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The Affective Core of Emotion: Linking Pleasure, Subjective Well-Being, and Optimal Metastability in the Brain

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Abstract

Arguably, emotion is always valenced—either pleasant or unpleasant—and dependent on the pleasure system. This system serves adaptive evolutionary functions; relying on separable wanting, liking, and learning neural mechanisms mediated by mesocorticolimbic networks driving pleasure cycles with appetitive, consummatory, and satiation phases. Liking is generated in a small set of discrete hedonic hotspots and coldspots, while wanting is linked to dopamine and to larger distributed brain networks. Breakdown of the pleasure system can lead to anhedonia and other features of affective disorders. Eudaimonia and well-being are difficult to study empirically, yet whole-brain computational models could offer novel insights (e.g., routes to eudaimonia such as caregiving of infants or music) potentially linking eudaimonia to optimal metastability in the pleasure system.

Keywords
anhedonia, eudaimonia, pleasure, reward

Introduction

Over the last 50 years there has been significant progress in the study of emotion within affective neuroscience, yet there is still no general consensus on the definition of emotion (Gendron & Barrett, 2009; Kringelbach & Phillips, 2014). Part of the problem has been the subjective element of emotional experience, which has been seen by early behaviourists and some contemporary neuroscientists to be an insurmountable roadblock to proper scientific enquiry (Ledoux, 2012), though others believe that emotion also carries objective features that are quite amenable to study (Berridge & Kringelbach, 2015). Many researchers, however, would agree that emotions rely on an affective core, that is, the pleasure system, which gives affective tone to emotion (Frijda, 2010; Russell, 2003) and interacts with cognitive appraisals using a complex choreography of interacting brain systems (Berridge & Kringelbach, 2015; Frijda, 1986; Gentsch, Grandjean, & Scherer, 2015; Schachter & Singer, 1962). An account of how hedonic psychological ingredients—which has also been called "primary appraisal" (Lazarus, 1991)—can be combined with conceptual knowledge to construct emotion was highlighted in a recent insightful history of ideas about emotion in psychology (Gendron & Barrett, 2009), showing the development from and tension between the two main "basic emotion" and "appraisal" traditions in the scientific study of emotion (Barrett, Lewis, & Haviland-Jones, 2016). These traditions might potentially be resolved as perhaps merely differences in emphasis; basic emotion theory emphasizes the preparedness for multiple separate mechanisms while the dimensional accounts propose two fundamental features (arousal and affective core) that when combined with higher level cognition result in emotions.

In this review we focus on the affective core ingredient of emotion components. We show how research has yielded significant new insights into underlying mechanisms of the pleasure system that originated for sensory pleasures, but may have

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extended to diverse and abstract emotions in human evolution (Kringelbach & Berridge, 2010). We define pleasure as positive hedonic valence, which can occur as either an objective 'liking' reaction or a subjective liking reaction to the hedonic impact of a stimulus—and usually both together (Berridge & Kringelbach, 2008). We therefore suggest that pleasure incorporates a simpler core 'liking' reaction generated by hedonic brain systems—whether a subjective feeling of pleasure is consciously felt or not. Note that this is similar to how 'wanting' (or incentive salience) is an objective motivational process within reward that makes stimuli attractive when attributed to them by mesolimbic brain systems. This can add impetus to a conscious feeling of wanting, but can also occur without that subjective feeling.

We have shown both 'liking' and 'wanting' are subsumed by the pleasure system which is a composite psychological process requiring multiple interacting and time-varying contributions from 'liking,' 'wanting,' and learning processes during the pleasure cycle (see Figure 1, where we show the evidence for different brain networks interacting during the sex cycle). This conceptualization is different from earlier behaviourist accounts positing simple self-stimulating pleasure centers (Dror, 2016; Olds & Milner, 1954), which have not stood the test of time. Instead we have shown how the pleasure system relies on the balanced interaction over time of key brain regions that change their relative contribution during the typical pleasure cycle (Berridge & Kringelbach, 2015). Importantly—in contrast to early views of dopamine as a pleasure neurotransmitter—this research has shown that dopamine is not linked to pleasure per se but instead to incentive salience, and so mostly active during the appetitive phase, as we show in detail in what follows (Berridge & Kringelbach, 2008; Leyton, 2010).

The conceptualization of a pleasure system with a cyclical flow of interacting processes creates the potential to describe anhedonia, the lack of pleasure, as the complete or partial breakdown of the interacting brain networks in the pleasure cycle. Anhedonia is major contributor to affective disorders, and for example, some distortions of 'wanting' can contribute to other disorders from addiction to schizophrenia (Rømer Thomsen, Whybrow, & Kringelbach, 2015). This has a strong impact on subjective well-being and happiness that depend on a well-functioning pleasure system, yet it has been difficult to study these elusive subjective experiences scientifically (Kringelbach & Berridge, 2009).

Hedonic research on animals and humans provides a useful foundation for understanding how positive affect can exert its influence on higher aspects of hedonic function in humans, including subjective well-being, for example, as demonstrated in the excellent psychological articles in this special issue. For example, Armenta and colleagues show evidence for how gratitude may play a role in self-improvement (Armenta, Fritz, & Lyubomirsky, 2017), while Cohen-Chen and colleagues demonstrate that hope can help resolve intergroup conflict (Cohen-Chen, Crisp, & Halperin, 2017).

Still, subjective well-being remains difficult to measure objectively and it would seem important to find ways to characterize the links to the pleasure system. We have previously followed Aristotle and more contemporary positive psychologists

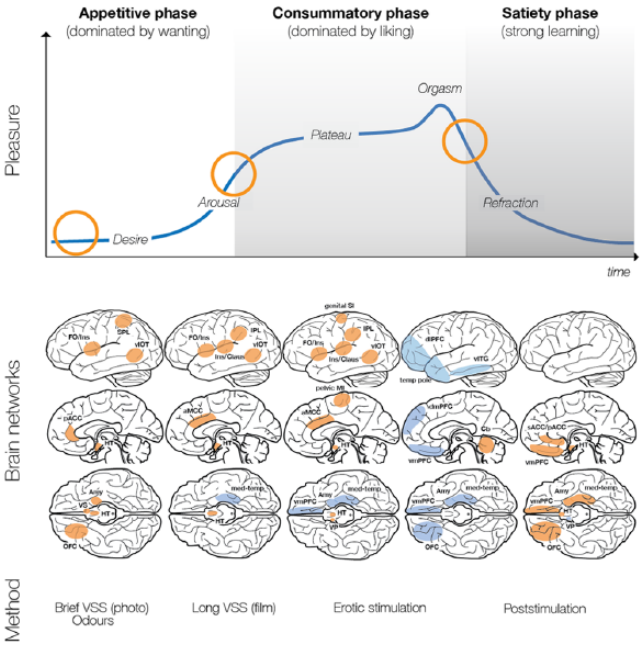

Figure 1. The pleasure cycle. Optimizing resource allocation for survival depends on the engagement with rewards and typically follows a cyclical time course common to many everyday moments of positive affect. Rewards act as motivational magnets to initiate, sustain, and switch state between appetitive, consummatory, and satiety phases. The pleasure system involves liking (hedonic impact), wanting (incentive salience), and learning (typically Pavlovian or instrumental associations and cognitive representations; Berridge & Kringelbach, 2013), which are interwoven during the complex choreography of the pleasure cycle. Wanting processing tends to dominate the appetitive phase, while liking processing dominates the consummatory phase. In contrast, learning can happen throughout the cycle. Here is shown the sexual pleasure cycle with representations of the brain regions involved at each phase. Anhedonia can usefully be defined as any perturbation to this cycle.
Note. Based on Georgiadis and Kringelbach (2012).

to distinguish conceptually between hedonia (pleasure) and eudaimonia (a life well-lived) ingredients of well-being, and also to note there is a close empirical link between them (Aristotle, 350BC/1976; Berridge & Kringelbach, 2011; Kesebir & Diener, 2008; Seligman, Steen, Park, & Peterson, 2005). Here, we expand our previous thoughts on how to potentially gain a toehold in the study of eudaimonia, to go beyond the use of correlational neuroimaging to using the new tools of probabilistic causal whole-brain computational modelling. In particular, towards the end of this review, we propose the need for optimality in pleasure systems of an important dynamical system parameter (*metastability*) in order to facilitate eudaimonia and well-being.

Pleasure and Motivation

The evolutionary imperatives of life imply that relevant stimuli for the survival of both individual and species (such as food, sex, and infants) are prioritized over other less important stimuli.

We and others have argued that a logical extension of this is that there must be an affective core evaluating the positively and negatively valenced stimuli selectively captured by attentional processes and made available for conscious appraisal (Barrett, Mesquita, Ochsner, & Gross, 2007; Frijda, 1986; Russell, 2003). This emotional brain processing is dependent on the proper functioning of the pleasure system, for which the core components have been identified by a large body of affective neuroscience research (Berridge & Kringelbach, 2015; see Figure 2).

Summarizing a large body of research, core brain networks have been identified where valenced stimuli are evaluated for their reward value based on the current state and made available for decision-making. This takes place during the pleasure cycle, which consists of appetitive, consummatory, and satiety phases (Figure 1; Georgiadis & Kringelbach, 2012; Georgiadis, Kringelbach, & Pfaus, 2012). Dissociable brain mechanisms linked to wanting, liking, and learning of rewards have been linked to specific brain regions and neurotransmitters, which govern the potential phase transitions within the pleasure cycle (Kringelbach & Berridge, 2009). The breakdown of any or all of these mechanisms leads to anhedonia, the lack of pleasure, which is a significant feature of neuropsychiatric disorders (Rømer Thomsen et al., 2015).

The progress in affective neuroscience in identifying the brain mechanisms of pleasure has been made possible by adopting the scientific strategy of dividing the concept of affect into two parts: the *affective reaction*, which includes objective aspects in behavioural and brain reactions; and *conscious affective feelings* linked to the subjective experience of emotion (Kringelbach, 2004a). In particular, affective reactions such as pleasure 'liking' and displeasure are prominent in the behaviour and brains of all mammals (Steiner, Glaser, Hawilo, & Berridge, 2001). In turn, swift progress has been made through the careful study of the objective features of reward behaviour and triangulating toward underlying brain substrates (Berridge & Kringelbach, 2008; Leknes & Tracey, 2008).

In general, this research has shown that pleasure is never merely a sensation nor a thought, but an additional hedonic gloss (Frijda, 2010), which is the pleasure versus displeasure affect that is actively generated by the brain and attached to its sensory or cognitive object (Berridge & Kringelbach, 2008). This hedonic gloss of an object is generated by the brain in dedicated networks of hedonic hotspots and coldspots (Berridge & Kringelbach, 2015; Peciña & Berridge, 2005; see Figure 2). Pleasure causation has been studied in other animals by changes in 'liking' reactions following direct brain manipulation of a hedonic hotspot (Smith, Mahler, Pecina, & Berridge, 2010). Hotspots and coldspots have been found in the rodent brain in subcortical regions (the nucleus accumbens, ventral pallidum, and parabrachial nucleus) and cortical regions (insula, medial and lateral orbitofrontal cortex) through direct neurochemical or optogenetic (i.e., direct and precise neuronal) manipulation generating positive or negative changes in 'liking' reactions to sensory pleasures such as sweetness (Berridge & Kringelbach, 2015). The evidence suggests that these nodes of the pleasure network form a functionally integrated circuit which obeys control rules that are largely hierarchical and where the top level functions as a cooperative heterarchy such that multiple unanimous "votes" from hotspots in, for example, the nucleus accumbens and the ventral pallidum, are required for a given brain manipulation to change 'liking' reactions (Smith & Berridge, 2007).

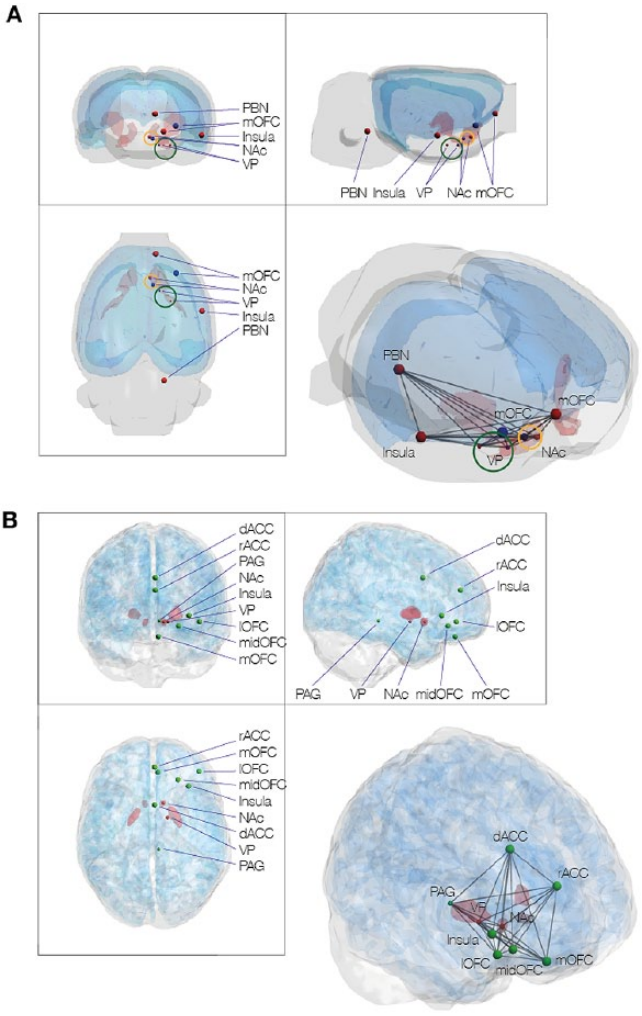

Figure 2. Hedonic hotspots in the rodent and human brain. **A.** Causal hedonic hotspots (red) and coldspots (blue) shown in the rat brain in coronal, sagittal, horizontal planes and in 3D fronto-lateral perspective view (clockwise from top left). **B.** Extrapolation of rat causal hotspots to analogous human sites in NAc and VP (red), as well as correlational information from fMRI for positive affective reactions (in green). Human views are also in coronal, sagittal, horizontal, and 3D perspective (clockwise from top left of B). To give an impression of the topology of the pleasure network, the tentative functional networks between the different hotspots and coldspots have been added but please note that the connection lines are not meant to imply direct anatomical projections between two connected structures, but rather a functional network in mediating hedonic 'liking' reactions and subjective pleasure ratings.
Note. Abbreviations: VP: ventral pallidum; NAc: nucleus accumbens; PBN: parabrachial nucleus; mOFC: medial orbitofrontal cortex; lOFC: lateral orbitofrontal cortex; midOFC: midanterior orbitofrontal cortex; dACC: dorsal anterior cingulate cortex; rACC: rostral anterior cingulate cortex; PAG: periaqueductal gray.
Based on Berridge and Kringelbach (2015).

The pleasure system relies on a second component of reward, 'wanting' or incentive salience making stimuli attractive when attributed to them by widespread mesolimbic brain systems (Berridge & Robinson, 2003). This process is primarily, but not exclusively, driven by the neurotransmitter dopamine, which is not linked to pleasure. During the pleasure cycle, the wanting system interacts closely with the pleasure system but is not identical to the hedonic impact or 'liking' of a reward (Berridge, 2007). Hence the incentive-sensitization theory of how an addict can come to "want" a reward intensely even if finding little or no 'liking' for this reward (Robinson & Berridge, 2003). The brain networks involved in 'wanting' are widespread and, for example, can become retuned by significant changes in the social environment (Reynolds & Berridge, 2008).

Much of what we know about pleasure causation networks has come from the animal literature but human neuroimaging has also started to provide insights into how pleasure is coded in human brain networks. The evidence suggests that hedonic evaluation of pleasure valence is anatomically distinguishable from earlier sensory computations (Kringelbach, 2004b), for example, how taste identification in the primary gustatory cortex in anterior insula is separate from valence processing in higher order areas such as orbitofrontal cortex (OFC; De Araujo, Kringelbach, Rolls, & Hobden, 2003; Kringelbach, de Araujo, & Rolls, 2004). A growing body of correlational human neuroimaging has shown involvement of subcortical and cortical regions (e.g., orbitofrontal, insula, medial prefrontal, and cingulate cortices) to hedonic evaluations including anticipation, appraisal, experience, and memory of pleasurable stimuli (Kringelbach, 2005; Simmons et al., 2014; see Figure 2b). The medial regions of orbitofrontal cortex, middle anterior regions of insula cortex, and ventromedial regions of prefrontal cortex have been shown to be involved in processing the fundamental pleasures of food, sex, and social stimuli, but many of these regions appear to be more concerned with monitoring and predicting reward value than in pleasure of the experience per se (Kahnt, Heinzle, Park, & Haynes, 2010; Kringelbach, 2010; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; O'Doherty, 2014; Schoenbaum & Roesch, 2005; Veldhuizen, Rudenga, & Small, 2010; Vuust & Kringelbach, 2010b).

In contrast to the regions just tracking reward, the midanterior subregion of the orbitofrontal cortex has emerged as an apex of pleasure system, linking reward with hedonic experience (Kringelbach, 2005; Kringelbach et al., 2003). Within this region there is strong, consistent activity correlating with the hedonic experience of a range of pleasures including when they are no longer pleasant, that is, during selective satiation (Blood & Zatorre, 2001; Georgiadis et al., 2006; Georgiadis & Kringelbach, 2012; Kringelbach, 2005; Kringelbach et al., 2003; Kringelbach & Rolls, 2004; Simmons et al., 2014; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001; Völlm et al., 2004).

A comparison of human and animal findings points to very similar systems preserved over mammalian evolution. Even some of the human cortical brain regions identified with neuroimaging are now being shown as potentially homologous to the distinct rodent hedonic hotspots and coldspots recently discovered in the orbitofrontal and insula cortices where opioid or orexin stimulating microinjections can enhance or suppress 'liking' reactions to sweetness, respectively (Castro, Chesterman, Wu, & Berridge, 2014; compare Figures 2A and 2B).

Taken together, a detailed causal understanding is emerging of the pleasure system where networks of brain regions are active during the different phases of the pleasure cycle. The switching between different networks depends on the state of the brain, where the role of the pleasure system is to facilitate the state transition between different points in the pleasure cycle to optimize survival. In this context, we propose that the anhedonia found in affective disorders can be thought of as perturbations to orchestration of state transitions (Rømer Thomsen et al., 2015).

As an example of a significant perturbation to the pleasure system, it has been demonstrated that damage to the rodent hedonic hotspot in posterior ventral pallidum will fully abolish the capacity for positive hedonic reactions, replacing 'liking' for sweetness with "disliking" gapes normally reserved for bitter or similarly noxious tastes (Aldridge & Berridge, 2010; Cromwell & Berridge, 1993). Equally in humans, there would seem to be a causal link to anhedonia following damage to the ventral pallidum. Evidence comes from a case report of anhedonia after accidental bilateral removal of the ventral pallidum following a neurosurgical intervention for removing parts of the globus pallidus to alleviate symptoms of Parkinson's disease patients (Miller et al., 2006).

Well-Being and Eudaimonia

This special issue illustrates how positive emotions contribute to states of subjective well-being. Intriguing evidence shows that complex emotions such as awe and wonder can drive scientific learning, over and above the mere effect of positivity (Valdesolo, Shtulman, & Baron, 2017). Yet, not all positive emotions are equal and there are very different nonverbal expressions between, for example, epistemological positive emotions (e.g., awe) and agency-approach emotions (such as pride; Sauter, 2017). These differences are interesting and must be linked to different routes from the affective core system to states of positive emotion, which may then in turn be linked to subjective well-being.

Still, in contrast to inducing pleasure with positive sensory or social stimuli, it is far more difficult to reliably induce subjective well-being in individuals. Since Aristotle, happiness has been thought of as consisting of the dual aspect of hedonia (pleasure) and eudaimonia (a life well-lived, embedded in meaningful values). Pleasure might be much easier to evoke but is often but a brief moment in happiness or in states of subjective well-being. Yet, it is clear that hedonia and eudaimonia empirically cohere together in happy people. In happiness surveys over 80% of individuals rate their overall eudaimonic life satisfaction as "pretty to very happy," and comparably, 80% also rate their current hedonic mood as positive (e.g., positive 6–7 on a 10-point valence scale where 5 is hedonically neutral;

Kesebir & Diener, 2008). However, it is well-known that subjective self-report measures are not always very reliable given that individuals are not particularly good at introspecting their emotional states (Schooler & Mauss, 2010).

Overall it would seem a reasonable assumption that eudaimonic happiness relies in part on the brain mechanisms of the pleasure system; especially given the direct link between the lack of pleasure, *anhedonia*, and affective disorders (Rømer Thomsen et al., 2015). We have previously shown that many of the key regions of the pleasure system are part of the brain's default-mode network, a key resting state network that is most active when we are not directly engaged in tasks (Gusnard & Raichle, 2001). There is also an emerging literature proposing that the default-mode network supports representations of self (Lou et al., 1999), internal modes of cognition (Buckner, Andrews-Hanna, & Schacter, 2008), and perhaps even states of consciousness (Laureys, Owen, & Schiff, 2004). We have previously speculated that the default-mode network may play a role in connecting eudaimonic and hedonic happiness (Kringelbach & Berridge, 2009) to the self, especially given the activity changes in the frontal regions such as the orbitofrontal and ventromedial prefrontal cortices correlating with pathological changes in subjective hedonic experience, such as in depressed patients (Drevets et al., 1997).

There is still a dearth of evidence for the link between subjective well-being and the default-mode network. Some intriguing evidence comes from the role of the precuneus which plays a key role in the default-mode network and has been shown to engage in self-related mental representations during rest (Cavanna & Trimble, 2006). Furthermore, recent anatomical evidence using voxel-based morphometry has purported to show a correlation between the gray matter volume of the right precuneus and self-reported questionnaire happiness scores (Sato et al., 2015). This is potentially interesting but preliminary findings, which will be important to replicate in a much larger independent sample of participants.

Still, the precuneus would be well-placed to be part of the imbalance involved in the pathological self-representations by the frontal default network and provide a potential link to the hedonic distortions of happiness that are accompanied by related hedonic and eudaimonic dissatisfaction, such as in cognitive rumination in depression (Addis, Wong, & Schacter, 2007; Schnider, 2003; Williams et al., 1996). As such, therapies that target the imbalances in dysphoria-activated depressogenic thinking, such as mindfulness-based cognitive therapy for depression, may conceivably modulate default network circuitry to help improve well-being via a linkage to the pleasure system (Teasdale et al., 2000).

Well-Being, Optimal Metastability, and Conscious Access

As mentioned in the Introduction, for many years one of the key roadblocks to the scientific study of emotion has been the subjective nature of feeling and the difficulty of making the link to brain mechanisms. It remains one of the important outstanding questions in neuroscience to establish causal links between subjective conscious experience and measurable neuronal activity. This is important for our fundamental understanding of brain function but also because it would potentially open up the possibility to develop novel treatments to rebalance pathological brain states, for example, loss of consciousness or affective disorders such as depression. This is especially pertinent for helping depressed individuals regain the elusive subjective experience of eudaimonia; a life well-lived, embedded in meaningful values together with a sense of engagement. But, as we saw before, the underlying causal mechanisms of eudaimonia have remained difficult to characterize with objective scientific measures.

A central problem for the lack of progress has been the lack of availability of causal animal models that can be used to study the full range of eudaimonia and affective disorders found in humans. While some features of affective disorders can be modelled in other animals (Ledoux, 2012), eudaimonia could potentially be a uniquely human experience. As such, human neuroimaging would seem a good tool to obtain further insight but has until now essentially only provided correlational rather than causal information on networks.

Yet, recent advances in whole-brain computational modelling of human neuroimaging data have now opened the possibility of providing probabilistic causal information on the underlying networks and mechanisms (Cabral, Kringelbach, & Deco, 2014; Deco & Kringelbach, 2014). Briefly, such models can capture the global dynamics of the human brain's large-scale network of local neural networks—or regions, linked by long-range connections (Kringelbach, McIntosh, Ritter, Jirsa, & Deco, 2015). The global dynamics of the whole-brain network are determined by the intrinsic dynamics of regions, that is, the dynamics of a region in absence of all couplings, as well as the extrinsic network couplings, allowing communication between the regions of the network. The local spontaneous dynamics of a single region can be modelled in different ways, for example, as a network of coupled spiking neurons. Importantly, when taken together, the emergent collective macroscopic behaviour of brain models has been shown to be only weakly dependent on the details of the regional dynamics (Breakspear & Jirsa, 2007; Deco & Jirsa, 2012).

Whole-brain models use the underlying anatomical skeleton of each individual obtained using diffusion tensor imaging to explicitly link regions, shaping the interplay between the local dynamics of each node, to fit with functional neuroimaging data from magnetoencephalography (MEG), electroencephalography (EEG), or fMRI (Cabral et al., 2014; Deco, Jirsa, McIntosh, Sporns, & Kotter, 2009). Indeed, such whole-brain models can then be manipulated off-line to provide probabilistic causal information on hedonic brain networks in health and disease, which has helped launch the field of computational neuropsychiatry (Deco & Kringelbach, 2014).

One important finding from this emerging literature is the importance of maximizing the optimal exploration of the dynamic repertoire inherent in the brain's structural connectivity (Deco & Kringelbach, 2016; Kringelbach et al., 2015). One way to describe this exploration of the dynamical repertoire is

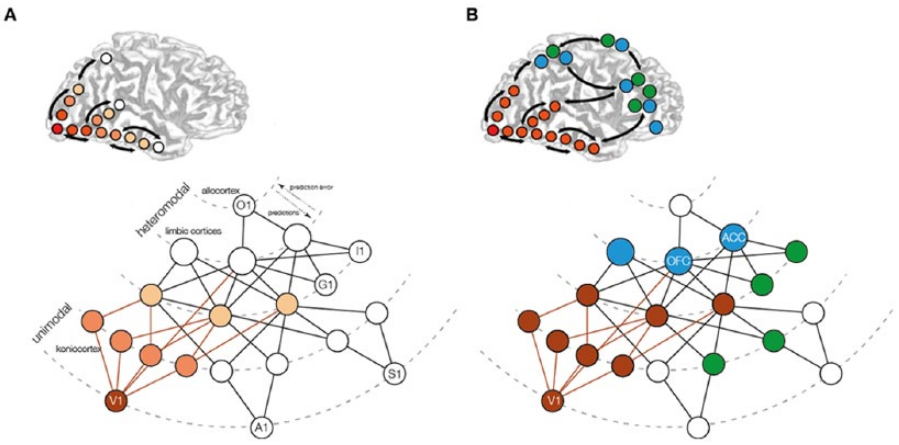

Figure 3. Rewards can become motivational agents with privileged access to consciousness. A. Subliminally presented stimuli typically fail to provide ignition of activity in regions of the global workspace (Dehaene & Changeux, 2011). Here is shown a representative schematic of hierarchical cortical processing demonstrating higher order limbic cortical regions (e.g., OFC) sending prediction signals to and receiving prediction error signals in return from multimodal, exteroceptive, and interoceptive systems. Each ring represents a different type of cortex, from less (interior circles) to greater (exterior circles) number of cortical layers. B. Incentive salience processing can make certain rewards motivational targets which have privileged routes to fast ignition of conscious access. Take for example the visual and auditory cuteness of infants, known to evoke fast activity in the adult brain. Given optimal metastability this can start a cascade of neural events that can help sustain the metastable state of pleasure with the necessary slowness for prosocial caregiving and play behaviours that may evoke eudaimonia.

Note. Abbreviations: A1: primary auditory cortex; G1: primary gustatory cortex; I1: primary interoceptive cortex; O1: primary olfactory cortex; S1: primary somatosensory cortex; V1: primary visual cortex; OFC: orbitofrontal cortex; ACC: anterior cingulate cortex.

Figure is adapted from Chanes and Barrett (2016), Kringelbach and Rapuano (2016), and Mesulam (1998).

through measuring *metastability.* This is a parameter from the field of dynamical systems that measures the variability of the states of phase configurations as a function of time, that is, how the synchronization between the different regions fluctuates across time (Cabral, Kringelbach, et al., 2014). It has been shown that when metastability is optimal, the system is best able to explore the dynamic repertoire, that is, an optimal point is reached between the fast and slow processing characterizing human cognition (Kringelbach et al., 2015).

Given these important results, we hypothesize as one possibility that such optimal metastability could be linked to a state of eudaimonia. In this brain state, there would be optimal flow of information in the pleasure system and connected emotion processing networks, which could correspond to the feelings of subjective well-being and flow anecdotally reported after a deeply meaningful experience of positive emotion. As such, this objective measure of metastability could link eudaimonia (and emotions) to more global theories of brain function. One such example is the global neuronal workspace model which has shown considerable promise for describing how conscious access is made possible by ignition of activity in self-supporting, reverberating, and metastable networks with information broadcast to the whole brain (Baars, 1989; Dehaene, Kerszberg, & Changeux, 1998; Lagercrantz & Changeux, 2009; Mesulam, 1998).

This novel framework of measuring the metastability of relevant brain states would allow for a mechanistic explanation of how certain kinds of stimuli evoke emotional reactions, and how the affective core of emotion is linked to subjective experience. Within the affective core, there are processes linked to wanting (i.e., incentive salience processes) that help make rewards into urgent motivational targets that are given privileged, fast ignition of the conscious workspace (Figure 3). Take for example parental care of human infants, a very important source of emotion and pleasure essential to the survival of our species. Humans are essentially helpless during infancy and childhood and require extensive caregiving behaviour (Bornstein et al., 2012; Parsons, Young, Murray, Stein, & Kringelbach, 2010), which depends on very fast processing of infant cues in the adult human brain. The sounds of infants has been shown to elicit significant activity already after only 50 ms in the brainstem (Parsons et al., 2014) while infant facial and auditory features elicit activity in the orbitofrontal cortex within around 130 ms (Kringelbach et al., 2008; Young, Parsons, Stevner, et al., 2016). This initial attentional orienting response may elicit pleasure (or distress) but it is only when later replaced with careful, slow caregiving behaviour addressing the specific needs of the infant that the deeply meaningful eudaimonic states of caregiving can emerge (Kringelbach, Stark, Alexander, Bornstein, & Stein, 2016; Young, Parsons, Stein, et al., in press). This slower, deliberate cognition has been shown to rely on slower brain activity in distributed networks including the very same regions of the orbitofrontal cortex recruited earlier for the fast response (Parsons, Stark, Young, Stein, & Kringelbach, 2013). For eudaimonia to arise it would seem important for the system to be optimally metastable (although this has not yet been experimentally demonstrated). When this is not the case, this puts at risk the future well-being of the infant given how slow, maladaptive parental cognitions such as rumination and worry can lead to significant disturbances in the parent–infant relationship (Stein et al., 2012). Interestingly, it has been

proposed that long-term social bonds can be fostered by positive moral emotions (Stellar et al., 2017).

Conclusion

In this article, we tried to summarize the significant recent progress in elucidating the affective core component of emotion. The pleasure system is complex and relies on the balanced interaction over time of key brain regions that change their relative contribution during the typical pleasure cycle of appetitive, consummatory, and satiety phases. This interaction is of course also shaped by neurotransmitters but contrary to early thoughts on pleasure, strong evidence has shown that dopamine is not a mechanism of pleasure 'liking' but instead to incentive salience or motivation 'wanting.' We have discussed the difficulties in fully characterizing eudaimonia with existing correlational neuroimaging methods.

We have also sketched how progress is now possible with the potential of probabilistic causal whole-brain computational modelling of human neuroimaging data. In particular, the evidence suggests that optimal metastability in pleasure systems could be a key ingredient in enabling eudaimonia and well-being, which could be an important topic of future research. These new whole-brain models have significant potential for representing the brain states in humans evoked by pleasurable and deeply meaningful stimuli such as infants and music (Vuust & Kringelbach, 2010a). In the future, such explorations hold the promise of more efficacious interventions for the treatment of affective disorders; thereby potentially enabling not only the greatest pleasure but also the greatest eudaimonia for the greatest number of people.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

References

Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, *45*(7), 1363–1377.

Aldridge, J. W., & Berridge, K. C. (2010). Neural coding of pleasure: "Rose-tinted glasses" of the ventral pallidum. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 62–73). New York, NY: Oxford University Press.

Aristotle. (1976). *The Nicomachean ethics, Book 10* (J. A. K. Thomson, Trans.). London, UK: Penguin Books. (350 BC)

Armenta, C. N., Fritz, M. M., & Lyubomirsky, S. (2017). Functions of positive emotions: Gratitude as a motivator of self-improvement and positive change. *Emotion Review, 9*(3), 183–190.

Baars, B. J. (1989). *A cognitive theory of consciousness*. Cambridge, UK: Cambridge University Press.

Barrett, L. F., Lewis, M., & Haviland-Jones, J. M. (2016). *Handbook of emotions*. New York, NY: Guildford Press.

Barrett, L. F., Mesquita, B., Ochsner, K. N., & Gross, J. J. (2007). The experience of emotion. *Annual Review of Psychology*, *58*, 373–403.

Berridge, K. C. (2007). The debate over dopamine's role in reward: The case for incentive salience. *Psychopharmacology*, *191*(3), 391–431.

Berridge, K. C., & Kringelbach, M. L. (2008). Affective neuroscience of pleasure: Reward in humans and animals. *Psychopharmacology*, *199*, 457–480.

Berridge, K. C., & Kringelbach, M. L. (2011). Building a neuroscience of pleasure and well-being. *Psychology of Well-Being: Theory, Research and Practice*, *1*, 1–3.

Berridge, K. C., & Kringelbach, M. L. (2013). Neuroscience of affect: Brain mechanisms of pleasure and displeasure. *Current Opinion in Neurobiology*, *23*(3), 294–303.

Berridge, K. C., & Kringelbach, M. L. (2015). Pleasure systems in the brain. *Neuron*, *86*, 646–664.

Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. *Trends in Neurosciences*, *26*(9), 507–513.

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

Bornstein, M. H., Putnick, D. L., Suwalsky, J. T., Venuti, P., de Falco, S., de Galperin, C. Z., . . . Tichovolsky, M. H. (2012). Emotional relationships in mothers and infants: Culture-common and community-specific characteristics of dyads from rural and metropolitan settings in Argentina, Italy, and the United States. *Journal of Cross-Cultural Psychology*, *43*(2), 171–197.

Breakspear, M., & Jirsa, V. K. (2007). Neuronal dynamics and brain connectivity. In V. K. Jirsa & A. R. McIntosh (Eds.), *Handbook of brain connectivity* (pp. 3–64). Berlin, Germany: Springer.

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, *1124*, 1–38.

Cabral, J., Kringelbach, M. L., & Deco, G. (2014). Exploring the network dynamics underlying brain activity during rest. *Progress in Neurobiology*, *114*, 102–131.

Cabral, J., Luckhoo, H., Woolrich, M., Joensson, M., Mohseni, H., Baker, A., . . . Deco, G. (2014). Exploring mechanisms of spontaneous functional connectivity in MEG: How delayed network interactions lead to structured amplitude envelopes of band-pass filtered oscillations. *Neuroimage*, *90*, 423–435.

Castro, D. C., Chesterman, N. S., Wu, M. K. H., & Berridge, K. C. (2014, November). *Two cortical hedonic hotspots: Orbitofrontal and insular sites of sucrose "liking" enhancement*. Paper presented at the Society for Neuroscience Conference, Washington, DC.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, *129*(Pt. 3), 564–583.

Chanes, L., & Barrett, L. F. (2016). Redefining the role of limbic areas in cortical processing. *Trends in Cognitive Sciences*, *20*(2), 96–106.

Cohen-Chen, S., Crisp, R. J., & Halperin, E. (2017). A new appraisal-based framework underlying hope in conflict resolution. *Emotion Review, 9*(3), 208–214.

Cromwell, H. C., & Berridge, K. C. (1993). Where does damage lead to enhanced food aversion: The ventral pallidum/substantia innominata or lateral hypothalamus? *Brain Research, 624*(1–2), 1–10.

De Araujo, I. E. T., Kringelbach, M. L., Rolls, E. T., & Hobden, P. (2003). The representation of umami taste in the human brain. *Journal of Neurophysiology*, *90*, 313–319.

Deco, G., & Jirsa, V. K. (2012). Ongoing cortical activity at rest: Criticality, multistability, and ghost attractors. *The Journal of Neuroscience*, *32*(10), 3366–3375.

Deco, G., Jirsa, V., McIntosh, A. R., Sporns, O., & Kotter, R. (2009). Key role of coupling, delay, and noise in resting brain fluctuations. *Proceedings of the National Academy of Sciences USA*, *106*(25), 10302–10307.

Deco, G., & Kringelbach, M. L. (2014). Great expectations: Using whole-brain computational connectomics for understanding neuropsychiatric disorders. *Neuron*, *84*, 892–905.

Deco, G., & Kringelbach, M. L. (2016). Metastability and coherence: Extending the communication through coherence hypothesis using

a whole-brain computational perspective. *Trends in Neurosciences*, *39*(3), 125–135.

Dehaene, S., & Changeux, J. P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*(2), 200–227.

Dehaene, S., Kerszberg, M., & Changeux, J. P. (1998). A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences USA*, *95*(24), 14529–14534.

Drevets, W. C., Price, J. L., Simpson, J. R., Jr., Todd, R. D., Reich, T., Vannier, M., & Raichle, M. E. (1997). Subgenual prefrontal cortex abnormalities in mood disorders. *Nature*, *386*(6627), 824–827.

Dror, O. E. (2016). Cold War "super-pleasure": Insatiability, self-stimulation, and the postwar brain. *Osiris*, *31*(1), 227–249.

Frijda, N. H. (1986). *The emotions*. Cambridge, UK: Cambridge University Press.

Frijda, N. H. (2010). On the nature and function of pleasure. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 99–112). New York, NY: Oxford University Press.

Gendron, M., & Barrett, L. F. (2009). Reconstructing the past: A century of ideas about emotion in psychology. *Emotion Review*, *1*, 316–339.

Gentsch, K., Grandjean, D., & Scherer, K. R. (2015). Temporal dynamics and potential neural sources of goal conduciveness, control, and power appraisal. *Biological Psychology*, *112*, 77–93.

Georgiadis, J. R., Kortekaas, R., Kuipers, R., Nieuwenburg, A., Pruim, J., Reinders, A. A., & Holstege, G. (2006). Regional cerebral blood flow changes associated with clitorally induced orgasm in healthy women. *The European Journal of Neuroscience*, *24*(11), 3305–3316.

Georgiadis, J. R., & Kringelbach, M. L. (2012). The human sexual response cycle: Brain imaging evidence linking sex to other pleasures. *Progress in Neurobiology*, *98*(1), 49–81.

Georgiadis, J. R., Kringelbach, M. L., & Pfaus, J. G. (2012). Sex for fun: A synthesis of human and animal neurobiology. *Nature Reviews. Urology*, *9*(9), 486–498.

Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews. Neuroscience*, *2*(10), 685–694.

Kahnt, T., Heinzle, J., Park, S. Q., & Haynes, J. D. (2010). The neural code of reward anticipation in human orbitofrontal cortex. *Proceedings of the National Academy of Sciences USA*, *107*(13), 6010–6015.

Kesebir, P., & Diener, E. (2008). In pursuit of happiness: Empirical answers to philosophical questions. *Perspectives on Psychological Science*, *3*, 117–125.

Kringelbach, M. L. (2004a). Emotion. In R. L. Gregory (Ed.), *The Oxford companion to the mind* (2nd ed., pp. 287–290). Oxford, UK: Oxford University Press.

Kringelbach, M. L. (2004b). Food for thought: Hedonic experience beyond homeostasis in the human brain. *Neuroscience*, *126*(4), 807–819.

Kringelbach, M. L. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. *Nature Reviews. Neuroscience*, *6*(9), 691–702.

Kringelbach, M. L. (2010). The hedonic brain: A functional neuroanatomy of human pleasure. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 202–221). New York, NY: Oxford University Press.

Kringelbach, M. L., & Berridge, K. C. (2009). Towards a functional neuroanatomy of pleasure and happiness. *Trends in Cognitive Sciences*, *13*(11), 479–487.

Kringelbach, M. L., & Berridge, K. C. (2010). *Pleasures of the brain*. New York, NY: Oxford University Press.

Kringelbach, M. L., de Araujo, I. E., & Rolls, E. T. (2004). Taste-related activity in the human dorsolateral prefrontal cortex. *Neuroimage*, *21*(2), 781–788.

Kringelbach, M. L., Lehtonen, A., Squire, S., Harvey, A. G., Craske, M. G., Holliday, I. E., . . . Stein, A. (2008). A specific and rapid neural signature for parental instinct. *PLoS ONE*, *3*(2), e1664. doi:1610.1371/journal.pone.0001664

Kringelbach, M. L., McIntosh, A. R., Ritter, P., Jirsa, V. K., & Deco, G. (2015). The rediscovery of slowness: Exploring the timing of cognition. *Trends in Cognitive Sciences*, *19*(10), 616–628.

Kringelbach, M. L., O'Doherty, J., Rolls, E. T., & Andrews, C. (2003). Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*, *13*(10), 1064–1071.

Kringelbach, M. L., & Phillips, H. (2014). *Emotion: Pleasure and pain in the brain*. Oxford, UK: Oxford University Press.

Kringelbach, M. L., & Rapuano, K. M. (2016). Time in the orbitofrontal cortex. *Brain*, *139*(4), 1010–1013.

Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: Evidence from neuroimaging and neuropsychology. *Progress in Neurobiology*, *72*(5), 341–372.

Kringelbach, M. L., Stark, E. A., Alexander, C., Bornstein, M. H., & Stein, A. (2016). On cuteness: Beyond caregiving to play, empathy and prosociality. *Trends in Cognitive Sciences*, *20*(7), 545–558.

Lagercrantz, H., & Changeux, J. P. (2009). The emergence of human consciousness: From fetal to neonatal life. *Pediatric Research*, *65*(3), 255–260.

Laureys, S., Owen, A. M., & Schiff, N. D. (2004). Brain function in coma, vegetative state, and related disorders. *The Lancet. Neurology*, *3*(9), 537–546.

Lazarus, R. (1991). *Emotion & adaptation*. New York, NY: Oxford University Press.

Ledoux, J. (2012). Rethinking the emotional brain. *Neuron*, *73*(4), 653–676.

Leknes, S., & Tracey, I. (2008). A common neurobiology for pain and pleasure. *Nature Reviews. Neuroscience*, *9*(4), 314–320.

Leyton, M. (2010). The neurobiology of desire: Dopamine and the regulation of mood and motivational states in humans. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 222–243). New York, NY: Oxford University Press.

Lou, H. C., Kjaer, T. W., Friberg, L., Wildschiodtz, G., Holm, S., & Nowak, M. (1999). A 15O-H2O PET study of meditation and the resting state of normal consciousness. *Human Brain Mapping*, *7*(2), 98–105.

Mesulam, M. M. (1998). From sensation to cognition. *Brain*, *121*, 1013–1052.

Miller, J. M., Vorel, S. R., Tranguch, A. J., Kenny, E. T., Mazzoni, P., van Gorp, W. G., & Kleber, H. D. (2006). Anhedonia after a selective bilateral lesion of the globus pallidus. *The American Journal of Psychiatry*, *163*(5), 786–788.

O'Doherty, J. P. (2014). The problem with value. *Neuroscience & Biobehavioral Reviews*, *43*, 259–268.

Olds, J., & Milner, P. (1954). Positive reinforcement produced by electrical stimulation of the septal area and other regions of rat brain. *Journal of Comparative and Physiological Psychology*, *47*, 419–427.

Parsons, C. E., Stark, E. A., Young, K. S., Stein, A., & Kringelbach, M. L. (2013). Understanding the human parental brain: A critical role of the orbitofrontal cortex. *Social Neuroscience*, *8*(6), 525–543.

Parsons, C. E., Young, K. S., Joensson, M., Brattico, E., Hyam, J. A., Stein, A., . . . Kringelbach, M. L. (2014). Ready for action: A role for the brainstem in responding to infant vocalizations. *Social Cognitive and Affective Neuroscience*, *9*(7), 977–984.

Parsons, C. E., Young, K. S., Murray, L., Stein, A., & Kringelbach, M. L. (2010). The functional neuroanatomy of the evolving parent–infant relationship. *Progress in Neurobiology*, *91*, 220–241.

Peciña, S., & Berridge, K. C. (2005). Hedonic hot spot in nucleus accumbens shell: Where do mu-opioids cause increased hedonic impact of sweetness? *The Journal of Neuroscience*, *25*(50), 11777–11786.

Reynolds, S. M., & Berridge, K. C. (2008). Emotional environments retune the valence of appetitive versus fearful functions in nucleus accumbens. *Nature Neuroscience*, *11*(4), 423–425.

Robinson, T. E., & Berridge, K. C. (2003). Addiction. *Annual Review of Psychology*, *54*, 25–53.

Rømer Thomsen, K., Whybrow, P. C., & Kringelbach, M. L. (2015). Reconceptualising anhedonia: Novel perspectives on balancing the pleasure networks in the human brain. *Frontiers in Behavioural Neuroscience*, *9*, 49. doi:10.3389/fnbeh.2015.00049

Russell, J. A. (2003). Core affect and the psychological construction of emotion. *Psychological Review*, *110*, 145–172.

Sato, W., Kochiyama, T., Uono, S., Kubota, Y., Sawada, R., Yoshimura, S., & Toichi, M. (2015). The structural neural substrate of subjective happiness. *Scientific Reports*, *5*, 16891. doi:10.1038/srep16891

Sauter, D. A. (2017). The nonverbal communication of positive emotions: An emotion family approach. *Emotion Review, 9*(3), 222–234.

Schachter, S., & Singer, J. (1962). Cognitive, social and physiological determinants of emotional state. *Psychological Review*, *69*, 387–399.

Schnider, A. (2003). Spontaneous confabulation and the adaptation of thought to ongoing reality. *Nature Reviews. Neuroscience*, *4*(8), 662–671.

Schoenbaum, G., & Roesch, M. (2005). Orbitofrontal cortex, associative learning, and expectancies. *Neuron*, *47*(5), 633–636.

Schooler, J. W., & Mauss, I. B. (2010). To be happy and to know it: The experience and meta-awareness of pleasure. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 244–254). New York, NY: Oxford University Press.

Seligman, M. E., Steen, T. A., Park, N., & Peterson, C. (2005). Positive psychology progress: Empirical validation of interventions. *The American Psychologist*, *60*(5), 410–421.

Simmons, W. K., Rapuano, K. M., Ingeholm, J. E., Avery, J., Kallman, S., Hall, K. D., & Martin, A. (2014). The ventral pallidum and orbitofrontal cortex support food pleasantness inferences. *Brain Structure & Function*, *219*(2), 473–483.

Small, D. M., Zatorre, R. J., Dagher, A., Evans, A. C., & Jones-Gotman, M. (2001). Changes in brain activity related to eating chocolate: From pleasure to aversion. *Brain*, *124*(Pt. 9), 1720–1733.

Smith, K. S., & Berridge, K. C. (2007). Opioid limbic circuit for reward: Interaction between hedonic hotspots of nucleus accumbens and ventral pallidum. *The Journal of Neuroscience*, *27*(7), 1594–1605.

Smith, K. S., Mahler, S. V., Pecina, S., & Berridge, K. C. (2010). Hedonic hotspots: Generating sensory pleasure in the brain. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 27–49). New York, NY: Oxford University Press.

Stein, A., Craske, M. G., Lehtonen, A., Harvey, A., Savage-McGlynn, E., Davies, B., . . . Counsell, N. (2012). Maternal cognitions and mother–infant interaction in postnatal depression and generalized anxiety disorder. *Journal of Abnormal Psychology*, *121*(4), 795–809.

Steiner, J. E., Glaser, D., Hawilo, M. E., & Berridge, K. C. (2001). Comparative expression of hedonic impact: Affective reactions to taste by human infants and other primates. *Neuroscience & Biobehavioral Reviews*, *25*(1), 53–74.

Stellar, J.E., Gordon, A.M., Piff, P.K., Cordaro, D., Anderson, C.L., Bai, Y., Maruskin, L.A., & Keltner, D. (2017). Self-transcendent emotions and their social functions: Compassion, gratitude, and awe bind us to others through prosociality. *Emotion Review, 9*(3), 200–207.

Teasdale, J. D., Segal, Z. V., Williams, J. M., Ridgeway, V. A., Soulsby, J. M., & Lau, M. A. (2000). Prevention of relapse/recurrence in major depression by mindfulness-based cognitive therapy. *Journal of Consulting and Clinical Psychology*, *68*(4), 615–623.

Valdesolo, P., Shtulman, A., & Baron, A. S. (2017). Science is awe-some: The emotional antecedents of science learning. *Emotion Review, 9*(3), 215–221.

Veldhuizen, M. G., Rudenga, K. J., & Small, D. (2010). The pleasure of taste flavor and food. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 146–168). Oxford, UK: Oxford University Press.

Völlm, B. A., de Araujo, I. E. T., Cowen, P. J., Rolls, E. T., Kringelbach, M. L., Smith, K. A., . . . Matthews, P. M. (2004). Methamphetamine activates reward circuitry in drug naïve human subjects. *Neuropsychopharmacology*, *29*(9), 1715–1722.

Vuust, P., & Kringelbach, M. L. (2010a). The pleasure of making meaning of music. *Interdisciplinary Science Reviews*, *35*(2), 168–185.

Vuust, P., & Kringelbach, M. L. (2010b). The pleasure of music. In M. L. Kringelbach & K. C. Berridge (Eds.), *Pleasures of the brain* (pp. 255–269). Oxford, UK: Oxford University Press.

Williams, J. M., Ellis, N. C., Tyers, C., Healy, H., Rose, G., & MacLeod, A. K. (1996). The specificity of autobiographical memory and imageability of the future. *Memory & Cognition*, *24*(1), 116–125.

Young, K. S., Parsons, C. E., Stein, A., Vuust, P., Craske, M. G., & Kringelbach, M. L. (in press). The neural basis of responsive caregiving behaviour: Investigating temporal dynamics within the parental brain. *Behavioural Brain Research*.

Young, K. S., Parsons, C. E., Stevner, A., Woolrich, M. W., Jegindø, E.-M., Hartevelt, T. J., & Kringelbach, M. L. (2016). Evidence for a caregiving instinct: Rapid differentiation of infant from adult vocalisations using magnetoencephalography. *Cerebral Cortex*, *26*(3), 1309–1321.