



Age differences in ventromedial prefrontal cortex functional connectivity during socioemotional content processing

Ryan T. Daley¹, Holly J. Bowen², Eric C. Fields³, Angela Gutchess⁴, Elizabeth A. Kensinger¹

¹Department of Psychology and Neuroscience, Boston College, United States

²Department of Psychology, Southern Methodist University, United States

³Department of Psychology and Neuroscience, Boston College, and Department of Psychology, Brandeis University, United States

⁴Department of Psychology, Brandeis University, United States

How to cite: Daley, R. T., Bowen, H. J., Fields, E. C., Gutchess, A., & Kensinger, E. A. (2020). Age differences in ventromedial prefrontal cortex functional connectivity during socioemotional content processing. *Social Behavior and Personality: An international journal*, 48(7), e9380

Self-relevance effects are often confounded by the presence of emotional content, rendering it difficult to determine how brain networks functionally connected to the ventromedial prefrontal cortex (vmPFC) are affected by the independent contributions of self-relevance and emotion. This difficulty is complicated by age-related changes in functional connectivity between the vmPFC and other default mode network regions, and regions typically associated with externally oriented networks. We asked groups of younger and older adults to imagine placing emotional and neutral objects in their home or a stranger's home. An age-invariant vmPFC cluster showed increased activation for self-relevant and emotional content processing. Functional connectivity analyses revealed age \times self-relevance interactions in vmPFC connectivity with the anterior cingulate cortex. There were also age \times emotion interactions in vmPFC functional connectivity with the anterior insula, orbitofrontal gyrus, inferior frontal gyrus, and supramarginal gyrus. Interactions occurred in regions with the greatest differences between the age groups, as revealed by conjunction analyses. Implications of the findings are discussed.

Keywords

socioemotional content processing; ventromedial prefrontal cortex; functional connectivity; human brain; age difference; self-relevance; emotion

The concept of the self has occupied the minds of scientists and philosophers over many centuries. Descartes (1641/1984) inextricably linked the self with introspection, subsequently distinguishing it from the body, and establishing Cartesian dualism. In his bundle theory, Hume (1739/2003) laid out a more materialist account, suggesting the self is not a unified whole, but rather the by-product of the individual's perceptions. Although a conclusive definition of the self is not provided in modern psychological accounts, research findings point to the neural and psychological representations of cognition, motivation, and affect as supporting this construct (Gillihan & Farah, 2005; Markus & Nurius, 1986). Importantly, while seeking to understand the self, in modern psychological accounts scholars have demonstrated that *self-relevant content*, or information that relates to an individual's identity or goals, can provide cognitive enhancements across the adult life span (Alexopoulos, Muller, Ric, & Marendaz, 2012; Cunningham, Brady-Van den Bos, & Turk, 2011; Glisky & Marquine, 2009; Grilli, Woolverton, Crawford, & Glisky, 2018; Gutchess, Kensinger, Yoon, & Schacter, 2007; Hou, Grilli, & Glisky, 2019; Leshikar, Dulas, & Duarte, 2015; Mueller, Wonderlich, & Dugan, 1986).

CORRESPONDENCE Ryan T. Daley, Department of Psychology and Neuroscience, Boston College, McGuinn Hall, Rm 300, 140 Commonwealth Avenue, Chestnut Hill, MA 02467, USA. Email: daleyrb@bc.edu

In neuroscientific accounts (Gusnard, Akbudak, Shulman, & Raichle, 2001; Kelley et al., 2002) the processing of information related to the self is associated with increased activation in the medial prefrontal cortex. What is intriguing for researchers is that the medial prefrontal cortex is also implicated in the processing and regulation of emotion (Etkin, Egner, & Kalisch, 2011; Goldin, McRae, Ramel, & Gross, 2008; Quirk & Beer, 2006). This has led to proposals that the medial prefrontal cortex may serve as a site of shared processing for self-referential and emotional information (D'Argembeau, 2013; Gutchess & Kensinger, 2018). However, much of the research on self-relevance has been conducted in the context of emotional content processing (Beer, 2017), such as deciding whether positive and negative personality traits are self-descriptive (Gutchess, Kensinger, & Schacter, 2007; Kelley et al., 2002; Rogers, Kuiper, & Kirker, 1977). Some scholars have intentionally examined regions implicated in self-relevance by emotion interactions (Moran, Macrae, Heatherton, Wyland, & Kelley, 2006)—as in the case of self-positivity bias (Fields, Weber, Stillerman, Delaney-Busch, & Kuperberg, 2019)—but to date none have attempted to separate the effects of these types of content on neural activity supporting information processing. More specifically, no prior studies have examined whether the medial prefrontal cortex is not only *activated* for self-referential and emotional material but also *functionally connected* in similar ways for processing the two types of content. Examining functional connectivity will provide a strong test of whether self-referential and emotional content recruit either a common processing network or a common hub (medial prefrontal cortex) that contributes to different functional networks.

It is also relevant to examine how age may affect the overlap between self-referential and emotional processing. Behaviorally, both older adults (defined here as individuals over the age of 60 years) and younger adults (defined here as individuals under the age of 40 years) elaborate on self-relevant content to a greater extent than they do non-self-relevant content (see, for a meta-analysis, Symons & Johnson, 1997), and findings reported in recent work suggest that self-relevant content can be processed with relative automaticity (Humphreys & Sui, 2016). This may account for other findings that both older and younger adults tend to have better memory for information that relates to the self, compared to information that relates to another person (Gutchess, Kensinger, Yoon, et al., 2007; Gutchess et al., 2015; Hamami, Serbun, & Gutchess, 2011; Yin, Sui, Chiu, Chen, & Egner, 2019). Older adults also demonstrate emotion enhancements, marked by paying increased attention to emotional compared to neutral content (Mather & Carstensen, 2005), particularly when the content is positive (Carstensen & Mikels, 2005; Reed, Chan, & Mikels, 2014). This positivity bias is thought to arise from older adults' motivation to engage in positive emotional experiences in light of a limited perceived temporal horizon (Carstensen & Mikels, 2005; Reed et al., 2014). At the same time, most individuals demonstrate bias toward positive self-related information (Alicke & Govorun, 2005). This can lead to self-relevance by emotion interactions, whereby younger adults also show enhanced performance on positive (vs. neutral or negative) self-relevant information, subsequently diminishing older age-related positivity biases in some cases (Leshikar et al., 2015; Yang, Truong, Fuss, & Bislimovic, 2012).

Alongside cognitive enhancements for self-relevant and emotional content, the literature points to the preservation of ventromedial prefrontal cortex (vmPFC) activation during the processing of these types of content across the adult life span (Kensinger & Gutchess, 2015; Mather, 2016). Although older adults show structural deterioration in prefrontal cortices (Fjell et al., 2014; Raz et al., 1997; Tisserand et al., 2002), there may be relative functional preservation of the vmPFC that allows for self-relevant and emotional processing enhancements as people age. Supporting this claim, older and younger adults both activate the vmPFC similarly during judgments about the self compared to another person (Gutchess, Kensinger, & Schacter, 2007). Gutchess and Kensinger (2018) recently proposed that an overlapping neural mechanism in the vmPFC may support representations of self-relevant and emotional content across the adult life span.

The vmPFC is an important region to examine because of its key role in the brain's default mode network (DMN), which comprises functional hubs along the cortical midline, including the medial prefrontal cortex, perigenual anterior cingulate cortex, posterior cingulate, and precuneus, along with the bilateral inferior

parietal cortices (Buckner et al., 2009; Greicius, Krasnow, Reiss, & Menon, 2003; Gusnard et al., 2001; Qin & Northoff, 2011; Raichle et al., 2001). Originally, the DMN was considered an explicitly task-negative network (Fox, Snyder, Vincent, Corbetta, & Raichle, 2005), whereby the greatest network activity was observed when people were at rest, and the network became deactivated when they focused on external stimuli. Since its discovery, however, the DMN has been shown to overlap with networks active during goal-oriented tasks that require the individual to create mental representations of self-relevant stimuli, as in autobiographical memory retrieval or imagining future scenarios (Buckner & DiNicola, 2019; Qin & Northoff, 2011; Soch et al., 2017). Whitfield-Gabrieli et al. (2011) demonstrated that both the vmPFC and the dorsomedial prefrontal cortex are associated with self-relevant content processing, but the vmPFC alone shows overlap with DMN activity at rest. Thus, the DMN and one of its cortical hubs, the vmPFC, are thought to disengage when external stimuli catch the individual's attention, and to engage during the creation or reflection of an internal mental representation.

It is possible, therefore, that the vmPFC could be functionally connected to similar networks during the processing of self-relevant and emotional content because of their motivational salience when creating internal representations. Indeed, fluctuations in functional connectivity of the vmPFC with DMN regions have been shown when individuals process emotional content in social contexts, such as facial expressions (Göttlich, Ye, Rodriguez-Fornells, Münte, & Krämer, 2017; Satpute & Lindquist, 2019; Sreenivas, Boehm, & Linden, 2012). Additionally, the processing of emotional stimuli is typically associated with activation of the salience network (Luo et al., 2014; Menon & Uddin, 2010), which includes hubs in the anterior insula and dorsal anterior cingulate that are functionally connected with the amygdala, orbitofrontal cortex, ventral tegmental area, and thalamus (Seeley et al., 2007). This network aids transitions between the internally oriented DMN and the externally oriented executive control network, including the dorsolateral prefrontal cortex, dorsal anterior cingulate, and lateral parietal cortices, during cognitively demanding tasks (Goulden et al., 2014; Menon & Uddin, 2010; Sridharan, Levitin, & Menon, 2008). In this case, processing emotional content in social contexts may lead to increased functional connection between the vmPFC and regions associated with salience and executive control networks.

The effects of aging on vmPFC connectivity are further complicated by the age-related deterioration of intrinsic functional networks. Deterioration of DMN architecture occurs in older adults and is marked by weaker within-network functional connectivity (Sala-Llonch, Bartrés-Faz, & Junqué, 2015) and stronger between-network functional connectivity between the DMN and externally oriented networks involved in cognitive control (Ng, Lo, Lim, Chee, & Zhou, 2016; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013). These network changes are thought to partially explain cognitive decline as people age (Andrews-Hanna et al., 2007; Spreng & Schacter, 2012; Spreng, Stevens, Viviano, & Schacter, 2016). Recently, however, scholars have suggested that increases in functional connectivity between the DMN and externally oriented networks may reflect age-related adaptive processes, whereby older adults rely on a wealth of stored semantic information during the generation of internal mental representations (Spreng et al., 2018; Turner & Spreng, 2015). Although Spreng et al. (2018) examined age interactions in DMN coupling with externally oriented networks during autobiographical memory retrieval, they suggested this coupling could reflect a domain-general process. We anticipated that older adults may rely on semantic knowledge to guide goal-directed content processing, as in the case of self-relevant or emotional content, which could be reflected in the functional coupling of regions between these networks.

As both older and younger adults engage the vmPFC when processing self-relevant and emotional content, we hypothesized that the vmPFC would show increased activation in these contexts compared to the processing of non-self-relevant and neutral information. There are two competing hypotheses regarding the functional networks that are connected to the vmPFC during the processing of self-relevant and emotional content. First, the vmPFC may be functionally connected to overlapping networks centered around the DMN. Second, the vmPFC may be functionally connected to distinct, nonoverlapping networks. Depending on which of the two patterns emerges, this will provide evidence either of further convergence between self-

relevant and emotional processing, or of a distinction between these processes, based on their associated functional networks.

Regarding age differences in vmPFC functional connectivity during the processing of self-relevant and emotional content, there are two more competing hypotheses. Because of the age-related cognitive benefits of self-relevant and emotional content, it is possible that the vmPFC is functionally connected to age-invariant networks when processing self-relevant and emotional content. Alternatively, age-related decreases in functional connectivity within the DMN and increases in functional connectivity between the DMN and regions associated with cognitive control networks may lead older adults to have decreased functional connectivity between the vmPFC and DMN regions for self-relevant content, but increased functional connectivity between the vmPFC and regions typically associated with the cognitive control networks during the processing of social content that is emotional but non-self-relevant in nature. Depending on which of these two patterns emerges, the results will either point to the maintenance of networks supporting the processing of emotion and self-relevance in older adults, or identify age-related shifts in functional networks supporting the processing of self-relevant and emotional content, respectively.

To test these hypotheses, we designed a paradigm adapted from Cunningham et al. (2011). To examine the effects of both self-relevance and emotion in the same paradigm, we presented younger and older adults with images of positive, negative, and neutral objects and asked them to imagine placing each object somewhere in their home (self) or in a stranger's home (other), depending upon a provided cue, while undergoing functional magnetic resonance imaging (fMRI) scans.

Method

Participants

As part of a larger event-based fMRI study, we collected data from a group of people aged 18–39 years (younger adults) and a second group aged 60–88 years (older adults). The cognitive testing process is summarized in Daley et al. (2020). No one in the participant groups reported a history of a serious mental illness or neurodegenerative disease.

For this study we focused on usable fMRI data obtained from a subsample of 50 younger adults (28 women, 22 men; $M_{\text{age}} = 22.26$ years, $SD = 3.91$; $M_{\text{education}} = 15.30$ years, $SD = 2.29$) and a subsample of 43 older adults (27 women, 16 men; $M_{\text{age}} = 68.28$ years, $SD = 6.78$; $M_{\text{education}} = 17.19$ years, $SD = 2.25$). All participants gave informed consent as approved by the Boston College Institutional Review Board.

Materials

The experimental stimuli comprised 420 images of objects (140 negative, 140 neutral, 140 positive) from the Open Affective Standardized Image Set (Kurdi, Lozano, & Banaji, 2017) and image sets used in prior laboratory research (e.g., Waring & Kensinger, 2009). Normative ratings of valence, arousal, and self-relevance are reported in Daley et al. (2020).

Procedure

Task. Participants viewed images (84 per valence) of positive (e.g., gold coins), negative (e.g., a gas mask), and neutral (e.g., a clothespin) objects, and imagined placing those objects in either their home or a stranger's home based upon the word that appeared above each image ("Self" or "Other"; $n = 126$ per category; see Figure 1). Following the initial presentation of each object (1,000 ms), pictures of two houses appeared below the object (one labeled "My house" and one labeled "Stranger's house"), which was the participants' cue to make a button press to indicate in which house they imagined placing the objects (3,000 ms).

Participants completed four full attention runs and two divided attention runs (42 objects per run), but the fMRI analyses reported here include the results from only the full attention runs (see supplementary materials for justification). Participants then completed a surprise recognition memory test (results reported in Daley et al., 2020) outside the scanner.

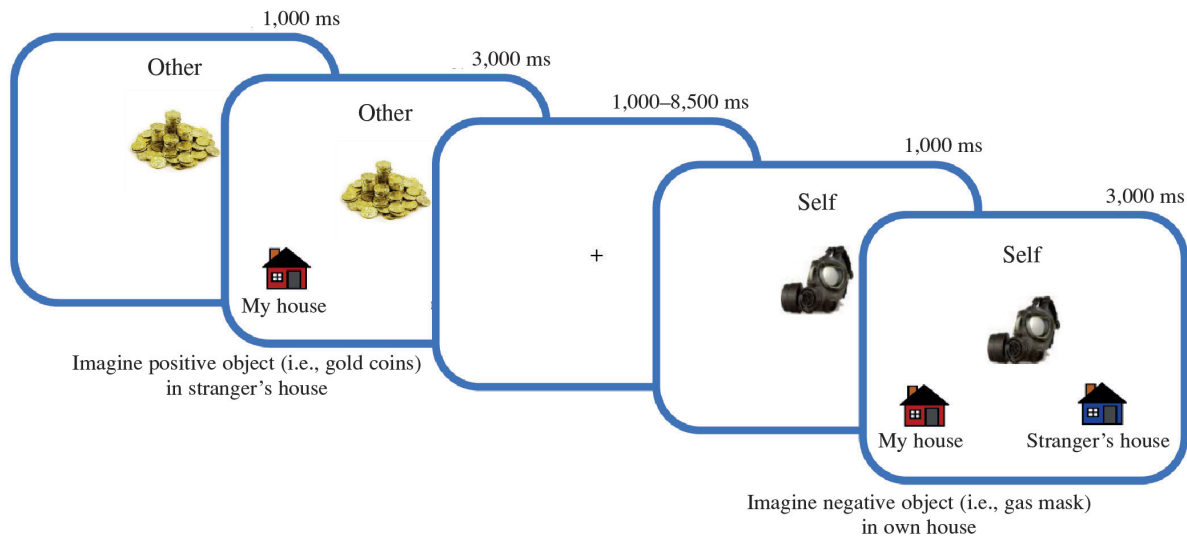


Figure 1. Socioemotional encoding task.

fMRI analyses to define a medial prefrontal cortex region. fMRI image acquisition, preprocessing, and visualization parameters are reported in the supplementary materials. We created a general linear model to examine neural activity during the processing of task stimuli independent of memory performance. Each participant's data were subjected to a fixed-effects model that consisted of six regressors of interest broken down by negative–self, neutral–self, positive–self, negative–other, neutral–other, and positive–other trials. A linear drift regressor was included as a regressor of no interest. We then included the results from each participant's model in a group-level random effects analysis of variance (ANOVA), with emotional valence (negative, neutral, positive) and self-relevance (self, other) as the within-subjects variables and age group (younger adults, older adults) as the between-subjects variable.

To define a medial prefrontal cortex region that was engaged for self-relevant or emotional information, we conducted a second-level *t* contrast to examine neural activity for the “*all conditions except neutral–other > neutral–other*” condition. Supporting our hypothesis about age-consistent activation during the processing of these types of information, a significant cluster appeared in the vmPFC (Montreal Neurological Institute space peak coordinate [MNI]: -2, 46, -20; see Figure 2).

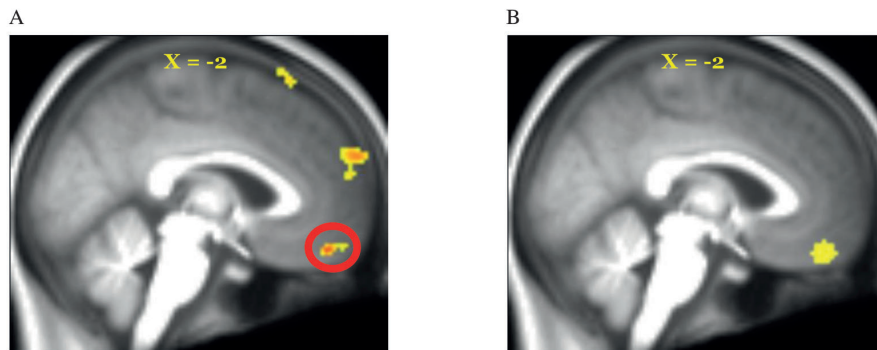


Figure 2. Age-invariant ventromedial prefrontal cortex (vmPFC) activation during socioemotional information processing.

A. Circled in red, a significant vmPFC (-2, 46, -20) cluster ($k = 34$) depicted in an activation map for the “all conditions except for neutral–other > neutral–other” t contrast, masked with the F test ($p = .005$).

B. A spherical volume of interest (6 mm) was created for each subject (yellow), centered around the vmPFC peak coordinate, as identified by the group activation map, and was used for the generalized psychophysiological interactions analyses.

Coordinates denote x coordinates in Montreal Neurological Institute space.

Effect of age on medial prefrontal cortex functional connectivity for self-relevant and emotional information.

To examine functional connectivity, we used the generalized psychophysiological interactions toolbox (gPPI; McLaren, Ries, Xu, & Johnson, 2012) in SPM12 with a seed region consisting of a 6 mm sphere around the peak voxel coordinate in the vmPFC (-2, 46, -20). The gPPI toolbox was used to model functional connectivity between the vmPFC and the rest of the brain at the individual subject level across all six conditions (negative–self, neutral–self, positive–self, negative–other, neutral–other, positive–other). We then conducted a group-level random effects ANOVA of the six contrasts generated by this subject-level analysis, with emotional valence (negative, neutral, positive) and self-relevance (self, other) as within-subjects variables and age group (younger adults, older adults) as the between-subjects variable.

We were interested in how age was related to vmPFC functional connectivity during self-relevant information processing, independent of emotion, so we conducted an F test for the age group \times self/other interaction (neutral content only). When significant results were revealed by each of these F tests, we conducted post hoc t contrasts to determine the direction of the interaction. We created two conjunction analyses using t tests from each age group, to determine whether the results from this interaction reflected (a) subtle age group differences in functional connectivity as shown by overlap in the functional networks recruited by the older and younger adult groups, or (b) regions with the greatest differences between the age groups, as shown by minimal overlap in the functional networks recruited by older and younger adults for self-relevant content. First, the “younger adult: neutral–other > neutral–self \cap older adult: neutral–other > neutral–self” contrast was created to determine the age overlap of regions showing greater functional connectivity with the vmPFC for non-self-relevant content compared to self-relevant content, independent of emotion. Next, we created the “younger adult: neutral–self > neutral–other \cap older adult: neutral–self > neutral–other” contrast to determine the age overlap of regions showing greater functional connectivity with the vmPFC for self-relevant content compared to non-self-relevant content, independent of emotion.

We were similarly interested in functional connectivity during positive and negative information processing independent of self-relevance; therefore, we conducted F tests for the age group \times positive/neutral (other content only) interaction and the age group \times negative/neutral (other content only) interaction. Again, when significant results were revealed we conducted post hoc t contrasts to determine the direction of the interaction, and to determine whether the F test results reflected subtle age group differences or highlighted the regions that show the greatest age group differences in functional connectivity with the vmPFC, we conducted four conjunction analyses using t contrasts. First, we created the “*younger adult: neutral–other > positive–other* \cap *older adult: neutral–other > positive–other*” and “*younger adult: neutral–other > negative–other* \cap *older adult: neutral–other > negative–other*” contrasts to determine the age overlap of regions showing greater functional connectivity with the vmPFC for neutral compared to positive content, and neutral compared to negative content, independent of self-relevance. We then created the “*younger adult: positive–other > neutral–other* \cap *older adult: positive–other > neutral–other*” and “*younger adult: negative–other > neutral–other* \cap *older adult: negative–other > neutral–other*” contrasts to determine the age overlap of regions showing greater functional connectivity with the vmPFC for positive compared to neutral content, and negative compared to neutral content, independent of self-relevance.

Last, we conducted three-way F tests to determine how age was related to self-relevance \times emotion interactions (age group \times self/other \times positive/neutral and age group \times self/other \times negative/neutral). These results are set out in the supplementary materials, Figure 1, and Table 1.

Results

Age Group Differences in Ventromedial Prefrontal Cortex–Anterior Cingulate Cortex Functional Connectivity for Self-Relevant Content

We examined how brain regions functionally connected with the vmPFC differed by age group during the processing of self-relevant and non-self-relevant information, independent of emotion. The F test used to examine this relationship revealed a significant age group \times self/other interaction for neutral content (see Figure 3). The directional breakdown of this F test revealed a significant cluster in the left perigenual anterior cingulate cortex (MNI peak coordinate: -12, 38, 12; $k = 34$) for the “*younger adult: neutral–self > neutral–other*, *older adult: neutral–other > neutral–self*” t contrast (see supplementary materials for t -test results in the opposite direction). Further interrogation of this cluster revealed that whereas the younger adults showed positive functional connectivity between the left perigenual anterior cingulate cortex and vmPFC for both self-relevant and non-self-relevant content, this relationship was stronger for self-relevant content. In contrast, older adults showed positive functional connectivity between these regions for non-self-relevant content, and negative functional connectivity for self-relevant content.

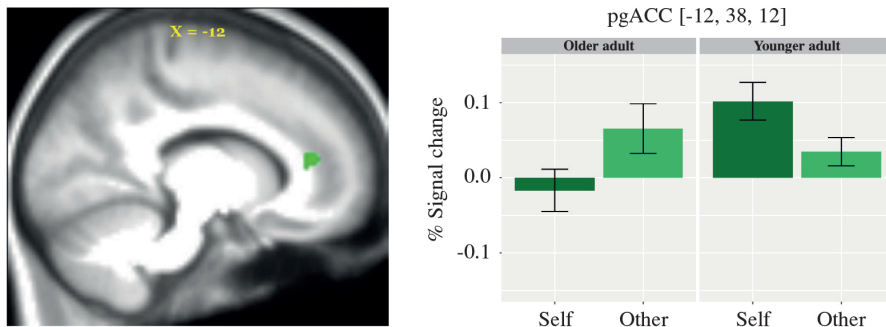


Figure 3. Age \times self-relevance interactions in ventromedial prefrontal cortex–perigenual anterior cingulate cortex (pgACC) functional connectivity. The directional t contrast (*younger adult: self > other*, *older adult: other > self*) masked with the F test ($p = .005$) revealed that, for neutral content only, younger adults had stronger vmPFC–perigenual anterior cingulate cortex positive functional connectivity for self compared to other, whereas older adults had positive connectivity between these regions for other content, and negative connectivity for self content. Coordinates reflect x coordinates in Montreal Neurological Institute space. Error bars reflect standard error of the mean.

Age Group Differences in Ventromedial Prefrontal Cortex Functional Connectivity for Positive Content

We examined how brain regions functionally connected with the vmPFC differed by age group during the processing of positive and neutral content, independent of self-relevance. The F test used to examine this relationship revealed a significant age group \times positive/neutral interaction for non-self-relevant content (see Figure 4 and Table 1). The directional t contrast of “*younger adult: positive–other > neutral–other*, *older adult: neutral–other > positive–other*” revealed no significant clusters. However, the t contrast in the other direction, “*older adult: positive–other > neutral–other*, *younger adult: neutral–other > positive–other*” revealed significant clusters in the left anterior insula, right supramarginal gyrus, and right inferior frontal gyrus. Younger adults showed positive connectivity between the vmPFC and the anterior insula, as well as the supramarginal gyrus, for both positive and neutral content, but showed negative functional connectivity between the vmPFC and the inferior frontal gyrus. Older adults showed positive connectivity for positive content, but negative functional connectivity for neutral content between the vmPFC and these regions.

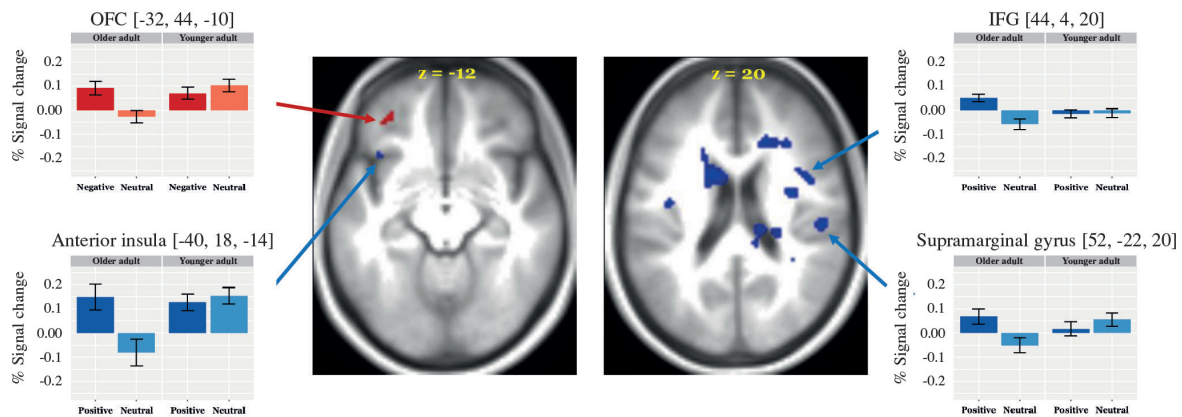


Figure 4. Age \times emotion interactions in the ventromedial prefrontal cortex and externally oriented network functional connectivity. The directional t contrast for the age \times positive/neutral interaction (*older adult: positive > neutral, younger adult: neutral > negative*) masked with the F test ($p = .005$) revealed vmPFC functional connectivity with the following regions (other content only): anterior insula, inferior frontal gyrus (IFG), and supramarginal gyrus (blue). Older adults showed positive connectivity between the vmPFC and these regions when processing positive content, but negative connectivity for neutral content. Younger adults showed equal positive connectivity for both types of content between the vmPFC and the anterior insula, as well as the supramarginal gyrus, but negative connectivity with the inferior frontal gyrus. The directional t contrast for the age \times negative/neutral interaction (*older adult: negative > neutral, younger adult: neutral > negative*) masked with the F test ($p = .005$) revealed positive vmPFC–orbitofrontal cortex connectivity (red) for both negative and neutral content (other content only) in younger adults, but positive connectivity for negative content and negative connectivity for neutral content in older adults. Coordinates reflect z coordinates in Montreal Neurological Institute space. Error bars reflect standard error of the mean. OFC = orbitofrontal cortex.

Table 1. *Regions Showing Greatest Age Differences in Ventromedial Prefrontal Cortex Functional Connectivity When Processing Positive and Neutral Content (Other Content Only)*

Lobe	Hemisphere	Region	BA	MNI (x, y, z)	Tal (x, y, z)	Cluster extent
Frontal	Right	Inferior frontal gyrus	44	44, 4, 20	39, 0, 23	38
Frontal	Left	Middle frontal gyrus	9	-34, 14, 30	-33, 9, 32	38
Frontal	Left	Precentral gyrus	6	-42, -10, 22	-40, -13, 22	61
Parietal	Right	Supramarginal gyrus	40	52, -22, 20	47, -24, 21	35
Other	Left	Anterior insula, Ventrolateral prefrontal cortex	13/47	-40, 18, -14	-38, 16, -7	80
Other	Left	Middle cingulate cortex, Caudate	31	-14, 6, 30	-14, 1, 31	403
Other	Right	Middle insula	13	34, -4, 18	30, -7, 20	68

Note. All regions reported reflect the directional t contrast of “older adult: positive–other > neutral–other, younger adult: neutral–other > positive–other” with a cluster threshold of $k = 30$ masked with the F test at $p = .005$. The rows in **boldface** indicate regions that we further interrogated to test our hypotheses. BA = Brodmann area, MNI = Montreal Neurological Institute coordinate, Tal = Talairach coordinate.

Age Group Differences in Ventromedial Prefrontal Cortex–Orbitofrontal Cortex Functional Connectivity for Negative Content

We examined how brain regions functionally connected with the vmPFC differ by age group during the processing of negative and neutral content, independent of self-relevance. The F test of this relationship revealed a significant age group \times negative/neutral interaction for non-self-relevant content (see Figure 4). The directional t test “younger adult: negative–other > neutral–other, older adult: neutral–other > negative–other” revealed no significant clusters. However, one cluster in the left orbitofrontal cortex (MNI peak coordinate: -32, 44, -10; $k = 31$) was revealed by the “older adult: negative–other > neutral–other, younger adult: neutral–other > negative–other” t contrast: Younger adults showed positive connectivity between the vmPFC and this region for both negative and neutral content, whereas older adults showed positive functional connectivity between these regions for negative content but negative functional connectivity for neutral content.

Age Group Interactions Reflect Greatest Differences in Ventromedial Prefrontal Cortex Functional Connectivity

We conducted six conjunction analyses to determine whether the results for the age group interactions with self-relevant and emotional content reflect brain regions that show (a) subtle differences by age group as demarcated by network overlap, or (b) the greatest differences between the two groups as demarcated by minimal network overlap. Results from all six analyses revealed no age group overlap in the networks functionally connected to the vmPFC. These results suggest the interactions reflect regions that showed the greatest difference between the age groups in functional connectivity with the vmPFC when the participants were processing self-relevant and emotional content.

For visualization purposes, the individual t contrasts contributing to these conjunction analyses are shown in Figure 5 with a threshold of $p < .005$ and a voxel extent of $k = 40$. There were no significant clusters for the t contrasts “younger adult: neutral–other > neutral–self,” “older adult: neutral–other > neutral–self,” “older adult: neutral–other > positive–other,” or “younger adult: negative–other > neutral–other.” These results suggest that both age groups showed negligible enhancement in functional connectivity between the vmPFC and other brain regions when neither self-relevance nor emotion were present.

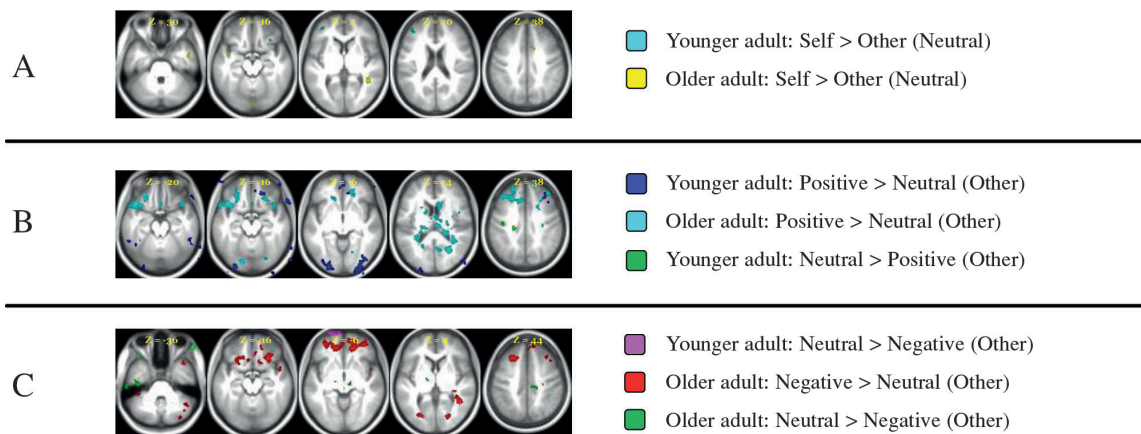


Figure 5. Directional *t* contrasts for conjunction analyses.

A. Regions functionally connected to the vmPFC during the processing of self > other content (neutral content only) are depicted for younger adults (cyan) and older adults (yellow).

B. Regions functionally connected to the vmPFC during the processing of positive > neutral content (other content only) are depicted for younger adults (blue) and older adults (cyan). Regions functionally connected to the vmPFC during the processing of neutral > positive content (other content only) are depicted for younger adults (green).

C. Regions functionally connected to the vmPFC during the processing of negative > neutral content (other content) are depicted for older adults (red). Regions functionally connected to the vmPFC during the processing of neutral > negative content (other content only) are depicted for younger adults (magenta) and older adults (green).

Coordinates denote z coordinates in Montreal Neurological Institute space.

Discussion

We sought to determine whether common or distinct functional networks are connected to the vmPFC during the processing of self-relevant and emotional information, and how these networks are impacted by advancing age. The results confirm that the vmPFC was engaged for both older and younger adults, and for both self-relevant and emotional content (Gutchess & Kensinger, 2018; Mather, 2016). Despite this overlap, the vmPFC appears to be functionally connected to distinct networks during the processing of self-relevant and emotional content, and we found age group differences in these distinct networks. Given that conjunction analyses revealed minimal network overlap between the two age groups, below we discuss the implications for the brain regions that showed the greatest age group differences in functional connectivity with the vmPFC during this study.

During the processing of self-relevant versus non-self-relevant content, independent of emotion, the greatest difference between the younger and older group was in vmPFC functional connectivity with the perigenual anterior cingulate cortex. Younger adults showed increased vmPFC–perigenual anterior cingulate cortex functional connectivity for self-relevant content, whereas older adults showed increased functional connectivity between these regions for non-self-relevant content. As the perigenual anterior cingulate cortex is associated with the DMN (Qin & Northoff, 2011), our result of increased coupling with

the vmPFC in younger adults for self-relevant content is consistent with prior work demonstrating an overlap between the DMN and self-relevance networks active during tasks that involve the internal representations of self-relevant content (Davey, Pujol, & Harrison, 2016; Molnar-Szakacs & Uddin, 2013; Qin et al., 2016; Soch et al., 2017). Older age is associated with decreased functional connectivity between DMN structures (Sala-Llonch et al., 2015), which may account for the decrease we observed among older adults in vmPFC–perigenual anterior cingulate cortex coupling for self-relevant content. It is also possible that creating mental representations of non-self-relevant content (i.e., imagining placing an object in a stranger’s house) is more computationally demanding for older adults (see, e.g., Dror & Kosslyn, 1994). This high task demand may account for the older adults’ increased vmPFC–perigenual anterior cingulate cortex coupling during the non-self-relevant condition, as more internally focused cognitive processing may be required than is needed in the self-relevant condition.

During the processing of emotional versus neutral content, independent of self-relevance, the greatest differences between the two age groups in vmPFC functional connectivity were in regions associated with the salience network. These age interactions were driven by the older adults’ positive functional connectivity between the vmPFC and the left anterior insula, right supramarginal gyrus, and right inferior frontal gyrus for positive content, but negative connectivity for neutral content. At the same time, younger adults showed positive connectivity between these regions for both types of content, with the exception of the right inferior frontal gyrus, where they showed negative connectivity. These age group differences in connectivity patterns in the anterior insula and supramarginal gyrus also characterized the connectivity patterns for the left orbitofrontal cortex when processing negative compared to neutral content, independent of self-relevance. These findings converge with prior work showing that older adults prioritize processing emotional over neutral content (Kensinger, Garoff-Eaton, & Schacter, 2007; Kensinger, Piquet, Krendl, & Corkin, 2005; Mather & Carstensen, 2005). The anterior insula and orbitofrontal cortex are implicated in the salience network, and the supramarginal gyrus, although not a functional hub, is sometimes identified with this network (Sadaghiani & D’Esposito, 2015; Seeley et al., 2007). As the salience network plays a role in transitioning between internally and externally focused attention (Goulden et al., 2014; Sridharan et al., 2008), it is possible that increased functional connectivity between the vmPFC and these regions may reflect beneficial integration of the DMN and the salience network. We speculate that this integration may enhance mental representations of emotional content for older adults specifically. Findings in recent work demonstrate that integration between the DMN and externally oriented networks reflects adaptive processes in older adults during autobiographical memory retrieval and future planning, rather than incipient cognitive decline (Spreng et al., 2018). Our findings extend this work by showing that increased functional connectivity between the vmPFC and regions associated with externally oriented networks was associated with processing non-self-relevant but socioemotional content in older adults. Younger adults, on the other hand, may integrate these networks more generally for emotional and neutral content in social contexts. These age group differences also reflect the idea that creating mental representations of non-self-relevant neutral content may be more computationally demanding, subsequently requiring older (vs. younger) adults to decouple internally and externally oriented networks to a greater extent. However, given that older, compared to younger, adults tend to show increased coupling between DMN and cognitive control networks (Esposito et al., 2018; Geerligs, Maurits, Renken, & Lorist, 2014; Grady, Sarraf, Saverino, & Campbell, 2016; Spreng et al., 2016), it is possible that the presence of non-self-relevant content that is neutral disrupts vmPFC functional connectivity with other networks. That is, neutral content may not trigger the same salience signals for older adults as it does for younger adults. Thus, neutral content may not be easily accessed by older adults during the creation of mental representations in social contexts.

In sum, we used a novel paradigm that differentiated between the effects of self-relevance and emotion to provide the first evidence that the vmPFC is a common activation hub during the processing of these types of content in older and younger adults. Despite being a common processing region, the vmPFC appears to be functionally connected to distinct networks during the processing of self-relevant and emotional content, and age further impacts on the makeup of these networks. The regions that showed the largest age

differences for self-relevance were associated with the DMN, whereas those for emotion were associated with the salience and executive control networks. Rather than age-related changes in vmPFC functional connectivity reflecting cognitive decline, we speculate that integration between the vmPFC and regions outside the DMN may reflect adaptive processes that assist older adults in the mental representation of emotional content in social contexts. Limitations to our research design are covered in Daley et al. (2020). We recommend that future researchers examine the relationship between large-scale functional networks and the creation of mental representations of emotional content in self-relevant and non-self-relevant contexts across the adult life span.

Acknowledgements

This work was supported by the National Institute on Aging (R21-AG051853; E.A.K and A.G.) and the National Institutes of Health Shared Instrument Grant (S10OD020039; Harvard Center for Brain Science).

The authors thank Jaelyn Ford for her assistance with fMRI analyses, and Katelyn Parisi, Tammy Moran, and Ross Mair for their assistance with fMRI data acquisition.

Supplementary materials can be retrieved from the Open Science Framework

<https://doi.org/10.17605/OSF.IO/RSXZM>

References

Alexopoulos, T., Muller, D., Ric, F., & Marendaz, C. (2012). I, me, mine: Automatic attentional capture by self-related stimuli. *European Journal of Social Psychology, 42*, 770–779.

<https://doi.org/10.1002/ejsp.1882>

Alicke, M. D., & Govorun, O. (2005). The better-than-average effect. In M. D. Alicke, D. A. Dunning, & J. I. Krueger (Eds.), *Studies in self and identity: The self in social judgment* (pp. 85–106). London, UK: Psychology Press.

Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E., & Buckner, R. L. (2007). Disruption of large-scale brain systems in advanced aging. *Neuron, 56*, 924–935.

<https://doi.org/10.1016/j.neuron.2007.10.038>

Beer, J. S. (2017). Current emotion research in social neuroscience: How does emotion influence social cognition? *Emotion Review, 9*, 172–180.

<https://doi.org/10.1177/1754073916650492>

Buckner, R. L., & DiNicola, L. M. (2019). The brain's default network: Updated anatomy, physiology and evolving insights. *Nature Reviews Neuroscience, 20*, 593–608.

<https://doi.org/10.1038/s41583-019-0212-7>

Buckner, R. L., Sepulcre, J., Talukdar, T., Krienen, F. M., Liu, H., Hedden, T., ... Johnson, K. A. (2009). Cortical hubs revealed by intrinsic functional connectivity: Mapping, assessment of stability, and relation to Alzheimer's disease. *Journal of Neuroscience, 29*, 1860–1873.

<https://doi.org/10.1523/JNEUROSCI.5062-08.2009>

Carstensen, L. L., & Mikels, J. A. (2005). At the intersection of emotion and cognition: Aging and the positivity effect. *Current Directions in Psychological Science, 14*, 117–121.

<https://doi.org/10.1111/j.0963-7214.2005.00348.x>

Cunningham, S. J., Brady-Van den Bos, M., & Turk, D. J. (2011). Exploring the effects of ownership and choice on self-memory biases. *Memory, 19*, 449–461.

<https://doi.org/10.1080/09658211.2011.584388>

Daley, R. T., Bowen, H. J., Fields, E. C., Parisi, K. R., Gutchess, A., & Kensinger, E. A. (2020). Neural mechanisms supporting emotional and self-referential information processing and encoding in older and younger adults. *Social Cognitive and Affective Neuroscience*, 2020, nsaa052.

<https://doi.org/10.1093/scan/nsaa052>

D'Argembeau, A. (2013). On the role of the ventromedial prefrontal cortex in self-processing: The valuation hypothesis. *Frontiers in Human Neuroscience*, 7, 372.

<https://doi.org/10.3389/fnhum.2013.00372>

Davey, C. G., Pujol, J., & Harrison, B. J. (2016). Mapping the self in the brain's default mode network. *NeuroImage*, 132, 390–397.

<https://doi.org/10.1016/j.neuroimage.2016.02.022>

Descartes, R. (1984). *The philosophical writings of Descartes* (Vol. 2; J. Cottingham, R. Stoothoff, & D. Murdoch, Trans.). Cambridge, UK: Cambridge University Press. (Original work published 1641.)

Dror, I. E., & Kosslyn, S. M. (1994). Mental imagery and aging. *Psychology and Aging*, 9, 90–102.

<https://doi.org/10.1037/0882-7974.9.1.90>

Esposito, R., Cieri, F., Chiacchiarretta, P., Cera, N., Lauriola, M., Di Giannantonio, M., ... Ferretti, A. (2018). Modifications in resting state functional anticorrelation between default mode network and dorsal attention network: Comparison among young adults, healthy elders and mild cognitive impairment patients. *Brain Imaging and Behavior*, 12, 127–141.

<https://doi.org/10.1007/s11682-017-9686-y>

Etkin, A., Egner, T., & Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Sciences*, 15, 85–93.

<https://doi.org/10.1016/j.tics.2010.11.004>

Fields, E. C., Weber, K., Stillerman, B., Delaney-Busch, N., & Kuperberg, G. R. (2019). Functional MRI reveals evidence of a self-positivity bias in the medial prefrontal cortex during the comprehension of social vignettes. *Social Cognitive and Affective Neuroscience*, 14, 613–621.

<https://doi.org/10.1093/scan/nsz035>

Fjell, A. M., McEvoy, L., Holland, D., Dale, A. M., Walhovd, K. B., & Alzheimer's Disease Neuroimaging Initiative. (2014). What is normal in normal aging? Effects of aging, amyloid and Alzheimer's disease on the cerebral cortex and the hippocampus. *Progress in Neurobiology*, 117, 20–40.

<https://doi.org/10.1016/j.pneurobio.2014.02.004>

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences*, 102, 9673–9678.

<https://doi.org/10.1073/pnas.0504136102>

Geerligs, L., Maurits, N. M., Renken, R. J., & Lorist, M. M. (2014). Reduced specificity of functional connectivity in the aging brain during task performance. *Human Brain Mapping*, 35, 319–330.

<https://doi.org/10.1002/hbm.22175>

Gillihan, S. J., & Farah, M. J. (2005). Is self special? A critical review of evidence from experimental psychology and cognitive neuroscience. *Psychological Bulletin*, 131, 76–97.

<https://doi.org/10.1037/0033-2909.131.1.76>

Glisky, E. L., & Marquine, M. J. (2009). Semantic and self-referential processing of positive and negative trait adjectives in older adults. *Memory*, 17, 144–157.

<https://doi.org/10.1080/09658210802077405>

Goldin, P. R., McRae, K., Ramel, W., & Gross, J. J. (2008). The neural bases of emotion regulation: Reappraisal and suppression of negative emotion. *Biological Psychiatry*, 63, 577–586.

<https://doi.org/10.1016/j.biopsych.2007.05.031>

Göttlich, M., Ye, Z., Rodriguez-Fornells, A., Münte, T. F., & Krämer, U. M. (2017). Viewing socio-affective stimuli increases connectivity within an extended default mode network. *NeuroImage*, *148*, 8–19.

<https://doi.org/10.1016/j.neuroimage.2016.12.044>

Goulden, N., Khusnulina, A., Davis, N. J., Bracewell, R. M., Bokde, A. L., McNulty, J. P., & Mullins, P. G. (2014). The salience network is responsible for switching between the default mode network and the central executive network: Replication from DCM. *NeuroImage*, *99*, 180–190.

<https://doi.org/10.1016/j.neuroimage.2014.05.052>

Grady, C., Sarraf, S., Saverino, C., & Campbell, K. (2016). Age differences in the functional interactions among the default, frontoparietal control, and dorsal attention networks. *Neurobiology of Aging*, *41*, 159–172.

<https://doi.org/10.1016/j.neurobiolaging.2016.02.020>

Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences*, *100*, 253–258.

<https://doi.org/10.1073/pnas.0135058100>

Grilli, M. D., Woolverton, C. B., Crawford, M., & Glisky, E. L. (2018). Self-reference and emotional memory effects in older adults at increased genetic risk of Alzheimer's disease. *Aging, Neuropsychology, and Cognition*, *25*, 186–199.

<https://doi.org/10.1080/13825585.2016.1275508>

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences*, *98*, 4259–4264.

<https://doi.org/10.1073/pnas.071043098>

Gutchess, A., & Kensinger, E. A. (2018). Shared mechanisms may support mnemonic benefits from self-referencing and emotion. *Trends in Cognitive Sciences*, *22*, 712–724.

<https://doi.org/10.1016/j.tics.2018.05.001>

Gutchess, A. H., Kensinger, E. A., & Schacter, D. L. (2007). Aging, self-referencing, and medial prefrontal cortex. *Social Neuroscience*, *2*, 117–133.

<https://doi.org/10.1080/17470910701399029>

Gutchess, A. H., Kensinger, E. A., Yoon, C., & Schacter, D. L. (2007). Ageing and the self-reference effect in memory. *Memory*, *15*, 822–837.

<https://doi.org/10.1080/09658210701701394>

Gutchess, A. H., Sokal, R., Coleman, J. A., Gotthilf, G., Grewal, L., & Rosa, N. (2015). Age differences in self-referencing: Evidence for common and distinct encoding strategies. *Brain Research*, *1612*, 118–127.

<https://doi.org/10.1016/j.brainres.2014.08.033>

Hamami, A., Serbun, S. J., & Gutchess, A. H. (2011). Self-referencing enhances memory specificity with age. *Psychology and Aging*, *26*, 636–646.

<https://doi.org/10.1037/a0022626>

Hou, M., Grilli, M. D., & Glisky, E. L. (2019). Self-reference enhances relational memory in young and older adults. *Aging, Neuropsychology, and Cognition*, *26*, 105–120.

<https://doi.org/10.1080/13825585.2017.1409333>

Hume, D. (2003). *A treatise of human nature*. Mineola, NY: Dover. (Original work published 1739–1740.)

Humphreys, G. W., & Sui, J. (2016). Attentional control and the self: The Self-Attention Network (SAN). *Cognitive Neuroscience*, *7*, 5–17.

<https://doi.org/10.1080/17588928.2015.1044427>

Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*, 785–794.

<https://doi.org/10.1162/08989290260138672>

Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007). Effects of emotion on memory specificity in young and older adults. *The Journals of Gerontology: Series B*, *62*, 208–215.

<https://doi.org/10.1093/geronb/62.4.P208>

Kensinger, E. A., & Gutchess, A. (2015). Memory for emotional and social information in adulthood and old age. In D. R. Addis, M. Barense, & A. Duarte (Eds.), *The Wiley handbook on the cognitive neuroscience of memory* (pp. 393–414). Hoboken, NJ: Wiley.

<https://doi.org/10.1002/9781118332634.ch19>

Kensinger, E. A., Piguet, O., Krendl, A. C., & Corkin, S. (2005). Memory for contextual details: Effects of emotion and aging. *Psychology and Aging*, *20*, 241–250.

<https://doi.org/10.1037/0882-7974.20.2.241>

Kurdi, B., Lozano, S., & Banaji, M. R. (2017). Introducing the Open Affective Standardized Image Set (OASIS). *Behavior Research Methods*, *49*, 457–470.

<https://doi.org/10.3758/s13428-016-0715-3>

Leshikar, E. D., Dulas, M. R., & Duarte, A. (2015). Self-referencing enhances recollection in both young and older adults. *Aging, Neuropsychology, and Cognition*, *22*, 388–412.

<https://doi.org/10.1080/13825585.2014.957150>

Luo, Y., Qin, S., Fernández, G., Zhang, Y., Klumbers, F., & Li, H. (2014). Emotion perception and executive control interact in the salience network during emotionally charged working memory processing. *Human Brain Mapping*, *35*, 5606–5616.

<https://doi.org/10.1002/hbm.22573>

Markus, H., & Nurius, P. (1986). Possible selves. *American Psychologist*, *41*, 954–969.

<https://doi.org/10.1037/0003-066X.41.9.954>

Mather, M. (2016). The affective neuroscience of aging. *Annual Review of Psychology*, *67*, 213–238.

<https://doi.org/10.1146/annurev-psych-122414-033540>

Mather, M., & Carstensen, L. L. (2005). Aging and motivated cognition: The positivity effect in attention and memory. *Trends in Cognitive Sciences*, *9*, 496–502.

<https://doi.org/10.1016/j.tics.2005.08.005>

McLaren, D. G., Ries, M. L., Xu, G., & Johnson, S. C. (2012). A generalized form of context-dependent psychophysiological interactions (gPPI): A comparison to standard approaches. *NeuroImage*, *61*, 1277–1286.

<https://doi.org/10.1016/j.neuroimage.2012.03.068>

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure and Function*, *214*, 655–667.

<https://doi.org/10.1007/s00429-010-0262-0>

Molnar-Szakacs, I., & Uddin, L. Q. (2013). Self-processing and the default mode network: Interactions with the mirror neuron system. *Frontiers in Human Neuroscience*, *7*, 571.

<https://doi.org/10.3389/fnhum.2013.00571>

Moran, J. M., Macrae, C. N., Heatherton, T. F., Wyland, C. L., & Kelley, W. M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience*, *18*, 1586–1594.

<https://doi.org/10.1162/jocn.2006.18.9.1586>

Mueller, J. H., Wonderlich, S., & Dugan, K. (1986). Self-referent processing of age-specific material. *Psychology and Aging, 1*, 293–299.

<https://doi.org/10.1037/0882-7974.1.4.293>

Ng, K. K., Lo, J. C., Lim, J. K. W., Chee, M. W. L., & Zhou, J. (2016). Reduced functional segregation between the default mode network and the executive control network in healthy older adults: A longitudinal study. *NeuroImage, 133*, 321–330.

<https://doi.org/10.1016/j.neuroimage.2016.03.029>

Qin, P., Grimm, S., Duncan, N. W., Fan, Y., Huang, Z., Lane, T., ... Northoff, G. (2016). Spontaneous activity in default-mode network predicts ascription of self-relatedness to stimuli. *Social Cognitive and Affective Neuroscience, 11*, 693–702.

<https://doi.org/10.1093/scan/nsw008>

Qin, P., & Northoff, G. (2011). How is our self related to midline regions and the default-mode network? *NeuroImage, 57*, 1221–1233.

<https://doi.org/10.1016/j.neuroimage.2011.05.028>

Quirk, G. J., & Beer, J. S. (2006). Prefrontal involvement in the regulation of emotion: Convergence of rat and human studies. *Current Opinion in Neurobiology, 16*, 723–727.

<https://doi.org/10.1016/j.conb.2006.07.004>

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences, 98*, 676–682.

<https://doi.org/10.1073/pnas.98.2.676>

Raz, N., Gunning, F. M., Head, D., Dupuis, J. H., McQuain, J., Briggs, S. D., ... Acker, J. D. (1997). Selective aging of the human cerebral cortex observed in vivo: Differential vulnerability of the prefrontal gray matter. *Cerebral Cortex, 7*, 268–282.

<https://doi.org/10.1093/cercor/7.3.268>

Reed, A. E., Chan, L., & Mikels, J. A. (2014). Meta-analysis of the age-related positivity effect: Age differences in preferences for positive over negative information. *Psychology and Aging, 29*, 1–15.

<https://doi.org/10.1037/a0035194>

Rogers, T. B., Kuiper, N. A., & Kirker, W. S. (1977). Self-reference and the encoding of personal information. *Journal of Personality and Social Psychology, 35*, 677–688.

<https://doi.org/10.1037/0022-3514.35.9.677>

Sadaghiani, S., & D'Esposito, M. (2015). Functional characterization of the cingulo-opercular network in the maintenance of tonic alertness. *Cerebral Cortex, 25*, 2763–2773.

<https://doi.org/10.1093/cercor/bhu072>

Sala-Llonch, R., Bartrés-Faz, D., & Junqué, C. (2015). Reorganization of brain networks in aging: A review of functional connectivity studies. *Frontiers in Psychology, 6*, 663.

<https://doi.org/10.3389/fpsyg.2015.00663>

Satpute, A. B., & Lindquist, K. A. (2019). The default mode network's role in discrete emotion. *Trends in Cognitive Sciences, 23*, 851–864.

<https://doi.org/10.1016/j.tics.2019.07.003>

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., ... Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience, 27*, 2349–2356.

<https://doi.org/10.1523/JNEUROSCI.5587-06.2007>

Soch, J., Deserno, L., Assmann, A., Barman, A., Walter, H., Richardson-Klavehn, A., & Schott, B. H. (2017). Inhibition of information flow to the default mode network during self-reference versus reference to others. *Cerebral Cortex, 27*, 3930–3942.

<https://doi.org/10.1093/cercor/bhw206>

Spreng, R. N., Lockrow, A. W., DuPre, E., Setton, R., Spreng, K. A. P., & Turner, G. R. (2018). Semanticized autobiographical memory and the default–executive coupling hypothesis of aging. *Neuropsychologia*, *110*, 37–43.

<https://doi.org/10.1016/j.neuropsychologia.2017.06.009>

Spreng, R. N., & Schacter, D. L. (2012). Default network modulation and large-scale network interactivity in healthy young and old adults. *Cerebral Cortex*, *22*, 2610–2621.

<https://doi.org/10.1093/cercor/bhr339>

Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. *Journal of Cognitive Neuroscience*, *25*, 74–86.

https://doi.org/10.1162/jocn_a_00281

Spreng, R. N., Stevens, W. D., Viviano, J. D., & Schacter, D. L. (2016). Attenuated anticorrelation between the default and dorsal attention networks with aging: Evidence from task and rest. *Neurobiology of Aging*, *45*, 149–160.

<https://doi.org/10.1016/j.neurobiolaging.2016.05.020>

Sreenivas, S., Boehm, S. G., & Linden, D. E. J. (2012). Emotional faces and the default mode network. *Neuroscience Letters*, *506*, 229–234.

<https://doi.org/10.1016/j.neulet.2011.11.012>

Sridharan, D., Levitin, D. J., & Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proceedings of the National Academy of Sciences*, *105*, 12569–12574.

<https://doi.org/10.1073/pnas.0800005105>

Symons, C. S., & Johnson, B. T. (1997). The self-reference effect in memory: A meta-analysis. *Psychological Bulletin*, *121*, 371–394.

<https://doi.org/10.1037/0033-2909.121.3.371>

Tisserand, D. J., Pruessner, J. C., Sanz Arigita, E. J., van Boxtel, M. P. J., Evans, A. C., Jolles, J., & Uylings, H. B. M. (2002). Regional frontal cortical volumes decrease differentially in aging: An MRI study to compare volumetric approaches and voxel-based morphometry. *NeuroImage*, *17*, 657–669.

<https://doi.org/10.1006/nimg.2002.1173>

Turner, G. R., & Spreng, R. N. (2015). Prefrontal engagement and reduced default network suppression co-occur and are dynamically coupled in older adults: The default–executive coupling hypothesis of aging. *Journal of Cognitive Neuroscience*, *27*, 2462–2476.

https://doi.org/10.1162/jocn_a_00869

Waring, J. D., & Kensinger, E. A. (2009). Effects of emotional valence and arousal upon memory trade-offs with aging. *Psychology and Aging*, *24*, 412–422.

<https://doi.org/10.1037/a0015526>

Whitfield-Gabrieli, S., Moran, J. M., Nieto-Castañón, A., Triantafyllou, C., Saxe, R., & Gabrieli, J. D. E. (2011). Associations and dissociations between default and self-reference networks in the human brain. *NeuroImage*, *55*, 225–232.

<https://doi.org/10.1016/j.neuroimage.2010.11.048>

Yang, L., Truong, L., Fuss, S., & Bislimovic, S. (2012). The effects of ageing and divided attention on the self-reference effect in emotional memory: Spontaneous or effortful mnemonic benefits? *Memory*, *20*, 596–607.

<https://doi.org/10.1080/09658211.2012.690040>

Yin, S., Sui, J., Chiu, Y.-C., Chen, A., & Egner, T. (2019). Automatic prioritization of self-referential stimuli in working memory. *Psychological Science*, *30*, 415–423.

<https://doi.org/10.1177/0956797618818483>