



Review article

The neuroscience of positive emotions and affect: Implications for cultivating happiness and wellbeing

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ABSTRACT

This review paper provides an integrative account regarding neurophysiological correlates of positive emotions and affect that cumulatively contribute to the scaffolding for happiness and wellbeing in humans and other animals. This paper reviews the associations among neurotransmitters, hormones, brain networks, and cognitive functions in the context of positive emotions and affect. Consideration of lifespan developmental perspectives are incorporated, and we also examine the impact of healthy social relationships and environmental contexts on the modulation of positive emotions and affect. The neurophysiological processes that implement positive emotions are dynamic and modifiable, and meditative practices as well as flow states that change patterns of brain function and ultimately support wellbeing are also discussed. This review is part of "The Human Affectome Project" (<http://neuroqualia.org/background.php>), and in order to advance a primary aim of the Human Affectome Project, we also reviewed relevant linguistic dimensions and terminology that characterizes positive emotions and wellbeing. These linguistic dimensions are discussed within the context of the neuroscience literature with the overarching goal of generating novel recommendations for advancing neuroscience research on positive emotions and wellbeing.

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1. Introduction

In the present global context of active threats of climate change, pandemics, and growing economic disparities and inequities, mental health concerns are rising worldwide (Burns, 2015; Hayes et al., 2018; Ip and Cheung, 2020; Twenge and Joiner, 2020). Considering the backdrop of these imminent societal challenges, advancing scientific research that focuses on wellbeing and healthy emotional outcomes is crucial (Hanlon and Jordans, 2020; Holmes et al., 2020). The experience of positive emotions, feelings, and affect are fundamental building blocks for cultivating resilience, flourishing, vitality, happiness, and life satisfaction (Bryant, 2003; Cohn et al., 2009; Diener et al., 2009; Silton et al., 2020), which ultimately contribute to physical and emotional wellbeing. Advancing our knowledge regarding how the central and peripheral nervous systems implement positive emotions and feelings (e.g., contentment, happiness, joy, and excitement, etc.) is critical to informing the development and dissemination of evidence-based strategies and interventions that enhance the experience of healthy positive emotions and associated wellbeing outcomes. However, while there has been a considerable amount of research focused on the neural correlates of negative emotions, the neuroscience literature on positive emotions and wellbeing is nascent by comparison. The existing research on positive emotions has been developed in relatively siloed academic subfields, often without much crosstalk occurring across disparate research agendas (Villanueva et al., 2020). As such, in order to identify critical areas for future research, this interdisciplinary review paper, informed by a linguistic perspective, provides an integrative account regarding the neurophysiological correlates of positive emotions that cumulatively contribute to scaffolding wellbeing.

This review paper emerged as part of the Human Affectome Project (<http://neuroqualia.org/background.php>), which used a Task Force model guided by a linguistic framework and analysis (Siddharthan et al., 2018) to work toward developing a more unified neuroscientific account of emotions, particularly considering the heterogeneity of affective constructs that are used in the scientific literature (Gruber et al., 2019). As a collaborative effort, the Human Affectome papers included in this Special Issue examined the extent to which organizing and conceptualizing discrete emotions and feelings can help advance affective neuroscience research. A task team within the Human Affectome Project created a linguistic inventory of emotion-related words in the English language to study a range of emotions that are articulated in everyday language (Siddharthan et al., 2018). The linguistic word inventory was sorted by 77 experts in the field into eight primary categories of feelings, including a category titled, “General Wellbeing,” based on the meaning of constituent words that were sorted into this category. The General Wellbeing category was described as follows, “feelings that relate to whether or not someone is happy, content, or sad, and refer in a nonspecific way to how someone is feeling overall (e.g., great, good, okay, fine, bad, terrible, etc.).” The General Wellbeing category was further subdivided into valenced categories of “sadness” (Arias et al., 2020) and “happiness.” We reviewed the articulated positive emotion

words within the “happiness” category and identified 62 words (see Supplemental Materials) that were grouped into eight categories (Table 1). Our review paper incorporates constructs associated with “feelings,” “actions,” and “outcomes” related to positive emotions across time, development, and environments/contexts, and explores how individual differences (e.g., cognitive control functions and social relationships) bidirectionally influence positive emotions, in conjunction with processes, strategies, and interventions that modify positive emotions to cultivate pleasant affectivity and wellbeing outcomes (see Fig. 1 for a conceptual model that guided topics covered in this paper).

Although our word list was designated broadly as the “happiness subcategory” within the framework of the Human Affectome Project, our review paper is focused on the role of neurophysiological correlates associated with positive emotions in cultivating wellbeing outcomes, which is consistent with the perspective that wellbeing should likely be prioritized over happiness as a transcendent human life goal (Jayawickreme et al., 2012a; Jongbloed and Andres, 2015; Seligman, 2011). Additionally, focusing on happiness as an end-goal appears to represent a highly Westernized value of striving toward experiencing positive, high arousal emotions and feelings (Shiota et al., 2014, 2017; Tsai et al., 2006), which may narrow the dominant scientific aperture and limit inclusivity of other cultural perspectives. Further, Suardi et al. (2016) noted that in the scientific literature, “happiness” is often used interchangeably with other related constructs, including “wellbeing,” “flourishing,” and “life-satisfaction,” to name a few. While some neuroscience research has indeed studied the neural correlates of these broader psychological outcomes, much of the literature has focused on narrower positive emotion and affective constructs. In order to employ consistent nomenclature throughout this paper, we used the term “positive emotions” to encompass positively valenced emotion constructs that range on the orthogonal dimension of arousal (e.g., happy, joyful, content, enthusiastic, etc.). In turn, “positive or pleasant affect” refers to the momentary state of experiencing a positive emotion, and “positive or pleasant affectivity” refers to a trait-like disposition reflecting the tendency to experience positive emotions on a regular basis.

This paper begins with a brief historical overview of psychological constructs (hedonia and eudaimonia) in order to establish these as distinct but related constructs, and to explore their relations with positive emotions and wellbeing (Section 2: Positive Emotions, Happiness, and Wellbeing in Humans and Animals). Next, we review the associations among neurotransmitters, hormones, brain networks (Section 3; Neurophysiological Response Associated with Positive Emotions and Affect), and cognitive functions (Section 4; Cognitive Control Functions in the Context of Positive Emotions) in the context of positive emotions and affect. Consideration of lifespan developmental perspectives are incorporated (Section 5; Positive Emotions and Wellbeing Across the Human Lifespan), and we also examine the impact of social relationships (Section 6, Healthy Social Contexts Bolster Positive Affect), and environmental contexts (Section 7; Environmental Factors Facilitate Positive Emotions and Healthy Outcomes) on the modulation of positive emotions. We view neurophysiological processes that implement positive emotions as dynamic and modifiable, and we discuss how meditative practices as well as flow states change patterns of brain function and ultimately promote wellbeing outcomes (Section 8; Cultivating Wellbeing: Modulating Neurophysiological Correlates of Positive Emotions). As a primary aim of the Human Affectome Project, we also examined and contextualized relevant linguistic dimensions and terminology that characterize emotions and feelings related to positive wellbeing outcomes in order to generate novel recommendations for enhancing neuroscience research on positive emotions (Section 9; Harnessing Linguistics to Guide Future Research on Positive Emotions).

Table 1
Eight Categories of Word Senses.

Category	Example
Content	okay, content
Very content	great, grand
Happy	happy
Very happy (general)	elated, overjoyed
Happy (acting)	buoyant, merry
Happy (feeling)	glow
Happy (outcome)	glad
Improvement (change)	better, improved, lightened

Note. We reviewed the articulated (positive) emotions within this category that people use to convey happiness and identified 62 word senses (see Supplemental Materials) that we grouped into eight categories.

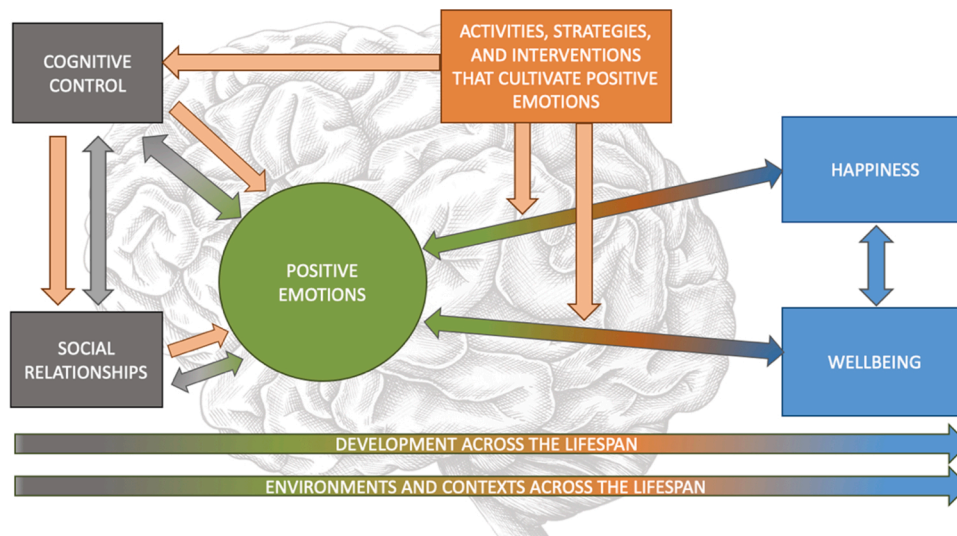


Fig. 1. A Conceptual Model of the Psychological Correlates of Positive Emotions that Influence Happiness and Wellbeing Outcomes.

Note: This is a graphical representation of the interrelated psychological constructs as well as the intervening processes, activities, and strategies that contribute to the scaffolding of pleasant affectivity and wellbeing. Cognitive control, social relationships (grey) represent key individual differences that are related to the experience of positive emotions and affect (green). These variables will be modulated in a dynamic manner throughout the lifespan by interacting developmental processes, environments, and contexts. Individual differences (grey) and positive emotions (green) can be measured using self-report (human research), behavior observations (human/animal research), and neurophysiological assessment (human/animal research). The psychological constructs in blue (happiness and wellbeing) represent outcome variables that reflect a combination of interacting constituent emotions, feelings, and behaviors, and they are not as well-suited for precise measurement with neuroscience methods, but may be correlated with variables yielded from neuroscientific research. Activities, interventions, and strategies are depicted in orange and reflect intentional behaviors and processes designed to positively influence happiness and wellbeing outcomes. There is an image of a human brain in the background to signify that the psychological constructs are implemented in the central nervous system, but cannot be reduced to constituent brain regions.

2. Positive emotions, happiness, and wellbeing in humans and animals

2.1. Psychological wellbeing constructs: *hedonia* and *eudaimonia*

Across cultures and eras, philosophical perspectives of happiness have offered diverse approaches in attempting to understand this psychological construct, many of which contribute to our present conceptions. Gautama Buddha (c.563/480 – c.483/400 BCE), the founder of Buddhism, believed that happiness is concerned with the good life, and starts from an understanding of the root cause of suffering. Living a good life involves avoiding extremes, specifically self-indulgence (*kāmasukhallikānuyoga*), and self-torture (*attakilamathānuyoga*), and instead following the ‘Middle Path’ of moderation (Hallisey, 1997). In Ancient Greece, Aristotle (384 – 322 BCE), following his predecessors Plato and Socrates, asserted that happiness resides in moral or ethical virtues, termed *eudaimonia* (Aristotle: *Nicomachean Ethics*, 2000). Such virtues include courage, justice, temperance, benevolence, and prudence. In order to be happy, one needed a good moral character to do the right thing even in difficult circumstances and to achieve virtue excellence. In contrast, while Epicurus (341 – 270 BCE) also viewed happiness as the ultimate purpose of human existence (Epicurus, 2020), its conception differed substantially from that of Aristotle. For Epicurus, happiness in its simplest terms is the pleasure that can be attained through the absence of physical pain and mental disturbances and via the pursuit of calmness and inner peace. As such, Epicurus’s philosophy, while hedonistic, does not emphasize the pursuit of high arousal pleasures. Instead, it recommends seeking the comfort of friendship and a simple life, highlights and values wisdom as well as the benefits of “sober reasoning, searching out the grounds of every choice and avoidance, and banishing those beliefs through which the greatest

tumults take possession of the soul” (Epicurus, 2020).

Also, contrasting the ‘Middle Path’ philosophy of Aristotle and Buddha, the British utilitarian Jeremy Bentham (1748–1832) held a more extreme *hedonistic* view, whereby happiness was defined as an experience of pleasure and a lack of pain (Bentham, 2007). Such pleasures included things as wealth, skill, friendship, a good reputation, power, piety, benevolence, memory, imagination, expectation, association, and relief (Bentham, 2007). In particular, Bentham conceived that each individual exhibited a natural self-interest, over social interest, towards their own wellbeing (Mill, 2008). Notably, these historical theories reflect Westernized patriarchal perspectives that have predominantly influenced current scientific thought and nomenclature. As discussed later in this review paper (see section 9), employing linguistic constructs from other languages will contribute to broadening the scope of neuroscientific research on positive emotions, which will, in turn, contribute to building a more inclusive science of wellbeing.

Related to these historical perspectives, three dominant paradigms of wellbeing presently exist in psychological research (Jayawickreme et al., 2012b): 1) *hedonia* (subjective wellbeing), 2) *eudaimonia* (psychological wellbeing), and 3) an integrative approach spanning *hedonia* and *eudaimonia*. In social psychology research, the literature on *hedonia* often covers the subjective evaluation of one’s quality of life (i.e., subjective wellbeing) and this area of research typically involves self-report measures of life satisfaction (Diener et al., 1999). *Eudaimonia* or psychological wellbeing refers to the extent that individuals are ‘doing well’ and uses terms related to improvement/change (Table 1) such as meaning, purpose, engagement, and flow (e.g., Ryff, 2017). Although closely related, hedonic and eudaimonic perspectives on wellbeing are perceived as distinct constructs (e.g., Di Fabio and Palazzeschi, 2015).

With regard to *hedonia*, based on a 30-year review of the hedonic literature, Diener et al., 1999 defined subjective wellbeing as consisting

of three primary components: *pleasant affect* such as joy, contentment, pride, affection, happiness, and elation, *unpleasant affect* including sadness, anxiety, stress, depression, guilt, and envy, and *life satisfaction* such as satisfaction with current, past and future life, and a desire to change. Our present review paper focuses predominantly on understanding how neuroscience approaches are used to advance knowledge about pleasant/positive affect and emotions (sections 3 – 5) as well as contexts, actions, and strategies (sections 6 – 8) that support healthy neuroplasticity associated with an increase or maintenance of positive emotions. Other theorists have since expanded on specific elements of the subjective wellbeing model, with an attempt to identify and measure positive psychological traits as ‘virtues’ including wisdom and knowledge, courage, humanity, justice, temperance, and transcendence (Peterson and Seligman, 2004). While these constructs all incorporate aspects of positive emotions, they remain beyond the scope of the present review paper.

Eudaimonia (or psychological wellbeing) defines wellbeing in terms of the development of human potential rather than anchored in positive psychological traits. As noted above, this perspective was originally derived from Aristotle’s philosophy of happiness and what it means to live a good life as articulated in *Nicomachean Ethics* (Broadie and Rowe, 2002). Consistent with the philosophical formulation of eudaimonia, psychological wellbeing refers to the conditions of optimal living and the effects of these conditions, whereas subjective wellbeing (i.e., hedonia) focuses on the experience of pleasure as a state that can be obtained through intrinsic goal-driven living or through extrinsic means such as living a life of greed, materialism, or exploitation (Ryan et al., 2008). Psychological and subjective wellbeing represent conceptually related, but empirically distinct streams of psychological functioning, although they may have overlapping features (Huta and Ryan, 2010). Some reported differences in research between eudaimonia and hedonia may be due to variability in operationalized definitions and/or measurement, or to other, cultural, cohort, and individual factors, and thus conceptualizing eudaimonia and hedonia as distinct orthogonal psychological constructs might be detrimental to advancing theory and research (Kashdan et al., 2008).

Integrating theoretical perspectives on subjective and psychological wellbeing, Gatt et al. (2014) have developed a composite scale of wellbeing called COMPAS-W (Composure, Own-worth, Mastery, Positivity, Achievement, Satisfaction). The COMPAS-W scale provides an overall measure of total wellbeing as well as specific subscales of subjective wellbeing and psychological wellbeing along a continuum that ranges from flourishing to languishing. Using this scale, Gatt et al. (2014) have shown that in a sample of 1486 healthy adult twins who were within the normal range on a measure of depression and anxiety (DASS-42), only 23 % could also be classified as ‘flourishing’ on the COMPAS-W wellbeing scale, with shared variance of 29 % (Routledge et al., 2016). This demonstrates the importance of measuring both composite wellbeing and psychological symptom scores as low levels of depression and anxiety symptoms do not necessarily indicate that a person is functioning optimally. Importantly, Gatt and colleagues have shown that composite wellbeing is a more powerful predictor of outcomes beyond subjective or psychological wellbeing alone, which the COMPAS-W scale has the ability to discriminate. For instance, they have shown that higher composite wellbeing using the COMPAS-W is associated with various other adaptive behavioral outcomes including attentional biases to happy emotions (Routledge et al., 2018), superior working memory and attention (Routledge et al., 2017), good sleep, diet, and exercise (Gatt et al., 2014), and lower work absenteeism (Gatt et al., 2014). With regard to neural correlates of wellbeing, a study with monozygotic and dizygotic adult twin pairs showed that increased levels of composite wellbeing were related to volumetric reductions in the brainstem, and environmental factors predominantly contributed to this relation (Gatt et al., 2018). A subsequent study showed that a specific resting state electroencephalography (EEG) profile (high alpha and delta, low beta) was related to increased composite wellbeing, and also

indicative of lower anxiety (Chilver et al., 2020). Most recently, Jamshidi et al. (2020) showed that the COMPAS-W scale of wellbeing also accounts for more genetic variance when examining polygenic scores derived from genome-wide association studies. Together, this evidence highlights the utility of examining composite wellbeing over subjective or psychological wellbeing alone and provides initial data implicating patterns of neural activity that are associated with higher levels of wellbeing.

Mounting evidence suggests that the cumulative experiences of positive emotions are critical building blocks supporting happiness, flourishing, and overall life satisfaction (Cohn et al., 2009). Yet, apart from the work from Gatt and colleagues (Chilver et al., 2020; Gatt et al., 2018; Jamshidi et al., 2020), the psychological research on eudaimonia and hedonia has primarily occupied a research terrain based on self-report measures and correlational studies and it has rarely been expanded upon through the use of neuroscience methods. The present interdisciplinary review focuses on positive affect and emotions, which is consistent with Diener et al.’s (1999) conceptualization of subjective wellbeing involving pleasant affect (along with dimensions of unpleasant affect and life satisfaction). As mentioned above, a separate review paper covered unpleasant affect (sadness) in the context of General Wellbeing (Arias et al., 2020). The emphasis on positive emotions and affect in our review paper reflects the language and constructs that are used in the neuroscience literature. As Gruber et al. (2019) noted, it is important for subfields to work collaboratively on unifying the language and constructs used to study positive emotions across development, temporal course, and contexts. The present paper integrates relevant neuroscience literature spanning cognitive, social, and developmental aspects of subjective wellbeing (hedonia) and psychological wellbeing (eudaimonia), with a predominant focus on the neurophysiological correlates of positive emotions and affect.

2.2. Are positive emotions unique to human experience?

Advancing knowledge about positive emotions in non-human animals (from now on referred to as “animals”) is not only important for improving the welfare of animals that are managed and cared for by humans (Boissy et al., 2007), but it also contributes to our understanding of positive emotions and happiness in humans (Anderson and Adolphs, 2014). In this respect, it has been argued that a detailed neuroscientific understanding of basic human emotions critically depends on understanding comparable animal emotions (Panksepp, 2005a, 2005b). Purposeful integration of human and animal approaches is critical to elucidating operating principles of relevant neural systems. This will contribute to advancing cross-species theories that make explicit behavioral and brain predictions. Whether happiness, and more fundamentally, emotion, is a uniquely human experience is a matter of ongoing debate (de Vere and Kuczaj, 2016; Panksepp, 2011; Webb et al., 2019). Since the existence of emotions in animals is increasingly accepted, particularly among behavioral biologists (Burgdorf and Panksepp, 2006), there are no reasonable grounds to deny the existence of positive emotions in animals, such as happiness, joy, or fun. Indeed, researchers that trained rats to play hide-and-seek observed that they “looked like they are having fun” (Reinhold et al., 2019, p. 4). More specifically, Reinhold et al. (2019) noted behaviors that signified eagerness, such as teasing of experimenters and *freudensprung*, or “joy jumps.” Furthermore, neurobiological as well as physiological analogues between humans and animals strongly argue for the existence of positive emotions in all mammalian species (Burgdorf and Panksepp, 2006). Increasing evidence for positive emotions in animals comes from numerous studies on play behavior (see section 6.2). Playful interactions with conspecifics or objects have been observed not only across mammalian taxa (e.g., dogs: Bekoff, 2015; dolphins: Janik, 2015; rats: Panksepp, 1981), but also in several bird (Bond and Diamond, 2003; Emery and Clayton, 2015) and reptile species (Burghardt, 2015). Moreover, playful pushing and pulling of objects has also been described

in two species of octopus (Zylinski, 2015), raising the question of the existence of basic positive emotional states even in invertebrates.

A major factor that distinguishes emotion research in animals from that in humans is that animals are unable to provide self-report to describe their inner states (Anderson and Adolphs, 2014); although, an adapted self-report methodology has been used to assess subjective well-being in captive primates (e.g., King and Landau, 2003; Weiss et al., 2012). Whereas not relying on self-report is often considered a beneficial aspect of animal work in that the behavioral manifestation of animals may be more precise compared to some of the issues (e.g., malleable memory, inaccurate reporting, etc.) when using self-report measures in humans, behavioral approaches also entail two main problems. First, it prevents us from gaining insight into the subjective component of emotions in animals, such as how an emotion “feels” for an animal (Mendl, Paul, et al., 2011). Second, we have to rely on objective parameters to assess the affective state of an individual while avoiding the “anthropomorphic trap” (Emery and Clayton, 2015). Nevertheless, great progress has been made in recent years regarding the identification of emotional states in animals as well as the associated neurobiological mechanisms. This research has predominantly focused on the assessment of negative affective states, as they are considered to be more intense, and thus more easily detectable, as well as more critical to animal welfare (Boissy et al., 2007; de Vere and Kuczaj, 2016; Proctor et al., 2013). However, as the welfare of both humans and animals also requires the presence of positive emotions, it is critical to analogously explore positive emotions in animals (Boissy et al., 2007; Burgdorf and Panksepp, 2006; de Vere and Kuczaj, 2016; Lawrence et al., 2019; Proctor et al., 2013).

Recognizing the significant value of behavioral neuroscience approaches to understanding the neurophysiological correlates of positive emotions, we have incorporated behavioral neuroscience research on positive emotions throughout this review in order to inform factors that promote human wellbeing and happiness. The inclusion of findings from animal research advances our understanding of the neuroscience of positive emotions via methods that allow for studying causal developmental relations among genes and behavioral outcomes, as well as methods that isolate the specific functions of brain structures and circuitry. In particular, animal research is integrated into section 3.1 (Neurochemical Processes Related to Positive Emotions and Affect), section 6.2 (Play), and section 7 (Environmental Factors Facilitate Positive Emotions and Healthy Outcomes).

3. Neurophysiological response associated with positive emotions and affect

While a myriad of psychological constructs has been developed to characterize the psychosocial building blocks of positive emotions and wellbeing, the majority of the human and animal neurophysiological research has focused more specifically on positive affective states (emotions, moods), and traits (for examples of research studies that have studied the neural correlates of wellbeing and/or happiness see Chilver et al., 2020; L. Luo et al., 2017; Routledge et al., 2018; Shi et al., 2018; Suardi et al., 2016). From the “core affect” perspective (e.g., Russell, 2003), positive emotions represent positively valenced affective states that range on orthogonal levels of arousal, per the circumplex model. For example, “calmness” is considered a positive emotion that represents relatively low levels of arousal compared to “happy” that represents approximately the same level of pleasant valence, but higher levels of arousal (Anderson and Adolphs, 2014). Positive affect is associated with flourishing and success across life domains including social, work, physical, and psychological health (Pressman et al., 2019). From an evolutionary perspective, the functional role of positive emotions has been theorized to build physical, intellectual, and social capacities that promote adaptation and long-term survival (Fredrickson, 1998). With regard to short-term functions, specific positive emotions, such as pleasure, have been theorized to reinforce activities that lead to survival

including food, procreation, and social ties (Berridge and Kringelbach, 2015). Although the special issue of the Human Affectome project includes a focused review on hedonics and reward (Becker et al., 2019), this section includes a brief review of the neurobiological processes associated with experiencing pleasure and reward as these experiences are implicated in positive emotions and wellbeing. Developing a better understanding of the neurophysiological correlates of positive affect and emotions is critical to understanding how to cultivate and promote societal happiness and wellbeing.

3.1. Neurochemical processes related to positive emotions and affect

At the neurochemical level, neurotransmitters, neuropeptides, and hormones have been implicated in the experience of pleasure, reward, and other positive emotions.

3.1.1. Hedonic brain networks and neurotransmitters

By far, the neurotransmitter dopamine has received the greatest amount of attention in relation to positive emotions, and dopamine has been implicated in reward-related processes. Reward is conceptualized as comprising of: (1) objective and subjective ‘liking’ reactions, which translate to the hedonic experience of pleasure, (2) ‘wanting’ or incentive salience, which describes the motivation to seek reward and (3) reward-based learning (Berridge and Kringelbach, 2008, 2013). The dopaminergic “wanting” network is a widespread mesolimbic system, whereas “liking” centers are located in the orbitofrontal cortex (OFC), insula, and ventral pallidum (Kringelbach & Berridge, 2017). Mounting evidence suggests that dopamine may play a specific role in wanting, rather than liking per se (Berridge and Kringelbach, 2015), and liking, wanting, and prediction of reward appear to be distinct constructs that are distinguishable via mesolimbic circuitry (Smith et al., 2011). The mesolimbic dopamine pathway is pivotal in the reward network and involves dopamine signaling from the ventral tegmental area (VTA) to the nucleus accumbens (NAc), which is a primary reward structure in the brain that implements responses to positive stimuli and integrates motivational valence and novelty (Bassareo et al., 2002). This signaling pathway also extends to regions such as the amygdala, hippocampus, and medial prefrontal cortex (mPFC) (Berridge and Kringelbach, 2011; Feder et al., 2009; Nestler and Carlezon, 2006). Dopamine projects from VTA and substantia nigra (SN) to various cortical and subcortical brain areas including the striatum, amygdala, hippocampus, anterior cingulate, olfactory cortex, and prefrontal cortex (Ashby and Isen, 1999; Burgdorf et al., 2017; Burgdorf and Panksepp, 2006).

Animal research has significantly contributed to advancing the identification of localized ‘hedonic hotspots’ in neural reward structures that generate ‘liking’ responses (Mahler et al., 2007; Pecina and Berridge, 2005; Smith and Berridge, 2005; Steiner et al., 2001). For example, mu opioid stimulation by MOR1 agonist (D-Ala2, NMe-Phe4, Gly-ol5)-enkephalin (DAMGO) micro-injection within a hotspot in NAc, or in a hotspot located in posterior ventral pallidum, was found to more than double the intensity of ‘liking’ reactions in response to sweet tastes in rodents (Pecina and Berridge, 2005; Smith and Berridge, 2005). These pleasure generating ‘hotspots’ in reward circuitry are highly localized, measuring just one cubic-millimeter in volume in rats (Berridge and Kringelbach, 2013). DAMGO microinjections to other parts of NAc have been shown to increase wanting but not liking in rodents, suggesting the highly localized and specialized function of the NAc ‘hotspot’ (Pecina and Berridge, 2005), and that liking, wanting, and prediction of reward are distinguishable constructs via specific patterns of NAc-VP neuronal firing pattern codes (K.S. Smith et al., 2011). However, other evidence in human research suggests that the subjective experience of pleasure is not purely stimulus driven, as pleasures are moderated by low and high states of satiety. OFC closely tracks subjective reports of a pleasurable sensation (Kringelbach et al., 2003). Kringelbach et al. (2003) showed that when participants in the scanner drank chocolate milk to satiety, OFC activity subsided, but it increased

again when they switched to a drink to which they had not habituated (i. e., tomato juice). While ‘liking’ only represents a limited component of the experience of positive affect, these studies provide insight into the role of reward-based circuitry in maintaining a positive hedonic tone.

Dopamine involvement has also been implicated in anhedonic responses to chronic stress in rodents. Anhedonia (diminished pleasure and/or interest) is a primary symptom of Major Depressive Disorder (MDD; American Psychiatric Association, 2013; Treadway and Zald, 2011). Human neuroscience research has illustrated that individuals with depression show reduced activity in reward-function circuitry, primarily including NAc and anterior cingulate regions (Mayberg et al., 2005; McNeely et al., 2008), and deep brain stimulation (DBS) has been shown to significantly reduce anhedonic symptoms in treatment-resistant depression (Sankar et al., 2020). The animal research on anhedonic depression is particularly well positioned to provide further insight into the role of the cellular mechanisms within the reward circuitry in modulating positive affect (Bessa et al., 2013; Francis et al., 2015; Heshmati and Russo, 2015). NAc dysfunction in particular has been repeatedly implicated in anhedonia and depression-like symptoms in animal models (Bessa et al., 2013; Di Chiara et al., 1999; Francis et al., 2015; Heshmati and Russo, 2015; Newton et al., 2002; Rada et al., 2003), particularly following exposure to a stressor.

Stress-induced anhedonic behavior in rodents is associated with changes in the morphology of dendrites of medium spiny neurons in NAc, which may modulate synaptic plasticity in a manner that confers future susceptibility to stress (Bessa et al., 2013; Heshmati and Russo, 2015). Chronic mild stress impacts dopamine responsiveness to rewarding stimuli in rats, inducing a stimulatory dopamine response to aversive stimuli and blunting stimulatory responses to rewarding stimuli (Di Chiara et al., 1999). Hedonic and anhedonic responses have also been elicited through other neurochemical actions in NAc. For example, the overexpression of cAMP response element-binding protein (CREB) in transgenic mice produced an antidepressant effect in a learned helplessness paradigm, whereas under-expression of CREB resulted in the opposite phenotype (Newton et al., 2002). The regulation in NAc has also been implicated in anhedonic responses to stress. Glutamate injected into the NAc of male Sprague–Dawley rats decreased motivated behavior in a forced swim paradigm, whereas *N*-methyl-D-aspartate glutamate antagonists increased motivated behaviors like an antidepressant would (Rada et al., 2003). Together, these findings indicate that stress exposure in rodents is associated with blunted reward responsiveness, likely via structural and functional changes in NAc. These findings are consistent with human research illustrating relationships between stressful life events and the onset of depression symptoms and episodes (Beck and Bredemeier, 2016; Hammen, 2005) and alterations in dopamine function in depression may be closely associated with stress (Treadway and Zald, 2011). While human research has broadly identified structural and functional abnormalities in ventral striatum in depression, future research should work to distinguish the impact of abnormalities in the anticipatory aspects of reward function from consummatory components (Treadway and Zald, 2011).

Regarding human research in positive affect, in their much-cited review, Ashby and Isen (1999) theorized that a) positive affect is associated with increased dopamine levels via dopamine release from VTA, and that b) dopamine mediates the relation between positive affect and cognitive function. Despite the popularity of this theory, many serious problems remain to be addressed. As noted in a more recent review, Goschke and Bolte (2014) stated that presently there is no *direct* evidence that dopaminergic input to fronto-striatal circuits is related to positive affect. Rather, much of the presently available evidence relies on the notion that effects of positive affect and dopamine appear to have similar effects on cognitive functions “from which it is inferred that effects of positive affect may partly be mediated by dopaminergic activity” (Goschke and Bolte, 2014, p. 412). Another essential problem with this

theory is that experiences of positive emotion, motivation, and reward often overlap in their occurrence and are frequently confounded with one another thus making isolation of unique links between positive affect and dopamine difficult (Ashby and Isen, 1999; Berridge and Kringelbach, 2008; Chiew and Braver, 2011, 2014; but see Kohls et al., 2009 for attempts to disentangle such effects). For example, Cohen et al. (2016) reported that being in a positive state (excitement condition due to ability to win \$100) generally increased performance on a go-no-go task and activation in a fronto-striatal neural network; however, reward responsivity to a monetary incentive and positive affect were confounded in this study. Similarly, Braem et al., 2013 used positive images (which served as mental placeholders for monetary reward on a trial-by-trial basis), and reported increased cognitive flexibility during the performance-contingent condition with activity being present in a medial vMPFC – PCC network. Although some research has begun to explore the extent to which the effects of reward and positive emotion on cognition are dissociable (Chiew and Braver, 2011, 2014), more comparative work is highly warranted, and accounting for motivational intensity, or arousal is critical (Feng et al., 2014; Harmon-Jones et al., 2013; Jefferies et al., 2008; Kensinger, 2008). Further, other neurobiological factors such as neurotransmitters, neuropeptides, or hormones, may also influence the role of the mesolimbic dopaminergic system in positive affect, positive emotions, and happiness.

3.1.2. Oxytocin

Oxytocin is a nonapeptide hormone released from the posterior pituitary and multiple organs (uterus, placenta, amnion, corpus luteum, testes, and heart) in response to social bonding, interactions, and the emotional context of social relationships (Shamay-Tsoory and Abu-Akel, 2016). Positive affect has been hypothesized to be associated with increases in oxytocin (S. Cohen and Pressman, 2006; IsHak et al., 2011; Pressman and Cohen, 2005). Experimentally administered oxytocin in humans is related to a myriad of findings that indicate a relationship with positive emotions. For example, administered oxytocin is associated with increased sustained attention to happy faces during an attention bias task in depressed patients (Domes et al., 2016), as well as increased emotion recognition in depressed patients (MacDonald et al., 2013) and volunteers (Marsh et al., 2010), and increased sensitivity to positive facial cues in healthy control participants (Domes et al., 2013a; 2013b; Tollenaar et al., 2013). Administered oxytocin is also associated with increased prosocial behaviors while receiving help from a stranger (Human et al., 2018). Related to studying the relationship between oxytocin and social behaviors, the density and distribution of oxytocin receptors are observed in parts of the prairie vole brain associated with social reinforcement such as NAc and amygdala (Insel and Shapiro, 1992). Animal studies using oxytocin knockout methods indicated reduced material behaviors such as decreased pup licking and impaired pup retrievals in knockout rats (for review, see Macbeth et al., 2010).

While these data indicate a link between sociocognitive cues and positive emotions, the precise neurochemical pathways mediating this link remain to be determined, and dopamine and endorphin systems have been theorized to mediate the link between oxytocin and social relationships (Pearce et al., 2017a). Indeed, there is emerging research charting interactions between oxytocin and dopamine, particularly with regard to complex socioemotional functions. Given the prosocial role commonly attributed to oxytocin, Shamay-Tsoory and Abu-Akel (2016) suggested that oxytocin attaches social salience to emotionally valenced stimuli, which then either stimulates or mediates dopamine in VTA (Groppe et al., 2013 or the NAc: Hurlmann and Scheele, 2016), depending, for example, on the valence of the face (Domes et al., 2013b). Such mediation could facilitate concurrent emotions such as happiness, joy, feelings of belonging, and contentment. Oxytocin release in the VTA elicits social reward and modulated dopaminergic neurons (Hung et al., 2017; Xiao et al., 2017), suggesting a setting of affective tone at the early stages of neural and neurochemical processing. While these data indicate a link between sociocognitive cues and positive emotions, the

precise neurochemical pathways mediating this link remain to be determined, and dopamine and endorphin systems have been theorized to mediate the link between oxytocin and social relationships (Pearce et al., 2017a).

3.1.3. Androgens/Estrogens

The explicit role of gonadal hormones (e.g., testosterone, estrogen, progesterone) in positive emotions is still largely unknown. Yet, mounting research documents the beneficial role of hormone replacement therapy to restore mood and wellbeing during aging processes. In aging men, decreasing testosterone levels are associated with increased symptoms of depression (Barrett-Connor and Kritz-Silverstein, 1999), and one in three women experiences anxiety and depression during menopause (Mishra and Kuh, 2012). To restore and maintain wellbeing and life satisfaction, supplementation of estrogen in perimenopausal women (Shaukat et al., 2005; Soares and Cohen, 2001) or of testosterone in aging or hypogonadal men (Alexander et al., 1997; Jockenhövel et al., 2009; Pope et al., 2003), reportedly increases mood, alleviates depressive symptoms, and/or increases sexual satisfaction. Whereas a recent U-curve model proposed that excess or deficiency of gonadal hormones increases mood and anxiety symptoms (Mueller et al., 2014), a converse model to explicitly address the contribution of gonadal hormones to positive emotions is at-large.

In sum, scientists have not yet reached a consensus with regard to the magnitude and specific mechanism of action of specific neurochemical substrates of positive emotions and affect (Ashby and Isen, 1999; Goschke and Bolte, 2014; Pearce et al., 2017a; Shamay-Tsoory and Abu-Akel, 2016), and this remains an important area for future research. Multifactorial processes within or between neurochemical groups (e.g., the interaction among dopamine and oxytocin in regulating a number of social behaviors; Liu and Wang, 2003; Pearce et al., 2017b) add to this presently opaque picture (Hung et al., 2017; Pearce et al., 2017b). Future research is needed to tease apart which precise boundary conditions influence the experience of positive emotions, affect, and ultimately wellbeing.

3.2. Flexible brain networks implement positive emotions and affect

In this section, we provide an overview of key cortical and subcortical brain structures that contribute to the experience of positive affect and emotions. We ultimately conclude that the brain processes positive affective stimuli and emotions via flexible and nimble brain networks that are sensitive to valence and arousal.

3.2.1. Prefrontal cortex (PFC)

Based on observations from lesion studies in the early 1970s (e.g., Gainotti, 1972), affect implementation in the brain was historically conceptualized as a lateralized function, with structures supporting positive affect lateralized to left prefrontal cortex (PFC) and negative affect lateralized to right PFC (Davidson, 1984; Heller, 1990). Whereas other early models of emotion focused solely on valence, Heller (1990) theorized that affect can be deconstructed into orthogonal dimensions of valence and arousal (per an earlier circumplex model of emotion; e.g., Russell, 1980) that are represented by specific patterns of lateralized brain activity spanning frontal and parietal cortices. This neuropsychological theory of lateralized affective function was supported by research using psychophysiological methods that illustrated that left frontal activity is associated with positive valence, whereas right frontal activity is associated with negative valence across a range of samples with clinical symptomatology (Borod, 1992; Engels et al., 2010; Heller et al., 1997, 1998; Henriques and Davidson, 1990, 1991; Herrington et al., 2005, 2010; Nitschke et al., 1999). Indeed, some EEG research has demonstrated an association between left dIPFC and positive affect (Davidson, 1992; Harmon-Jones, 1997), as well as decreased left dIPFC activity in individuals with depression (Grimm et al., 2008; Nitschke et al., 2004). Left dIPFC activity is also enhanced in response to positive

stimuli, even when compared to arousal-matched negative stimuli, which is illustrative of a valence effect (Herrington et al., 2005). Translational research has shown that left dIPFC is commonly targeted during repetitive transcranial magnetic stimulation (rTMS) treatment for Major Depressive Disorder, and stimulation is associated with a reduction in anhedonia symptoms (Sonmez et al., 2019). rTMS stimulation of left dIPFC also facilitates memory retrieval of positively valenced stimuli (Balconi and Ferrari, 2012), implicating that left dIPFC stimulation in individuals with depression may be effective via modifying psychological mechanisms related to processing positive stimuli. With specific relevance to wellbeing outcomes, a resting state EEG study showed lateralized findings, such that greater left than right frontal activity was related to higher levels of hedonic and eudaimonic wellbeing (Urry et al., 2004). Thus, left dIPFC in particular appears to play a specific role in processing positive affect and emotions. While bilateral dIPFC has been broadly implicated in emotion regulation across many studies (Buhle et al., 2014), additional research is needed to better characterize its role in the regulation of positive emotions.

3.2.2. Orbitofrontal Cortex (OFC)

Beyond the contributions of left dIPFC with regard to processing positively valenced stimuli and emotions, other cortical and subcortical brain regions are frequently implicated in studies of pleasure, and reward function. These brain regions commonly include orbitofrontal cortex (OFC), medial PFC (mPFC), anterior cingulate cortex (ACC), and insula as well as subcortical structures involved in hedonics such as nucleus accumbens, ventral pallidum, and amygdala (Berridge and Kringelbach, 2015; Panksepp, 2011). OFC codes for subjective affective valence (pleasantness) related to reward across a range of stimuli types (for review see Rolls, 2019). Via projections to other brain regions (e.g., ventromedial prefrontal cortex, pregenual cingulate cortex) and networks, OFC provides inputs to judgment, decision-making processes, and learning (Rolls, 2019). Lesions to OFC in macaques are associated with impairment in tasks that involve associating reward with stimuli and show impairments in changing behavior in response to altered reinforcement contingencies (Pujara et al., 2019; Stalnaker et al., 2015). Moreover, a central region of medial OFC (mOFC; involved in pleasure encoding) and ventral pallidum (the only region to completely abolish pleasure in animals when lesioned) appear to be strongly associated with the experience of pleasure (Kringelbach, 2005; Kringelbach and Berridge, 2010). mOFC is related to subjective reports of experiencing pleasure across a range of sensory experiences (e.g., olfactory, taste, and texture; Rolls, 2019). With implications for healthy postpartum recovery, subjective pleasant mood ratings while new mothers viewed photos of their infants were related to bilateral OFC activity, indicative of positive emotions such as joy, warmth, love, and nurturance (Nitschke et al., 2004). Although OFC is implicated in state pleasantness, a direct link between self-reported trait happiness and OFC activity was not observed during a social decision making task; rather, OFC was related to coding the value of social rewards involved in generosity (Park et al., 2017). While OFC undoubtedly plays a critical role in motivation, liking and experiencing pleasure, future research contextualizing the role of OFC during the experience of a range of positive emotions would advance our understanding of how the myriad of OFC functional capabilities contribute to health and wellbeing. Further, research disentangling how OFC codes for arousal in addition to valence will be useful for gaining insight about transdiagnostic symptoms of impulsive response to high-arousal positive emotions and stimuli (Johnson et al., 2020).

3.2.3. Anterior Cingulate Cortex (ACC)

In conjunction with other frontal and subcortical regions, anterior cingulate cortex (ACC) implements different aspects of cognitive control functions (e.g., top-down attentional, control, response inhibition, conflicting and error monitoring, etc.; Banich, 2009; Shenhav et al., 2016; Silton et al., 2010). Based on cytoarchitecture parcellations, ACC

is typically subdivided into dorsal ACC (dACC), and rostral ACC (rACC; Bush et al., 2000). dACC has connections to other frontal cortical regions (e.g., dlPFC; Banich, 2009; Mohanty et al., 2007; Siltan et al., 2010) and is commonly associated with top-down control and monitoring functions involved with regulating emotions (Joormann and Stanton, 2016), including positive emotion regulation (Kim and Hamann, 2007). Further, individuals may fail to control impulses in response to a positive stimulus or emotion (Johnson et al., 2020), or positive stimuli and emotions may specifically facilitate how attention is directed (Gable and Harmon-Jones, 2008). Dorsal regions of PFC and ACC are theorized to contribute to appraisal or labeling emotions while rACC has subcortical connections to limbic structures and likely plays a role in regulating and generating affective responses (Etkin et al., 2011).

rACC projects directly to subcortical regions such as amygdala and hippocampus (Devinsky et al., 1995) and is commonly associated with guiding attention to emotion and is broadly implicated in affective processing. For example, rACC is involved with evaluating stimuli for affective salience and reducing interference from task-irrelevant affective interference, as well as monitoring for errors (Brassen et al., 2011; Mohanty et al., 2007). rACC also subsumes subgenual region cg25 which is considered a key target of deep brain electrical stimulation for individuals with intractable depressive disorders (Mayberg et al., 2005; McNeely et al., 2008), and stimulation of this region reduces feelings of apathy and anhedonia symptoms and increases experience of pleasure in social and family activities (Mayberg et al., 2005). Abnormalities in reward functions represent critical components of anhedonia (e.g., motivational and consummatory anhedonia; Treadway and Zald, 2011), and likely are directly related to differences in rACC function given that rACC is directly associated with coding the value of receiving a reward (Treadway and Zald, 2011) and also predicting future rewards (Treadway and Zald, 2011; Vassena et al., 2014). Possibly related to reward function, rACC also contributes to enhancing positive emotions. Scharnowski et al. (2020) showed that positive emotion upregulation in response to social stimuli was associated with increased dorsal medial PFC-amygdala connectivity via subgenual ACC. In a sample of elderly adults, increased rACC activity was associated with enhanced attention to happy faces (Brassen et al., 2011), which may be related to a propensity for bias to positive emotions per the socioemotional selectivity theory (see section 5.2). Another study showed that subjective happiness was associated with increased rACC density and state happiness (via mood induction) was related to increased rACC activity (Matsunaga et al., 2016). In sum, the limited available evidence indicates that rACC, perhaps via its intricate connectivity with cortical and limbic regions, may facilitate the healthy experience of positive emotions via guiding attention toward positive stimuli when contextually relevant. Further elucidating the distinct ways that rACC contributes to positive emotion regulation remains an important area of future research, particularly with regard to the role of rACC in the anticipation of future positive events, outcomes and rewards both in healthy and clinical populations.

3.2.4. Insula

The insula integrates interoception and emotional awareness and it functions as a junction box with bidirectional communications with numerous cortical and subcortical brain regions (e.g., amygdala, hippocampus, etc.) involved respectively in aspects of top-down and bottom-up features of emotional appraisal, response, and regulation (Gasquoine, 2014; Giuliani et al., 2011; Li et al., 2018). More specifically, anterior insula cortex (AIC) is theorized to represent salient body and environmental experiences, updating this information in a moment-to-moment manner (Craig, 2009). As such, the insula likely contributes to the visceral experience of all emotions (Craig, 2009), including positive emotions (Li et al., 2018), and wellbeing (Lewis et al., 2013). AIC has direct projections to the frontal cortex (Gasquoine, 2014), and appears to be involved in implementing top-down circuitry that regulates amygdala response to affective stimuli in a goal-driven manner (Cromheeke and Mueller, 2014; Giuliani et al., 2011; Li et al.,

2018; Menon and Uddin, 2010). Akin with models of lateralized frontal affective function discussed earlier (e.g., Davidson, 1984; Heller, 1990) left AIC may be associated with positive emotions and feelings of affiliation; whereas right AIC may be more involved with processing negatively valenced information (Craig, 2009). Craig (2009) has extended this model of AIC to understanding human awareness of time perception such that he predicts that when individuals are in a content or positive state within the context of an affiliative setting, left AIC will be more active and time durations are underestimated. In contrast, when individuals are in a negatively taxing situation, right AIC is expected to be more active and time durations are overestimated and time appears to pass more slowly. Alternations of time perception based on valenced mood states may shed some light on the subjective experience of flow (see Section 6.2) wherein an individual enters a sustained positive mood state and becomes so engaged in the task at hand that they lose track of time. Minimal research has specifically focused on the role of insula in positive emotions and this remains an area of growth for future research.

3.2.5. Amygdala

While an abundance of research has predominantly focused on the role of amygdala in negative emotions and fear-conditioning, animal and human research has also implicated amygdala in a range of affect-related processes involving positive emotions and stimulus reward learning, particularly implicating the role of basolateral amygdala in updating representations of value (Baxter and Murray, 2002). With regard to positive emotions, previous research has theorized that the amygdala processes valence in a bipolar manner, with amygdala activity increasing in response to negative stimuli and emotions and decreasing in response to positive stimuli and emotion (Burgdorf and Panksepp, 2006; Koeppe et al., 2009). Building on this theory, release of endogenous opioids in amygdala was related to decreased amygdala activity during the experience of positive emotion in humans (Koeppe et al., 2009). Other research has shown that amygdala response to viewing negative and positive images was comparable, and that amygdala activity was increased in response to both positive and negative images relative to neutral images, suggesting that amygdala tracks arousal rather than valence (Garavan et al., 2001). Consistent with the role of the left hemisphere in positive emotions, amygdala response to positive images appears to be preferentially lateralized to left amygdala (Hamann et al., 2002). Providing additional support for this affective lateralization, a magnetoencephalography (MEG) study showed that right laterobasal amygdala activity mediated negative valence, while left centromedial amygdala was activated in response to pleasantly valenced stimuli (Styliadis et al., 2014). Styliadis et al., (2014) reported that amygdala did not mediate arousal effects. Further research striving to specifically identify the role of amygdala in processing dimensions of arousal and valence in response to positive stimuli would help clarify the role of amygdala in the experience of positive emotions.

3.2.6. Flexible brain networks implement affective processes

While distinct cortical and subcortical brain structures are associated with processing positively valenced stimuli and emotions, these brain regions are theorized to work in conjunction as part of flexible networks that respond to perpetually shifting contextual task demands. Lindquist et al. (2016) provided data from a meta-analysis that support the neural implementation of a “flexible affective workspace,” such that “at the level of regional brain activity, there is no single region or even voxel that uniquely represents positivity or negativity.” In general, cortical and subcortical brain regions involved with processing affective stimuli (mPFC, ACC, AI, amygdala, ventral striatum, etc.) showed increased activity across the neuroimaging studies included in the meta-analysis. Thus, per fMRI data, affective stimuli, regardless of whether they are positive or negative, appear to be processed by a flexible affective workspace, which is consistent with constructionist theories of emotion (Satpute and Lindquist, 2019). However, as reviewed in the subsequent section (3.3), once temporal resolution is considered, distinct

contributions of brain regions emerge such that valence and arousal are distinguished via time course. Indeed, [Kringelbach and Berridge \(2017\)](#) have hypothesized that various brain networks are activated at various times during a pleasure cycle and that a key function of the pleasure system is to support transitioning across different brain networks in order to facilitate survival. In particular, they theorized that the Default Mode Network (DMN) may play a critical role in these processes and in connecting eudaimonic and hedonic experiences to the self and other emotion processing networks and also map on to the experience of flow (see section 8.2) that may accompany a state of positive emotion during deeply task-focused attention.

The specific neural mechanisms of the hypothesized flexible affective workspace remain under investigation. However, the DMN, which represents a widely distributed brain network of constituent cortical brain regions (e.g., the dlPFC, mPFC ACC, OFC, precuneus, posterior parietal cortex) that are implicated in the hedonic network (reviewed in section 3.1), as well as affective processing, related internal thought processes, and representations of the self ([Berridge and Kringelbach, 2011](#); [Buckner, 2012](#); [Raichle et al., 2001](#); [Satpute and Lindquist, 2019](#)) may play a critical function in supporting wellbeing, positive emotions, and possibly happiness ([Berridge and Kringelbach, 2011](#)). The DMN has been associated with indices of wellbeing (L. [Luo et al., 2017](#); [Shi et al., 2018](#)) as well as maintaining representational content that distinguishes between discrete emotions ([Satpute and Lindquist, 2019](#)). There is emerging evidence for the existence of the DMN in human infants as well as non-human animals ([Buckner, 2012](#); [Satpute and Lindquist, 2019](#)), which provides additional support for the plausible existence of positive emotions in non-human animals. With regard to wellbeing research, increased functional connectivity within mPFC and precuneus was associated with increased meaning in life, which is associated with eudaimonic wellbeing (see section 2.1) and possibly a greater capacity to extract meaningful memories from past or future events (L. [Luo et al., 2017](#)). Hedonic wellbeing (see section 2.1) may be associated with increased flexibility and neuroplasticity across various brain networks implicated in both cognitive control and affective processing ([Shi et al., 2018](#)). Recent research also has been focused on whether DMN activity and connectivity is modulated by mindfulness-based interventions which are theorized to enhance positive emotions and wellbeing (see section 8.1).

3.3. Affective chronometry distinguishes positive emotions and affect

As noted above, the spatial resolution afforded by fMRI methods has illustrated that overlapping brain regions and networks function in a flexible manner to process a range of affective stimuli ([Lindquist et al., 2012, 2016](#)); however, the time course of brain activity is not well characterized by fMRI research. Our present understanding of affective chronometry, or the temporal dynamics of affective response ([Davidson, 1998](#)), is based predominantly on EEG and MEG methods that provide information about time-resolution on the order of milliseconds. Affective response reflects dynamic processes that change over time; however, temporal course as a fundamental characteristic of positive emotions is rarely addressed in the present literature. Identifying the specific time window that information flows within brain networks provides insight into how brain regions may be selectively engaged during a specific time window while processing specific affective stimuli types.

Emotion-specific temporal signatures ([Costa et al., 2014](#); [Esslen et al., 2004](#); [Styliadis et al., 2015, 2018](#); [Waugh et al., 2015](#)) are often influenced by a range of individual differences (e.g., [Fisher et al., 2014](#); [Sass et al., 2010](#); [Silton et al., 2010](#); [Stockdale et al., 2015, 2017](#)). Studying the temporal dynamics of emotional processing is critical due to the distinct aspects of emotional responses (e.g., reactivity, regulation, and repair) that develop across time. Such responses may unfold prior to stimulus presentation ([Nitschke et al., 2006](#); [Poli et al., 2007](#); [Sabatinelli et al., 2001](#)), during stimulus presentation, and through the

post-stimulus period ([Garrett and Maddock, 2001](#)). EEG studies using event related potential (ERP) methods have shown that affective modulations take place around 100 ms after stimulus onset and can be sustained for as long as several seconds ([Brosch et al., 2008](#); [Olofsson et al., 2008](#)). Valence and arousal modulate ERP components at distinct temporal stages of emotional visual processing, with a rather diverse but typically early latency range for valence (usually 100–300 ms) and a consistent and later emerging arousal effect (200–1000 ms; [Olofsson et al., 2008](#)).

Further, affective stimuli representing different categories of emotions appear to be processed at different latencies. For example, a study using ERP methods reported that the processing of pleasant stimuli occurred after 160 ms, while the processing of unpleasant (disgust) stimuli was prioritized at around 140 ms after the stimulus onset ([Hot and Sequeira, 2013](#)). Similarly, another study showed that after 200 ms post-stimulus onset, fear processing occurred prior to that of disgust, and was followed by that of happiness (at 266–277 ms and 414–422 ms post-stimulus) and sadness ([Costa et al., 2014](#)). In both temporal windows, the processing of pleasant stimuli was characterized by higher activity in medial prefrontal cortex and ACC compared with fear and disgust. [Esslen et al. \(2004\)](#) investigated neural responses to facial expressions (happy, sad, angry, fearful, and disgust), and the responses to each facial expression were associated with distinct onset times and durations within different time windows. Activity for happy faces was significant during 138–205 ms in the left and right frontal areas, at 244–290 ms in the left and right ventromedial frontal and temporal areas and right parietal areas, and at 361–467 ms in the ACC and the right frontal areas ([Esslen et al., 2004](#)). Together, these research findings illustrate that a pattern of brain activity is distributed across time while processing positive stimuli and emotions.

Resolving the temporal course of valence and arousal remains a critical issue as well, since positive emotions range in arousal (e.g., contentment is theorized to be a lower arousal state than happiness, [Anderson and Adolphs, 2014](#)). A recent MEG study provided additional evidence for the spatiotemporal evolution of emotion in terms of valence (pleasant/unpleasant) and arousal (high/low; [Styliadis et al., 2018](#)). Valence and arousal were distinguished via the temporal course of regional brain activity. Emotional processing involves neural pathways for pleasant valence at a very early stage (60–110 ms) and the interaction of pleasant valence with high arousal at both early and later stages of processing (170–280 ms, 210–400 ms, 220–300 ms, 270–1000 ms, 330–500 ms, and 640–820 ms; [Styliadis et al., 2018](#)). Although all positive stimuli activated inferior frontal gyrus (IFG), it is the temporal evolution of brain activity that offers a complete assessment of the selective engagement of IFG across dimensions of affective characteristics. In sum, the affective chronometry of basic emotions occurs during specific but not continuous time segments, with accumulating evidence that 1) positive affective stimuli are processed later relative to negative affective stimuli and 2) valence and arousal are associated with distinct patterns of spatiotemporal activity. Continuing to study the spatiotemporal patterns of neural activity constituting brain circuitry associated with positive affect contributes to advancing our understanding of the specific roles of cortical brain structures engaged in affective processing. For example, depression symptoms appear to impact the early temporal course of processing positive stimuli ([Deldin et al., 2000](#); [Zhang et al., 2018](#)), and identifying these temporal differences in processing could help inform interventions and treatment strategies. We have incorporated findings regarding the temporal course of neural activity into other sections of this paper whenever relevant, especially considering that affective chronometry often provides insights into developmental processes as well as individual differences associated with psychological disorders.

Across Section 3, we have explored a myriad of interconnected neurophysiological processes ranging from neurochemicals to flexible brain networks in humans and animals that are associated with positively valenced emotions and affect. These neurophysiological processes

adapt and unfold in different ways over time and they are sensitive to stimulus properties (e.g., arousal), individual differences, including psychological disorders, and they are also influenced by developmental, social, and environmental factors (see sections 5, 6, & 7). Critical to supporting positive emotions and wellbeing in our current milieu that is wrought with societal-based stressors and increasing mental health problems, emerging research is beginning to focus on advancing our understanding regarding how interventions function to regulate and/or boost positive emotions as well as modify associated neurobiological functions (see section 8).

4. Cognitive control functions in the context of positive emotions

Cognitive control is an umbrella term that includes critical executive functions (e.g., working memory, set shifting, and inhibitory control; Miyake et al., 2000) that are needed to guide behavior throughout our daily lives and actions. Mood state and traits are associated with cognitive processes that interact with our own emotions, other peoples' emotions, and affective stimuli in our environments; thus, top-down cognitive control is frequently required in order to efficiently execute daily tasks in the face of continuous affective distractors. However, much of the research from the past two decades has focused on how negative moods, emotions, and stimuli influence basic cognitive control functions and vice-versa (Cromheeke and Mueller, 2014; Inzlicht et al., 2015; Lopes et al., 2005; Okon-Singer et al., 2015; Pessoa, 2008). In comparison, minimal research has focused on the specific influence of positive moods, emotions, and stimuli on cognitive control (and vice-versa), although initial research suggests that positive stimuli (e.g., faces, words, images) generally improve various cognitive control functions (see Goschke and Bolte, 2014 for review). In this section, we examine the associations between positive stimuli and/or mood (i.e., naturalistic state or induction) and cognitive control, integrating relevant electrophysiological and neuroimaging studies with behavioral evidence. Positive affect and cognitive control may influence each other bidirectionally or positive emotions may serve as a moderator. However, some of these effects may be sensitive to arousal, and/or modality, or are task dependent. Thus, to take into account the effect of various task demands, the subsequent sections review the effects of positive stimuli and affect on three key components of cognitive control functions: inhibition, working memory, and shifting.

4.1. Inhibition

The construct of inhibition broadly refers to the capability to stop an automatic or dominant prepotent response to a stimulus (Miyake et al., 2000). Inhibitory control function is implemented by a network of cortical brain regions including dorsomedial and lateral prefrontal cortex, right inferior frontal cortex, and dorsal anterior cingulate (dACC; Aron et al., 2014; Banich et al., 2009; Miller and Cohen, 2001). Critical to experiencing positive affectivity and wellbeing, intact inhibitory control abilities contribute to navigating healthy social relationships and activities (see section 6.1), particularly in the context of navigating affective stimuli that are interwoven into the fabric of daily social interactions. Inhibitory control functions are also critical to promoting behaviors that facilitate a healthy lifestyle since implementing inhibitory control is important for achieving long-term goals (Katzir et al., 2010). Flexible patterns of thought and behavior engendered by positive emotions increase enjoyment of positive health behaviors (Van Cappellen et al., 2018). For example, the presence of positive emotions predicts meditation habits (Cohn and Fredrickson, 2010) and physical activity adherence (Rhodes and Kates, 2015). Advancing our understanding of inhibitory control functions against the backdrop of affective experiences is critical as inhibitory functions are arguably always engaged in an affect-laden context (Todd et al., 2008).

The dual mechanisms of control (DCM) theory (Braver, 2012) is a

neuroscience-based theory of cognitive control that is closely related to response inhibition and is relevant to understanding positive affective constructs, including moods and emotions. DCM separates cognitive control into *proactive* and *reactive* control subprocesses. Whereas proactive control is anticipatory and can be engaged in advance to execute the upcoming task adequately, reactive control is ad hoc and occurs only transiently in response to a high demand cognitive challenge. Proactive control may be more associated with shaping actions in light of goal-oriented behaviors, and in contrast, reactive control may help guide attention toward novel threats and rewards (Grimshaw et al., 2018). These control subprocesses may be related to experiencing positive emotions in various ways. For example, proactive control may help strategically guide behavior over time toward achieving a long-term goal or positive life event, and reactive control might be more instrumental in steering attention toward more immediate rewards and positive experiences. In addition to proactive and reactive control, evaluative control occurs later and involves the monitoring of action outcomes (Ridderinkhof et al., 2004; van Wouwe et al., 2011). Electrophysiological studies have examined differential effects of positive and negative stimuli on proactive, reactive, and evaluative control which provides insights regarding how affective stimuli influence different temporal aspects of response inhibition.

In order to ascertain how positive mood influences proactive control, Vanlessen and colleagues (2015) collected EEG data during an inhibitory control task following positive mood induction. Their results indicated that the CNV (contingent negative variation), an ERP indicator of proactive control, was reduced after positive mood induction. Yet, van Wouwe et al. (2011) reported that positive mood did not modulate proactive control as indexed by CNV. Proactive control may thus vary depending on the task context, or perhaps on the nature of the positive mood or emotion that is being experienced. Gable and Harmon-Jones (2008) postulated that positive mood states vary in levels of approach motivation and they suggested that high approach motivation narrows the scope of attention whereas low approach motivation broadens attention. However, arousal may be confounded with motivation such that high approach motivation states are presumably high arousal states and low approach motivation states are presumably low arousal states. Thus, arousal, rather than approach motivation per se, may serve as the primary aperture for attentional scope. Fröebeer and Dreisbach (2012) have conducted experimental research illustrating that low arousal positive affect reduces proactive control, which is consistent with a broadened scope of attention. Additional research is warranted to advance our understanding of the constituent and interactive contributions of arousal and positive valence states on proactive control functions.

There is emerging evidence that arousal, rather than valence, also impacts reactive control functions. A behavioral experiment evaluating the differential effect of proactive control compared to reactive control found that task-irrelevant positive and negative images functioned as distractors during reactive, but not proactive control (Grimshaw et al., 2018), indicating an arousal effect during reactive control. Consistent with the direction of these findings, another study reported that positive mood increased N2 amplitude during reactive control, and as noted above, this research team also observed that positive mood was related to less efficient proactive control (indexed by CNV) which indicates that positive mood may distinctly influence how proactive and reactive control processes are engaged (Vanlessen et al., 2015). Other research focusing on conflict resolution generally supports the findings of increased reactive control following positive mood induction and has similarly documented increased amplitude for N200 (Kanske and Kotz, 2011; Zinchenko et al., 2017) and slightly later components (N300–400, N450–550; Xue et al., 2013) that may be implicated in evaluative control. Across cognitive tasks involving attentional control and response inhibition, positive mood induction has been associated with increased P3 amplitude (Albert et al., 2010), attenuated error-related negativity (ERN; van Wouwe et al., 2011) as well as

subsequent error-related positivity, such that negative feedback may be perceived as a mood-incongruent event if an individual is in a positive mood (Paul and Pourtois, 2017). In sum, evidence from electrophysiological research increasingly suggests that positive mood reduces *pro-active* and *evaluative* control processes while increasing *reactive* control processes.

While positively valenced moods, emotions, and stimuli influence inhibitory control functions in various ways, these findings may hinge on the specific positive emotions that are experienced along with associated motivational and contextual factors as well as varying levels of arousal. For example, positive emotions such as “pride” and “self-worth” have been implicitly associated with behaviors indicative of increasing inhibitory control and thus facilitating reaching long-term goals, while other positive emotions such as “happiness”, “joy” and “fun” were implicitly related with achieving short-term goals and behaviors indicative of less self-control such as eating more chocolate or failing to persist on a difficult task (Fishbach et al., 2010; Katzir et al., 2010). Additional research is warranted to study a broader range of positive emotions and stimuli on subsequent inhibitory control functions, and it will be particularly important to disentangle the roles of arousal in the context of positive stimuli (e.g., how does inhibitory control function differ in the context of viewing low-arousal positive stimuli such as an image portraying a feeling of contentment compared to high-arousal positive stimuli such as an image of cliff-diving). It is important for future neuroscience research to account for motivational and contextual factors in experimental task design/stimulus properties as well as levels of arousal in order to further refine theories regarding how different types of positive emotion constructs and stimuli influence inhibitory control functions and vice-versa.

4.2. Working memory

Working memory refers to the ability to retain information for immediate processing in order to accomplish complex tasks such as learning, reasoning, decision-making, and implementing goal-directed behavior (Baddeley, 2010). Relatedly, affective working memory, or maintaining mental representation of feelings, is theorized to be fundamental to driving goal-directed behaviors (Mikels and Reuter-Lorenz, 2019). Additional research is needed to characterize how neural correlates of feelings are integrated into working memory networks to contribute to the experience and regulation of emotions. Notably, increased capacity for working memory is associated with improved emotion regulation (Hendricks and Buchanan, 2016; Messina et al., 2016; Schweizer et al., 2017; Scult et al., 2017). Thus, it is not surprising that Pe et al. (2013) reported that the ability to effectively update positive stimuli in working memory is related to increased life satisfaction and wellbeing. Higher levels of life satisfaction and subjective wellbeing have also been associated with attentional biases toward positive stimuli (Blanco and Vazquez, 2020; Sanchez and Vazquez, 2014), and these positive biases may influence working memory and subsequent recall of information.

As noted earlier in section 3.2., lateral PFC plays a critical role in modulating working memory in the presence of positive stimuli. In an early neuroimaging study at the intersection of affect and working memory, Gray et al. (2002) used video clips to induce a pleasant, unpleasant, or neutral mood, and then asked participants to complete a 3-back working memory task using either words or face stimuli. An interaction between mood and stimulus type indicated that lateral PFC was particularly sensitive to face stimuli after positive mood induction. Similarly, Dolcos et al. (2004) documented lateralized findings with left dlPFC activity associated with attending to positive stimuli, and right vlPFC activity associated with attending to negative stimuli. However, successful encoding of images (evaluated on an unexpected cue-recall task) was specifically enhanced by arousal in left vlPFC and dlPFC, indicating that it is critical for researchers to attend to both valence and arousal dimensions of stimuli in interpreting the role of attention to

emotion in working memory. Perlstein et al. (2002) observed increased right dlPFC activity in response to pleasant stimuli (contrasted to unpleasant and neutral stimuli), which suggests that right dlPFC may be sensitive to coding valence during working memory.

In order to disentangle the specific effects of valence and arousal on cerebral networks Jordan and Dolcos (2017) investigated how patterns of network activity are recruited in the face of positive and negative distractors during a working memory task. Behavioral results showed that positive distractors had less of an impact on working memory performance than negative distractors. Valence-specific effects were observed in “dorsal executive system” regions (e.g., LPC, dlPFC), and overlapping arousal and valence effects were observed in “ventral affective system” regions (e.g., amygdala, vlPFC, mPFC, visual cortex). During negative distraction, decreased activity in LPC and vACC was observed, and increased activity in vlPFC and mPFC was observed during positive distraction. Arousal effects were also identified in vlPFC; although the valence-related effects noted during positive distraction were slightly more posterior and lateral than the arousal-related effects. Overlapping valence and arousal effects were also observed in the visual cortex extending to the fusiform gyrus and superior parietal lobe. Network analyses indicated that during negative distraction (compared to positive distraction), mPFC and vACC showed increased functional connectivity with the left parietal cortex, suggesting increased communication between the default mode network (DMN) and the fronto-parietal executive network (FPN) as goal-irrelevant negative emotions impact cognitive control functions. Together, the findings from this study suggest that valence/arousal dissociations have a differential impact on working memory performance.

Individual differences related to anxiety and mood disorders may further impact the relationship between affective stimulus properties and working memory. For example, consistent with the lateralized findings reported above, Fales et al. (2010) reported lateralized findings implicating increased left IFG activity while viewing happy (compared to neutral) stimuli. However, this finding was only present in individuals with low (but not high) trait anxiety. Keresztes and colleagues (2012) showed that individuals with remitted depression exhibited significantly lower activity in right dlPFC and left vlPFC compared to healthy comparisons in response to positive emotional distractors when working memory load was high. For individuals with mood disorders, reduced PFC activity in the presence of positive distractors during high cognitive load may be related to difficulties engaging in inhibitory control or emotion regulation processes. Mirroring the fMRI research conducted by Keresztes et al. (2012), EEG studies have provided additional information regarding the temporal resolution of these effects. Zhang and colleagues (2018) found that individuals with depression demonstrated a working memory impairment for positive stimuli that appeared to be associated with poor selective attention to positive stimuli during encoding, as indexed by reduced occipital P1 amplitude, paired with poor efficiency at later memory stages (matching and maintaining) as measured by reduced frontal P2 and parietal LPP amplitudes, regardless of stimuli valence. Relatedly, Levens and Gotlib (2010) reported that individuals with depression (compared to healthy controls) were slower to disengage from facial stimuli with sad expressions and quicker to disengage from facial stimuli with happy expressions during a working memory task. The control group showed the opposite pattern of behavioral responses. Levens and Gotlib (2010) speculated that these patterns of working memory behavior might be associated with difficulties repairing negative mood due to difficulties with sustained engagement with positive emotions and information and less processing and elaboration of positive events and stimuli in memory.

Harnessing developmental perspectives, other studies (Mueller et al., 2017; Ziaei et al., 2017, 2018) have examined how positive mood influences the neural correlates of working memory across the lifespan. As discussed in section 5.2, the socioemotional selectivity theory postulates that as individuals age, they experience enhanced levels of positive affect (Carstensen, 1998; Carstensen et al., 1995). Providing additional

support for this theory, Ziaei and colleagues (2018) illustrated that older adults had more difficulties inhibiting task-related positive information than younger adults during a working memory task, and that older adults engaged left IFG and ACC activity whereas younger adults activated the striatum and posterior cortex. Left IFG activity in older adults was negatively correlated with reaction time, indicating that it was likely associated with the implementation of top-down cognitive control functions during the task (Ziaei et al., 2018). These findings show that positivity bias, or the automatic tendency to have attention preferentially captured by positive stimuli, is associated with enhanced distraction in the context of positive distractors during a working memory task. Individual differences related to positivity bias may be associated with some of the discrepant findings in this literature given that positive information facilitated behavioral response in younger adults in the study (Ziaei et al., 2018). In another study by the same research team and using the same task, younger adults recruited vIPFC during both positive and negative distraction conditions, while older adults recruited a different pattern of frontal brain activity and demonstrated reduced activity in frontoparietal task regions and reduced DMN activity (Ziaei et al., 2017). In addition, positive stimuli activated the amygdala more so in older, but not younger, adults, and was related to increased memory performance and faster response time in older adults. This observed shift in subcortical amygdala activity during processing positive stimuli along with a more differentiated recruitment of PFC regions may have implications for the positivity bias commonly observed in older adults (Ziaei et al., 2017). On the other end of the age spectrum, young adults recruited the lateral and medial PFC more so than adolescents, who, in turn, relied on amygdala and nucleus accumbens involvement when dealing with emotional working memory (Mueller et al., 2017). Taken together, these findings indicate a U-curve of PFC and amygdala engagement in response to positive stimuli across adolescents, young adulthood, and older adulthood.

Although the associated neuromolecular mechanisms of positive affect on working memory are not yet understood, research has been exploring potential genetic candidates. For example, the ADRA2B polymorphism encodes a protein that increases noradrenergic (NA) transmission in the brain by inhibiting its release presynaptically (Fairfield et al., 2019). As a result, increased NA availability is hypothesized to facilitate the encoding of emotionally salient events in long-term memory (de Quervain et al., 2007). However, whether this effect also aids emotional working memory remains to be confirmed. Whereas Mammarella et al. (2016) found that ADRA2B deletion carriers (vs. non-carriers) were better at remembering positive words during a working memory task and had better recognition memory for words read with a positive intonation, the effect was not replicated in a later study by the same team (Fairfield et al., 2019). There, the presence of a second neurotransmitter regulating gene (cannabinoid receptor type 1, CB1) together with the ADRA2B was necessary to enhance positive working memory. Taken together, while promising, the set of disparate findings was recently confirmed by a meta-analytic investigation of neuroimaging emotional working memory studies, which failed to identify brain regions that were consistently more activated during positive relative to neutral stimuli (Schweizer et al., 2019). As such, the search for the boundary conditions (e.g., task-relevance, stimulus type, trait anxiety, stress level, etc.) under which positive mood and stimuli influence the neural correlates of working memory will necessitate additional research.

4.3. Shifting

Shifting broadly refers to the capability to move between cognitive mental sets in a flexible manner. In general, the prefrontal, medial, cingulate premotor, and parietal brain regions are implicated across a range of shifting tasks (Collette et al., 2005; Wager et al., 2004). In the earliest cognitive science work on this topic, Dreisbach and Goschke (2004) induced positive mood states by showing participants positive

images before performing a switching task. This positive mood manipulation selectively increased or abolished the switch costs (i.e., the cognitive effort required to move between tasks), depending on the relevance of the learned stimulus-response associations (i.e., learned irrelevance and perseveration, respectively); however, positive mood enhanced cognitive flexibility at the cost of decreased perseveration and increased distractibility (Dreisbach and Goschke, 2004). Since this seminal finding, minimal neuroimaging research has directly focused on understanding how positive mood, emotions, and stimuli influence switching capabilities. One series of lab studies illustrated that in some contexts, positive emotions and moods increase shifting and cognitive flexibility relative to other mood states (Putkinen et al., 2017; Storbeck et al., 2019), which is theorized to facilitate selective attention toward new opportunities and rewards in the environment (Carver, 2003; Tamir and Robinson, 2007). Providing additional support for the notion that positive emotions increase cognitive flexibility, an fMRI study showed that switch costs were reduced after viewing positively valenced images and increased after viewing negatively valenced images (Wang et al., 2017). These behavioral results were related to decreased activity in dACC in the positive viewing condition and increased dACC activity in the negative viewing condition, potentially indicating a need for additional top-down control following the presentation of negatively valenced images. Subramaniam et al. (2009) relatedly reported that individuals in a positive mood were able to solve insight problems more readily, and this behavioral outcome was associated with preparatory ACC activity during the interval preceding each problem. While this is an indirect measure of cognitive flexibility, the findings from this study suggest that positive mood may improve insight and related cognitive flexibility via modulating attentional control mechanisms related to ACC function. In order to contribute to optimizing human capacity for solving problems in a flexible manner, additional neuroscience research in this area is warranted, especially work that accounts for the role of arousal and motivation, in order to elucidate how brain networks that implement cognitive flexibility are biased by positive emotions.

In summary, positive mood, emotions, and stimuli appear to differentially modulate specific cognitive control processes, and additional neuroscience research across cognitive domains would contribute to developing more unified theories regarding how positive moods, emotions, and stimuli influence cognitive control and vice versa. Moreover, depending on the cognitive control function being probed, studies have either used positively valenced emotional faces (e.g., happy faces) and to a lesser extent positive scenes or positive words (reflecting a range of positive emotions). Yet, investigation of other positive affective experiences and emotions are lacking (e.g., contentment, pride, joy, elation, or merriment, etc.). While there is some evidence that positive moods and emotions promote the capability to direct selective attention towards new opportunities and rewards in the environment (Carver, 2003; Putkinen et al., 2017; Storbeck et al., 2019; Tamir and Robinson, 2007), other research suggests otherwise (Harmon-Jones et al., 2013; Hunt-singer et al., 2012). Many studies have neglected to assess and account for arousal and motivation which may be contributing to the contradictory findings and theories. Advancing our understanding regarding how positive emotions and moods could influence cognitive control in a beneficial manner also has significant potential to strategically inform innovations in evidenced-based treatments for psychological disorders that are hallmarked by impairments in cognitive function, such as depression (Levin et al., 2007).

5. Positive emotions and wellbeing across the human lifespan

Global population research shows that general happiness and its constituent parts - eudemonia, hedonia, and life satisfaction - change over the course of the human lifespan (Stephens et al., 2015). Measures of happiness and life satisfaction modeled over the lifespan tend to follow a U-shaped curve in most world populations (Blanchflower and Oswald, 2008). Thus, happiness decreases progressively from early adulthood

into the mid-to-late forties where it reaches a nadir and progressively increases again. These findings also show that average happiness levels reached by individuals in their sixties are very similar to those experienced by individuals in their twenties. However, evidence of a decline in happiness in very old age has been suggested (Blanchflower and Oswald, 2008). For example, centenarians show significantly lower levels of positive affect than their octogenarian peers (Cho et al., 2013), although positive affect among centenarians is enhanced in the presence of better cognitive and physical function at levels similar to the positive affect reported by octogenarians. Other studies suggest that this decline in positive affect seen in very late life may be driven by a small proportion of individuals with the vast majority (~90 %) reporting stable levels of wellbeing until death (R. A. Burns and Ma, 2015). Similarly, other measures of mental health tend to improve with age with the prevalence of anxiety and depressive disorders generally decreasing linearly across the adulthood years (Alonso and Lépine, 2007; Gum et al., 2009; Hollingworth et al., 2010).

Contrary to conventional wisdom and expectations that normative late life physical and cognitive declines would be mirrored in declines in emotional wellbeing, happiness and positive affectivity often show significant stability and even increases in the later years (Carstensen et al., 1999; Charles and Carstensen, 2010). Indeed, greater capacity for emotion regulation is observed as age increases from childhood into adulthood (Charles and Carstensen, 2007). By the time individuals enter late adulthood, the increased capacity for emotion regulation in healthy adults is often contrary to changes that the body experiences via increased physiological challenges and demands. The decline in physiological function that is normative in late adulthood may augment the capacity for superior emotion regulation (Carstensen et al., 1999; Charles and Carstensen, 2010).

Emotion regulation refers to processes that govern the type, occurrence, and intensity of felt and expressed emotions that are inextricably linked to distinct but overlapping neural emotion circuits (Gross, 1998; Urry and Gross, 2010). Emotion regulation varies considerably over the lifespan in concordance with individuals' changing capacities – increases or declines in such capacities – for emotion regulation (Gross, 2013). Gross (2013) explains that emotion regulation during the early years is predominantly influenced by external agents (e.g., adults such as parents and caregivers); with maturation and the further development of motor and higher-order cognitive abilities as well as the prefrontal regions of the brain, emotion regulation processes become increasingly internally controlled; finally, in the late life years, improved capacity for emotion regulation may explain the higher levels of self-reported happiness and positive affectivity. However, the neurocognitive and psychological aging processes involved in emotion regulation that facilitate happiness are not well characterized. In order to address this gap and to provide a comprehensive developmental framework for understanding happiness, the following sections review the evidence on changes in happiness and wellbeing across the lifespan and consider the extent to which brain aging, neurodegeneration, and cognitive decline may underlie some of these changes.

5.1. Brain aging and neurodegeneration: implications for wellbeing

Neurobiological theories of positive emotion and happiness should, if robust, be compatible with happiness trajectories and changes in brain function observed across the lifespan. Based on the hallmarks of brain aging research, this section yields insights into the neurophysiological correlates associated with positive emotions and wellbeing.

Brain Structure and Function. Extensive research has aimed to characterize macro- and microscopic cerebral changes with age (Coffey et al., 1998; Esiri, 2007; Ge et al., 2002a, 2002b; Raz, 2000; Raz et al., 2010). Imperfect, but useful, indices of these changes include volumetric measures of cortical and subcortical brain regions measured at different ages across adulthood. These studies show that after reaching a maxima in approximately the mid-twenties, the vast majority of brain structures

decrease in volume at a progressively accelerating rate (Pfefferbaum et al., 2013; Potvin et al., 2016; Walhovd et al., 2011). There is evidence for lateralized effects with regard to aging in the cerebrum, with the left hemisphere experiencing greater shrinkage across the lifespan (Thambisetty et al., 2010), which is another counterintuitive finding since approach-related and positive emotions have historically been conceptualized as lateralized to the left hemisphere (Davidson, 1992; Davidson and Irwin, 1999; Demaree et al., 2005; Wheeler et al., 1993; also see section 3.2).

In addition to structural brain changes observed in aging, several functional changes also occur, particularly in cerebral activity in response to emotions. The amygdala, mPFC, and anterior cingulate cortex (ACC) are key structures implicated in affective processing (Mather, 2016). During aging, functional connectivity between amygdala and mPFC decreases (Nashiro et al., 2012), which is correlated with an improved recall of positive emotions compared to negative emotions. Another study comparing younger and older adults found that older people remembered relatively more positive feelings and that retrieval of negative memories elicited more activation in mPFC and ACC and less activity in the amygdala in older individuals while the reverse pattern was observed in younger individuals (Ge et al., 2014). Activity in mPFC/ACC was inversely correlated with the reported intensity of negative events which is consistent with a down-regulation of negative feelings by the mPFC in older adults. The decrease in mPFC/ACC connectivity observed in aging is also associated with increased positive bias in emotion processing (Sakaki et al., 2013). Relating structural and functional findings, an age-related shrinkage of the amygdala may contribute to decreased salience of negative feelings (Cacioppo et al., 2011).

Affective modulation of hippocampus also appears to play a significant role in facilitating a positive memory bias in older adults (Addis et al., 2010). Compared to younger adults, older adults showed increased functional connectivity among vmPFC, dmPFC and OFC along with affective modulation of hippocampus that was distinctly observed during encoding positive images, but not negative images (Addis et al., 2010). In particular, Addis et al. (2010) showed that vmPFC and amygdala strongly influenced hippocampal activity when older adults encoded positive information, but in contrast, thalamic influence on hippocampal activity was observed for younger adults. There were no age-related differences observed in connectivity during encoding negative stimuli. This may indicate that the bias for remembering positive emotions in older adults – the positivity effect (Carstensen and Mikels, 2005) – is due, at least in part, to age-related differences in encoding stimuli of positive (but not negative) valence. Together, the neurophysiological research in this area suggests that the positivity effect and associated experiences of happiness are supported by distributed brain networks that are more resilient and/or more adaptive to neurodegenerative processes associated with aging; moreover, the relative resilience of the right hemisphere may contribute to preserved or increased levels of happiness in aging. However, this cannot explain the decrease in wellbeing, happiness, and life satisfaction observed until middle-age, and this explanation is also not consistent with the fact that brain regions associated with the DMN generally follow a pattern of progressive decline in volume and connectivity with age (Vidal-Piñeiro et al., 2014). In sum, it appears that cerebral structures implicated in positive emotions and happiness (e.g., OFC, dlPFC, insula) may be less affected by neurodegenerative processes, and may at least partly explain the relative resilience and increase in happiness during aging. Moreover, changes in connectivity and activation patterns in mPFC, ACC, hippocampus, and amygdala are also likely to contribute to this effect.

5.2. Improving with age: socioemotional selectivity and emotion regulation enhance experience of positive emotions

Socioemotional selectivity theory states that with age, individuals are characterized by a stronger motivation for emotion regulation so as

to enhance their experience of positive affect (Carstensen, 1998; Carstensen et al., 1995). This motivational focus replaces the emphasis on information-seeking as a motivational goal, which is more normative during the earlier developmental periods in life. The socioemotional selectivity theory (Carstensen, 1998; Carstensen et al., 1995) explains that the increased salience of emotion regulation as people age derives from the perspective that one's future time is limited such that the need for feeling good at the present time surpasses the need for information related to the future. From this perspective, happiness and, more generally, positive emotional states, gain premium value as we grow older. This greater value comes from a desire to gain greater emotional meaning from life in the late adulthood years rather than a desire for greater hedonism per se (Carstensen et al., 2003).

One mechanism through which enhanced positive emotion regulation occurs as people age is through changes in cognitive processing, including greater attention to and encoding of positive information relative to negative information (Carstensen et al., 1999; Carstensen and Mikels, 2005). Isaacowitz and Blanchard-Fields (2012) proposed that cognitive processes (e.g., selective attention and cognitive control) in older adults are closely related to emotion regulation, which in turn, determines success in the ability to enhance positive affect. Another mechanism is through a more selective approach in choosing individuals with whom to engage socially (Carstensen, 1998; Carstensen et al., 1995, 2003). With aging, a shift is observed toward restructuring one's social networks and contacts such that they are constituted of fewer but maximally emotionally meaningful relationships that can be expected to bring happiness and gratification (Carstensen, 1992; Lang and Carstensen, 1994). In long-term relationships that are not easily terminated (e.g., with a spouse or family member), older adults are more likely to emphasize the positive aspects of the relationship while deemphasizing the negative aspects (Bookwala and Jacobs, 2004; Carstensen et al., 1995).

Cacioppo and colleagues offer an explanation rooted in age-related changes in the brain to account for the greater experience of happiness in late life that is predicted by the socioemotional selectivity theory (Todorov et al., 2011). Using their aging-brain model, Cacioppo et al. (2011) theorized that functional changes in the amygdala occur with age, whereby activation of the amygdala is diminished to negative stimuli but remains stable to positive stimuli. The aging-brain model views this age-related change in the amygdala as responsible for the lower emotional arousal to negative stimuli and, in turn, diminished cognitive processing and memory for negatively-valenced material. Ochsner and Gross (2005) have followed a different line of reasoning and proposed the cognitive-control model, according to which age related decreases in amygdala activity do not exhibit amygdala impairments, as the aging-brain model implies, but are due to prefrontal emotion regulation processes that decrease amygdala response for negative but not for positive stimuli. In sum, the aging-brain model assumes that the higher levels of happiness evidenced with age is the result of the age-related functional decline in the amygdala, while the cognitive control model argues it is explained by the prefrontal regulation of emotional processing. Additional research is needed to reconcile the discrepancies in these models of age-related changes in positive emotion regulation.

One area contributing to neuroprotective processes and relevant to explaining eudaimonia trajectories across the lifespan relates to meditative practice (also see section 8.1). Mounting evidence suggests that mindfulness and other forms of meditation result in lower levels of anxiety, depression, and pain, and higher levels of wellbeing and life satisfaction (Allen et al., 2017; Goyal et al., 2014; Kumar and Ali, 2003). Neurobiologically, differences in brain volume, activity, and connectivity between meditators and non-practitioners have been found in brain areas overlapping substantially with those thought to be implicated in hedonics and eudaimonia (Fox et al., 2014, 2016). The brains of meditators appear "younger" than those of non-meditators (Luders et al., 2016) and show less activity in the DMN (Brewer et al., 2011). Since

lower levels of DMN activity is associated with higher measures of happiness (Y. Luo et al., 2016) and with lower anxiety and depressive symptomatology (Coutinho et al., 2016), its contribution to wellbeing and eudaimonia appears justified. Moreover, less neurodegeneration, most notably in the hippocampus might suggest neuroprotective effects (Kurth et al., 2015, 2015; Luders et al., 2016). From an aging perspective, meditative practice appears to be associated with increased cortical thickness in the right insula and right dlPFC, with a stronger effect seen in older participants (Lazar et al., 2005).

6. Healthy social contexts bolster positive affect

From an evolutionary perspective, positive emotions are theorized to facilitate survival via fostering strong social relationships and connections (Fredrickson, 1998). Healthy social relationships and connections across the lifespan augment positive emotions and promote overall wellbeing. Humans are innately social beings and a multitude of physical and psychological benefits are gained from positive social support and healthy relationships with others. From early infancy through adulthood, play (section 6.2) is a social behavior infused with positive emotions that serves to strengthen bonds and connections. However, the research presented in this next section highlights the critical role of healthy social relationships in laying the groundwork for happiness and wellbeing across the lifespan.

6.1. Social relationships and connectedness promote thriving

Strong interdependent and healthy relationship bonds are critical for human survival, and positive emotions contribute in complex ways to this equation (Pressman et al., 2019; Sbarra and Coan, 2018; Shiota et al., 2014, 2017). Whereas evolutionary theories generally suggest that negatively valenced emotions support short-term survival (Stockdale et al., 2020), positive emotions such as joy, contentment, interest, and love have been broadly theorized to increase physical, intellectual, and social capacities, connections, and resources that facilitate survival in the long run (Fredrickson, 1998). Relatedly, the size of social networks increases longevity and enhances the capability to cope with stressors (Pearce et al., 2017a). However, specific positive emotions such as pleasure may also serve to reinforce behaviors that lead to short-term survival, such as goal-directed consummatory behaviors related to food, procreation, and social connections (Berridge and Kringelbach, 2015). Momentary happiness often increases when spending time with friends and family (Csikszentmihalyi and Hunter, 2003), and our social relationships are enriched through the sharing of positive emotions (Campos et al., 2013). Capitalization, or the upregulation in a relationship partner's positive emotion has beneficial bonding effects for both members of the relationship (Gable et al., 2004). Strong relationship bonds mitigate the neural response to threat, especially while holding hands with a romantic partner (e.g., less threat-related activity in the right anterior insula, superior frontal gyrus and hypothalamus; Coan et al., 2006), and research implementing a similar hand-holding paradigm illustrated that social touch reduced the neural response to pain (e.g., reduction in activity in the posterior insula, ACC, OFC, vmPFC, and dlPFC; López-Solà et al., 2019). Collaborative social relationships appear to lead to increased capabilities across a range of functions that reduce threat response, support thriving, and in turn, cultivate positive emotions and wellbeing.

Social thriving is also associated with more connected, longer, happier lives, quicker recovery from illness, and reduced risk for physical or mental health problems (Brackett et al., 2011; Holt-Lunstad et al., 2010; Pearce et al., 2017a; Sbarra and Coan, 2018). Notably, the social experience of positive emotions in humans is communicated and shared through embodied expressions. Physical expressions that signal emotion states capture attention particularly well (Calvo and Nummenmaa, 2008). This is in part the case because emotion states must be navigated and regulated for social success (Fridlund and Russell, 2006). Humans

automatically and seemingly effortlessly send information through the channel of expression (Ambady and Rosenthal, 1992; Darwin, 1873). We signal pride when we raise our arms in joy (Tracy and Matsumoto, 2008), prosocial orientations when we smile (Ruiz-Belda et al., 2003), and intense happiness when we cry tears of joy (Aragón and Bargh, 2018; Aragón and Clark, 2018). Expressing, perceiving, and regulating positive emotions remains critical to facilitating healthy social connections and the positive benefits that they confer.

The Social Baseline Theory (SBT; Coan et al., 2014; Coan and Sbarra, 2015; Sbarra and Coan, 2018) offers a transdisciplinary neuroscience-based perspective regarding the critical nature of social relationships in enabling wellbeing and positive health outcomes. SBT is based on the premise that the human brain evolved in order to maintain social relationships that facilitate the achievement of shared goals. Per this theory, adaptation occurred to support optimal function within the context of interdependent social environments and the human brain constructs the representation of social partners as “efficacy-enhancing extensions of the self, which allows it to budget its cognitive and physiological resources as if the cognitive and physiological resources available to others were available to the self as well” (Sbarra and Coan, 2018, p. 43).

Expending neural and associated behavioral resources to meet environmental demands is theorized to be more efficient in the context of available social resources (Coan et al., 2014; Coan and Sbarra, 2015). Social resources are theorized to influence affective responses, which in turn modulate neurophysiology and related health outcomes (Sbarra and Coan, 2018), yet additional research is needed to support the postulated neurophysiological and psychological pathways in this theory, especially with regard to the specific role of positive emotions, which are generally linked with high-quality social relationships and positive health outcomes (Pressman et al., 2019). As discussed above in section 3.1, oxytocin, a hormone neuropeptide, is implicated in both affiliative behaviors (Eisenberger and Cole, 2012) and processing positive socioemotional cues and stimuli (Marsh et al., 2010) and may play a critical role in understanding the link between social relationships and positive emotions. Affiliative caregiving behaviors modify neural correlates in caregivers (Nitschke et al., 2004), and offspring alike (Eisenberger and Cole, 2012). Animal research has robustly highlighted the critical role of subcortical reward-related circuitry (e.g., ventral striatum, septal area) in caregiving behaviors, and activity in these regions (in conjunction with reduced amygdala activity) is increased in humans experiencing social connections (Eisenberger and Cole, 2012). Ventral striatum, septal area, and amygdala contain a high density of oxytocin and opioid receptors (Eisenberger and Cole, 2012), which in part may modulate the experience of positive emotions that emerge during healthy social connectedness. Much of the research in this area has been conducted in an experimental, but cross-sectional manner. It is critical that future developmental neuroscience research longitudinally investigate the impact of caregiving behaviors and attachment on the development of positive emotions in offspring (as well as the caregivers) in order to identify how social connection modifies neural function and neurotransmitters associated with positive emotions to mitigate negative experiences of threat, pain, and stress and ultimately promote thriving and wellbeing over the lifespan.

6.2. Play

Across the human lifespan, positive emotions are generally experienced during play which is a critical form of social interactions that builds relational capacities and facilitates general wellbeing (Nijhof et al., 2018; Russ et al., 2009; Storli and Sandseter, 2019). Play occurs across cultures, and play is observed in mammalian species, certain bird species and reptiles (Nijhof et al., 2018). Given that play requires a significant time and energy expenditure for humans and animal species alike, play likely serves an important evolutionary purpose facilitating survival (Nijhof et al., 2018). For children, play enables the development

of a broad repertoire of social capacities as well as affective processes, including understanding and regulating emotions as well as empathy (Nijhof et al., 2018; Russ et al., 2009). Play also scaffolds cognitive development in the domains of problem-solving and creativity (Nijhof et al., 2018). While the scientific literature has not reached a consensus regarding the definition of play, it is typically agreed upon that play does not have any readily obvious practical purpose in the moment that it is occurring and it typically reflects repeated behaviors that are spontaneous, pleasurable, and rewarding (Nijhof et al., 2018). In humans, play represents a wide range of experiences and activities, including attunement/mimic play, body play and movement, object play, social play, imaginative and pretend play, storytelling-narrative play, and creative play (National Institute for Play, 2018). Despite the importance of play for supporting healthy development and wellbeing, minimal neuroscience research has been conducted regarding play in humans, so we have focused this section on the findings from the animal literature where play is less multifaceted and typically divided into three primary domains: locomotor play, object play, and social play (Nijhof et al., 2018).

Play has long fascinated behavioral scientists around the globe (e.g., Brownlee, 1984), since animals often appear to be enjoying themselves when playing (Martin and Bateson, 1985). While this intuitive impression of joy may be a good first indication (Bekoff, 2015), more conclusive evidence comes from recent advances in neuroscience that support the view that play is a rewarding behavior. In order to evaluate the theory that play is governed by older brain circuitry, early research studied play in decorticated rats, and confirmed that rats still initiate play in the absence of the neocortex, albeit with some subtle changes relative to controls (e.g., Panksepp et al., 1994). Greater detail about the neural structures associated with play has emerged through the application of techniques such as deep brain stimulation and mapping of brain ‘activation’ using immediate early genes such as *c-fos* (Gordon et al., 2002). This research has implicated a number of subcortical centers in play although as yet no clear ‘play circuitry’ has emerged (Siviy and Panksepp, 2011). These subcortical areas include: the parafascicular region of the thalamus (PFA) likely because of its role in processing somatosensory inputs (e.g., Bell et al., 2009), the prefrontal cortex (Gordon et al., 2002) and striatum (Siviy and Panksepp, 1985) that likely contributes to creating the fluid motor movements seen in play; and the periaqueductal gray (PAG; Gordon et al., 2002) that may have a role in switching between the different behaviors involved in play. In more recent research, other regions have been implicated in play including: the habenula (van Kerkhof et al., 2013), amygdala, and nucleus accumbens (e.g., Trezza et al., 2012) all of which have roles in reward processing and coordinating emotional responses.

In terms of neurotransmitters and neuromodulators, brain reward systems are involved in social play in rats (Vanderschuren et al., 1997), and social play in rats is used as a model to study the neuropharmacology of ‘pleasure’ (Trezza et al., 2010). Although it is rather difficult to separate play into discrete hedonic (‘liking’) and motivational (‘wanting’) components, it is clear that several neurotransmitter systems play overlapping roles in control of rat social play (Berridge et al., 2009). Endogenous opioids, for example, are widely released in the brain during play (Vanderschuren et al., 1995) while low doses of opioid agonists increase and opioid antagonists decrease play (Niesink and Van Ree, 1989). Dopamine has also long been implicated in play behavior, as dopamine antagonists generally inhibit play (e.g., however, the role of dopamine in play is not particularly straightforward as dopamine agonists can both increase or decrease play and with only modest sized effects; Beatty et al., 1984). More recent work has shown other neurotransmitters to be implicated in play including endocannabinoids, as indirectly enhancing activity of the endocannabinoid system makes rats more playful, although direct endocannabinoid agonists paradoxically reduce play (Trezza and Vanderschuren, 2008). Most recently, there has been renewed interest in the role of the neuropeptides vasopressin and oxytocin in play and specifically whether they provide an explanation for sex differences in play behavior (Reppucci et al., 2018). The

complexity of the neurochemical substrates for play becomes even more apparent when the interactions between neurotransmitter systems are considered. For example, opioids and cannabinoids interact to modulate social play, while dopaminergic neurotransmission reduces the effects of endocannabinoids but not opioids on play behavior (Trezza and Vanderschuren, 2008). The recent finding that oxytocin neurons directly control dopamine signaling (Xiao et al., 2017) perhaps to bias behavior towards socially rewarding interactions at the expense of exploration, also gives further indication of the intricate system implemented in the neurotransmitter modulation of play behavior (Trezza et al., 2010). The involvement of neurotransmitters in play provides support for play being a positive (enjoyable) experience.

Likewise, infants of all great apes have been found to display typical vocalizations in positively reinforcing situations (e.g. when they are tickled; Ross et al., 2009). There is evidence that these vocalizations are evolutionarily homologous to human laughter (Panksepp, 2005b; Ross et al., 2009). Accordingly, vocalizations in response to positive stimuli have also been increasingly investigated in other species (Panksepp, 2005b). Rats for example emit typical ultrasonic vocalizations (USVs) in the range of about 50 kHz, while engaging in playful interactions (Burgdorf et al., 2001; Knutson et al., 1998; Panksepp, 2005b) or being tickled by a human experimenter (Panksepp and Burgdorf, 2000). Interestingly, these 50 kHz USVs, referred to as “rat laughter” in the literature, are also of interest to the discussion that positive emotion (‘liking’) and motivation (‘wanting’) components of reward-seeking behaviors are dissociable (see also Berridge et al., 2009). For example, they tend not to be sustained following optogenetic stimulation of dopamine neurons despite the persistence of motivated behavior (Scardocho et al., 2015). Pharmacologically, cues associated with psychostimulants (whether they directly elicit USVs or not) have been shown to increase USVs in drug free tests (e.g., Panksepp and Burgdorf, 2000). This suggests that 50 kHz USVs reflect the positive emotional state engendered by the anticipation of positively rewarding outcomes, and perhaps further that such positive emotional states have a role in organizing appropriate behavioral responses (Barker, 2018). However, whether such “laughing-like” vocalizations also occur in other species and can therefore be used as an “across-species-indicator” of positive emotional states, is not clear yet. With regard to humans, the literature on laughter is complex, but it is mainly considered to be a social emotion associated with bonding, agreement, affection, and emotional regulation (Oveis et al., 2016). Laughter shapes social behavior (e.g., play, cooperation, cohesion), indicates safety, and also serves to detect and communicate status and dominance in some contexts (Oveis et al., 2016).

7. Environmental factors facilitate positive emotions and healthy outcomes

Beyond contextual factors such as strong social relationships and healthy social interactions, environmental factors are also critical to cultivating positive emotions and wellbeing (Townsend et al., 2018). With the advent of mobile EEG technologies, human neuroscience research has recently begun to study changes in brain function as people ambulate around a park or bike in natural settings (Scanlon et al., 2020). Other research has focused on studying how “built-environments” such as schoolyard park designs facilitate play, physical exercise, and positive emotions, and enhance community-based relationships (Bates et al., 2018). It is becoming increasingly common for city planners and architects to guide structural and interior design implementations for public spaces such as hospitals, libraries, schools, and parks in a manner that facilitates wellbeing (Panagopoulos et al., 2016), with the general notion that increased access to green space improves wellbeing (Conniff and Craig, 2016; Panagopoulos et al., 2016). Biophilic, salutogenic, and restorative designs are becoming increasingly popular approaches for building internal and external spaces that promote healing and optimize wellbeing (Africa et al., 2019; Coburn et al., 2017; Mazuch, 2017). On a

smaller scale, researchers are beginning to explore how architectural characteristics of home foster (or hinder) family relationships and developmental trajectories (Graham et al., 2015). These newer research arenas are critical to informing strategies to enhance wellbeing for individuals and their communities and ambulatory devices that garner psychophysiological measurements remain promising for advancing our understanding of how people perceive and experience different environmental contexts (Coburn et al., 2017; Scanlon et al., 2020). Despite limited human neuroscience research in this area, the animal literature has developed a large body of research focused on “environmental enrichment,” which refers to the addition of social and physical resources into the environments of domesticated and confined animals, and has been defined as environmental manipulation that improves the biological function of the animal (Newberry, 1995).

Since the discovery that enrichment leads to positive effects on brain development and behavior (Rosenzweig et al., 1962), enrichment has been widely used to study the effects of the environment on brain development and particularly on neuroplasticity and neurogenesis (Praag et al., 2000). A variety of environmental manipulation approaches have been used to manipulate affective state, ranging from unpredictable housing events (Harding et al., 2004) and the removal/provision of environmental enrichment (Brilot et al., 2010; Burman et al., 2008) to the variation of lighting conditions (Burman et al., 2009) or the use of pharmacological treatments (Rygula et al., 2014, 2014, 2015; Stracke et al., 2017). However, within this domain, there has been surprisingly less of a focus on the role of enrichment in generating positive affect.

Due to the increasing awareness of the importance of exploring not only negative but also positive emotional states, several studies have explicitly applied ‘positive treatments,’ such as the provision of environmental enrichment (Brydges et al., 2011; Richter et al., 2012) or food-based rewarding events (e.g., Burman et al., 2011). Although explicit indicators for the existence of happiness or happy moods in animals do not exist, a recent study in Syrian hamsters concluded that “we cannot say whether the hamsters in our study felt happy in their enriched housing, but the changes in cognitive processing of ambiguous cues certainly suggest enriched hamsters became more optimistic about the likelihood of future reward when faced with uncertain information” (Bethell and Koyama, 2015, p. 15). Similarly, children and families experience increased emotional and physical wellbeing when they have access to stable, good quality, and affordable housing resources that are not overcrowded (Clair, 2019).

7.1. Environmental manipulations influence cognitive biases reflecting affective states

Cognitive components of emotional processing in animals have been proposed to constitute a novel and powerful tool for the assessment of emotional valence (Mendl et al., 2010b). Affective states in animals are often inferred from different physiological and/or behavioral measures (Abou-Ismael et al., 2007; Burman et al., 2007; Hurst et al., 1999; Mason et al., 2001), yet these assessment tools have certain limitations such as difficulties of interpretation or sensitivity to emotional arousal but not valence (Paul et al., 2005). Indeed, housing conditions have been shown to impact cognitive function in animals. In a seminal study, Harding and colleagues (Harding et al., 2004) introduced a novel technique to determine the affective state of rats by quantifying changes in judgment bias by training the animals on a simple discrimination task. Animals in a negative affective state were more likely to interpret an ambiguous cue as predicting a ‘bad event’ (“the glass is half empty”), while those being in a positive affective state were more likely to judge it in a positive or optimistic way (“the glass is half full”). Since then, cognitive bias studies have been accumulating to gain insight into affective states in a range of animal species, including rats (e.g., Burman et al., 2009; Enkel et al., 2010), mice (Kloke et al., 2014; Novak et al., 2015), starlings (Brilot et al., 2010; Matheson et al., 2008), dogs (Burman et al., 2011; Mendl

et al., 2010a), sheep (Doyle et al., 2010), chicks (Salmeto et al., 2011), pigs (e.g., Murphy et al., 2013; Stracke et al., 2017), horses (Briefer Freymond et al., 2014; Hintze et al., 2017), and rhesus macaques (Bethell et al., 2007).

In pigs, the application of a cognitive enrichment task was found to down-regulate both opioid and neuropeptide Y (NPY) receptors in the amygdala (Kalbe and Puppe, 2010). A comprehensive analysis of protein expression in the nucleus accumbens of enriched and cocaine self-administering rats found uniquely different proteomic expressions in response to cocaine self-administration and enrichment (Lichti et al., 2014). Neurotrophins such as IGF1 may have a role in linking physical exercise to positive affect (Burgdorf et al., 2016; Torres-Aleman, 2010), and it is also known that immediate early genes (IEG; Bahrami and Drablos, 2016) which can be rapidly induced by the sensory experience of enrichment (Brown et al., 2018) have roles in both neuroplasticity and consolidation of emotional memories (Mukherjee et al., 2017). Given this knowledge, further work is required to understand the neural basis for enrichment-induced changes in positive affect including de-confounding the effects of exercise from those of social and environmental interactions and the relationships between neuroplasticity processes and positive affect.

7.2. Environment enrichment attenuates illness

There has been growing interest in human research regarding the link between mental wellbeing and physical health as indicated by immune response (Pressman et al., 2019). Environmental enrichment in mice attenuated the effects of a flu infection (Jurgens and Johnson, 2012) and lipopolysaccharides (Ji et al., 2017) and enriched housing of pigs reduced the impact of a co-infection with two common respiratory viruses (van Dixhoorn et al., 2016) and affected levels of autoantibodies (L. Luo et al., 2017). In humans, there is some evidence for a relationship between positive emotions and inflammatory cytokines with more positive emotional states being associated with lower levels of IL-6 (Stellar et al., 2015). However, there is no data in animals to substantiate these findings. Although Boissy et al. (2007) highlighted the need for more research in this area, there appears to have been little progress in identifying direct immune markers for positive emotional states in animals.

8. Cultivating wellbeing: modulating neurophysiological correlates of positive emotions

As cumulatively illustrated in the previous sections of this review, human and animal neurophysiology implemented in positive emotions and wellbeing reflect dynamic, flexible, and adaptive processes that occur throughout the lifespan. Given the persistent malleability of the human brain and nervous system, it follows that engaging in practices and interventions that enhance positive emotions and associated neural correlates will contribute to promoting happiness and wellbeing. Focusing attention on present moment experiences is prospectively related to happiness (Killingsworth and Gilbert, 2010); thus, in this section we review the neural correlates of mindfulness meditation practices (section 8.1) and flow states (section 8.2), both of which involve a deep focus on the present moment and are linked to experiencing positive emotions.

8.1. Meditation and contemplative practices

Mindfulness meditation refers to secular practices that are derived from Buddhist contemplative traditions (Wielgosz et al., 2019), and typically involves modulating the focus of attention on experiences unfolding in the present moment, coupled with a nonjudgmental awareness (Kabat-Zinn, 2003). A range of attentional capabilities is honed via mindfulness meditation including initiating, directing, and sustaining attention while also increasing one's meta-awareness of

interoceptive experiences (Dahl et al., 2015). According to Buddhist contemplative wisdom, rather than happiness per se, *sukha* is thought to result from sustained engagement in meditative practices. *Sukha* refers to a "state of flourishing that arises from mental balance and insight into the nature of reality. Rather than a fleeting emotion or mood aroused by sensory and conceptual stimuli, *sukha* is an enduring trait that arises from a mind in a state of equilibrium and entails a conceptually unstructured and unfiltered awareness of the true nature of reality." (Ekman et al., 2005, p. 60).

Grounded in contemporary affective science theories, meditation practices are postulated to enhance the capacity for and experience of positive emotions (Garland et al., 2015; Wielgosz et al., 2019), and promote wellbeing (Dahl et al., 2015). Despite the burgeoning neuroscience research on mindfulness and positive emotion, few theoretical models exist to map the processes via which mindfulness specifically enhances the experience of positive emotions. Garland, Farb, Goldin, and Fredrickson (2015) propose that mindfulness broadens cognitive scope which, in turn, bolsters the capacity for savoring, or positive emotion regulatory processes. Wielgosz et al. (2019) theorize that mindfulness meditation practices modify positive valence systems related to approach-related behaviors through enhanced emotion awareness, modulations in emotional reactivity, increased use of cognitive reappraisal, and alterations in reward processes.

Changes in neurophysiological activity (Davidson et al., 2003; Davidson and Lutz, 2008; Desbordes et al., 2012; Fox et al., 2016) and immune function (Davidson et al., 2003) have been observed during and following mindfulness meditation. A meta-analysis showed that convergent changes in cortical brain function are observed in structures (e.g., insula, dACC, left PFC/dlPFC, premotor and supplementary motor cortex) across a range of mindfulness meditation practices (Fox et al., 2016). Relatedly, some studies have reported reduced amygdala activity (Desbordes et al., 2012), and increased prefrontal cortical activity (Davidson et al., 2003; Davidson and Lutz, 2008; Fox et al., 2016; Weng et al., 2013). Increased functional connectivity in the DMN has also been observed in individuals who have a long-term meditation practice (Brewer et al., 2011; Jang et al., 2011). Further, many of the brain regions and networks reviewed here (and in section 3.2) are associated with attentional control functions (e.g., dlPFC, dACC; Silton et al., 2010), and are also related to emotion regulation strategies, such as reappraisal (Braunstein et al., 2017; Buhle et al., 2014).

Loving-kindness meditation (LKM) translated from the term *metta*, as "the wish that others find genuine happiness and well-being," (Mascaro et al., 2015, p. 2) is a type of mindfulness meditation that is related to increasing insight regarding human interconnectedness and awareness that we all share the same wish to be happy (Salzberg, 2011). A study that administered six weekly 60-minute sessions of LKM found associations with positive emotions such that LKM was associated with experiencing positive emotions during practice and that these emotions continued after the session ended. Repeated engagement with LKM practice was associated with a cumulative increase in positive emotions (Fredrickson et al., 2008). LKM is also associated with increases in empathy, compassion, prosocial behavior, altruism, and social connectedness (discussed in section 6.1), as well as specific patterns of physiological activity including modulating vagal tone (Kok et al., 2013) and regional brain activity (e.g., dlPFC, orbitofrontal cortex, striatum, ventral tegmental area) that support intertwined social and emotional functions related to positive emotions, reward, and self-referential processing (Bankard, 2015; Fredrickson et al., 2008; Garrison et al., 2014; Kok et al., 2013; Leppma and Young, 2016; Lutz et al., 2008; Mascaro et al., 2015). Compassion training (i.e., a two-week protocol that involved 30 min a day of guided audio instructions to facilitate feelings of compassion toward others) and subsequent altruistic behavior are associated with increased connectivity among dlPFC and nucleus accumbens, which may reflect the capacity to consider others' wellbeing and experience positive emotions in response to caring for others (Weng et al., 2013). A range of mindfulness meditation practices

appear to beneficially enhance the quality and frequency of experiencing positive emotions and modulate associated neurophysiological correlates, and additional research is needed to clarify the key mechanisms (e.g., meditation type, duration, frequency, etc.) that promote an enduring experience of beneficial emotions.

Interventions and strategies for modulating positive emotions should be interpreted within situational and cultural contexts (Miyamoto and Ma, 2011). For example, Miyamoto and Ma (2011) illustrated that participants who followed an Easternized dialectal cultural script that involved striving for balance between positive and negative emotions tended to opt for strategies that regulated positive emotions in a less hedonic manner than Westernized participants. In Japan, experiencing a balance of positive and negative emotions was related to improved ratings of subjective health and fewer physical health symptoms, but this profile was not related to improved health ratings for individuals living in the United States who tended to highly value positive emotions and minimize negative emotions (Miyamoto and Ryff, 2011). These findings point toward the importance of identifying patterns of emotion regulation strategies that are contextually adaptive or maladaptive.

8.2. Flow

Flow is a positive emotional state of optimal experience that involves sustained, task-oriented, goal-driven attention during an intrinsically rewarding activity (Csikszentmihalyi, 2002). Flow is experienced in a broad array of different problem solving situations from artistic activities (de Manzano et al., 2010), to athletics (Jackson et al., 1998, 2001), computer programming, video gaming (Harmat et al., 2015), and many occupational activities. According to Csikszentmihalyi (1988), any activity, mental or physical, can produce flow as long as it is a challenging task that demands intense concentration and commitment, contains clear goals, provides immediate feedback, and is perfectly matched to the person's skill level. A flow state ensues when one becomes so deeply focused on a task that all else disappears. The person experiences a euphoric state of joy and pleasure without strain or effort. Thus, flow is frequently associated with eudaimonia, or self-actualization of the individual (Bonaiuto et al., 2016). While certain activities can certainly increase the likelihood of experiencing flow there also appear to be a variety of other factors, including an autotelic personality that influences whether an individual is likely to experience the flow state (Ullén et al., 2010).

While Csikszentmihalyi and his colleagues (Csikszentmihalyi, 1990, 2014; Peifer and Engeser, 2020) have described numerous situations where people experience flow, much less is known about associated neurocognitive function. One perspective is the characterization of flow as a circumstance where the explicit processing system is relatively inactive and highly practiced implicit behaviors are able to solve the problems at hand (Dietrich, 2004). Dietrich (2004) has argued that this state may be characterized by relatively reduced frontal activity. When the flow state is interrupted or the activity has ended, individuals once again become aware of their past satisfaction. While Dietrich's theory is conceptually appealing, efforts to confirm reduced frontal activity during flow state have not been substantiated. For instance, Harmat et al. (2015) asked participants to report their subjective experience of flow while playing the computer game TETRIS at different levels of difficulty. The self-reported flow state was positively related to several measures of parasympathetic nervous system engagement, but no relationship between frontal engagement as measured by Near-Infrared Resonance Spectroscopy was identified.

The importance of the reward system in flow has been highlighted by several recent studies using several different cognitive neuroscience methods. Using an adaptive difficulty mental arithmetic task with fMRI, Ulrich et al. (2014) found increased activation in the putamen in the dorsal striatum during an experimentally induced flow state. Increases in lateral PFC were also observed. Other research exploring the relationship between flow and the reward system has focused on the

individual's tendency to experience flow states. This has typically been measured using the Swedish Flow Proneness Questionnaire (Ullén et al., 2010), a self-report measure that assesses the frequency of the flow experience in work, maintenance, and leisure activities. Using this measure, several studies have identified the importance of the dopamine D2-receptor such that flow proneness was linked to the higher availability of the dopamine D2-receptor particularly in the dorsal striatum (de Manzano et al., 2013). A recent behavioral genetics twin study suggested that the ability to achieve a flow state is moderately heritable (Mosing et al., 2012). A related study found a link between a striatal dopamine D2-receptor polymorphism and flow proneness establishing the causal importance for the striatal dopamine reward system and flow (Gyurkovics et al., 2016). Thus, it appears that flow critically depends on synchronization of the attentional and reward networks (see Weber et al., 2017 for a review).

Achieving a flow state is a multifaceted process involving multiple neural systems and physiological processes implicated in reward and positive emotions, happiness, and life satisfaction. Given that flow states often occur during an activity, future research investigating flow may consider implementation of a mobile EEG and other wearable sensors to characterize the neurophysiological correlates of flow as they occur in the moment.

9. Harnessing linguistics to guide future research on positive emotions and wellbeing

As noted earlier, The Human Affectome Project set out to capture a broad spectrum of emotions and feelings through linguistics in order to develop an inclusive linguistic framework through which we might examine our scientific efforts in affective neuroscience. The present review examined neurophysiological correlates associated with positive emotions, with implications for happiness and wellbeing. In parallel, other discrete emotions were directly addressed in companion papers included in this Special Issue, such as those examining *sadness*, *fear*, *anger*, *motivation*, and *hedonics*. In addition, other articles focused on actions (*physiological feelings*), temporal dimensions (e.g., *actions*, *anticipatory feelings*), and contextualized emotions within the notion of *the self* and *the social environment*. Although our present work in this review paper is most closely linked to the articles on *hedonics* and *motivation*, many of the topics are deeply intertwined and illustrate many interconnections across these areas of research.

With regard to the pursuit of pleasure, the review on *hedonics* (Becker et al., 2019), found that about two-thirds of the hedonic-classified emotion words were related to concepts of pleasure, while one-third of the words were associated with concepts of displeasure, thus situating hedonics within the frameworks of positive emotions and general wellbeing (present review paper) and also discrete negative emotions (e.g., sadness, anger) reviewed in the other articles (Alia-Klein et al., 2020; Arias et al., 2020). A number of words on the positive emotions/wellbeing word list was related to contentment, which may be associated with reward functions that contribute to a perpetual striving toward homeostasis. Related, Pace-Schott et al., 2019 illustrated the role of physiological feelings in evaluating homeostasis, including feelings related to primitive drives (sex, food, water, air) but also extends to interoceptive/internal sensations (e.g., stomach/bowels, nausea), as well as external states (e.g., temperature, pressure) or energy-related concepts (e.g., sleep). Perturbations to homeostasis may be associated with fundamental drives and motivated/appetitive behaviors in both animals and humans. Reward-seeking behaviors may lead to consummatory actions (e.g., ingestion) as homeostasis is restored (Hsu et al., 2018), and contentment or calmness is achieved. Since these processes are frequently repeated for many homeostatic needs (e.g., hunger, thirst, etc.), perhaps it is not surprising that a good portion of the language that is used for wellbeing is related to contentment. Relatively low arousal positive emotions such as contentment or calmness may represent low-cost affective states that serve to restore physiological resources.

High arousal positive emotions, which are reflected by feeling words such as “radiate,” rejoice,” “triumph,” or “rejoice” likely serve as more effective reinforcers compared to low arousal positive emotions, but high arousal positive emotions may be more costly in terms of physiological resources. The feedback loops created by physiological feelings to restore and maintain homeostasis will be important for future research to take into consideration for generating a comprehensive neurophysiological theory of positive emotions.

A useful outcome of the present analysis of positive emotion words involved the identification of temporal dynamics within these linguistic constructs including being content (present-focused), acting happy, being happy as an outcome (e.g., glad), or seeking improvement (through change; future-oriented). In order to work toward providing cohesion for researchers studying positive emotions, Gruber et al. (2019) offered a conceptual framework for positive emotion constructs that is organized with regard to level of analysis (state, mood, individual differences, and temperament) as well as temporal course (pre-stimulus, online, post-stimulus). The positive emotion (“happiness”) words that were part of the Siddharthan et al. (2018) linguistic study, largely reflected online and post-stimulus states and moods. This is consistent with the notion that while happiness can reflect a mood or state (Watson et al., 1988) it is also often treated as a trait (Lyubomirsky and Lepper, 1999), or an outcome (Myers and Diener, 1996). We observed that an assumed temporal chronology is inherently incorporated into positive emotion words that may parallel psychological constructs from a model of cognitive control (proactive, reactive, and evaluative control; van Wouwe et al., 2010). For example, many human experimental studies have focused on the neural response to perceiving happy facial expressions and positive scenes using trial-by-trial designs to evoke discrete emotional reactivity (reactive component). On the other hand, positive scenes and memory induction procedures have been used to induce (proactive component) a sustained positive mood prior to engaging in task performance. This is mirrored by positive feeling words that refer to general states of being (i.e., mood states) such as being happy (lighthearted, light), or very happy (triumphant, elated, overjoyed, etc.), content (being good, fine, content, ok), or being very content (marvelous, great, keen, tremendous). Similarly, the Siddharthan et al. (2018) linguistics project also indicated words related to ways of acting (buoyant, joyful, merry, jovial - reactive or proactive components) and as a result of a desired outcome (glad - evaluative component). Research on savoring, or the upregulation of positive emotional experiences, has also highlighted the importance of distinguishing the temporal course of savoring from anticipation to savoring the moment to reminiscing (Bryant, 2003). Likewise, work in the temporal course of the reward system has also delineated pursuit from pleasure (Berridge and Kringelbach, 2015). Clarifying the chronological sequelae of emotions and feelings evoked by a positive experience may be a critical link with regard to understanding the neurophysiological correlates of distinct temporal dimensions of positive emotions. For example, anticipating a positive event could be physiologically similar to “wanting”, appreciating an event in the moment may approximate “liking,” and reminiscing about a positive event after it occurs could map onto “contentment.”

Moreover, knowledge obtained by the *actions* group as well as the *anticipatory feelings* group could aid in future development of gaining knowledge of these temporal distinctions. The *anticipatory feelings* group identified twice as many linguistic concepts for their topic as we found in our review of General Wellbeing words, pointing toward the importance of a pending change in the emotional state (e.g., from being apprehensive to being in a state of fear after the event occurred) to achieve homeostasis as an endpoint. Another positive emotion word category that is related to *anticipatory feelings* involves improvement and change (ameliorated, improved, cheered, humored, lightened, etc.) from a less desired state. The nature of emotions that arise out of a change from a negative toward a positive state is relatively unstudied. While positive emotions could arise due to the improved state, negative emotions from

memory or regret of the negative states may simultaneously exist, as is described in mixed emotions, (Larsen and McGraw, 2014). Alternatively, there could be singular positive valence of emotions when a struggle or negative experience is removed or ameliorated (Aragón, 2017; Aragón and Bargh, 2018). Additionally, the positive experiences that arrive from such a shift could represent a blend of positive emotions such as relief and joy (C. A. Smith and Ellsworth, 1987). These positive feelings, whether singular, mixed, or blended in nature have been studied in opponent-process theory (Solomon and Corbit, 1974) and in research on anatomical and functional alterations of reward/motivation circuits in chronic pain that have shown that relief from pain activates reward circuitry (Leknes et al., 2013; Navratilova et al., 2015; Navratilova and Porreca, 2014).

Finally, all of these concepts are central to the interaction of the organisms with their environment and, in a few species, how they perceive themselves. Indeed, the implications of positive emotion constructs for the individual at the neurobiological level of the *self* remains a future area of exploration for affective scientists. In their review of the self, Frewen et al. (2020) conducted a meta-analysis (via the neurosynth database) and highlighted some overlap between the processing of the self (self-referential processing; SRP) and reward-related brain circuitry, indicated a potential entanglement of the two. However, additional brain areas emerged during self-referential processing that were not activated during reward including more abstract concepts of the self, such as Theory of Mind. While this suggests that processing of the self is rewarding, or implicates reward that inherently involves self-reference, it appears solely to be a piece to the puzzle regarding what positive emotions constitute for organisms and the actions needed to bring about that state or to remain in that state (e.g., reward being a rather short-lived experience). From a linguistic perspective, many of the word senses found in the articulated feelings that have been documented (Siddharthan et al., 2018) may offer useful clues for positive emotion researchers to expand research into new horizons.

As a limiting factor, the Siddharthan et al. (2018) linguistics project focused on linguistic terms found in English which retains its hegemony as the “lingua franca” for science communication. While some emotion words may approximate similar cross-cultural meanings, there are emotion words in specific languages that carry unique meanings, such as the Danish term *hygge* which encompasses feelings of coziness, warmth, and wellness, or the term *gigil* in Tagalog that translates as the gritting of teeth and the urge to pinch or squeeze something that is unbearably cute. Related to the positive emotions derived from mindfulness meditation (Section 6.1), *sukha* is a Buddhist (Sanskrit) term that refers to an enduring trait of flourishing resulting from balance, insight, and awareness (Ekman et al., 2005). Related, Ekman et al. (2005) wrote that the “traditional languages of Buddhism, such as Pali, Sanskrit, and Tibetan, have no word for “emotion” as such. The fact that there is no term in Buddhism for “emotion” is quite consistent with modern neuroscience perspectives regarding how affect is implemented in the brain, such that the neural circuitry that supports affective and cognitive processes are intertwined (Mohanty et al., 2007). A Westernized account of affective neuroscience that is predominantly based in English may result in overlooking the study of critical wellness-related constructs and perspectives that exist in other cultures. Researchers need to recognize the limitations inherent in any word set existing in a single language (e.g., English) given that many cross-cultural differences are known to exist in affect and language, so any conclusions that are drawn must account for these differences (Wierzbicka, 2013).

10. Conclusions

Arguably, it is the experience, interpretation, and regulation of positive stimuli and emotions whose cumulative effects ultimately lead to the experience of happiness, life satisfaction, and wellbeing (Bryant, 2003; Cohn et al., 2009; Diener et al., 2009; Silton et al., 2020). As this present review illustrates, experiencing positive emotions benefits

psychological and physical wellbeing in numerous, intersecting ways, including modulating neurophysiological correlates within the central and peripheral nervous systems. Yet, rates of mental health problems are rising and negatively impacting daily life function for an increasingly large number of people across the lifespan (World Health Organization, 2017). At the societal level, this poses problematic implications for complicating the recovery from co-occurring noncommunicable health disorders (e.g., obesity, diabetes, asthma, etc.; World Health Organization, 2014) and these issues are often accompanied by deteriorating social bonds and community support.

Noting the importance of happiness and wellbeing in social progress at the global level, the United Nations commissioned its first World Happiness Report (WHR) in 2012 (Helliwell et al., 2012). This report, based on a single rating of happiness, suggests some geographical regions score above (Northern America, Australia, and New Zealand; Western, Central, and Eastern Europe; and Latin America and the Caribbean) and below (sub-Saharan Africa and South Asia) the mean global level of happiness. According to the 2018 WHR (Helliwell et al., 2018), nearly 75 % of the variability in global levels of happiness is explained by six factors: 1) the perceived availability of social support, 2) national gross domestic product (GDP), 3) average healthy life expectancy, 4) the perceived freedom to make life choices, 5) generosity as indicated by self-reported monetary donations to a charity, and 6) perceived levels of corruption. Other research based on multiple waves of the World Value Survey has shown that the greater the inequality in income within nations, the greater the inequalities in national happiness and life satisfaction (Ovaska and Takashima, 2010). While many of the items reflect high-level structural factors that governing bodies can aim to influence, the findings from our present review highlight the importance of strong social bonds for achieving happiness and wellbeing (section 6.1) which remain an area that individuals and community-based organizations can work to cultivate via strategic urban design and built environments (section 7) that create space and opportunities for meaningful social connections (Bates et al., 2018).

While scholars and policymakers have increasingly recognized the importance of happiness and wellbeing in assessing progress and development around the globe, one nation in particular – the small nation of Bhutan nestled between India and China – has explicitly committed to the national goal of enhancing happiness (Helliwell et al., 2012; Nidup et al., 2018). In Bhutan, happiness is defined holistically as encompassing economic, spiritual, social, cultural, and ecological perspectives and the government has been actively engaged in increasing the proportion of citizens who meet sufficiency standards on a range of indicators of deprivation (e.g., water, sanitation, electricity, education; Nidup et al., 2018). Bhutan's culture is strongly rooted in the Buddhist religion and spirituality as well as compassion are core components of Bhutanese life and are viewed by the Bhutanese authorities as essential to the domain of Gross National Happiness Index (Helliwell et al., 2012). While global levels of happiness are related to GDP and income, psychological wellbeing also contributes to national levels of happiness resulting in the assessment of these factors by the United Nations in recent years with Bhutan having explicitly committed to increasing happiness levels among its citizens. Ostensibly, many of the components of happiness reviewed in the present paper are incorporated into the everyday fabric of life in Bhutan.

Short of living in Bhutan, actively engaging in behaviors that are associated with happiness and wellbeing may need to be actively practiced in contemporary society across the lifespan. As reviewed in section 8.1., mindfulness meditation and loving-kindness meditation have been linked with positive emotion outcomes and wellbeing, but additional research is needed to understand how “dosage,” and specific components of contemplative practices modulate positive emotions and associated neurophysiological correlates. Similarly, the positive psychology literature has developed a number of evidence-based strategies designed to increase and enhance positive emotions (Quoidbach et al., 2015), yet very little is known about how human neurophysiology might change in

response to these strategies, and this remains an area for future research (Silton et al., 2020). Given that increased happiness is frequently observed in late life, future research may benefit from harnessing some of the strategies that are naturally employed by older individuals to enhance the experience of positive emotions (see section 5.2).

Since the present review paper is largely focused on happiness and wellbeing outcomes, we have skirted the topic regarding the relation between positive emotion dysregulation and psychopathology. Needless to say, the experience of excessive happiness and positive emotions can have negative implications for psychological wellbeing, such that experiencing positive emotions in excess is related to bipolar disorder (e.g., Gruber, 2011). Other disturbances in positive emotion regulation have been associated with depressive disorders (Silton et al., 2020). Research on “emodiversity” postulates that experiencing a range of positive and negative emotions is associated with positive health outcomes (Quoidbach et al., 2014) and additional research may be warranted to contextualize the role of positive emotions within individuals' affective repertoire, with close to consideration of environmental and contextual factors, including the role of culture.

Given the importance of positive emotions to psychological health, the Research Domain Criteria (RDoC) initiative within the United States' National Institute of Mental Health has a distinct domain dedicated to positive emotions titled “Positive Valence Systems.” However, the terminology employed in positive emotion research, or in the linguistic adjudication in the present review is much broader and diverse than the terminology associated with the Positive Valence Systems domain in the RDoC matrix, which has become a prominent multidimensional model used to classify mental disorders for research purposes. Progress in theoretical and treatment development will benefit from the reconciliation of the terms and constructs represented in the RDoC matrix with those typically employed in the field (Gruber et al., 2019). The RDoC initiative is aiming to move the needle on enhancing prevention and intervention approaches to psychological disorders. The stakes are high, and linguistics may be important to guide the inclusion of broader positive emotion constructs into the RDoC that go beyond reward, learning, efforts, and habit. Much of the neurophysiological research reviewed in the present paper is correlational, and by expanding the RDoC Positive Valence Systems to incorporate a broader positive emotions nomenclature, longitudinal, experimental, and intervention research will accelerate and more specific mechanisms of positive emotions may be identified.

Finally, animal research pertaining to happiness and positive emotions is integrated throughout this review. With regard to the study of positive emotional states in animals has progressed over the last years, much remains to be learned. A better understanding of positive emotions in animals, across taxa, will contribute to advancing knowledge regarding human positive emotions and their evolutionary origins (Anderson and Adolphs, 2014; de Vere and Kuczaj, 2016). Additionally, it is an important tool to improve the welfare of captive animals (Boissy et al., 2007). Thus, we echo previous calls made by other researchers to counterbalance the bias toward studying negative emotions in animals and humans and continue to shift the focus toward the study of positive emotions in order to enhance our understanding of critical factors and strategies that contribute to societal happiness and wellbeing.

Author contribution

This review is the outcome of a collaborative work process. As such, the author order is alphabetical and the intellectual contributions from each author are noted below:

Rebecca Alexander wrote original text for Section 3.1 and she assisted with editing the manuscript.

Oriana R. Aragón wrote original text for Sections 6.1 and 9, and she assisted with editing the manuscript, and conducted the linguistic sorting investigation.

Jamila Bookwala wrote original text for Sections 5, 8.1 and 10 and

assisted with editing the manuscript.

Nicolas Cherbuin wrote original text for Sections 2.1 and 5, and he provided editorial direction.

Justine M. Gatt wrote original text for Section 2.1 and assisted with developing Fig. 1 and editing the manuscript.

Ian J. Kahrilas contributed original text to Section 3.2 and assisted with editing and revising the manuscript, collating references, and creating Fig. 1.

Niklas Kästner wrote original text for sections 2.2, 6.2 and 7, and he assisted with editing the manuscript.

Alistair Lawrence wrote original text for Sections 2.2, 3.1, 6.2 and 7, and he provided assistance with editing and revising the manuscript.

Leroy Lowe is the architect of the Human Affectome Project. He wrote original text for Sections 1 and 9. He also assisted with editing this manuscript.

Robert G. Morrison wrote original text for section 8.2

Sven C. Mueller wrote original text for Sections 1, 2.1, 3, 4, and 9 and provided significant editorial direction throughout the project and contributed significantly throughout the revision process. He also contributed to creating Fig. 1.

Robin Nusslock contributed to editing and revising the manuscript.

Christos Papadelis contributed to formulating the team of co-authors and helped generate ideas for the framework of the paper.

Kelly L. Polnaszek contributed to editing the manuscript and collating references.

S. Helene Richter wrote original text for Sections 2.2, 6.2, and 7 and assisted with editing the manuscript.

Rebecca L. Siltan wrote original text for Sections 1–10 and provided team leadership and editorial vision throughout writing and revising the manuscript. She is the corresponding author.

Charis Styliadis wrote original text for Section 3.3, and 5 and assisted with editing the manuscript.

Oriana Aragon, Nicolas Cherbuin, Leroy Lowe, and Christos Papadelis were present at the initial Human Affectome Project launch meeting and workshop which was held in Halifax, Nova Scotia, 4–5 August 2016.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neubiorev.2020.12.002>.

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