Greater Good Science Center

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Positive Neuroscience

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JOHN TEMPLETON FOUNDATION

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EXECUTIVE SUMMARY

Showing care and affection to our loved ones, acting compassionately toward others who are suffering, being moved by an emotional song, and being resilient in the face of stressful situations—these feelings and behaviors are all crucial parts of being human and living a good life. But where do they come from? How do our brains help foster our capacity to flourish in the face of adversity, show kindness to those in despair, and enjoy life to the fullest? An emerging field of study—positive neuroscience—aims to answer these questions.

Positive neuroscience focuses on the nervous system mechanisms that underlie human flourishing and well-being. This emerging field of study was significantly bolstered by the John Templeton Foundation's $5.8 million Positive Neuroscience Project, an initiative led by Martin E.P. Seligman. The project included the Templeton Positive Neuroscience Awards competition, which awarded funding to 15 groups conducting research at the intersection of neuroscience and positive psychology.

This white paper focuses on the research that has emanated from these awards. In particular, it discusses the neuroscience of social attachment and relationships ("the social brain"), compassion and generosity ("the compassionate brain"), musical talent and musical appreciation ("the musical brain"), and emotional regulation and resiliency ("the resilient brain").

The Social Brain

Humans are social animals, and with good reason: Relationships are key to our happiness and health—and to our survival. Is our social nature rooted at least in part in our neurobiology? And if so, what biological mechanisms underlie our abilities to form attachments to other people?

Addressing this question typically involves looking at our earliest attachments in life: Decades of studies on rodents and non-human primates have identified several hormones and brain regions that are likely involved in forming

and maintaining the bonds between parents and children. Indeed, research suggests that the human brain is wired for parental care. For example, human neuroimaging studies have found that there are unique patterns of brain activity that respond to baby cries and photos of children. These include brain areas known to be involved in empathy and reward.

Other studies suggest that becoming a parent changes the brain's structure and function. In addition, there seem to be brain activity differences between more and less sensitive mothers and more and less involved fathers. Intriguingly, some work suggests that parental brain activity when children are babies may influence children's later social and emotional abilities. For example, in one study, fathers who had more positive thoughts about parenting their one-month-old—and greater brain activation in response to their child's cries in regions associated with sensory information processing and parental motivation—also had toddlers with better socio-emotional skills, such as empathy and positive peer relations.

Many of the same mechanisms that are involved in these early bonds—including hormones, brain circuits, and synced behavior and neural responses—also underlie other relationships. For example, one study found that both maternal and romantic love activated some of the same areas of the brain's reward system; another study found that romantic partners displayed more synchronized behavior and brain responses than did strangers—mechanisms that are also thought to be involved in the parent-child bond. This suggests these biological mechanisms play a central role in our relationships, across stages of life.

A relatively new line of research has focused on the "social touch" system—a touch pathway that is particularly sensitive to touch that feels pleasant and which is often involved in social interactions. Remarkably, studies have found that the same brain areas that responded when people had their arms touched softly at a pleasant speed also responded when those people viewed other people receiving a similar touch—suggesting that this may be a form of "neural empathy" that helps us to interpret the relationships and alliances among people in our proximity.

The Compassionate Brain

We tend to think that "human nature" is synonymous with violence, selfishness, and aggression—and that those behaviors are our evolutionary and biological legacy. But in recent years, neuroscience research actually suggests a more complicated story.

Studies of the brain have identified a neurobiological basis to compassion and generosity. They have identified areas of the brain associated with kind, helpful—or "prosocial"— thoughts, feelings, and behaviors. For example, one recent neuroimaging study found that the brain circuits involved in two gut-level responses to seeing people suffering—distress and tenderness—could be dissociated from one another, and that activity in either one could predict charitable behavior. Another line of research demonstrates that people's brains assign an inherent "value" to generosity and fairness: We experience vicarious rewards when we view others benefiting.

Other research has examined activity in the brains of so-called "extraordinary altruists"—people who have voluntarily donated a kidney to a total stranger. Studies have found that these people have exceptionally strong neural responses to fearful faces, suggesting that they are especially attuned to the suffering of others.

Through neuroscience studies, researchers have also identified a number of factors that seem likely to increase or decrease compassion and generosity such as how we perceive other people, whether we're primed to think of ourselves as individuals or as part of a group, and how much we care about similarities between ourselves and other people. There is also some evidence to suggest that stress—either felt personally or "caught" from someone else—may inspire prosocial behavior.

Evidence also suggests that compassion is a skill that can be practiced and improved. For example, one study found that two weeks of daily compassion training increased activity in brain regions involved in emotion regulation and social cognition. Participants who completed this training also gave more money to someone who had been snubbed in a previous round of a money distribution game than participants who completed memory training did.

The Musical Brain

Making and enjoying music is an essential component of human cultures across the globe. Yet despite its longstanding importance to humanity, researchers have only recently started to understand how the brain allows us to produce, understand, and appreciate music. This emerging line of neuroscience research has started to produce valuable insights into humans' relationship to music.

In particular, studies have found that brain "hyperconnectivity"—that is, increased structural and/or functional connectivity between specific brain regions—underlies the extraordinary musical abilities of two unique populations: people with absolute (or "perfect") pitch—who can identify musical pitches without a reference—and people with sound-color synesthesia—for whom hearing particular musical sounds triggers perception of colors.

Additionally, other research suggests that hyperconnectivity may also underlie people's aesthetic responses to music. In one study, people who experienced chills while listening to music had thicker white fiber bundles connecting their brain's auditory areas to brain areas involved in social and emotional processing and reward. Additionally, because similar brain areas are involved in our emotional responses to music and experiences of empathy, this may suggest that these two experiences are related in some way.

The Resilient Brain

We are constantly barraged with stimuli and situations that can evoke emotion. Walking down a city street, we may see people hugging (or fighting), hear a baby crying, smell food that reminds us of our childhood, and receive a text with sad news—all within a few seconds. Over the past few decades, neuroscientists have published hundreds of studies exploring how our brains respond to emotional stimuli and how we can improve our ability to thrive in the face of stressful situations.

Neuroimaging studies have found that a part of the brain's limbic system called the amygdala responds to both positive and negative emotional stimuli. However, people vary in the extent to which their amygdalae respond to different stimuli. For example, one study found that the amygdalae of happier participants responded more to positive images than the amygdalae of less happy people, but there was no relationship between people's happiness levels and their amygdala responses to negative images. These results suggest that happier people are more motivated to see opportunities in their environments, but that they don't wear "rose-colored glasses" that prevent their brains from recognizing nearby negative stimuli.

In contrast, people with more of a negative "affective style"—people less prone to happiness—are more reactive to emotional stimuli and have less ability to regulate their emotions in response to stressful circumstances. Fortunately, mounting evidence suggests that various techniques can change how our brains respond to emotional situations.

One of the most widely studied techniques is "cognitive reappraisal," a strategy for changing the emotional impact of a situation by changing how you think about that situation. Reappraisal can be used to lessen negative emotions (negative reappraisal) as well as to increase positive emotions (positive reappraisal). Evidence suggests that reappraisal can change the emotional impact of emotional stimuli and that this result correlates with activity changes in specific parts of the brain. There are multiple factors that may influence the effectiveness of reappraisal, including the specific tactics that are used, the frequency with which one engages in reappraisal, age, gender, genetics, and socioeconomic status.

Besides cognitive reappraisal, research also suggests that certain forms of meditation can improve mood and change how the brain responds to emotional stimuli. For example, one study found that short-term mindfulness training increased the functional connectivity between the amygdala and the ventromedial prefrontal cortex, an area involved in emotion regulation, suggesting that even a few weeks of meditation training may build up emotion-regulation abilities.

A different form of meditation, compassion meditation, may be another effective method for emotion regulation. One study found that this technique increased the positive emotion participants experienced when shown images of people suffering and also activated a network of brain regions involved in positive emotion and affiliation.

Future Directions

Positive neuroscience is a new subfield of neuroscience and thus there are many research areas ripe for further exploration. These include studying the neuroscience of caregiving by non-parents, further elucidating the neural mechanisms of friendship, mapping how neural markers of compassionate behavior in the lab do or do not extend to real-world behaviors, exploring the role of brain hyperconnectivity in aesthetic responses to different forms of art, determining the neural mechanisms underlying other emotion regulation strategies, and discovering what strategies can best help children develop their emotion regulation skills.

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Introduction

Love. Compassion. Generosity. Empathy. Creativity. Resilience. These virtues help give life meaning. They are the very essence of what it means to thrive. But where do they come from? What is it about the brain that fosters our capacity to live up to the ideals of The Good Life? An emerging field of study—positive neuroscience—aims to answer these questions.

What is positive neuroscience? "Positive neuroscience research describes the brain mechanisms that enable human flourishing, illuminating the mechanisms behind our unmatched ability to form cooperative relationships, to value one another's well-being, and to build social structures that expand the scope of human flourishing," write Joshua Greene and India Morrison in the introduction to the book *Positive Neuroscience* (Greene & Morrison, 2016).

As its name implies, positive neuroscience can be considered a subfield of neuroscience, the study of the structure and function of the nervous system. Neuroscience itself is a relatively young field, having only been considered a unique scientific discipline for the past 50 years or so. In this time, most studies in neuroscience focused on identifying mechanisms for how the nervous system works and on elucidating the causes of various nervous system pathologies. Positive neuroscience research, by contrast, is explicitly focused on how the structure and function of the nervous system relate to the aspects of life that help people thrive. With this focus, positive neuroscience research often overlaps with other fields of study, including positive psychology—the scientific study of positive experiences, traits, and institutions—and social neuroscience—the study of how biological systems relate to social behavior.

<u>Origins and Evolution of the Field</u>

While research that could fit within the scope of positive neuroscience has been ongoing for decades, this line of research advanced considerably with the advent of neuroimaging technologies. These technologies, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), allow for the non-invasive study of healthy human brains. Additional forms of support—both in funds, interest, collaboration, and recognition—came from the John Templeton Foundation's $5.8 million Positive Neuroscience Project, an initiative established in 2008 by Martin E.P. Seligman. This project included the Templeton Positive Neuroscience Awards competition, whose 15 winning groups received funding to conduct research focused on the intersection of neuroscience and positive psychology.

"Research has shown that positive emotions and interventions can bolster health, achievement, and resilience, and can buffer against depression and anxiety. And while considerable research in neuroscience has focused on disease, dysfunction, and the harmful effects of stress and trauma, very little is known about the neural mechanisms of human flourishing," said Seligman when announcing the recipients of the Templeton Positive Neuroscience Awards. "Creating this network of positive neuroscience researchers will change that."

What research came out of these awards? And what can it teach us about the brain mechanisms that underlie human flourishing? These questions are the subject of this paper.

About This Paper

The field of positive neuroscience can be conceptualized as quite broad, including anything that touches on the neural basis of a positive aspect of life. This white paper will be considerably more limited in scope, focusing on subject areas within positive neuroscience that received significant funding from subgrants stemming from the John Templeton Foundation's Positive Neuroscience Project.

In particular, this paper is broken into chapters discussing main research themes emanating from the Templeton Positive Neuroscience Awards. The first chapter, "The Social Brain," discusses the biological processes that support human relationships. The second, "The Compassionate Brain," discusses the ways in which our brains are wired for generosity and compassion. The third, "The Musical Brain," dives into the brain mechanisms behind our ability to perceive and appreciate music, and the fourth chapter, "The Resilient Brain," tackles the neuroscience of how brains respond to emotional stimuli and situations. The final section discusses limitations of the research described in this paper, as well as possible directions it can take in the future.

In this white paper, the number of citations (as of September 2018) for a particular study or review paper is indicated in brackets [ ] next to that citation; highly cited studies (>50 citations) are indicated in **bold**.

It is important to note that, because this area of study is so new, some of the findings presented in this paper stem from only a few studies (and sometimes a single study) and thus should be considered preliminary until they are validated by future studies.

CHAPTER 1

The Social Brain

Humans are social animals, and with good reason: Relationships are key to our happiness and health. As babies and young children, we are dependent on caregivers to keep us alive and teach us about the world. As we grow and age, relationships provide us with love and support, give us opportunities for joy and play, combat stress, and add meaning to our lives. In fact, a considerable body of evidence from evolutionary biology suggests that our skills of bonding and cooperation have been essential to our survival as a species **(Henrich & Henrich, 2006) [143]** (Warneken, 2015) [25].

Over the past several decades, researchers have explored the neuroscience underlying social behavior and have discovered much about how humans and other animals form and maintain attachments. This research suggests both that humans are 'wired to connect'—we are born with innate biological mechanisms that allow us to start forming connections with others beginning at birth—and also that our relationships with others can change the structure and function of our brains. This chapter will describe some of the mechanisms that underlie social attachment, with a primary focus on the neuroscience of human relationships.

The research covered in this chapter can help us better understand: the parental drive to care for young children, and how being a parent changes the brain; the biological processes involved in the parent-child bond, romantic relationships, and friendships; and how our brains process social touch—the touch that we use to convey affection and provide emotional support to our friends and loved ones. Taken together, this research can shed light on humans' social nature and also how we might better nurture and support our relationships across the lifespan.

Wired to Connect: The Parental Brain and the Origins of Attachment

Most of the early work on the neuroscience of social connection was performed on non-human animals, including rodents and non-human primates, and focused on the parent-child bond (most frequently the mother-infant bond). These studies showed that a constellation of hormones, neuropeptides (small protein-like molecules used by neurons to communicate with each other), and neurotransmitters—including oxytocin, vasopressin, estrogen, testosterone, and dopamine—play important roles in parenting behaviors (see review: **(Rilling & Young, 2014) [250]**). Additionally, animal studies identified several brain regions involved in mammalian parental care, including the medial preoptic area, the nucleus accumbens, the ventral tegmental area, the prefrontal cortex, and the periaqueductal gray, among others **(Dulac, O'Connell, & Wu, 2014) [141]**.

While much of what is known about the brain mechanisms underlying the parent-child bond and parenting behavior comes from animal studies, in the last few decades, researchers have developed ways to study the brain regions involved in different aspects of human parent-child bonds. This is thanks, in large part, to the advent of functional magnetic resonance imaging (fMRI) technology, which allows researchers to record human neural activity non-invasively by measuring changes in oxygenated blood in different brain regions during a specific task—essentially showing which brain regions are "activated" during that task.

As will be evident, most of the earliest fMRI studies on the neuroscience underlying the parent-child bond focused almost entirely on the mother-child relationship, with the neuroscience of fatherhood being largely overlooked. But in the last five years or so there has been growing interest in studying the neuroscience of fathering, shedding new light on the field. These studies will be discussed throughout the chapter.

Which areas of the brain are implicated in parental care?

One way to study parents' brains is to have them listen to baby cries while having their brain activity recorded. The logic behind this method is that babies cry when they need their parents; these cries, and parents' responses, form the basis of parent-child attachment and bonding **(Bell & Ainsworth, 1972)** [1343]. Thus, understanding how a parent's brain responds to an infant's cries may help us understand the neural basis of our earliest social bond: parent-baby attachment.

In the first studies to use a cry-and-fMRI experiment, Jeffrey Lorberbaum and colleagues had mothers with young children listen to audio clips of a baby crying alternating with audio clips of white noise at a similar volume and intensity **(Lorberbaum et al., 1998)** [219] **(Lorberbaum et al., 2002)** [443]. The studies found that several brain areas were more active when mothers listened to the infant crying. Areas activated by crying included the thalamus (a region involved in processing sensory information) as well as the mesial prefrontal cortex and right orbitofrontal cortex (brain areas involved in motivation and reward), largely consistent with brain lesion studies in rodents and monkeys, which found that damaging these areas disrupted maternal behavior **(Kling & Steklis, 1976)** [262] **(Stamm, 1955)** [158] **(Slotnick, 1967)**[168] **(Slotnick & Nigrosh, 1975)** [99] (Wilsoncroft, 1963) [34].

In a later study, mothers who perceived that their own mothers had provided them with high levels of maternal care when they were children had larger volumes of grey matter in several brain areas (including the middle frontal gyrus, superior temporal gyrus and fusiform gyrus), and showed significantly more activity in these areas when they heard a baby cry than did mothers who perceived their mother has having been less attentive. While correlational, this result may suggest that having a responsive mother changes the brain in a way that predisposes daughters to become more responsive mothers themselves **(P. Kim, Leckman, Mayes, Newman, et al., 2010)** [152]. Mothers who had perceived that their own mothers had been less attentive, on the other hand, had greater activation in their left hippocampus when they heard the crying, which may indicate that these mothers had more of a stress response when they heard their own infant cry.

Another common method for studying the neuroscience of parent-child attachment involves showing parents photos or videos of children while their brain activity is recorded. One such study found that mothers had greater activation in brain regions involved in arousal and emotion (the amygdala and insula) as well as empathy (such as the posterior superior temporal sulcus and anterior paracingulate cortex) when they viewed photos of their own children versus other familiar children, suggesting that activity in these circuits may reflect maternal attachment **(Leibenluft, Gobbini, Harrison, & Haxby, 2004)** [397].

Multiple studies found that viewing their own babies (versus unknown babies) increased activity in mothers' orbitofrontal cortex (OFC), suggesting that activity in this reward-related region may reflect maternal love and attachment **(Nitschke et al., 2004)** [373] **(Noriuchi, Kikuchi, & Senoo, 2008)** [308] **(Minagawa-Kawai et al., 2009)** [194]. Some studies have shown that the extent of this OFC activation was associated with the extent of the positive feelings evoked upon seeing their infant **(Nitschke et al., 2004)** [373] **(Minagawa-Kawai et al., 2009)** [194]. This suggests that the OFC may be involved in the positive feelings brought on in mothers by their infants. Additionally, another study found the same response in infants: Viewing movies of their smiling mother increased the infant's OFC activation **(Minagawa-Kawai et al., 2009)** [194]. These findings suggest that OFC activity is an important component of the social attachment system, and that this mechanism for attachment is already online in children as young as 12 months old.

Besides determining how a mother's brain responds uniquely to their own child, studies have also uncovered how a mother's brain responds differently when their baby is happy versus distressed. One study found that when a mother watched a video of her infant in distress, activity increased in a number of brain areas (e.g. dorsal OFC, caudate nucleus, tempoparietal junction, prefrontal cortex, etc.) more than it did when she watched a video of her infant playing, suggesting that mothers have more complicated neural responses to their infants when the infants are in need **(Noriuchi et al., 2008)** [308]. The researchers note that this may be because mothers feel both positive emotions (like love) and negative emotions (worry, anxiety) at the same time when they see their upset child. Additionally, mothers may try to regulate their own emotional state and mood so as not to display negative expressions to their already distressed infant. A different study found that some reward-related regions containing dopamine neurons were specifically activated when mothers viewed photos of their baby smiling, but not when they saw their child crying **(Strathearn, Li, Fonagy, & Montague, 2008)** [322], a finding that might help explain the unique pleasure that parents experience when seeing their baby smile.

Interestingly, one recent study found that how a father's brain responded to seeing photos of his happy child depended on the gender of the child (Mascaro, Rentscher, Hackett, Mehl, & Rilling, 2017) [11]. Fathers looking at a daughter's happy expression had a stronger response in brain regions involved in reward and emotion regulation (the medial and lateral orbitofrontal cortex) than did fathers looking at a son's happy expression. In contrast, fathers looking at a son's neutral facial expression had a stronger medial OFC response than fathers looking at a daughter's neutral facial expression, and this brain response was positively related to the extent to which these dads engaged in rough and tumble play with their sons.

What are some possible explanations for these findings? One possibility is that fathers may derive more pleasure from seeing their daughters smile than their sons. Another possibility is that fathers may interpret their sons' neutral expressions as being less neutral—i.e., they see them as being more positive or negative—than their daughters' neutral expressions. And a third possibility is that fathers may find sons' ambiguous expressions more rewarding, which may help explain why they engage in more rough-and-tumble play with sons, since ambiguous expressions are typical in this type of play.

Interestingly, this study also found that fathers of daughters used more language related to emotions with their daughters, leading the researchers to hypothesize that fathers may tend to use two different routes for helping their children develop empathy and emotion regulation skills: noticing and talking about emotions with daughters and engaging in rough-and-tumble play with sons.

How does parenting change the brain?

The research described above shows how humans have hard-wired brain systems in place to direct our attention to, empathize with, and be motivated to help young children. Other research, however, shows how becoming parents and caring for babies and children can actually change our brains, often in service of improving our ability to help vulnerable offspring.

- ***Changes in brain activity in parents***

One example of a study showing how parental brains change in response to parenthood is an fMRI study that found that areas of the brain involved in processing emotional stimuli—the amygdala and other limbic regions—responded more to infant laughing than crying in non-parents. In parents, however, the pattern was reversed: The limbic system responded more to infant cries than laughs **(Seifritz et al., 2003)** [**379**].

In another study, fathers and childless men looked at photos of children with different facial expressions and tried to feel the emotion depicted by the child. The fathers had stronger activation than the other men in brain regions involved in processing facial emotions (the caudal middle frontal gyrus), understanding the mental states of other people (the temporoparietal junction), and processing reward (the medial orbitofrontal cortex) (Mascaro, Hackett, & Rilling, 2014) [34]. Also, men with lower testosterone levels had higher brain activity in the area involved in processing facial emotions, which may suggest that the "the decline in testosterone that accompanies the transition to fatherhood may be important for augmenting empathy toward children."

Interestingly, this study also found that non-fathers had stronger activation in brain regions involved in reward and motivation when looking at sexually provocative photos than did fathers. According to the researchers, this may suggest that fatherhood dampens the brain's reward responses to sexual stimuli (although the researchers note that differences in relationship status between these two groups may also be at play). This finding suggests that there may be a trade-off between mating and parenting behaviors that can be visible in the brain activity of new dads.

Results from another study suggest that becoming a new parent—mother or father—activates a "global caregiving brain network" (**Abraham et al., 2014**) [**113**]. This study, which is one of the first to directly compare the brains of mothers and fathers and to look at the neuroscience of parenting in same-sex couples, recorded brain activity in heterosexual primary-caregiving mothers, heterosexual secondary-caregiving fathers, and primary-caregiving homosexual fathers while they watched videos of themselves interacting with their infant.

The results showed that parents who spent more time providing childcare had more activity and integration in a network of brain structures involved in vigilance, reward, motivation, cognitive empathy, and social understanding. On average, primary-caregiving heterosexual mothers had more activation in the areas involved in emotion processing (like the amygdala) and secondary-caregiving heterosexual fathers had more activation in the cortical circuits involved in social understanding (like the superior temporal sulcus). Primary-caregiving homosexual fathers showed similar amygdala activation to the mothers and similar superior temporal sulcus activation to the secondary-caregiving fathers. According to the researchers, these findings suggest becoming a committed parent who is actively engaged in caring for young children may activate this neural caregiving circuit, regardless of the parent's gender or genetic relationship to the child.

- ***Changes in brain structure in parents***

Other studies have found evidence that parenting can induce structural changes in the brains of parents. One longitudinal study looked at new mothers' brains two to four weeks after giving birth, then found that that gray matter in several brain areas had increased roughly three months later, and that the growth of some of these areas (the amygdala, substantia nigra, and hypothalamus) had a positive relationship with how positively the mothers felt about their babies (**P. Kim, Leckman, Mayes, Feldman, et al., 2010**) [**287**].

A study of new fathers looked at their brains two to four weeks after birth and then again at 12-16 weeks after birth. Results showed that their gray matter volume in brain regions associated with parental motivation (hypothalamus, amygdala, striatum, and lateral prefrontal cortex) increased over time, while the volumes of other brain regions (orbitofrontal cortex, posterior cingulate cortex, insula) decreased (**P. Kim et al., 2014**) [**118**]. Interestingly, decreased gray matter in the OFC was correlated with more intrusive parenting ("a parental style that overrides the infant's signals and imposes the parental agenda"). These findings have some provocative implications. "Although maternal intrusiveness tends to be considered negative for infants," write the researchers, "paternal intrusiveness, particularly paternal stimulatory behavior with infants, has been characterized as sensitive parenting."

What brain mechanisms underlie differences in parenting styles?

The research discussed thus far in this chapter highlights the many brain areas involved in the parent-child bond. However, we also know that humans show a wide variety of parenting styles, temperaments, and behaviors. For example, some parents are more nurturing than others, some are more anxious than others, some are more responsive than others, and some engage in more active play than others. Over the past several years, there has been a growing interest in determining what neural mechanisms underlie these differences.

- ***The neuroscience of sensitive mothering***

Neuroimaging studies of mothers of young children have identified some brain regions that are likely involved in sensitive parenting. One study found that "synchronous mothers"—those whose behaviors seem well-coordinated with their infants—showed greater activity in brain regions involved in reward and affiliation (like the left nucleus accumbens) when they watched a video of their baby playing, compared with when they watched a video of another baby playing **(Atzil, Hendler, & Feldman, 2011) [244]**. Intrusive mothers—those who provided stimulation when their babies needed to rest—showed greater activity in brain regions involved in fear and anxiety (like the right amygdala). According to the researchers, these results suggest that "well-adapted parenting appears to be underlay by reward-related motivational mechanisms, temporal organization, and affiliation hormones, whereas anxious parenting is likely mediated by stress-related mechanisms and greater neural disorganization."

Another study, this time of mothers of toddlers, found more sensitive mothers had more activation in prefrontal brain areas known to be involved in emotion regulation (the right frontal pole and inferior frontal gyrus) when they heard their own child's cry than when they heard another child's cry. This may suggest that activation in these areas helps sensitive mothers override the negative emotions they feel when they hear their child cry, enabling them to figure out the best way to engage with their infant to ameliorate the child's distress **(Musser, Kaiser-Laurent, & Ablow, 2012) [100]**.

- ***The neuroscientific basis of fathering styles***

Other studies have focused on understanding the biological basis of variations in fathering behavior. In particular, there is evidence that sensitive and involved fathering likely involves brain areas implicated in motivation, reward, emotion regulation, and empathy.

For example, one study found that fathers who showed the greatest activity in the ventral tegmental area—an area involved in motivation and reward—while looking at their child's picture also reported engaging in more caregiving activities **(Mascaro, Hackett, & Rilling, 2013) [83]**. And another study showed fathers videos of their own child and of another child. The fathers who were more sensitive and displayed more reciprocal behaviors with their infants, such as mirroring their facial expressions and emotions, showed less of a difference in activation of their OFC between when they were watching their own child versus another child (this is different from studies in mothers) (Kuo, Carp, Light, & Grewen, 2012) [46]. The researchers suggest that this result could mean that these more sensitive fathers are more highly interested in children in general.

On the flip side, another study found that fathers who had more restrictive attitudes toward parenting, meaning that they endorsed strict and punitive rules, had less activity in brain regions involved in empathy (anterior insula, bilateral inferior frontal gyrus) and regulating emotions (the orbitofrontal cortex) (Mascaro, Hackett, Gouzoules, Lori, & Rilling, 2014) [39].

This study also found that dads with an intermediate level of activation in the anterior insula were the most involved fathers. Since this area is involved in empathy but also arousal, the researchers suggest that too much activity in this area may be due to anxiety and catastrophizing (e.g. "I am a terrible father"), which could make these fathers find playing with their babies less pleasant (too little activity may suggest a deficit in being able to empathize with their child).

How does the parent-child bond influence the child's future relationships?

Research suggests that a parent's brain activity can influence their child's socioemotional behavior and future relationships. Particularly useful are longitudinal studies that allow researchers to track parents and children over time and see to what extent various variables influence a child's later social abilities.

One longitudinal study found that the kinds of thoughts that parents had about parenting their new baby, along with the ways their brains responded to their infant's cries, were associated with their child's socioemotional abilities as a toddler **(P. Kim et al., 2015) [50]**. In particular, mothers who reported more anxious thoughts and actions when their child was one month old (but not three to four months old), had lower activity in their substantia nigra, a brain area associated with reward, when hearing their baby cry, and their child had poorer socioemotional skills as a toddler. For fathers, those who had more positive thoughts about parenting when their baby was a month old (but not three to four months), had more activation in the auditory cortex and caudate in response to their child's cries, and also had toddlers with greater socioemotional skills.

These findings suggest that interventions that help parents feel better about their new role will likely be more successful, as far as child outcomes go, if they occur early on (within the first month). Additionally, the researchers say that their findings suggest that such interventions may be best targeted by the parent's gender: Efforts to reduce anxious thoughts about parenting and baby well-being may be most helpful for mothers, whereas efforts to increase positive thoughts about parenting may be most helpful for fathers.

Another longitudinal study that followed parents and their children for the first four years of the child's life found that parents who had stronger caregiving circuits when their child was an infant had children who later showed more social engagement and better emotion regulation abilities as preschoolers than did parents with less connectivity in these circuits (Abraham, Hendler, Zagoory-Sharon, & Feldman, 2016) [11]. Additionally, this relationship could be explained by the level of behavioral synchrony that parents showed with their babies at the beginning of the study. In other words, parents who had stronger caregiving circuits also showed more coordinated behavior with their infants—their gaze, emotional displays, talk, and touch were more in tune with their infants' cues—and this is what led to later positive social outcomes among the kids, according to the researchers' analysis.

Finally, a recently published longitudinal study found that parents who had stronger neural empathy networks at the beginning of the study, when their children were babies, had children with better physiological responses to stress (as measured by the level of the stress hormone cortisol in their saliva) and stronger emotion regulation skills six years later (Abraham, Raz, Zagoory-Sharon, & Feldman, 2018) [7]. This study, which included both mothers and fathers, found no gender differences in these networks between mothers and fathers who acted as primary caregivers.

Beyond the Parent-Child Bond: The Neuroscience of Other Relationships

The studies discussed above show the importance of the parent-child bond as well as the neural circuits that underlie it. This research suggests that the relationships that we have with our parents as babies and young children physically shape our brains and set the stage for how we interact with other people throughout the course of our lives.

While the parent-child bond is likely the most studied relationship in positive neuroscience, research suggests that some of the same mechanisms that are involved in these early bonds—including hormones, brain circuits, and synchrony—underlie other relationships as well.

Romantic relationships

How do the neural underpinnings of the parent-child bond mirror and differ from those that underlie romantic relationships? One particularly highly cited study compared the brain regions involved in maternal and romantic love **(Bartels & Zeki, 2004) [1605]**. This study used fMRI to determine which brain areas responded more when mothers viewed pictures of their own children versus other children they knew. These results were then compared to those from an earlier fMRI study that compared how participants' brains responded to pictures of their romantic partners versus pictures of their friends **(Bartels & Zeki, 2000) [1169]**. The researchers found that both forms of attachment—maternal love and romantic love—activated some of the same areas of the reward system, and both decreased activity in areas involved in social judgment, negative emotion, and "mentalizing" (assessing other people's emotions and intentions).

According to the researchers, these results suggest a "push–pull mechanism of attachment" that is present in the brains of both parents and romantic partners. Both forms of attachment appear to involve turning down activity in brain regions involved in negative emotion, avoidance behavior, and social judgment while simultaneously turning up activity in brain areas involved in reward.

Several studies have examined the role of oxytocin—a neuropeptide that regulates a whole host of social behaviors—in romantic love. One study found that oxytocin was higher in people in new romantic relationships than in single people, and oxytocin levels correlated with how interactive and in sync couples were, paralleling discoveries about oxytocin's role in the parent-infant bond **(Schneiderman, Zagoory-Sharon, Leckman, & Feldman, 2012) [193]**. Another study found that people with a certain variant of the oxytocin receptor were at greater risk of having empathic communication difficulties in the beginning stages of their romantic relationships **(Schneiderman, Kanat-Maymon, Ebstein, & Feldman, 2014) [51]**, and a third found that oxytocin was higher in periods of new bond formation, including in new parents and new lovers (Ulmer-Yaniv et al., 2016) [12].

Another mechanism thought to underlie romantic bonds is brain-to-brain synchrony. One study used electroencephalography (EEG) to record the brain activity of 104 adults while they engaged in a social interaction with a stranger or a romantic partner (Kinreich, Djalovski, Kraus, Louzoun, & Feldman, 2017) [3]. The researchers found that couples, but not strangers, showed neural synchrony—for instance, when they were interacting with one another, partners displayed similar brain signals (but this wasn't the case when they were resting).

Additionally, neural synchrony was associated with behavioral synchrony: Pairs that engaged in more coordinated behaviors—such as looking at each other or another object at the same time or displaying the same emotion—also showed more synchronized brain activity via EEG, and this neural synchrony was localized to temporal-parietal structures in the brain, regions previously implicated in processing social information.

What's more, couples looked at each other's faces more than strangers did, which anchored their brain-to-brain synchrony, suggesting that this type of "social gaze" may play a important role in neural synchrony and in solidifying romantic bonds.

Friendships

"Friendships are [a] central, albeit under-researched, component of the individual's well-being and social adaptation," wrote Ruth Feldman, professor of developmental social neuroscience, and colleagues in a 2013 study. "As social creatures, humans need close friendships not only for survival but also for health, longevity, and life satisfaction" **(Feldman, Gordon, Influs, Gutbir, & Ebstein, 2013) [138]**.

While there's much we don't know about the neuroscience of friendship, the research that does exist suggests that friendships, like romantic relationships, build on the same biological systems that underlie the early child-parent bond and may even be influenced by the care that people received when they were infants.

For example, that 2013 study by Feldman and colleagues found that preschoolers who had more attentive mothers as infants displayed evidence of stronger friendship bonds as three-year-olds: They played more harmoniously with their best friend and showed greater increases in oxytocin in their saliva after playing with them. This study also found evidence that certain genes, as well as parental oxytocin levels, may influence a child's later social abilities.

These results suggest that biological factors and early parenting behaviors may set the stage so that some children struggle more in forming relationships. However, the researchers also suggest that preschool—the "initial stage of friendship formation"—may provide an ideal time for helping at-risk children develop relationship skills, which could reap lasting benefits.

A growing body of work suggests that, as in the parent-child bond and romantic relationships, both behavioral and neural synchrony likely also play a role in our friendships **(Wheatley, Kang, Parkinson, & Looser, 2012) [50]** (Wheatley & Sievers, 2016) [0]. For example, one study found that strangers who were assigned to disclose personal information to one another showed more synchronized movements in their interactions than did pairs who were assigned another task that didn't involve self-disclosure **(Vacharkulksemsuk & Fredrickson, 2012) [95]**. Additionally, people who were more behaviorally in sync reported feeling a stronger rapport with their experimental partner. And a recent study found that close friends had "exceptionally similar" neural responses while watching the same video in an fMRI scanner; more socially distant friends had less similar brain responses. However, the researchers note that this study cannot tell us whether we're more likely to become friends with people who see the world similarly or whether our friendships influence how our brains respond to our environments (Parkinson, Kleinbaum, & Wheatley, 2018) [9].

Finally, a recent fMRI study of a first-year cohort of MBA students found evidence that social closeness is encoded in the temporal-parietal cortex. Thus, when we encounter a particular person we know, neurons in a particular part of the temporal-parietal cortex become active. Which neurons become active depends on how socially close we are to that particular person (such as whether we are acquaintances or close friends). The temporal-parietal cortex was already known to be involved in spatial navigation, but this study is the first to suggest that this brain region may have been co-opted for coding social network positions as well (Parkinson, Kleinbaum, & Wheatley, 2017)[19].

Social Touch: Further Evidence for the Biological Roots of Connection

Further evidence for the deep biological roots of human connection comes from a fascinating line of research that is less than 10 years old: the identification and exploration of a unique sensory system for social touch.

Touch can convey emotion, help initiate new relationships, and strengthen our existing bonds. From the moment we are born and throughout life, touch plays important roles in our social-emotional development and well-being. For example, studies have found that parental touch can increase parents' oxytocin levels **(Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010)** [97] and decrease infants' physiological responses to stress **(Feldman, Singer, & Zagoory, 2010)** [225], and that increasing physical affection between spouses can increase oxytocin and decrease blood pressure **(Holt-Lunstad, Birmingham, & Light, 2008)** [285].

What is social touch?

But how is the touch that we use to convey affection different from other forms of touch? Until fairly recently not much was known about the physiology underlying this form of pleasant social touch; more attention had been paid to other forms of tactile sensations such as pain, itch, and heat/cold.

But in 2009, Line Löken, Håkan Olausson, India Morrison, and colleagues found that a specific type of touch receptor found in human skin responded to soft brushing of the arm at a medium velocity, a type of touch that subjects found pleasant **(Löken, Wessberg, Morrison, McGlone, & Olausson, 2009)** [457]. There was also a direct correlation between how much these receptor fibers (called "C-tactile afferents" or "CT fibers") fired and how pleasant humans rated the touch sensation that initiated the firing. In contrast, participants found being brushed on the palm, which does not contain these receptors, as being less pleasant.

What's more, Morrison and her colleagues connected this finding to brain activity: CT fibers project to the insular cortex, a brain area known for processing information about emotions and interpersonal experiences.

This led the researchers to propose their "Social Touch Hypothesis," a prediction that C-tactile afferents are the first step in processing the social touch that facilitates interpersonal bonds, such as those between parents and infants, between close friends, and between romantic partners **(Morrison, Löken, & Olausson, 2010)** [242].

Social touch and "neural empathy"

Morrison and her colleagues—as well as other groups—have gone on to make several discoveries about the social touch system. For instance, using fMRI, they found that when people viewed videos of other people having their arms stroked at a pleasant speed, their posterior insula was activated in the same way as when they had been stroked themselves **(Morrison, Bjornsdotter, & Olausson, 2011)** [147]. This form of "neural empathy" may help people extract important social information that can be conveyed via touch, helping them to piece together the nature of the relationships and alliances among the people around them.

Morrison and colleagues also discovered that people who have fewer C-tactile afferents, due to a genetic mutation, perceived arm stroking as less pleasant and did not show activation in their insular cortex in response to others receiving this form of touch. This provides additional evidence that C-tactile afferent fibers are likely involved in transmitting pleasant touch, and that people may require firsthand experience to develop the ability to interpret other people's touch experiences **(Morrison, Löken, et al., 2011)** [83]. Additionally, a recent study found that people who reported having less tender physical contact with family members, partners, or close friends reported finding affective touch to be significantly less pleasant than participants who received more interpersonal touch in their day-to-day lives, suggesting that there might be an element of use-it-or-lose-it involved in perceiving CT-optimal touch as pleasant (Sailer & Ackerley, 2018) [4].

Processing social touch in the brain

Other studies have examined how social touch is processed in the brain. One fMRI study found that arm brushing activates a network of brain areas recognized for their involvement in social perception and social cognition, including the right posterior superior temporal sulcus, the medial prefrontal cortex, and the dorsal anterior cingulate cortex **(Gordon et al., 2013)** [129]. By contrast, other studies using fMRI and functional near-infrared spectroscopy (fNIRs) have found that people with more autistic traits had less activity in parts of this "social brain" in response to arm brushing **(Voos, Pelphrey, & Kaiser, 2013)[95]** (Bennett, Bolling, Anderson, Pelphrey, & Kaiser, 2014) [33].

When given a choice, people in one study chose to be brushed at speeds that maximally activated their C-tactile afferent fibers, and this brushing activated brain areas involved in decision-making and reward-related activities (Perini, Morrison, & Olausson, 2015) [22] (the activation of decision-making areas may have been due to the participants needing to decide which stroking speeds they preferred). Interestingly, this study found that stroking the arm (which contains CT fibers) and the palm (which does not) similarly activated these brain regions. This finding may help explain why we feel motivated to (and often enjoy) being touched by our loved ones and touching them ourselves.

In 2016, Morrison conducted a meta-analysis study to distinguish between the brain areas involved in processing discriminative touch (touch used to identify or learn about a tactile stimulus) and the social/affective aspects of touch. She found that the posterior insula (which is generally involved in processing emotions related to sensory experience) was more likely to be activated by social touch whereas discriminatory touch was more likely to activate the primary somatosensory cortex (which is generally involved in processing tactile information) (Morrison, 2016) [18]. However this does not mean the two forms of touch can be totally separated, notes Morrison. “In daily life, tactile interactions with other people may prompt both simultaneously,” she writes, “providing means for not only reaching out and touching someone, but also for feeling and evaluating their touches in return.”

CHAPTER 2

The Compassionate Brain

We tend to think that "human nature" is synonymous with violence, selfishness, and aggression—and that those behaviors are our evolutionary and biological legacy. But in recent years, neuroscience research actually suggests a more complicated story. Studies of the brain have identified a neurobiological basis to compassion and generosity, suggesting that these positive traits are not just cultural constructs that we try to force on people to counter their more vicious "natural" instincts. Instead, they too are part of our biology.

What regions of the brain are associated with those prosocial thoughts, feelings, and behaviors—and what do those associations suggest about the origins and function of prosocial behavior? Do some people seem to have a stronger innate propensity for compassion? And is it possible to train the brain to become more compassionate? Those are some of the key scientific questions that this chapter will cover.

Mapping the Prosocial Brain

Before diving into what is known about the neuroscience of compassion, it is important to note that compassion can be difficult to define scientifically, and researchers have proposed various definitions (for discussion see reviews **(Goetz, Keltner, & Simon-Thomas, 2010) [961] (Singer & Klimecki, 2014) [234] (Strauss et al., 2016) [79]**). This paper will use the definition put forth by Tor Wager, Sona Dimidjian, and colleagues in a recent book chapter. They define compassion as "a mental state arising in response to another's suffering that motivates behavior intended to relieve their suffering" (Ashar, Andrews-Hanna, Dimidjian, & Wager, 2016) [0].

In their chapter, Wager and colleagues present a model for understanding the neural systems that underlie this mental state. According to Wager, three major processes contribute to the experience of compassion, each with its own underlying (and interrelated) brain mechanisms. These processes are: affective responses, social inferences, and emotional meanings.

What are these processes and how do they fit together?

Let's consider a scenario where a person may or may not feel compassion. When confronted with someone in need—say, a person asking for money—we have an immediate emotional response. We may feel distress, disgust, or tenderness (or a mix of those or other feelings). These are basic affective responses.

At the same time, we may be making judgments about this person: Are they to blame for their situation or not? Can they be trusted if we help them? These are social inferences.

These affective responses and social inferences may become integrated into a more complex cognitive-emotional response. For example, we may angrily blame the person if we feel they are responsible for their suffering, or we may feel compassion for them because we feel they deserve help. These are emotional meanings.

According to Wager, these three processes—affective responses, social inferences, and emotional meanings—can interact and influence each other, and that interaction can result in a behavioral decision such as giving the person money—or walking away.

While these are theoretical categories—different researchers view the processes that go into compassion differently—they provide us with a framework for understanding what brain systems are likely involved in compassion.

Affective responses

According to Wager, seeing someone suffer can lead to two types of affective responses. The first, called distress responses (sometimes referred to as "empathic distress"), are the negative feelings that arise in response to seeing others in pain or suffering. And the second, called tender responses (sometimes referred to as "empathic care"), are feelings of warmth, care, and a motivation to help. Distress responses motivate us to reduce our own negative feelings, either by escaping the situation or by helping the suffering person, whereas tender responses motivate us to want to relieve the other person's suffering, most likely by helping them **(Batson, Fultz, & Schoenrade, 1987) [921]**. This framework suggests that either type of gut-level response—distress or tenderness—can lead to compassionate actions.

In fact, a recent fMRI study by Wager's group found that the brain circuits involved in these two responses could be dissociated from one another, and that activity in either one could predict charitable behavior (Ashar, Andrews-Hanna, Dimidjian, & Wager, 2017) [18]. In this study, participants listened to a series of true stories involving human suffering (stories of people with cancer, homelessness, congenital diseases, etc.) and provided real-time ratings of either how distressed or how tender they felt. The participants were supposed to receive some money for participating in the study; after hearing the stories of suffering, they were asked how much of that money they would be willing to give to a charity that had helped the person in the story.

The researchers found that activity in two brain regions, the nucleus accumbens and the medial orbitofrontal cortex, was associated with tenderness and empathic care; these brain regions are involved in processing reward and have previously been implicated in prosocial behavior. By contrast, activity in two other brain regions, the premotor and somatosensory cortex, was associated with empathic distress; these brain regions are involved in producing emotional facial expressions and other bodily actions, as well as in processing the expressions and actions made by others. Additionally, the activity levels in the associated brain regions for either empathic care or empathic distress predicted how much participants chose to donate that round—increased activity in either case predicted higher donations, less activity predicted less in donations. The results provide further evidence for the association between compassion and these brain regions, again suggesting that both empathic care and empathic distress can lead to compassionate behavior.

Social inference

Making social inferences requires imagining another person's internal states. Because of this connection, social inferences likely rely at least in part on the empathy areas in the brain, including the network involved in "mentalizing"—the process of trying to understand another person's thoughts, feelings, beliefs, and motivations. This network comprises various cortical structures, including the dorsal medial prefrontal cortex, the posterior cingulate cortex, and the temporoparietal junction, among others (for reviews of the neuroscience of empathy see **(Frith & Frith, 2006)[1263]**, **(Zaki & Ochsner, 2012) [479]** and (Marsh, 2018) [2]).

Research suggests that activity in these empathy networks translates into compassionate behavior. For example, one study found that participants who had the most activation in their mentalizing network (dorsomedial prefrontal cortex, medial prefrontal cortex, precuneus) in response to watching another participant being excluded in a game wrote the most helpful and comforting emails to the excluded participant **(Masten, Morelli, & Eisenberger, 2011) [276]**. Another study that explicitly asked participants to make social inferences of people based on biographical information and a photograph—such as the extent to which they "have a positive outlook on life" or "like to gossip"—found that people with the most activity in their dorsomedial prefrontal cortex during this task were the most altruistic when they later had the opportunity to give the people in the photographs money or problem-solving assistance **(Waytz, Zaki, & Mitchell, 2012) [101]**. These findings suggest that our ability to consider what it is like to be another person—an ability reflected in our brain activity—may motivate us to help that other person.

Emotional meaning

Activity in brain areas involved in affective responses and mentalizing may inform the construction of the "emotional meaning" component of compassion, which itself is thought to involve a complex network of regions called the ventromedial prefrontal-subcortical system **(Roy, Shohamy, & Wager, 2012) [494]**.

Evidence for this system's role in compassion comes in part from studies that have explicitly asked participants to channel feelings of compassion. For example, researchers in one fMRI study asked participants to adopt a compassionate or passive attitude while they viewed pictures of people with sad or neutral expressions **(J. W. Kim et al., 2009) [131]**. Adopting a compassionate attitude towards the people with sad expressions was associated with greater activity in this brain network, which has also been implicated in both motivating people to behave prosocially and in generating the rewarding feeling that occurs in the wake of such generous behavior.

The neural basis of the "helper's high"

Indeed, many studies suggest that behaving generously involves the same brain areas that are involved in other inherently rewarding behaviors, such as eating and sex. These findings help explain why behaving with compassion and generosity gives us a pleasurable, uplifting feeling, known as the "helper's high."

For example, fMRI studies have found that cooperating in an economic game activated brain areas—the nucleus accumbens, the caudate nucleus, ventromedial frontal/orbitofrontal cortex, and rostral anterior cingulate cortex—involved in reward processing **(Rilling et al., 2002) [1481]**; that when people gave money to a charity, parts of their brain's reward system—the ventral tegmental area, dorsal striatum, and ventral striatum—activated as when they received money themselves **(Moll et al., 2006)** [844]; that giving money to a charity—even when people were forced to do so—increased activity in a brain region linked to the "processing of concrete rewards such as money, food, and drugs" called the ventral striatum **(Harbaugh, Mayr, & Burghart, 2007)** [882]; and that the amount of activity in one reward-related region—the ventromedial prefrontal cortex—correlated with the amount of money that people chose to give to a particular charity **(Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010)** [382].

Our brains "value" generosity

Other studies suggest that giving feels good because our brains place an inherent value on helping others. In an fMRI study by Jamil Zaki and Jason Mitchell, participants played rounds of an economic game called the "Dictator Game" in which they had to decide to give money either to themselves or a person they had just met **(Zaki & Mitchell, 2011) [131]**. In some rounds the dictator stood to earn more (e.g., they could get $2, but the other person could only get $1); in others, the receiver did.

The neuroimaging results showed that deciding to give the money to the person who could benefit the most—the most efficient choice—activated the orbitofrontal cortex, an area of the brain involved in assessing the subjective value of rewarding stimuli. Additionally, the anterior insula, which is involved in aversive emotions like pain and disgust, was more active when participants chose inefficient decisions, and people with more robust responses made fewer inefficient choices. These findings suggest that prosocial behavior may be initiated, at least in part, by an intrinsic weighing of the subjective value of helping other people. They also suggest that people are not intrinsically selfish, but instead show an intrinsic value for fairness.

A follow-up study tested specific ratios between what the dictator and the receiver stood to gain. This study found that activity in the ventromedial prefrontal cortex—an area that is active when people receive something rewarding—mapped to the subjective value that participants placed on giving money to themselves and to another person, as determined via their distribution choices **(Zaki, López, & Mitchell, 2014) [57]**. Importantly, this does not mean that people valued giving other people money the same as they valued getting money themselves; participants, on average, valued giving $1.26 as much as they valued receiving $1.00 for themselves. These findings do suggest, however, that our brain processes the value of giving to others on the same scale that it uses to value receiving things for ourselves (although the exchange rate is different).

However, people differ in the extent to which they are sensitive to such "vicarious rewards," and this influences their behavior. A recent study found that participants who had the greatest activation in the ventral striatum, a reward-related brain region, when a friend or a stranger received money in a lab experiment also reported having more prosocial tendencies in their day-to-day lives (Morelli, Knutson, & Zaki, 2018) [0]. This finding supports the idea that brain responses to vicarious rewards may be related to how generously people behave in different contexts. Indeed, other studies have found evidence that individuals may have their own stable "cooperative phenotype," **(Peysakhovich, Nowak, & Rand, 2014) [155]** or tendency to act altruistically (Hubbard, Harbaugh, Srivastava, Degras, & Mayr, 2016) [13].

Differences in Activity of the Prosocial Brain

Despite the deep neural roots of compassion, research suggests that, not surprisingly, there is variation in how and when we see the prosocial brain activate. Some of these differences are caused by individual differences among people—some people are more compassionate than others—while others are caused by external circumstance—some situations are more likely to elicit a compassionate response.

The brains of "extraordinary altruists"

Research has documented a wide range in people's innate tendency toward compassion and altruism. Sitting at one end of the spectrum are people with psychopathic tendencies and at the other are "extraordinary altruists," people whose generosity goes above and beyond societal norms.

Studies about a rare population of extraordinary altruists—people who have voluntarily donated a kidney to a stranger—have provided important insights about the neurobiological mechanisms that underlie compassion and generosity.

There are compelling reasons not to donate a kidney to a total stranger you may never meet, as Abigail Marsh describes in a recent book chapter (Marsh, 2016) [0]. Recovering from the procedure can be very painful, and the long-term health effects are unknown. Donors can lose weeks of work; some have even lost their health insurance for donating. Some hospitals (and whole countries) even ban the practice out of the fear that people who choose such a risky procedure may have some form of mental illness. It was only in 1999 that people in the United States were first allowed to donate kidneys to strangers.

Thus, people who choose to donate a kidney to a stranger are a rare breed. As of 2016, only about 1,400 people in the United States had done so. Yet these people do exist, which suggests that there is something unique about them that drives them to be so extraordinarily generous.

Marsh's studies suggest that individual differences in altruism stem from differences in what she terms "empathic concern"—"an other-oriented motivational state associated with wanting to improve another's welfare"—but what could also be called compassion.

Remarkably, using neuroscience techniques, Marsh's studies of the brain suggest that some people—like altruistic kidney donors—are more compassionate in part because they are better able to perceive other people's distress.

Marsh hypothesized that people who have donated kidneys to a stranger may be exceptionally good at recognizing when others are in distress. She developed this idea after conducting studies that showed that: 1) people had greater sympathy for and were more willing to help someone with a fearful expression than someone with a neutral expression **(Marsh & Ambady, 2007) [80]**, and 2) people with the greatest ability to recognize fearful expressions were also the most willing to help the distressed **(Marsh & Blair, 2008) [626]**.

Marsh and colleagues tested this theory using functional magnetic resonance imaging (fMRI) to scan the brains of altruistic kidney donors, and of control participants who weren't altruistic kidney donors, while they viewed pictures of faces with various expressions **(Marsh et al., 2014) [108]**. The researchers not only found that the kidney donors were better than the other participants at recognizing fearful (but not angry) faces but also that they had significantly larger right amygdalae, and that they experienced more activation in this brain region when viewing fearful facial expressions. Strikingly, these results were the opposite of what Marsh and others had found in earlier studies of people with psychopathic tendencies—i.e., those people had more difficulty identifying fearful facial expressions and had reduced amygdala responses to these expressions **(Marsh et al., 2008) [652] (Viding et al., 2012)[208]**.

According to Marsh, these findings suggest that kidney donors are not "pathological" or "superhuman." Instead, "extraordinary altruism in humans may be associated with variations in established neuro-cognitive phenomena that support social responsiveness and caring for others' welfare, especially enhanced sensitivity to others' fear" **(Marsh et al., 2014) [108]**.

Other studies from Marsh's group further support the idea that the generous behavior exhibited by extraordinary altruists—such as kidney donors—relies on the same neural systems that underlie day-to-day prosocial behavior.

One study found that kidney donors had greater activity in their left amygdalae and periaqueductal gray (PAG)—an area important for parental caregiving—and greater connectivity between these regions; they also reported feeling greater sympathy when they heard distressing stories than did control participants (Brethel-Haurwitz et al., 2017) [2]. Another recent study found that kidney donors showed greater emotional empathy (Brethel-Haurwitz et al., 2018) [1]. Specifically, when kidney donors observed a stranger experience pain, their brain activity in an empathy-related brain region called the anterior insula was more similar to when they themselves experienced pain than it was for non-kidney donors when they observed a stranger in pain. Since this degree of similarity between our own experience and our observation of someone else's experience usually only occurs when we observe people we know well, this result provides additional evidence that kidney donors have an enhanced capacity for empathic concern and compassion toward more socially distant people.

Together these studies suggest that the brains of extraordinary altruists function differently from the average person—but not that differently. In fact, in several of the studies there was a sizeable overlap between the brain activity in some of the control participants and in some of the kidney donors. This overlap suggests two things: 1) that becoming a kidney donor likely requires other influences beyond having a "super-altruistic brain" (in fact, Marsh has found that societal factors, such as geographic differences in subjective well-being, likely help promote acts of extreme altruism (Brethel-Haurwitz & Marsh, 2014) [22]), and 2) while most of us are not extreme altruists, our brains share the same general neural foundation for empathy and compassion. Increasing our ability to emotionally empathize with others in need may help us, too, to become more compassionate and altruistic.

Factors that elicit more compassion and generosity

Even within the same individual person, he or she is sometimes more inclined to feel compassion for, and to help, certain people or causes over others.

What are the factors that drive these differences? Research points us toward a few: how we perceive other people, whether we're primed to think of ourselves as individuals or as part of a group, and how much we care about similarities between ourselves and other people.

- ***Our perceptions of other people***

One study showed more activity in the reward-related regions of participants' brains when they saw two categories of people win money: people who had answered questions about personal, social, and ethical issues in a more socially desirable way and people who participants found to be more similar to themselves in attitudes and values. This result suggests that we may ascribe a higher subjective value to these two categories of people (**Mobbs et al., 2009**) [**230**].

Another study found that the nucleus accumbens, a reward-related region, was more active when participants viewed actual photos of orphans than when they viewed only the orphans' silhouettes, and that this activity difference could account for the difference in how much money participants said they were willing to donate to help the orphans depicted in the photos versus the silhouettes (**Genevsky, Vastfjall, Slovic, & Knutson, 2013**) [**82**]. This is an example of the "identifiable victim effect," the observation that people behave more generously toward a person when they are more aware of specific details about that person, such as their photo, name, or age.

- ***Whether we're thinking more independently or interdependently***

In another study, participants who were primed to think independently (by reading a story that contained independent, first-person singular pronouns, such as "I" or "mine") had greater activation in the ventral striatum in the times they won money in a gambling game than when their friend won money in the same game. However, when they were primed to think interdependently (by reading a story that contained first-person plural pronouns, such as "we" or "ours"), they had similar ventral striatum activation when they won and when their friend won (Varnum, Shi, Chen, Qiu, & Han, 2014) [45]. This result suggests that feeling more interdependent may cause us to experience our loved ones' good fortune as strongly as we experience our own.

- ***How invested we are in an identity we share with others***

Another study found that NYU students who were more invested in being part of the NYU student body had more activation in the ventral striatum when they viewed a fellow NYU student receive money than they did when they viewed a Columbia University student receive money. They also gave more money to NYU students than to Columbia students in a money distribution task; the reverse was true for students who were less invested in their NYU identity (Hackel, Zaki, & Van Bavel, 2017) [7]. This finding suggests that when we feel more invested in our membership within a particular social group, we place more value on the well-being of others in that group, thus inflating the vicarious rewards we experience when we see them benefit.

Together these findings suggest that various factors—factors relating to other people, our state of mind, and our feelings about our own identity—can shift how the subjective value of a particular person is coded in the reward regions of our brains. These brain changes can, in turn, modulate our compassion and our actions.

Stress and generosity

There are other factors that can shape whether we feel compassion for a person in need and the extent to which we put this compassion to use through generous actions. For example, we are unlikely to help someone if we fear for our own safety or if we feel like our assistance would be ineffective (Buchanan & Preston, 2016) [0]. On the flip side, seeing a particularly vulnerable person or a person in immediate need may activate our caregiving circuits, driving us to act altruistically without thinking **(Preston, 2013) [188]**.

In particular, psychologists Tony Buchanan and Stephanie Preston suggest that observing and resonating with another person's stress can activate our caregiving circuit, motivating us to help the distressed.

Evidence that people have a physiological resonance response when seeing someone experiencing stress comes from a study by Preston and Buchanan in which they measured levels of the stress hormone cortisol in the saliva of two categories of people: first, people engaged in public speaking and mental arithmetic tasks; and second, people observing the first set of people doing these stressful tasks. They found that cortisol responses in observers increased after watching someone perform the stressful tasks. Additionally, the amount that the observer's cortisol went up was related to the cortisol increase in the person performing the stressful tasks, indicating that you can indeed "catch" another person's stress **(Buchanan, Bagley, Stansfield, & Preston, 2012)[96]**.

While it has yet to be shown experimentally that this stress resonance leads people to help more, Preston and Buchanan say in a review, "The caregiving model predicts that observers who become contagiously activated by the immediate plight of the target should be more likely to help, but this is only for situations that require an immediate response that the observer can enact" (Buchanan & Preston, 2016) [0].

Indeed, there is some existing research that suggests that experiencing stress ourselves—albeit not stress induced by social resonance—can lead to more generous behavior (Buchanan & Preston, 2014) [45]. In one study, participants who had completed a public speaking and mental arithmetic task were more generous during a series of economic games than participants who had engaged in a non-stressful activity **(von Dawans, Fischbacher, Kirschbaum, Fehr, & Heinrichs, 2012) [200]**. In another study, participants who were forced to make their decisions quickly were more cooperative and generous than those who were given time to deliberate **(Rand, Greene, & Nowak, 2012) [820]** [Note: a recent replication of this study did not find this effect (Camerer et al., 2018) [0]. The original study's lead author, David Rand, suggests that this non-replication result may be due to increased familiarity with economic games among participants (Rand, 2018)[0]); other studies have found similar effects to the original study—see **(Rand, 2016) [130]** for a meta-analysis of multiple studies].

However, there is also evidence that this prosocial stress response may be limited to certain scenarios. For example, a study where participants were given the opportunity to donate to charitable organizations found that stressed participants actually gave less than control participants, perhaps suggesting the generosity that stressed people provide to individuals does not extend to organizations **(Vinkers et al., 2013) [50]**.

There are likely other factors that increase generosity in stressful situations, according to Buchanan and Preston. As they write in a review: "Research and theory suggest that individuals will actually respond prosocially during stress when the target is vulnerable, distressed, socially bonded or interdependent and when the observer does not fear for their own safety or security, does not have conflicting personal goals, and knows what needs to be done" (Buchanan & Preston, 2014) [45].

Why might being stressed lead people to be more generous? Mounting evidence suggests that stress can shift how people process potential rewards and risks. To explain this shifting phenomenon, psychologists Mara Mather and Nichole Lighthall proposed a model they named STARS (Stress Triggers Additional Reward Salience) **(Mather & Lighthall, 2012)[129]**. This model, and the studies that informed it, suggests that people (and animals) experiencing acute stress are more likely to select decisions that have previously been rewarding. Studies conducted on both humans and animals have found that stressful scenarios increase dopamine release in reward-related brain regions, and the STARS model suggests that this increased dopamine can make rewarding behavior (such as food or drugs) seem extra rewarding, driving our desires to obtain such rewards.

Since giving and helping others are known to activate brain regions involved in processing reward, it makes sense that stress may make these behaviors seem more rewarding as well.

Does Practicing Compassion Change Our Brains?

While the research above suggests that brains may come "prewired" for compassion and generosity, other studies suggest that compassion is a skill that can be practiced and improved—and that this practice can change how our brains function.

One method for increasing compassion is to practice loving-kindness meditation, a type of meditation designed to fill the mind with feelings of love, kindness, and compassion. Research has found that practicing loving-kindness can lead to a variety of positive outcomes, including increases in personal resources (e.g. increased purpose in life, mindfulness, and feelings of social support) and more positive relations with others **(Fredrickson, Cohn, Coffey, Pek, & Finkel, 2008) [1955]**.

Importantly, research suggests that meditation may have the potential to increase a practitioner's empathy for others. An fMRI study that compared novice meditators with expert meditators—people who had practiced at least 10,000 hours of Buddhist meditation, including loving-kindness practices—found that participants had greater activation in neural circuits associated with empathy when they heard emotional sounds (sounds of a distressed woman or a baby laughing) while in a meditative state than in a control state, and this difference was greater for the expert meditators **(A. Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008) [967]**. And another fMRI study found that participants randomly assigned to a compassion meditation program were more accurate at identifying others' emotions and had increased activation in brain regions involved in empathy, including the inferior frontal gyrus (IFG) and dorsomedial prefrontal cortex, when they were asked to identify people's emotional states just by viewing their eyes **(Mascaro, Rilling, Tenzin Negi, & Raison, 2013) [176]**.

These studies suggest that meditation may increase empathy, but can it increase compassion as well? Some research suggests that it can. One study found that completing eight weeks of either mindfulness or compassion meditation training increased the likelihood that participants helped someone in need in a real-world setting: While sitting in a crowded medical office, they were more willing to give up their seat to someone on crutches than were participants who hadn't yet completed either of those trainings **(Condon, Desbordes, Miller, & DeSteno, 2013)** [**244**]. This small study suggests that meditation may increase not just people's compassion, but also how they act on that compassion when confronted with someone in need.

Participants in another study who were assigned to use a smartphone-based compassion meditation/loving-kindness app were more generous when given the chance to donate some money to charity than were control participants (Ashar, Andrews-Hanna, Yarkoni, et al., 2016) [13]. This, again, is evidence that compassion meditation may successfully increase compassion as well as generosity.

Other studies have found hallmarks of increased compassion in the brain following compassion training. In one study, participants who completed 30 minutes of daily compassion training for two weeks were presented with an opportunity to give their money to someone who had been snubbed in a previous round of a money distribution game. Compared to people who had completed a memory training program, the people who received compassion training gave away more of their money **(Weng et al., 2013)** [**309**]. Furthermore, compared to their brain activity before they began the training, participants who had undergone compassion training also showed increased activity in brain regions involved in emotion regulation and social cognition, including the dorsolateral prefrontal cortex and the inferior parietal cortex, when they viewed images of people suffering. The participants who had the greatest brain activity changes were the most altruistic with their money distributions, suggesting that compassion can be cultivated with training and that increased compassion can be apparent not only through generous behavior but in brain activity as well.

Another study found that after participants underwent compassion training, they had more positive emotion when witnessing videos of people in distress than did people who underwent memory training and then watched the same videos. The people in the compassion condition also had increased activation in brain regions previously implicated in love and affiliation, suggesting that the neural underpinnings of compassion (and accompanying positive emotion) can be strengthened with compassion training **(Klimecki, Leiberg, Lamm, & Singer, 2013)** [**361**]. In other words, research suggests that yes, brains can indeed become more compassionate.

CHAPTER 3

The Musical Brain

Making and enjoying music is an essential component of human cultures across the globe—and it has likely been that way for thousands of years: The first instruments, flutes made of mammoth ivory and bird bone, are thought to be 42,000 years old **(Higham et al., 2012)** **[212]**.

Yet despite its longstanding importance to humanity, researchers have only recently started to understand how the brain allows us to produce, understand, and appreciate music. This emerging line of neuroscience research has started to produce valuable insights into humans' relationship to music—it both builds on and contributes to the field of positive neuroscience.

This chapter will focus on two research questions that have received significant attention from neuroscientists so far: What can the brains of people with extraordinary musical abilities teach us about the neural circuits that we all use to perceive and understand music? And what brain mechanisms undergird our emotional and aesthetic responses to music?

What Can the Brains of People with Extraordinary Musical Abilities Teach Us About Musical Perception?

Just as the brains of extraordinary altruists can teach us about how humans are wired for empathy and compassion, the brains of people with exceptional musical abilities can teach us about how humans are wired to produce and appreciate music. This section will discuss research that has showed that brain "hyperconnectivity"—that is, increased structural and/or functional connectivity between brain regions—underlies the extraordinary musical abilities of two unique populations: people with absolute pitch and people with sound-color synesthesia.

Absolute pitch

Absolute pitch (AP), sometimes called "perfect pitch," is the ability to identify musical pitches without a reference. For example, someone with absolute pitch can name or recreate an individual pitch (G, A, F#, etc.) presented out of the blue and can also name the pitches of non-musical everyday sounds, like car alarms. This is a rare ability: Only 0.01 to one percent of people are thought to have absolute pitch (Loui, 2016) [3]. Among these people are many of the world's greatest composers; AP is also common in people with neurodevelopmental disorders, including autism and Williams syndrome.

- ***Nature or nurture?***

While there is evidence that AP has a genetic component, it is also influenced by one's environment. For example, it is more common in people who speak tonal languages and those who receive earlier musical training (Loui, 2016) [3]. Additionally, one's AP abilities appear to be influenced by their instrument of choice. For example, players of the violin—a high-pitched instrument—are more likely to have AP for high pitches, whereas players of the cello—a low-pitch instrument—are more likely to have AP for low pitches.

- ***What's different about the brains of people with absolute pitch?***

What is it about the brains of AP musicians that allows for their exceptional perceptual abilities? Scientists have identified several structural and functional differences between the brains of people with and without AP that may underlie this ability. For instance, multiple studies have found that AP musicians have greater left-right asymmetry in the planum temporale, a brain region that is involved in auditory and language processing. While most right-handed people have a larger planum temporale in their left hemisphere than their right hemisphere, studies have shown that this asymmetry is even stronger in AP musicians **(Schlaug, Jancke, Huang, & Steinmetz, 1995)** [**913**] **(Keenan, Thangaraj, Halpern, & Schlaug, 2001)** [**294**], and that the extent of this asymmetry correlates with pitch naming ability **(Zatorre, Perry, Beckett, Westbury, & Evans, 1998)** [**337**]. Other studies have found differences, albeit inconsistent differences, in cortical thickness between AP musicians and control participants **(Bermudez, Lerch, Evans, & Zatorre, 2009)** [**268**], (Dohn et al., 2015) [31].

While these differences may very well play a vital role in AP ability, work by Psyche Loui, an assistant professor of creativity and creative practice at Northeastern University, and colleagues suggests that there is another important mechanism at play: connectivity between brain regions. In one study, Loui and colleagues used an MRI technique called diffusion tensor imaging (DTI) to compare white matter connections in the brains of 12 AP and 12 non-AP musicians. They found that a bundle of nerve fibers called the arcuate fasciculus, which connects auditory and language areas in the brain to the frontal lobes, was thicker in AP musicians than in non-AP musicians. Additionally, AP musicians with thicker tracts connecting parts of their left temporal lobe were also better at accurately identifying pitches **(Loui, Li, Hohmann, & Schlaug, 2011)** [**104**]. This is evidence that "hyperconnectivity" in the brains of AP musicians may underlie their unique perceptual ability.

Further evidence comes from a study that found that people with tone deafness, who have difficulties discriminating between pitches, had reduced connectivity in their arcuate fasciculus **(Loui, Alsop, & Schlaug, 2009)** [**232**]. In addition, a later study that used a made-up music system to probe how people learn musical grammar rules, such as the relationships between pitches, found that people who were better at learning the new pitch system had a larger right ventral arcuate fasciculus **(Loui, Li, & Schlaug, 2011)** [**57**].

Together, this research suggests that these structural connections are important for music learning, both for those of us with and without AP ability. And while we may not all have the capacity to become AP musicians, there is evidence that white matter can change with musical training **(Halwani, Loui, Rüber, & Schlaug, 2011)** [**170**].

- ***How is the activity in the brains of AP musicians different?***

Given these structural differences, it should follow that there are likely functional differences in brain activity between people with and without AP—and, indeed, some studies have found such differences.

For example, an fMRI study by Loui's group found that AP musicians had increased activity and functional connectivity in parts of their brains—particularly in the temporal cortex (a brain area involved in auditory perception), as well as in regions involved in emotion processing and reward—when they listened to music (Loui, Zamm, & Schlaug, 2012) [40]. This study also found differences in brain activity between AP and non-AP musicians when they weren't listening to music, suggesting that people with AP have intrinsic differences in brain function. Interestingly, this result may help explain why people with AP sometimes can identify pitches in non-musical sounds like the wind or sounds from a washing machine—even when they aren't listening to music, their brains seem to be tuned to perceive it.

Sound-color synesthesia

Research suggests that people with another unique perceptual ability related to music—sound-color synesthesia—also have enhanced connectivity in parts of their brains. For people with sound-color synesthesia, hearing particular musical sounds (chords, pitches, timbres) triggers perception of colors. For example, a person with sound-color synesthesia may perceive a particular chord to be a particular color—C major, say, could provoke the color yellow while B flat major provokes aqua.

- ***Nature or nurture?***

Evidence suggests that synesthesia, like AP, is influenced by both genetics and environment. In fact, there is some overlap between these two abilities. One study found that 20 percent of AP musicians also had synesthesia; that study even identified a particular genomic location (chromosome 6q) that may be linked to both abilities (Gregersen et al., 2013) [43].

- ***What's different about the brains of people with sound-color synesthesia?***

Like AP, sound-color synesthesia may involve brain hyperconnectivity. A study by Loui's group found that, compared with people without synesthesia, people with sound-color synesthesia have a thicker bundle of nerves in their right hemisphere that connects visual and auditory areas to attention areas in the frontal lobe. Additionally, the strength of these connections correlated with the strength of their synesthesia (Zamm, Schlaug, Eagleman, & Loui, 2013) [48].

Together, these results suggest that people with AP and synesthesia can thank certain "hyperconnective" pathways for their unique perceptual abilities. Interestingly, research suggests that a similar connectivity continuum underlies another capability, one that many—but not all—of us possess: the ability to be emotionally moved by music.

How Does Music Evoke Emotion?

Whether or not they are musicians—or even whether they have any innate musical ability—most people enjoy music. The evidence? In 2017, Americans spent an average of 32 hours a week listening to music (Nielsen, 2017). That's four and a half hours a day.

There are likely many reasons why we spend so much of our days engaging with music. Some music is religiously or culturally significant; other music may help us concentrate. But there's another big reason why we may spend so much time listening to our favorite tunes: Music has an uncanny ability to evoke strong emotion. Music can make us sad, nostalgic, cheerful, or ecstatic. It can make us cry, prompt us to dance, or give us the chills.

This section will describe some of what researchers have uncovered about the mechanisms that underlie our emotional and aesthetic responses to music.

What characteristics of a song make it convey emotion?

Some elements of a song are more likely to induce strong emotional (and physical) reactions. One study found that sequences and appoggiaturas (a particular sort of ornamental note) most reliably evoke tears, while new or unexpected harmonies commonly evoke shivers **(Sloboda, 1991) [896]**. Another study found that musical performances and vocal expressions rely on the same specific patterns of acoustic cues to evoke emotion. For example, sadness was conveyed through slow speech or music tempo and a low voice or song intensity; happiness, by contrast, was conveyed through faster speech or music tempo and a medium-high voice or song intensity **(Juslin & Laukka, 2003) [1446]**. Furthermore, songs that contain vocals are more emotionally arousing **(Grewe, Nagel, Kopiez, & Altenmüller, 2007) [294]** (Loui, Bachorik, Li, & Schlaug, 2013) [17].

How do our brains respond to emotional music?

One key to unlocking the neural underpinnings of our emotional responses to music is the observation that people tend to find listening to music, even sad music **(Sachs, Damasio, & Habibi, 2015) [92]**, pleasurable. One study found that there was a strong correlation between when participants reported experiencing chills while listening to a song excerpt they found pleasurable and activation of their sympathetic nervous system, which can reflect emotional arousal **(Salimpoor, Benovoy, Longo, Cooperstock, & Zatorre, 2009) [378]**. Additionally, people who did not report experiencing pleasure while listening to the same excerpt did not have a change in emotional arousal. These findings suggest that that the strong emotional arousal people experience while listening to music may be rewarding.

A series of neuroimaging studies provides further evidence that listening to music is inherently rewarding due to its emotional content. One study used positron emission tomography (PET) scanning, which uses a dye containing radioactive tracers to track changes in blood flow, to measure brain activity while 10 musicians listened to a classical song that they selected because it "consistently elicited intensely pleasant emotional responses, including chills" **(Blood & Zatorre, 2001) [2471]**. There was a correlation between the intensity of chills felt while listening to their song and the amount of cerebral blood flow, a marker of neural activity, in brain areas involved in reward and motivation.

Other fMRI studies suggest that familiar songs may be especially good at activating our brain's reward pathways. One study found that people had more activation in reward circuitry when listening to familiar songs than they did when listening to unfamiliar songs, suggesting that familiarity may be crucial for emotional engagement **(Pereira et al., 2011) [179]**. A similar result was found in another study in which researchers asked participants to rate how strongly they felt different emotions while listening to a range of song clips in an fMRI scanner **(Trost, Ethofer, Zentner, & Vuilleumier, 2012)[178]**. Activation in brain areas associated with feelings of reward correlated with song familiarity ratings, and these areas were more active when participants reported feeling pleasant emotions while listening to a song clip than when they reported feeling less pleasant emotions. These results may help explain why people often find listening to familiar songs more enjoyable than listening to new music.

But what about new music? Can neuroscience help explain how we decide to add new songs to our music collections? In one novel fMRI study, participants listened to 30-second samples of new songs and were given the opportunity to offer money to buy the song in its entirety **(Salimpoor et al., 2013)** [338]. Researchers found that activity in a brain region called the nucleus accumbens, which is part of the reward system, correlated with the amount of money listeners were willing to pay to hear the whole song. Thus, some new songs also activate our reward circuitry, prompting us to want to listen to them again (which, in turn, makes them familiar songs).

What brain differences underlie differences in aesthetic responses to music?

These studies show that activity in certain brain regions may help explain the intensity of people's emotional responses to music and the amount of pleasure they derive from particular songs. Another line of research, however, shows that there are likely differences in brain structure that help determine one's aesthetic responses to music.

One study, for example, compared the brains of 10 people who said they frequently get chills from music and 10 who said they never have (Sachs, Ellis, Schlaug, & Loui, 2016) [22]. The people who experienced chills had thicker white fiber bundles connecting their brain's auditory areas with brain areas involved in social and emotional processing and reward (their insula and medial prefrontal cortex). Furthermore, people who experienced chills the most frequently had the thickest connections between these regions.

Additional evidence for the importance of connections between these brain regions and aesthetic responses to music comes from a study that looked at the other end of the spectrum: a person with musical anhedonia, a rare condition in which people receive no enjoyment from listening to music. The subject reported: "Music doesn't particularly change my mood or give me an emotional response. . . . Mostly I'd say that I'm neutral about music, because I just don't care (and I don't care that I don't care)" (Loui et al., 2017) [3].

As expected, the person with musical anhedonia had decreased volume in their white matter connections between auditory and reward areas. "Individual differences in structural connectivity between the auditory and reward networks likely represent normal variation in musical reward sensitivity, with some additional patterns that give rise to extreme cases such as musical anhedonia," write the authors.

An exciting potential implication of this finding is that there may be individual differences in other aesthetic responses (say, to dance or poetry) (Sachs et al., 2016) [22]. Indeed, there is already some evidence supporting the role of hyperconnectivity in other abilities. For example, one study found that people with higher empathic concern had stronger white matter tracts linking action, perception, and limbic areas of the brain (and also temporal and frontal lobe regions) (Parkinson & Wheatley, 2014) [40].

In fact, similar brain mechanisms may underlie our emotional responses to music, creativity, and empathy, notes Loui in a book chapter (Loui,

2016) [3]. All three of these abilities rely, at least in part, on the medial prefontal cortex (MPFC). Loui notes how creative musical improvisation, for example, has been associated with increased activity in the MPFC in fMRI studies of jazz-improvising musicians **(Limb & Braun, 2008) [558]** and freestyle rappers **(Liu et al., 2012) [124]**. Empathic skills also involve this brain region. One fMRI study found that people who had more activity in their MPFC (and superior temporal sulcus) while watching a person discuss an event showed more empathic accuracy when they were asked to describe how the person felt—in other words, they were better at identifying the emotion that the person reported feeling at the time **(Zaki, Weber, Bolger, & Ochsner, 2009)[285]**.

Of course, just because studies suggest that the MPFC is involved in all these functions, that doesn't necessarily mean that there are relationships between the functions themselves—but Loui thinks those relationships may well exist. "Because the MPFC plays a crucial role in creativity as well as with emotionally empathizing with others," writes Loui "our finding of increased auditory-to-MPFC activity in people who get chills from music may relate creativity in music to empathy, thus informing theories about the evolutionary function of music." (Loui, 2016) [3]. She further speculates:

Perhaps the reason that humans have evolved to create music is to identify emotionally with each other via an auditory mode of communication. . . . If emotional experiences to music involve areas of the brain that are important for empathizing with other people, then perhaps the purpose of music is to arouse emotional responses that resonate with other minds. Music, then, is a social artifact for empathy.

Experimental support for this idea comes from two studies in particular. The first found that children who were taught to play music together showed greater improvements in emotional empathy than did a control group of children who were not trained to play music together **(Rabinowitch, Cross, & Burnard, 2013) [149]**. The second found that people who showed greater variations in their brain activity patterns as they listened to clips of music engineered to convey different emotions also had higher levels of cognitive and affective empathy (Sachs, Habibi, Damasio, & Kaplan, 2018) [1].

While there is much more to discover about the neuroscience that underlies our understanding and appreciation of music, the research discussed in this section shines some light on the brain connections that allow us to learn about music—sometimes to an exceptional extent—as well as the circuits that underpin our deep, perhaps innate, ability to be moved by music.

CHAPTER 4

The Resilient Brain

Every day, we are barraged with stimuli and situations that can evoke emotion. Walking down a city street, we may see people hugging (or fighting), hear a baby crying, smell food that reminds us of our childhood, and receive a text with sad news—all within a few seconds. People vary in how they respond to situations like these, both in how they perceive these emotional stimuli and in how emotionally affected they actually are by them.

Over the past few decades, neuroscientists have published hundreds of studies exploring how our brains respond to emotional stimuli and ways we can improve our ability to thrive in the face of stressful situations. This chapter will focus on three specific areas of research: how brains respond to positive and negative information in general, how people differ in how their brains respond to positive and negative information, and how certain activities may help make people become more emotionally resilient.

How Do Brains Respond to Positive and Negative Stimuli?

How do our brains respond when we see a baby smile or watch someone get hurt? Many brain regions are involved in processing emotional stimuli, from the sensory neurons that first receive external sensations to the limbic system that helps us process the emotional content of this stimuli to parts of the frontal cortex that help us contextualize what we see and sort out what it means. While later sections of this chapter will discuss some of these other brain regions, this brief section will first focus on a part of the limbic system that has been implicated in our emotional responses more than perhaps any other: the amygdala.

The critical role of the amygdala in our emotional responses

For years, study after study showed the amygdalae, two almond-shaped structures toward the middle of our brains (one in each hemisphere), were involved primarily in detecting and processing negative stimuli, such as fearful faces **(Morris et al., 1996)** [2245]. This is why the amygdala is still often referred to as the "fear center" of the brain.

However, in the early 2000s, studies found that the amygdala preferentially responds to emotionally-laden stimuli—both negative and positive—over more neutral stimuli **(Garavan, Pendergrass, Ross, Stein, & Risinger, 2001)** [325]**(Hamann & Mao, 2002)** [407]**(Hamann, Ely, Hoffman, & Kilts, 2002)** [416].

Amygdala activity may reflect stimulus intensity

In fact, research has found that amygdala activity maps to the emotional intensity of stimuli, regardless of whether stimuli are positive or negative **(Anderson et al., 2003)** [1038]**(Small et al., 2003)** [730] **(Cunningham, Raye, & Johnson, 2004)** [367]. For example, one fMRI study found that amygdala activity was highest for very pleasant and very unpleasant odors **(Anderson et al., 2003)** [1038], while another found a similar result with tastes **(Small et al., 2003)** [730]. However, one fMRI study that used sounds and photos found that participants' amygdalae responded more to stimuli that participants rated as negative than those they rated as positive, suggesting that audiovisual stimuli may have a different effect on amygdala activity from chemical stimuli like odors and tastes **(Anders, Eippert, Weiskopf, & Veit, 2008)**[86].

The role of the amygdala in detecting intensely positive and negative stimuli even appears to extend to abstract concepts, at least according to one study. In this fMRI study, participants were given various concepts—such as "murder," "love," "freedom," "multiculturalism," "technology," "recycling," "immigration," "terrorism," and "poetry"—and were asked to indicate how good or bad they thought each concept was **(Cunningham, Raye, & Johnson, 2004)** [367]. The degree of amygdala activation was associated with the emotional intensity of the concepts to the participants: The concepts participants rated as either very good or very bad elicited the strongest amygdala response.

People's Brains Differ in How they Respond to Emotional Stimuli

However, neuroimaging studies have also found that people differ in how their amygdalae respond to positive and negative stimuli. For example, studies found that the amygdalae of more extroverted people responded more to positive emotional stimuli than did the amygdalae of less extroverted people **(Canli et al., 2001)** [627], and participants who were more neurotic and predisposed to anger and agitation had increased amygdala responses to negative images **(Cunningham, Arbuckle, Jahn, Mowrer, & Abduljalil, 2011)** [73]. What might explain such individual variability in amygdala responses to the same stimuli?

In a recent book chapter, neuroscientist William Cunningham and colleagues suggest "conceptualizing the amygdala as a structure involved in the processing of motivationally relevant stimuli"(Man, Ames, Todorov, & Cunningham, 2016)[0]. They argue that the amygdala—which is highly integrated with several other brain regions—serves a function vital to survival: It "informs us about what is important in the environment, and then facilitates the modulation of appropriate perceptual, attentional, autonomic, or conceptual processes in order to respond to present challenges or opportunities." In this way, it makes sense that amygdala activity may vary depending on an individual's unique goals, needs, and values.

Evidence that our amygdala is flexibly attuned to our current goals comes from an fMRI study by Cunningham and colleagues in which they presented participants with a series of celebrity names (e.g., Adolph Hitler, Paris Hilton, Mother Teresa, George Clooney) and asked participants to rate—depending on the round—only how positive, only how negative, or both how positive and negative their overall attitude was toward the presented name **(Cunningham, Van Bavel, & Johnsen, 2008)** [243]. Amygdala activity was highest in response to positive stimuli presented in the positive rating trials and to negative stimuli in the negative rating trials, although there was still some activation for negative names in the positive rating condition. This finding suggests that the amygdala responds to positive stimuli when we are motivated to focus on positive stimuli and to negative stimuli when we are motivated to focus on them, but the amygdala always has some baseline processing for negative stimuli regardless of our goals. (A recent, albeit statistically underpowered, replication study reproduced some of these findings (Lumian & McRae, 2017) [3].)

Results from another study also support the idea that, although it does respond to motivationally relevant positive stimuli, the amygdala is always attuned to negative stimuli (Stillman, Van Bavel, & Cunningham, 2015) [14]. In this fMRI study, participants were shown two photos and were asked to concentrate on just one of them. Negative photos elicited strong amygdala responses whether or not the participant was paying attention to them. Positive images, however, resulted in strong amygdala activity only when they were task-relevant (i.e., the participant was told to focus on positive images).

Why might this occur? From an evolutionary perspective, it is crucial that humans and other animals always pay special attention to potentially threatening stimuli. The salience of positive stimuli, such as food or socializing, may be more dependent on context. "Thus, the same brain region that allows us to identify opportunities for a long, cold drink can also help maintain a constant vigilance for predators," write the researchers. "This may allow humans and other animals to navigate the environment in a way that will maximize goal pursuit while minimizing catastrophic mistakes." In that light, it would make sense that the amygdala would be especially sensitive to positive stimuli only when those stimuli seem necessary to helping achieve a critical goal.

Happy people have balanced amygdalae

But not everyone sees threats and opportunities the same way. There are individual differences in which stimuli people find motivating, and these differences may explain differences in amygdala activity. For example, one fMRI study found that the amygdalae of happier participants responded more to positive images than the amygdalae of less happy people, but there was no relationship between happiness and amygdala responses to negative images (Cunningham & Kirkland, 2013) [41].

These results may suggest that happier people are more motivated to see opportunities in their environments, but that they don't wear "rose-colored glasses" that prevent their brains from recognizing nearby negative stimuli. "[H]appy people are joyful, yet balanced: They notice and seek positive experiences while also being sensitive to potential costs to well-being," write the researchers. "This strategy helps them to function optimally across the variety of situations that can arise in the social world."

Why do different people's amygdalae respond differently to the same stimuli?

So happier people may have more balanced amygdala responses. What factors account for this? According to Cunningham and his colleagues, the reactivity that a given person's amygdala shows in response to emotional stimuli is a manifestation of their "affective style": People with more of a positive affect style are less reactive to emotional stimuli, have a greater capacity for emotion regulation, and tend to have a more positive disposition. By contrast, people with more of a negative affect style are more reactive to emotional stimuli, have less ability to regulate their emotions, and tend to have a more negative disposition.

According to Cunningham, a person's affect style originates in genetics and early environmental influences. And this is born out by studies that have found that biological and social factors can influence how an individual person's amygdalae respond to emotionally laden stimuli. These factors include: genetics **(Hariri et al., 2002)** [2453] **(Montag, Reuter, Newport, Elger, & Weber, 2008)** [123], attachment style **(Vrtička, Andersson, Grandjean, Sander, & Vuilleumier, 2008)** [233], early life adversity **(Tottenham et al., 2011)** [300] **(van Harmelen et al., 2013)** [135], and mental disorders including depression, anxiety, and post-traumatic stress disorder **(Arnone et al., 2012)** [110]**(Thomas et al., 2001)** [548] **(Rauch et al., 2000)** [1150] **(Armony, Corbo, Clément, & Brunet, 2005)** [251].

Fortunately, research also suggests that we aren't beholden to our DNA and early life experiences when it comes to our emotions. Mounting studies suggest that various factors can change how our brains respond to emotional situations. In fact, the number of studies containing the phrase "emotion regulation" published each year has grown exponentially since 2001**(Gross, 2015)** [636].

How Do Emotion Regulation Techniques Change the Brain?

Emotion regulation involves "attempts to influence which emotions one has, when one has them, and how one experiences or expresses these emotions," writes psychologist James J. Gross **(Gross, 2015)** [636]. People use many different methods to regulate—or attempt to regulate—their emotions. These methods can be conscious or subconscious and can include avoiding a situation, focusing on one's breath, reaching out to a friend, forcing a smile, or going for a run—among many other possibilities. It's important to note that not all emotion regulation strategies are beneficial—for instance, some people attempt to change their emotions by binge eating.

While people vary in their natural ability to regulate their emotions, due to factors such as their attachment experiences as children **(Cassidy, 2008)** [1853] and differences in connectivity between their amygdala and prefrontal cortex **(Lee, Heller, van Reekum, Nelson, & Davidson, 2012)** [117], research also suggests that emotion regulation skills can be taught. In fact, many successful psychotherapy interventions influence emotion regulation, and improvements in emotion regulation abilities are related to positive clinical outcomes (Gratz, Weiss, & Tull, 2015) [41].

However, there is still much we don't know about how emotion regulation strategies work, and how they can best be used to help people become more emotionally resilient and to thrive in the face of stressful situations. One way to gain insight into these questions is to study how emotion regulation activities change brain function. The remainder of this chapter will focus on the neural mechanisms underlying two activities that, research suggests, can improve our emotional responses: cognitive reappraisal and meditation.

Cognitive reappraisal

Cognitive reappraisal is a strategy for changing the emotional impact of a situation by changing how you think about the situation. You can use reappraisal to lessen negative emotions (negative reappraisal). But, as psychologists Kateri McRae and Iris Mauss, and colleagues have explored, you can also use reappraisal to explicitly increase positive emotions (positive reappraisal) (McRae & Mauss, 2016) [9].

For example, imagine a parent witnessing their toddler having a tantrum in the middle of the grocery store. Negative reappraisal might involve the parent reminding himself or herself that the tantrum, while frustrating, is developmentally appropriate behavior. Positive reappraisal might involve thinking about how they are grateful that their child trusts them enough to be vulnerable around them.

The goal behind positive reappraisal is to increase positive emotions without necessarily changing negative ones (the grateful parent is likely also a frustrated one). This is important not only because there are many psychological benefits to experiencing positive emotion **(Fredrickson, 2001)** [**10518**] but also because some negative emotion may be unavoidable, or even constructive, in a stressful situation. For example, one would not expect a person grieving the death of their spouse to experience only positive emotions.

While most of the studies looking into the neuroscience of cognitive reappraisal have focused on negative reappraisal paradigms, this chapter will examine positive and negative reappraisal, since evidence suggests most of our day-to-day attempts to regulate our emotions have the goal of increasing positive emotions and decreasing negative ones **(Gross, Richards, & John, 1994)** [**734**].

So does reappraisal work? Can reframing our thinking about a stimulus or experience change our emotional response? Multiple studies suggest that reappraisal can successfully decrease negative and/or increase positive emotion **(Gross, 1998)** [**3812**] **(Jackson, Malmstadt, Larson, & Davidson, 2000)** [**512**] **(Dillon & LaBar, 2005)** [**86**] **(Giuliani, McRae, & Gross, 2008)** [**172**]**(Ray, McRae, Ochsner, & Gross, 2010)** [**149**] **(McRae, Ciesielski, & Gross, 2012)** [**184**].

Some of these studies have found that using cognitive reappraisal correlates with activity changes in specific parts of the brain **(Hajcak & Nieuwenhuis, 2006)** [**416**] **(Foti & Hajcak, 2008)** [**294**] **(McRae et al., 2010)** [**422**]. When participants in one study successfully used reappraisal to dampen their negative emotional responses to negative scenes, fMRI imaging showed increased activity in the lateral and medial prefrontal cortex—areas involved in working memory and cognitive control—along with decreased activity in the medial orbitofrontal cortex and amygdala—areas involved in processing emotions **(Ochsner, Bunge, Gross, & Gabrieli, 2002)** [**2418**].

A meta-analysis of 48 neuroimaging studies, the majority of which used negative reappraisal to lower negative emotions in response to negative stimuli, found that reappraisal activated regions involved in cognitive control and semantic representation and dampened activity in both amygdalae **(Buhle et al., 2014)** [**674**]. This suggests that negative cognitive reappraisal works by changing the meaning that we give to a particular stimulus or situation, which reduces amygdala activity, making the potentially stressful stimuli feel less salient.

The goal of reappraisal is not just to change the intensity of an emotional response (how positive or negative one feels about a certain situation) but also to change its duration (how long one feels these positive or negative emotions). The first study to examine the duration of brain responses to emotional stimuli during reappraisal—and the first to use neuroimaging to directly compare negative and positive reappraisal to negative stimuli—found that both forms of reappraisal shortened responses in the amygdala, insula, and superior temporal gyrus and lengthened responses in prefrontal regions (Waugh et al., 2016) [8]. The researchers note that some prefrontal areas are thought to be involved in monitoring regulation success, which may explain the prolonged activation in those areas.

Interestingly, while negative reappraisal also decreased amygdala activity intensity, positive reappraisal did not. In contrast, the intensity of activity in the medial prefrontal cortex—an area involved in the cognitive control of emotion—increased only in the positive reappraisal condition. According to the researchers, this result suggests that "increasing positive emotion may involve more engagement with the emotional stimulus relative to decreasing negative emotion." Thus, using positive reappraisal may require more active cognitive effort into thinking about the potential meanings associated with a particular stimulus.

While it may seem that such increased cognitive engagement with the negative images would impede reappraisal performance and thereby increase negative emotions, this wasn't the case. Participants actually reported the largest increase in positive emotion and decrease in negative emotion following positive reappraisal, when they were apparently engaging more deeply with the negative stimuli.

Another study suggests that repeated reappraisal of particular emotion-evoking stimuli could have lasting effects on the brain. Participants who were told to use reappraisal to decrease their emotional response to the same negative photos four times in one session still showed dampened amygdala responses to these images one week later—their amygdala response to these images was lower one week later than it was in response to images they had reappraised only once **(Denny, Inhoff, Zerubavel, Davachi, & Ochsner, 2015)** [**56**]. However, increased activation in the prefrontal cortex during reappraisal did not persist one week later. These findings suggest that "reappraisal can exert long-lasting 'dose-dependent' effects on amygdala response that may cause lasting changes in the neural representation of an unpleasant event's emotional value," write the researchers.

Factors that can influence the effectiveness of cognitive reappraisal

While this paper has reviewed evidence that reappraisal is an effective emotion regulation strategy, other studies have identified factors that can influence how well reappraisal works. These factors include the reappraisal tactics used and how frequently a person tends to use reappraisal, as well as their age, gender, and socioeconomic status.

- ***Reappraisal tactics***

One study suggests that reappraisal's success can depend on a person's emotional goals and the reappraisal tactics they use **(McRae, Ciesielski, et al., 2012)** [**184**]. Specifically, this study found that participants who used positive reappraisal when looking at negative pictures had greater increases in positive emotion than participants who were told to use negative reappraisal. But the success of positive reappraisal depended on the tactics deployed. For example, when participants tried to challenge the reality or authenticity of what they saw—i.e., they told themselves that the pictures were fake or from a movie—they showed smaller increases in positive emotion than participants who used other tactics, such as changing how they viewed future consequences of the situation—i.e., by telling themselves that the situation depicted in the picture would improve over time.

- ***Frequency of reappraisal***

In one study, frequent reappraisers experienced and expressed more positive emotion (and less negative emotion) and had greater well-being than people who reappraised less frequently. By contrast, using the technique of suppression—denying or trying not to feel one's emotions—was associated with poorer well-being (**Gross & John, 2003)** [**6106**].

- ***Age***

Multiple studies have shown that age may influence reappraisal efficacy. One fMRI study that compared cognitive reappraisal abilities in children aged 10-13, adolescents (14-17), and young adults (18-22) found that reappraisal success increased with age, as did activity in part of the prefrontal cortex during reappraisal (no age-dependent difference in amygdala activation was evident) **(McRae, Gross, et al., 2012)** [**334**].

Another study also found that young adults were more successful than adolescents at using reappraisal to regulate negative emotions (Silvers, Shu, Hubbard, Weber, & Ochsner, 2015) [43]. Additionally, this study found that older participants had greater decreases in amygdala activity during reappraisal than younger participants, and this effect persisted when participants were reshown stimuli that they had previously reappraised. According to the researchers, these findings "suggest that one source of heightened emotionality in adolescence is a diminished ability to cognitively down-regulate aversive reactions." An earlier study of older adults (age 62 to 94) found similar results **(Urry, 2006)** [**922**].

- ***Gender***

Gender is another factor that may influence the effectiveness of cognitive reappraisal. One fMRI study found that while men and women reported similar changes in negative affect after using cognitive reappraisal to decrease their emotional response to negative pictures, their brain activity during this task was quite different **(McRae, Ochsner, Mauss, Gabrieli, & Gross, 2008)** [**518**]. During reappraisal, men's amygdala activity decreased more than women's did, but activity in women's prefrontal regions and the ventral striatum increased more than men's. The researchers offer two possible explanations for these findings: (1) reappraisal may take less cognitive effort for men (hence the less intense increase in prefrontal activation), and/or (2) women may use positive emotion more than men in their reappraisals (this could explain why they had less of a decrease in amygdala activity—increasing positive emotion could cancel out part of this effect). However, this study was not designed to test such hypotheses.

It is important to note that several of the studies in this chapter only used female participants as a way of minimizing variation in brain activity during reappraisal. This is a major limitation in interpreting this research.

- ***Genetics***

Genetics may also influence one's tendency to use reappraisal as an emotion regulation strategy, although this effect is likely limited. A recent study of twins found that one's tendency to use reappraisal as an emotion regulation strategy is significantly less heritable than one's tendency to use suppression, another emotion regulation strategy (McRae et al., 2017) [2]. These findings suggest that environment plays a larger role than genetics in influencing whether an individual tends to use cognitive reappraisal as an emotion regulation strategy, although future studies will need to determine which environmental factors play the biggest roles.

- ***Socioeconomic status***

One environmental factor that can be highly influential on an individual is socioeconomic status (SES), and, according to one recent study, SES may affect who benefits the most from cognitive reappraisal (Troy, Ford, McRae, Zarolia, & Mauss, 2017) [11]. This study found that people with stronger reappraisal ability had fewer depression symptoms, but this was only true for people with lower socioeconomic status.

Why might this be? One theory put forth by the researchers is that people who have more difficulty changing their environments may benefit more from strategies that allow them to change themselves (or at least their reactions). According to the researchers, these findings suggest that cognitive reappraisal and other emotion regulation strategies may be an important factor in the resilience of people in lower SES environments—and, as a corollary, lower SES people who struggle with cognitive reappraisal may be more at risk.

"Although ideally we should keep stress and inequality from occurring in the first place, this is not always possible," write the researchers. "Thus, increasing resilience through cognitive reappraisal—a learnable skill—provides a cost-effective and promising target for prevention and intervention for those lower in SES."

- ***Intersection between cognitive reappraisal and mental health***

Studies have suggested that cognitive reappraisal is less effective both for people with a history of self-harm behaviors (Davis et al., 2014) [26] and for people with social anxiety disorder (Jacob, Shany, Goldin, Gross, & Hendler, 2018)[0], and measures of participants' brain activity have backed this up. One study found that people who were experiencing elevated life stress benefitted from frequently attempting reappraisal—they had fewer depression symptoms—but only if the reappraisal was successful. People who frequently attempted reappraisal unsuccessfully actually had more depressive symptoms (Ford, Karnilowicz, & Mauss, 2017) [6].

Mindfulness meditation

Besides cognitive reappraisal, research also suggests that certain forms of meditation can improve people's mood and their ability to regulate their emotions **(Chambers, Gullone, & Allen, 2009)[898] (Roemer, Williston, & Rollins, 2015)[62]**.

Additionally, multiple studies have explored how meditation training can change how the brain responds to emotional stimuli. In particular, mindfulness meditation—which "encompasses focusing attention on the experience of thoughts, emotions, and body sensations, simply observing them as they arise and pass away"—has been used in several studies exploring the neuroscience of emotion regulation **(Hölzel et al., 2011) [1565]**.

One fMRI study showed participants—either experienced or novice mindfulness meditators—a series of photos intended to elicit emotional responses; sometimes the participants saw the photos when they were in a mindful state of awareness, other times when they weren't focused on being mindful **(Taylor et al., 2011) [251]**. This study found that people rated photos as being less intensely emotional when they were in a mindful state, suggesting that mindfulness is an effective emotion regulation strategy.

Neuroimaging data suggest that different mechanisms supported this effect for the two groups. For expert meditators, mindfulness dampened activity in the default mode network, an interconnected set of brain regions that is active when people are thinking about themselves and their emotions. For new meditators, mindfulness decreased amygdala responses to the emotional images. These findings may reflect how long-term meditators are better able to accept their emotions, whereas people newer to the practice may engage in more active emotion regulation by dampening their amygdala reactivity to the stimulus.

Another very recent study compared how short- and long-term mindfulness meditation changed how brains responded to emotional stimuli (Kral et al., 2018) [0]. This study found that, relative to control participants without any mindfulness training, short-term meditators (those who had completed an eight-week Mindfulness-Based Stress Reduction course) showed a decreased amygdala response to positive photos but not to negative photos. For more experienced meditators, however, the more hours of retreat practice they had completed, the less activity their amygdala demonstrated in response to negative pictures.

This study also found that short-term training increased the functional connectivity between the amygdala and the ventromedial prefrontal cortex, an area involved in emotion regulation, further suggesting that even a few weeks of meditation training may build up emotion regulation abilities (another study suggests that this same eight week meditation course strengthens structural connections between these brain regions (Hölzel et al., 2016) [7]). However, this increased functional connectivity was not seen in long-term meditators.

Why might this be? The researchers suggest that long-term training makes the reduction in reactivity to emotional stimuli more automatic so that it doesn't require as much activity in cognitive control areas. "This explanation aligns with subjective reports from practitioners, and with the goals and expectations of mindfulness meditation practice: to practice being aware and accepting of (affective) experience so that over time this process becomes more automatic," they write.

A similar effect was observed in another fMRI study: Participants who reported being more mindful overall showed decreased activity in prefrontal regions—those involved in cognitive control—when they were told they were about to view a negative photo than did people who were naturally less mindful, suggesting that mindful people may require less regulatory resources to inhibit their emotional arousal **(J. Lutz et al., 2013) [135]**.

Compassion meditation

A different form of meditation, compassion meditation, may be another effective method for emotion regulation. One study found that compassion training—completing a course "aimed at fostering benevolent and friendly attitudes toward oneself and other persons based on techniques from Eastern contemplative tradition"—increased the positive affect participants experienced when shown images of people suffering and also activated a network of brain regions involved in positive affect and affiliation **(Klimecki et al., 2013)** [**367**].

Another study compared the neural networks involved when 15 long-term practitioners of Nyingma meditation (a Tibetan Buddhist practice that specifically focuses "on the cultivation of loving-kindness, altruism and compassion") used reappraisal or compassion meditation to regulate their emotions while watching short videos of people in distress (Engen & Singer, 2015) [48]. While both strategies were effective, they were effective in different ways. Compassion meditation increased positive affect, whereas reappraisal decreased negative affect. Additionally, neuroimaging showed that, relative to reappraisal and passive viewing, compassion meditation techniques "increased activation in regions involved in affiliation, positive affect and reward processing including ventral striatum and medial orbitofrontal cortex."

Given that compassion training has been shown to increase altruistic and prosocial behavior, as discussed in Chapter 2, these findings suggest that it may also be an effective method for increasing our resilience in the face of stressful situations—especially those involving the suffering of others—on top of facilitating social connection and generosity.

Other emotion regulation strategies

Besides cognitive reappraisal and various forms of meditation, there are several other strategies that can be deployed before, during, and after emotional events to help people regulate their emotional responses, though these other strategies have not yet been studied neuroscientifically to the same degree as cognitive reappraisal and meditation.

Some of these other strategies involve "direct training" that helps people regulate their emotional response to a particular situation. Other "indirect training" strategies strengthen processes used in emotion regulation in general. For example, multiple studies have found that working memory training, a type of indirect training, can help bolster people's emotion regulation abilities and is associated with increased activity in cognitive control brain areas (frontoparietal brain region) (for a review of this emotion regulation strategy and others see (Cohen & Ochsner, 2018)[0]).

There are also emotion regulation strategies, besides positive reappraisal, that people use to try to increase their positive emotions **(Quoidbach, Mikolajczak, & Gross, 2015)** [**139**]. As Gross and his colleagues note in a recent review, these can include methods like trying to "pump yourself up" before an event—such as by playing your favorite song on the drive to the event—savoring the good aspects of a particular experience, taking more ownership of your role in a particular situation (e.g., by thinking, "I worked hard for this" instead of, "I got lucky"), "social sharing"—talking about positive emotional experiences with a friend or loved one—and "counting your blessings"—focusing on the good things that happened to you that day. While studies have explored the neural mechanisms behind some of these strategies—such as how expressing gratitude can change the brain (Kini, Wong, McInnis, Gabana, & Brown, 2016) [23]—there is much left to be explored neuroscientifically in this arena.

Limitations and Future Directions

This paper presents an overview of four areas of positive neuroscience research, but by no means does it encompass all the work being done in this subfield. For example, there is research underway about the neuroscience of creativity, gratitude, awe, and optimism—to name just a few topics. And with the continuing advancement of brain imaging techniques, and a new generation of neuroscientists who have been trained in positive neuroscience methods, the field is certain to grow in both depth and breadth.

This section of the white paper will both discuss some limitations inherent to much of the existing research covered in this paper and also highlight exciting future research directions for it.

Limitations

The vast majority of the studies covered in this paper involved functional magnetic resonance imaging (fMRI). While fMRI is an important tool in neuroscience—especially in human neuroscience, which largely relies on non-invasive methods—the technique does have some limitations. For example, because the technique is costly and time-intensive, many fMRI studies have included very small sample sizes (sometimes fewer than 10 participants), particularly in the first years that the technique was used. These limitations can be problematic because such small samples can result in low statistical power, which both lowers the chance of detecting a true effect and also lessens the likelihood that a result is statistically significant due to a true effect (as opposed to chance) **(Button et al., 2013)** [**2910**]. Additionally, because neuroimaging studies are expensive and time-consuming, replication studies are rare, which can exacerbate statistical analysis problems. In recent years, researchers have combatted these issues by conducting consortium studies and sharing neuroimaging data among groups **(Poldrack et al., 2017)** [**220**].

Another limitation common to many fMRI studies is that their participants do not reflect the larger population in terms of age, race/ethnicity, education, socioeconomic status, etc., which can result in findings that are not generalizable (Lewinn, Sheridan, Keyes, Hamilton, & McLaughlin, 2017) [19]. For example, since several of the emotion-regulation studies included in this paper only recorded brain activity from female participants, it is unclear whether similar results would be found in male participants. Concerns related to this topic have spurred the emergence of a new subfield of study, population neuroscience, which places questions of participant demographics at the fore **(Falk et al., 2013)** [75].

In addition, there are more theoretical limitations to fMRI. For example, neuroscientists still do not know exactly how changes in fMRI activity map to changes in neural activity **(Logothetis, 2008)** [**2658**]. And, as is clear from this paper, the same brain areas are active in many different tasks, and each task results in activation in several areas, thus it is difficult to characterize the function(s) of a particular brain region (Genon, Reid, Langner, Amunts, & Eickhoff, 2018) [7].

Despite these limitations, fMRI is still a very valuable technique that provides important insights into the inner workings of the human brain. Furthermore, many of these limitations will be addressed with improvements in the use of the technique, including by conducting studies with large sample sizes, making data sets open to analysis and aggregation by multiple labs, increasing the spatial and temporal resolution of the technique, and using machine learning algorithms to analyze fMRI data.

Other techniques discussed in this paper also have limitations. For example, several of the studies discussed in this paper used self-report surveys to measure attributes such as prosociality, parenting behavior, and musical ability, which can lead to data reliability issues. Similarly, some of the laboratory tasks, such as those in which participants are given the option to behave generously or compassionately, can suffer from participants' desire to demonstrate what they assume to be socially appropriate behavior. However, researchers generally try to whatever extent possible to minimize the potential effects of these factors, such as by using multiple techniques to measure prosociality (not just self-report) or by rendering participants' data anonymous (reducing their incentive for the socially desirable behavior).

Future directions

Positive neuroscience is ripe for expansion, and the research presented in this paper will likely be expanded upon in many different directions. Here are a few particularly interesting possibilities.

- ***The Social Brain***

There are several intriguing areas for further exploration when it comes to the neuroscience of social relationships. Despite the attention that the parent-child bond has already received from positive neuroscientists, there are still many unanswered questions related to the topic, including how to develop interventions to strengthen this essential primary attachment. For instance, neuroscientists James Rilling and Jennifer Mascaro have made the provocative proposal that fathers at risk of committing child abuse or experiencing postpartum depression could receive doses of oxytocin—and they suggest that neuroimaging could be used to predict which fathers would likely find such treatment effective (Rilling & Mascaro, 2016) [1]. They also suggest that there should be increased research on the neuroscience of "alloparenting"—the childcare provided by step-parents, grandparents, aunts, uncles, older siblings, day care workers, teachers, and other caregivers. For example, studies could further elucidate which parts of the brain make up the universal caregiving circuit present in all adults as well as how the neuroscience of parenting is similar to and different from the neuroscience of caring for a large group of children.

There is also still much we don't know about the neurobiological factors that underlie friendship and the different stages of romantic love. When it comes to the neuroscience of friendship, one interesting future research avenue is determining to what extent people tend to become friends with people who have similar neural reactions to various stimuli—versus whether friends become more neutrally similar over time (Parkinson, Kleinbaum, & Wheatley, 2018) [9].

Finally, there is much left to discover around the science of touch, including the mechanisms that underlie precisely how touch serves to buffer people against the negative effects of stress, along with the ways that touch facilitates important social behaviors, such as relationship formation, consolation, and reconciliation (Morrison, 2016) [12].

- ***The Compassionate Brain***

Research related to the neuroscience of compassion, empathy, and prosocial behavior may eventually lead to a more compassionate world—or at least according to a recent paper by Tor Wager and his colleagues (Ashar, Andrews-Hanna, Dimidjian, & Wager, 2017) [18]. Because their research has already started to identify the factors that can predict empathy and charitable giving, they argue that advances in this line of research will help us better understand precisely how to elicit compassion and generosity. Demonstrating the strength of this research will likely require measuring compassionate behavior in real-world settings where people are not aware that they are being observed (Ashar, Andrews-Hanna, Dimidjian, & Wager, 2016) [0].

Additional research will also need to be done to identify which factors—individual and societal—can facilitate or inhibit compassionate action and whether these factors respond to training. Of particular importance is the refinement of interventions, such as compassion meditation, that can counteract the effects of "burnout" and compassion fatigue in people who repeatedly encounter others in distress, such as first responders and medical professionals (Ashar, Andrews-Hanna, Yarkoni, et al., 2016) [13].

Research also needs to identify the exact mechanisms involved in vicarious rewards—those feelings of reward evident in the brain when we see others enjoying some kind of benefit—and their link to specific outcomes (Morelli, Knutson, & Zaki, 2018) [0]. For example, could methods (such as perspective-taking) that might change the value that one's brain places on vicarious rewards have observable effects on prosocial behavior? Likewise, what could explain the correlation between neural sensitivity to vicarious rewards and psychological well-being? Neuroscientist Jamil Zaki and colleagues speculate the correlation may be due to feeling more connected to friends and less lonely.

There's likely much more to be learned about extraordinary altruists as well. For example, do the findings from altruistic kidney donors apply to other highly altruistic people, such as heroic rescuers? And studies have found that, when extraordinary altruists observe people in pain, their brain activity suggests they are responding similarly to if they themselves were in pain. But does that kind of response extend to less severely distressing situations? Furthermore, it would be good to know if the neural signatures of altruism found in kidney donors can be used to predict prosocial behavior in less altruistic people (Brethel-Haurwitz et al., 2018)[1].

- ***The Musical Brain***

Studies have found that people who have the strongest aesthetic response to music also had increased connectivity between social and emotional parts of their brain and their frontal regions. That result invites the question: Does this finding extend to other forms of aesthetic stimuli, such as art or poetry (Sachs, Ellis, Schlaug, & Loui, 2016) [22]? Since this kind of neural connectivity has also been observed in highly empathic people, researchers also have reason to explore whether people who have a stronger aesthetic response to music are also more empathic (Parkinson & Wheatley, 2014) [40].

- ***The Resilient Brain***

While researchers have come a long way in elucidating the role of the amygdala in processing positive and negative stimuli, there are still many remaining questions. For example, do happier people always have increased amygdala responses to positive stimuli, or do these responses only occur when people are asked to pay attention to these stimuli? And what does it mean, if anything, that happier people had greater—albeit non-significantly—amygdala responses to negative images (Cunningham & Kirkland, 2013) [41]?

Additionally, much remains to be explored regarding positive reappraisal (McRae & Mauss, 2016) [9]. Important questions include: Does positive reappraisal lead to increased resilience? Does this relationship hold for all people? What factors could mediate and/or moderate the relationship between positive reappraisal and resiliency? And, importantly, what effect does positive reappraisal have on negative emotions—and does any such effect change depending on circumstances?

Research also still needs to elucidate the circumstances under which different emotion-regulation strategies will be most effective. For example, research suggests that distraction may be more useful than reappraisal in situations that are intensely emotional or when a person has a limited amount of time in which to regulate their emotions (McRae, 2016) [9]. There may also be situations in which it would be best to use a combination of emotion regulation strategies, such as using distraction first to dampen the immediate intensity of emotions, followed by reappraisal **(Gross, 2015) [636]**. Studies looking at the neural mechanisms underlying other emotion regulation strategies could help inform this work.

Other avenues for future research include determining the developmental trajectory in which children learn different forms of emotion regulation and whether or not interventions could help children develop these skills more quickly **(McRae et al., 2012) [334]**.

Finally, there is some evidence that emotion regulation approaches can be used to mitigate negative emotions between groups of people. For example, one study found that Israeli participants who were randomly assigned to reappraisal training and then presented with anger-inducing information about the Israeli-Palestinian conflict showed greater support for conciliatory policies and less support for aggressive policies toward Palestinians both one week and five months later **(Halperin, Porat, Tamir, & Gross, 2013) [120]**. Understanding how the neural mechanisms that underlie successful cognitive reappraisal of personal emotions are similar and/or distinct from those involved in moderating intergroup emotion may aid in developing interventions for seemingly intractable conflicts between couples, families, and even nations **(Goldenberg, Halperin, van Zomeren, & Gross, 2015) [55]**.

The outlook for positive neuroscience certainly looks…positive. While the field's growth and development will of course depend on funding, the research covered by this paper—and these promising future directions—suggest that understanding the neural underpinnings of human flourishing is not only a subject worth pursuing but one that is likely to produce invaluable insights.

References

Abraham, E., Hendler, T., Shapira-Lichter, I., Kanat-Maymon, Y., Zagoory-Sharon, O., & Feldman, R. (2014). Father's brain is sensitive to childcare experiences. *Proceedings of the National Academy of Sciences*, 111(27), 9792–9797. https://doi.org/10.1073/pnas.1402569111

Abraham, E., Hendler, T., Zagoory-Sharon, O., & Feldman, R. (2016). Network integrity of the parental brain in infancy supports the development of children's social competencies. *Social Cognitive and Affective Neuroscience*, 11(11), 1707–1718. https://doi.org/10.1093/scan/nsw090

Abraham, E., Raz, G., Zagoory-Sharon, O., & Feldman, R. (2018). Empathy networks in the parental brain and their long-term effects on children's stress reactivity and behavior adaptation. *Neuropsychologia*, 116, 75-85. https://doi.org/10.1016/j.neuropsychologia.2017.04.015

Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D. G., Glover, G., … Sobel, N. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience*, 6(2), 196–202. https://doi.org/10.1038/nn1001

Armony, J. L., Corbo, V., Clément, M. H., & Brunet, A. (2005). Amygdala response in patients with acute PTSD to masked and unmasked emotional facial expressions. *American Journal of Psychiatry*, 162(10), 1961–1963. https://doi.org/10.1176/appi.ajp.162.10.1961

Arnone, D., McKie, S., Elliott, R., Thomas, E. J., Downey, D., Juhasz, G., … Anderson, I. M. (2012). Increased Amygdala Responses to Sad But Not Fearful Faces in Major Depression: Relation to Mood State and Pharmacological Treatment. *American Journal of Psychiatry*, 169(8), 841–850. https://doi.org/10.1176/appi.ajp.2012.11121774

Ashar, Y. K., Andrews-Hanna, J. R., Dimidjian, S., & Wager, T. D. (2016). Toward a Neuroscience of Compassion. In *Positive Neuroscience* (pp. 125–142). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199977925.003.0009

Ashar, Y. K., Andrews-Hanna, J. R., Dimidjian, S., & Wager, T. D. (2017). Empathic Care and Distress: Predictive Brain Markers and Dissociable Brain Systems. *Neuron*, 94(6), 1263–1273.e4. https://doi.org/10.1016/j.neuron.2017.05.014

Ashar, Y. K., Andrews-Hanna, J. R., Yarkoni, T., Sills, J., Halifax, J., Dimidjian, S., & Wager, T. D. (2016). Effects of compassion meditation on a psychological model of charitable donation. *Emotion*, 16(5), 691–705. https://doi.org/10.1037/emo0000119

Atzil, S., Hendler, T., & Feldman, R. (2011). Specifying the neurobiological basis of human attachment: Brain, hormones, and behavior in synchronous and intrusive mothers. *Neuropsychopharmacology*, 36(13), 2603–2615. https://doi.org/10.1038/npp.2011.172

Bartels, A., & Zeki, S. (2000). The neural basis of romantic love. *NeuroReport*, 11(17), 3829–3834. https://doi.org/10.1097/00001756-200011270-00046

Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage*, 21(3), 1155–1166. https://doi.org/10.1016/j.neuroimage.2003.11.003

Batson, C. D., Fultz, J., & Schoenrade, P. A. (1987). Distress and Empathy: Two Qualitatively Distinct Vicarious Emotions with Different Motivational Consequences. *Journal of Personality*, 55(1), 19–39. https://doi.org/10.1111/j.1467-6494.1987.tb00426.x

Bell, S. M., & Ainsworth, M. D. (1972). Infant crying and maternal responsiveness. *Child Development*, 43(4), 1171–1190. http://dx.doi.org/10.2307/1127506

Bennett, R. H., Bolling, D. Z., Anderson, L. C., Pelphrey, K. A., & Kaiser, M. D. (2014). fNIRS detects temporal lobe response to affective touch. *Social Cognitive and Affective Neuroscience*, 9(4), 470–476. https://doi.org/10.1093/scan/nst008

Bermudez, P., Lerch, J. P., Evans, A. C., & Zatorre, R. J. (2009). Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cerebral Cortex*, 19(7), 1583–1596. https://doi.org/10.1093/cercor/bhn196

Blood, A. J., & Zatorre, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences*, 98(20), 11818–11823. https://doi.org/10.1073/pnas.191355898

Brethel-Haurwitz, K. M., Cardinale, E., Vekaria, K., Robertson, E., Walitt, B., VanMeter, J., & Marsh, A. A. (2018). Extraordinary altruists exhibit enhanced self-other overlap in neural responses to distress. *Psychological Science*. 29(10),1631-1641. https://doi.org/10.1177/0956797618779590

Brethel-Haurwitz, K. M., & Marsh, A. A. (2014). Geographical Differences in Subjective Well-Being Predict Extraordinary Altruism. *Psychological Science*, 25(3), 762–771. https://doi.org/10.1177/0956797613516148

Brethel-Haurwitz, K. M., O'Connell, K., Cardinale, E. M., Stoianova, M., Stoycos, S. A., Lozier, L. M., … Marsh, A. A. (2017). Amygdala–midbrain connectivity indicates a role for the mammalian parental care system in human altruism. *Proceedings of the Royal Society B: Biological Sciences*, 284(1865), 20171731. https://doi.org/10.1098/rspb.2017.1731

Buchanan, T. W., Bagley, S. L., Stansfield, R. B., & Preston, S. D. (2012). The empathic, physiological resonance of stress. *Social Neuroscience*, 7(2), 191–201. https://doi.org/10.1080/17470919.2011.588723

Buchanan, T. W., & Preston, S. D. (2014). Stress leads to prosocial action in immediate need situations. *Frontiers in Behavioral Neuroscience*, 8(January), 1–6. https://doi.org/10.3389/fnbeh.2014.00005

Buchanan, T. W., & Preston, S. D. (2016). When Feeling and Doing Diverge. In *Positive Neuroscience* (pp. 89–104). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199977925.003.0007

Buhle, J. T., Silvers, J. A., Wager, T. D., Lopez, R., Onyemekwu, C., Kober, H., … Ochsner, K. N. (2014). Cognitive reappraisal of emotion: A meta-analysis of human neuroimaging studies. *Cerebral Cortex*, 24(11), 2981–2990. https://doi.org/10.1093/cercor/bht154

Camerer, C. F., Dreber, A., Holzmeister, F., Ho, T.-H., Huber, J., Johannesson, M., … Wu, H. (2018). Evaluating the replicability of social science experiments in Nature and Science between 2010 and 2015. *Nature Human Behaviour*, 2(September). https://doi.org/10.1038/s41562-018-0399-z

Canli, T., Zhao, Z., Desmond, J. E., Kang, E., Gross, J. J., & Gabrieli, J. D. E. (2001). An fMRI study of personality influences on brain reactivity to emotional stimuli. *Behavioral Neuroscience*, 115(1), 33–42. https://doi.org/10.1037/0735-7044.115.1.33

Cassidy, J. (2008). EMOTION REGULATION: INFLUENCES OF ATTACHMENT RELATIONSHIPS. *Monographs of the Society for Research in Child Development*, 59(2–3), 228–249.https://doi.org/10.1111/j.1540-5834.1994.tb01287.x

Chambers, R., Gullone, E., & Allen, N. B. (2009). Mindful emotion regulation: An integrative review. *Clinical Psychology Review*, 29(6), 560–572. https://doi.org/10.1016/j.cpr.2009.06.005

Cohen, N., & Ochsner, K. N. (2018). From surviving to thriving in the face of threats: the emerging science of emotion regulation training. *Current Opinion in Behavioral Sciences*, 24, 143–155. https://doi.org/10.1016/j.cobeha.2018.08.007

Condon, P., Desbordes, G., Miller, W. B., & DeSteno, D. (2013). Meditation Increases Compassionate Responses to Suffering. *Psychological Science*, 24(10), 2125–2127. https://doi.org/10.1177/0956797613485603

Cunningham, W. A., Arbuckle, N. L., Jahn, A., Mowrer, S. M., & Abduljalil, A. M. (2011). Reprint of: Aspects of neuroticism and the amygdala: Chronic tuning from motivational styles. *Neuropsychologia*, 49(4), 657–662. https://doi.org/10.1016/j.neuropsychologia.2011.02.027

Cunningham, W. A., & Kirkland, T. (2013). The joyful, yet balanced, amygdala: Moderated responses to positive but not negative stimuli in trait happiness. *Social Cognitive and Affective Neuroscience*, 9(6), 760–766. https://doi.org/10.1093/scan/nst045

Cunningham, W. A., Raye, C. L., & Johnson, M. K. (2004). Implicit and explicit evaluation: fMRI correlates of valence, emotional intensity, and control in the processing of attitudes. *Journal of Cognitive Neuroscience*, 16(10), 1717–1729. https://doi.org/10.1162/0898929042947919

Cunningham, W. A., Van Bavel, J. J., & Johnsen, I. R. (2008). Affective Flexibility. *Psychological Science*, 19(2), 152–160. https://doi.org/10.1111/j.1467-9280.2008.02061.x

Davis, T. S., Mauss, I. B., Lumian, D. S., Troy, A. S., Shallcross, A. J., Zarolia, P., … McRae, K. (2014). Emotional reactivity and emotion regulation among adults with a history of self-harm: Laboratory self-report and functional MRI evidence. *Journal of Abnormal Psychology*, 123(3), 499–509. https://doi.org/10.1037/a0036962

Denny, B. T., Inhoff, M. C., Zerubavel, N., Davachi, L., & Ochsner, K. N. (2015). Getting over it: Long-lasting effects of emotion regulation on amygdala response. *Psychological Science*, 26(9), 1377–1388. https://doi.org/10.1177/0956797615578863

Dillon, D. G., & LaBar, K. S. (2005). Startle modulation during conscious emotion regulation is arousal-dependent. *Behavioral Neuroscience*, 119(4), 1118–1124. https://doi.org/10.1037/0735-7044.119.4.1118

Dohn, A., Garza-Villarreal, E. A., Chakravarty, M. M., Hansen, M., Lerch, J. P., & Vuust, P. (2015). Gray-and white-matter anatomy of absolute pitch possessors. *Cerebral Cortex*, 25(5), 1379–1388. https://doi.org/10.1093/cercor/bht334

Dulac, C., O'Connell, L. A., & Wu, Z. (2014). Neural control of maternal and paternal behaviors. *Science*, 345(6198), 765–770. https://doi.org/10.1126/science.1253291

Engen, H. G., & Singer, T. (2015). Compassion-based emotion regulation up-regulates experienced positive affect and associated neural networks. *Social Cognitive and Affective Neuroscience*, 10(9), 1291–1301. https://doi.org/10.1093/scan/nsv008

Feldman, R., Gordon, I., Influs, M., Gutbir, T., & Ebstein, R. P. (2013). Parental oxytocin and early caregiving jointly shape children's oxytocin response and social reciprocity. *Neuropsychopharmacology*, 38(7), 1154–1162. https://doi.org/10.1038/npp.2013.22

Feldman, R., Singer, M., & Zagoory, O. (2010). Touch attenuates infants' physiological reactivity to stress. *Developmental Science*, 13(2), 271–278. https://doi.org/10.1111/j.1467-7687.2009.00890.x

Ford, B. Q., Karnilowicz, H. R., & Mauss, I. B. (2017). Understanding reappraisal as a multicomponent process: The psychological health benefits of attempting to use reappraisal depend on reappraisal success. *Emotion*, 17(6), 905–911. https://doi.org/10.1037/emo0000310

Foti, D., & Hajcak, G. (2008). Deconstructing reappraisal: Descriptions preceding arousing pictures modulate the subsequent neural response. *Journal of Cognitive Neuroscience*, 20(6), 977–988. https://doi.org/10.1162/jocn.2008.20066

Fredrickson, B. L. (2001). The role of positive emotions in positive psychology. The broaden-and-build theory of positive emotions. *The American Psychologist*, 56(3), 218–226. https://doi.org/10.1037/0003-066X.56.3.218

Fredrickson, B. L., Cohn, M. A., Coffey, K. A., Pek, J., & Finkel, S. M. (2008). Open hearts build lives: Positive emotions, induced through loving-kindness meditation, build consequential personal resources. *Journal of Personality and Social Psychology*, 95(5), 1045–1062. https://doi.org/10.1037/a0013262

Frith, C. D., & Frith, U. (2006). T*he Neural Basis of Mentalizing. Neuron*, 50(4), 531–534. https://doi.org/10.1016/j.neuron.2006.05.001

Garavan, H., Pendergrass, J. C., Ross, T. J., Stein, E. A., & Risinger, R. C. (2001). Amygdala responses to both positively and negatively valenced stimuli. *Neuroreport*, 12(12), 2779–2783.

Genevsky, A., Vastfjall, D., Slovic, P., & Knutson, B. (2013). Neural Underpinnings of the Identifiable Victim Effect: Affect Shifts Preferences for Giving. *Journal of Neuroscience*, 33(43), 17188–17196. https://doi.org/10.1523/JNEUROSCI.2348-13.2013

Giuliani, N. R., McRae, K., & Gross, J. J. (2008). The up- and down-regulation of amusement: Experiential, behavioral, and autonomic consequences. *Emotion*, 8(5), 714–719. https://doi.org/10.1037/a0013236

Goetz, J. L., Keltner, D., & Simon-Thomas, E. (2010). Compassion: An evolutionary analysis and empirical review. *Psychological Bulletin*, 136(3), 351–374. https://doi.org/10.1037/a0018807

Gordon, I., Voos, A. C., Bennett, R. H., Bolling, D. Z., Pelphrey, K. A., & Kaiser, M. D. (2013). Brain mechanisms for processing affective touch. *Human Brain Mapping*, 34(4), 914–922. https://doi.org/10.1002/hbm.21480

Gordon, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2010). Oxytocin, cortisol, and triadic family interactions. *Physiology and Behavior*, 101(5), 679–684. https://doi.org/10.1016/j.physbeh.2010.08.008

Gratz, K. L., Weiss, N. H., & Tull, M. T. (2015). Examining emotion regulation as an outcome, mechanism, or target of psychological treatments. *Current Opinion in Psychology*, 3, 85–90. https://doi.org/10.1016/j.copsyc.2015.02.010

Gregersen, P. K., Kowalsky, E., Lee, A., Baron-Cohen, S., Fisher, S. E., Asher, J. E., … Li, W. (2013). Absolute pitch exhibits phenotypic and genetic overlap with synesthesia. *Human Molecular Genetics*, 22(10), 2097–2104. https://doi.org/10.1093/hmg/ddt059

Grewe, O., Nagel, F., Kopiez, R., & Altenmüller, E. (2007). Listening To Music As A Re-Creative Process: Physiological, Psychological, And Psychoacoustical Correlates Of Chills And Strong Emotions. *Music Perception: An Interdisciplinary Journal*, 24(3), 297–314. https://doi.org/10.1525/mp.2007.24.3.297

Gross, J. J. (1998). Antecedent- and response-focused emotion regulation: divergent consequences for experience, expression, and physiology. *Journal of Personality and Social Psychology*, 74(1), 224–237. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9457784

Gross, J. J. (2015). Emotion Regulation: Current Status and Future Prospects. *Psychological Inquiry*, 26(1), 1–26. https://doi.org/10.1080/1047840X.2014.940781

Gross, J. J., & John, O. P. (2003). Individual Differences in Two Emotion Regulation Processes: Implications for Affect, Relationships, and Well-Being. *Journal of Personality and Social Psychology*, 85(2), 348–362. https://doi.org/10.1037/0022-3514.85.2.348

Gross, J. J., Richards, J. M., & John, O. P. (1994). Emotion Regulation in Everyday Life. *Emotion Regulation in Couples and Families: Pathways to Dysfunction and Health.*, 13–35. https://doi.org/10.1037/11468-001

Hackel, L. M., Zaki, J., & Van Bavel, J. J. (2017). Social identity shapes social valuation: Evidence from prosocial behavior and vicarious reward. *Social Cognitive and Affective Neuroscience*, 12(8), 1219–1228. https://doi.org/10.1093/scan/nsx045

Hajcak, G., & Nieuwenhuis, S. (2006). Reappraisal modulates the electrocortical response to unpleasant pictures. *Cognitive, Affective and Behavioral Neuroscience*, 6(4), 291–297. https://doi.org/10.3758/CABN.6.4.291

Halwani, G. F., Loui, P., Rüber, T., & Schlaug, G. (2011). Effects of practice and experience on the arcuate fasciculus: Comparing singers, instrumentalists, and non-musicians. *Frontiers in Psychology*, 2(JUL), 1–9. https://doi.org/10.3389/fpsyg.2011.00156

Hamann, S. B., Ely, T. D., Hoffman, J. M., & Kilts, C. D. (2002). Ecstasy and Agony: Activation of the Human Amygdala in Positive and Negative Emotion. *Psychological Science* (Wiley-Blackwell), 13(2), 135. https://doi.org/10.1111/1467-9280.00425

Hamann, S. B., & Mao, H. (2002). Positive and negative emotional verbal stimuli elicit activity in the left amygdala. *Neuroreport*, 13(1), 15–19. http://www.ncbi.nlm.nih.gov/pubmed/11924878

Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007). Neural Responses to Taxation and Voluntary Giving Reveal Motives for Charitable Donations. *Science*, 316(5831), 1622–1625. https://doi.org/10.1126/science.1140738

Hare, T. A., Camerer, C. F., Knoepfle, D. T., O'Doherty, J. P., & Rangel, A. (2010). Value Computations in Ventral Medial Prefrontal Cortex during Charitable Decision Making Incorporate Input from Regions Involved in Social Cognition. *Journal of Neuroscience*, 30(2), 583–590. https://doi.org/10.1523/JNEUROSCI.4089-09.2010

Hariri, A. R., Mattay, V. S., Tessitore, A., Kolachana, B., Fera, F., Goldman, D., … Weinberger, D. R. (2002). Serotonin transporter genetic variation and the response of the human amygdala. *Science*, 297(5580), 400–403. https://doi.org/10.1126/science.1071829

Henrich, J., & Henrich, N. (2006). Culture, evolution and the puzzle of human cooperation. *Cognitive Systems Research*, 7(2–3), 220–245. https://doi.org/10.1016/j.cogsys.2005.11.010

Higham, T., Basell, L., Jacobi, R., Wood, R., Ramsey, C. B., & Conard, N. J. (2012). Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: The radiocarbon chronology of Geißenklösterle. *Journal of Human Evolution*, 62(6), 664–676. https://doi.org/10.1016/j.jhevol.2012.03.003

Holt-Lunstad, J., Birmingham, W. A., & Light, K. C. (2008). Influence of a "warm touch" support enhancement intervention among married couples on ambulatory blood pressure, oxytocin, alpha amylase, and cortisol. *Psychosomatic Medicine*, 70(9), 976–985. https://doi.org/10.1097/PSY.0b013e318187aef7

Hölzel, B. K., Brunsch, V., Gard, T., Greve, D. N., Koch, K., Sorg, C., … Milad, M. R. (2016). Mindfulness-Based Stress Reduction, Fear Conditioning, and The Uncinate Fasciculus: A Pilot Study. *Frontiers in Behavioral Neuroscience*, 10(June), 1–12. https://doi.org/10.3389/fnbeh.2016.00124

Hölzel, B. K., Lazar, S. W., Gard, T., Schuman-Olivier, Z., Vago, D. R., & Ott, U. (2011). How does mindfulness meditation work? Proposing mechanisms of action from a conceptual and neural perspective. *Perspectives on Psychological Science*, 6(6), 537–559. https://doi.org/10.1177/1745691611419671

Hubbard, J., Harbaugh, W. T., Srivastava, S., Degras, D., & Mayr, U. (2016). A general benevolence dimension that links neural, psychological, economic, and life-span data on altruistic tendencies. *Journal of Experimental Psychology: General*, 145(10), 1351–1358. https://doi.org/10.1037/xge0000209

Jackson, D. C., Malmstadt, J. R., Larson, C. L., & Davidson, R. J. (2000). Suppression and enhancement of emotional responses to unpleasant pictures. *Psychophysiology,* 37(4), 515–522. https://doi.org/10.1017/S0048577200990401

Jacob, Y., Shany, O., Goldin, P. R., Gross, J. J., & Hendler, T. (2018). Reappraisal of Interpersonal Criticism in Social Anxiety Disorder: A Brain Network Hierarchy Perspective. *Cerebral Cortex*, 1–14. https://doi.org/10.1093/cercor/bhy181

Juslin, P. N., & Laukka, P. (2003). Communication of Emotions in Vocal Expression and Music Performance: Different Channels, Same Code? *Psychological Bulletin*, 129(5), 770–814. https://doi.org/10.1037/0033-2909.129.5.770

Keenan, J. P., Thangaraj, V., Halpern, A. R., & Schlaug, G. (2001). Absolute pitch and planum temporale. *NeuroImage*, 14(6), 1402–1408. https://doi.org/10.1006/nimg.2001.0925

Kim, J. W., Kim, S. E., Kim, J. J., Jeong, B., Park, C. H., Son, A. R., … Ki, S. W. (2009). Compassionate attitude towards others' suffering activates the mesolimbic neural system. *Neuropsychologia*, 47(10), 2073–2081. https://doi.org/10.1016/j.neuropsychologia.2009.03.017

Kim, P., Leckman, J. F., Mayes, L. C., Feldman, R., Wang, X., & Swain, J. E. (2010). The plasticity of human maternal brain: Longitudinal changes in brain anatomy during the early postpartum period. *Behavioral Neuroscience*, 124(5), 695–700. https://doi.org/10.1037/a0020884

Kim, P., Leckman, J. F., Mayes, L. C., Newman, M. A., Feldman, R., & Swain, J. E. (2010). Perceived quality of maternal care in childhood and structure and function of mothers' brain. *Developmental Science*, 13(4), 662–673. https://doi.org/10.1111/j.1467-7687.2009.00923.x

Kim, P., Rigo, P., Leckman, J. F., Mayes, L. C., Cole, P. M., Feldman, R., & Swain, J. E. (2015). A prospective longitudinal study of perceived infant outcomes at 18-24 months: Neural and psychological correlates of parental thoughts and actions assessed during the first month postpartum. *Frontiers in Psychology*, 6(NOV), 1–14. https://doi.org/10.3389/fpsyg.2015.01772

Kim, P., Rigo, P., Mayes, L. C., Feldman, R., Leckman, J. F., & Swain, J. E. (2014). Neural plasticity in fathers of human infants. *Social Neuroscience*, 9(5), 522–535. https://doi.org/10.1080/17470919.2014.933713

Kini, P., Wong, J., McInnis, S., Gabana, N. T., & Brown, J. W. (2016). The effects of gratitude expression on neural activity. *NeuroImage*, 128, 1–10. https://doi.org/10.1016/j.neuroimage.2015.12.040

Kinreich, S., Djalovski, A., Kraus, L., Louzoun, Y., & Feldman, R. (2017). Brain-to-Brain Synchrony during Naturalistic Social Interactions. *Scientific Reports*, 7(1), 1–12. https://doi.org/10.1038/s41598-017-17339-5

Klimecki, O. M., Leiberg, S., Lamm, C., & Singer, T. (2013). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex*, 23(7), 1552–1561. https://doi.org/10.1093/cercor/bhs142

Kling, A., & Steklis, H. D. (1976). A neural substrate for affiliative behavior in nonhuman primates. *Brain, Behavior and Evolution*, 13(2–3), 216–238. https://doi.org/10.1159/000123811

Kral, T. R. A., Schuyler, B. S., Mumford, J. A., Rosenkranz, M. A., Lutz, A., & Davidson, R. J. (2018). Impact of short- and long-term mindfulness meditation training on amygdala reactivity to emotional stimuli. *NeuroImage*, 181(February), 301–313. https://doi.org/10.1016/j.neuroimage.2018.07.013

Kuo, P. X., Carp, J., Light, K. C., & Grewen, K. M. (2012). Neural responses to infants linked with behavioral interactions and testosterone in fathers. *Biological Psychology*, 91(2), 302–306. https://doi.org/10.1016/j.biopsycho.2012.08.002

Lee, H., Heller, A. S., van Reekum, C. M., Nelson, B., & Davidson, R. J. (2012). Amygdala-prefrontal coupling underlies individual differences in emotion regulation. *NeuroImage*, 62(3), 1575–1581. https://doi.org/10.1016/j.neuroimage.2012.05.044

Leibenluft, E., Gobbini, M. I., Harrison, T., & Haxby, J. V. (2004). Mothers' neural activation in response to pictures of their children and other children. *Biological Psychiatry*, 56(4), 225–232. https://doi.org/10.1016/j.biopsych.2004.05.017

Limb, C. J., & Braun, A. R. (2008). Neural substrates of spontaneous musical performance: An fMRI study of jazz improvisation. *PLoS ONE*, 3(2). https://doi.org/10.1371/journal.pone.0001679

Liu, S., Chow, H. M., Xu, Y., Erkkinen, M. G., Swett, K. E., Eagle, M. W., … Braun, A. R. (2012). Neural correlates of lyrical improvisation: An fMRI study of freestyle rap. *Scientific Reports*, 2. https://doi.org/10.1038/srep00834

Löken, L. S., Wessberg, J., Morrison, I., McGlone, F., & Olausson, H. (2009). Coding of pleasant touch by unmyelinated afferents in humans. *Nature Neuroscience*, 12(5), 547–548. https://doi.org/10.1038/nn.2312

Lorberbaum, J. P., Newman, J. D., Dubno, J. R., Horwitz, A. R., Nahas, Z., Teneback, C., … George, M. S. (1998). Feasibility of using fMRI to study mothers responding to infant cries. *NeuroImage*, 7(4 PART II), 99–104. Retrieved from http://www.scopus.com/inward/record.url?eid=2-s2.0-21944454359&partnerID=40&md5=1441ab931891bf78b70b1f7e59aff9a4

Lorberbaum, J. P., Newman, J. D., Horwitz, A. R., Dubno, J. R., Lydiard, R. B., Hamner, M. B., … George, M. S. (2002). A potential role for thalamocingulate circuitry in human maternal behavior. *Biological Psychiatry*, 51(6), 431–445. https://doi.org/10.1016/S0006-3223(01)01284-7

Loui, P. (2016). The Role of Brain Connectivity in Musical Experience. In J. D. Greene, I. Morrison, & M. E. P. Seligman (Eds.), *Positive Neuroscience* (First). Oxford University Press. Retrieved from http://mindlab.research.wesleyan.edu/files/2014/01/Connectivity-in-Music-text-figs.pdf

Loui, P., Alsop, D., & Schlaug, G. (2009). Tone Deafness: A New Disconnection Syndrome? *Journal of Neuroscience*, 29(33), 10215–10220. https://doi.org/10.1523/JNEUROSCI.1701-09.2009

Loui, P., Bachorik, J. P., Li, H. C., & Schlaug, G. (2013). Effects of voice on emotional arousal. *Frontiers in Psychology*, 4(OCT), 1554–1564. https://doi.org/10.3389/fpsyg.2013.00675

Loui, P., Li, H. C., Hohmann, A., & Schlaug, G. (2011). Enhanced Cortical Connectivity in Absolute Pitch Musicians: A Model for Local Hyperconnectivity. *Journal of Cognitive Neuroscience*, 23(4), 1015–1026. https://doi.org/10.1162/jocn.2010.21500

Loui, P., Li, H. C., & Schlaug, G. (2011). White matter integrity in right hemisphere predicts pitch-related grammar learning. *NeuroImage*, 55(2), 500–507. https://doi.org/10.1016/j.neuroimage.2010.12.022

Loui, P., Patterson, S., Sachs, M. E., Leung, Y., Zeng, T., & Przysinda, E. (2017). White matter correlates of musical Anhedonia: Implications for evolution of music. *Frontiers in Psychology*, 8(SEP), 1–10. https://doi.org/10.3389/fpsyg.2017.01664

Loui, P., Zamm, A., & Schlaug, G. (2012). Enhanced functional networks in absolute pitch. *NeuroImage*, 63(2), 632–640. https://doi.org/10.1016/j.neuroimage.2012.07.030

Lumian, D. S., & McRae, K. (2017). Preregistered Replication of "Affective Flexibility: Evaluative Processing Goals Shape Amygdala Activity." *Psychological Science*, 28(9), 1193–1200. https://doi.org/10.1177/0956797617719730

Lutz, A., Brefczynski-Lewis, J., Johnstone, T., & Davidson, R. J. (2008). Regulation of the neural circuitry of emotion by compassion meditation: Effects of meditative expertise. *PLoS ONE*, 3(3), 1–10. https://doi.org/10.1371/journal.pone.0001897

Lutz, J., Herwig, U., Opialla, S., Hittmeyer, A., Jäncke, L., Rufer, M., … Brühl, A. B. (2013). Mindfulness and emotion regulation-an fMRI study. *Social Cognitive and Affective Neuroscience*, 9(6), 776–785. https://doi.org/10.1093/scan/nst043

Man, V., Ames, D. L., Todorov, A., & Cunningham, W. A. (2016). Amygdala Tuning Toward Self and Other. In *Positive Neuroscience* (pp. 105–124). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199977925.003.0008

Marsh, A. A. (2016). Extraordinary Altruism. In *Positive Neuroscience* (pp. 143–156). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199977925.003.0010

Marsh, A. A. (2018). The neuroscience of empathy. *Current Opinion in Behavioral Sciences*, 19, 110–115. https://doi.org/10.1016/j.cobeha.2017.12.016

Marsh, A. A., & Ambady, N. (2007). The influence of the fear facial expression on prosocial responding. *Cognition and Emotion*. https://doi.org/10.1080/02699930600652234

Marsh, A. A., & Blair, R. J. R. (2008). Deficits in facial affect recognition among antisocial populations: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, 32(3), 454–465. https://doi.org/10.1016/j.neubiorev.2007.08.003

Marsh, A. A., Finger, E. C., Mitchell, D. G. V, Reid, M. E., Sims, C., Kosson, D. S., … Blair, R. J. R. (2008). Reduced amygdala response to fearful expressions in children and adolescents with callous-unemotional traits and disruptive behavior disorders. *American Journal of Psychiatry*, 165(6), 712–720. https://doi.org/10.1176/appi.ajp.2007.07071145

Marsh, A. A., Stoycos, S. A., Brethel-Haurwitz, K. M., Robinson, P., VanMeter, J. W., & Cardinale, E. M. (2014). Neural and cognitive characteristics of extraordinary altruists. *Proceedings of the National Academy of Sciences*, 111(42), 15036–15041. https://doi.org/10.1073/pnas.1408440111

Mascaro, J. S., Hackett, P. D., Gouzoules, H., Lori, A., & Rilling, J. K. (2014). Behavioral and genetic correlates of the neural response to infant crying among human fathers. *Social Cognitive and Affective Neuroscience*, 9(11), 1704–1712. https://doi.org/10.1093/scan/nst166

Mascaro, J. S., Hackett, P. D., & Rilling, J. K. (2013). Testicular volume is inversely correlated with nurturing-related brain activity in human fathers. *Proceedings of the National Academy of Sciences*, 110(39), 15746–15751. https://doi.org/10.1073/pnas.1305579110

Mascaro, J. S., Hackett, P. D., & Rilling, J. K. (2014). Differential neural responses to child and sexual stimuli in human fathers and non-fathers and their hormonal correlates. *Psychoneuroendocrinology*, 46(404), 153–163. https://doi.org/10.1016/j.psyneuen.2014.04.014

Mascaro, J. S., Rentscher, K. E., Hackett, P. D., Mehl, M. R., & Rilling, J. K. (2017). Child gender influences paternal behavior, language, and brain function. *Behavioral Neuroscience*, 131(3), 262–273. https://doi.org/10.1037/bne0000199

Mascaro, J. S., Rilling, J. K., Tenzin Negi, L., & Raison, C. L. (2013). Compassion meditation enhances empathic accuracy and related neural activity. *Social Cognitive and Affective Neuroscience*, 8(1), 48–55. https://doi.org/10.1093/scan/nss095

Masten, C. L., Morelli, S. A., & Eisenberger, N. I. (2011). An fMRI investigation of empathy for "social pain" and subsequent prosocial behavior. *NeuroImage*, 55(1), 381–388. https://doi.org/10.1016/j.neuroimage.2010.11.060

Mather, M., & Lighthall, N. R. (2012). Risk and reward are processed differently in decisions made under stress. *Current Directions in Psychological Science*, 21(1), 36–41. https://doi.org/10.1177/0963721411429452

McRae, K., Ciesielski, B., & Gross, J. J. (2012). Unpacking cognitive reappraisal: Goals, tactics, and outcomes. *Emotion*, 12(2), 250–255. https://doi.org/10.1037/a0026351

McRae, K., Gross, J. J., Weber, J., Robertson, E. R., Sokol-Hessner, P., Ray, R. D., … Ochsner, K. N. (2012). The development of emotion regulation: An fMRI study of cognitive reappraisal in children, adolescents and young adults. *Social Cognitive and Affective Neuroscience*, 7(1), 11–22. https://doi.org/10.1093/scan/nsr093

McRae, K., Hughes, B., Chopra, S., Gabrieli, J., Gross, J. J., & Ochsner, K. N. (2010). The neural bases of distraction and reappraisal: An fMRI study of emotion regulation. *Journal of Cognitive Neuroscience*, 22, 248–262. https://doi.org/10.1162/jocn.2009.21243

McRae, K., & Mauss, I. B. (2016). Increasing Positive Emotion in Negative Contexts. In *Positive Neuroscience* (pp. 159–174). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199977925.003.0011

McRae, K., Ochsner, K. N., Mauss, I. B., Gabrieli, J. J. D., & Gross, J. J. (2008). Gender Differences in Emotion Regulation: An fMRI Study of Cognitive Reappraisal. *Group Processes & Intergroup Relations*, 11(2), 143–162. https://doi.org/10.1177/1368430207088035

McRae, K., Rhee, S. H., Gatt, J. M., Godinez, D., Williams, L. M., & Gross, J. J. (2017). Genetic and environmental influences on emotion regulation: A twin study of cognitive reappraisal and expressive suppression. *Emotion*, 17(5), 772–777. https://dx.doi.org/10.1037/emo0000300

Minagawa-Kawai, Y., Matsuoka, S., Dan, I., Naoi, N., Nakamura, K., & Kojima, S. (2009). Prefrontal activation associated with social attachment: Facial-emotion recognition in mothers and infants. *Cerebral Cortex*, 19(2), 284–292. https://doi.org/10.1093/cercor/bhn081

Mobbs, D., Yu, R., Meyer, M., Passamonti, L., Seymour, B., Calder, A. J., … Dalgleish, T. (2009). A Key Role for Similarity in Vicarious Reward. *Science*, 324(5929), 900–900. https://doi.org/10.1126/science.1170539

Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. *Proceedings of the National Academy of Sciences*, 103(42), 15623–15628. https://doi.org/10.1073/pnas.0604475103

Montag, C., Reuter, M., Newport, B., Elger, C., & Weber, B. (2008). The BDNF Val66Met polymorphism affects amygdala activity in response to emotional stimuli: Evidence from a genetic imaging study. *NeuroImage*, 42(4), 1554–1559. https://doi.org/10.1016/j.neuroimage.2008.06.008

Morelli, S. A., Knutson, B., & Zaki, J. (2018). Neural sensitivity to personal and vicarious reward differentially relates to prosociality and well-being. *Social Cognitive and Affective Neuroscience*, (July 2018). https://doi.org/10.1093/scan/nsy056

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, 383(6603), 812–815. https://doi.org/10.1038/383812a0

Morrison, I. (2016). ALE meta-analysis reveals dissociable networks for affective and discriminative aspects of touch. *Human Brain Mapping*, 37(4), 1308–1320. https://doi.org/10.1002/hbm.23103

Morrison, I., Bjornsdotter, M., & Olausson, H. (2011). Vicarious Responses to Social Touch in Posterior Insular Cortex Are Tuned to Pleasant Caressing Speeds. *Journal of Neuroscience*, 31(26), 9554–9562. https://doi.org/10.1523/JNEUROSCI.0397-11.2011

Morrison, I., Löken, L. S., Minde, J., Wessberg, J., Perini, I., Nennesmo, I., & Olausson, H. (2011). Reduced C-afferent fibre density affects perceived pleasantness and empathy for touch. *Brain*, 134(4), 1116–1126. https://doi.org/10.1093/brain/awr011

Morrison, I., Löken, L. S., & Olausson, H. (2010). The skin as a social organ. *Experimental Brain Research*, 204(3), 305–314. https://doi.org/10.1007/s00221-009-2007-y

Musser, E. D., Kaiser-Laurent, H., & Ablow, J. C. (2012). The neural correlates of maternal sensitivity: An fMRI study. *Developmental Cognitive Neuroscience*, 2(4), 428–436. https://doi.org/10.1016/j.dcn.2012.04.003

Nielsen. (2017). Time with tunes: how technology is driving music consumption. Retrieved from https://www.nielsen.com/us/en/insights/news/2017/time-with-tunes-how-technology-is-driving-music-consumption.html

Nitschke, J. B., Nelson, E. E., Rusch, B. D., Fox, A. S., Oakes, T. R., & Davidson, R. J. (2004). Orbitofrontal cortex tracks positive mood in mothers viewing pictures of their newborn infants. *NeuroImage*, 21(2), 583–592. https://doi.org/10.1016/j.neuroimage.2003.10.005

Noriuchi, M., Kikuchi, Y., & Senoo, A. (2008). The Functional Neuroanatomy of Maternal Love: Mother's Response to Infant's Attachment Behaviors. *Biological Psychiatry*, 63(4), 415–423. https://doi.org/10.1016/j.biopsych.2007.05.018

Ochsner, K. N., Bunge, S. A., Gross, J. J., & Gabrieli, J. D. E. (2002). Rethinking Feelings: An fMRI Study of the Cognitive Regulation of Emotion. *Journal of Cognitive Neuroscience*, 14(8), 1215–1229. https://doi.org/10.1162/089892902760807212

Parkinson, C., Kleinbaum, A. M., & Wheatley, T. (2017). Spontaneous neural encoding of social network position. *Nature Human Behaviour*, 1(5), 1–7. https://doi.org/10.1038/s41562-017-0072

Parkinson, C., Kleinbaum, A. M., & Wheatley, T. (2018). Similar neural responses predict friendship. *Nature Communications*, 9(1). https://doi.org/10.1038/s41467-017-02722-7

Parkinson, C., & Wheatley, T. (2014). Relating anatomical and social connectivity: White matter microstructure predicts emotional empathy. *Cerebral Cortex*, 24(3), 614–625. https://doi.org/10.1093/cercor/bhs347

Pereira, C. S., Teixeira, J., Figueiredo, P., Xavier, J., Castro, S. L., & Brattico, E. (2011). Music and Emotions in the Brain: Familiarity Matters. *PLoS ONE*, 6(11). https://doi.org/10.1371/journal.pone.0027241

Perini, I., Morrison, I., & Olausson, H. (2015). Seeking pleasant touch: neural correlates of behavioral preferences for skin stroking. *Frontiers in Behavioral Neuroscience*, 9(February), 1–9. https://doi.org/10.3389/fnbeh.2015.00008

Peysakhovich, A., Nowak, M. A., & Rand, D. G. (2014). Humans display a 'cooperative phenotype' that is domain general and temporally stable. *Nature Communications*, 5, 4939. https://doi.org/10.1038/ncomms5939

Preston, S. D. (2013). The origins of altruism in offspring care. *Psychological Bulletin*, 139(6), 1305–1341. https://doi.org/10.1037/a0031755

Quoidbach, J., Mikolajczak, M., & Gross, J. J. (2015). Positive interventions: An emotion regulation perspective. *Psychological Bulletin*, 141(3), 655–693. https://doi.org/10.1037/a0038648

Rabinowitch, T. C., Cross, I., & Burnard, P. (2013). Long-term musical group interaction has a positive influence on empathy in children. *Psychology of Music*, 41(4), 484–498. https://doi.org/10.1177/0305735612440609

Rand, D. G. (2016). Cooperation, Fast and Slow: Meta-Analytic Evidence for a Theory of Social Heuristics and Self-Interested Deliberation. *Psychological Science*, 27(9), 1192–1206. https://doi.org/10.1177/0956797616654455

Rand, D. G. (2018). Non-naïvety may reduce the effect of intuition manipulations. *Nature Human Behaviour*, 81(2017), 190560. https://doi.org/10.1038/s41562-018-0404-6

Rand, D. G., Greene, J. D., & Nowak, M. A. (2012). Spontaneous giving and calculated greed. *Nature*, 489(7416), 427–430. https://doi.org/10.1038/nature11467

Rauch, S. L., Whalen, P. J., Shin, L. M., McInerney, S. C., Macklin, M. L., Lasko, N. B., … Pitman, R. K. (2000). Exaggerated amygdala response to masked facial stimuli in posttraumatic stress disorder: a functional MRI study. *Biological Psychiatry*, 47(9), 769–776. https://doi.org/10.1016/S0006-3223(00)00828-3

Ray, R. D., McRae, K., Ochsner, K. N., & Gross, J. J. (2010). Cognitive reappraisal of negative affect: Converging evidence from EMG and self-report. *Emotion*, 10(4), 587–592. https://doi.org/10.1037/a0019015

Rilling, J. K., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S., & Kilts, C. D. (2002). A neural basis for social cooperation. *Neuron*, 35(2), 395–405. https://doi.org/10.1016/S0896-6273(02)00755-9

Rilling, J. K., & Young, L. J. (2014). The biology of mammalian parenting and its effect on offspring social development. *Science*, 345(6198), 771–776. https://doi.org/10.1126/science.1252723

Roemer, L., Williston, S. K., & Rollins, L. G. (2015). Mindfulness and emotion regulation. *Current Opinion in Psychology*, 3, 52–57. https://doi.org/10.1016/j.copsyc.2015.02.006

Roy, M., Shohamy, D., & Wager, T. D. (2012). Ventromedial prefrontal-subcortical systems and the generation of affective meaning. *Trends in Cognitive Sciences*, 16(3), 147–156. https://doi.org/10.1016/j.tics.2012.01.005

Sachs, M. E., Damasio, A., & Habibi, A. (2015). The pleasures of sad music: a systematic review. *Frontiers in Human Neuroscience*, 9(July), 1–12. https://doi.org/10.3389/fnhum.2015.00404

Sachs, M. E., Ellis, R. J., Schlaug, G., & Loui, P. (2016). Brain connectivity reflects human aesthetic responses to music. *Social Cognitive and Affective Neuroscience*, 11(6), 884–891. https://doi.org/10.1093/scan/nsw009

Sachs, M. E., Habibi, A., Damasio, A., & Kaplan, J. T. (2018). Decoding the neural signatures of emotions expressed through sound. *NeuroImage*, 174(March), 1–10. https://doi.org/10.1016/j.neuroimage.2018.02.058

Sailer, U., & Ackerley, R. (2018). Exposure shapes the perception of affective touch. *Developmental Cognitive Neuroscience*, (July). https://doi.org/10.1016/j.dcn.2017.07.008

Salimpoor, V. N., Benovoy, M., Longo, G., Cooperstock, J. R., & Zatorre, R. J. (2009). The rewarding aspects of music listening are related to degree of emotional arousal. *PLoS ONE*, 4(10). https://doi.org/10.1371/journal.pone.0007487

Salimpoor, V. N., Van Den Bosch, I., Kovacevic, N., McIntosh, A. R., Dagher, A., & Zatorre, R. J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science*, 340(6129), 216–219. https://doi.org/10.1126/science.1231059

Schlaug, G., Jancke, L., Huang, Y., & Steinmetz, H. (1995). In vivo evidence of structural brain asymmetry in musicians. *Science*, 267(5198), 699–701. https://doi.org/10.1126/science.7839149

Schneiderman, I., Kanat-Maymon, Y., Ebstein, R. P., & Feldman, R. (2014). Cumulative risk on the oxytocin receptor gene (OXTR) underpins empathic communication difficulties at the first stages of romantic love. *Social Cognitive and Affective Neuroscience*, 9(10), 1524–1529. https://doi.org/10.1093/scan/nst142

Schneiderman, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2012). Oxytocin during the initial stages of romantic attachment: Relations to couples' interactive reciprocity. *Psychoneuroendocrinology*, 37(8), 1277–1285. https://doi.org/10.1016/j.psyneuen.2011.12.021

Seifritz, E., Esposito, F., Neuhoff, J. G., Lüthi, A., Mustovic, H., Dammann, G., … Di Salle, F. (2003). Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents. *Biological Psychiatry*, 54(12), 1367–1375. https://doi.org/10.1016/S0006-3223(03)00697-8

Silvers, J. A., Shu, J., Hubbard, A. D., Weber, J., & Ochsner, K. N. (2015). Concurrent and lasting effects of emotion regulation on amygdala response in adolescence and young adulthood. *Developmental Science*, 18(5), 771–784. https://doi.org/10.1111/desc.12260

Singer, T., & Klimecki, O. M. (2014). Empathy and compassion. *Current Biology*, 24(18), R875–R878. https://doi.org/10.1016/j.cub.2014.06.054

Sloboda, J. A. (1991). Musical structure and emotional response: some empirical findings. *Psychology of Music*, 19, 110–120. https://doi.org/10.1177/0305735691192002

Slotnick, B. M. (1967). Disturbances of maternal behavior in the rat following lesions of the cingulate cortex. *Behaviour*, 29(2), 204–236. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/6073421

Slotnick, B. M., & Nigrosh, B. J. (1975). Maternal behavior of mice with cingulate cortical, amygdala, or septal lesions. *Journal of Comparative and Physiological Psychology*, 88(1), 118–127. https://doi.org/10.1037/h0076200

Small, D. M., Gregory, M. D., Mak, Y. E., Gitelman, D., Mesulam, M. M., & Parrish, T. (2003). Dissociation of neural representation of intensity and affective valuation in human gustation. *Neuron*, 39(4), 701–711. https://doi.org/10.1016/S0896-6273(03)00467-7

Stamm, J. S. (1955). The function of the median cerebral cortex in maternal behavior of rats. *Journal of Comparative and Physiological Psychology*, 48(4), 347–356. https://doi.org/10.1037/h0042977

Stillman, P. E., Van Bavel, J. J., & Cunningham, W. A. (2015). Valence Asymmetries in the Human Amygdala: Task Relevance Modulates Amygdala Responses to Positive More than Negative Affective Cues. *Journal of Cognitive Neuroscience*, 27(4), 842–851. https://doi.org/10.1162/jocn_a_00756

Strathearn, L., Li, J., Fonagy, P., & Montague, P. R. (2008). What's in a Smile? Maternal Brain Responses to Infant Facial Cues. *Pediatrics*, 122(1), 40–51. https://doi.org/10.1542/peds.2007-1566

Strauss, C., Lever Taylor, B., Gu, J., Kuyken, W., Baer, R., Jones, F., & Cavanagh, K. (2016). What is compassion and how can we measure it? A review of definitions and measures. *Clinical Psychology Review*, 47, 15–27. https://doi.org/10.1016/j.cpr.2016.05.004

Taylor, V. A., Grant, J., Daneault, V., Scavone, G., Breton, E., Roffe-Vidal, S., … Beauregard, M. (2011). Impact of mindfulness on the neural responses to emotional pictures in experienced and beginner meditators. *NeuroImage*, 57(4), 1524–1533. https://doi.org/10.1016/j.neuroimage.2011.06.001

Thomas, K. M., Drevets, W. C., Dahl, R. E., Ryan, N. D., Birmaher, B., Eccard, C. H., … Casey, B. J. (2001). Amygdala response to fearful faces in anxious and depressed children. *Archives of General Psychiatry*, 58(11), 1057–1063. https://doi.org/10.1001/archpsyc.58.11.1057

Tottenham, N., Hare, T. A., Millner, A., Gilhooly, T., Zevin, J. D., & Casey, B. J. (2011). Elevated amygdala response to faces following early deprivation. *Developmental Science*, 14(2), 190–204. https://doi.org/10.1111/j.1467-7687.2010.00971.x

Trost, W., Ethofer, T., Zentner, M., & Vuilleumier, P. (2012). Mapping aesthetic musical emotions in the brain. *Cerebral Cortex*, 22(12), 2769–2783. https://doi.org/10.1093/cercor/bhr353

Troy, A., Ford, B., McRae, K., Zarolia, P., & Mauss, I. B. (2017). Change the Things You Can: Emotion Regulation Is More Beneficial for People From Lower Than From Higher Socioeconomic Status. *Emotion*, 17(1), 141–154. https://doi.org/10.1037/emo0000210

Ulmer-Yaniv, A., Avitsur, R., Kanat-Maymon, Y., Schneiderman, I., Zagoory-Sharon, O., & Feldman, R. (2016). Affiliation, reward, and immune biomarkers coalesce to support social synchrony during periods of bond formation in humans. *Brain, Behavior, and Immunity*, 56, 130–139. https://doi.org/10.1016/j.bbi.2016.02.017

Urry, H. L. (2006). Amygdala and Ventromedial Prefrontal Cortex Are Inversely Coupled during Regulation of Negative Affect and Predict the Diurnal Pattern of Cortisol Secretion among Older Adults. *Journal of Neuroscience*, 26(16), 4415–4425. https://doi.org/10.1523/JNEUROSCI.3215-05.2006

Vacharkulksemsuk, T., & Fredrickson, B. L. (2012). Strangers in sync: Achieving embodied rapport through shared movements. *Journal of Experimental Social Psychology*, 48(1), 399–402. https://doi.org/10.1016/j.jesp.2011.07.015

van Harmelen, A. L., van Tol, M. J., Demenescu, L. R., van der Wee, N. J. A., Veltman, D. J., Aleman, A., … Elzinga, B. M. (2013). Enhanced amygdala reactivity to emotional faces in adults reporting childhood emotional maltreatment. *Social Cognitive and Affective Neuroscience*, 8(4), 362–369. https://doi.org/10.1093/scan/nss007

Varnum, M. E. W., Shi, Z., Chen, A., Qiu, J., & Han, S. (2014). When "Your" reward is the same as "My" reward: Self-construal priming shifts neural responses to own vs. friends' rewards. *NeuroImage*, 87, 164–169. https://doi.org/10.1016/j.neuroimage.2013.10.042

Viding, E., Sebastian, C. L., Dadds, M. R., Lockwood, P. L., Cecil, C. A., De Brito, S. A., & McCrory, E. J. (2012). Amygdala Response to Preattentive Masked Fear in Children With Conduct Problems: The Role of Callous-Unemotional Traits. *American Journal of Psychiatry*, 169(10), 1109–1116. https://doi.org/10.1176/appi.ajp.2012.12020191

Vinkers, C. H., Zorn, J. V, Cornelisse, S., Koot, S., Houtepen, L. C., Olivier, B., … Joëls, M. (2013). Time-dependent changes in altruistic punishment following stress. *Psychoneuroendocrinology*, 38(9), 1467–1475. https://doi.org/10.1016/j.psyneuen.2012.12.012

von Dawans, B., Fischbacher, U., Kirschbaum, C., Fehr, E., & Heinrichs, M. (2012). The Social Dimension of Stress Reactivity: Acute Stress Increases Prosocial Behavior in Humans. *Psychological Science*, 23(6), 651–660. https://doi.org/10.1177/0956797611431576

Voos, A. C., Pelphrey, K. A., & Kaiser, M. D. (2013). Autistic traits are associated with diminished neural response to affective touch. *Social Cognitive and Affective Neuroscience*, 8(4), 378–386. https://doi.org/10.1093/scan/nss009

Vrtička, P., Andersson, F., Grandjean, D., Sander, D., & Vuilleumier, P. (2008). Individual attachment style modulates human amygdala and striatum activation during social appraisal. *PLoS ONE*, 3(8). https://doi.org/10.1371/journal.pone.0002868

Warneken, F. (2015). Precocious prosociality: Why do young children help? *Child Development Perspectives*, 9(1), 1–6. https://doi.org/10.1111/cdep.12101

Waugh, C. E., Zarolia, P., Mauss, I. B., Lumian, D. S., Ford, B. Q., Davis, T. S., … McRae, K. (2016). Emotion regulation changes the duration of the BOLD response to emotional stimuli. *Social Cognitive and Affective Neuroscience*, 11(10), 1550–1559. https://doi.org/10.1093/scan/nsw067

Waytz, A., Zaki, J., & Mitchell, J. P. (2012). Response of dorsomedial prefrontal cortex predicts altruistic behavior. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience,* 32(22), 7646–7650. https://doi.org/10.1523/JNEUROSCI.6193-11.2012

Weng, H. Y., Fox, A. S., Shackman, A. J., Stodola, D. E., Caldwell, J. Z. K., Olson, M. C., … Davidson, R. J. (2013). Compassion training alters altruism and neural responses to suffering. *Psychological Science*, 24(7), 1171–1180. https://doi.org/10.1177/0956797612469537

Wheatley, T., Kang, O., Parkinson, C., & Looser, C. E. (2012). From Mind Perception to Mental Connection: Synchrony as a Mechanism for Social Understanding. *Social and Personality Psychology Compass*, 6(8), 589–606. https://doi.org/10.1111/j.1751-9004.2012.00450.x

Wheatley, T., & Sievers, B. (2016). Toward a Neuroscience of Social Resonance. In *Positive Neuroscience* (pp. 37–54). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199977925.003.0004

Wilsoncroft, W. E. (1963). Effects of Median Cortex Lesions on the Maternal Behavior of the Rat. *Psychological Reports*, 13(3), 835–838. https://doi.org/10.2466/pr0.1963.13.3.835

Zaki, J., López, G., & Mitchell, J. P. (2014). Activity in ventromedial prefrontal cortex co-varies with revealed social preferences: Evidence for person-invariant value. *Social Cognitive and Affective Neuroscience*, 9(4), 464–469. https://doi.org/10.1093/scan/nst005

Zaki, J., & Mitchell, J. P. (2011). Equitable decision making is associated with neural markers of intrinsic value. *Proceedings of the National Academy of Sciences*, 108(49), 19761–19766. https://doi.org/10.1073/pnas.1112324108

Zaki, J., & Ochsner, K. (2012). The neuroscience of empathy: Progress, pitfalls and promise. *Nature Neuroscience*, 15(5), 675–680. https://doi.org/10.1038/nn.3085

Zaki, J., Weber, J., Bolger, N., & Ochsner, K. (2009). The neural bases of empathic accuracy. *Proceedings of the National Academy of Sciences*, 106(27), 11382–11387. https://doi.org/10.1073/pnas.0902666106

Zamm, A., Schlaug, G., Eagleman, D. M., & Loui, P. (2013). Pathways to seeing music: Enhanced structural connectivity in colored-music synesthesia. *NeuroImage*, 74(617), 359–366. https://doi.org/10.1016/j.neuroimage.2013.02.024

Zatorre, R. J., Perry, D. W., Beckett, C. A., Westbury, C. F., & Evans, A. C. (1998). Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. *Proceedings of the National Academy of Sciences*, 95(6), 3172–3177. https://doi.org/10.1073/pnas.95.6.3172

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