



Published in final edited form as:

*Parent Sci Pract.* 2012 ; 12(2-3): 115–123. doi:10.1080/15295192.2012.680409.

## Parenting and Beyond: Common Neurocircuits Underlying Parental and Altruistic Caregiving

**James E. Swain,**

Department of Psychiatry, University of Michigan, Rachel Upjohn Building, 4250 Plymouth Road, Ann Arbor, Michigan 48109-2700 USA.

**Sara Konrath,**

University of Michigan.

**Stephanie L. Brown,**

University of Michigan.

**Eric D. Finegood,**

University of Michigan.

**Leyla B. Akce,**

University of Michigan.

**Carolyn J. Dayton,** and

University of Michigan.

**S. Shaun Ho**

University of Michigan.

James E. Swain: jamesswa@med.umich.edu

### SYNOPSIS

Interpersonal relationships constitute the foundation on which human society is based. The infant-caregiver bond is the earliest and most influential of these relationships. Driven by evolutionary pressure for survival, parents feel compelled to provide care to their biological offspring. However, compassion for non-kin is also ubiquitous in human societies, motivating individuals to suppress their own self-interests to promote the well-being of non-kin members of the society. We argue that the process of early kinship-selective parental care provides the foundation for non-exclusive altruism via the activation of a general *Caregiving System* that regulates compassion in any of its forms. We propose a tripartite structure of this system that includes (1) the perception of *need* in another, (2) a *caring motivational or feeling* state, and (3) the delivery of a *helping response* to the individual in need. Findings from human and animal research point to specific neurobiological mechanisms including activation of the insula and the secretion of oxytocin that support the adaptive functioning of this Caregiving System.

### INTRODUCTION

The human capacity to form enduring social relationships is central to individual and collective mental health in a society. These relationships can manifest as “care for others”, whether parental care in parent-child dyads, care within kinship relationships, altruistic helping behaviors towards friends and even strangers, or compassion for all. High quality social relationships between parents and children, siblings, spouses, friends, co-workers, or any two people create recurring fulfilling emotional experiences (i.e., “bonds” or “connections”), and a society that maintains the strength of such experiences functions at a high level.

## THE PRIMACY OF PARENTAL CARE

The bond between the primary caregiver and the infant constitutes the earliest and most influential relationship that humans experience (Feldman, 2007). Building on the work of Bowlby and colleagues (Bowlby, 1978), efforts to characterize this reciprocal interaction between mother and infant and to assess its impact on infant and child development have provided a powerful theoretical and empirical framework within social and developmental psychology (Cassidy & Shaver, 1999). Parenting quality modulates gene expression and the brain systems underlying emotion and stress regulation in human children (McGowan et al., 2009). Better parenting can diminish anxiety and aggression (NICHD Early Care Research Network, 2006) and cultivate resilience after stress (Korosi & Baram, 2010). Thus, adults' disposition of caring for others may have roots in their own early-life experiences with primary caregivers such that people who experienced quality parenting as children may express stronger compassion and altruistic behaviors towards others. This connection between early life experience and later caring is supported by the continuity of parent-infant attachment styles into adult relationships (Fraley, 2002). Debated at least since Darwinian times, it has been recently theorized that the origins of altruistic behaviors lie in the quality of parent-infant interactions across species (De Waal, 1996, 2009; Sober & Wilson, 1998).

## FROM KIN TO NON-KIN TO GENERALIZED CARE AND GENEROSITY

How can *kinship-selective* parental care (e.g., a mother brings home her baby from daycare everyday instead of an unrelated baby) be generalized to *kinship-non-selective* caregiving (e.g., a maternal care for an unrelated baby)? We argue that exclusive parenting is the ultimate foundation of non-exclusive altruism, via the proximate mechanisms of deep emotional bonds. This is also not a new idea: "Tender emotion and the protective impulse are, no doubt, evoked more readily and intensely by one's own offspring... but the distress of any child will evoke this response to a very intense degree in those in whom the instinct is strong.... In a similar direct fashion the distress of any adult (towards whom we harbor no hostile sentiment) evokes the emotion" (McDougall, 1908), p. 72–74).

Here, we refer to this deep sense of emotional connection as *compassion*, defined as "the feeling that arises in witnessing another's suffering and that motivates a subsequent desire to help" (Goetz, Keltner, & Simon-Thomas, 2010). We construe compassion as a psychological construct encompassing facets of empathy (social cognitive ability), loving kindness (caring feelings), and generosity (helping actions) toward others regardless of kinship (Brown & Brown, 2006). Thus, compassion is a motivation that may suppress our own self-interest to promote the well-being of others. Compassion is subserved by a general *Caregiving System* (Brown, Brown, & Preston, 2011), that operates in both parental and altruistic caregiving and makes genuine non-exclusive altruism possible.

In this article, we describe potential neurobiological and hormonal mechanisms of this general *Caregiving System* in humans. We review a subset of the human neuroimaging literature elucidating functional and structural neurobiological and hormonal mechanisms underlying parental and altruistic care. Namely, we highlight the functional brain region of the insula and the neurohormone oxytocin as key components of both specific parenting *and* general caregiving systems. We also discuss how parenting and compassion may be mutually cultivated through practice.

## NEUROBIOLOGICAL MECHANISMS OF PARENTAL CAREGIVING

Classical lesion studies in rodent model systems (rats, mice, and voles) have implicated the medial pre-optic area (MPOA) of the hypothalamus, the ventral part of the bed nucleus of the stria terminalis (BNST), and the lateral septum (LS) as regions pivotal for regulation of

pup-directed maternal behavior via a limited number of key genes and hormones, such as estrogen, prolactin and oxytocin. Importantly, maternal responsiveness necessarily includes hypothalamic control of both approaching distressed offspring *and* inhibiting competing stress responses that would interfere with providing help (Numan, 2006). *Approach motivation* is increased via the nucleus accumbens-ventral pallidum circuit, and *avoidance motivation* is reduced by interrupting threat signals transmitted from the amygdala to the periaqueductal grey (PAG). The possibility that maternal behavior depends on the simultaneous regulation of avoidance and approach motivation raises intriguing questions about possible health implications of maternal caregiving because both motivations are intimately tied to the regulation of the sympathetic stress response system (Brown, Brown, & Preston, 2011).

Maternal licking and grooming behavior in the days following birth serves to contribute to the pups' level of stress response in hypothalamic-pituitary-adrenal axis, which in turn can affect subsequent maternal behavior of the offspring by means of altering their stress reactivity and emotionality (Jensen & Champagne, 2012). There is also growing evidence that, at least in part, early-life programming of young affects their later adult parenting behavior through altered expression of genes, as with the estrogen receptor alpha gene in an animal model (Champagne et al., 2006), and in development of brain circuitry that is directly implicated in the regulation of maternal behavior in humans (Kim, Leckman, Mayes, Newman, et al., 2010). Although we do not know whether the epigenetic activation of maternally related genes is transmitted across multiple generations of female offspring, the intergenerational cycle of parenting style, behavior, and related physiology clearly repeats itself across multiple generations (Champagne, 2010; Gonzalez, Lovic, Ward, Wainwright, & Fleming, 2001; Kaffman & Meaney, 2007; Veenema, 2009). Importantly, early adversity effects on the HPA stress system and its intergenerational transmission can be reversed or contribute to resiliency with environmental alterations (Beery & Francis, 2011). It remains to be studied, whether a similar reversal can occur with respect to the effects of early adversity and later enrichment or targeted parenting psychotherapeutic interventions on the maternal system.

In humans, homologous neurocircuits to those that regulate rodent parenting behaviors are being described using safe structural and functional magnetic resonance neuroimaging (MRI) techniques. MRI techniques combine non-invasive magnetic fields and radiofrequency signals to determine the properties of brain tissue. For functional studies, infant auditory and visual stimuli events are used to elicit blood-oxygen-dependent signals that relate to brain activity with millimeter resolution. An important caveat throughout the interpretation of fMRI studies, however, is that that the resultant measurements represent integrations of brain activity and relate blood flow changes that require several seconds to develop. On one hand, short events may capture briefly held mental states, but miss sustained emotion; on the other hand, longer events may capture more complex brain responses, but also average them out making subtle phenomena more difficult to separate from the noise.

Lorberbaum and colleagues (2002) were the first group to study brain activity in mothers while they listened to other-baby cries, highlighting the importance of a thalamocingulate circuit for emotion response and regulation in mammals. Since then, researchers have confirmed the importance in humans of a broad array of brain regions for response to own-infant stimuli and which relate to parenting thoughts and behaviors, including parts of the amygdala (alarm), striatum/nucleus accumbens (NA; motivation and reward), and cingulate (decision-making). In humans, cortical regions that have not been highlighted so much in the rodent literature have also been described, including the inferior frontal gyrus (IFG), orbitofrontal cortex (OFC), insula, periaqueductal grey (PAG) and dorsomedial prefrontal

cortex (dmPFC), that regulate complex social-cognitive functions that are selectively engaged when the maternal brain responds to infant stimuli (cries or pictures). (For reviews, see (Barrett & Fleming, 2011; Swain, 2010, 2011).

## PARENTAL BRAIN IMAGING RESPONSES AND STRUCTURAL PLASTICITY

Recent human neuroimaging studies have demonstrated the functional significance of many of the parental caregiving-related brain circuits mentioned above, with increasing emphasis on cortical areas. Conceptualizing empathy as a key aspect of parenting, Lenzi and colleagues (Lenzi et al., 2009) scanned mothers while observing and imitating faces of their own child and found that mothers responded to emotional expressions of their child with activations in the insula and other cortical regions involved in motor imitation (mirror neuron system), in addition to the amygdala. Moreover, right anterior insular activation was correlated positively with levels of maternal empathy assessed with independent validated interviews. It is interesting to speculate as to whether babies' brains are also mirroring parents' brains with activations relating to long term consequences and in accord with animal models above.

Direct studies of baby brain structure and function in response to parenting cues have not been done; however, a pioneering neuroimaging study of mothers showed how perceived maternal care (a proxy for the animal models' licking and grooming behaviors) affects both brain structures and functional response to own-baby cries (Kim, Leckman, Mayes, Newman et al., 2010). In this study, mothers who reported higher maternal care in their own childhood showed higher gray matter density, proportional to the number of neurons, in a range of higher cortical areas and executive function areas, including the insula, superior and middle frontal gyri, orbital gyrus, superior temporal gyrus and fusiform gyrus. There were also increased functional responses in a number of frontal brain regions and the insula in response to own-baby cries.

Strikingly, besides the effects of mothers' own early-life experiences, the transition to parenthood also involves a degree of maternal brain plasticity around the time of childbirth. In the first prospective longitudinal study of gray matter changes over the first few months of parenthood, there were increases in gray matter volume of the insula, prefrontal cortex, parietal lobes, and midbrain areas between 2–4 weeks and 3–4 months postpartum (Kim, Leckman, Mayes, Feldman et al., 2010). Furthermore, increased gray matter volume in the midbrain (including the hypothalamus, substantia nigra, and amygdala) was associated with maternal positive perceptions of her baby. Because the hypothalamus contains neurons responsible for oxytocin secretion, the increased hypothalamus volume may result from potentially bolstered oxytocin neurons, which may lead to increased positive maternal feelings towards infants. Direct evidence for the involvement of oxytocinergic cell involvement is lacking, but these results at least suggest that the first months of motherhood in humans are accompanied by hypothalamic-fortifying structural plasticity that may potentiate positive feelings toward babies.

## THE IMPORTANCE OF OXYTOCIN IN PARENTING

Among the factors that may account for variations in parent-infant interactions is the neurohormone oxytocin (Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010). One aspect of motherhood is the mode of delivery, such that vaginal (VD) versus caesarean deliveries (CD) is associated with higher oxytocin (Marchini, Lagercrantz, Winberg, & Uvnas-Moberg, 1988). Consistent with this, mothers with VD vs. CD show greater brain responses to baby-cries in the insula, striatum, and anterior cingulate cortex (Swain et al., 2008). Regardless of delivery type, mothers show higher oxytocin levels during breastfeeding (Nissen et al., 1996). In accord, breastfeeding versus formula-feeding

mothers show greater brain responses to their own infant's cry in insula, striatum, amygdala, and superior frontal gyrus (Kim et al., 2011). Although other hormones may be involved, serum oxytocin has been directly related to brain responses to baby pictures of different emotions in emotion regulation areas (cingulate), reward regions (striatum) and hormone-control regions (hypothalamus) (Strathearn, Fonagy, Amico, & Montague, 2009; Strathearn, Li, Fonagy, & Montague, 2008).

In addition, women administered intranasal oxytocin showed increased neural responses to unrelated baby cries in the inferior frontal gyrus and insula compared to women in the placebo group. Evidently, a causal relation between oxytocin and women's brain responses was demonstrated with two groups in a randomized control trial (Riem et al., 2011). These regions are linked with empathy and mother-infant bonding. Oxytocin administration also led to decreased neural responses in the right amygdala, which is linked to anxiety and aversion. This study shows that oxytocin may modulate maternal behaviors by *enhancing positive motivation* by sensitizing care-related insula activity, and by *reducing negative motivation* by desensitizing anxiety-related amygdala responses as infant pictures themselves has been shown to do to mother brains (Bartels & Zeki, 2004). This is also consistent with administration of oxytocin increasing parental behaviors (Naber, van IJzendoorn, Deschamps, van Engeland, & Bakermans-Kranenburg, 2010).

## NEUROBIOLOGICAL MECHANISMS OF NON-KIN CAREGIVING

Human neuroimaging research has also advanced our understanding of neural mechanisms underlying pro-social altruistic behaviors suggesting the key importance of a limited group of brain regions that overlap with those important for parenting. For example, hypothesizing that altruistic motivation is driven by empathy and affected by perceived group membership, Hein and colleagues (Hein, Silani, Preuschoff, Batson, & Singer, 2010) scanned participants as they witnessed an in-group or out-group partner (a fan of the same or different soccer team) experiencing painful stimuli (electric shocks). Participants could help their partner by receiving half of their partner's shocks (a costly option), watch a soccer video, or watch their partner receive pain. The neural responses in the anterior insula while witnessing another in-group member in pain strongly predicted later helping behavior. Additionally, the anterior insula was the only region that correlated positively with both helping behavior and a separate measure of empathic concern. These results display how the willingness to engage in costly altruistic behavior may critically depend on the insula.

A related fMRI study investigated neural correlates of charitable donations (Hare, Camerer, Knoepfle, & Rangel, 2010). In half of the trials, participants were given the option to donate \$0-\$100 of their own study compensation to numerous charities. In the other half, participants were forced to donate a certain amount to a charity. At the conclusion of the study, one charity would be chosen at random and the money would actually be donated (either forcibly or willingly). The researchers found that three key brain areas were implicated in donation behaviors: the ventral medial prefrontal cortex (vmPFC), the bilateral anterior insula, and the posterior superior temporal cortex (pSTC). Activation and interaction between these regions modulated the actual charitable donations made by participants.

The insula is also related to feelings of loving-kindness as shown in brain imaging of meditation practices (Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008). Long-term compassion-based meditators vs. novice meditators, while they were engaged in an experimental state of loving-kindness meditation, showed greater activation in the insula and areas of the somatosensory cortex in response to emotional stimuli. Furthermore, insular activation during meditation correlated positively with self-reported meditation intensity.

These findings underline the key role of the insula in maintaining the capacity for empathic concern, a quality necessary in both successful parental and non-kin caring.

Along similar lines, studies on brain structural plasticity have found that long-term compassion-based mindfulness meditation, which includes compassion-based exercises, increased cortical thickness and gray matter volume of the anterior insula in long-term practitioners of mindfulness meditation versus matched controls (Holzel et al., 2008; Lazar et al., 2005). These human brain imaging studies demonstrate an effect of meditation on structural plasticity in the key brain region underlying compassion which parallels changes in structural plasticity that occur in new mothers.

Finally, a link between the insula and oxytocin was also found in empathy as an aspect of compassion. Pincus and colleagues (Pincus et al., 2010) manipulated intranasal oxytocin in depressed patients and matched controls while they underwent an emotional mental attribution task. They found an increased neural activation in insula and cingulate in depressed patients during the emotional mental attribution. This study shows that oxytocin might reverse a possible impairment of emotional empathy in the depressed patients.

## SUMMARY AND FUTURE DIRECTIONS

In many ways our understanding of the neurobiology of human parental and altruistic caregiving is in its infancy. However, there may be enough pieces of the puzzle at this time to see an emerging picture. Across the studies reviewed above, the insula and oxytocin emerge as prominent anatomical and hormonal mechanisms, respectively, underlying both parenting and non-kin caring. Hence, it is suggested that the insula and oxytocin are key players in a general *Caregiving System* (Brown, Brown, & Preston, in press), which may regulate compassion in any of its forms (Frost, 2003; Goetz, Keltner, & Simon-Thomas, 2010). This system can be formulated as having a tripartite structure starting with (1) perception of an individual's *need* for assistance, which can elicit (2) a *caring motivational or feeling* state, and consequently (3) *helping responses* to the individual in need are made – for the child in the instance of parenting in response to baby-cry (Swain, 2010; Swain, Kim, & Ho, 2011; Swain et al., 2012).

Advances in technology in terms of brain imaging and hormone assays may help us to understand the ways that the human brain has evolved to motivate and regulate caring motivations. This information may help to create an infrastructure for understanding how human prosocial tendencies are represented in the brain with implications for optimizing resilience, mood, and mental and physical health.

As yet, our studies have not addressed the complexities of how parenting style variations may be reflected in variations in brain activation patterns. There is no one way to be a parent, and we predict that mothers who communicate primarily by talking and facial and eye-movements face-to-face with an infant may show a different pattern from those whose primary mode of interaction involves primarily carrying, somatosensory, or vestibular adjustments – behaviors that may also vary with cultural input. Hence, we imagine that there are not only differences among mothers in their motivation to mother and their caregiving feelings, as described above; there may also be variations in the elaborate brain patterns associated with the quality and intensity of parenting exhibited, and these brain patterns may well vary across cultures, across parity, and across different infants within a family. Such differences in brain patterns will need to be addressed in addition to unifying caring circuits that may be critical to “good-enough” parenting (Winnicott, 1960).

In practice, several parenting interventions have already employed methods that can cultivate compassion. For example, *Circle of Security* provides a program model for

working with parents of toddlers to enhance reflective functioning on themes of attachment, which is relevant for compassionate parenting during preschool ages (Hoffman, 2006; Marvin, Cooper, Hoffman, & Powell, 2000). Several other mindfulness-based parenting programs aim to develop the qualities of listening with full attention when interacting with their children, cultivating emotional awareness and self-regulation in parenting, and bringing compassion and nonjudgmental acceptance to their parenting interactions (Duncan, Coatsworth, & Greenberg, 2009). It would be interesting to investigate how interventions like these modulate the insula and connected brain circuits as well as oxytocin and related endocrine systems to promote caring. Such research may increase adults' and children's well-being and collectively our society's capacity to be more compassionate and tolerant.

## Acknowledgments

Dr. Swain is supported by grants the National Alliance of Research on Schizophrenia and Depression (narsad.org), the Klingenstein Third Generation Foundation (ktgf.org), NIH/NIMHD IRC2MD004767-01, and the Michigan Institute for Clinical Health Research UL1RR024986 (JES).

## REFERENCES

- Barrett J, Fleming AS. Annual Research Review: All mothers are not created equal: neural and psychobiological perspectives on mothering and the importance of individual differences. *Journal of Child Psychology and Psychiatry*. 2011; 52:368–397. [PubMed: 20925656]
- Bartels A, Zeki S. The neural correlates of maternal and romantic love. *Neuroimage*. 2004; 21(3): 1155–1166. [PubMed: 15006682]
- Beery AK, Francis DD. Adaptive significance of natural variations in maternal care in rats: A translational perspective. *Neuroscience Biobehavioral Reviews*. 2011; 35(7):1552–1561.
- Bowlby J. Attachment theory and its therapeutic implications. *Adolescent Psychiatry*. 1978; 6:5–33. [PubMed: 742687]
- Brown SL, Brown RM. Selective Investment Theory: Recasting the Functional Significance of Close Relationships. *Psychological Inquiry*. 2006; 17(1–29)
- Brown, SL.; Brown, RM.; Preston, S. A model of human caregiving motivation. In: Brown, SL.; Brown, RM.; Penner, L., editors. *Moving Beyond Self Interest: Perspectives from Evolutionary Biology, Neuroscience, and the Social Sciences*. New York: Oxford University Press; 2011.
- Cassidy, J.; Shaver, PR. *Handbook of Attachment*. Guilford Press; 1999.
- Champagne FA. Epigenetic influence of social experiences across the lifespan. *Developmental Psychobiology*. 2010; 52(4):299–311. [PubMed: 20175106]
- Champagne FA, Weaver IC, Diorio J, Dymov S, Szyf M, Meaney MJ. Maternal care associated with methylation of the estrogen receptor- $\alpha$ 1b promoter and estrogen receptor- $\alpha$  expression in the medial preoptic area of female offspring. *Endocrinology*. 2006; 147(6):2909–2915. [PubMed: 16513834]
- De Waal, F. *Good natured: The origins of right and wrong in humans and other animals*. Cambridge: Harvard University Press; 1996.
- De Waal, F. *The Age of Empathy: Nature's Lessons for a Kinder Society*. New York: Three Rivers Press/Random House; 2009.
- Duncan LG, Coatsworth JD, Greenberg MT. A model of mindful parenting: implications for parent-child relationships and prevention research. *Clinical Child and Family Psychology Reviews*. 2009; 12(3):255–270.
- Feldman R. Parent-infant synchrony and the construction of shared timing; physiological precursors, developmental outcomes, and risk conditions. *Journal of Child Psychology and Psychiatry*. 2007; 48(3–4):329–354. [PubMed: 17355401]
- Feldman R, Gordon I, Schneiderman I, Weisman O, Zagoory-Sharon O. Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent-infant contact. *Psychoneuroendocrinology*. 2010

- Fraley RC. Attachment Stability From Infancy to Adulthood: Meta-Analysis and Dynamic Modeling of Developmental Mechanisms. *Personality and Social Psychology Review*. 2002; 6(2):123–151.
- Frost, PJ. *Toxic Emotions as Work: How Compassionate Managers Handle Pain and Conflict*. Boston, MA: Harvard Business School Press; 2003.
- Goetz JL, Keltner D, Simon-Thomas E. Compassion: an evolutionary analysis and empirical review. *Psychological Bulletin*. 2010; 136(3):351–374. [PubMed: 20438142]
- Gonzalez A, Lovic V, Ward GR, Wainwright PE, Fleming AS. Intergenerational effects of complete maternal deprivation and replacement stimulation on maternal behavior and emotionality in female rats. *Developmental Psychobiology*. 2001; 38(1):11–32. [PubMed: 11150058]
- Hare TA, Camerer CF, Knopfle DT, Rangel A. Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. *Journal of Neuroscience*. 2010; 30(2):583–590. [PubMed: 20071521]
- Hein G, Silani G, Preuschhoff K, Batson CD, Singer T. Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron*. 2010; 68(1):149–160. [PubMed: 20920798]
- Hoffman KT. Changing toddlers' and preschoolers' attachment classifications: The circle of security intervention. *Journal of Consulting and Clinical Psychology*. 2006; 74(6) 1017-10260022-10260020.
- Holzel BK, Ott U, Gard T, Hempel H, Weygandt M, Morgen K, et al. Investigation of mindfulness meditation practitioners with voxel-based morphometry. *Social Cognitive and Affective Neuroscience*. 2008; 3(1):55–61. [PubMed: 19015095]
- Jensen CL, Champagne F. Epigenetic and neurodevelopmental perspectives on variation in parenting behavior. *Parenting: Science & Practice*. 2012; 12 xx-xx.
- Kaffman A, Meaney MJ. Neurodevelopmental sequelae of postnatal maternal care in rodents: clinical and research implications of molecular insights. *Journal of Child Psychology and Psychiatry*. 2007; 48(3–4):224–244. [PubMed: 17355397]
- Kim P, Feldman R, Mayes LC, Eicher V, Thompson N, Leckman JF, et al. Breastfeeding, brain activation to own infant cry, and maternal sensitivity. *Journal of Child Psychology and Psychiatry*. 2011; 52(8):907–915. [PubMed: 21501165]
- Kim P, Leckman JF, Mayes LC, Feldman R, Wang X, Swain JE. The plasticity of human maternal brain: longitudinal changes in brain anatomy during the early postpartum period. *Behavioral Neuroscience*. 2010; 124(5):695–700. [PubMed: 20939669]
- Kim P, Leckman JF, Mayes LC, Newman MA, Feldman R, Swain JE. Perceived quality of maternal care in childhood and structure and function of mothers' brain. *Developmental Science*. 2010; 13(4):662–673. [PubMed: 20590729]
- Korosi A, Baram TZ. Plasticity of the stress response early in life: mechanisms and significance. *Developmental Psychobiology*. 2010; 52(7):661–670. [PubMed: 20862706]
- Lazar SW, Kerr CE, Wasserman RH, Gray JR, Greve DN, Treadway MT, et al. Meditation experience is associated with increased cortical thickness. *Neuroreport*. 2005; 16(17):1893–1897. [PubMed: 16272874]
- Lenzi D, Trentini C, Pantano P, Macaluso E, Iacoboni M, Lenzi GL, et al. Neural basis of maternal communication and emotional expression processing during infant preverbal stage. *Cerebral Cortex*. 2009; 19(5):1124–1133. [PubMed: 18787229]
- Lutz A, Brefczynski-Lewis J, Johnstone T, Davidson RJ. Regulation of the neural circuitry of emotion by compassion meditation: effects of meditative expertise. *PLoS One*. 2008; 3(3):e1897. [PubMed: 18365029]
- Marchini G, Lagercrantz H, Winberg J, Uvnas-Moberg K. Fetal and maternal plasma levels of gastrin, somatostatin and oxytocin after vaginal delivery and elective cesarean section. *Early Human Development*. 1988; 18(1):73–79. [PubMed: 2906866]
- Marvin, R.; Cooper, G.; Hoffman, K.; Powell, B. Attachment-based Intervention with at-risk Head Start Child-parent Dyads. Paper presented at the Conference Name; 2000. from URL.
- McDougall, W. *An introduction to social psychology*. London: Methuen; 1908.



- McGowan PO, Sasaki A, D'Alessio AC, Dymov S, Labonte B, Szyf M, et al. Epigenetic regulation of the glucocorticoid receptor in human brain associates with childhood abuse. *Nature Neuroscience*. 2009; 12(3):342–348.
- Naber F, van Ijzendoorn MH, Deschamps P, van Engeland H, Bakermans-Kranenburg MJ. Intranasal oxytocin increases fathers' observed responsiveness during play with their children: a double-blind within-subject experiment. *Psychoneuroendocrinology*. 2010; 35(10):1583–1586. [PubMed: 20457491]
- NICHD Early Care Research Network. Infant-mother attachment classification: risk and protection in relation to changing maternal caregiving quality. *Developmental Psychology*. 2006; 42(1):38–58. [PubMed: 16420117]
- Numan M. Hypothalamic neural circuits regulating maternal responsiveness toward infants. *Behavioral Cognitive Neuroscience Reviews*. 2006; 5(4):163–190.
- Pincus D, Kose S, Arana A, Johnson K, Morgan PS, Borckardt J, et al. Inverse effects of oxytocin on attributing mental activity to others in depressed and healthy subjects: a double-blind placebo controlled fMRI study. *Frontiers in Psychiatry*. 2010; 1:134. [PubMed: 21423444]
- Riem MM, Bakermans-Kranenburg MJ, Pieper S, Tops M, Boksem MA, Vermeiren RR, et al. Oxytocin Modulates Amygdala, Insula, and Inferior Frontal Gyrus Responses to Infant Crying: A Randomized Controlled Trial. *Biological Psychiatry*. 2011; 70:291–297. [PubMed: 21470595]
- Sober, E.; Wilson, DS. *Unto others: The evolution and psychology of unselfish behavior*. Cambridge: Harvard University Press; 1998.
- Strathearn L, Fonagy P, Amico J, Montague PR. Adult attachment predicts maternal brain and oxytocin response to infant cues. *Neuropsychopharmacology*. 2009; 34(13):2655–2666. [PubMed: 19710635]
- Strathearn L, Li J, Fonagy P, Montague PR. What's in a smile? Maternal brain responses to infant facial cues. *Pediatrics*. 2008; 122(1):40–51. [PubMed: 18595985]
- Swain JE. The human parental brain: In vivo neuroimaging. *Progress in Neuro-Psychopharmacological and Biological Psychiatry*. 2010; 35:1242–1254.
- Swain JE. Becoming a parent-biobehavioral and brain science perspectives. *Curr Probl Pediatr Adolesc Health Care*. 2011; 41(7):192–196. [PubMed: 21757136]
- Swain JE, Kim P, Ho SS. Neuroendocrinology of parental response to baby-cry. *Journal of Neuroendocrinology*. 2011; 23(11):1036–1041. [PubMed: 21848646]
- Swain JE, Konrath S, Brown S, Finegood E, L B-A, Ho SS. Parenting and beyond: common neurocircuits underlying parental and altruistic caregiving. *Parenting, Science and Practice*. 2012 *in press*.
- Swain JE, Tasgin E, Mayes LC, Feldman R, Constable RT, Leckman JF. Maternal brain response to own baby-cry is affected by cesarean section delivery. *Journal of Child Psychology and Psychiatry*. 2008; 49(10):1042–1052. [PubMed: 18771508]
- Veenema AH. Early life stress, the development of aggression and neuroendocrine and neurobiological correlates: what can we learn from animal models? *Frontiers in Neuroendocrinology*. 2009; 30(4): 497–518. [PubMed: 19341763]
- Winnicott DW. The theory of the parent-infant relationship. *International Journal of Psychoanalysis*. 1960; 41:585–595. [PubMed: 13785877]