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Patterns of brain activity associated with nostalgia: a social-cognitive neuroscience perspective

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Abstract

Nostalgia arises from tender and yearnful reflection on meaningful life events or important persons from one's past. In the last two decades, the literature has documented a variety of ways in which nostalgia benefits psychological well-being. Only a handful of studies, however, have addressed the neural basis of the emotion. In this prospective review, we postulate a neural model of nostalgia. Self-reflection, autobiographical memory, regulatory capacity and reward are core components of the emotion. Thus, nostalgia involves brain activities implicated in self-reflection processing (medial prefrontal cortex, posterior cingulate cortex and precuneus), autobiographical memory processing (hippocampus, medial prefrontal cortex, posterior cingulate cortex and precuneus), emotion regulation processing (anterior cingulate cortex and medial prefrontal cortex) and reward processing (striatum, substantia nigra, ventral tegmental area and ventromedial prefrontal cortex). Nostalgia's potential to modulate activity in these core neural substrates has both theoretical and applied implications.

Key words: nostalgia; self-reflection; emotion regulation; autobiographical memory; reward

Introduction

Nostalgia has a checkered history. The term was originally coined by a Swiss medical student, Johannes Hofer (Hofer, 1934), who, in his dissertation, labeled nostalgia a medical or neurological disease accompanied by maladaptive psychological and physiological symptoms, such as despondency, anorexia, fever and pain. The view of nostalgia as a disease persevered in the 18th and 19th centuries. By the turn of the 20th century, the perception of nostalgia as a psychiatric or psychosomatic disorder was well-entrenched. The list of symptoms included anxiety, sadness, pessimism and insomnia. This perception was softened near the end of that century when nostalgia came to be regarded as a form of depression. Taken together, although its conceptualization changed over time, nostalgia has consistently been seen as dysfunctional (for historical overviews, see Sedikides *et al.*, 2004; Batcho, 2013).

Currently, however, nostalgia is being rehabilitated. It is now considered a predominantly positive, albeit bittersweet, self-conscious emotion that arises from personally relevant, tender and longful memories of one's past (Wildschut *et al.*, 2006; Batcho, 2007; Hepper *et al.*, 2012). Nostalgia is elicited by a variety of triggers, such as objects, events or close others from one's childhood or youth (Schuman and Scott, 1989; Holbrook and Schindler, 1996), music or songs (Routledge *et al.*, 2011; Sedikides *et al.*, 2021) and photographs (Gilboa *et al.*, 2004; Cox *et al.*, 2015), as well as odors and tastes (Supski, 2013; Reid *et al.*, 2014). Furthermore, nostalgia is prevalent (i.e. experienced several times a week), universal (i.e. occurring in many cultures across five continents) and observed across ages (i.e. among older children, teenagers and adults; Zhou *et al.*, 2008; Hepper *et al.*, 2014, 2021; Madoglou *et al.*, 2017; Wildschut *et al.*, 2019).

Crucially, the emotion has emerged as a psychological resource that confers a variety of intrapersonal and interpersonal benefits (Sedikides *et al.*, 2008, 2015; Frankenbach *et al.*, 2021). In particular, nostalgia boosts self-esteem or self-positivity (Vess *et al.*, 2012; Cheung *et al.*, 2013, 2016), increases meaning in life (Routledge *et al.*, 2011, 2012; Sedikides and Wildschut, 2018), fosters social connectedness and social support (Wildschut *et al.*, 2010; Reid *et al.*, 2014; Sedikides and Wildschut, 2019), encourages help seeking (Juhl *et al.*, 2021), enhances psychological health and well-being (Routledge *et al.*, 2013; Baldwin and Landau, 2014; Baldwin *et al.*, 2015; Layous *et al.*, 2021) and attenuates dysphoric states such as loneliness, boredom, stress or death anxiety (Zhou *et al.*, 2008, 2021a; Routledge *et al.*, 2011; Van Tilburg *et al.*,

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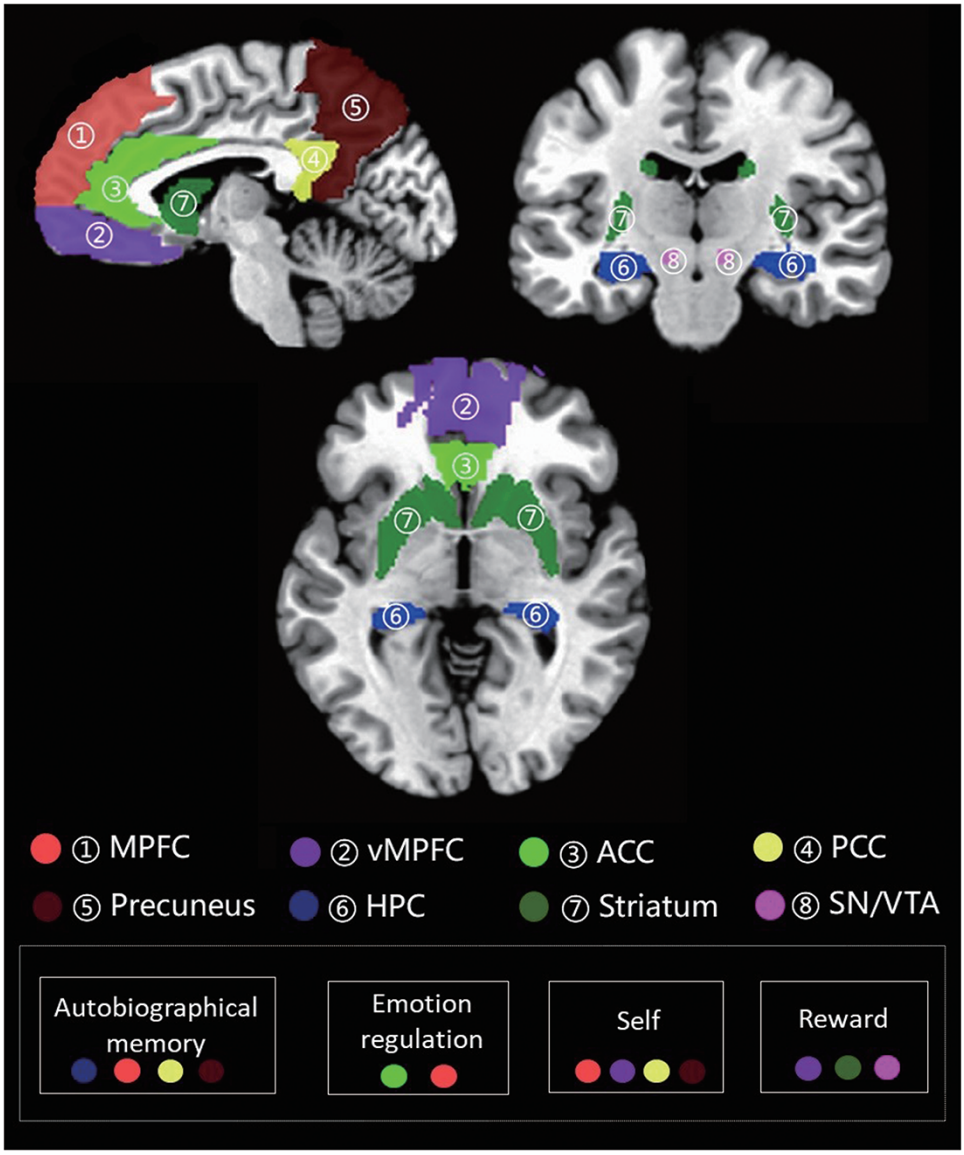

Fig. 1. The nostalgic brain model: brain regions activated in nostalgia *vs* control conditions. mPFC = medial prefrontal cortex; vmPFC = ventromedial prefrontal cortex; ACC = anterior cingulate cortex; PCC = posterior cingulate cortex; HPC = hippocampus; SN = substantia nigra; VTA = ventral tegmental area. Nostalgia involves neural substrates known to be engaged in self-reflection, autobiographical memory, emotion regulation and reward processing.

2013). Furthermore, in stark contrast to historical views (Batcho, 2013; Sedikides *et al.*, 2015), nostalgia can be implemented in interventions among older adults to maintain and improve emotional and memory functions (Yamagami *et al.*, 2007), enrich psychological well-being (Bohlmeijer *et al.*, 2007) and ameliorate depression (Chiang *et al.*, 2010).

Over the past decade, the behavioral literature has covered extensively the nature (what it is) and functions (what it does) of nostalgia. Evidence from social cognitive neuroscience has now begun to address the neural substrates of the emotion. Although brain research on nostalgia has progressed rapidly, it is still in its early stage. The field is, to paraphrase Winston Churchill,[1] at the end of the beginning. Therefore, the time is ripe to synthesize the state of the art and identify promising directions for the next stage of neuroscientific research into nostalgia.

[1] The paraphrase is based on a Winston Churchill 1942 speech referring to the Second Battle of El Alamein.

We present the first synthesis of brain research into nostalgia. Given its multifaceted nature, it is reasonable to assume that the emotion involves different interacting brain regions. This view is consistent with meta-analyses of neuroimaging studies on basic emotions (e.g. fear, anger, sadness, happiness, disgust and surprise), which show that each basic emotion involves multiple distributed functional networks rather than being specifically related to a single distinct brain region (e.g. fear = amygdala; Kober *et al.*, 2008; Lindquist *et al.*, 2012; Saarimäki *et al.*, 2018). We identified four components of nostalgia based on its definition and relevant theory: self-reflection, autobiographic memory, emotion regulation and rewards. Accordingly, we first offer several key propositions regarding the neural networks of nostalgia. We then review the neural literature on nostalgia and illustrate its relevance to, and support for, the propositions. Next, we introduce a neural model of nostalgia (Figure 1) that aspires to integrate the empirical findings. We conclude with a discussion of the key issues to be addressed in future neuroimaging

research. Overall, this prospective review is intended to attract researchers' attention to and nurture their interest in the emotion while offering focused hypotheses in need of empirical scrutiny.

Core components of nostalgia

Self-reflection

Nostalgia is regarded as a prima facie self-conscious emotion (Van Tilburg *et al.*, 2019) and is accompanied by self-reflection (Sedikides *et al.*, 2015). The central and defining character of nostalgia is the self, as the emotion originates from one's meaningful experiences. Indeed, the self is featured prominently in nostalgic recollections. Nostalgic narratives, for example, are filled with highly self-relevant events, as well as exchanges between the self and close others, featuring the self as a protagonist (Wildschut *et al.*, 2006; Abeyta *et al.*, 2015). The trajectory of these narratives is redemptive (i.e. from humble beginnings to a happy ending), thus depicting the self in favorable light (Wildschut *et al.*, 2006; Luo *et al.*, 2016).

The medial prefrontal cortex (mPFC) is the key brain region involved in self-reflection processing, which requires integrating stimuli in the context of personal thoughts, goals and traits (Northoff and Bermpohl, 2004; Lieberman, 2007; Lieberman *et al.*, 2019). The posterior cingulate cortex (PCC) is also a key region in self-reflection as well as self-consciousness (Northoff and Bermpohl, 2004; Cavanna and Trimble, 2006; Northoff *et al.*, 2006). For example, both the mPFC and PCC show heightened activation when individuals reflect on the information that is highly self-relevant and self-descriptive (Moran *et al.*, 2006; Wagner *et al.*, 2012). We therefore propose the following:

Proposition 1: Nostalgia involves brain regions associated with self-reflection.

Autobiographical memory

Autobiographical memory involves the processing of the self in mental time travel into the past (Sedikides *et al.*, 2015), which is distinguished from self-reflection (Lieberman *et al.*, 2019). At the trait level, nostalgia serves basic autobiographical memory functions (i.e. greater overall recruitment of memories) as do two other types of autobiographical memory, rumination (brooding and reflection) and counterfactual thinking (downward or upward), but is different from them in terms of its comparatively strong positive associations with self-regard and intimacy maintenance (i.e. acquiring symbolic proximity or strengthening social bonds) and its weak association with bitterness revival (i.e. rekindling resentment from having presumably been wronged; Cheung *et al.*, 2018). When experimentally manipulated, nostalgia (compared to brooding or reflection) leads to (i) greater intimacy maintenance, conversation, teach/inform, death preparation, boredom reduction and bitterness revival reduction and (ii) elevated positive affect, self-esteem, social connectedness, meaning in life and self-continuity (Jiang *et al.*, 2021). Taken together, nostalgic recollection can be considered a special case of autobiographical memory (Sedikides *et al.*, 2015; Wildschut and Sedikides, 2020).

According to the neuroscience literature, autobiographical memory processing mainly involves the brain regions of hippocampus (Cabeza and Nyberg, 2000; Addis *et al.*, 2004; Svoboda *et al.*, 2006), as well as mPFC and PCC (Gilboa, 2004; Svoboda *et al.*, 2006; Kim, 2012). We therefore propose the following:

Proposition 2: Nostalgia involves brain regions associated with autobiographical memory.

Emotion regulation

Nostalgia is distinct from general autobiographical memory in another important way. Autobiographical memory implicates acts of remembering past events in one's life, but such events are not necessarily dipped in affect. Nostalgia, however, has a potent affective signature (Sedikides *et al.*, 2015; Van Tilburg *et al.*, 2018). The New Oxford Dictionary of English (The New Oxford Dictionary of English, 1998) defines nostalgia as 'a sentimental longing or wistful affection for the past' (p. 1266), and researchers are unanimous in labeling it an emotion (Sedikides *et al.*, 2015; Wildschut and Sedikides, 2020). The emotional potency of autobiographical memories predicts the level or strength of nostalgia (Barrett *et al.*, 2010; Barrett and Janata, 2016).

Nostalgia's affective signature is ambivalent, as it involves the co-occurrence of positive and negative affect (Barrett *et al.*, 2010), but mostly positive, as it encompasses more positive than negative affect (Sedikides and Wildschut, 2016) and elicits more positive than negative affect (Leunissen *et al.*, 2021). Ambivalent emotions entail neural mechanisms both of simultaneously positive and negative states and a rapid vacillation between positive and negative states (Vaccaro *et al.*, 2020). As such, nostalgia is not only bittersweet but also regulates negative states, soothing emotional conflict. This process may be associated with a specific mode of emotion regulation, cognitive reappraisal. When experiencing nostalgia, people generally feel well even when this sentiment is somewhat unwarranted by the valence of the pertinent past event (Cheung *et al.*, 2018; Sedikides *et al.*, 2015). That is, people reframe the nostalgic memory in a rose-colored manner. In addition, nostalgia regulates negative emotionality in itself (Josephson, 1996; Folkman, 2008): when triggered by a discomforting state (e.g. loneliness and meaninglessness), nostalgia counters it through the evocation of upbeat, social and meaningful memories (Routledge *et al.*, 2011; Maher *et al.*, 2021; Wildschut *et al.*, 2006; Zhou *et al.*, 2008).

Several brain regions, especially the anterior cingulate cortex (ACC) and mPFC, are known to play key roles in emotion regulation, particularly cognitive reappraisal (Bush *et al.*, 2000; Ochsner and Gross, 2005; Pezawas *et al.*, 2005). We therefore propose the following:

Proposition 3: Nostalgia involves brain regions associated with emotion regulation processing.

Reward

As we mentioned, despite its bittersweetness, nostalgia is a predominantly positive emotion (Sedikides and Wildschut, 2016). An integrative data analysis based on 41 experiments showed that nostalgia inductions increase positive rather than negative affect (Leunissen *et al.*, 2021). In addition to positive affect or pleasure, nostalgia is related to motivation and reward seeking. A stream of empirical studies has indicated that nostalgia is approach-oriented such that it strengthens approach motivation, encourages risk-taking toward reward and promotes the pursuit of one's important goals (Stephan *et al.*, 2014; Zou *et al.*, 2019; Sedikides and Wildschut, 2020). Various regions of the reward network,

especially ventral striatal dopamine systems, are involved in positive emotion and, moreover, approach motivation (Burgdorf and Panksepp, 2006; Lindquist *et al.*, 2012; Berridge and Kringelbach, 2015).

Key structures in the reward network include the striatum, substantia nigra (SN), ventral tegmental area (VTA) and ventromedial prefrontal cortex (vmPFC, including medial orbitofrontal cortex or mOFC; Haber and Knutson, 2010). The striatum, for example, is a core region of the mesolimbic dopamine system and is critical in reward processing (O'Doherty, 2004; Delgado, 2007). The striatum, and particularly the ventral striatum (VS), is consistently activated by rewarding outcomes. The VS is sensitive to primary rewards such as food, drugs or sex, and to secondary rewards such as money and power (Sescousse *et al.*, 2013). Reward-related brain regions are often activated by satisfying stimuli (e.g. picture of a loved one, positive social feedback, music and art; Bartels and Zeki, 2004; Berridge and Kringelbach, 2015). We therefore propose the following:

Proposition 4: Nostalgia involves brain regions associated with reward processing.

Overview

Taken together, nostalgia entails self-reflection, autobiographical memory, emotion regulation and a reward orientation (Sedikides *et al.*, 2015; Van Tilburg *et al.*, 2018; Sedikides and Wildschut, 2020). We thus asked whether nostalgia involves brain regions associated with (i) self-reflection processing, (ii) autobiographical memory processing, (iii) emotion regulation processing and (iv) reward processing. To answer these questions (*Propositions 1–4*), we reviewed the emerging literature on patterns of brain activity associated with nostalgizing.

We concentrate on specific brain regions that are most strongly implicated in nostalgia, and we do not aim to cover exhaustively and comprehensively all pertinent brain activity. Also, as we have alluded earlier, we frame our review in terms of brain regions rather than specific cortical networks; after all, within a given cortical network (e.g. the default mode network or DMN), different brain regions may exercise distinct roles (Wen *et al.*, 2020). Hence, a focus on brain regions is more informative. Furthermore, a brain region could be linked with more than one of the four core components of nostalgia. For example, mPFC is broadly involved in most of the components. However, it is unclear whether mPFC is activated in conjunction with the specific component under consideration (i.e. mPFC activity might indicate self-reflection or emotion regulation). Put otherwise, although we offered *Propositions 1–4* based on existing nostalgia theory and research, our foci on patterns of brain activity relied to some extent on reverse inference. Lastly, the core components are not independent from each other; for example, self-reflection, autobiographical memory retrieval and emotion regulation could occur simultaneously. Consequently, we posit that the core components of nostalgia—and relevant processes—are interdependent and coordinated (see also the 'Summary' section).

Neural substrates of nostalgia

Review of neuroscientific studies investigating the neural basis of nostalgia

To the best of our knowledge, six studies have directly addressed the neural bases of nostalgia. We discuss them below. The results provide initial empirical evidence for our propositions.

In a functional magnetic resonance imaging (fMRI) study (Oba *et al.*, 2015), participants were instructed to view passively nostalgic pictures that described objects or scenes experienced in childhood (e.g. a pencil case from childhood), as well as similar but non-nostalgic (i.e. control) pictures (e.g. a contemporary pencil case). After scanning, participants rated their memory, along with their emotional experience (i.e. personal significance and emotionality), that accompanied each picture during scanning. Nostalgic (compared to control) pictures elicited stronger activity in the hippocampus. Prior work had shown that hippocampal engagement during autobiographical memory retrieval is modulated by qualities such as vividness, emotionality and personal significance (Addis *et al.*, 2004; Gilboa *et al.*, 2004). Consistent with these findings, hippocampal activity was correlated with ratings of the emotional and personal significance of nostalgic objects (Oba *et al.*, 2015). Nostalgizing, then, involves autobiographical memory that is more vivid, emotional and personally significant than non-nostalgic recollection.

In addition, nostalgic (compared to control) pictures enhanced responses in the reward system, including the SN/VTA and striatum (Oba *et al.*, 2015). Further, hippocampus-VS co-activation was positively correlated with participants' dispositional nostalgia under the influence of experimentally induced nostalgia. Based on these two sets of findings, Kikuchi and Noriuchi (2017) speculated that memory and reward systems coproduce nostalgia, and each system plays a pivotal role in the experience of the emotion.

Compared with visual triggers, odor-evoked autobiographical memories are more emotionally significant (Herz *et al.*, 2004). In a positron emission tomography study with venous catheter (injection of $H_2{}^{15}O$), participants were instructed to smell a personalized nostalgic odor as well as a control odor that was irrelevant to nostalgia (Matsunaga *et al.*, 2013). The nostalgic odor induced more autobiographical memories and positive emotions and, importantly, elicited stronger activation in the vmPFC and precuneus/PCC. Furthermore, across participants, activity in these two regions was positively correlated.

The vmPFC responds to pleasant, emotionally valenced odorants (Gottfried and Zald, 2005). More generally, vmPFC is involved in reward-related processing, responding preferentially to positive (as opposed to negative) outcomes (O'Doherty *et al.*, 2001; Liu *et al.*, 2011). Therefore, Matsunaga *et al.*'s (2013) finding of a positive neural correlation between PCC and vmPFC might represent the association of autobiographical memory and reward system. Given that the precuneus/PCC is thought to be a neural correlate of self-reflection processing (Cavanna and Trimble, 2006), the precuneus/PCC activity is consistent with nostalgia's self-reflection. In addition, Matsunaga *et al.*'s (2013) showed that nostalgia-induced vmPFC and precuneus/PCC activation was negatively associated with levels of peripheral proinflammatory cytokines measured from blood samples, such as the tumor necrosis factor-α and interferon-γ. Although these across-participant correlations need to be interpreted with caution due to the small sample size ($N = 10$), the researchers suggested that nostalgia might confer benefits on health and well-being via the inhibition of systemic inflammation.

Nostalgia is commonly elicited by music (Janata *et al.*, 2007; Sedikides *et al.*, 2021). Music evokes complex emotions, varying in both valence and arousal (Koelsch, 2014). Behavioral evidence indicates that nostalgia is a low-arousal and positively valenced emotion (Van Tilburg *et al.*, 2018). Trost *et al.* (2012) tested this idea in an imaging study. They used nine musical epochs to elicit different emotions, with each representing a specific

emotion (e.g. nostalgia, joy and sadness), and instructed participants to assess the degree of arousal and valence of each musical epoch. Compared with positive and high-arousal emotions (e.g. joy and wonder), positive but low-arousal emotions (e.g. nostalgia and tenderness) increased brain activity in limbic and medial prefrontal areas.

Irrespective of valence, low-arousal emotions (e.g. nostalgia) also engage a network centered on the hippocampus and vmPFC, including the subgenual ACC. The hippocampus is involved in music-induced emotions (Koelsch, 2014) and is susceptible to chronic stressors (Jacobson and Sapolsky, 1991). Stress and depression conduce to atrophy and loss of neurons in the hippocampus (Warner-Schmidt and Duman, 2006). It is possible, then, that the psychological health benefits of nostalgia (e.g. decreased stress; Routledge *et al.*, 2013) derive in part from the neural change in hippocampus during nostalgizing. We note, however, that Trost *et al.* (2012) did not differentiate nostalgia from other emotions with similar valence or arousal (e.g. peacefulness and tenderness). Accordingly, the extent to which the above evidence is specific to nostalgia will need to be addressed in follow-up investigations.

Barrett and Janata (2016) examined the neural correlates of music-evoked nostalgia. In an fMRI study, each participant listened to 30 musical excerpts, which were selected from the Billboard Top-100 Pop, Hip Hop and R&B lists when the participant was between 7 and 19 years old. Immediately after listening to each excerpt, participants reported their level of nostalgia. Although overall results did not reveal significant neural correlates of music-evoked nostalgia, informative individual differences emerged. Among those who were dispositionally lower on nostalgia, activity in the midbrain and left amygdala increased when listening to more nostalgia-evoking music (i.e. when they felt more nostalgic). In contrast, among those who were dispositionally higher on nostalgia, activity in these regions decreased when listening to more nostalgia-evoking music.

The amygdala is one of the most critical brain regions for emotion. It has a germane role in processing social signals of emotion and in the consolidation of emotional memories (Dalgleish, 2004). The amygdala responds to socio-affective stimuli that encourage approach, such that music-evoked joy elicits stronger brain responses in the superficial amygdala (Koelsch *et al.*, 2013). Accordingly, Barrett and Janata's (2016) finding that individuals higher on dispositional nostalgia manifested decreased amygdala activation during music-evoked nostalgia may suggest that nostalgic listeners may experience less positive affect in response to nostalgic music. Alternatively, as the amygdala also plays an important role in the processing of negative emotion (Kober *et al.*, 2008; Lindquist *et al.*, 2012), their finding may indicate that individuals high (compared to low) on dispositional nostalgia experience less negative emotion when listening to nostalgic music. Stated otherwise, individuals high on dispositional nostalgia may be better at regulating their negative mood elicited by nostalgic music. This possibility is consistent with research demonstrating that high-nostalgia individuals derive greater well-being benefits from a nostalgia induction (Cheung *et al.*, 2016; Layous *et al.*, 2021). Barrett and Janata's results should be interpreted with caution, however, considering the small sample size ($N = 12$).

More recently, Yang *et al.* (2021) induced nostalgia through pictures that depicted events or objects in participants' childhood. Following nostalgia induction, participants judged whether two death-related (*vs* neutral) words belonged in the same category. Participants who viewed nostalgic (*vs* control) pictures evinced more intense activation in right amygdala in response to death-related (*vs* neutral) words and also manifested greater accuracy in word judgments. Their findings indicate that nostalgia, as an approach-oriented emotion, enhances detection of death threat.

In addition to experimentally induced nostalgia, researchers have investigated attendees' reported nostalgia in Double-A Minor League Baseball games. In a recent electroencephalography (EEG) study, Hungenberg *et al.* (2020) recorded attendees' neurological responses as well as their self-reported nostalgia in the games. Attendees' brainwave frequencies (i.e. theta power in the frontal and temporal lobes, and alpha power in the posterior) that were indicative of self-reflection correlated positively and significantly with reported nostalgia. Furthermore, more self-reflection processing predicted, via reported nostalgia, attendees' desire to attend a future game and recommend a game to a friend.

Review of other relevant studies

Next, we review studies that, although not addressing nostalgia directly, are highly relevant to it, as they implement manipulations or stimuli that are common in nostalgia research and could elicit nostalgia. Typically, nostalgia is induced by either nostalgic stimuli or cues, such as music, photos and odors dating to one's childhood (Reid *et al.*, 2014; Oba *et al.*, 2015), or by recalling personal memories of nostalgic events (Sedikides *et al.*, 2015; Leunissen *et al.*, 2021). First, we will discuss work that involved stimuli deemed nostalgic, and subsequently, we will turn to work that involved memories of events deemed nostalgic.

Studies that involved stimuli deemed nostalgic

In an fMRI study, Janata (2009) presented participants with 30 excerpts of popular music from the Apple iTunes Music Store dating to their childhood. Following each excerpt, participants rated the familiarity, affective valence and autobiographical salience of the music. Strongly autobiographical songs were rated as more vivid, emotional and strongly associated with a specific memory (i.e. a discrete event). Brain activity in the dorsal mPFC (dmPFC) was positively related to the autobiographical salience of musical excerpts, whereas rostral and ventral mPFC (rmPFC and vmPFC), as well as PCC, responded to familiar, autobiographically salient and positive affective music pieces. Although based on a small sample ($N = 13$), these results suggest that the mPFC is engaged when people experience emotionally salient memories triggered by familiar songs from their personal past. The mPFC also engaged, along with lateral prefrontal and posterior cortices, to familiar and autobiographically salient songs. Therefore, the autobiographical salience and positive value produced by music-evoked personal memories were manifested mainly in the mPFC and its subregions. The mPFC is typically recruited not only during the processing of self-related information (D'Argembeau *et al.*, 2007) but also in autobiographical memory (Gilboa *et al.*, 2004) and in self-conscious emotion (Somerville *et al.*, 2013). Indeed, a meta-analysis indicated that autobiographical memory and self-reflection activated the same region within the mPFC (Martinelli *et al.*, 2013). Thus, the mPFC may serve as a hub that links self-reflection processing with autobiographical memories and emotions and plays an integrative role in the experience of nostalgia.

Another fMRI study, using songs popular in the past, also demonstrated the engagement of mPFC in specific autobiographical memories (Ford *et al.*, 2011). Participants listened to such songs and retrieved whatever autobiographical memory came to

mind. Certain neural regions of the core autobiographical memory network, including vmPFC, PCC and medial temporal lobe (MTL—along with the hippocampus), were engaged in all autobiographical memories. Moreover, the authors of this fMRI study examined how autobiographical memory specificity modulated activation of the autobiographical memory network by instructing participants to rate the level of specificity (i.e. lifetime period, general event and specific event) of their memory. Relative to retrieval of abstract personal knowledge, event retrieval was accompanied by stronger activation in dorsolateral and dorsomedial prefrontal regions. In addition, participants rated event-specific memories as most vivid, emotional, positive and subject to reliving. These memories were associated with enhanced activity in the MTL (including the hippocampus) and dmPFC (Ford *et al.*, 2011). Similarly, other studies revealed greater engagement of the mPFC, hippocampus (Maguire and Mummery, 1999) and regions associated with self-reference (anteromedial PFC; Levine *et al.*, 2004) during specific event memory.

Personal photos, as common cues for nostalgia, allow participants to re-experience their memories. Gilboa *et al.* (2004) induced distant or recent autobiographical memories via photographs of participants ranging from their fifth year of age to the present. Although the retrieval of both distant and recent memories activated the hippocampus, there was a greater distribution of activation along the hippocampus in distant than recent memories. As opposed to personal semantic information, recalling detailed, vivid and distant autobiographical experiences determined the involvement of hippocampus and two posterior regions, precuneus and lingual gyrus.

In addition to music and pictures, an fMRI study implemented a personally meaningful odor that linked to one's childhood time with family (Herz *et al.*, 2004). This kind of odor could elicit more intense emotional responses and greater activation in the amygdala and hippocampal regions during recall than pertinent control odor or visual stimuli. Autobiographical memory triggered by the olfactory stimuli was more emotional than when triggered by alternate sensory stimuli. This effect might be due to the direct neural link between the olfactory system and the amygdala-hippocampal system implicated in emotion and memory processing (LeDoux, 2000).

Studies that involved memories of events deemed nostalgic

Nostalgic memories are predominately positive, specific, vivid and distant (Van Tilburg *et al.*, 2019). We now discuss neuroimaging studies that examined positive, specific, vivid and distant autobiographical memories induced through nostalgizing. Evidence indicates that recalling positive autobiographical memories involves reward-related circuitry. In a study by Speer *et al.* (2014), participants first wrote about their personal memories prompted by life event cues (analogous to the Event Reflection Task typically used to induce nostalgia; Sedikides *et al.*, 2015). Subsequently, participants were given either positive (e.g. visiting Disneyland) or neutral (e.g. packing for a trip) personalized event cues and asked to savor these memories during scanning. Compared with neutral memories, positive memories enhanced not only self-reported positive mood but also activity in the striatum and mPFC. Crucially, the increase in positive mood was associated with higher striatum and mPFC activity. Additionally, participants preferred to recall positive past experiences even at the cost of tangible reward (i.e. money) in a gambling task; that is, positive autobiographical memories were valued more than monetary reward. Based on their findings, Nature (2014) concluded that 'Nostalgia rewards the brain, and people will even give up money for the chance to enjoy some nostalgia' (p. 11). As such, although Speer *et al.* did not explicitly highlight nostalgia, their findings point to the rewarding basis of nostalgia. Similarly, Lempert *et al.* (2017) asked participants to write about memories prompted by typical nostalgic life event cues (e.g. family vacation). Positive memory retrieval increased activity in the striatum and temporoparietal junction, and this brain modulation was linked to reduced temporal discounting. Hence, the extent to which memory recall is rewarding influences future reward-related decision-making.

In a study by Van Schie *et al.* (2019), participants used a first-person perspective to relive (rather than retrieve) positive autobiographical memories and evaluated the vividness of these memories. Positive compared to neutral memories enhanced mood and activation in the mPFC, ACC and precentral as well as postcentral gyrus. Higher vividness was related to more pleasurable, distant and longer memories; it was also related to greater activation in amygdala, hippocampus and insula, indicating increased awareness of oneself.[2] In the related work, effective vmPFC to hippocampus connectivity was observed when participants relived memories of events that were highly emotionally arousing or elicited stronger positive affect (Nawa and Ando, 2019). Returning to the Van Schie *et al.* study, participants' state self-esteem increased after reliving positive autobiographical memories in line with findings that nostalgia elevates self-esteem (Hepper *et al.*, 2012; Wildschut *et al.*, 2006) and augments self-positivity even when contrasted against an imagined positive future event in one's life (Vess *et al.*, 2012).

Cooney *et al.* (2007) investigated the neural correlates of positive autobiographical recall in recovery from negative mood. Retrieving positive autobiographical memories from one's high school years while in a negative mood state improved one's mood. Moreover, such retrieval was associated with activation in the orbitofrontal cortex and in ACC, highlighting an important role of the vmPFC and specifically of the subgenual cingulate, in regulating negative mood. These findings suggest that recall of positive memories could counteract affective negativity and regulate mood, consistent with the emotion regulatory capacity of nostalgia (Wildschut and Sedikides, 2022).

Summary

Nostalgia is an emotional experience that arises from memories featuring the self in social contexts (Sedikides *et al.*, 2008, 2015). Nostalgia is a complex emotion, involving multiple psychological processes. Existing studies, although limited in number, have shown that nostalgia involves brain structures known to be engaged in self-reflection (mPFC, PCC and precuneus), autobiographical memory (hippocampus, mPFC, PCC and precuneus), emotion regulation (ACC and mPFC) and reward processing (SN, VTA, STA and vmPFC). We summarize in Table 1, the research findings, including both fMRI studies, directly examining the neural basis of nostalgia and studies relevant to the neural basis of nostalgia. Further, we propose, in Figure 1, a 'nostalgic brain' model based exclusively on studies that directly addressed the neural basis of nostalgia. Lastly, we highlight, in Box 1, core brain regions activated more strongly in nostalgia than in control conditions (studies represented in Figure 1), and we incorporate core components of the emotion in describing its neural substrates.

[2] Piefke *et al.* (2003) reported hippocampal engagement for recent (5 years pre-interview), but not distant (up to participants' 10th year of age), autobiographical memories.

Table 1. Summary of functional magnetic resonance imaging (fMRI) studies and findings directly or indirectly relevant to nostalgia

Studies	Sample Size	Trigger	mPFC	ACC	PCC	Precuneus	HPC	Striatum	SN/VTA
1. Barrett and Janata, 2016	12	Music							√
2. Matsunaga *et al.*, 2013	10	Odor	√		√	√			
3. Oba *et al.*, 2015	15	Picture					√	√	√
4. Trost *et al.*, 2012	16	Music	√	√		√	√	√	
5. Cooney *et al.*, 2007	14	Event	√	√					
6. Ford *et al.*, 2011	16	Music	√		√		√		
7. Gilboa *et al.*, 2004	9	Photo			√	√	√		
8. Herz *et al.*, 2004	5	Odor					√		
9. Janata, 2009	13	Music	√		√				
10. Lempert *et al.*, 2017	35	Event	√		√			√	
11. Nawa and Ando, 2019	36	Event	√				√		
12. Piefke *et al.*, 2003	20	Event	√				√		
13. Speer *et al.*, 2014	28	Event	√	√				√	
14. Van Schie *et al.*, 2019	47	Event	√	√			√		

HPC = hippocampus; mPFC = medial prefrontal cortex; ACC = anterior cingulate cortex; PCC = posterior cingulate cortex; SN = substantia nigra; VTA = ventral tegmental area.
Studies 1–4 directly addressed the neural basis of nostalgia. Studies 5–14 used stimuli or manipulations common in nostalgia research that were likely to elicit nostalgia. We did not include the Yang *et al.* (2021) study, because it examined the neural modulation of nostalgia on death threat rather than the neural basis of nostalgia. Also, we did not include the Hungenberg *et al.* (2020) study, because it used EEG rather than fMRI.

Box 1. Neural Substrates of Nostalgia

Nostalgia is considered a combination of self-reflection processing, autobiographical memory, emotion regulation and reward processing. The mPFC serves as a hub, integrating these four components.
We summarize below the functional significance of brain structures highlighted in the nostalgic brain model.

- mPFC: it is involved in tasks of high self-relevance and tasks that require self-reflection. The mPFC also functions in autobiographical memory, self-conscious emotion and emotion regulation. Its subregions, such as vmPFC, are also relevant to the model. The vmPFC is involved in assigning personal significance to self-related contents, playing an important role in reward processing.
- ACC: it is involved in monitoring and in functions associated with the cognitive control of emotion. The ACC also acts as an affective component of the self.
- PCC: it is involved in self-reflection and in autobiographical memory.
- Precuneus: it is involved in a wide spectrum of highly integrated tasks, including visuospatial imagery, episodic memory retrieval and self-reflection. Precuneus has been proposed as neural correlate of self-consciousness.
- Hippocampus: it plays a key role in memory function, particularly in the retrieval of autobiographical memory.
- Striatum: a core region of the mesolimbic dopamine system, and a critical component of reward systems. The VS is sensitive to primary rewards such as food, drugs or sex and to secondary rewards such as money and power.
- SN/VTA: it plays a central role in reward processing, such as reward anticipation, and has been associated with the experience of positive affect during music listening.

We emphasize that the evidence for the abovementioned propositions is suggestive at best. Granted, experimental inductions of nostalgia yielded activation in the brain regions we discussed (Figure 1). However, as we mentioned, our interpretations relied on reverse inference, an issue that needs to be addressed by future research (see also the 'Multivariate approach to testing the propositions' section). We have listed brain regions most consistently associated with the four components of nostalgia (i.e. self-reflection, autobiographical memory, emotion regulation and reward processing) based on the social neuroscience literature. However, each component is associated with other brain regions as well; for example, amygdala and insula are also implicated in reward processing (Sescousse *et al.*, 2013), whereas temporal cortex and cerebellum are also implicated in autobiographical memory (Svoboda *et al.*, 2006). For example, key brain regions involved in nostalgia (specifically self-reflection), such as mPFC and PCC, are also core regions of the DMN (Philippi and Koenigs, 2014), raising the possibility that DMN is implicated in nostalgizing. Yet, to the extent that a given brain region is associated with one of the four components, it should also be involved in nostalgia. Thus, when testing the propositions, it is more informative to demonstrate that nostalgia and a given component share a neural basis rather than simply showing that nostalgia activates the listed brain regions (see the 'Multivariate approach to testing the propositions' section).

Further, we observe that the components (and relevant processes) are interdependent and coordinated. First, autobiographical memories have high emotional potency and, vice versa, emotional experiences attain a privileged status in memory (Bluck and Li, 2001; Talarico *et al.*, 2004; Schaefer and Philippot, 2005; LaBar and Cabeza, 2006). This emotion-memory interaction may make the nostalgic experience more lasting and significant. Second, autobiographical memory, emotion-imbued autobiographical memories and self-reflection overlap (Lieberman *et al.*, 2019). In both positive and negative autobiographical memory processing, the precuneus shows connections with the mPFC, a key region of the self-processing network (Xu *et al.*, 2018). Also, the mPFC and PCC play a role in integrating self-relevance into autobiographical memory (Northoff and Bermpohl, 2004; Cabeza and St Jacques, 2007), whereas the mPFC and ACC play a role in integrating emotion into self-reflection processing (Moran *et al.*, 2006).

Third, memory and reward systems interact closely in the nostalgic experience. High-value (e.g. nostalgic) stimuli engage reward-related regions such as the VTA and VS, promoting memory formation and better subsequent recall (Scimeca and Badre, 2012), potentially owing to the interactions with memory-related regions such as the hippocampus (Wittmann *et al.*, 2005; Adcock *et al.*, 2006). Dopamine release supports hippocampal plasticity and memory formation and increased dopamine release may

make memories more self-relevant and salient, strengthening them over time and rendering them more accessible in the future (Shohamy and Adcock, 2010). Indeed, the simultaneous involvement of autobiographic memory and reward system during nostalgia was manifested by hippocampus-VS (Oba *et al.*, 2015) and PCC-vmPFC (Matsunaga *et al.*, 2013) co-activation. Jointly, these findings highlight the function of memory and reward networks: the association between autobiographical memory and its reward property would be reinforced by dopamine transmission when experiencing nostalgia, such that the nostalgic memory would be re-encoded and re-stored in the network. The reinforced memory and reward association would further improve the reward value of the future nostalgic experiences (Oba *et al.*, 2015). Given that nostalgia is thought to 'bestow an endearing luster on past selves' (Davis, 1979, p. 41), it may add more lustrous elements to autobiographical events that may not have seemed all that positive at the time.

Brain activity involved in nostalgizing could be modulated by the triggered memories' emotional significance, distance and vividness. For example, greater activation in amygdala, hippocampus and insula (Van Schie *et al.*, 2019), as well as effective vmPFC to hippocampus connectivity (Nawa and Ando, 2019), was detected when details about a personal event were recalled. Indeed, nostalgia could be considered a more specific, vivid and emotionally salient form of distant autobiographical memories (Van Tilburg *et al.*, 2019). Thus, when examining nostalgia-specific brain activities and cognitive processes, the control condition (e.g. equally vivid and emotional salient non-nostalgic autobiographical memories) is vital in helping researchers pinpoint a unique neural signature of nostalgia.

Future directions in neuroimaging research on nostalgia

Multivariate approach to testing the propositions

Our four propositions pertain to which brain regions are activated when an individual nostalgizes and why (e.g. mPFC because it is involved in autobiographical memory). Thus, to test each proposition, one ought to document not only that nostalgizing activates the corresponding brain region but also that the activation is due to a specific component (e.g. autobiographical memory). Consider the case of ACC, known to be one of the most functionally heterogeneous brain regions (Poldrack, 2011; Wager *et al.*, 2016). Even if a study found activation in ACC when participants were presented with nostalgia-evoking stimuli, one could not infer that this activation was due to emotion regulation (i.e. Proposition 3) as opposed to another component. Therefore, to test our propositions, one would need to compare directly brain regions activated by nostalgia with brain regions activated by a component of interest (e.g. emotion regulation).

Furthermore, in doing so, it does not suffice to show that there are activation overlaps because such overlaps do not necessarily mean that they involve a common component (i.e. the same brain region could be activated for different reasons). Recently, a multivariate pattern analysis (MVPA) approach has been proven useful in discriminating between conditions that involve a common component (Woo *et al.*, 2014; Wake and Izuma, 2017; Levorsen *et al.*, 2021). For example, suppose that each of two conditions—for example, nostalgia and emotion regulation—significantly activated the same 100 voxels within the ACC. If activation patterns across the 100 voxels were similar between conditions (i.e. significantly positive voxel-by-voxel correlation), these patterns would constitute strong evidence of a common component (e.g. nostalgia involves emotion regulation).

Furthermore, a multivariate approach is suitable for testing the idea that multiple brain regions (Figure 1) collectively contribute to the subjective experience of nostalgia. As an example, a recent MVPA study has demonstrated that activation patterns across distributed brain regions (i.e. prefrontal, midcingulate, insular cortices, thalamus and amygdala) can predict subjective fear ratings (Zhou *et al.*, 2021b). This finding constitutes another critical piece of evidence against the idea that each emotion is specifically related to a single distinct brain region. Similarly, the attempt to predict the subjective experience of nostalgia using a whole-brain multivariate pattern is promising. The endeavor to unveil the neural signatures of nostalgia via a multivariate approach will add to the understanding of neural mechanisms of emotions in general—for example, how activation patterns in brain regions linked to different functions converge to produce a specific felt emotion.

Differentiating nostalgia from positive affect

Nostalgia is bittersweet, but more sweet than bitter (Van Tilburg *et al.*, 2019; Leunissen *et al.*, 2021). However, although the affective signature of nostalgia is predominantly positive, it should be distinguished from general positive affect (Stephan *et al.*, 2012; Sedikides *et al.*, 2015). Nostalgic engagement involves co-activation of positive and negative affect, a pattern that produces an emotional dynamic felt as ambivalence. The ambivalence of nostalgia may, at least in part, be responsible for its psychological benefits (Sedikides and Wildschut, 2016). There is evidence that individuals who experience mixed emotions show improved well-being (Adler and Hershfield, 2012).

To differentiate nostalgia from positive affect, psychologists have compared the effects of recalling nostalgic *vs.* positive memories (e.g. a lucky event). These studies have documented unique effects of nostalgia (compared to positive memory per se) on ingroup evaluation and motivation to approach ingroup members (Wildschut *et al.*, 2014), social connectedness, self-esteem and ensuing inspiration (Stephan *et al.*, 2015), openness to experience and ensuing creativity (Van Tilburg *et al.*, 2015), social connectedness and ensuing self-continuity (Sedikides *et al.*, 2016) and perceived social support (Zou *et al.*, 2019). Other research that compared listening to nostalgic *vs* cheerful songs demonstrated unique effects of music-evoked nostalgia on self-esteem and ensuing optimism (Cheung *et al.*, 2013). These diverse findings illustrate the distinctiveness of nostalgia, above and beyond general positive recollection and concomitant positive affect.

Future neuroimaging research could emulate these procedures by comparing the neural activation associated with nostalgic stimuli (e.g. autobiographical recall, music and scent) to patterns of activation associated with equally positive, but non-nostalgic, stimuli. This would address a limitation of existing studies, which generally did not systematically control for stimulus valence. For example, in Oba *et al.* (2015), the nostalgic (*vs* control) stimuli elicited greater self-reported happiness.

Regulatory function of nostalgia

According to the regulatory model (Sedikides *et al.*, 2015; Wildschut and Sedikides, 2022), nostalgia counteracts or down-regulates diverse psychological threats. One account for the regulatory (e.g. threat-buffering) capacity of nostalgia is the engagement of top-down processes, including cognitive emotion

regulation. These processes involve the PFC and ACC (Ochsner *et al.*, 2004; Ochsner and Gross, 2005; Cisler and Koster, 2010). Given that activation in these regions is also associated with nostalgia, PFC and ACC may represent the neural substrate of nostalgia's regulatory function (Janata, 2009; Trost *et al.*, 2012; Barrett and Janata, 2016). Stated otherwise, when encountering a psychological threat, nostalgia may modulate activity in the emotion regulation network. This regulatory mechanism has been documented in an fMRI study on self-esteem and mortality salience (Yanagisawa *et al.*, 2016). Individuals with high self-esteem showed increased amygdala-ventrolateral prefrontal cortex connectivity in response to death-related stimuli, and this stronger functional connectivity predicted a reduction in defensive reactions following exposure to these stimuli. Notably, nostalgia inductions boost self-esteem (Wildschut *et al.*, 2006; Hepper *et al.*, 2012), which may shed light on the mechanisms underlying the self-regulatory potential of nostalgia.

Another regulatory mechanism may be indirect and derive from nostalgia's rewarding potential. Rewarding stimuli decrease physiological stress reactivity (Creswell *et al.*, 2013), and this may explain the beneficial influence of nostalgia (a predominantly positive emotion) in the context of threat. Given that the VS shows resting-state functional connectivity with the vmPFC (Di Martino *et al.*, 2008), it is possible that striatum activity is accompanied by heightened vmPFC activity, which regulates psychological and behavioral responses to threat information (Falk *et al.*, 2015; Dutcher *et al.*, 2016). When individuals experience nostalgia, their reward-related neural activity intensifies, which may modulate their neural responses to threat allowing them to be more resilient and less defensive. Overall, nostalgia might modulate neural responses to threats, thereby buffering their impact (Juhl *et al.*, 2010; Routledge *et al.*, 2011) and reducing defensive responding (Routledge *et al.*, 2013; Sedikides and Wildschut, 2018). Future neuroscience research would do well to focus on providing further evidence for this proposed regulatory function of nostalgia.

Individual differences

Nostalgia proneness

Neural responses to nostalgia-evoking music are modulated by individual differences in nostalgia proneness. Barrett and Janata (2016) found that high (*vs* low) dispositional nostalgia attenuated the relation between music-evoked nostalgia and brain activity in regions implicated in affect and reward processing (i.e. left amygdala and a midbrain region including the SN and VTA). As mentioned before, for individuals who were more chronically nostalgic, activity in these regions decreased when they experienced music-evoked nostalgia, whereas, for those less chronically nostalgic, activity in these areas increased when exposed to music-evoked nostalgia. The findings highlighted the importance of incorporating individual differences in future research on neural responses to complex and idiosyncratic emotional experiences.

Genetic influences are also relevant. A twin study demonstrated that dispositional nostalgia is partly shaped by heredity (Luo *et al.*, 2016). More recently, Luo *et al.* (2017) uncovered a biological basis for nostalgia's heritability. These researchers focused on a polymorphism in the promoter of the serotonin transporter gene (5-HTTLPR) as a possible biological basis. Participants with the 5-HTTLPR short allele were higher on dispositional nostalgia than those without this allele. Given that the serotonin system is linked with sensitivity to negative experiences, the findings suggest that individuals with the 5-HTTLPR short allele may recruit nostalgia to cope with the psychological consequences of aversive events. This interpretation is consistent with evidence from an EEG study, indicating that relative right-frontal EEG asymmetry, a neural correlate of withdrawal from aversive stimulation (Davidson, 1998), is positively associated with dispositional nostalgia (Tullett *et al.*, 2015). Future research should consider the role of serotonin in modulating the neurological networks implicated in nostalgia (Hensler, 2006).

Attachment avoidance

Nostalgia functions as a social resource, decreasing attachment-related anxiety and avoidance (Wildschut *et al.*, 2006). Individual differences in attachment-related avoidance moderate the sociality function of nostalgia. Nostalgic reflection fosters social connectedness, interpersonal competence (Wildschut *et al.*, 2010) and relationship satisfaction (Juhl *et al.*, 2012) among low-avoidance, but not among high-avoidance, individuals. Moreover, attachment-related avoidance is implicated in the extent to which people recruit nostalgia to cope with social distress, such as loneliness and social exclusion. Specifically, low-avoidance (compared to high-avoidance) individuals are more likely to respond to social distress with increased nostalgia (Wildschut *et al.*, 2010; Abakoumkin *et al.*, 2017). Notably, attachment-related avoidance has been linked to hippocampal reduction (Quirin *et al.*, 2009), suggesting that the hippocampus is involved in the formation and maintenance of social attachment (Koelsch, 2014). This suggestion aligns with the results of neuroimaging studies that document changes in hippocampal activity during nostalgic reflection (Trost *et al.*, 2012; Oba *et al.*, 2015). Signal changes in hippocampus in response to nostalgic stimuli might be contingent upon individual differences in attachment style. Future research could examine whether a person low (than high) on attachment avoidance evinces greater changes in hippocampal and reward-network activity when nostalgizing.

Resilience

Resilience is defined as the ability to experience positive emotions (Bonanno, 2005) and to use personal and social resources for bouncing back effectively from adversity (Tugade and Fredrickson, 2004). Resilience can moderate the relation between loneliness and nostalgia, such that highly resilient individuals are more likely or able to recruit nostalgia when feeling lonely (Zhou *et al.*, 2008). When recollecting positive memories, resilience was associated with greater striatal activity (Speer *et al.*, 2014). That is, resilient individuals, who have a greater tendency to experience positive emotions (i.e. improvement of positive mood), are also those who exhibit more reward-related activity in the striatum when engaging in positive autobiographical memories. In addition, the memory and reward network (i.e. the hippocampal-VTA loop) involved in nostalgia may be related to resilience (Oba *et al.*, 2015). To be precise, when nostalgia is experienced, the connection between the nostalgic memory and its reward value would be reinforced by dopamine transmission, with the memory re-encoded and re-stored in the network. Consequently, the reinforced association is likely to produce more rewards when nostalgia is re-experienced, thereby strengthening resilience (Oba *et al.*, 2015). Future neuropsychological studies could assess more closely the association between resilience and nostalgia's role in threat or adversity regulation.

Multisensory nostalgia

Neuroscientists have used auditory (Janata, 2009; Ford *et al.*, 2011; Trost *et al.*, 2012; Barrett and Janata, 2016), visual (including

semantic and image; Speer *et al.*, 2014; Oba *et al.*, 2015) and olfactory (Matsunaga *et al.*, 2013) stimuli to induce nostalgia. However, these differing nostalgia inductions may produce distinct effects. For example, odor-evoked autobiographical memories are more emotionally potent than memories evoked by other stimuli (Herz *et al.*, 2004), yielding stronger activity in MTL regions and precuneus (Arshamian *et al.*, 2013). Also, music- and odor-induced nostalgia may elicit stronger activity in regions implicated in emotion and visual vividness (e.g. precuneus; Trost *et al.*, 2012; Matsunaga *et al.*, 2013; Barrett and Janata, 2016). In the case of musical memory, an amnesia patient study suggested that memory for music depends on brain networks that are distinct from those involved in episodic and semantic memory (Finke *et al.*, 2012). These findings underscore the importance of addressing the mechanisms that underlie different nostalgia inductions. Furthermore, it is useful to investigate the neural bases of nostalgia through different inductions within the same group of participants. This would allow researchers to test whether the brain regions proposed above are actually *core* structures (thus, activated regardless of induction methods) and to identify other brain regions that are contingent on specific induction methods.

Conclusion

In recent years, social cognitive neuroscience has begun to offer valuable insights into the neural bases of nostalgia, as well as human emotion and memory in general. Based on psychological understanding, we postulated that nostalgia involves several neural regions, specifically those involved in self-reflection, autobiographical memory, emotion regulation and reward processing. The results of recent neuroscientific studies are at least partially consistent with these propositions, although some evidence is indirect (i.e. based on reverse inference).

Nostalgia's influence on neural activity within multiple brain structures suggests the potential for applications of nostalgia-based therapy and treatment to emotional and memory dysfunctions. The social cognitive neuroscience approach can provide evidence and novel explanations for the psychological benefits of nostalgia. Involvement of the reward network may further elucidate nostalgia's benefits and could be mediated by nostalgia's capacity to fulfill personal and social needs. Future research could explicate the functional mechanisms underlying nostalgia through a multivariate approach as well as elucidate the connectivity among the core regions associated with this emotion. Future research could also compare nostalgia with positive emotion or memory, examine multisensory nostalgia by various triggers and explore individual differences that may modulate brain responses during nostalgic engagement.

Emotion is one of the most elusive topics in both psychology and neuroscience, and advances in neuroscience testify to how complex the neural representation of emotion is (Lindquist *et al.*, 2012; Adolphs, 2017; Barrett, 2017; Saarimäki *et al.*, 2018). Yet, we hope that our review provides a good starting point for unraveling the neural basis of nostalgia.

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Conflict of interest

The authors declare no conflicts of interest.

Data Availability

None declared.

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