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# The neural correlates of happiness: A review of PET and fMRI studies using autobiographical recall methods

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**Abstract** Although very difficult to define, happiness is becoming a core concept within contemporary psychology and affective neuroscience. In the last two decades, the increased use of neuroimaging techniques has facilitated empirical study of the neural correlates of happiness. This area of research utilizes procedures that induce positive emotion and mood, and autobiographical recall is one of the most widely used and effective approaches. In this article, we review eight positron emission tomography and seven functional magnetic resonance imaging studies that have investigated happiness by using autobiographical recall to induce emotion. Regardless of the neuroimaging technique used, the studies conducted so far have shown that remembering happy events is primarily associated with the activation of many areas, including anterior cingulate cortex, prefrontal cortex, and insula. Importantly, these areas are also found to be connected with other basic emotions, such as sadness and anger. In the conclusion, we integrate these findings, discussing important limitations of the extant literature and suggesting new research directions.

**Keywords** Happiness · Autobiographical recall · PET · fMRI · Mood induction methods

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Defining happiness is a difficult task for natural and social scientists, including psychologists, economists, sociologists, geneticists, and neuroscientists. Indeed, *happiness* is a term often used to refer to and that is interchangeable with many other concepts, such as *well-being*, *flourishing*, *optimal functioning*, *life satisfaction*, *quality of life*, and *health* (Chemali, Chahine, & Naassan, 2008; David, Boniwell, & Conley Ayers, 2013; Diener, Lucas, & Oishi, 2002; Easterlin, 2010; Kahneman, Diener, & Schwarz, 1999; Keyes & Haidt, 2003; Layard, 2006; Lykken, 1999; Seligman, 2011; Veenhoven, 2000).

Insightful reflections about the happiness concept and its semantic space may be drawn from psychological research. Scholars working in this field have conceptualized happiness on the basis of two approaches: eudaimonic and hedonic (Deci & Ryan, 2008; Haybron, 2008; McMahon, 2006; Ryan & Deci, 2000; Sotgiu, 2013; White, 2006). *Eudaimonic* happiness is a concept originally defined by Aristotle in his *Nicomachean Ethics*. He stated that happiness is only attainable by living virtuously. Similarly, on the basis of Stoicism, Seneca and Epictetus affirmed that the main path to happiness is through virtuous living, by facing and resisting temptations that could corrupt personal inner harmony. The eudaimonic trend was followed by Christian philosophers including Augustine and Tommaso d'Aquino. Conversely, *hedonic* happiness is a concept that refers to the Cyrenaic school of Aristippus and Epicurus, who considered the pursuit of pleasure and the avoidance of pain to be the main path to happiness.

Empirical research on happiness began in the 1960s with Gurin's survey of the American population (Gurin, Veroff, & Feld, 1960), and evolved in the 2000s with the inception of Positive Psychology (Seligman & Csikszentmihalyi, 2000). Contemporary psychological sciences include eudaimonic approaches, which focus on happiness as the development of

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personal potential and virtue and the achievement of subjective targets and goals (Ryan, Huta, & Deci, 2006; Ryff & Singer, 2008; Waterman, 2008, 2012), as well as hedonic approaches, which focus on how pleasure can contribute to happiness (Diener, Oishi, & Lucas, 2003; Huta & Ryan, 2010; Kahneman et al., 1999).

The debate about the distinction between eudaimonia and hedonia is wide and transcends the boundaries of the psychological sciences (Huta & Waterman, 2014; Kashdan, Biswas-Diener, & King, 2008; Keyes & Annas, 2009). Within the neurosciences, the study of happiness has focused on the neurobiology of pleasure because it is easier to evoke hedonic happiness with concrete stimuli, and laboratory studies have shown that animals react to pleasant stimuli similarly to humans (Berridge & Kringelbach, 2008). In studies conducted with rodents, researchers have observed different hotspots of the brain that are able to elicit pleasure reactions when stimulated. These hotspots include nucleus accumbens (Mahler, Smith, & Berridge, 2007), ventral pallidum (Ho & Berridge, 2013), limbic regions of prefrontal cortex (PFC)—especially orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), and midinsular cortex (Berridge & Kringelbach, 2011, 2013)—and parabrachial nucleus (Peciña & Berridge, 2005; Peciña, Smith, & Berridge, 2006; Smith & Berridge, 2007). All of these structures are connected, forming a "pleasure network" in which greater activation correlates with greater pleasure reactions. Empirical evidence has also shown that the amygdala, a limbic structure mostly involved in the activation of negative emotions, codes for pleasure (Chemali, Chahine, & Naassan, 2008; Fernando, Murray, & Milton, 2013; Mahler & Berridge, 2012).

Little neuroscientific research has focused on human eudaimonic happiness, and no studies on its neural correlates. Only a hypothesis by Kringelbach and Berridge (2009; see also Berridge & Kringelbach, 2011) has addressed this question, arguing for the involvement of the brain's default network. The default network is a resting-state network, which includes the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), retrosplenial cortex (Rsp), and inferior parietal lobule, together with the hippocampus and other memory-related areas (Buckner, Andrews-Hanna, & Schacter, 2008; Gusnard, Akbudak, Shulman, & Raichle, 2001). This system has often been described as important for self-representation and self-consciousness. Following Kringelbach and Berridge's hypothesis, eudaimonic happiness could be coded by pleasure hotspots placed in the brain's default network. More specifically, this hypothesis assumes that frontal regions having a high density of opiate receptors, such as the anterior cingulate and orbitofrontal cortices, may play a significant role in connecting eudaimonic and hedonic happiness. However, the debate concerning this topic is still ongoing.

In the last few decades, the increased use of neuroimaging techniques has contributed significantly to the definition of the neural correlates of cognitive functions, such as perception, attention, language, and memory. More recently, neuroimaging techniques have also been used to investigate the neural correlates of affective phenomena and emotions, including happiness (for reviews, see Phan, Wager, Taylor, & Liberzon, 2002; Vytal & Hamann, 2010). This area of research requires mood induction procedures (see Westermann, Spies, Stahl, & Hesse, 1996, for a review), and one of the most effective is autobiographical recall (Baker & Gutterfreund, 1993; Jallais & Gilet, 2010).

It is worth noting that the recollection of autobiographical memories involves both emotion and vividness. With regard to emotion, some studies (e.g., Dolcos, LaBar, & Cabeza, 2004; Hamann, Ely, Grafton, & Kilts, 1999) have reported a correlation between increased memory for emotional stimuli and activation of the amygdala and hippocampus. Specifically, whereas negative emotions have been shown to elicit right temporal activity, positive emotions activate mPFC, entorhinal, and temporo-polar regions. As for the contribution of vividness, the intensity of imagery during autobiographical recollection correlates with activity in the occipital cortex, cuneus, and precuneus; on the other hand, the vividness of other sensory details is associated with activity in related sensory areas (Addis, Pan, Vu, Laiser, & Schacter, 2009; Cabeza & St Jacques, 2007). Furthermore, there is evidence that the mPFC is involved in placing the self in the memory (Daselaar et al., 2008; Greenberg & Rubin, 2003; Svoboda, McKinnon, & Levine, 2006).

In this article, we review neuroimaging studies of happiness that have used autobiographical recall as the mood induction task. It is worth noting that, although the theoretical distinction between hedonic and eudaimonic happiness is gaining great attention in contemporary science, none of the studies in the present review discussed it. Instead, they considered happiness as a broad category of positive emotional experiences, all of which are assumed to have the same impact on autobiographical memory.

The remainder of this article includes four sections. In the next section, we describe the main characteristics of autobiographical recall methods. In the subsequent two sections, we summarize findings from positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies that have used this procedure to identify the neural correlates of happiness, as well as the correlates of other basic emotions (e.g., fear, anger, and sadness). In the last section, we integrate the findings from all of the studies reviewed, identifying a limited number of brain areas that are typically involved in autobiographical memory for happiness and discussing their functions. We also critically discuss key limitations of the extant literature and suggest new research directions.

Importantly, throughout the article, we will attempt to highlight whether the neural correlates of happiness coincide with

brain areas that are believed to be involved in the experiences of eudaimonia and hedonia (e.g., Kringelbach & Berridge, 2009). Consistent with theoretical and empirical advances within both psychology (e.g., Linley, Joseph, Harrington, & Wood, 2006; Pawelski, 2013; Sotgiu, 2010; Sotgiu & Rusconi, 2014) and neuroscience (e.g., Habel, Klein, Kellermann, Shah, & Schneider, 2005; Murphy, Nimmo-Smith & Lawrence, 2003), special attention will also be devoted to the similarities and differences between the neural correlates of happiness and those for its oppositely valenced basic emotions. More specifically, since happiness and sadness radically differ in terms of their semantics and subjective experience (cf. Russell & Carroll, 1999), we will focus on the comparison between these two emotions.

## Autobiographical recall as a mood induction procedure

Autobiographical recall is a procedure used to induce mood or emotion. It is a component of the more general category of imagination mood induction procedures, in which participants are required to evoke the emotion felt during a personally experienced event. Usually, participants have to recollect the event as vividly as possible, relieving and reexperiencing the emotions, sensations, perceptions, and reactions (Westermann et al., 1996). This procedure can be used alone or combined with other mood induction procedures (Jallais & Gilet, 2010). Studies comparing different mood induction procedures have demonstrated the greater effectiveness of autobiographical recall relative to other approaches (Gilet, 2008; Jallais & Gilet, 2010; Zhang, Yu, & Barrett, 2014), especially when it is used to induce positive emotions (Strack, Schwarz, & Gschneidinger, 1985).

Neuroimaging studies of happiness have implemented autobiographical recall in many different ways. In general, almost all studies have included a prescan interview in which participants were required to select and write down a number of personally experienced events. The events were then reviewed and selected by the experimenters. During PET or fMRI, autobiographical memories were elicited by generic or specific retrieval cues (Cabeza & St. Jacques, 2007). Different cues have been used: written instructions, pictures, emotion-related words, human faces expressing emotion, or film clips or auditory scripts (with a predetermined structure and length based on the written reports originally made by the participants). These cues guided each participant in reliving emotional experiences during the scanning session.

## PET studies

Table 1 summarizes the main characteristics and findings from eight PET studies that used an autobiographical mood induction procedure to elicit happiness. Notably, the four studies by Lane and his colleagues (Lane et al., 2009; Lane, Reiman, Ahern, Schwartz, & Davidson, 1997; Lane et al., 1998; Reiman, Lane, Ahern, & Schwartz, 1997) followed the same research methodology and used the same sample of participants.

For each study, the following features are indicated: (1) the emotional conditions contrasted, (2) the specific recall induction techniques used by researchers, (3) the demographic characteristics of the participants (age and gender), and (4) the main findings about the elicited neural correlates of happiness. It is noteworthy that the brain regions reported in Table 1 were selected from the original publications on the basis of significant activation peaks obtained from the contrast between happiness and a neutral condition.

### Emotional conditions

All of the studies included in Table 1 contrasted happiness with sadness. The four studies by Lane and his colleagues (Lane et al., 2009; Lane et al., 1997; Lane et al., 1998; Reiman et al., 1997) also contrasted happiness and disgust. However, only two studies (Damasio et al., 2000; Marci, Glick, Loh, & Dougherty, 2007) investigated happiness versus anger, and only one (Damasio et al., 2000) investigated happiness versus fear. Remarkably, we were not able to find any PET studies comparing happy and surprising conditions.

### Recall induction techniques

Five of the eight studies (Lane et al., 2009; Lane et al., 1997; Lane et al., 1998; Marci et al., 2007; Reiman et al., 1997) asked participants to listen to prerecorded audio scripts of autobiographical emotional experiences referring to each contrasted condition. In the remaining three studies (Damasio et al., 2000; George, Ketter, Parekh, Herscovitch, & Post, 1996; George et al., 1995), participants were cued to recall and relive personally experienced emotional events they had selected during a preexperimental session. All of the reviewed studies used normal adult participants, but only three (Damasio et al., 2000; George et al., 1996; Marci et al., 2007) recruited participants of both genders.

### Correlates of happiness

No clear activation pattern is apparent across all studies. As is reported in Table 1, distinctive cortical or subcortical areas showed increased activity in each study. However, some areas showed increased activity in more than one study. For example, three studies (Damasio et al., 2000; George et al., 1996; George et al., 1995) reported activation in ACC. On the other hand, both George et al. (1995) and Lane et al. (1997) identified PFC as a crucial area. Specifically, whereas George and

**Table 1** PET studies (in chronological order of publication date)

| Study | Contrasted Conditions | Technique of Recall Induction | Participants' Characteristics | Neural Correlates of Recalled Happiness | |
|---|---|---|---|---|---|
| George et al. (1995) | Happiness, sadness, neutral | REC/REL<br>Two experiences per condition cued with pictures of human emotional faces | 11 females, age: 33.3, *SD*: 12.3 | + ACC<br>– R PFC<br>– TPC | |
| George et al. (1996) | Happiness, sadness, neutral | REC/REL<br>two experiences per condition cued with pictures of human emotional faces | ten females, age: 34.5, *SD*: 12.1<br>ten males, age: 35, *SD*: 8.8 | Men<br>+ R caudate<br>+ L putamen<br>+ L superior FG | Women<br>+ L ACC<br>+ R caudate<br>+ L inferior FG<br>+ precentral gyrus<br>+ cerebellum |
| Lane et al. (1997); Reiman et al. (1997); Lane et al. (1998); Lane et al. (2009) | Happiness, sadness, disgust, neutral | LIS.SCRIPTS<br>Three experiences per condition and film clips | 12 females, age: 23.3, *SD*: 3.2 | + ventral mesial FC<br>+ ventral striatum<br>+ caudate<br>+ medial PFC<br>+ midbrain<br>+ L mid insula | |
| Damasio et al. (2000) | Happiness, sadness, fear, anger, neutral | REC/REL<br>One experience per condition | 21 females, 20 males divided in four cohorts, age: from 24 to 42 | + R INS<br>+ R somatosensory cortices<br>+ R PC<br>+ R/L posterior cingulate<br>+ L ACC<br>–/+ R ACC<br>+ R OFC<br>+ L basal forebrain<br>+ R hypothalamus<br>+ L midbrain. | |
| Marci et al. (2007) | Happiness, anger, sadness, neutral | LIS.SCRIPTS<br>Two experiences per emotion | five females, five males, age: 33.9, *SD*: 11.9 | + L ventral striatum<br>+ L anterior/ R superior/L middle TG | |

REC/REL = recalling and relieving past emotional experiences, LIS.SCRIPTS = listening autobiographical scripts, + = activation, – = deactivation, R = right, L = left, ACC = anterior cingulate cortex, FC = frontal cortex, FG = frontal gyrus, INS = insula, OFC = orbitofrontal cortex, PC = parietal cortex, PFC = prefrontal cortex, TG = temporal gyrus, TPC = temporo-parietal cortex

colleagues (1995) found deactivation in right PFC, Lane and colleagues (1997) reported activation in mPFC. Two studies (George et al., 1996; Lane et al., 1997) showed increased activity in caudate nucleus, and two others (Lane et al., 1997; Marci et al., 2007) revealed increased activity in ventral striatum. Furthermore, the studies by both Lane et al. (1997) and Damasio et al. (2000) reported activation in the midbrain and insula. Notably, many of the neural sites detected in these studies overlap with brain areas hypothesized to be involved in the experience of either eudaimonic happiness (especially frontal regions, such as ACC and PFC) or hedonic happiness (especially subcortical regions, such as the basal ganglia and insula; see, e.g., Berridge & Kringelbach, 2011; Kringelbach & Berridge, 2009).

### Neural correlates of other emotions

A clearer pattern of activation was found for sadness, which was investigated in all eight studies reported in Table 1. Indeed, four of the studies (Damasio et al., 2000; George et al., 1996; Lane et al., 1997; Marci et al., 2007) showed activation in caudate nucleus, three in ACC and left PFC (Damasio et al., 2000; George et al., 1996; George et al., 1995), and three in insula (Damasio et al., 2000; George et al., 1996; Lane et al., 1997). Few of the studies investigated disgust, anger, or fear. Taken together, they showed that the negative emotions were associated with the activation of a number of neural sites, including PFC, cingulate cortex, insula, temporal cortices, midbrain, and cerebellum.

## fMRI studies

Table 2 summarizes the main characteristics and findings from seven fMRI studies that used an autobiographical mood induction procedure to elicit happiness. To facilitate comparative analyses between the PET and fMRI studies, the data included in Tables 1 and 2 are analogous. One exception is the information regarding the neural correlates associated with recalled happiness (last column of Table 2). Whereas the brain

**Table 2** fMRI studies (in chronological order of publication date)

| Study | Contrasted Conditions | Technique of Recall Induction | Participants' Characteristics | Neural Correlates of Recalled Happiness |
|---|---|---|---|---|
| Markowitsch et al. (2003) | Happiness, sadness, rest | REC/REL<br>18 experiences for condition with key words as reminder | seven females, six males, age: 30 (range: 19–43) | + R posterior TG<br>+ R ACC<br>+ L medial/superior FG<br>+ L precuneus<br>+ L ventral pallidum<br>+ L amygdala |
| Pelletier et al. (2003) | Happiness, sadness, neutral | REC/REL<br>One experience for condition | four females, five males professional actors, age: 33 (range: 25–41) | + OFC<br>+ medial PFC<br>+ Lventrolateral PFC<br>+ L anterior temporal pole<br>+ R pons |
| Cerqueira, et al. (2008); Cerqueira et al. (2010) | Happiness, irritability, neutral | LIS.SCRIPTS<br>Three experiences for condition | five females, six males, age: 32.4 ± 7.2 | + L PFC<br>+ L anterior/R posterior INS<br>+ L ACC<br>+ L hypothalamus/ thalamus<br>+ L/R middle TG<br>+ R TC |
| Sitaram et al. (2011) | Happiness, disgust, sadness | REC/REL<br>One experience or more for condition with pictures (International Affective Picture System) as reminder | 12 volunteers, age: N/A | + medial OFC/antero-rostral FC<br>+ ACC<br>+ INS |
| Zotev et al. (2011) | Happiness, count, rest | REC/REL<br>three experiences for condition with the word "happy" as cue | 28 males, age: 28 ± 9 | + R PFC<br>+ L superior FG<br>+ L/R TG<br>+ L amygdala<br>+ L hippocampal regions<br>+ L/R hippocampus<br>+ ACC<br>+ PCC |
| Zotev et al. (2014) | Happiness, count, rest | REC/REL<br>Three experiences for condition with the word "happy" as cue | four females, two males, age: 24 ± 9 | + L/R INS<br>+ R OFC<br>+ R PFC<br>+ ACC<br>+ R superior TG<br>+ lingual gyrus |

N/A = not available, REC/REL = recalling and relieving past emotional experiences, LIS.SCRIPTS = listening autobiographical scripts, + = activation, – = deactivation, R = right, L = left, ACC = anterior cingulate cortex, FC = frontal cortex, FG = frontal gyrus, INS = insula, OFC = orbitofrontal cortex, PCC = posterior cingulate cortex, PFC = prefrontal cortex, TC = temporal cortex, TG = temporal gyrus

regions for PET studies in Table 1 refer to contrasts between happiness and neutral conditions, such contrasts were reported in only six of the seven fMRI studies (Cerqueira et al., 2008; Cerqueira et al., 2010; Markowitsch, Vandekerckhove, Lanfermann, & Russ, 2003; Pelletier et al., 2003; Zotev et al., 2011; Zotev, Phillips, Yuan, Misaki, & Bodurka, 2014); the final fMRI study (Sitaram, Lee, Ruiz, Rana, Veit, & Birbaumer, 2011) only reported contrasts between three emotional conditions (i.e., happiness, sadness, and disgust). However, since the researchers followed a block-design experimental protocol interleaving emotional and rest conditions, we determined this study to be appropriate for inclusion in this review. Importantly, as for the PET studies in Table 1, the neural correlates of recalled happiness for the fMRI studies in Table 2 were selected from the original articles on the basis of significant activation peaks.

## Emotional conditions

Three of the seven studies (Markowitsch et al., 2003; Pelletier et al., 2003; Sitaram et al., 2011) contrasted happiness with sadness. However, only two (Cerqueira et al., 2008; Cerqueira et al., 2010) contrasted happiness with anger-related emotions (i.e., irritability), and only one (Sitaram et al., 2011) contrasted happiness and disgust. Importantly, we did not find any fMRI studies contrasting happiness with fear or surprise. Furthermore, Table 2 includes two studies by Zotev and colleagues (Zotev et al., 2011; Zotev et al., 2014) in which

happiness was not contrasted with an emotional condition, but only with two control conditions (i.e., mentally counting backward and rest).

### Recall induction techniques

Unlike the PET studies reviewed in the preceding section, only two of the fMRI studies (Cerqueira et al., 2008; Cerqueira et al., 2010) evoked happiness by presenting prerecorded auditory scripts of personal events. Instead, the authors of the remaining five studies (Markowitsch et al., 2003; Pelletier et al., 2003; Sitaram et al., 2011; Zotev et al., 2011; Zotev et al., 2014) instructed participants to imagine and relive autobiographical emotional events using different types of cues (e.g., words or pictures). All studies focused on adults with no history of neurological or psychiatric disorders. Notably, all of the participants recruited by Pelletier et al. (2003) were professional actors.

### Neural correlates of happiness

As compared to the PET studies, the fMRI studies had greater agreement about the cerebral areas associated with happiness. Five of the seven studies (Cerqueira et al., 2008; Markowitsch et al., 2003; Sitaram et al., 2011; Zotev et al., 2011; Zotev et al., 2014) reported neural activation in ACC. Four showed activation in PFC—specifically, right PFC (Zotev et al., 2011; Zotev et al., 2014), left PFC (Cerqueira et al., 2008), and left and medial PFC (Pelletier et al., 2003). Furthermore, four studies (Cerqueira et al., 2008; Markowitsch et al., 2003; Zotev et al., 2011; Zotev et al., 2014) revealed activation in the temporal gyrus, three (Cerqueira et al., 2008; Sitaram et al., 2011; Zotev et al., 2014) in the insula, three (Pelletier et al., 2003; Sitaram et al., 2011; Zotev et al., 2014) in OFC, three (Markowitsch et al., 2003; Pelletier et al., 2003; Zotev et al., 2011) in hippocampal regions and temporal pole, and two (Markowitsch et al., 2003; Zotev et al., 2011) in left amygdala. As Table 2 shows, distinctive cortical or subcortical activations were found in each study. Importantly, as we observed with regard to the PET studies, the neural correlates of happiness from fMRI studies encompassed many brain areas hypothesized to be involved in the experience of either eudaimonic or hedonic happiness (e.g., Berridge & Kringelbach, 2011; Kringelbach & Berridge, 2009).

### Neural correlates of other emotions

Among the three studies that contrasted happiness with sadness, two (Markowitsch et al., 2003; Pelletier et al., 2003) showed activation in OFC in both emotional conditions, and Pelletier et al. found common activations in ventrolateral PFC. For irritability, Cerqueira et al. (2010) reported activations in left ACC and left PFC. For disgust, Sitaram et al. (2011) reported activation in a number of brain regions, including right ACC, frontal gyrus, middle temporal gyrus, postcentral gyrus, cuneus, and precuneus.

## Conclusions

### Summary and integration of findings

Taken together, the PET and fMRI studies reviewed in the present article showed that remembering happy autobiographical events is primarily associated with the activation of three neural sites: PFC, ACC, and insula. Clear contributions were identified from many other areas, including parietal sensory cortices, thalamus, hypothalamus, basal ganglia (e.g., caudate nucleus and ventral striatum), and various limbic structures located in frontal and temporo-parietal regions (e.g., amygdala, hippocampus, and cingulate gyrus).

All of the aforementioned regions may be considered part of a broad neural network responsible for processing the different features defining happy autobiographical memories. Within this network, the thalamus, sensory cortices, and parietal regions may play a key role in recalling the sensory, visuospatial, and motor details associated with happy memories. Limbic regions may account for the subjective feelings experienced during retrieval. Both basal-ganglia and limbic structures may be responsible for the pleasure reactions and bodily changes associated with recalling happy experiences. Finally, frontal regions might account for the cognitive processes involved in the subjective appraisal of recalled happy experiences.

Notably, the number of studies included in the present article was too small and the focus of these investigations was too narrow to draw any conclusions about a specific neural model of happiness. We argue that, whereas the network described above greatly overlaps with those postulated in other models of happiness proposed to date (e.g., Chemali et al., 2008; Funahashi, 2011), the available empirical evidence does not permit us to identify distinctive brain areas associated with remembering happy events. As we emphasized, PFC, ACC, and insula were the most frequently reported areas to show activation across the reviewed studies. However, these areas also played a crucial role in the recall of negative emotions, such as sadness and anger. For example, a clear difference between recalled happiness and sadness is evident only in the prefrontal and orbitofrontal cortices: Happy memories seem to activate more medial regions, whereas sad memories activate more lateral regions (see George et al., 1996; George et al., 1995; Markowitsch et al., 2003; Pelletier et al., 2003).

Interestingly, other empirical evidence from contemporary neuroscience suggests that PFC, ACC, and insula serve complex psychological functions, which are not uniquely related to happy memories or, more generally, to happiness. For

example, it has been shown that PFC is important for self-referential mental activity (D'Argembeau et al., 2007; Johnson et al., 2006; Kelley et al., 2002; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Ochsner et al., 2005; Philippi, Duff, Denburg, Tranel, & Rudrauf, 2012; Zhu, Zhang, Fan, & Han, 2007), the representation of decision values (Chib, Rangel, Shimojo, & O'Doherty, 2009), and reward-related behavior (Kringelbach, 2005; Öngür & Price, 2000). ACC is mostly activated during cognitively demanding tasks aimed at inducing either positive or negative emotions (Phan et al., 2002); similar to PFC, this structure also appears to be involved in self-referential processing (D'Argembeau et al., 2007; Han et al., 2010; Johnson et al. 2006; Zhu et al., 2007).

Furthermore, it has been suggested that the insula plays a critical role in the processing of interoceptive information associated with both positive and negative emotions (Cauda et al., 2012; Gasquoine, 2014; Phan et al., 2002). Finally, recent studies have shown the involvement of PFC, ACC, and insula in mood disorders, including depression (e.g., Davey, Harrison, Yücel, & Allen, 2012; Philippi, Motzkin, Pujara, & Koenigs, 2015; Sperduti et al., 2013; Takahashi et al., 2010; Yoshimura et al., 2014; for a review, see Nejad, Fossati, & Lemogne, 2013).

To summarize, at present, it is difficult to propose a heuristic model describing the neural correlates of happy memories. Indeed, some brain areas (i.e., PFC, ACC, and insula) were frequently reported across the studies in this review. However, their activation may depend on the nature of the emotional induction procedures employed in the various studies (i.e., recall of self-relevant information), rather than on the valence and typology of the emotions investigated (regarding this point, see also George et al., 1995; Sitaram et al., 2011).

## Limitations of the current literature and future research directions

In addition to the arguments discussed above, we believe there are other reasons why it is difficult to identify a distinctive neural network associated with happy memories. In our opinion, these reasons concern two methodological limitations affecting the neuroimaging studies included in the present review.

The first limitation concerns the way the autobiographical recall method has been implemented to date. Indeed, in all of the studies reviewed in the present article, the researchers asked participants to retrieve happy events from their past. However, the researchers did not collect any information about the various features defining these recollections, such as physiological reactions, sensory details, and subjective feelings. We contend that, in the absence of specific experimental directions, the characteristics of autobiographical recollections may vary significantly from one participant to another, and even within the same participant when he or she is asked to recall more than one event. In turn, interindividual and intra-individual variability in recalling happy memories may hinder the identification of distinctive neural networks associated with remembering happy experiences.

The second limitation concerns the absolute lack of studies investigating the neural correlates of happiness defined as either eudaimonia or hedonia. As we noted in the introduction, Berridge and Kringelbach (2011, 2013) speculated that even though distinctive neural networks could be activated by eudaimonic and hedonic happiness, these two brain circuits could strongly overlap. Specifically, they proposed that both eudaimonic and hedonic happiness might be correlated with activity in orbitofrontal and cingulate cortices, although it is still unclear how these cortices differentially participate in eudaimonia or hedonia. We note that, although similar regions were also detected in a number of studies included in the present review, the methods of happiness elicitation used so far have not permitted us to establish whether these areas would play equivalent roles during experimental tasks asking participants to selectively recall hedonic or eudaimonic events.

We believe that neuroscientists can overcome both of these limitations. Regarding the first limitation, future neuroimaging studies using autobiographical recall methods should follow procedures of emotion induction that control the content of happy memories. For example, researchers could provide participants with specific directions and criteria regarding how to self-select happy events during preexperimental sessions (e.g., "Please recall a happy event in which you performed a lot of movement."). Furthermore, participants undergoing brain scans could be cued with stimuli (e.g., sentences) referring to distinct classes of memory contents (e.g., physiological changes, sensory details, or subjective feelings). Hopefully, both of these strategies would help reduce inter- and intra-individual variability in neural network activation, thus controlling potential confounding factors affecting brain mapping.

Regarding the second limitation, we propose that future neuroimaging research use emotion induction procedures that ask participants to imagine or recollect happy autobiographical events reflecting the two aforementioned conceptions of happiness (either eudaimonic or hedonic). In particular, eudaimonic events should refer to the achievement of life goals and self-actualizing experiences. By contrast, hedonic events should include experiences characterized by strong sensations of physical or psychological pleasure.

To conclude, we note that the research developments illustrated above may provide further opportunities to identify distinctive neural circuits associated with happy autobiographical memories. Hopefully, this will advance our knowledge of the neural substrates of positive mental states.

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