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Changes in Well-Being: Complementing a Psychosocial Approach with Neurobiological Insights

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Abstract The sustainability of changes in well-being achieved via positive interventions is challenged by findings that happiness levels are constrained by a homeostatic set-point. In this paper, we propose that while generally stable, the neurological and psychophysiological bases of well-being demonstrate plasticity. The neurobiological underpinnings of the hedonic component of well-being are first reviewed, demonstrating the value of both central (such as frontal asymmetry) and peripheral (such as heart rate variability) indices. Convergent evidence that certain well-being interventions are capable of modifying subjective, central and peripheral indices of positive affect or regulation of negative affect is then reported, although there is a clear need for longitudinal research to demonstrate the longevity of changes. It is recommended that a multi-level approach to evaluating positive interventions incorporating subjective psychosocial and neurobiological indices of affective change is adopted by researchers in an attempt to identify interventions most likely to achieve sustained positive outcome. Accumulating evidence through rigorous research that positive interventions can enhance psychosocial and neurophysiological factors can provide a compelling case for more widespread dissemination through public health policy.

Keywords Positive affect · Affective style · Emotion regulation · Psychophysiology · Neurological · Positive interventions · Set Point Theory · Positive psychology

1 Introduction

The assumption that subjective well-being is amenable to change underpins all efforts to promote better mental health and happiness. The long-term benefit of well-being

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interventions is however challenged by evidence that an individual's happiness and satisfaction levels tends to be fairly consistent and positively biased across the lifespan, regardless of major life events or efforts to modify them. This homeostatic-like stability has been argued to be evolutionarily adaptive and under the control of "dispositional, genetically pre-wired, neurological systems" (Cummins 2010, p. 4). Nonetheless, the scope to improve well-being remains. There is also evidence that certain interventions can impact even at the very fundamental neurophysiological substrates of well-being, which may result in more persistent improvements.

The aim in this paper is to critically evaluate the scientific and practical progress made towards promoting well-being and to identify more integrated and strategic methods for accelerating research insights and practical knowledge transfer. First, a brief overview of various well-being conceptualisations will be provided. This will be followed by a discussion about whether or not well-being is static and immune to intervention. Then a range of approaches and interventions for enhancing well-being will be evaluated to determine some of the most effective approaches and to explore other viable approaches less usually considered. The paper will conclude with some recommendations advocating a more multifaceted framework for evaluating and promoting well-being and will endorse inclusion of neurobiological approaches in this endeavour.

2 Defining Well-Being

Within the domain of positive psychology, well-being and happiness have commonly been referred to and operationalised as "subjective well-being". According to this perspective well-being involves a cognitive assessment of satisfaction with life and affective (positive and negative) judgements, and is experienced when the positive aspects considerably outweigh the negative aspects so that pleasure is maximised and pain is minimised (Diener 1994). Similarly, neurobiological paradigms focus on affective style and emotion regulation as indicative of well-being (Davidson 2003, 2004a, b). Defined in these ways, well-being is closely aligned with emotional factors and the concept of hedonia. While this is a valid association, adopting such a narrow scope can exclude important eudaimonic aspects (Delle Fave et al. 2011; Keyes 2002; Ryff 1989; Waterman 2008). Subsequently, more contemporary perspectives are emerging which emphasise the multidimensional nature of well-being by including additional factors such as psychological growth, positive relationships and life meaning to supplement the works on subjective well-being. Two examples of this more integrated and comprehensive approach to conceptualising well-being are the Orientations to Happiness (OTH) framework (Peterson et al. 2005; Seligman 2002) and the Complete State Model of Mental Health (Keyes 2005, 2007). The former model espoused pleasure, engagement and meaning pathways for happiness, and has recently been extended in Seligman's (2011) PERMA model to include relationships and accomplisment. The latter model articulates emotional, social and psychological factors as fundamental to sound mental health and flourishing. Recommendations to governments for measuring well-being via evaluations of life satisfaction, momentary mood and eudaimonia are also being espoused (Dolan and Metcalfe 2012).

3 Is 'Trait' Well-Being Pre-determined and Static or Can It be Enhanced?

While well-being states clearly fluctuate across the day, and in response to positive and negative life events, individuals are widely regarded to also exhibit a more general level of well-being that appears to endure despite changes in state well-being, much like a personality trait. Happiness Set Point Theory, also known as the Dynamic Equilibrium Theory, asserts that happiness levels remain stable over time despite changes in life circumstances, even major events (Headey 2006). The happiness set point is thought to operate similarly to other human homeostatic systems whereby the body endeavours to maintain a predetermined level of happiness irrespective of external factors. While happiness levels may alter temporarily after significant life events, they soon return to a physiologically determined set point. This adaptation is commonly referred to as the hedonic treadmill (Brickman and Campbell 1971) or "homeostatic control" (Cummins 2003). This stability has a genetic basis, with twin studies showing that genetic similarity accounts for at least half of the variance observed in well-being and emotionality (Tellegen et al. 1988; Nes et al. 2006; Roysamb et al. 2003).

While there is some evidence to support the stability of life satisfaction and happiness (Cummins 2003), this evidence is somewhat limited and overgeneralised. For example, a study by Brickman et al. (1978) found that the happiness of 22 major lottery winners and 29 paralysis accident victims was within the normal range shortly after their major life event. However, the sample size was small restricting the generalisability of the findings, and no baseline data on happiness were collected hence, the level of *change* in happiness for each participant could not be established. Instead, post-event happiness for these lottery winners and paralysis victims was compared with a control group of 22 participants who presumably did not collectively experience any significant positive or negative life events. Such a comparison does not consider within-subject variability, thus restricting the conclusions that can be drawn.

There are also pockets within the population, however, for whom well-being change is substantial. When well-being data from panel studies are examined, the variation in well-being across time for some individuals becomes more apparent. For example, using data from the German Socio-Economic Panel (SOEP), Headey (2006) examined 20 years of data from an initial sample of 12,541 respondents. Data were collected annually commencing from 1985. It was found that when the first 5 years of life satisfaction data were compared with the last 5 years of data (a sample size of 2,843), that 172 (5.5 %) of the respondents reported an increase of at least 20 % in their scores, while 357 respondents (11.4 %) reported a decrease of at least 20 %. These changes were considered "substantial" given standard deviations of around 1.5. Analysis of these longitudinal data, in conjunction with personality data, revealed correlations between life satisfaction and the personality factors of extraversion and neuroticism diminished over time. This suggests that despite the long term stability of these personality traits, they are not able to maintain equilibrium with regard to life satisfaction. Moreover, respondents who were more extraverted and open to experience displayed the greatest gains in long term life satisfaction whereas those who were more neurotic reported the greatest reductions in long term life satisfaction. These findings prompted Headey (2006) to recommend major revisions to the set point theory to accommodate the evidence of malleability in well-being for some people, especially those with particular personality profiles. Interestingly, Cummins (2012) also presents evidence that people with low baseline levels of well-being can exhibit significant changes in well-being, but argues that this simply reflects a return to their homeostatic set-point.

Diener et al. (2006) have also provided several revisions to the original hedonic treadmill theory. These revisions acknowledge individual differences in adaptation based on temperament. Life satisfaction has been most commonly used when exploring the notion of adaptation and a set point, however, the malleability of positive and negative emotions and of eudaimonic components of well-being is less well understood. Moreover, it is argued that an individual can have numerous set points, given the multifaceted nature of well-being, each of which be malleable to differing extents. Essentially these revisions underscore that well-being set points can change depending on circumstances, the individual and the type of well-being under investigation.

Consistent with the changing perspectives and evidence on set point theory is Lyubomirsky et al.'s (2005b) *Architecture of Sustainable Change* model. Although the model estimates that 50 % of the variance in happiness is attributable to genetics and 10 % to circumstantial factors such as socio-economic status, their model also acknowledges that 40 % of one's happiness depends on the extent to which an individual engages in intentional activities aimed at fostering well-being. Such activities can be cognitive (e.g., adopting an optimistic outlook), behavioural (e.g., physical activity), or volitional (e.g., using signature strengths to help others). More recent discourse and evidence, particularly among scholars within the field of positive psychology, points to views that initiatives to enhance well-being are worthwhile, provided the right factors are targeted. The *Architecture of Sustainable Change* model emphasises that if well-being is to be enhanced, then deliberate attention needs to be directed towards factors which are susceptible to change. Although a number of significant correlates of well-being have been consistently identified in the literature, such as genetics and personality, and to a lesser extent, socio-demographic factors including gender, age, income and education (see Diener et al. 1999), it is difficult to alter these circumstances. Subsequently, there has been great interest in whether well-being can be enhanced by factors which are under the volition of the individual such as lifestyle determinants, emotion regulation strategies and positive interventions.

4 Development and Evaluation of Positive Interventions

For some years now researchers have examined the effects of various strategies aimed at improving well-being. Noteworthy is Fordyce's (1977, 1983) work exploring a range of different happiness interventions in comparison to control conditions. Based on reviews of the happiness literature focusing on malleable methods rather than on personality and objective indicators of happiness, and on what worked best in Fordyce's (1977) previous research, Fordyce (1983) developed a "14 fundamentals for happiness program". Happiness strategies in this program included socialising more, focusing on the present, being organised and adopting an optimistic mindset. Participants in the happiness program reported increased happiness compared to control participants. According to Fordyce (1983), the program fostered "the development of new behaviors and attitudes, changes in life-style, new insights and understandings, better copings with bad moods, enhancement of happy moods, to a better awareness of happiness itself" (p. 495). Fordyce's (1977, 1983) work provided some preliminary evidence that happiness could be improved using deliberate strategies.

In more recent years, particularly with the inception of "positive psychology", additional interventions have been developed and evaluated. For example, the *three good things* activity, whereby individuals write down three positive things that happened during their day and why they think these good things occurred, *the gratitude visit*, which involves writing and delivering a letter to thank someone who had been kind to them in the past, and *using signature strengths in a new way*, which involves identifying signature strengths and using one of these in a new and different way every day for a week, were found to decrease depression and increase happiness for 3 months (gratitude visit) or 6 months (three good things and strengths use) post-intervention (Seligman et al. 2005).

Similarly, Sheldon and Lyubomirsky (2006) found support for the *best possible self* activity which involves imagining yourself in the future, after everything has gone as well as it possibly could and imagining what this would be like. Numerous other well-being interventions focused on forgiveness (Reed and Enright 2006), kindness (Otake et al. 2006) and life coaching (Green et al. 2006) have also been undertaken with many showing favourable outcomes (e.g., increased hope, positive affect, satisfaction with life and decreased depression).

Sin and Lyubomirsky's (2009) meta-analysis summarises the efficacy of 51 different positive psychology interventions (PPIs; N = 4,266) including mindfulness (Bédard et al. 2003), positive writing (King 2001) and Well-Being Therapy (Fava et al. 1998). Essentially this meta-analysis found that PPIs are effective in increasing well-being and decreasing depression with effect sizes of .29 and .31, respectively. This demonstrates that although effects are not very strong and tend to be limited to short-term assessments, substantial progress is being made with the development of well-being interventions. As greater awareness is gained regarding individual difference factors, interaction effects and underlying mechanisms, more refined and robust positive psychology interventions can be developed. Of particular interest is the claim by Cummins (2012) that PPIs are only effective in shifting trait well-being for those who exhibit below average levels initially. According to this view, PPIs are simply facilitating a biological disposition to return to the individual's set-point.

The investigation of neurobiological mechanisms underlying various aspects of well-being may provide significant insight into the efficacy, or otherwise, of positive interventions. As with all subjective states, well-being rests on biological foundations. Importantly, the homeostatic 'set-point' hypothesized by Cummins (2003) has a biological basis, and therefore if significant changes occur at that level, we suggest that the set-point should be theoretically capable of undergoing a permanent shift. Such a fundamental shift can be likened to the persistent change that can occur in resting heart rate following a sustained physical exercise regime, and is not unusual in physiological systems. Attempts to modify well-being would therefore be well-informed by a consideration of biological mechanisms supporting this subjective state. The success or otherwise of positive psychology or lifestyle interventions will ultimately depend on the plasticity of these systems; if the neurobiological substrates underlying well-being are not malleable, then attempts to modify them may be futile. In contrast, an understanding of the mechanisms underlying well-being will help identify those interventions which have a significant impact on these substrates, and consequently interventions that may have greater longevity over time. In the following sections, some of the key neurobiological mechanisms associated with well-being will be described. The neurobiological profiles of affective styles and emotion regulation processes will be reviewed, and the stability of these mechanisms will be examined to shed light on the malleability of these substrates. Such findings provide insight into the neuroplasticity of well-being, but also raise the possibility that interventions might be able to target malleable substrates to deliver more powerful outcomes.

5 Stable Neurobiological Patterns Underlying Well-Being

The majority of research into the neurobiological bases of well-being has explored subjective well-being or hedonic constructs, such as affective style, core affect, regulation of positive and negative affective states, and pleasure and reward, all of which shape global well-being. Affective style is a relatively stable disposition which refers to an individual's general emotional reactivity and regulation (Davidson 2004a, b). Affective disposition (or 'homeostatically protected mood') is also one of the key components determining the 'set-point' in Cummins' homeostatic model of well-being (Cummins 2012; Cummins et al. 2003). Individuals with a positive affective style show a tendency to approach and respond to positive stimuli with positive emotions, and to recover from negative events more quickly than do individuals with a negative affective style. Emotion regulation is one of the core means of optimising well-being; for instance, positive affect can be maintained by savouring positive emotions (Bryant and Veroff 2007), while negative affect can be reduced by suppression or reappraisal (Gross 2008; Quoidbach et al. 2010).

Biologically, regulation of emotions is a means of being flexible in the face of environmental demands (Thompson 1994). Perceived dangers trigger basic emotions, such as fear and anger, which initiate a protective survival response (withdrawal or approach, respectively) (Davidson et al. 1990; Davidson 1993). Physiologically, this translates to activation of the 'fight-flight' response, driven by sympathetic nervous system activity. While this 'default mode' optimizes survival from an evolutionary perspective, it is also costly in terms of energy use (Thayer and Lane 2009) and can be detrimental to well-being. Many situations involving novelty or change will also trigger this response, despite no real risk to the individual (Davidson et al. 2000). The capacity to down-regulate the full emotional response to such stimuli is thus beneficial, enabling greater flexibility in the behavioural repertoire of responses to the environment. In contrast, there is also the potential to amplify emotional responses that serve important functions. For example, life experiences which trigger positive responses can be savoured in the present or stored as a source of coping for use in challenging times or as a means to reignite and appreciate the positive experience in the future. Also of note is that some regulation strategies are likely to be more adaptive than others. For example, cognitive reappraisal strategies tend to be positively associated with well-being, while suppression of emotional expression has been negatively associated with well-being (Gross and John 2003; Haga et al. 2009).

5.1 Central Measures of Well-Being

A network of brain regions has been implicated in affective style and emotion regulation, consisting of prefrontal cortex (including dorsolateral, ventrolateral and ventromedial prefrontal cortex, and orbitofrontal cortex), insula and anterior cingulate cortex (ACC). These distributed regions have strong connections with subcortical regions, consisting of the limbic system (including the amygdala and hippocampus), basal ganglia (including the nucleus accumbens), thalamus and reticular activating system (Davidson et al. 2000, 2003; see also Fig. 1). They also overlap with the cortical circuitry underlying the subjective experience of pleasure, which includes the orbitofrontal cortex, the ACC and the insula (Kringelbach and Berridge 2009), as well as key pathways such as the median forebrain bundle (Hernandez et al. 2006).

One of the most consistently reported neurobiological profiles associated with well-being is an asymmetry in prefrontal cortex (PFC) activity. Initially, stroke patients with damage to their left PFC were observed to be more likely to experience extreme anxiety and depression than comparable right lesion patients (e.g., Robinson and Sztela 1981; Starkstein et al. 1987). This phenomenon, known as a 'catastrophising' effect, implied that the experience of positive affect may depend on a module located in the left PFC. Similarly, an 'indifference reaction' was observed more often in patients with right PFC lesions, which implied a right hemisphere based PFC module for negative affect. A similar

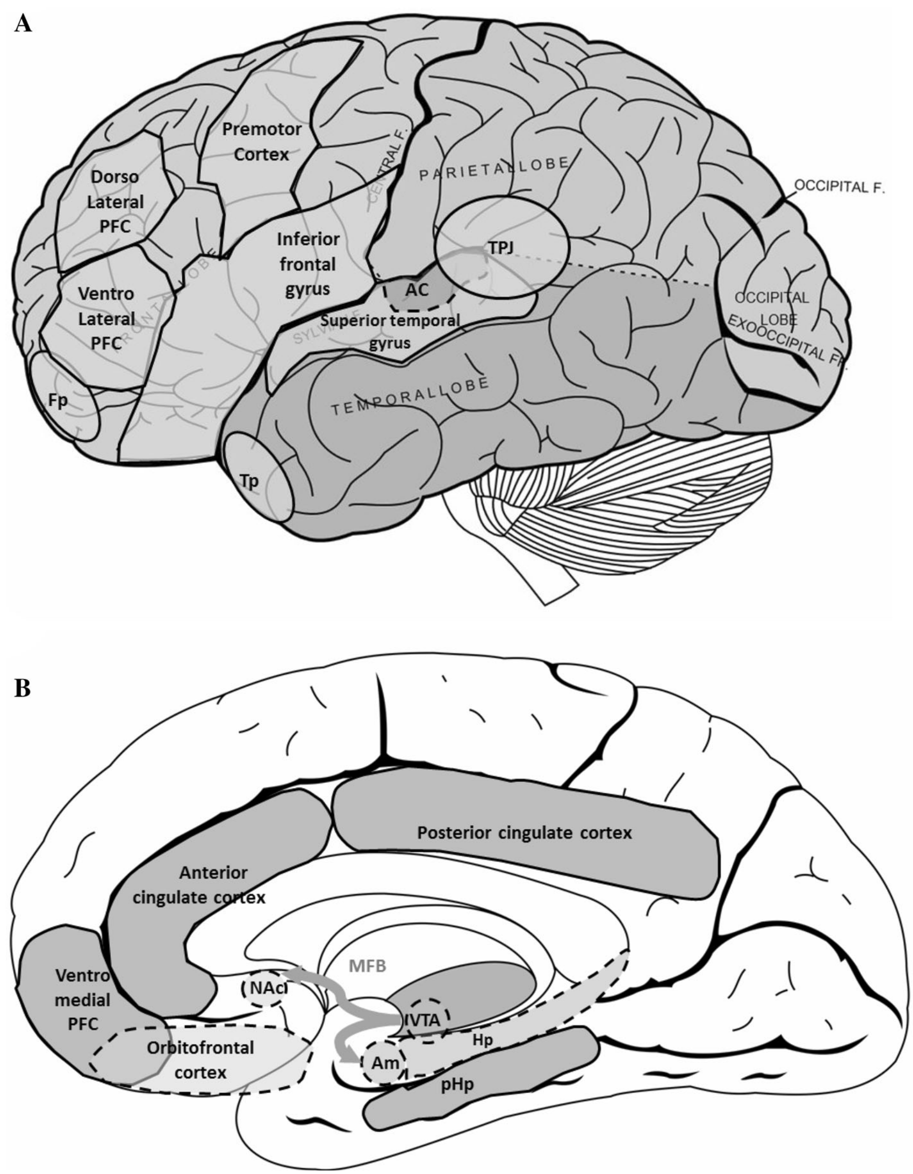

Fig. 1 Central regions implicated in well-being from **a** lateral view; **b** medial view. *NAc* nucleus accumbens, *Am* amygdala, *Hp* hippocampus, *pHp* parahippocampal gyrus, *Fp* frontal pole, *AC* primary auditory cortex, *VTA* ventral tegmental area, *MFB* median forebrain bundle, *TPJ* temporal parietal junction

asymmetry in emotional function is observed following temporary anesthetization of each hemisphere via sodium amytal injections (Lee et al. 1990).

There is now a large corpus of research using electroencephalographic methods which supports an association between frontal asymmetry and positive affect and well-being. For instance, Tomarken et al. (1992) recorded brain activity from 90 undergraduate females over 3 weeks. They found that a left bias asymmetry was positively associated with a stable positive affective style, and inversely associated with negative affect. For participants whose asymmetry was stable over this period, a left bias asymmetry was also associated with a stronger emotional response to positive films, while a right bias asymmetry was also associated with a stronger emotional response to negative films (Wheeler et al. 1993). Individuals with higher baseline left prefrontal activity are also more effective at voluntary suppression of emotional responses to negative pictures (Jackson et al. 2000). Davidson et al. have similarly shown that a resilient affective style is associated with greater activity in the left PFC (Davidson et al. 2000; Davidson 2004a; Davidson and Irwin 1999). In contrast, individuals with greater right frontal activation show stronger reactivity to negative film clips than their left frontal counterparts. This association between frontal asymmetry and emotional responses has been observed in infants as young as 4 months of age (Fox 1994), and was predictive of approach or withdrawal behaviours 10 months later. More specifically, 4 year olds with increased left frontal activity were more likely to be sociable in group settings, while children with reduced left frontal activation were more likely to be inhibited (Fox et al. 1995).

It has been proposed that the left PFC is involved in approach-related, goal-directed planning of actions, while right PFC activation might relate to threat-related vigilance (Davidson et al. 1990, 2003; Davidson 2004b; Kinsbourne 1978). Importantly, Fox (1994) provides evidence that individual differences in trait affect may arise from either hyper- or hypo-activation of either hemisphere. The finding that people with left-sided prefrontal asymmetry report higher levels of positive affect and well-being (Davidson 2004a, b; Ochsner et al. 2002) could therefore result from greater activation of left frontal cortex or reduced activity in right frontal cortex. Several meta-analyses have confirmed that greater left PFC activation underlies positive affect or approach-related emotions (Murphy et al. 2003; Wager et al. 2003). For instance, Wager et al. (2003) found a trend towards greater left lateralization in the lateral frontal cortex (activation peak counts: 26 left, 14 right, $p < .01$) for approach-related emotions. Similarly, Murphy et al. (2003) found left lateralization for approach related emotions, but for whole brain rather than frontal regions (activation peak counts: 165 left, 134 right; $p < .05$). Interestingly, this asymmetry may be moderated by sex, with some evidence for stronger left-bias asymmetry in men than in women (Flores-Gutierrez et al. 2009; Wager et al. 2003). In sum, individuals who show a left bias in frontal asymmetry are likely to report higher scores on subjective well-being scales, show more positive affect generally and in response to positively valenced stimuli, and tend to be approach- rather than withdrawal-oriented than do people with a right bias(Coan and Allen 2004; Fox 1991; Harmon-Jones and Allen 1997; Jacobs and Snyder 1996; Sutton and Davidson 1997; Tomarken et al. 1992; Wheeler et al. 1993). Conversely, individuals with greater left frontal activation should exhibit resilience in response to aversive events or stimuli. Whether this relationship means that frontal asymmetry can be directly targeted to effect changes in positive affect is an exciting possibility, and is explored further in a later section in this review.

Frontal regions of the brain are also implicated in well-being through emotion regulation. In particular, there is evidence that frontal cortical regions such as the PFC and ACC are responsible for top-down regulation of activity in subcortical limbic structures, such as the amygdala (Davidson 2004a, b; Fox 1994; Gross 2008; LeDoux 1996; Ochsner and Gross 2004; Quirk et al. 2003). Greater activity in these regions results in inhibition of basic emotional responses, and predicts quicker recovery from aversive events (Davidson et al. 2000, Davidson 2004a, b). In support, people reporting higher well-being show greater activation of the ACC and reduced amygdala activation in response to negative images (van Reekum et al. 2007). Recent studies have also found that the dorsal ACC is larger (Giuliani et al. 2011) and several prefrontal regions are more active (Urry et al. 2009) in people who used an adaptive emotion regulation strategy (reappraisal). In contrast, amygdala activity increases in participants who are instructed to consciously maintain or prolong their (negative) emotional response to aversive pictures (Schaefer et al. 2002). Consistent with prefrontal asymmetry observations, individuals characterized by negative effect (e.g., depression) show asymmetry in amygdala activation with a right amygdala bias (Davidson et al. 2000).

5.2 Peripheral Measures of Well-Being

A positive affective style also involves cortical regulation of the body's homeostatic systems; the hypothalamic-pituitary axis, the sympathetic nervous system and the immune system. In their meta-analysis, Pressman and Cohen (2005) reported evidence for an association between trait positive affect and reduced release of stress hormones, such as cortisol, adrenaline and noradrenaline, and enhanced immune function. One of the targets of amygdala activation during aversive conditions is the hypothalamic pituitary axis, in which cortisol is released from the adrenal glands. Individuals with a positive affective style have been found to have lower basal cortisol levels than those with a negative affective style (Cohen et al. 2003; Davidson et al. 2000; Davidson 2004a, b; Polk et al. 2005; but see also Ryff et al. 2004). Similarly, individuals who are poor at regulating their emotions (in response to aversive images, despite training in suppression or reappraisal of their emotional response) exhibited abnormally high cortisol levels in the evening (Urry et al. 2006). In contrast, release of cortisol and time taken for blood pressure to return to baseline levels following a stressor were found to be reduced in individuals with a positive affective style (Bostock et al. 2011). A range of factors thought to impact on emotion regulation (including personal control, self-soothing behaviour and social companionship) have also been associated with lowered cortisol release in children (see Stansbury and Gunnar 1994).

One of the functions of cortisol is to suppress the immune system, so it is not surprising that individuals with a negative affective style also show a suppressed immune response (Rosenkranz et al. 2003). In contrast, individuals with a positive affective style showed an enhanced immune response (Cohen et al. 2003; Davidson et al. 2000, Davidson 2004a, b; Diener and Chan 2011; Friedman et al. 2007; Lyubomirsky et al. 2005a). For instance, Cohen et al. (2003) exposed 334 volunteers to two rhinoviruses which produce the common cold, and assessed symptoms 5 days later. They found that participants reporting a more positive emotional style were dose-dependently less likely to develop disease symptoms than were participants with lower positive emotional style. Further, Kang et al. (1991) found suppressed immune function (natural NK cell activity) in women with strong right prefrontal asymmetry, suggesting the relationship between positive affective style and immune function is mediated by prefrontal asymmetry.

Emotion regulation is also reflected in cortical control of cardiovascular activity (Bernston et al. 2007; Thayer and Lane 2009). Heart rate variability (HRV) is the degree to which the intervals between heart pulses vary. This variability is the result of a balance between sympathetic (which increases the heart rate) and parasympathetic (which decreases the heart rate) nervous systems, and reflects the flexibility of the cardiovascular system to changing demands (Beauchaine 2001). A flexible autonomic nervous system is thought to be required for the appropriate expression and regulation of emotional responses (Thayer and Lane 2009), and HRV provides a simple, direct measure of this capacity.

Individuals with a low resting HRV are thought to have difficulty adapting to changes in the environment, and regulating their emotions (Beauchaine et al. 2007; Lane et al. 2009;

Thayer and Lane 2009). HRV is reduced in affective disorders, such as anxiety and depression (Friedman and Thayer 1998a, b; Kemp et al. 2010; Thayer et al. 2000; Thayer and Lane 2000). HRV has also, however, been associated with affective style in non-clinical populations. For instance, Bleil et al. (2008) operationalized trait 'negative affect' as the variance shared across depressed, anxious and angry emotions. They assessed 653 individuals from a community sample and found that negative affect was inversely related to the high frequency component of HRV, which reflects parasympathetic control. In contrast, a higher resting HRV has been associated with greater emotional expressivity. Butler et al. (2006) assessed respiratory sinus arrhythmia (RSA), which equates with the high frequency band of the HRV when respiration rate is controlled (and thus indicative of parasympathetic regulation of the heart period) in a sample of women. They found that a high resting RSA was associated with greater emotional expressivity in discussing a distressing video (as measured by video recordings of both verbal and non-verbal expressions). Shook et al. (2007) demonstrated that individuals with a higher resting HRV showed a greater willingness to approach positive novel objects, and were less likely to attend extensively to negative objects, than people with a lower resting HRV.

Individuals with a higher resting HRV also demonstrated more effective emotion regulation of the eyeblink startle response (Melzig et al. 2009; Ruiz-Padial et al. 2003). The reflex eyeblink response to a loud noise is exaggerated under negative affective conditions, and reduced under positive affective conditions. Melzig et al. (2009) potentiated the eyeblink response by threatening participants with shock, and found that it returned to baseline more quickly following a loud noise in participants with high HRV than in participants with low HRV, implying that the latter were less able to regulate their anxiety. Ruiz-Padial et al. (2003) found that participants with low HRV showed greater startle magnitudes to both negative and neutral stimuli, which they interpret as reflecting poor prefrontal cortical control of the amygdala-mediated defence system. In support, Lane et al. (2001) found that HRV was associated with activity in the medial PFC, which suggests that HRV may also be an indirect index of PFC-governed emotion regulation.

5.3 Different Aspects of Well-Being

The debate regarding how hedonic and eudaimonic well-being should be conceptualized is ongoing (Biswas-Diener et al. 2009). The neurobiological literature can potentially provide insight into this ambiguity by exploring whether there are distinct neurobiological profiles for these constructs.

The majority of this work has isolated neural networks associated with hedonic well-being. For instance, a meta-analysis of imaging studies on emotion processing performed by Phan et al. (2002) found that over 70 % of studies which induced happiness reported activation in the basal ganglia. Importantly, the functional neuroanatomy of these hedonic hotspots is moderated by neurotransmitters, with endorphins strongly implicated in pleasure (or 'liking') (Smith and Berridge 2005; Stewart and Vezina 1988), while dopamine appears to be more involved in desire or 'wanting' (Berridge and Robinson 1998; Berridge and Kringelbach 2011; Wachtel et al. 2002). Cannabinoids have also been associated with pleasure, with this action likely to be mediated also by dopamine release in the mesolimbic reward regions of the brain (French et al. 1997; Lupica et al. 2004). A full profile of biochemical markers of well-being is yet to be established, although it is likely that they will yield differences in basal levels of transmitters implicated in pleasure, such as dopamine and beta-endorphins, as well as those involved in social bonding such as oxytocin and prolactin (Depue and Collins 1999; Panksepp 1998; Ryff and Singer 1998).

To date, there are considerably fewer studies which have attempted to isolate neural underpinnings of eudaimonic well-being. Ryff et al. (Friedman et al. 2007; Ryff et al. 2004, 2006) found a number of psychobiological indices were associated with eudaimonic well-being, measured by the Psychological Well-Being Scales (Ryff 1989), in a sample of older women. These included lower levels of basal cortisol, higher levels of noradrenaline and lower inflammation responses as measured by pro-inflammatory cytokines. More specifically, daily cortisol slopes were positively associated with personal growth and purpose in life in women 75 years and over who reported strong personal growth and purpose in life. In women 65 years and older, adrenaline levels were positively associated with positive relations and noradrenaline levels were positively associated with autonomy, while inflammatory markers (interleukin-6 and soluble interleukin 6 receptors) were negatively correlated with purpose in life. Urry et al. (2004) examined neural predictors of eudaimonic (also measured by Ryff's PWBS) and hedonic well-being, measured by the Satisfaction with Life Scale (Diener et al. 1985) and the PANAS (Watson et al. 1988). They found left frontal activity was correlated with both forms of well-being. When positive affect was controlled, psychological well-being (but not satisfaction with life) still accounted for some prediction in left frontal activity, implying that increased left frontal activation is also associated with eudaimonic well-being in a manner that extends beyond positive affect alone.

More broadly, neurobiological concomitants have been observed for a range of constructs associated with eudaimonic well-being, including transcendence, spirituality and mindfulness. Dispositionally mindful people, for example, have been found to exhibit more effective PFC functioning during emotional categorization tasks (Creswell et al. 2007). The dorsal ACC (which plays a key role in attention) is also thicker, and more active during meditation, in expert meditators than in non-meditators (Grant et al. 2010; Hölzel et al. 2007; see also Hölzel et al. 2011 for review). There have also been a number of brain regions (or 'God spots') implicated in spirituality, religiosity or transcendence, although these appear to be quite distributed (including the PFC, temporal and parietal lobe; Esel 2009; Kapogiannis et al. 2009; Persinger et al. 2010; Ramachandran et al. 1997). In one recent study, Newberg et al. (2010) found that long-term meditators exhibited increased activation in the frontal lobes, with some evidence of left bias asymmetry. Higher pleasures, such as transcendent states, aesthetic appreciation of music and arts, altruism, and social relationships, may also be represented in identifiable brain circuits. For instance, strong emotional experiences with music activate regions that are associated with reward and emotion, including the thalamus, insula, orbitofrontal cortex and ventral striatum, and reduce activation in the amygdala and ventromedial prefrontal cortex (Blood and Zatorre 2001). Further, Griffiths et al. (2004) found that left hemisphere lesions to the amygdala and insula resulted in selective loss of intensely positive experiences of music, suggesting that this higher pleasure may also be reflected in a left-bias asymmetry.

In sum, there is substantial evidence for particular neurobiological profiles on which well-being rests. People with a positive affective style, and who are able to regulate their emotions well, show superior prefrontal inhibition of limbic system regions responsible for generating basic emotions. They also show lower levels of circulating and reactive cortisol than people characterized by negative affect, and appear to be immunologically resilient. Flexibility in adapting to the environment in a positive way is also reflected in a more variable heart rate, indicative of an effective balance of the parasympathetic and sympathetic nervous systems. While the data suggest that hedonic and eudaimonic well-being share some neural substrates, the possibility of distinct but overlapping networks needs to be explored with more extensive mapping. In the next section, we explore whether these neurobiological substrates of well-being are trait-like, or whether evidence supports their modification by interventions.

6 Are Neurobiological Substrates of Well-Being Modifiable?

There are a number of convincing arguments supporting the malleability of neurobiological substrates of well-being. First, although there is a substantial genetic component to well-being (Nes et al. 2006; Roysamb et al. 2003; Tellegen et al. 1988; Lykken and Tellegen 1996), there is also considerable scope for environmental influence. Heritability of well-being is estimated to be variously 50 % (Lyubomirsky et al. 2005b), 72 % (Keyes 2010) or even 80 % (Lykken and Tellegen 1996). Regardless of the figure, at least 20 % of the variability appears to be independent of genetic or demographic factors. For instance, while Tellegen et al. found that 40 % of the variance in pleasant emotionality was accounted for by genetic similarity in twins, they also found that 20 % was accounted for by family environment. Similarly, while 48 % of the variance in well-being was inherited, 13 % was a result of family environment. Similarly, while there appears to be a heritable component of frontal asymmetry, this component is relatively small (e.g., between 27 and 32 %), indicating considerable flexibility (Anokhin et al. 2006; Smit et al. 2005).

Second, even the heritable component of well-being is subject to environmental interaction (see Nesse 2004). Lyubomirsky et al. (2005a, b) argue that "even a high heritability coefficient for a particular trait (such as happiness) does not rule out the possibility that the mean level of that trait for a specific population can be raised. Under the right conditions, perhaps everyone can potentially become happier." (p. 9). Genes code for proteins, which can direct the growth of neurons in particular brain regions, increase the receptor sensitivity to certain neurotransmitters or a range of other neurobiological events that may predispose an individual to certain traits. A number of transmitter receptor systems implicated in mood have been hypothesized to mediate the genetic contribution to well-being (Roysamb et al. 2003). For instance, a gene which codes for transport of the neurotransmitter serotonin is associated with a positive bias in attending to affective stimuli (Fox et al. 2009). This gene (5-HTT) is however subject to gene by environment interactions and therefore its expression shows considerable variability between individuals (see Caspi et al. 2010). The expression of heritable components of well-being (the well-being 'phenotype') is therefore also clearly influenced by lifestyle or volitional factors. Positive interventions could therefore theoretically provide the appropriate environmental conditions to enhance well-being, despite its strong genetic component.

Third, processes underlying well-being demonstrate both state and trait-like characteristics. Prefrontal asymmetry associated with affective style is reported to be quite reliable over time, and therefore trait-like (Davidson 2004a). However, it is not stable for all people. In particular, children's frontal asymmetry is not reliable over time (Davidson and Rickman 1999), supporting a developmental basis for this substrate. A developmental basis for emotion regulation has also been well established (Goldsmith et al. 1997, 2008). Such data imply that a propensity for well-being may be consolidated early, but does not necessarily imply it is resistant to modulation later in life. Frontal brain regions involved in emotion regulation and well-being are still undergoing development well after puberty (Keverne 2004), so the onset of interventions during childhood or adolescence may be particularly fruitful.

Neuroplasticity is well-established throughout the lifespan, and a range of enriching lifestyle activities have been found to enhance the connectivity or density of neural networks (e.g., Johansson 2006; Kempermann et al. 2002; Merzenich 2005, Rosenzweig and Bennett 1996; Scarmeas and Stern 2003). Substantial research also suggests that even stable asymmetries can be modified by experience. Coan and Allen (2004) found that variances in EEG asymmetry were equally attributable to trait and state effects (8 and 10 % respectively). Most notably, a shift in prefrontal asymmetry has been observed following a range of manipulations including presentation of affective stimuli (see Coan and Allen 2004 for review). Even a short period of massage or uplifting music exposure was found to significantly shift right frontal asymmetry in depressed adolescents immediately post-exposure (Jones and Field 1999). However, whether such shifts in frontal asymmetry persist beyond the treatment period is unclear as there are very few studies which have re-tested after a delay to determine longevity.

Finally, there is emerging evidence of changes to these substrates following interventions in theory-consistent directions (see Pressman and Cohen 2005, and Coan and Allen 2004, for reviews). This evidence is most clear in studies which have investigated emotion regulation, mindfulness and meditation.

Emotion regulation: One paradigm which has been effective for illustrating the effects of emotion regulation involves instructing participants to either ‘enhance’, ‘maintain’ or ‘suppress’ their emotional response to emotionally valenced images. Effective suppression or reappraisal of a response to negative images increases activation of left ventromedial PFC and dorsal ACC and reduces activation of the right amygdala (Ochsner et al. 2002, 2004; Ochsner and Gross 2005; Urry et al. 2006; Levesque et al. 2003; Goldin et al. 2008), as well as reducing the magnitude of the eyeblink startle response (Dillon and LaBar 2005; Jackson et al. 2000) and release of the stress hormone, ACTH (Abelson et al. 2005). Further, participants in the enhance condition were found by Jackson et al. (2000) to experience increased eyeblink startle responses. In contrast, suppression of emotional responses to positive stimuli (erotic pictures) resulted in activation of right prefrontal regions (Beauregard et al. 2001). Schaefer et al. (2002) asked participants to either maintain, regulate or be passive about their emotion response to negative pictures. Amygdala activity was greatest in the maintenance condition, although it is noted that suppression was also observed to increase amygdala activation in one study (Goldin et al. 2008).

HRV is also a sensitive marker of phasic changes in response to emotion regulation interventions. For example, Butler et al. (2006) instructed participants to either suppress (‘act as if feel nothing’), reappraise (‘look for the positive’) or respond normally to an aversive film about WWII bombings. They found that both emotion regulation groups exhibited significantly higher HRV in the high frequency band than did the control participants. In addition, Lane et al. (2008) demonstrated that increases in HRV associated with emotion regulation are also associated with activation in the ACC, a region implicated in emotion regulation (see also Matthews et al. 2004; O’Connor 1990).

Mindfulness/Meditation: Interventions aimed at increasing eudaimonic well-being also appear to increase left-sided frontal asymmetry, possibly by promoting emotion regulation. Davidson et al. (2003) randomly assigned participants to either an 8 week mindfulness meditation training program or a wait-list. Significant increases in left-sided anterior brain activation and immunoprotection (influenza antibody titres) were observed from baseline to post-intervention for the meditation group. Importantly, both the asymmetry and immunoprotection index were maintained when tested 4 months after the mindfulness meditation intervention. A focussed attention meditation condition yielded increased activation in the dorsolateral PFC, an effect which was stronger in practitioners than novices (Brefczynski-Lewis et al. 2008). In addition to emotion regulation, mindfulness also promotes attention regulation. Consistent with the role of the ACC in attention, 5 days of mediation results in increased activation of the rostral ACC (Tang et al. 2009). ACC white matter was also increased after 11 h of meditative training (Tang et al. 2010).

In sum, the neurobiological circuits underlying well-being appear to exhibit considerable plasticity, even in adulthood. Interventions targeted at increasing positive affect on the whole are capable of shifting frontal asymmetry to the left, mimicking the left bias present in trait positive affective style. A consistent caveat of this research however is the absence of longitudinal studies, and therefore the persistence of effects on both well-being and its neurobiological substrates remains to be determined. Nonetheless, one study to date (Davidson et al. 2003) has demonstrated that mindfulness meditation causes an increase in left frontal asymmetry and immune functioning for at least 4 months after the meditation intervention. Interestingly, two studies in which eudaimonic well-being was explored revealed a pattern of asymmetry that was more central than prefrontal (Davidson et al. 2003; Urry et al. 2004), which may suggest a broader neural circuitry extending beyond the prefrontal centre implicated in hedonic well-being. Peripheral markers of well-being, such as HRV, also appear to be influenced by interventions such as emotion regulation, which has exciting implications for physical health benefits. Overall, the findings indicate that the neural basis of well-being can be modified by interventions, which may provide useful foci for designing interventions which target these substrates. For instance, interventions which exploit left prefrontal activation, such as those which engage approach motivations, might be particularly effective (Urry et al. 2004).

7 Conclusion

Community and practitioner interest in cognitive and behavioural interventions which enhance well-being is expanding at a rapid rate (Seligman et al. 2005; Sin and Lyubomirsky 2009). It is therefore timely that empirical research on such interventions is also beginning to accelerate. Nonetheless, because of the multidisciplinary nature of well-being, this research has been fragmented. Positive psychological interventions have tended to be evaluated quite independently of research exploring the underlying mechanisms of well-being, and the efficacy of well-being interventions is typically conceptualized via subjective and psychosocial reports quite separately from their effects on central or peripheral physiology. Clearly there is an element of multidisciplinary interdependence and expertise which when fused promises to deliver a more effective and efficient approach to facilitating individual well-being.

By reviewing the literature on both stable and malleable physiological substrates of well-being, this paper highlights the importance of a neurobiological perspective to well-being intervention research. Interventions which influence emotion regulation and affective style can also influence the biological underpinnings of those processes. The importance of these findings for those in the field of health promotion is that the value or efficacy of interventions may be at least partly determined by whether they can stimulate measurable changes at this very fundamental level of well-being. The interventions that are most likely to yield a sustained increase in well-being over time may be those with effects that permeate down to the biological foundations of well-being, demonstrating a profound shift in affective disposition, and potentially, the hypothesized homeostatic 'set-point' of an individual's well-being. In contrast, interventions which appear to impact only on the phenomenology of well-being may be more difficult to sustain, and may be subject to the substantial forces of the hedonic treadmill. Subsequently, well-being scholars are encouraged to: (1) adopt a multi-level approach in their evaluations of positive psychology interventions, incorporating subjective psychosocial factors and neurobiological indices of affective change; (2) obtain assessments at multiple time-points in an effort to gauge the sustainability of well-being enhancement; and (3) aim to differentiate between various mechanisms responsible for improvements in well-being, by specifically targeting well-being processes, such as emotion regulation. Such endeavours should contribute to a significantly more systematic, integrated and collaborative approach to understanding and promoting well-being and will provide more substantial and compelling evidence necessary for influencing public health policy and creating more widespread health benefits.

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