Chapter 5.

NEUROSCIENCE OF HAPPINESS

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Introduction

The past decade has seen robust scientific attention to the neural bases of human emotion. While this research area lay dormant for many earlier decades,[1] the global scientific community has taken up questions related to both normal or typical emotion as well as pathological changes in emotion associated with psychopathology. For many years, emotion and reason were thought to be associated with separate brain systems – with emotion associated with subcortical structures and reason associated with the cerebral cortex. However, extensive developments in neuroimaging techniques over the past two decades have given us a much more nuanced understanding of the interactive interplay between cortical and subcortical zones in the circuitry of emotion and emotion regulation.

Progress in understanding the neural bases of emotion, and happiness more specifically, has been tremendously helped by the availability of imaging methods to interrogate both the function and structure of the human brain. These methods have contributed importantly to our understanding of the different constituents of happiness and well-being.

This review will emphasize recent developments in affective and social neuroscience that showcase four constituents of well-being: sustained positive emotion; recovery from negative emotion; pro-social behavior and generosity; and mind-wandering, mindfulness and "affective stickiness" or emotion-captured attention. The first two constituents have been studied within the framework of affective chronometry,[2] the time course of emotional responding. In several early publications we argued that the ability to recover quickly from adversity was a key constituent of well-being and can be measured objectively.[3] More recently, we have extended these studies by directly measuring the time course of brain activity in specific circuits underlying both negative[4] and positive[5] emotion. Moreover, some of these new findings suggest that these patterns of brain function are related not just to reports of emotion and life satisfaction, but also to systemic biological measures that are associated with physical health. These studies help to provide an understanding of the mechanisms connecting psychological well-being and physical health. The third constituent—pro-social behavior and generosity—has recently been shown to play a very important role in promoting well-being, and the neural bases of these social behaviors are now the subject of more intensive study. The fourth and final constituent we consider—mind wandering, mindfulness and affective stickiness—is also receiving more serious research attention, though it still remains understudied.

Nevertheless, this last constituent is particularly important since it underscores the difference between well-being, as measured by life evaluation, and happiness, as measured by emotional reports. An individual can potentially have high levels of subjective well-being and yet not be happy at every moment. For example, such a person might respond with intense sadness, upon learning of a tragic event involving loss. An individual with high levels of well-being could conceivably also feel and express anger in response to a moral transgression or in response to an individual who is perceived to be thwarting an important goal. If the individual recovers quickly and there is no lingering resentment—affective stickiness—then it is likely that high levels of well-being can persist even in the face of these seemingly inconsistent emotions. These considerations lead to two important conjectures. One is that from a neuroscientific perspective, there must be something different in the baseline patterns of brain function that distinguish those with high versus low levels of well-being, since well-being does not depend upon momentary or short-lived emotional states. And second, there is an important distinction between happiness (which can be momentary and short-lived) and well-being (most likely more enduring and related to life satisfaction). Whether happiness or well-being in the senses that are being used here differentially contribute to other aspects of mental and physical health will be considered in the following sections.

In the concluding section of this chapter, we consider the implications of the fact that the circuits that have been implicated in well-being all exhibit plasticity, the ability to grow and change.[6] Such plasticity occurs wittingly or unwittingly and most of the influences on our well-being that shape these circuits are unwitting. We are exposed to adversity and stressful life events that are often beyond our control. These contextual influences induce plastic changes in brain function and structure that clearly impact our well-being. However, plasticity in these circuits could also be harnessed for intentional cultivation and shaping. Engaging in specific forms of training to cultivate well-being through psychotherapy, meditation and other forms of mental training have been found to induce functional and structural changes in the brain and have also been found to benefit well-being.[7] Some of the most promising evidence of this sort will be reviewed in the concluding section of the chapter.

Positive Emotion

Often, well-being is defined in two different but related ways—hedonia (pleasure or momentary well-being) and eudaimonia (flourishing, living a meaningful life) first described by Aristotle.[8] There has been much work done exploring the neural correlates of hedonic well-being in animals by studying the brain response to reward.[9] These mechanisms are very similar across species and research across human and animal populations have informed each other. Further, hedonic and eudaimonic well-being are highly correlated in humans[10] and many of the brain mechanisms involved in the hedonic experience of sensory pleasure are also active in the more eudaimonic experience of altruistic and higher order pleasurable experiences.[11]

By combining state-of-the-art cellular recording, microinjection and nuanced behavioral measurements, Berridge and his colleagues[12] were able to isolate separate neural representations within ventral striatal circuitry—specifically within the nucleus accumbens and ventral pallidum—for wanting, liking and prediction components of the same reward. The ventral striatum is a region deep in the center of the brain that is associated with wanting, liking, and reward in a large number of species. We refer to it as subcortical, which means the structure is located below the cortex (which covers the surface of the brain). In humans, the region most activated by hedonic pleasure is the ventral prefrontal cortex (a region in the front of the brain directly above the eyeballs), but there is also activity in ventral striatum (the same region identified in rodents).

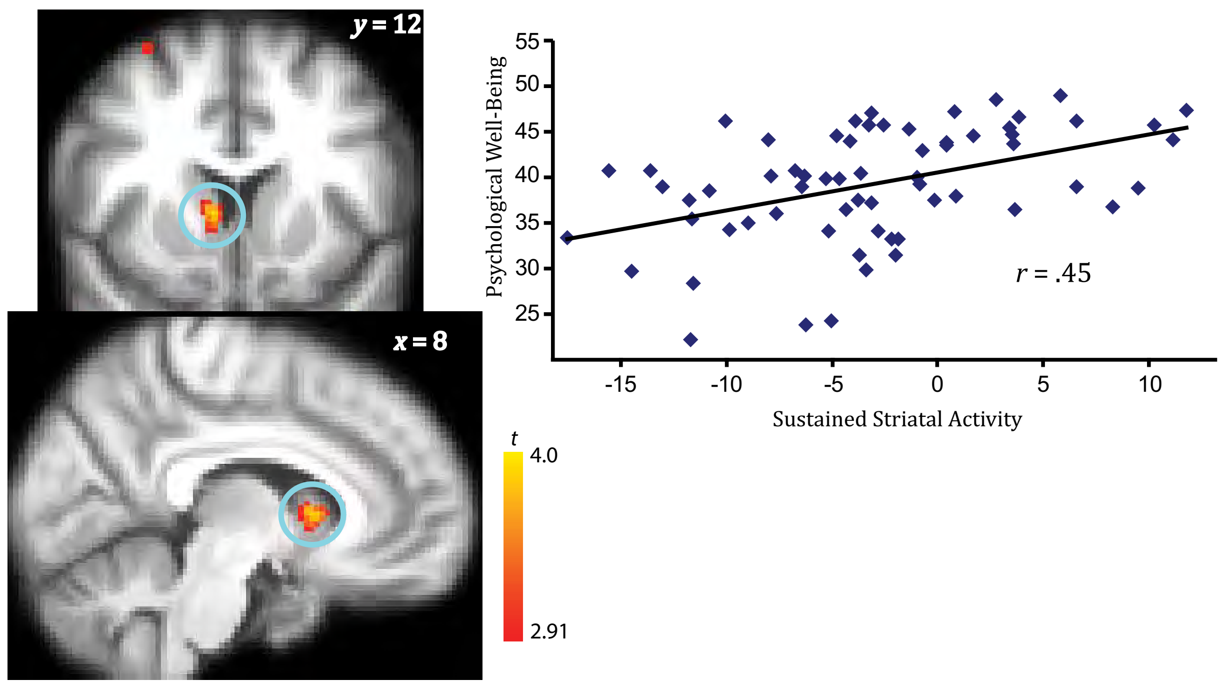
In a typical experiment designed to investigate circuitry activated during hedonic pleasure,[13] participants were presented with text that had been rated as highly positive (e.g., winning the lottery) and then asked to generate imagery related to this text for 12 seconds during which brain function was monitored with fMRI. When the positive imagery condition was contrasted with an unpleasant condition, greater activation for the former was found in the nucleus accumbens (within the ventral striatum) and a region of the ventromedial prefrontal cortex. Functional connectivity between the nucleus accumbens and amygdala (a brain region commonly activated by positive and negative emotional stimuli) and between the ventral prefrontal cortex and amygdala was significantly increased during the positive compared to negative imagery conditions. A similar pattern of prefrontal activation was observed in a study conducted in our laboratory[14] with mothers soon after the birth of their first child. While in the scanner, mothers were presented with pictures of their own infants, a stranger infant or an adult. We found greater ventrolateral prefrontal activation in response to pictures of their own infants. These pictures also elicited significantly greater positive affect and the magnitude of prefrontal activation predicted the intensity of positive mood ratings. Using positron emission tomography at rest to index baseline patterns of glucose metabolism (a measure of brain activation), Volkow found that individuals with increased activation in the ventromedial prefrontal cortex reported increased baseline levels of positive emotionality.[15]

The studies reviewed above all examined the regions of the brain activated by short-lived emotional stimuli. While some of the findings indicate that these short-term neural responses correlate with present moment measures of happiness, it is not clear if such short-term neural responses correlate with more enduring forms of well-being and life satisfaction or whether other patterns of neural activity better predict these more trait-like measures. Moreover, the studies reviewed above all focus on positive affect, yet some have suggested that enduring well-being is also associated with a more resilient response to adversity, operationalized by some as faster recovery following negative events.[16] In the sections that follow, we take up these different issues.

Savoring: The Neural Bases of Sustaining Positive Emotion

The first clue that the neural bases of sustaining happiness might be different from the short-term elicitation of positive emotion came from studies with depressed patients. We investigated whether depressed patients showed the typical pattern of activation in response to positive stimuli compared with controls. Using conventional analysis methods, we were unable to detect robust differences in activation in reward-related brain regions between clinically depressed patients and non-depressed controls.[17] However, when we examined the capacity to sustain activation in

Figure 5.1: *Psychological well-being is predicted by sustained activation of the ventral striatum across trials in response to positive pictures, p<.005, corrected for multiple comparisons. Modified from Heller et al. (2013).*

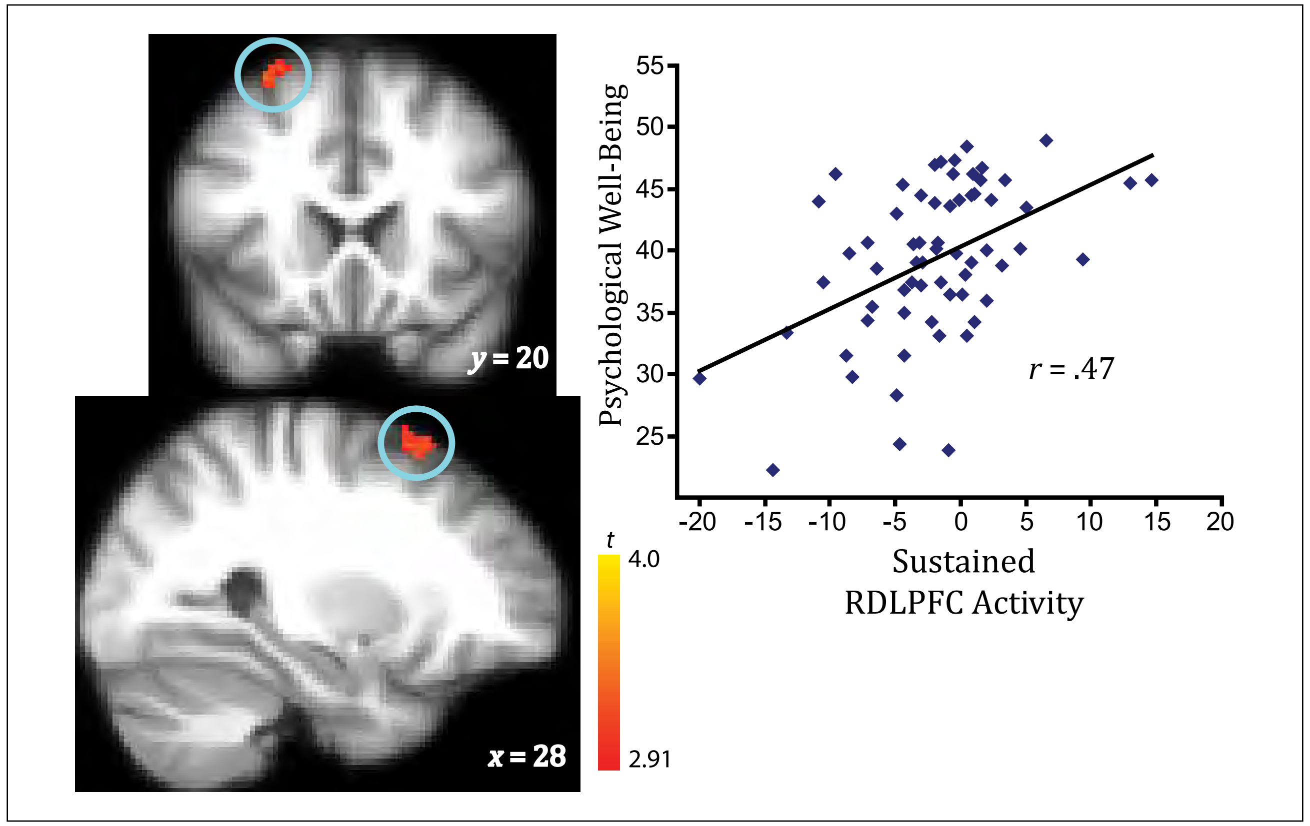


the nucleus accumbens over time (across trials in the experiment), robust differences between patients and controls became apparent. The depressed patients and the controls showed a very similar response during the early trials in the experiment, but as the experiment progressed, across trials of positive stimulus presentations, the controls sustained activation in the nucleus accumbens, while the depressed patients did not. The nucleus accumbens is a cluster of neurons in the ventral striatum that is commonly associated with positive affect and reward. Moreover, when connectivity between the accumbens and other brain regions was examined, it was connectivity between the accumbens and the middle frontal gyrus (a region that has been associated with regulation and goal-directed behavior) that showed sustained activation among the controls but dropped off with increased trials in the depressed patients. Finally we also demonstrated[18] that patients' reports of positive emotion were most strongly predicted by the metric that captured their sustained activation across trials over time, rather than the conventional measure of mean activation. This study provided the first strong experimental evidence that the neural correlates of savoring, the ability to maintain positive emotion over time, are associated with sustained activation in the ventral striatum and with sustained connectivity between regions of prefrontal cortex and the ventral striatum. Moreover, depressed patients differ from controls on these metrics.

In a direct follow-up to this initial study,[19] we examined whether sustained activation in the ventral striatum would change over the course of antidepressant treatment and whether an increase in the ability to sustain activity would specifically predict increases in reported positive affect. We found that when medication is taken, the greater the increase of sustained ventral striatum activation, the greater the rise in reports of positive affect among clinically depressed patients. These findings indicate that metrics of sustained activation in the ventral striatum can be used to index sustained happiness and are an important outcome measure for studies of antidepressant impact.

In a recent study involving a large community sample derived from the MIDUS study,[20] we experimentally examined relations between individual differences in sustained activation in the ventral striatum and psychological well-being.[21] We found that individuals with higher levels of sustained activation across trials in the ventral striatum in response to positive pictures reported higher levels of psychological well-being on Ryff's[22] composite measure of well-being (see Figure 5.1). In addition, we found a similar pattern in the dorsolateral prefrontal cortex, a region often involved in working memory and attention, but also active when a person is regulating his or her emotion (Figure 5.2). We also looked at the relationship between activity in these brain regions and an individual's cortisol output over the course of the day. Cortisol can be understood as a measure of a body's response to stress, with higher amounts over the course of the day indicating more stress signals being communicated in the body. We found that participants with greater sustained activation in both the ventral striatum and the dorsolateral prefrontal region had lower levels of cortisol output, which suggests less activation of the body's stress response (see Figure 5.3). These findings indicate that the initial clues we gleaned from studies with depressed patients generalize to healthy individuals, and indicate that sustained activation across time in response to positive incentives in the ventral striatum and dorsolateral prefrontal cortex predicts psychological well-being, a form of sustained happiness that may not depend directly upon external circumstances. Moreover, our findings indicate that these neural patterns predict not only reports of well-being but also peripheral biological measures (such as cortisol output) that may reflect both psychological and physical well-being.

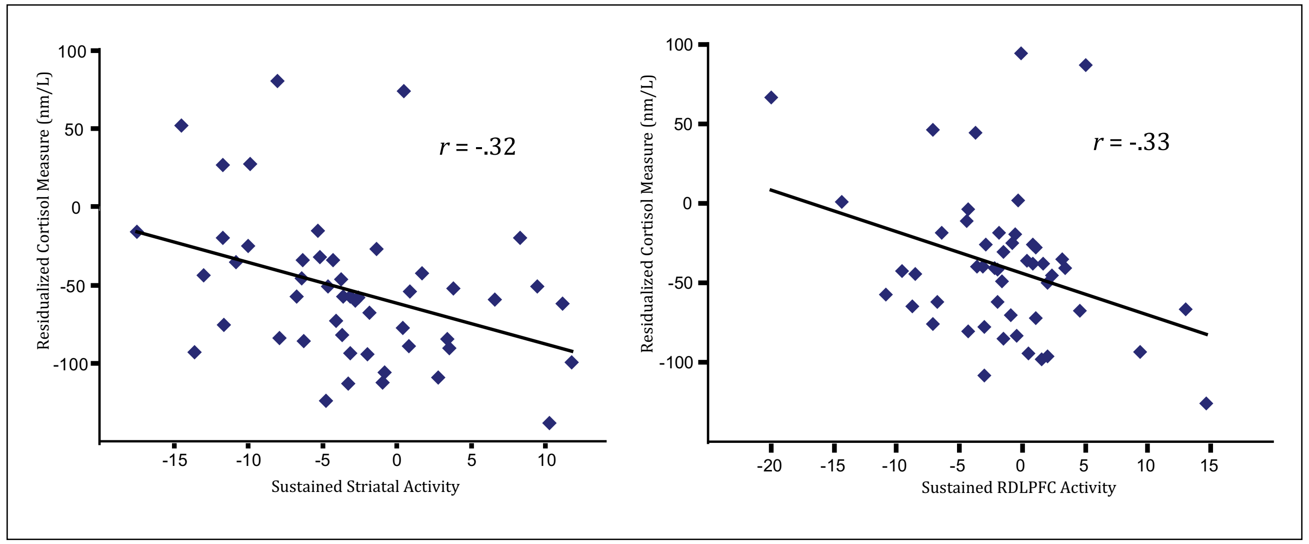
Figure 5.2: *Psychological well-being is predicted by sustained activation of the right dorsolateral prefrontal cortex (RDLPFC) across trials in response to positive pictures, p<.005, corrected for multiple comparisons. Modified from Heller et al. (2013).*



Our laboratory has developed methods to probe the duration of positive and negative affect using peripheral physiological measures.[23] Using measures of facial electromyography (fEMG), facial expression behavior that follows the offset of emotional stimuli can be used to probe the extent to which positive and negative affect persist beyond the eliciting stimulus. We would predict that short-lived responses to positive stimuli should be associated with lower levels of well-being and should be impacted by stressful life experiences. In a sample of 116 participants who were part of the MIDUS study,[24] we[25] found that individuals exposed to prolonged marital stress exhibited short-lived responses to positive stimuli. And the findings above indicate that individuals with short-lived responses to positive stimuli show lower levels of well-being compared with those who show more prolonged reactivity to such stimuli. These findings suggest that some of the key chronic obstacles to well-being such as marital stress may undermine well-being by specifically diminishing the capacity to sustain positive affect.

In a novel recent report, Telzer and colleagues[26] studied adolescents longitudinally over a two year age span. They assessed brain activity with fMRI in response to two separate tasks that putatively engaged hedonic and eudaimonic happiness respectively. They found that ventral striatal activation in response to the task that engaged eudaimonic happiness (a family donation task that involved personal loss in the service of overall family gain) predicted longitudinal

Figure 5.3: *Sustained activation in the ventral striatal and dorsolateral prefrontal cortex regions in response to positive pictures is associated with lower levels of overall total daily cortisol output. Modified from Heller et al. (2013).*



decrease in depressive symptoms while activation in this same region in response to a hedonic reward task did not. This suggests that the context in which ventral striatal activation is observed is significant and determines the network with which it associates. What is not known from this study is whether a more sensitive analytic method might have revealed differences in the pattern of activation (within the ventral striatum and related regions) between these conditions.

Both brain function and concepts of positive affect are complex and so it should not be surprising that there are interesting relationships between positive affect and other regions of the brain as well. Though they are not as straightforward as the findings within the ventral striatum, we discuss some of these thought-provoking findings in Annex 1.

Resilience and the Recovery from Adversity

The study of resilience is receiving increased neuroscientific attention.[27] Much of this work is being conducted at the rodent level and entails the study of experimental manipulations that have resilience-promoting effects, including variations of maternal care, early handling, and partially restricted foraging schedules. While there are many definitions of resilience, the maintenance of high levels of well-being in the face of adversity seems to be a common theme among the differing definitions. One key way in which high levels of well-being can be sustained in the face of adversity is through effective recovery from negative events. We have conceptualized recovery as a form of automatic emotion regulation.[28] It is automatic in the sense that it does not require explicit effortful control; rather, there are large individual differences in the naturally occurring rate at which we recover from negative events. Just as we described above in the case of savoring, the time course of recovery from negative events is the flip side of savoring. Measures of recovery from negative events can be obtained using peripheral psychophysiological measures[29] or can be assessed with direct measures of brain function[30] where the actual time course of responding in specific neural circuits can be assessed. In both cases, the key time window for measuring recovery is the period after a negative emotional stimulus ceases to be present. Prolonged or slow recovery would be reflected in greater signal in the period that follows the end of a negative emotional stimulus, reflecting a continuation of the emotional response when it ceases to be relevant. We suggest that a key constituent of well-being is fast recovery following a negative stimulus. Moreover, we have proposed that the time course of responding in the amygdala represents a central node through which peripheral signs of recovery are modulated. The rationale for considering the amygdala a central node for resilience is the extensive literature implicating this structure in fear and anxiety.[31] Faster recovery of the amygdala would therefore imply more adaptive coping with adversity, since the central and peripheral changes associated with fear and anxiety would be diminished more quickly if the amygdala exhibited a faster time course of decreased activation following exposure to a negative event.

To test these ideas, we recruited 120 middle-aged adults (mean age=48 years) and brought them into the laboratory for an imaging session during which an automatic emotion regulation paradigm was presented.[32] In this paradigm, positive, negative or neutral pictures were presented for four seconds, after which a neutral face was presented one or three seconds after the image, or not at all. Three days after the scanning session, participants rated the likeability of the faces they had seen, along with novel unfamiliar faces that acted as foils.

In response to the emotional pictures, the time course was divided into separate reactivity and recovery periods. We measured amygdala activity in the four seconds while the image was on the screen (reactivity) and in the four seconds after the image disappeared (recovery). We found that individual differences in neuroticism, one of the key attributes of trait negative affect and a personality variable that is inversely related to well-being,[33] was predicted by greater amygdala signal during the recovery period, but not during the reactivity period. This implies that a person's initial reaction to a negative event (either large or small) has little effect on that person's trait levels of neuroticism. The process that results in less neuroticism is how well the person recovers once the negative stimulus is no longer relevant. We also found that ratings of less likeability of the neutral faces were associated with greater amygdala signal during both the reactivity and recovery periods. These findings suggest that individual differences in amygdala recovery may play an important role in resilience and well-being, and argue for increased attention to this construct in future studies of well-being.

Is there more direct evidence that recovery following negative events is connected with well-being, and is there a particular component of well-being that may be more strongly associated with recovery than others? We studied these questions in a sample of 331 participants from the MIDUS study between the ages of 34-84 years.[34] Using an automatic emotion regulation task very similar to that described above for the imaging study, we examined emotion-modulated startle at different latencies during and following emotional picture presentation. After viewing emotional images, participants were sometimes subjected to a loud burst of sound, and the amount of startle in response to the sound was used as a measure of sustained emotional arousal. Evidence for better recovery following negative events would be reflected in greater startle diminution after negative pictures were removed from the participants' view. We used startle magnitude during the picture presentation as a measure of recovery that was unconfounded by reactivity. We found that participants with higher scores on the Purpose in Life subscale of well-being exhibited the most robust recovery following negative events. This finding holds with measures of reactivity statistically removed. The other subscales of the Ryff well-being measure to reach statistical significance were the Personal Growth and Self-Acceptance subscales. These findings suggest that better recovery from negative events may be an important constituent of well-being. They further raise the possibility that strategies that might promote the learning of more effective recovery might serve to increase well-being.

Russo et al.[35] review the growing literature in non-human animals (mostly rodents) that is focused on the mechanisms underlying resilience. For the purposes of these studies, resilience is operationalized as not succumbing to the deleterious effects of stress-inducing manipulations. In mice exposed to predators or chronic defeat stressors, those exhibiting a resilient behavioral profile showed higher levels of early gene expression in glutamatergic neurons in the medial prefrontal cortex (a region commonly involved in the regulation of emotion in humans). Activation in this brain region has been interpreted as a pro-resilience adaptation. Consistent with this interpretation, Covington et al.[36] showed that direct stimulation of neurons in this region promotes resilience to social defeat stress, underscoring the causal role of this brain region in the expression of resilience. In squirrel monkeys, Katz et al.[37] found that exposure to intermittent maternal separation (which has been found to promote resilience) increases cortical volume in the ventromedial prefrontal cortex, a pattern that is opposite to what is observed in depression. These and other related findings are consistent with human data in suggesting an important role for prefrontal regulatory regions in the promotion of resilience, and they further underscore the role of these circuits in well-being. These findings are also consistent with the evidence introduced in an earlier section of this chapter showing that individuals with sustained dorsolateral prefrontal activation in response to positive stimuli report higher levels of well-being.[38] The general view suggested here is that opportunities with moderate levels of adversity may facilitate the learning of emotional regulatory strategies that help promote better recovery and result in changes in prefrontal engagement.

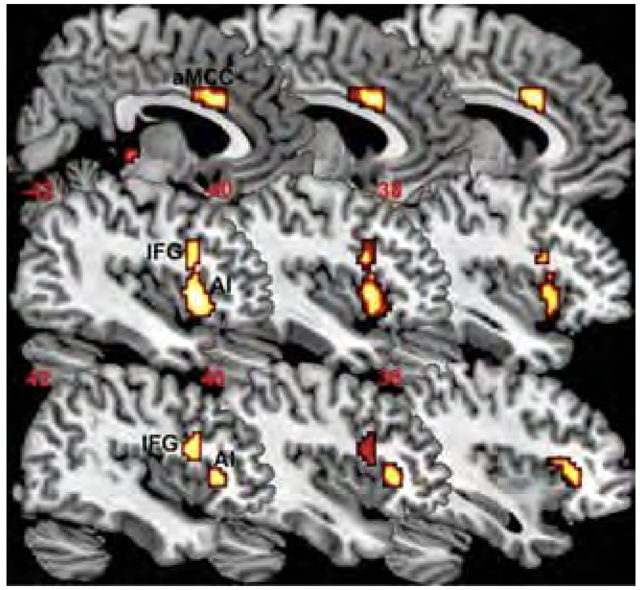
Empathy, Altruism, and Well-Being

One of the strongest predictors of well-being is the quality of an individual's social relationships.[39] In fact, when individuals are made to experience social isolation many of the same brain regions become active that are active in the experience of physical pain.[40] Behavior that increases social bonds (altruism and pro-social behavior) reliably increases well-being in children[41] and adults[42] and appears to be consistent across cultures.[43] In fact, individuals asked to recall a purchase they made for another person were happier immediately following the memory, and were subsequently more likely to spend money on another person. This type of behavior could result in a feedback loop, where pro-social behavior increases well-being, which then results in more pro-social behavior.[44] Pro-social behavior is even associated with better health[45] and longer life expectancy[46] and these improved health outcomes in turn can also contribute to greater well-being.

Neural Correlates of Empathy and Altruism

A vital precursor to the development of pro-social behavior is the activation of empathy, or the ability of an individual to recognize and share the emotions of others. The neuroscience of empathy is in its nascent stages, but one thing that is clear is that many of the brain regions involved in empathy are the same as those involved in experiencing our own emotions.[47] For example, when individuals watch other people being exposed to a painful stimulus, they show activation in the anterior insula (a region just behind the temples) and anterior medial

Figure 5.4: *The anterior insula (AI) and anterior/medial cingulate cortex (aMCC) are activated during the experience of pain and also to witnessing pain in another. The inferior frontal gyrus (IFG) is also identified. From top left to bottom right are slices from the center of the brain outward showing regions that respond to witnessing another in pain. (From Lamm et al. [2011]).*



cingulate cortex (an area of cortex just above the corpus callosum in the medial part of the brain). This overlaps with the activity shown when those individuals are exposed to pain themselves.[48] The anterior insula is not only active when witnessing the pain of another – it activates in response to a person's own positive and negative experiences. Similarly, increases activity when witnessing both positive and negative emotions of another, thus suggesting that it does not code valence but rather something that is common across different types of emotion. For example, Jabbi et al. found activation of the anterior insula when individuals witnessed others drinking both pleasant and unpleasant drinks.[49]

Activity in empathy-related regions is also affected by the degree of social connectedness between the observer and the individual experiencing pain. Hein et al. studied fans of two different sports teams and found that anterior insula activation was decreased in individuals observing the pain of a rival versus a fan of the same team.[50] The anterior insula is a region that is involved in the feeling of bodily sensation, so this suggests that individuals observing others in pain "feel" some level of that pain themselves, and the feeling is stronger if the individual receiving the pain is someone that the person feels more socially connected to. In Hein's study of sports fans, they further found that the more anterior insula activity an individual showed, the more likely they were to help the individuals in pain when given the opportunity.[51] In a study of African Americans and Caucasian Americans, Mathur et al.[52] found that both groups showed anterior insula and anterior cingulate cortex activity in response to witnessing both African Americans and Caucasian Americans in pain. However, African Americans additionally recruited the medial prefrontal cortex (a region generally implicated in self-related processing) when witnessing the suffering of other African Americans as opposed to Caucasian Americans. Further, the magnitude of medial prefrontal activity positively predicted the amount of money participants indicated later ~~that~~ that they would be willing to donate to help members of their in-group.[53]

One step beyond the experience of empathy (and more directly related to well-being) is the ability of an individual to engage in pro-social behavior. In a study of individuals deciding whether to donate money to charity, it was found that people showed activity in the same brain regions (ventral tegmental area and dorsal and ventral striatum) both when they donated money and when they received it.[54] In fact, in that study the ventral striatum was even more active when participants donated money than when they received it. Given the role of the ventral striatum in the experience of positive affect (discussed in a previous section), these data corroborate the adage that "it is better to give than to receive." Additionally, participants with greater magnitude of striatal activity also made a greater number of charitable donations than individuals with less striatal activity. This suggests that participants are more likely to engage in charitable donations if they find the activity more intrinsically rewarding.

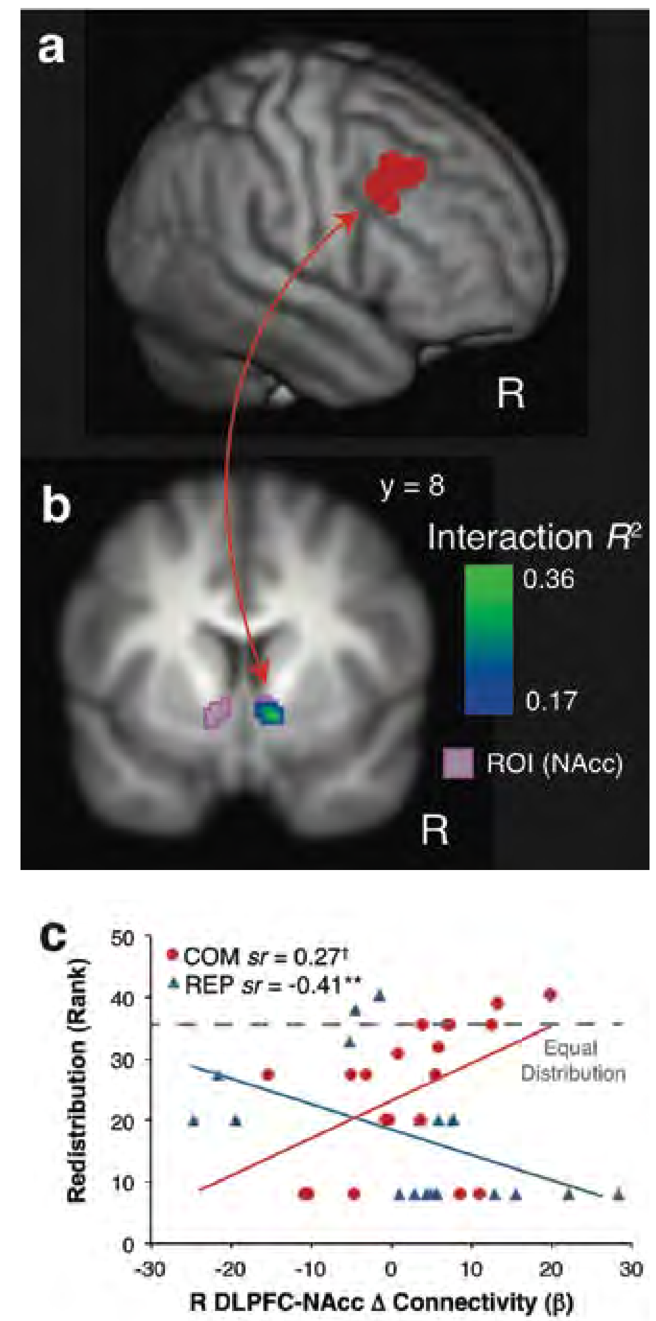
Another interesting avenue of research in this area is the study of the brains of extraordinarily altruistic individuals. Marsh et al. found just such a population when they recruited voluntary organ donors, specifically individuals who donated a kidney to a stranger. They deemed these individuals "extraordinary altruists," as kidney donation is a significant cost to the donor to benefit an anonymous stranger. They found that extraordinary altruists showed increased amygdala response to faces of people in fear, and greater amygdala volume on average than a group of control participants. Further, greater amygdala response in the whole sample predicted better recognition of fearful faces one to two hours later.[55] Given the role of the amygdala in emotional arousal, these results suggest a heightened sensitivity to the suffering of others in this group of extraordinary altruists, specifically others that are experiencing fear.

Neural Changes in Response to Compassion Training

The expression of empathy and compassion has been a mainstay of many contemplative traditions for millennia, and some traditions have even evolved extensive methods to train these qualities. We define empathy here as sharing the feelings of others, whereas compassion is a feeling of concern for another, along with a desire to improve his or her well-being. Recent years have seen a gain in momentum towards the study of mindfulness and concentration trainings. However, it is only recently that scientists have begun to study the efficacy of methods that specifically train compassion on an individual's well-being, and the well-being of those around them. Kemeny and colleagues enrolled female school teachers in a secular eight-week training with a focus on mindfulness, empathy, compassion, and recognition of emotions in oneself and others. They found that after the training, the women reported higher levels of positive emotion and lower levels of negative emotion compared to a wait-list control group. In addition to changes in their own emotions, they had an increased ability to recognize the emotions of others, a precursor for empathy and compassion.[56] In a study of a much shorter training, Leiberg et al.[57] studied the effects of just one day of compassion training compared to a day of memory training. They found that people trained in compassion reported increases in positive emotions, accompanied by greater helping behavior in a pro-social game.

Several studies provide insight into the brain mechanisms underlying these increases in the ability to recognize emotion and engage in helping behavior. Mascaro et al. investigated the effects of an eight-week cognitive-based compassion training versus a health discussion control group, and found that the compassion group was better able to recognize emotions after training. Further, the increases in recognition were predicted by activity in the ventral and dorsomedial prefrontal cortex.[58] Since these regions are involved in the regulation of emotion and goal-directed behavior, this activity might indicate the compassion training led to the development of greater motivation to recognize the emotions of others, and thus a more compassionate response. In our laboratory, Weng et al.[59] studied individuals who completed a two-week training in either compassion or cognitive reappraisal, and found that people engaged in more helping behavior after compassion training (versus reappraisal). We also studied the brain response to images of people suffering, before and after the trainings. We found that a greater increase in the connection between dorsolateral prefrontal cortex and nucleus accumbens predicted greater helping behavior in the compassion group, but less helping behavior in the reappraisal group (see Figure 5.5). These data suggest that the regulation of emotion by the dorsolateral prefrontal cortex serves different purposes in the two different groups. In the reappraisal group it might allow the individual to more effectively disengage from another's suffering, while in the compassion group it might allow the individual to manage their own emotional response in order to have more resources to direct towards helping.[60]

Figure 5.5: *Stronger increases in connectivity between right dorsolateral prefrontal cortex (R DLPFC, shown in red) and nucleus accumbens (NAcc, shown in green) predicts more helping behavior in people trained in compassion, but less helping behavior in people trained in reappraisal (from Weng et al. [2013]). Participants were ranked by how much they chose to distribute.*



In another study of the effects of compassion training on an individual's response to suffering, Klimecki et al. studied the effects of a one-day compassion training versus a one-day memory training on participants' response to short clips of strangers in distress. Before training, both groups showed increases in negative affect, accompanied by increases in anterior insula and anterior cingulate cortex, in response to the video clips. After the compassion training, participants watched another set of video clips of people in distress but this time reported a very different emotional response and exhibited a different neural signature. They reported greater positive affect (with respect to the memory training group) and showed activation in brain regions commonly associated with positive affect, namely the ventromedial prefrontal cortex, putamen, pallidum, ventral tegmental area.[61] These findings suggest that after compassion training, an individual witnessing another's suffering might buffer the debilitating effects of a negative empathic response with the generation of positive emotion to better allow the individual to respond with helping behavior.

A follow up on the previously mentioned study of a day of compassion training looked at the specific effects of empathy training versus compassion. Participants first watched videos of people suffering before any training, then after a day-long empathy training, and finally a third time after a day of compassion training. They found that the empathy training alone led to increases in insula and anterior middle cingulate cortex activity as well as to an increase in negative affect in response to viewing people in distress. However, after the completion of both empathy and compassion trainings the participants again showed increases in positive affect, decreases in negative affect, and increases in regions more commonly associated with positive emotion, including the ventromedial prefrontal cortex and ventral striatum.[62]

Mind Wandering, Mindfulness and Affective Stickiness

In a well-known study, Killingsworth & Gilbert[63] developed a smartphone app to sample the experience of more than 2,000 individuals (mean age=34 years) while they went about their daily activities in the world. They were interested in the frequency with which people reported their minds to be wandering (i.e., not focused on the activity in which they were predominantly engaged). At the same time, they also asked participants to rate the degree to which they were happy or unhappy at that moment. They found that on average, these participants reported their minds to be wandering 47% of the time. Moreover, when they reported their minds to be wandering, they also reported significantly more unhappiness than when they were focused on the activity at hand. In a very recent report, Wilson and colleagues[64] found that across 11 different studies, college student participants typically did not enjoy spending 6-15 minutes in a room by themselves with nothing to do. They preferred to engage in external activities much more, even ones that were mundane, and some even preferred to receive electric shocks than to sit alone. In light of the high prevalence of mind wandering and negative affect during "resting" conditions, the findings from Wilson et al.[65] clearly indicate that the typical college student finds his/her thoughts during an uninstructed condition to be unpleasant.

Neuroscientists have begun to discover specific characteristics of the brain's function at rest, when no formal task or instruction is given and the mind is allowed to wander. When functional MRI data is collected from participants at rest (not completing any task), a very reliable network of brain regions becomes active. Because these regions are active specifically in the absence of a task, we refer to them as the default mode network. Connectivity between regions in this network, in the absence of explicit instruction or a task, has been found to be related to various aspects of mind wandering.[66] For example, Mason et al.[67] found increased activity in several areas of the default mode (including the medial prefrontal cortex and the posterior cingulate) related to an increased frequency of mind wandering reports.

Mindfulness is a construct that is receiving serious attention in the scientific literature for the first time.[68] Mindfulness is often defined as paying attention, on purpose, non-judgmentally, and, when cultivated through training, is said to promote increased well-being.[69] Recent evidence suggests that mindfulness meditation training results in a decrease in the same regions of the default mode that are increased in activation during mind wandering.[70] These authors suggest that their findings "demonstrate differences in the default-mode network that are consistent with decreased mind-wandering."

Mindfulness is also said to be associated with decreased attachment, reflected in part by a decreased influence of wanting, which may at least in part underlie the association between mindfulness and well-being. Wanting, defined as an incentive to approach, can be irrationally inconsistent with cognitive goals and lead to decreases in well-being. This occurs in a striking way in addiction. Using a newly developed behavioral measure of mindfulness based on breath counting accuracy,[71] we recently examined the relation between individual differences in this behavioral measure of mindfulness and a behavioral measure of reward-related attention capture, a proxy for emotional distraction. We used a task based upon Anderson et al.[72] that assesses how much individuals are slowed by attending to a distractor formerly paired with reward, despite their cognitive goal of completing a visual search as quickly as possible. We found that participants with greater breath counting accuracy (i.e., higher levels of mindfulness) showed less attention capture by a previously rewarded stimulus, indicating decreased attachment to affect-relevant stimuli and less "stickiness"—involuntarily being attentionally pulled by irrelevant emotional distractors. Strengthening attentional skills through mindfulness or similar types of training may decrease stickiness and mind wandering and increase well-being by transforming default mode activity.

Summary

This review emphasizes four novel constituents of well-being and their underlying neural bases: 1. Sustained positive emotion; 2. Recovery from negative emotion; 3. Empathy, altruism and pro-social behavior; and 4. Mind-wandering, mindfulness and "affective stickiness" or emotion-captured attention. Well-being has been found to be elevated when individuals are better able to sustain positive emotion; recover more quickly from negative experiences; engage in empathic and altruistic acts; and express high levels of mindfulness. In each case, a growing body of evidence is pointing towards the importance of these four constituents to well-being. In some cases, effects are stronger for certain components of well-being, such as purpose in life, or positive relations with others. In other cases, the findings hold for measures of overall well-being. The neural circuits that underlie each of these four constituents are partially separable, though there is some overlap. The prefrontal cortex and ventral striatum are especially important in sustained positive emotion. Connectivity between the prefrontal cortex and amygdala is a key node through which effective recovery following negative events is mediated. The anterior insula and regions of the anterior cingulate cortex are implicated in empathic responding and the prefrontal cortex-ventral striatum are critical here in subserving altruistic behavior. Mind-wandering and mindfulness engage the default networks that can be detected at rest. Two key nodes of the default mode—the medial prefrontal cortex and the precuneus/posterior cingulate cortex—have both been implicated in mind-wandering. These regions exhibit decreased activation during the explicit voluntary cultivation of mindfulness, and increased levels of mindfulness are associated with decreased behavioral signs of stickiness.

Just how these four constituents may synergistically work together has not been studied, nor has their relative contributions to well-being been rigorously dissected. There are two overall lessons that can be taken from the neuroscientific evidence. The first is the identification of the four constituents we highlight, which are not commonly emphasized in well-being research. The second concerns the profound implications of the fact that the circuits we identify as underlying these four constituents of well-being all exhibit plasticity, and thus can be transformed through experience and training. Training programs are now being developed to cultivate mindfulness, kindness, generosity etc. As we reviewed above, data are available that indicate that some of these training regimes, even those as short as two weeks, can induce measurable changes in the brain. These findings highlight the view that happiness and well-being are best regarded as skills that can be enhanced through training.

1 See Davidson & Begley (2012).
2 Davidson et al. (2000).
3 See Davidson (2000) for review.
4 Schuyler et al. (2012).
5 E.g., Heller et al. (2014).
6 Davidson & McEwen (2012).
7 Ibid.
8 Aristotle (2004).
9 See e.g., Berridge & Kringelbach (2011) for review.
10 Diener et al. (2008).
11 Berridge & Kringelbach (2011), Kringelbach & Berridge (2009).
12 Smith et al. (2011).
13 Costa et al. (2010).
14 Nitschke et al. (2004).
15 Volkow et al. (2011).
16 E.g., Davidson (2004).
17 Heller et al. (2009).
18 Ibid.
19 Heller et al. (2013).
20 See http://www.midus.wisc.edu/
21 Heller et al. (2013).
22 Ryff & Keyes (1995), Ryff (1989).
23 See e.g., Jackson et al. (2003).
24 See http://www.midus.wisc.edu/
25 Lapate et al. (2014).
26 Telzer et al. (2014).
27 E.g., Russo et al. (2012).
28 Schuyler et al. (2012).
29 E.g., Jackson et al. (2003), Schaefer et al. (2013).
30 E.g., Schuyler et al. (2012).
31 E.g., LeDoux (2014).
32 Schuyler et al. (2012).
33 E.g., Wink & Staudinger (2014).
34 Schaefer et al. (2013).
35 Russo et al. (2012).
36 Covington et al. (2010).
37 Katz et al. (2009).
38 Heller et al. (2013).
39 Diener & Seligman (2002).
40 Eisenberger (2012).
41 Aknin et al. (2012).
42 Dunn et al. (2008), Hofmann et al. (2014).
43 Aknin et al. (2013).
44 Aknin et al. (2011).
45 Borgonovi (2008), Brown et al. (2005).
46 Brown et al. (2003).
47 Singer & Klimecki (2014).
48 Lamm et al. (2011); see Figure 4.
49 Jabbi et al. (2007).
50 Hein et al. (2010).
51 Ibid.
52 Mathur et al. (2010).
53 Ibid.
54 Moll et al. (2006).
55 Marsh et al. (2014).
56 Kemeny et al. (2012).
57 Leiberg et al. (2011).
58 Mascaro et al. (2013).
59 Weng et al. (2013).
60 Ibid.
61 Klimecki et al. (2012).
62 Klimecki et al. (2013).
63 Killingsworth & Gilbert (2010).
64 Wilson et al. (2014).
65 Ibid.
66 Callard et al. (2013), Mason et al. (2007) for review.
67 Mason et al. (2007).
68 See Davidson (2010).
69 Brown & Ryan (2003).
70 Brewer et al. (2011).
71 Levinson et al. (2012).
72 Anderson et al. (2011).

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