstein, J. S. & Stern, J. M. (1997). Role of the midbrain periaqueductal gray in maternal nurturance and aggression: C-fos and electrolytic lesion studies in lactating rats. *The Journal of Neuroscience*, 17, 3364-3378.
- Lorberbaum, J. P., Newman, J. D., Dubno, J. R., Horwitz, A. R., Nahas, Z., Teneback, C. C., et al. (1999). Feasibility of using fMRI to study mothers responding to infant cries. *Depression and Anxiety*, 10(3), 99-104.

- Lorberbaum, J., Newman, J. D., Horwitz, A. R., Dubno, J. R., Lydiard, R. B., Hamner, M. B., et al. (2002). A potential role for thalamocingulate circuitry in human maternal behavior. *Biological Psychiatry*, 51(6), 431 - 445.
- Marsh, A. (under review). Fear and empathy: A cognitive neuroscience perspective
- Molavi, Diana Weedman et al. *Neuroscience Tutorial: Hypothalamus and Autonomic Nervous System*. ST. LOUIS: Washington Univ. School of Medicine, 1997.
(<http://thalamus.wustl.edu/course/hypoANS.html>)
- Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. *Proc Natl Acad Sci U S A*, 103(42), 15623-15628.
- Numan, M. (1990). "Long-term effects of preoptic area knife cuts on the maternal behavior of postpartum rats." *Behav Neural Biol* 53(2): 284-290.
- Numan, M. (2006). "Hypothalamic neural circuits regulating maternal responsiveness toward infants." *Behav Cogn Neurosci Rev* 5(4): 163-190.
- Numan, M. (2007). Motivational systems and the neural circuitry of maternal behavior in the rat. *Developmental Psychobiology*, 49(1), 12-21.
- Numan, M. and K. P. Corodimas (1985). "The effects of paraventricular hypothalamic lesions on maternal behavior in rats." *Physiol Behav* 35(3): 417-425.
- Numan, M., & Insel, T. R. (2003). *The Neurobiology of Parental Behavior*. New York:
- Numan, M., Numan, M. J., Pliakou, N., Stolzenberg, D. S., Mullins, O. J., Murphy, J. M., & Smith, C. D.(2005a). The effects of D1 or D2 dopamine receptor antagonism in the medial preoptic area, ventral pallidum, or nucleus accumbens on the maternal retrieval response and other aspects of maternal behavior in rats. *Behav. Neurosci.* 119, 1588-1604.
- Numan, M., Numan, M. J., Schwarz, J. M., Neuner, C. M., Flood, T. F., & Smith, C. D.(2005b). Medial preoptic area interactions with the nucleus accumbens-ventral pallidum circuit and maternal behavior in rats. *Behav. Brain Res.* 158, 53-68.

- Ongür, D. and J. L. Price (2000). "The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans." *Cerebral Cortex* 10: 206-219.
- Preston, S. D. & deWaal, F. B. M (in press). Altruism. *The Handbook of Social Neuroscience*. Jean Decety and John Cacioppo eds. Oxford University Press.
- Post, S. G., Ed. (2007). *Altruism and Health: Perspectives from empirical research*. New York, Oxford University Press.
- Poulin, M., Brown, S., Dillard, A. & Smith, D. (under review). Health benefits of helping behavior: Stress-buffering as a potential mechanism.
- Preston, S. & Brown, S. Fools rush in: The ultimate and proximate bases of active altruism. *Neuroscience and Biobehavioral Reviews* (revise and resubmit).
- Rolls, E. T., Z. J. Sienkiewicz, et al. (1989). "Hunger modulates the responses to gustatory stimuli of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey." *European Journal of Neuroscience* 1: 53-60.
- Rosenblatt, J. S. (1992). Hormone-behavior relations in the regulation of maternal behavior. In J. B. Becker, S. M. Breedlove & D. Crews (Eds.), *Behavioral Endocrinology* (1st ed., pp. 219-259). Cambridge, MA: MIT Press/Bradford Books.
- Sanchez, M., Ladd, C., & Plotsky, P. (2001). Early adverse experience as a developmental risk factor for later psychopathology: Evidence from rodent and primate models. *Development and Psychopathology*, 13, 419-449.
- Stratford, T. R. and A. E. Kelley (1999). "Evidence of functional relationship between NAc shell and lateral hypothalamus subserving the control of feeding behavior." *J Neurosci* 19: 11040-11048.
- Tanabe, T., M. Lino, et al. (1975). "Discrimination of odors in olfactory bulb, pyriform-amygdaloid areas, and orbitofrontal cortex of the monkey." *Journal Neurophysiology* 38: 1284-1296.

- Terkel, J., Bridges, R. S., & Sawyer, C. H. (1979). Effects of transecting lateral neural connections of the medial preoptic area on maternal behavior in the rat: Nest building, pup retrieval and prolactin secretion. *Brain Research*, 169, 369-380.
- Trivers, R. L. (1971). "The evolution of reciprocal altruism." *Quarterly Review of Biology* 46: 35-57.
- Ueno, A. & Matsuzawa, T. (2004). Food transfer between chimpanzee mothers and their infants. *Primates*, 45, 231-239.
- Uvnas-Moberg, K. (1997). "Physiological and endocrine effects of social contact." *Ann NY Acad Sci* 807: 146-163.
- Uvnas-Moberg, K. (1998). "Antistress pattern induced by oxytocin." *News Physiol Sci* 13: 22-25.
- Uvnas-Moberg, K. (1998). "Oxytocin may mediate the benefits of positive social interaction and emotions." *Psychoneuroendocrinology* 23: 819-835.
- Warneken, F., Hare, B., Melis, A.P., Hanus, D., & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. *PLoS Biology*, 5, 1414 – 1420.
- Wong, L., Kolditz, T. A., Millen, R. A., & Potter, T. M. (2003). *Why they fight: Combat motivation in the Iraq War*. Carlisle Barracks, PA: Strategic Studies Institute.
- Wright, J. and M. L. Leonard (2002). *The evolution of nestling begging: competition, cooperation & communication*. Dordrecht: Kluwer Academic Press.
- Zahavi, A. (1995). "Mate selection-a selection for handicap." *Journal of Theoretical Biology* 53: 205-214.
- Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. New York, Oxford University Press.
- Zak, P. J., R. Kurzban, et al. (2004). "The neurobiology of trust." *Ann N Y Acad Sci* 1032: 224-227.

Zald, D. H. and S. W. Kim (1996). "Anatomy and function of the orbital frontal cortex, II: function and relevance to obsessive-compulsive disorder." *Journal of Neuropsychiatry* 8(3): 249-261.

Zatorre, R. J. and M. Jones-Gotman (1991). "Human olfactory discrimination after unilateral frontal or temporal lobectomy." *Brain* 114(part A): 71-84.