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Affect in the aging brain: A neuroimaging meta-analysis of older vs. younger adult affective experience and perception

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Abstract

We report the first functional neuroimaging meta-analysis on age-related differences in adult neural activity during affect. We identified and coded experimental contrasts from 27 studies (published 1997-2018) with 490 older adults (55-87 years, M_{age}=69 years) and 470 younger adults (18-39 years, M_{age} =24 years). Using multilevel kernel density analysis, we assessed functional brain activation contrasts for older vs. younger adult affect across in-scanner tasks (i.e., affect induction and perception). Relative to older adults, younger adults showed more reliable activation in subcortical structures (e.g., amygdala, thalamus, caudate) and in relatively more posterior aspects of specific brain structures (e.g., posterior insula, mid- and posterior cingulate). In contrast, older adults exhibited more reliable activation in the prefrontal cortex and more anterior aspects of specific brain structures (e.g., anterior insula, anterior cingulate). Meta-analytic coactivation network analyses further revealed that in younger adults, the amygdala and mid-cingulate were more central, locally efficient network nodes, whereas in older adults, regions in the superior and medial prefrontal cortex were more central, locally efficient network nodes. Collectively, these findings help characterize age differences in the brain basis of affect and provide insights for future investigations into the neural mechanisms underlying affective aging.

Keywords: aging, affective neuroscience, brain, emotion, meta-analysis, functional neuroimaging

1. Introduction

Affect is the mental representation of ongoing bodily states (e.g., autonomic, immune, metabolic, and temperature shifts) and predictions about how objects and events (e.g., a rabid dog, meeting a stranger) will impact those states; as such, affect is thought to form the basis of emotion, motivated behavior, and even consciousness (Barrett & Bar, 2009; Cabanac, 2002; Craig, 2009; Damasio, 1999; Duncan & Barrett, 2007; LeDoux & Brown, 2017; MacCormack & Lindquist, 2017; Northoff, 2012; Schwarz & Clore, 1983; Seth, 2018). Affect is most frequently characterized as having two subjective qualities: *valence*, or subjective pleasantness vs. unpleasantness ("positive" vs. "negative"), and *arousal*, or subjective activation vs. relaxation ("high arousal" vs. "low arousal") (Bradley & Lang, 1994; Posner, Russell, & Peterson, 2005; Satpute, Kragel, Barrett, Wager, & Bianciardi, 2019). Although it is often assumed that the neurobiology underlying affect remains stable after reaching adulthood (Davidson, 2003), behavioral findings show age-related shifts in affect from young adulthood (i.e., 18 years old) into late life (i.e., >60 years old).

For example, cross-sectional and longitudinal studies suggest that older adults tend to experience greater positive and less negative affect, greater low arousal and less high arousal affect, greater affective stability and less affective reactivity than younger adults (Birditt, Fingerman, & Almeida, 2005; Brose, Scheibe, & Schmiedek, 2013; Bruine de Bruin, van Putten, van Emden, & Strough, 2018; Carstensen, Pasupathi, Mayr, & Nesselroade, 2000; Charles & Piazza, 2009; Charles, Reynolds, & Gatz, 2001; Cheng, 2004; Coats & Blanchard-Fields, 2008; English & Carstensen, 2014; Gross et al., 1997; Kan, Garrison, Drummey, Emmert, & Rogers, 2018; Kessler & Staudinger, 2009; MacCormack, Henry, Davis, Oosterwijk, & Lindquist, 2019; Mather & Carstensen, 2005; Mikkelsen, O'Toole, Lyby, Wallot, & Mehlsen, 2019; Mogilner, Kamvar, & Aaker, 2011; Neupert, Almeida, & Charles, 2007; Shallcross, Ford, Floerke, & Mauss, 2013). Similar patterns emerge when perceiving affect in nonverbal expressions such as on faces. In some studies, older adults performed well at identifying positive expressions (e.g., happiness) but were less able to infer the meaning of posed facial expressions conveying negative affect (e.g., sadness; Calder et al., 2003; McDowell, Harrison, & Demaree, 1994; Moreno, Borod, Welkowitz, & Alpert, 1993; but see differing meta-analytic evidence in Ruffman et al., 2008 and see Mather & Knight, 2006 for work on threat perception preservation across adulthood). Other studies find that older adults perceive posed angry and happy faces to be less highly arousing than do younger adults (Svärd, Fischer, & Lundqvist, 2014).

Although there is clear behavioral evidence for age-related shifts in affect, we still know relatively little about how neural activity during affect might differ across adulthood. Since the late 1990s, more than two dozen functional magnetic resonance imaging (fMRI) studies have examined differences in functional brain activity during healthy older vs. younger adult affect. Herein, we applied quantitative meta-analysis to statistically summarize this growing literature, identifying which brain regions show the most reliable age-related differences in functional activation during affect across studies of older versus younger adults. Furthermore, we used network-based meta-analytic coactivation analyses to pinpoint the groups of brain regions that most reliably co-activate during affective states for younger and older adults and then identify which of these regions serve as influential hubs. Ultimately, this research has the potential to (i) identify neural mechanisms that may be associated with observed affective differences across adulthood and more generally (ii) underscore how aging nervous systems produce aging minds.

1.1. The brain basis of affect

Over a hundred years of research have examined the peripheral and, more recently, central nervous system representations of affect. For instance, since the late 19th century, it was recognized that affect is related to and represented in peripheral nervous system changes (e.g., heart rate and skin conductance; Fere, 1888; James, 1890; Tarchanoff, 1890). In recent decades, human functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have investigated functional brain differences during affect. Meta-analytic summaries of this work in young adults reveal that pleasant and unpleasant states are represented by brain regions spanning subcortical, limbic, and cortical regions (Fusar-Poli et al., 2009; Kober et al., 2008; Lindquist, Satpute, Wager, Weber, & Barrett, 2016; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; F. C. Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2004; Vytal & Hamann, 2010; Wager, Phan, Liberzon, & Taylor, 2003). More specifically, affective states are associated with increased activity across the brain within regions such as the brainstem, cerebellum, amygdala, basal ganglia, anterior, mid, and posterior insula, ventromedial prefrontal cortex (vmPFC), dorsomedial prefrontal cortex (dmPFC), motor and premotor cortex, ventrolateral and dorsolateral prefrontal cortex, anterior, mid, and posterior regions of the cingulate cortex (ACC, MCC, PCC), temporoparietal cortex, lateral temporal cortex, and visual cortex (e.g., Kober et al., 2008; Lindquist et al., 2012, 2016). These regions interact as sets of broadly distributed functional networks that are thought to perform domain-general functions (i.e., functions not just specific to affect) and are undergirded by the brain's structural architecture

(Barrett & Satpute, 2019; Bressler & Menon, 2010; Kelly et al., 2008; Park & Friston, 2013; Petersen & Sporns, 2015; Power et al., 2011; Yeo et al., 2011).

Candidate functional networks that likely contribute to affect include the central autonomic, salience, default mode, dorsal attention, and frontoparietal networks. The *central autonomic network* (i.e., insular cortex, ACC, amygdala, hypothalamus, periaqueductal gray, and parts of the ventrolateral medulla) helps regulate preganglionic sympathetic and parasympathetic neurons and is thought to support the management and integration of visceral signals and functions, including during affect (Benarroch, 1993; Ding et al., 2020; Kleckner et al., 2017). The *salience network* (i.e., anterior insula, ACC, middle frontal gyrus, MCC, amygdala, ventral striatum, and substantia nigra/ventral tegmental area) helps direct attention and behavior to motivationally relevant stimuli (e.g., noticing a threat, being distracted by cake) (Kleckner et al., 2017; Lindquist & Barrett, 2012; Menon, 2015; Menon & Uddin, 2010; Seeley et al., 2007; Touroutoglou, Andreano, Adebayo, Lyons, & Barrett, 2019; C. Xia, Touroutoglou, Quigley, Barrett, & Dickerson, 2017). Finally, the *default mode network* (i.e., vmPFC, dmPFC, PCC, lateral prefrontal cortex, and lateral temporoparietal and temporal cortex) supports mentalizing, autobiographical memory, and self-referential, introspective processes, whereas the *dorsal attention network* (i.e., the intraparietal sulcus, frontal eye fields, superior parietal lobule, and ventral premotor cortex) and the *frontoparietal control network* (i.e., the dorsolateral and lateral parietal cortex) support perceptual attention, executive function, and some aspects of cognitive control (Buckner, Andrews-Hanna, & Schacter, 2008; Cole, Repovš, & Anticevic, 2014; Denny, Kober, Wager, & Ochsner, 2012; Dixon et al., 2018; Dixon, Thiruchselvam, Todd, & Christoff, 2017; Spreng, Mar, & Kim, 2009; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). In the context of affect, the default mode network in particular may support the concepts, autobiographical narratives, and mentalization that help the brain predict and categorize experiences and stimuli as affective in nature (Barrett, 2017; Satpute & Lindquist, 2019). Ultimately, these functional networks show evidence of functional connectivity within and between nodes during affective states or affect perception (see reviews in Barrett & Satpute, 2013; Lindquist & Barrett, 2012; Satpute & Lindquist, 2019; Touroutoglou, Lindquist, Dickerson, & Barrett, 2015). What remains in question is whether and how these brain regions and networks associated with affect differ in their functional profiles across age.

1.2 The neuroscience of aging

Although much research has examined how brain regions and networks activate during affective states in young adults, less work examines how such functional activation differs and changes across adulthood. Yet there are multiple reasons why one might predict age-related shifts in functional brain activity during affect. First, healthy aging is generally accompanied by structural and functional brain changes (although the severity and types of change can vary across individuals, e.g., "super-agers": Rogalski et al., 2013; Zhang et al., 2020). For example, older adult brains tend to exhibit increased grey matter atrophy (especially in frontal regions) and decreases in overall white matter volume when compared to younger adult brains (J. S. Allen, Bruss, Brown, & Damasio, 2005; Bagarinao et al., 2018; Fjell & Walhovd, 2010; Fjell et al., 2013; Good et al., 2001; Smith, Chebrolu, Wekstein, Schmitt, & Markesbery, 2007). These structural differences may impact functional activation in degree and/or kind. During cognitive tasks, older adult brains are typically characterized by increased functional activation in prefrontal regions and greater recruitment across both brain hemispheres relative to younger adults (e.g., Cabeza, Anderson, Locantore, & McIntosh, 2002; Park & Reuter-Lorenz, 2009; Turner & Spreng, 2012). A meta-analysis of functional neuroimaging studies on cognitive aging revealed that older adults exhibit more reliable activation in the prefrontal cortex during cognitive tasks relative to younger adults, whereas younger adults exhibit more reliable activation in exteroceptive sensory regions such as the occipital lobe (Spreng, Wojtowicz, & Grady, 2010). This pattern has been called the posterior-anterior shift in aging (PASA) and describes the increasing functional involvement of prefrontal regions over sensory processing regions as age increases (e.g., Davis et al., 2008; McCarthy et al., 2014).

The healthy aging brain also demonstrates reorganization of functional brain networks that may influence the neural basis of affect (see review in Sala-Llonch, Bartrés-Faz, & Junqué, 2015). The default mode and dorsal attention networks appear especially sensitive to age-related disruptions, with relative maintenance of somatosensory and subcortical networks (Tomasi & Volkow, 2012). Indeed, some of the most consistent findings are that late life is accompanied by reductions in default mode and frontoparietal network connectivity both at rest and during cognitive tasks (Andrews-Hanna et al., 2007; Betzel et al., 2014; Campbell, Grady, Ng, & Hasher, 2012; Esposito et al., 2008; He et al., 2014; Nashiro, Sakaki, Braskie, & Mather, 2017; Onoda, Ishihara, & Yamaguchi, 2012; Shaw, Schultz, Sperling, & Hedden, 2015; Liang Wang et al., 2010; Lubin Wang, Su, Shen, & Hu, 2012; Ward et al., 2015; L. Zhang et al., 2020). More recent work suggests that older adults' brains are characterized by changes in network integration, with greater between-network connectivity and lower within-network connectivity

in visual, sensorimotor, and frontoparietal control networks during cognitive control and attention tasks (Bagarinao et al., 2019). Collectively, these findings could be interpreted as evidence that older adult brains shift function to prefrontal regions to compensate for structural or functional changes elsewhere (Cabeza et al., 2018; Grady et al., 1994) or alternatively that prefrontal regions are increasingly recruited because neural activity in frontal regions becomes less efficient with age due to structural declines predominating in these prefrontal regions (Morcom & Henson, 2018).

1.3. Hypotheses about age-related nervous system shifts during affect

In addition to structural and functional brain changes associated with cognitive aging more generally, there are known structural and functional changes in the brain and peripheral nervous system that may specifically contribute to age-related differences in affect. First, there are peripheral nervous system changes that may alter affect in later life. The theory of maturational dualism suggests that these structural changes may result in a disconnect between peripheral signals and mental processes such as affect and cognition (MacCormack et al., 2019; Mendes, 2010; Mikkelsen et al., 2019). Although it is debated whether peripheral signals are necessary for affective experience (Barrett, 2017; Barrett & Bliss-Moreau, 2009; Berntson, Gianaros, & Tsakiris, 2018; Cannon, 1927; Ekman & Cordaro, 2011; Feinstein et al., 2016; Friedman, 2010; Garfinkel & Critchley, 2013; Harrison, Gray, Gianaros, & Critchley, 2010; MacCormack & Lindquist, 2017), there is increasing experimental evidence that ongoing efferent signals to and afferent signals from the body can indeed contribute to the quality of affective experiences and perceptions (Durso, Luttrell, & Way, 2015; Eisenberger, Moieni, Inagaki, Muscatell, & Irwin, 2017; Garfinkel et al., 2014; Gray et al., 2012; MacCormack et al., 2020; MacCormack & Muscatell, 2019; Muscatell et al., 2016).

The theory of maturational dualism suggests that peripheral nerve demyelination and neuropathy (i.e., cell death) that occur from mid-to-late life may be a source of age-related changes in affect (Melcangi, Magnaghi, & Martini, 2000; Mendes, 2010; Sato, Sato, & Suzuki, 1985; Verdú, Ceballos, Vilches, & Navarro, 2000). For instance, older adults tend to show less autonomic nervous system reactivity during high arousal affect inductions such as stress, conflict, and amusement (Levenson, Carstensen, Friesen, & Ekman, 1991; Levenson, Carstensen, & Gottman, 1994; Neiss, Leigland, Carlson, & Janowsky, 2009; Tsai, Levenson, & Carstensen, 2000; Uchino, Birmingham, & Berg, 2010). One the one hand, older adults' reduced autonomic reactivity could be due to them finding certain affective stimuli or situations less aversive or arousing to begin with or due to improved affect

regulation, but it is also possible that structural and functional peripheral aging could be contributing to their autonomic blunting. Consistent with the latter explanation, older adults show reduced sensitivity to internal bodily signals (i.e., "interoception") than younger adults (Khalsa, Rudrauf, & Tranel, 2009; J. Murphy, Geary, Millgate, Catmur, & Bird, 2018), perhaps reflecting changes to both afferent pathways and how the brain represents those afferent signals.

Although the theory of maturational dualism has focused primarily on the peripheral nervous system (Mendes, 2010), it follows that changes to peripheral nerve involvement in emotion might be reflected in central nervous processing of this information. Specifically, relative to older adults, younger adult brains might show greater activation and coactivation of regions and networks involved in autonomic regulation and interoception such as the central autonomic and salience networks. To our knowledge, little research has examined shifts in the autonomic network across adulthood. There are, however, known structural and functional late-life shifts in the salience network. For example, older adult brains show decreased grey matter volume within hubs of the salience network (e.g., insula, dorsal anterior cingulate cortex or dACC) relative to younger adults (He et al., 2014; Sun et al., 2016) as well as altered functional connectivity between hubs within the salience network and between the salience network and other functional networks. Yet some findings are inconsistent: some studies show either preservation or increased age-related salience network connectivity (Cao et al., 2014; Xiao et al., 2018) whereas others show age-related declines in connectivity (E. A. Allen et al., 2011; He et al., 2013, 2014; Onoda et al., 2012; Roski et al., 2013). Still other work finds divergent patterns of aging depending on which salience subnetwork is examined (Touroutoglou, Zhang, Andreano, Dickerson, & Barrett, 2018). For example, as age increased, there were *decreases* in coactivation within a dorsal salience subnetwork (e.g., between the dorsal anterior insula and MCC) thought to support attention to affect and cognitive control. On the other hand, as age increased, there was *increased* coactivation within the ventral subsystem (e.g., between the ventral anterior insula and amygdala) thought to support visceromotor processes and felt arousal.

Beyond the aging of systems supporting visceromotor control and interoception, there are known age-related differences in other functional networks that point to other potential mechanisms for affective aging. For instance, there are age-related shifts in default mode network and frontoparietal network function during affect (see discussions in Martins & Mather, 2016; Mather, 2016). The role of these networks in self-reflective processes and cognitive control have been taken as evidence for socioemotional selectivity theory (SST), which proposes that as

older adults approach the end of their lives, they are more likely to prioritize socioemotional goals (e.g., close relationships), including being more motivated to attend to pleasant stimuli and select situations or regulate feelings that promote greater positivity and well-being (Carstensen & DeLiema, 2018; Carstensen, Isaacowitz, & Charles, 1999; Carstensen & Mikels, 2005; Scheibe, English, Tsai, & Carstensen, 2013). These goals may lead older adults to implicitly regulate their affective states in different ways than younger adults. Indeed, it has been suggested that, after building a lifetime of affective "expertise," older adults may rely more on self-referential processes supported by the default mode network than do younger adults during affect (Martins & Mather, 2016). As such, SST might predict that older adult brains are characterized by greater activity in prefrontal regions within the default mode and frontoparietal networks during affect—as well as altered functional connectivity between frontal and limbic regions in order to facilitate the pursuit of positive and avoidance of negative stimuli and experiences (Martins & Mather, 2016; Mather, 2012; Mather & Carstensen, 2005; Mather & Knight, 2005). Furthermore, older adults might show increased or maintained activity within the salience network during the experience or perception of positive affective stimuli (i.e., the "positivity" effect) relative to younger adults, but conversely, younger adults might show greater activity herein during negative affect.

Of course, the predictions outlined by affective aging theories such as maturational dualism and SST may not be mutually exclusive. A first step is to examine which brain regions are most reliably activated during affect in older and younger adults across the literature. The present meta-analysis examined (i) age differences in which brain regions are reliably activated during affect as well as (ii) age differences in which brain regions show reliable functional coactivation, in order to begin clarifying possible neural mechanisms underlying age-related differences in affect.

1.4. The present meta-analysis

Roughly two decades of neuroimaging studies have directly compared differences in functional brain activity when younger vs. older adults experience affective states and perceive portrayals of affective behaviors (e.g., affective facial, bodily, and vocal expressions). The primary goal of this meta-analysis was to quantitatively summarize this literature to reveal which regions and sets of coactivated regions most reliably co-occur with affect in older relative to younger adults and vice versa. As a secondary goal, we sought to examine age-related neural differences in valence and arousal, with the hopes of shedding light on theories of affective aging outlined above.

Although individual neuroimaging studies are valuable in their own right, meta-analysis overcomes the limitations associated with sample size, power, and limited experimental designs inherent in individual studies (Cremers, Wager, & Yarkoni, 2017; Turner, Paul, Miller, & Barbey, 2018). Meta-analysis can also reveal the functional neuroanatomy or "neural reference space" (see Lindquist et al., 2012) consistently related to a process of interest and begin weighing in on questions about how those processes might be instantiated in the brain. Our primary aim was to identify the neural reference spaces for younger and older adult brains during affect in general and with respect to valence and arousal. Our second goal was to examine which brain regions were most reliably coactivated for older adults than younger adults and vice versa. We used network-based statistics to reveal which brain regions were most central (i.e., influential) within networks and which were most locally efficient (i.e., tightly interconnected).

2. Methods

2.1. Literature search and study selection

We conducted a review of all functional neuroimaging studies that assessed affective processing in older versus younger adults. Using PRISMA standards (Liberati et al., 2009), we identified and coded individual study-level experimental contrasts from 27 studies containing a total N= 960 healthy participants, with 490 older adults (58% female; M_{age}=69.04 years, 55-87 years) and 470 younger adults (53% female; M_{age}=24.22 years, 18-39 years). See **Table 1** for study-specific demographics and design details. We only included studies that had contrasts for healthy samples of adults. For example, we did not include special population samples such as individuals with Alzheimer's disease, diabetes, depression, etc. We also strove to only include samples where the older adults were cognitively healthy (i.e., no evidence of clinically significant cognitive declines or impairments). See the Supplementary Materials (SMs) **Table S1** for study-specific information on older adult cognitive assessments.

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2.1.1. Inclusion and exclusion criteria. Prior to performing the literature search, we established inclusion and exclusion criteria on the basis of our prior published neuroimaging meta-analyses (Brooks et al., 2017; Kober et al., 2008; Lindquist et al., 2016, 2012; Satpute et al., 2015). Studies could either use fMRI or PET methods, must have included a sample of healthy (non-clinical) older and younger adults (as defined in the given study), and must have used an affect induction or any task where affective stimuli were passively viewed, categorized, or rated in the scanner. Per our prior meta-analytic work, we specifically focused on studies designed to manipulate *affective*

experiences (e.g., feelings of emotion) or *affective perceptions* (e.g., seeing or hearing affect or emotion in others' facial, bodily, or vocal behaviors) and excluded studies designed to explicitly measure the neural basis of learning, memory, priming, or pain given that these types of tasks are likely to involve additional psychological and hence neural processes (e.g., studies assessing brain activity during affective learning reveal neural processes linked to learning in addition to affect). Furthermore, although there are hypotheses that older adults might be better at engaging explicit emotion regulation (Birditt & Fingerman, 2005; Sands, Garbacz, & Isaacowitz, 2016; Scheibe & Blanchard-Fields, 2009; although see Livingstone & Isaacowitz, 2019), we excluded these kinds of studies, as explicit emotion regulation involves effortful cognitive control processes that may be distinct from affective experiences or perceptions. This exclusion criterion is consistent with our prior meta-analytic work which also excludes emotion regulation studies (Brooks et al., 2017; Lindquist et al., 2016, 2012; Satpute et al., 2015).

To be included in our database, papers had to (i) conduct functional neuroimaging analyses, (ii) report peak coordinates from an experimental contrast, and (iii) report a contrast that was relevant to the research question (e.g., a contrast examining older adult affect on a drug vs. placebo would not be eligible because the contrast was confounded with drug effects rather than age effects on affect). We considered any peer-reviewed publications in press or published up until January 2019 that met our search parameters. Literature searches were conducted using UNC Libraries (Web of Science, Elsevier, ScienceDirect) and Google Scholar, with Boolean that included combinations of the following words: [Emotion OR Arousal OR Valence OR Affect] AND [Aging OR Old Age OR Older Adult OR Late Adulthood] AND [Brain OR fMRI OR Positron Emission Tomography OR Neural]. Theses, dissertations, and book chapters were excluded. We found 64,724 papers in UNC Libraries using this Boolean, sorted by relevance. In Google Scholar, using the same Boolean, we found roughly 49,700 results, sorted by relevance.

Our literature search team included two trained research assistants plus the first and second authors. The process was overseen by the senior author. The research assistants and second author jointly looked through the combined results for relevant papers. The first author also examined the first 5,000 hits on each search to confirm that all relevant papers had been found by the first team. Many items were duplicates, significantly inflating the number of papers. Additionally, although many papers discussed older adult affect or the brain, they did not actually study the brain. Through these concerted efforts, we identified 82 possible papers.

We excluded 14 papers that used EEG or structural/functional connectivity approaches, unless those papers also provided functional activation peak coordinates from relevant contrasts, given that the MKDA method we used does not analyze functional connectivity data. Eight papers were review articles that were examined for other relevant studies but did not contain original data. A further six papers were excluded because they only reported continuous age analyses, but results derived from such analyses are not compatible with MKDA. Another 13 papers contained only contrasts that did not fit our inclusion criteria (e.g., contrasts only compared healthy vs. unhealthy groups; compared older adults on drug vs. placebo). Finally, 15 papers did not actually investigate affective experience or perception, but instead assessed constructs such as empathy, theory of mind, prejudice, or social cognition which we *a priori* excluded on the basis that these constructs are related to, but distinct from, affective experience or perception. Importantly, we cross-checked papers by the same authors to ensure that all included studies were independent and did not represent different publications from the same sample or analyses.

Thus, the search concluded with a final set of 26 papers spanning 27 studies, of which 26 studies used fMRI and 1 study used PET. (See **Figure S1** in SMs for PRISMA flowchart.) We included the single PET study given that PET and fMRI both measure blood flow and use the same coordinate system; PET inclusion is also common practice in other neuroimaging meta-analyses (e.g., Kraynak, Marsland, Wager, & Gianaros, 2018; Lindquist et al., 2016, 2012; Phan, Wager, Taylor, & Liberzon, 2002; Thayer et al., 2012; Wager, Jonides, & Reading, 2004). Note that the single PET study included in the database only contains within-age contrasts and no between-age contrasts. Given our meta-analytic focus on between-group age differences, contrasts from the single PET study only appear in supplementary analyses that include within-age contrasts.

2.1.2. Coding. After all relevant papers were identified, the first and second authors read all papers, independently coded them, and extracted peak coordinates for the database. Coders met every 5 papers to review coding and ensure that codes were applied correctly and consistently between coders. Coded variables included *sample characteristics* (e.g., sample size, age, sex), *task characteristics* (e.g., passive viewing of affective stimuli, judging or categorizing stimuli into emotion categories, etc.), and *contrast characteristics*—specifically, the age groups (older adults or OAs, younger adults or YAs), valence (negative, neutral, positive), and arousal (high, medium, low) of each target and comparison within the contrast. Of note, all study stimuli were either normed for discrete emotions that differed in valence and arousal (e.g., in face perception tasks) or normed for valence and arousal (e.g., International Affective Picture System; IAPS). Although discrete emotion categories included *happy*,

sad, *angry*, *fear*, *disgust*, *contempt*, and *surprise*, the most prevalent category studied was *fear*. In studies that used affective images such as IAPS, studies generally compared negative, positive, and neutral images that were normed at mid-to-high arousal.

In total, coding produced 72 contrasts that directly contrasted older vs. younger adults, with 41 contrasts where younger adults were the target (YA > OA) and 31 contrasts where older adults were the target age group (OA > YA). See **Table 2**. There were an additional 92 contrasts that contrasted within-age group effects (e.g., OA negative affect > OA neutral affect) which are relevant for additional results presented in the SMs.

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2.2. Meta-analytic approach

2.2.1. Functional activations. To assess age differences in functional activations during affect, we used multilevel kernel density analysis (MKDA; Kober et al., 2008; Kober & Wager, 2010; Salimi-Khorshidi et al., 2009; Wager et al., 2009, 2007), which has been extensively validated and used in functional neuroimaging meta-analyses of human affect, pain, and cognition over the past decade. MKDA is used to compute meta-analytic summary contrasts of brain regions that are more reliably active than would be expected by chance during one condition vs. another (e.g., OAs > YAs) across the literature. Using the Matlab toolbox NeuroElf (http://neuroelf.net/), the MKDA uses voxel-wise peak activations within study contrasts to generate a meta-analytic map of neural activity.

As per standard MKDA and neuroimaging meta-analytic procedures (Kober et al., 2008; Müller et al., 2018; Wager et al., 2007), contrast coordinates in Talairach space were first converted to MNI space and then convolved using a smoothing kernel of 12mm to produce binary indicator contrast maps. In most neuroimaging meta-analyses, coordinates are convolved with spheres between 10-15mm and we picked 12mm, building off prior data-driven approaches and other similar studies using MKDA (Brooks et al., 2017; Lindquist et al., 2016, 2012; Salimi-Khorshidi et al., 2009). MKDA weights study contrasts by sample size and down-weights study contrasts that do not model random effects in their analyses, with the goal of ensuring that adequately powered, more generalizable studies contribute more strongly to the meta-analytic findings. Thus, contrast maps were weighted by the square root of the sample size. Studies that used only fixed effects analysis techniques were then down weighted by 0.75. These weighted averages of the kernels across individual study contrasts were then used to derive a map of proportional brain activation from *N* contrasts. Ultimately, MKDA treats contrasts as independent and nests coordinates within contrasts to control for dependencies therein. We carried out Monte Carlo tests to assess the

significance of each voxel in the MKDA maps. In particular, we simulated 5000 samples to create a null distribution of the expected maximum proportion of voxels with significant activation that is greater than expected by chance, according to which all MKDA maps were thresholded. For all analyses, we set this *a priori* threshold to a stringent height-based threshold of $p<.01$ (using family-wise error or FWE-correction for multiple comparisons) to determine whether voxels were significant. However, given the small size of our database and given that this is the first meta-analysis to examine age-related differences in functional brain activity during affect, we also report exploratory findings for regions that showed significant differences at the less stringent FWE-correction thresholds of $p<.02$ and $p<.05$. As part of quality control, we confirmed that coordinates for all meta-analytic maps were located in grey matter and not ventricles.

We performed two different rounds of MKDAs. Of primary interest, we first examined brain regions that were reliably active across affective contrasts comparing older and younger adults. Specifically, we compared YA>OA and OA>YA study contrasts across all tasks and dimensions of affect (e.g., negative affect > neutral affect and positive affect > neutral affect). The goal with these analyses was to produce a "neural reference space" representing functional brain activations that are reliably more activated across studies for younger adults compared to older adults or that are reliably more activated for older adults compared to younger adults during any affective experience or perception. These maps are akin to assessing the reliable brain activity for younger and older adults across the literature. (For full neural reference space across affect, see SMs **Table S2**). After determining age differences across all affective contrasts, we next examined age differences in functional activation for specific *dimensions* of affect, broken down by valence (e.g., negative affect > neutral affect, positive affect > neutral affect) and arousal (e.g., high arousal > low and medium arousal, medium arousal > high and low arousal, low arousal > high and medium arousal). These maps are akin to assessing the average reliable brain activity for each condition of interest: i.e., brain activation in younger adults (YA>OA) or older adults (OA>YA) for a specific aspect of valence or arousal. These maps also are the most specific analyses, allowing us to pinpoint age differences in affect.

In addition to the primary analyses examining between-age group contrasts (e.g., OA>YA or YA>OA) across affect, valence, and arousal, we also conducted secondary analyses that contrasted both sets of age contrasts against each other, i.e., [(YA>OA)>(OA>YA)] and [(OA>YA)>(YA>OA)]. The motivation for these additional analyses was to determine the specificity of contrast effects observed by subtracting out anything due to chance within each age group. Although less straightforward to interpret than the simpler YA>OA and OA>YA contrasts,

these secondary analyses allowed us to combine all YA>OA and OA>YA contrasts and thus provided more power to provisionally examine contrast effects. These secondary results are reported in the SMs (**Tables S3-S4**). Finally, we were most interested in age differences across affective processes overall and by valence vs. arousal. However, we did conduct supplementary analyses to assess potential age differences by affective experience vs. perception. Interestingly, there were only some age differences by type of affective process. These findings are presented in the SMs (**Table S5-S6**).

2.2.2. Functional coactivation. To assess age differences in functional coactivation during affect, we followed a method similar to Robinson and colleagues' (2009) approach to meta-analytic coactivation modeling. First, we extracted separate functional activation coordinates from the neural reference spaces for YA>OA and OA>YA that were identified by MKDA as being the most reliably activated across studies. Using these MKDA-thresholded coordinates, we extracted study-level activation frequencies for each coordinate at the level of the MKDA contrast, coded as 1=*coordinate activation was observed*, 0=*coordinate activation was not observed*. From these binary variables, we then computed phi-coefficients (which are computationally equivalent to Pearson correlations) between coordinates to determine coactivation of regions at the meta-analytic level. To test the significance of these phi-coefficients, we used the χ_2 test of independence for binary variables. To correct for multiple comparisons and minimize false positives, we used the Benjamani-Hochberg correction to control for false discovery rate at the nominal level of .05 (Benjamini & Hochberg, 1995). All coactivation analyses were conducted in R. Coactivation visualizations of the significant nodes that survived multiple comparisons correction were created using BrainNet Viewer (M. Xia, Wang, & He, 2013) (https://www.nitrc.org/projects/bnv/).

To characterize coactivation patterns, we computed network statistics on the coactivation patterns between functional coordinates ("nodes") that survived multiple comparisons correction. Specifically, we computed three network statistics for the YA>OA and OA>YA coactivation networks: (1) eigenvector centrality (Borgatti, 2005), (2) betweenness centrality (Freeman, 1977), and (3) local efficiency (Latora & Marchiori, 2001). *Eigenvector centrality* indicates how central a node is to the network overall (e.g., how many edges a node shares with other nodes, taking into account whether related nodes are also central). Nodes with high eigenvector centrality indicate that a given node shares many edges with other central nodes; nodes with high eigenvector centrality are thus particularly influential in relation to other nodes. *Betweenness centrality* indicates whether a node is more likely to serve as a "bridge" or "bottleneck" when connecting other sets of nodes. Nodes with higher betweenness help

connect other nodes with each other and thus may help "gate" the flow of information across a network. Finally, *local efficiency* is a measure of how closely connected a node's immediate neighbors are. A node with high local efficiency has nodal neighbors that are tightly interconnected, making it more efficient for information to flow between nearby nodes.

We focused on these three network statistics because they provide a broad descriptive view of network topology. Given that the YA>OA and OA>YA networks have different node sets and edge densities, it is important to note that the value of network statistics are not directly comparable across YA>OA and OA>YA networks (van Wijk, Stam, & Daffertshofer, 2010). Rather, these statistics characterize key nodes *within* each network. Moreover, network statistic values are not standardized scales so values cannot be compared between metrics (e.g., between eigenvector centrality and betweenness centrality). Values can, however, be interpreted relative to other node values *within* the same metric (e.g., within local efficiency). It is also possible to compare the *relative* rankings of nodes between networks (e.g., if the insula were to have the highest eigenvector centrality in both networks) for descriptive purposes. Network properties were analyzed and visualized with the igraph (http://igraph.org) and brainGraph (https://github.com/cwatson/brainGraph) packages in R (Csardi & Nepusz, 2006; Watson, 2018). Layouts for network metrics were computed using the Fruchterman-Reingold algorithm (Fruchterman & Reingold, 1991).

3. Results

3.1. Age differences in functional activation during affect

3.1.1. Age differences in affect. We first examined brain regions that were more frequently activated in YA>OA across affect (375/553 points; 40/72 contrasts). We observed three clusters centered on the right amygdala (27, 3, -36; k=420, p<.01), left rostral parahippocampal gyrus (-24, -33, -15; k=745, p<.01), and the mid-cingulate cortex (MCC; 6, 6, 24; k=386, p<.01). The right amygdala cluster extended into the hippocampus, the entorhinal and perirhinal cortex, the inferior frontal gyrus including some anterior (more ventral) insula, and other parts of the parahippocampal gyrus. The left rostral parahippocampal cluster extended into the left amygdala, hippocampus, fusiform gyrus, superior temporal gyrus, posterior insula extending into the somatosensory cortex, the agranular retrolimbic area extending into the lingual gyrus, as well as the lingual gyrus and thalamus. The MCC cluster included the anterior MCC and extended into the left caudate body. See **Table 3 and Fig. 1**.

Next, we examined brain regions that more frequently activated in OA>YA across affect (192/553 points; 31/72 contrasts). Here, we did not observe any significant clusters of activation at p<.01. However, at p<.02, we

observed one large cluster centered on the right dACC (11, 46, -1; k=1149), that also included a large cluster in the medial prefrontal cortex (primarily dmPFC but also some vmPFC), with some activation also in the rostral superior frontal cortex, right anterior insula, and left and right caudate. See **Table 4 and Fig. 1**.

-- INSERT TABLE 3 AND 4 ABOUT HERE –

-- INSERT FIGURE 1 ABOUT HERE --

3.1.2. Age differences in valence. Next, we examined brain regions that more frequently activated in YA>OA during negative and positive affect. Negative affect contrasts (197/553 points; 20/72 contrasts) included study contrasts wherein negative > neutral or negative > positive affect. Here, we observed one cluster in the left amygdala (-18, -5, -16, k= 388, p<.01), which also included the hippocampus, rostral parahippocampal gyrus, parts of the entorhinal and perirhinal cortices, as well as the sublobar lateral geniculum body in the thalamus. There were only a few positive affect contrasts for younger > older adults (71/553 points; 8/72 contrasts including contrasts with positive > neutral or positive > negative affect). We found no significant clusters, even at exploratory p<.02 and p<.05 thresholds, although it should be noted that this analysis is likely underpowered due to the small sample of contrasts. See **Table 5**.

Turning to older adults, we examined brain regions that more frequently activated in OA>YA for contrasts where negative affect was the target (60/553 points; 13/72 contrasts). We observed one cluster in the right somewhat more dorsal ACC (14, 39, 9, k= 435, p<.01) that extended primarily into the dmPFC but also included some dorsolateral prefrontal cortex (dlPFC) and rostral parts of the superior and middle frontal gyrus. For positive affect (68/553 points; 8/72 contrasts), there were no significant clusters of activation at p<.01, again likely due to the small number of contrasts. At p<.02, we found a very large cluster of activation centered in the left caudate head and left ACC (-10, 23, 5, k= 5093), but this large cluster also extended into the retrosplenial cortex, putamen, postcentral gyrus which included the primary somatosensory cortex, the pulvinar, thalamus, and the dorsolateral prefrontal cortex along with other activations in the medial and superior frontal cortex. Note that as a general rule of thumb, an MKDA with 10 contrasts or fewer is considered relatively unreliable, so such results should be taken as provisional. See **Table 6,** but also **Table S7** for additional exploratory analyses with positive affect.

-- INSERT TABLE 5 AND 6 ABOUT HERE --

3.1.3. Age differences in arousal. Next, we examined brain regions that reliably activated in younger > older adults during high and low arousal affect. For YA>OA contrasts where high arousal affect was the target

relative to low and medium arousal (238/553 points; 20/72 contrasts), there were no significant clusters of activation at the *a priori* threshold of $p<.01$. Exploratory analyses at $p<.02$ revealed two significant clusters. The first cluster centered in the right mid-cingulate cortex (MCC; 3, -3, 27, $k=467$, $p<.02$) extending into the anterior MCC (aMCC), left and right caudate body, and left thalamus. The second cluster centered in the ventromedial prefrontal cortex (vmPFC; 15, 54, 1, $k=477$, $p<.02$) extending into aMCC, dACC, and dmPFC. For YA>OA low arousal affect, there were insufficient contrasts (i.e. only 2) to compute this MKDA comparison. See **Table 5**.

For OA>YA contrasts where high arousal affect was the target relative to low and medium arousal (132/553 points; 18/72 contrasts), there was one significant cluster of activation centered in the middle frontal gyrus and anterior portions of the right vmPFC (25, 43, -2, $k=561$, $p<.01$) extending into the dACC, right caudate, and more dorsal, anterior parts of the insula. For OA>YA low arousal affect, there were insufficient contrasts (i.e. only 1) to compute this MKDA comparison. See **Table 6**.

3.1.5. Secondary meta-analytic contrasts. Finally, we contrasted both sets of age contrasts against each other, i.e., [(YA>OA)>(OA>YA)] and [(OA>YA)>(YA>OA)] in order to determine the specificity of contrast effects observed by subtracting out anything due to chance within each age group. Results largely replicated those reported for the YA>OA and OA>YA contrasts. See **Tables S3-S4** in SMs. For example, when YA>OA was the target contrast (relative to OA>YA), activations in the left and right amygdala and parahippocampal gyrus predominated across affect as well as within negative affect. On the other hand, when OA>YA was the target contrast (relative to YA>OA), a single cluster of activation centered in the dmPFC and dACC emerged as significant across affect. For negative affect when OA>YA was the target, we observed a single cluster with its peak of activation in the superior frontal gyrus spanning the dmPFC into the dACC and inferior frontal gyrus. With a few more contrasts afforded by this less conservative analysis, we also observed greater activation in the left caudate and right thalamus for positive affect when YA>OA was the target. However, we still did not find any significant effects for positive affect when OA>YA was the target.

For high arousal affect when YA>OA was the target, significant peak activation was also observed in the left lentiform nucleus, caudate, and thalamus. In high arousal contrasts where OA>YA was the target, significant clusters emerged in the left prefrontal cortex and caudate. Importantly, with this less conservative analysis, we were also able to examine age differences in low arousal affect. For low arousal contrasts with YA>OA as the target, one large cluster occurred in the left uncus extending throughout the superior temporal gyrus and parts of the vmPFC as

well as a second large cluster with its peak of activation in the right culmen. For low arousal contrasts wherein OA>YA was the target, activation centered in the dorsal and pregenual ACC extending into the vmPFC. Analyses with positive and low arousal affect still include fewer contrasts relative to contrasts with negative and high arousal affect; therefore, we caution that the positive and low arousal affect findings should be viewed as provisional.

3.2. Age differences in functional coactivation during affect

3.2.1. Coactivations. Using the whole-brain meta-analytic coordinates identified in the primary YA>OA affect and OA>YA affect neural reference spaces, we next analyzed patterns of functional coactivation between these meta-analytically thresholded regions (**Fig. 2**). For YA>OA, nodes in the amygdala and parahippocampal gyrus, inferior and superior temporal gyrus, posterior insula, thalamus, lingual gyrus, caudate, and MCC were most reliably coactivated during affect, even after correcting for multiple comparisons. In particular, younger adults showed greater coactivation between multiple nodes within the parahippocampus (extending into amygdala and hippocampus). There was also a cluster of coactivating nodes centered in the mid-cingulate and caudate, as well as coactivations between the posterior insula with the thalamus, MCC, and caudate.

On the other hand, for OA>YA, nodes in the ACC, caudate, anterior insula, and frontal gyrus were most reliably coactivated during affect, even when correcting for multiple comparisons. In particular, nodes in the ACC, dmPFC, mid-frontal, superior frontal, and caudate tended to co-activate together during affect. To a lesser extent, there were also coactivations between the inferior frontal gyrus, anterior insula, and parts of the medial and mid-frontal cortex. Full coactivation correlation matrices are reported in the SMs.

-- INSERT FIGURE 2 ABOUT HERE --

Finally, to better identify important nodes within the YA>OA and OA>YA networks for affect, we computed the eigenvector centrality, betweenness centrality, and local efficiency of nodes within each network. See **Fig. 3** and relevant tables in the SMs. For the YA>OA network, nodes with the highest eigenvector centrality (*EC*) values were the right MCC (x=7, y=5, z=23; *EC*=.48), left caudate (-16, 8, 17; -16, 9, 23; -6, 8, 16; -13, 11, 9; *ECs*=.42, .40, .37, .25 respectively), anterior MCC (-4, 15, 23; *EC*=.28), left MCC (-3, -6, 28; *EC*=.26), and left posterior insula (-34, -19, 12; *EC*=.23). Nodes with highest betweenness centrality (*BC*) were the right inferior frontal gyrus (35, 6, -13; 30, 14, -20; *BC*=.17, .12 respectively), right amygdala (29, 0, -25; *BC*=.11), left fusiform (-22, -66, -4; *BC*=.11), and left parahippocampus (-25, -57, 3; *BC*=.10). Nodes with the highest local efficiency (*LE*) were the left and right MCC (-3, -6, 28; 10, 8, 33; both *LE*=1.00), right hippocampus (34, -8, -19; *LE*=.83), several

nodes in the left caudate (*LE*=.83-.80), as well as the right parahippocampus (22, 0, -11; *LE*=.73) and left anterior MCC (-4, 15, 23; *LE*=.72).

For the OA>YA network, nodes with the highest eigenvector centrality values were nodes in the right caudate (20, 29, 2, *EC*=1.00), right mid-frontal gyrus (25, 43, -2; *EC*=.99), right ACC (11, 46, -1; *EC*=.95), right medial frontal gyrus (10, 38, -6; *EC*=.87), and the right superior frontal gyrus (21, 44, -14; *EC*=.79). Nodes with the highest betweenness centrality were the right medial frontal gyrus (10, 38, -6; *BC*=.28), left caudate (-3, 14, 11; *BC*=.25), right ACC S1 (11, 46, -1; *BC*=.19), right medial frontal gyrus (11, 47, 7; *BC*=.19), and the right and left caudate S7 S4 (20, 29, 2; -13, 27, 8; *BC*=.16, .15 respectively). Finally, the nodes with greatest local efficiency were the left superior frontal gyrus S3 S10 (-29, 60, 5; -15, 60, 9; both *LE*=1.00), right anterior insula (33, 18, 5; *LE*=.83), right inferior frontal gyrus (38, 35, 0; *LE*=.83), right mid-frontal gyrus (25, 43, -2; *LE*=.76), and the right medial frontal gyrus (12, 60, 12; *LE*=.7). See SMs for additional tables.

-- INSERT FIGURE 3 ABOUT HERE –

4. Discussion

4.1. Age differences in the neural reference space for affect

We present the first known meta-analysis that examines age differences between younger and older adults' functional brain activation and coactivation during affect. When pooling across the experience and perception of affective valence and arousal, we found that younger adults exhibited more reliable activation than older adults in subcortical structures such as the bilateral amygdala, hippocampus, and thalamus, whereas older adults had more reliable activation in prefrontal cortical regions such as medial (especially dmPFC), middle, superior, and inferior frontal gyrus. Relative to older adults, younger adults also exhibited more posterior activation both within specific brain structures and with respect to the whole brain. For instance, younger adults had more reliable activity in the posterior insula and MCC during affect, whereas older adults had more reliable activity in the anterior insula and dACC during affect. These findings may be consistent with evidence on age-related changes in domain-general brain function, insofar as they may indicate a possible posterior-to-anterior shift in aging from sensory processing regions to prefrontal regions with increasing age (i.e., PASA; Davis et al., 2008; McCarthy et al., 2014). As such, our findings are consistent with some effects found in cognitive aging neuroscience.

We also found that younger adults had more reliable activity than older adults in regions that form a central autonomic network such as the amygdala, thalamus, and posterior insula. Younger adults exhibited reliable

coactivation between subcortical and limbic structures such as parahippocampal gyrus (extending into amygdala and hippocampus), the posterior insula, thalamus, and MCC. The MCC and amygdala were particularly central and locally efficient hubs amongst this group of regions, and younger adults' coactivation regions were more likely to cluster in segregated neighbors than older adults. In contrast, older adults had more reliable activity in regions that comprise the dorsal salience network (i.e., dACC) and default mode network (i.e., dmPFC; Benarroch, 1993; Cersosimo & Benarroch, 2013; Goswami, Frances, & Shoemaker, 2011; see Ding et al., 2020; Sie, Chen, Shiau, & Chu, 2019 for recent work). Older adults showed more reliable coactivations amongst the dACC, dmPFC, and mid-to-superior frontal cortex as well as the inferior frontal gyrus, anterior insula, and more anterior parts of the caudate. Amongst these regions, the dACC, caudate, and middle frontal gyrus were more central, locally efficient nodes, and older adult's patterns of coactivation were less segregated than those of younger adults. Collectively, these findings have implications for theories of age-related differences in affect.

First, our findings lend provisional support for the theory of maturational dualism. The finding that younger adults had more reliable activation within and coactivation amongst brain regions associated with autonomic control and interoceptive representations may suggest that younger adults' affective experiences and perceptions are characterized by relatively greater involvement of visceral signals than those of older adults. In contrast, the finding that older adults had more reliable activation within and coactivation amongst brain regions comprising the dorsal salience network and default mode network may suggest that older adults are engaging in relatively more mentalizing, autobiographical memory, and self-regulation during affective experiences and perceptions than younger adults. Indeed, proponents of SST have predicted such outcomes as evidence that older adults are using different forms of emotion regulation than younger adults (e.g., Martins & Mather, 2016).

It may be tempting to interpret these results as evidence that older adults are engaging in emotion regulation to a greater extent than younger adults during these in-scanner affect tasks. We did not include studies of explicit emotion regulation in our database but cannot rule out that older adults may be either engaging in emotion regulation or approaching affective tasks differently than younger adults (e.g., due to motivational differences, increased semantic knowledge, greater cognitive effort, greater expertise, etc.). Notably, in our meta-analysis of negative affect, older adults exhibited more reliable activity than younger adults in regions associated with the frontoparietal control network (e.g., dlPFC). In prior work with younger adults, the dlPFC shows consistent increases during emotion regulation (see Buhle et al., 2014 for meta-analysis). Yet individual studies of emotion

regulation have shown that older adults engage dlPFC to a similar extent as younger adults (Winecoff, LaBar, Madden, Cabeza, & Huettel, 2011). The dlPFC is also commonly activated in younger adults across studies of emotion in which participants are not explicitly engaging in emotion regulation (Lindquist et al., 2012). Consequently, we caution against the reverse inference that activation of dlPFC in older adults implies that older adults are engaging in emotion regulation to a greater extent than younger adults.

Taken together, both maturational dualism and SST fit the overall pattern of findings and may suggest compatible (rather than competing) neural mechanisms of affective aging. Nevertheless, the above meta-analytic interpretations are reverse inferences that warrant verification in future studies. Another caveat is that greater activity in prefrontal regions for older adults could be unrelated to psychological processes but may instead reflect prefrontal structural declines resulting in stronger BOLD activity in these regions due to more diffuse, less efficient neuronal activity (Morcom & Henson, 2018). This alternative explanation should be addressed in future.

4.1.1. Age differences in neural representations of valence. We separately examined the neural representation of valence to further weigh in on predictions from different theories of affective aging. The findings for negative affect largely replicate the overall affect findings. This is unsurprising given that there were relatively more studies of negative than positive affect in our database. During negative affect, younger adults had the most reliable activity (relative to older adults) in the left amygdala, with some activation extending throughout the left and right parahippocampal gyrus. As in the overall neural reference space findings, the amygdala is linked to the generation of autonomic states, consistent with maturational dualism. SST also suggests that younger adults should experience relatively more robust negative affect. To the extent that the left amygdala reflects the intensity of negative affect, these findings would also support SST. Of note, our prior meta-analytic work also found that the left amygdala was most frequently activated during negative relative to positive affect in the literature on young adults (Lindquist et al., 2016).

Although most studies in the database tested for age differences in positivity (20/27 studies), it is striking that so few studies reported significant age differences in positive affect, especially given predictions from SST and the large number of behavioral studies testing the positivity effect in affective aging. We found no significant regions of activation for younger > older adult positive affect, regardless of corrected thresholds explored (*ps*<.01, .02, .05). Note that we did observe significant activation for older > younger adults at the exploratory FWE-corrected threshold of $p<.02$ in the left caudate, which is sometimes associated with reward learning (Haruno &

Kawato, 2006) and motivated behavior (Delgado, 2004). Given the lesser threshold, we caution against strong inferences, but these findings may be provisional support for SST. This finding should be interpreted against the backdrop of the null effects of OA>YA comparisons for positivity in the broader literature however. Future studies should prioritize evaluating age differences in positive affect with larger samples and more diverse methods of targeting positive affect in the scanner.

4.1.2. Age differences in neural representations of arousal. There were a large number of high arousal contrasts in the database but almost no low arousal contrasts, due to the kinds of studies and stimuli that predominate in the existing literature. It is also worth noting that many studies in the meta-analytic database examined negative valence that was mid-to-high arousal, so it is likely that arousal and valence are confounded in our findings (see Lindquist et al., 2016 for a discussion). When examining high arousal contrasts, findings replicate the general pattern of findings observed for negative affect but include several additional regions not observed in the overall and negative affect contrasts. In line with maturational dualism, younger adults again showed reliable activation relative to older adults in regions implicated in visceromotor control and autonomic nervous system representations (Beissner, Meissner, Bar, & Napadow, 2013; Gianaros et al., 2017; Kleckner et al., 2017; Satpute et al., 2019; Touroutoglou et al., 2019) such as the mid-cingulate (including aMCC), caudate, thalamus and the posterior vmPFC/ACC.

In contrast, older adult high arousal affect was again more related to dorsal, anterior parts of the salience network such as the middle frontal gyrus, anterior portions of the vmPFC, as well as the dACC and more dorsal, anterior parts of the insular cortex. Interestingly, in healthy young adults, the dorsal salience subsystem is related to executive function, whereas the ventral salience subsystem is related to subjective arousal (Touroutoglou, Hollenbeck, Dickerson, & Barrett, 2012; Touroutoglou et al., 2018). One might assume that relatively greater activation of the dorsal salience network in older adults during high arousal affect may reflect greater regulation efforts. A separate interpretation is that due to age-related decreases in dorsal salience functional connectivity (as found in Touroutoglou et al., 2018), older adults have more diffuse (less efficient) neuronal processing in the dorsal salience network, resulting in greater activity during states of heightened arousal. Again, these findings should be addressed in future research.

4.2. Strengths, limitations, and future directions for the affective neuroscience of aging

In the present study, we used functional neuroimaging meta-analytic techniques to summarize three decades of literature on age-related neural differences during affective experience and perception. This work sheds light on what we know to date about how the aging brain and affect are related. However, this work is not without limitations. Below, we discuss both merits and limitations and then highlight critical future directions that will help further the affective neuroscience of aging.

4.2.1. The power and limits of meta-analysis. This meta-analysis identified the most consistent (i.e., reliable) effects in the affective neuroscience of aging literature. Doing so is critical, given that any one study is prone to false positives, sampling biases, and method-specific confounds (Wager et al., 2007). However, due to the nature of the existing literature, our meta-analysis best speaks to reliable age differences in the neural bases of negative and high arousal affect. The published literature contained too few significant age differences in positive affect, despite the fact that nearly three-quarters of included studies did test for age differences in positive affect. Furthermore, low arousal affect was especially underrepresented in the meta-analytic database, due to its infrequent inclusion in study designs. Given recent behavioral work showing that older adults are more likely to report experiencing and may even prefer low arousal affective experiences and stimuli (Bjalkebring, Västfjäll, & Johansson, 2015; MacCormack et al., 2019; Sands & Isaacowitz, 2017), future neuroimaging studies should strive to understand age differences in arousal, not just valence.

In addition to biases or limitations in the existing literature, coordinate-based neuroimaging meta-analyses further limit the scope of possible data that can be included. Coordinate-based neuroimaging meta-analyses remain the gold-standard for assessing the reliability of functional brain activity but require that coordinates be derived from contrasts rather than correlations or functional connectivity approaches. Consequently, we focused on studies with functional coordinates that contrasted age groups but did not include studies that treated age as a continuous variable or that focused exclusively on functional connectivity. We were able to produce coactivation analyses to approximate network function, yet meta-analytic coactivation is not equivalent to within-study functional connectivity. Nevertheless, these findings help reveal which brain regions were reliably coactivating as a unit together across aging studies during affect, which may prove useful for future functional connectivity studies of affective aging.

4.2.2. Generalizability and specificity. One strength of our meta-analysis is that the adults included are relatively generalizable to healthy community samples. On average across studies, young adults were frequently from the community (rather than university students), ranged in age from 21-26 years, and were often matched with older adults on key demographics such as sex and education. Of course, our findings generalize to the population only insofar as most Western scientific studies do—participants in our sample were mostly North American adults and it is unclear how these neuroimaging findings (or even affective aging findings) replicate and generalize across cultures and ethnicities (see Grossmann, Karasawa, Kan, & Kitayama, 2014).

In addition to generalizability across populations, it remains unknown how findings might generalize across other psychological domains vs. might be specific to affect. Some of the age-related differences we observed (e.g., older adult greater dmPFC and superior frontal activity) parallel findings in the cognitive aging neuroscience literature. This may suggest that there are domain-general aging processes—such as structural declines—that in turn impact multiple psychological functions. As such, it is unclear how the present findings are driven by domain-general vs. affect-specific neural aging. Although this meta-analysis cannot quantitatively speak to shared vs. unique patterns of neural aging for "cognitive" and "affective" tasks, future work should build on these findings to investigate domain-general vs. domain-specific patterns associated with aging during tasks that are relatively more vs. less affect-laden.

4.2.3. Mapping within-person trajectories of affective aging. Another crucial limitation is that all included studies were cross-sectional in nature and, as such, cannot account for within-person changes, individual differences (e.g., different rates of aging), or generational differences (Hoffman & Stawski, 2009; Salthouse, 2012; Sliwinski, Hoffman, & Hofer, 2010). This means that the present findings only reveal age *differences* rather than age-related *changes*, which would require within-person longitudinal assessments across ideally three or more timepoints. For instance, it is possible that effects observed herein are confounded with cohort or generational effects (e.g., older adults who grew up in a different historical context compared to young adult samples). Hence, it remains unclear if the neural differences found between older vs. younger adults are due to the process of aging itself or due to generational, historical, or cultural shifts across time. Similarly, even if effects observed are due to aging, the exact causal relation between brain aging and affective aging remains unclear. Although in this meta-analysis we assume that age-related changes in brain morphology and function likely precede and give rise to age-related changes in affective processes, this need not be the case. For example, shifts in affect over time may also

influence the nature and time course of brain aging (e.g., chronic stressors and depression likely accelerate brain aging whereas more positive social affective experiences may help buffer against certain forms of brain aging). Multi-site studies like the Midlife in the United States Study (Brim et al., 1996) and the Lifespan Human Connectome Project in Aging (Bookheimer et al., 2019) represent important next steps for clarifying how within-person aging might causally predict downstream affective processes in later life and vice versa.

4.2.4. Linking structure and function, brain and body. Lastly, we do not yet know how these observed age differences in functional brain activation and coactivation during affect are grounded in age-related structural changes to the central and peripheral nervous system. A broader challenge facing neuroscience is to link brain function such as in functional connectivity fMRI with brain structure using techniques such as diffusion tensor imaging to map structural connectivity (Damoiseaux, 2017; Meier et al., 2016; Poldrack, 2010; Snyder & Bauer, 2019; Vázquez-Rodríguez et al., 2019). Indeed, although functional connectivity must be grounded in the structural limitations of the brain's architecture, structural connectivity alone is insufficient for explaining functional connectivity (Friston, 2011).

Many studies in both humans and non-human animals already document aging effects on brain structure, broadly finding that even in healthy aging, the brain shrinks in volume (especially in the frontal and temporal cortices, as well as the putamen, thalamus, and accumbens), an effect that is partially explained by neuronal shrinkage, shortening of synaptic spines, and fewer synapses (J. S. Allen et al., 2005; Bagarinao et al., 2018; Fjell & Walhovd, 2010; Fjell et al., 2013; Good et al., 2001; Meunier, Achard, Morcom, & Bullmore, 2009; Raz et al., 2005; Scheibel, Lindsay, Tomiyasu, & Scheibel, 1975; Smith et al., 2007). Furthermore, myelination deteriorates throughout the central and peripheral nervous systems, leading to slower, less efficient neuronal signaling (Hill, Li, & Grutzendler, 2018; Marner, Nyengaard, Tang, & Pakkenberg, 2003; Melcangi et al., 2000; Palve & Palve, 2018; Peters, 2002, 2009; Verdú et al., 2000). Despite these broad findings, there remain many mixed and contradictory results, as neuroscientists seek to understand how diverse markers of brain structure and function shift and relate to each other in multidimensional ways, be they markers of structural integrity and connectivity, functional activity and connectivity, amyloid deposition, glucose metabolism, or neuroinflammation.

Finally, it remains unclear how peripheral nervous system aging interacts with central nervous system aging, and what implications these together may hold for affective aging. We interpret some of our findings as potential evidence for shifts in the neural representation of visceral and interoceptive processing, but ultimately,

future research must measure and examine these relations between central and peripheral aging. Bridging measures of the aging brain and body will further clarify how health and disease in later life may mitigate vs. accelerate affective aging, and in turn, how affective aging could itself drive late life health and disease. In the future, an affective neuroscience of aging should account for both within- and between-system changes in the periphery and brain, bringing us one step closer to understanding how the aging nervous system interfaces with affective aging.

4.3. Conclusions

Our meta-analysis revealed reliable differences in neural activation and coactivation between younger and older adults during affect. Meta-analytic findings were consistent with multiple theories of affective aging and do not provide evidence in clear favor for one model over other models. This may be in part because affective aging is a heterogeneous process, driven by multiple temporal, situational, and individual factors. Future experimental neuroimaging work should explicitly articulate and falsify hypotheses associated with each model of affective aging and rule out alternative interpretations that may be confounded with observed effects. For example, does greater prefrontal activity in late life during affect reflect structural declines in these regions, increased cognitive effort during in-scanner tasks, improved regulation strategies, greater reliance on semantic knowledge and accumulated predictions, or compensation for structural and functional age-related changes happening elsewhere in the brain? This meta-analysis cannot adjudicate between these possible mechanisms. Instead, careful study design and experimentation are needed in future work. In the meantime, these findings begin to pinpoint specific neuronal patterns of affective aging across the healthy adult lifespan and shore up behavioral findings demonstrating that even processes as basic as affective experience and perception do not remain stable across adulthood.

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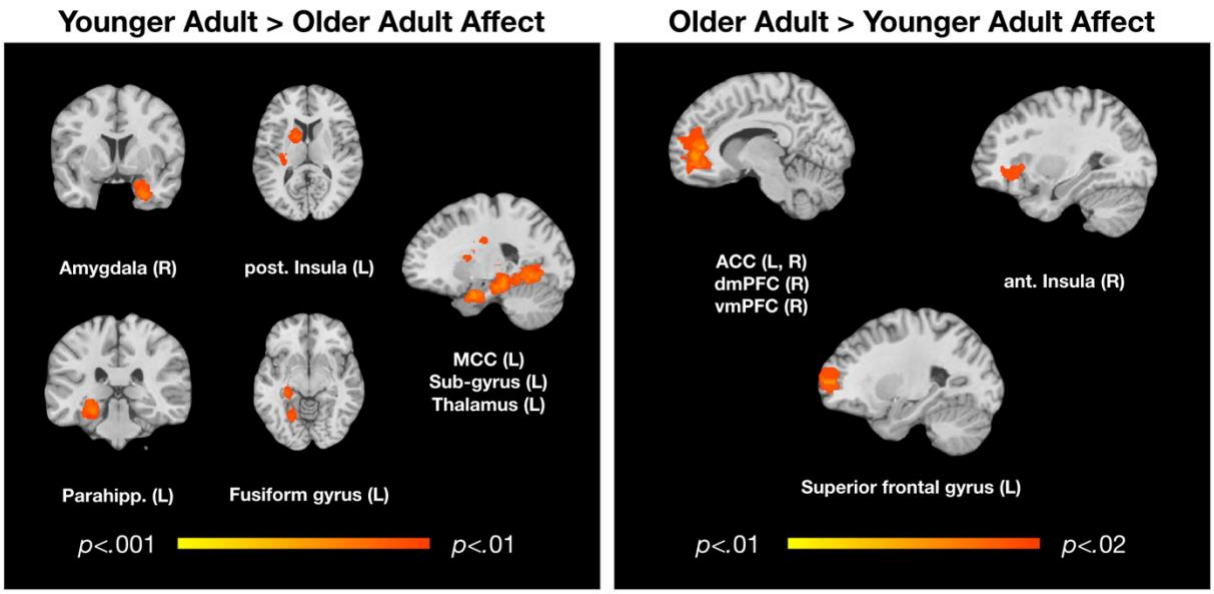

Figure 1. Regions of significant, reliable functional activations differing by age across affect. *P*-values represent thresholds with FWE-corrections for multiple comparisons.

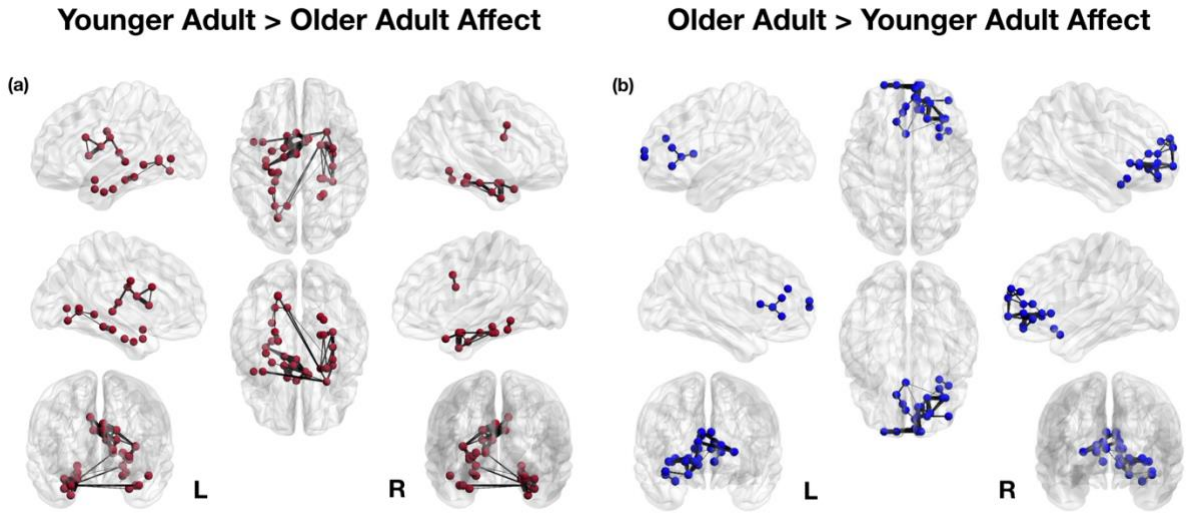

Figure 2. Meta-analytic coactivation of older and younger adult brain regions during affect, corrected for false discovery rate.

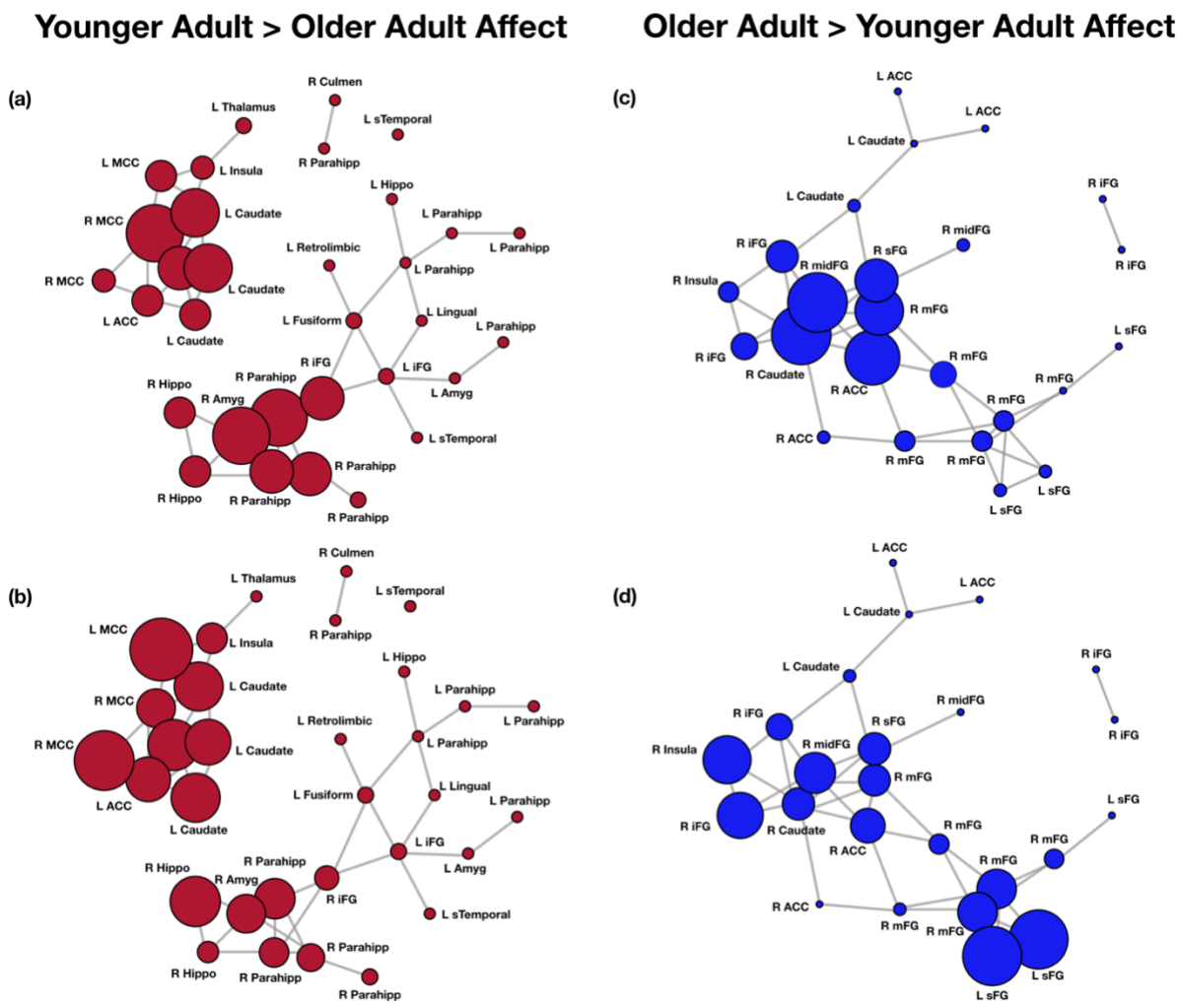

Figure 3. Network depictions of meta-analytic regions varying by centrality and efficiency in older vs. younger adult brains during affect. (a) Eigenvector centrality for YA>OA affect, with greater centrality in the right and left mid-cingulate cortex (MCC), left caudate, right amygdala (amyg), and parts of right parahippocampus (parahipp). (b) Local efficiency for YA>OA affect, with greater efficiency in the right and left mid-cingulate cortex (MCC), left caudate and insula, right amygdala (amyg), and parts of right hippocampus and parahippocampus (hippo; parahipp). (c) Eigenvector centrality for OA>YA affect, with greater centrality revealed for right caudate, mid-frontal gyrus (midFG), medial frontal gyrus (mFG), and right anterior cingulate (ACC). (d) Local efficiency for OA>YA affect, with greater efficiency in right anterior insula, inferior, medial, and mid-frontal gyrus (iFG, mFG, midFG), as well as left superior frontal gyrus (sFG).

Table 1. Summary of included studies in the final meta-analytic database.

Study	Older Adult N (#female), M_{age}	Younger Adult N (#female), M_{age}	In-Scanner Task Description	Affective Categories
Allard et al. (2014)	30 (20), *68.47 years*	34 (16), *23.79 years*	Passive affect induction and perception task using video clips	positive, negative, neutral
Brassen et al. (2011)	21 (14), *65.80 years*	22 (8), *25.20 years*	Spatial cueing paradigm with affect perception of faces	happy, fearful, sad, neutral
Cassidy et al. (2013)	18 (12), *75.56 years*	19 (11), *24.32 years*	Passively viewed facial expressions	positive, negative, neutral
Dolcos et al. (2014)	16 (11), *68.56 years*	18 (10), *23.61 years*	Affect induction with pictures	high arousal negative, medium arousal negative, low arousal negative, neutral
Ebner et al. (2012)	32 (18), *68.2 years*	30 (16), *25.1 years*	Judged facial expressions	happy, angry, neutral
Everaerd et al. (2017)	25 (0), *66.7 years*	25 (0), *21.5 years*	Movie clip stress induction followed by in-scanner passive viewing facial expressions	happy, fearful
Fischer et al. (2005)	22 (11), *74.1 years*	24 (12), *24.7 years*	Passively viewed facial expressions	angry, neutral
Fischer et al. (2010)	18 (9), *74.3 years*	24 (12), *24.7 years*	Judged facial expressions	fearful, neutral
Gunning-Dixon et al. (2003)	8 (4), *72.3 years*	8 (4), *25.8 years*	Judged facial expressions	happy, sad, angry, fearful, disgusted, neutral
Iidaka et al. (2002)	12 (6), *65.2 years*	12 (6), *25. 1 years*	Judged facial expressions	positive, negative, neutral
Kehoe et al. (2013)	23 (23), *61.0 years*	23 (23), *23.0 years*	Affect induction with pictures; subjects categorized whether things in the pictures were living or non-living	high arousal positive, high arousal neutral, low arousal positive, low arousal neutral
Keightley et al. (2007)	11 (6), *69.6 years*	10 (5), *27.2 years*	Judged facial expressions	angry, contempt, disgusted, fearful, happy, sad, surprised, neutral
Kensinger et al. (2008)	17 (11), *73.3 years*	17 (12), *21.6 years*	Affect induction with pictures; subjects judged the size of objects in pictures	high arousal negative, high arousal positive, neutral
Leclerc et al. (2008)	20 (13), *n/a*	17 (12), *n/a*	Affect induction with pictures; subjects judged the size of objects in pictures	high arousal negative, high arousal positive, neutral
Leclerc et al. (2010): Study 1	18 (10), *72.2 years*	18 (10), *21.5 years*	Affect induction with pictures using a visual search task	high arousal negative, high arousal positive, neutral

Leclerc et al. (2010): Study 2	24 (14), *73.7 years*	24 (9), *23.9 years*	Affect induction with pictures; subjects judged whether objects were animate or common objects	high arousal negative, high arousal positive, neutral
Leclerc et al. (2011)	19 (11), *71.7 years*	20 (10), *23.4 years*	Affect induction with pictures and words while judging whether objects were animate or common objects	high arousal negative, high arousal positive, neutral
Murty et al. (2009)	30 (14), *61.2 years*	30 (14), *25.6 years*	Affect induction with pictures while judging whether picture was indoors or outdoors	"aversive" (high arousal negative), neutral
Paradiso et al. (1997)	8 (6), *62.6 years*		Affect induction with film clips	happy, fearful, "fear-disgust," neutral
Paradiso et al. (2003)	17 (8), *65.0 years*		Affect induction and perception with pictures and facial expressions	happy, sad, neutral
Ritchey et al. (2011)	15 (7), *66.7 years*	19 (10), *23.2 years*	Affect induction with pictures	high arousal positive, high arousal negative, low arousal neutral
Roalf et al. (2011)	22 (13), *72.5 years*	14 (7), *25.2 years*	Affect induction with passive viewing of pictures	high arousal negative, high arousal positive, low arousal neutral
St. Jacques et al. (2009) *	15 (15), *70.2 years*	15 (15), *24.8 years*	Affect induction with pictures	positive, negative, neutral
St. Jacques et al. (2010) *	15 (15), *70.2 years*	15 (15), *24.8 years*	Affect induction with pictures	positive, negative, neutral
Tessitore et al. (2005)	14 (7), *67.0 years*	12 (6), *25.0 years*	Judged facial expressions	fearful, angry, control (a shape)
Wright et al. (2006)	18 (12), *71.6 years*	18 (12), *24.0 years*	Passively viewed facial expressions	fearful, neutral
Zsoldos et al. (2016)	17 (8), *68.6 years*	17 (11), *24.9 years*	Judged facial expressions	fearful, neutral

* Note that St. Jacques et al. (2009) and St. Jacques et al. (2010) are likely from the same study and sample but report different analyses and contrasts, and thus are both retained in the database. However, we only included the St. Jacques papers once in sample size and demographic counts so as to avoid overestimating the number of unique individuals in the meta-analytic database.

Table 2. Study and between-age contrast characteristics within the meta-analytic database.

Characteristic	# Studies	OA>YA # Contrasts	YA>OA # Contrasts
Affective Process			
Experience	15	23	29
Perception	10	7	11
Both	2	1	1
Affective Stimuli			
Facial expressions	12	9	12
Affective images	13	21	27
Film clips	1	1	0
Words	1	0	2
Affective Task			
Emotion judgment	15	16	23
Passive viewing	6	10	9
Likert rating	6	5	9

Table 3. Coordinates for younger > older adult affect, k-threshold of *p*<.01, FWE-corrected for multiple comparisons.

Region	*BA*	*x*	*y*	*z*	*k*	*max*	*mean*
R Amygdala (cluster)		**29**	**0**	**-25**	**420**	**.21**	**.13**
R Amygdala		29	0	-25		.21	.15
R Hippocampus		34	-8	-19		.18	.14
R Parahippocampal Gyrus	34	22	0	-11		.18	.14
R Parahippocampal Gyrus	36	23	-30	-12		.15	.12
R Inferior Frontal Gyrus	13	35	6	-13		.15	.13
R Culmen		24	-44	-11		.14	.11
R Parahippocampal Gyrus	35	20	-30	-7		.14	.11
R Hippocampus		33	-20	-11		.14	.12
R Inferior Frontal Gyrus	47	30	14	-20		.13	.12
R Parahippocampal Gyrus	36	33	-33	-13		.11	.11
R Parahippocampal Gyrus	19	21	-48	-4		.11	.11
L Parahippocampal Gyrus (cluster)	**27**	**-23**	**-31**	**-8**	**745**	**.21**	**.13**
L Parahippocampal Gyrus	27	-23	-31	-8		.21	.14
L Amygdala		-27	-4	-20		.20	.14
L Parahippocampal Gyrus	28	-20	-23	-9		.19	.14
L Parahippocampal Gyrus	18	-25	-57	3		.18	.14
L Fusiform Gyrus	19	-22	-66	-4		.18	.13
L Superior Temporal Gyrus	38	-37	5	-18		.15	.12
L Hippocampus		-33	-12	-17		.15	.12
L Superior Temporal Gyrus	38	-46	4	-10		.15	.13
L Posterior Insula	13	-34	-19	12		.14	.11
L Agranular Retrolimbic Area	30	-23	-70	6		.13	.11
L Hippocampus		-27	-41	1		.13	.12
L Lingual Gyrus	18	-12	-57	6		.11	.11
L Thalamus		-27	-24	4		.11	.11
R Mid-Cingulate (cluster)	**24**	**7**	**5**	**23**	**396**	**.19**	**.12**
R Mid-Cingulate	24	7	5	23		.19	.13
L Caudate Body		-16	9	23		.18	.12
L Caudate Body		-16	8	17		.16	.12
L Anterior Mid-Cingulate	24	-4	15	23		.14	.12
L Mid-Cingulate	24	-3	-6	28		.15	.12
L Caudate		-6	8	16		.13	.12
L Caudate		-13	11	9		.12	.12
R Mid-Cingulate	24	10	8	33		.11	.10

Notes. *BA* = Brodmann Area; *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm_3; *max* = maximum value within cluster; *mean* = average value within cluster. L = left, R = right.

Table 4. Coordinates for older > younger adult affect, k-threshold of *p*<.02, FWE-corrected for multiple comparisons.

Region	*BA*	*x*	*y*	*z*	*k*	*max*	*mean*
R Anterior Cingulate (cluster)	**32**	**11**	**46**	**-1**	**1149**	**.16**	**.10**
R Anterior Cingulate	32	11	46	-1		.16	.11
R Anterior Cingulate	32	14	39	9		.16	.11
L Superior Frontal Gyrus	10	-29	60	5		.16	.11
L Caudate Body		-13	27	8		.15	.10
R Medial Frontal Gyrus	10	11	47	7		.15	.10
R Middle Frontal Gyrus	10	25	43	-2		.13	.11
R Caudate Head		20	29	2		.13	.10
R Superior Frontal Gyrus	11	21	44	-14		.13	.10
R Medial Frontal Gyrus	10	10	38	-6		.13	.10
L Superior Frontal Gyrus	10	-15	60	9		.12	.10
L Medial Frontal Gyrus	9	-4	42	22		.12	.10
L Anterior Cingulate	32	-7	36	14		.12	.09
R Anterior Insula	13	33	18	5		.12	.09
L Caudate Body		-3	14	11		.12	.09
R Medial Frontal Gyrus	9	8	49	18		.12	.09
L Anterior Cingulate	32	-7	35	-2		.12	.09
R Inferior Frontal Gyrus	47	40	26	1		.09	.09
R Inferior Frontal Gyrus	47	38	35	0		.09	.09
R Medial Frontal Gyrus	10	15	60	-5		.09	.09
R Medial Frontal Gyrus	10	12	60	12		.09	.09
R Medial Frontal Gyrus	10	8	57	20		.09	.09

Notes. *BA* = Brodmann area; *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm^3; *max* = maximum value within cluster; *mean* = average value within cluster. L = left, R = right.

Table 5. Coordinates for younger > older adult negative and high arousal affect, k-threshold of *p*<.01 and .02, FWE-corrected for multiple comparisons.

Region	*BA*	*x*	*y*	*z*	*k*	*max*	*mean*
Negative Affect							
L Amygdala (cluster)		**-18**	**-5**	**-16**	**388**	**.29**	**.21**
L Amygdala		-18	-5	-16		.29	.23
L Parahippocampal Gyrus	28	-20	-28	-10		.26	.21
L Hippocampus		-33	-12	-17		.26	.18
L Parahippocampal Gyrus	27	-27	-29	-3		.26	.19
L Parahippocampal Gyrus	35	-20	-21	-9		.21	.21
L Sublobar Laternal Geniculum Body		-24	-21	-2		.16	.16
High Arousal Affect							
R Mid-Cingulate (cluster)	**24**	**3**	**-3**	**27**	**467**	**.25**	**.18**
R Mid-Cingulate	24	3	-3	27		.25	.18
R Mid-Cingulate	24	7	5	23		.25	.18
L Mid-Cingulate	24	-7	0	28		.25	.18
L Caudate Body		-16	-9	23		.25	.20
L Caudate Body		-13	11	14		.20	.17
L Anterior Mid-Cingulate	33	-3	18	16		.20	.16
L Posterior Cingulate	23	-3	-11	33		.20	.17
L Thalamus		-22	-15	16		.20	.15
L Caudate Body		-16	2	21		.15	.15
R Mid-Cingulate	24	10	0	39		.15	.15
R Medial Frontal Gyrus (cluster)	**10**	**15**	**54**	**1**	**477**	**.25**	**.15**
R Medial Frontal Gyrus	10	15	54	1		.25	.17
R Anterior Cingulate	24	4	38	3		.25	.18
R Medial Frontal Gyrus	10	4	57	9		.20	.17
R Medial Frontal Gyrus	9	8	42	14		.20	.15
L Anterior Cingulate	32	-8	39	14		.20	.17
R Anterior Cingulate		0	47	1		.20	.16
L Medial Frontal Gyrus	9	-4	44	24		.19	.16
R Medial Frontal Gyrus	10	19	62	-7		.15	.15
R Medial Frontal Gyrus	9	12	47	21		.15	.15
R Medial Frontal Gyrus	10	8	60	17		.15	.15
R Medial Frontal Gyrus	10	18	41	9		.15	.15

Notes. *BA* = Brodmann Area; *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm_3; *max* = maximum value within cluster; *mean* = average value within cluster. L = left, R = right. Nothing was significant for YA>OA Positive Affect at *p*<.01, .02, or .05. There were insufficient contrasts to examine YA>OA Low Arousal Affect.

Table 6. Coordinates for older > younger adult negative and high arousal affect, k-threshold of *p*<.01, FWE-corrected for multiple comparisons.

Region	*BA*	*x*	*y*	*z*	*k*	*max*	*mean*
Negative Affect							
R Anterior Cingulate (cluster)	**32**	**14**	**39**	**9**	**435**	**.23**	**.15**
R Anterior Cingulate	32	14	39	9		.23	.14
R Medial Frontal Gyrus	9	19	41	23		.21	.14
R Superior Frontal Gyrus	9	15	41	36		.21	.15
R Middle Frontal Gyrus	11	20	37	-1		.16	.16
R Middle Frontal Gyrus	9	35	45	36		.15	.15
High Arousal Affect							
R Middle Frontal Gyrus (cluster)	**10**	**25**	**43**	**-2**	**561**	**.23**	**.15**
R Middle Frontal Gyrus	10	25	43	-2		.23	.17
R Anterior Cingulate	32	15	46	-1		.23	.17
R Caudate Head		20	29	2		.23	.15
R Inferior Frontal Gyrus	13	32	9	-13		.16	.13
R Medial Frontal Gyrus	10	15	51	-10		.16	.16
R Inferior Frontal Gyrus	47	40	26	1		.16	.16
R Inferior Frontal Gyrus	47	38	35	0		.16	.16
R Medial Frontal Gyrus	10	19	47	11		.16	.16
R Inferior Frontal Gyrus	47	42	14	-8		.12	.12

Notes. *BA* = Brodmann Area; *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm^3; *max* = maximum value within cluster; *mean* = average value within cluster. L = left, R = right. There were insufficient contrasts to examine OA>YA Positive Affect and Low Arousal Affect.

Supplementary Materials for MacCormack, J. K., Stein, A. G., Kang, J., Giovanello, K. S., Satpute, A. B., & Lindquist, K. A. (2020). Affect in the aging brain: A neuroimaging meta-analysis of older vs. younger adult affective experience and perception. *Affective Science.*

In these supplementary materials, we provide more thorough and extensive information about additional and secondary analyses that support and complement the primary findings presented in the main text. We report these supplementary findings in hopes that these additional details will prove useful for future neuroimaging studies on affective aging. Below are listed the tables provided herein. Note that OA=Older Adult, YA=Younger Adult.

Figure S1. PRISMA diagram. This PRISMA diagram summarizes the literature search and study screening, eligibility, and inclusion process.

Table S1. Descriptive summary of cognitive assessments. This table summarizes how different studies assessed and ensured that older adult participants did not have significant cognitive declines that could impair or confound their performance on in-scanner affect tasks.

Table S2. Overall neural reference space for affect across age. We report the regions that are more reliably activated during affect for contrasts [OA>YA]+[OA>OA]+[YA>OA]+[YA>YA].

Tables S3-S4. Meta-analytic contrasts. Here, we report findings for [OA>YA]>[YA>OA] and [YA>OA]> [OA>YA] meta-analytic contrasts. The motivation for these additional analyses was to determine the specificity of contrast effects observed by subtracting out anything due to chance within each age group. Although less straightforward to interpret than the simpler YA>OA and OA>YA contrasts (as presented in the main text), these secondary analyses allowed us to combine all YA>OA and OA>YA contrasts and provide more power to provisionally examine contrast effects.

Tables S5-S6. Age differences in functional activation for affective experience and perception. We report neural differences for age differences in affective experiences and affective perception.

Table S7. Exploratory analyses of positive affect. Given much emphasis on the positivity effect in the affective aging literature, we conducted exploratory analyses on positive affect. We first conducted an exploratory analysis of OA > YA adult functional brain activation during positive > neutral and positive > negative affect tasks (k-threshold corrected), but results should be interpreted with caution given that these findings are based on few contrasts (8/72 between-age contrasts). There were no significant clusters of activation for YA > OA adult positive affect. It is also possible that the positivity effect found in older adults may not just apply to between-age differences (e.g., older adults experience greater positive affect than younger adults) but could also encompass within-age differences (e.g., older adults experience greater positive affect relative to neutral or negative affect). As such, we also present within-age older adult positive affect findings (OA>OA), but again caution that findings should be taken as preliminary (10/92 within-age contrasts).

Tables S8-S9. Functional coactivation correlations. We present the full correlations for regions of functional coactivation, corrected for multiple comparisons.

Tables S10-S11. Supplementary graph theory metrics for OA>YA and YA>OA regions of functional connectivity across affect. These tables detail the full set of values for the network statistics of eigenvector centrality, betweenness centrality, and local efficiency that are also reported in the main text.

Figure S1. PRISMA diagram summarizing the literature search and study screening, eligibility, and inclusion process. Note there were 26 articles but 27 studies in total (as one paper contained two independent studies).

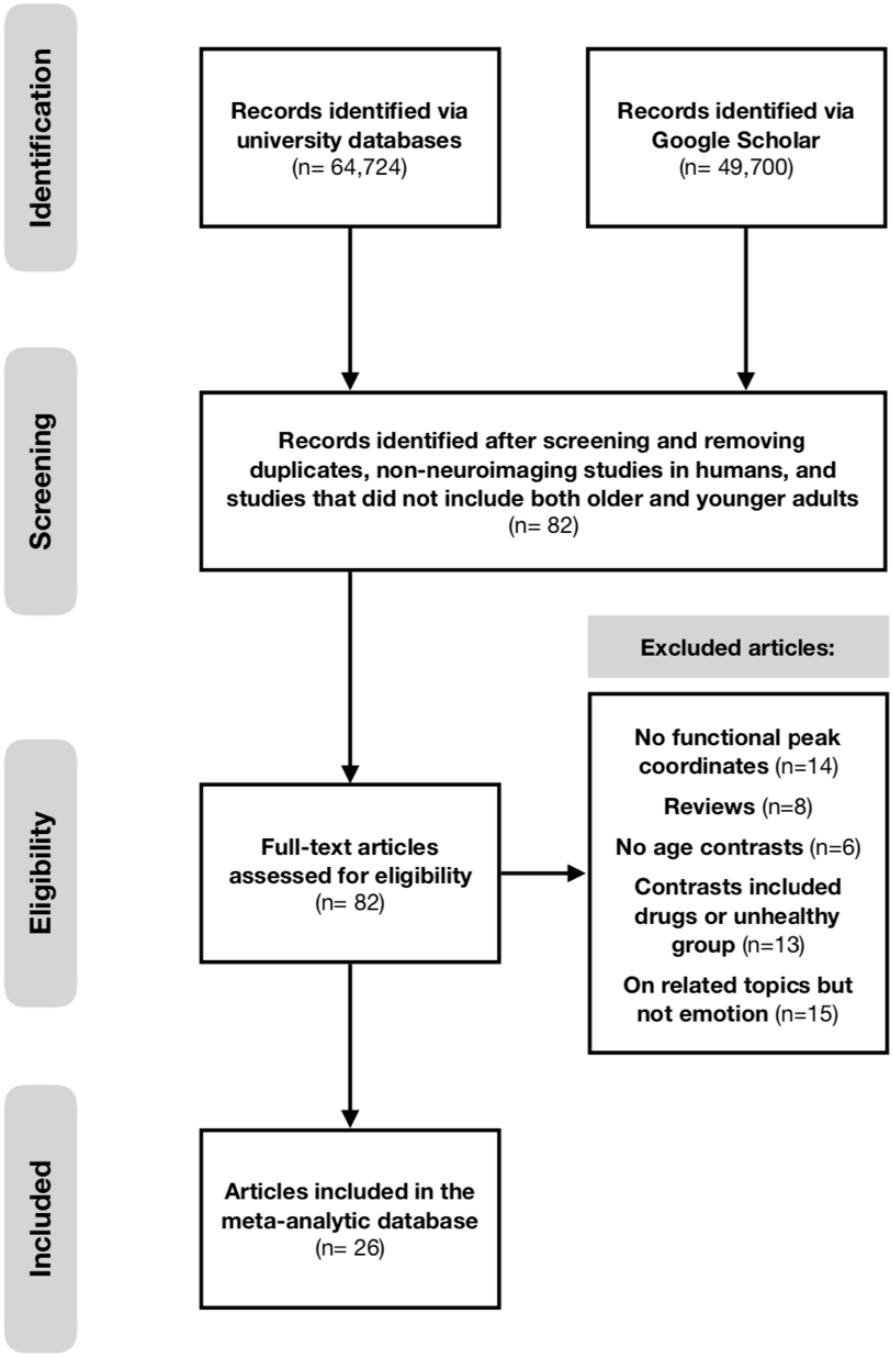

Table S1. Cognitive testing and screening conducted with older adults in meta-analytic database studies.

Study	Cognitive Processes	Cognitive Assessments
Allard et al. (2014)	• Verbal intelligence • Verbal fluency • Working memory • Cognitive reasoning	• Shipley Institute of Living Scale • Wisconsin Card Sorting Test • Controlled Oral Word Association Test (FAS) • Wechsler Adult Intelligence Scale (WAIS-III) – mental arithmetic subtest • Wechsler Memory Scale (WMS-III) – mental control subtest & backward digit span subtest
Brassen et al. (2011)	• Subclinical dementia and mild cognitive impairments • Verbal fluency • Verbal intelligence • Executive function	• Mini-Mental State Examination • Boston Naming Test • CERAD Verbal Fluency Task • CERAD Word List Learning, Recall, and Recognition Tasks • CERAD Constructional Praxis Task and Recall Task • Multiple-Choice Vocabulary Test, Version B
Cassidy et al. (2013)	• Subclinical dementia and mild cognitive impairments • Verbal fluency • Verbal intelligence • Processing speed • Working memory	• Mini-Mental State Examination • Shipley Institute of Living Scale – vocabulary subtest • Digit-Comparison Task • Wechsler Memory Scale – letter-number sequencing subtest
Dolcos et al. (2014)	• Cognitive impairments	• "A number of questionnaires and cognitive measures were used for inclusion/exclusion purposes" – although not specified which ones
Ebner et al. (2012)	• Subclinical dementia and mild cognitive impairments • Verbal fluency • Verbal intelligence • Processing speed • Episodic memory • Working memory	• Mini-Mental State Examination • Verbal Fluency Task • Synonyms Reasoning Blocks: 1 • Letter Comparison Task • Free Word Recall Task • 2-Back Digits Task
Everaerd et al. (2017)	• Cognitive impairments	• Cognitive screening conducted by a physician
Fischer et al. (2005)	• Subclinical dementia and mild cognitive impairments	• Mini-Mental State Examination

Study (Continued)	Cognitive Processes (Continued)	Cognitive Assessments (Continued)
Fischer et al. (2010)	• Subclinical dementia and mild cognitive impairments • Memory capacity	• Mini-Mental State Examination • Synonyms Reasoning Blocks: 1 • Experimental memory task
Gunning-Dixon et al. (2003)	• None mentioned	• None mentioned
Iidaka et al. (2002)	• Subclinical dementia and mild cognitive impairments • Verbal and visual memory	• Trail Making Test: Part A • Digit Symbol Test • Wechsler Memory Scale: verbal paired associates, word recall, figure recall subtests
Kehoe et al. (2013)	• Subclinical dementia and mild cognitive impairments • Verbal fluency • Verbal intelligence • Executive function	• Mini-Mental State Examination • Boston Naming Test • CERAD Verbal Fluency Task • CERAD Word List Learning, Recall, and Recognition Tasks • CERAD Constructional Praxis Task and Recall Task • National Adult Reading Test
Keightley et al. (2007)	• Subclinical dementia and mild cognitive impairments • Verbal fluency	• Mini-Mental State Examination • Vocabulary Test
Kensinger et al. (2008)	• Subclinical dementia and mild cognitive impairments • Verbal intelligence • Working memory • Processing speed	• Mini-Mental State Examination • Forward and Backward Digit Span Tasks • Wechsler Adult Intelligence Scale (WAIS-III) – digit/symbol substitution subtest • Wechsler Adult Intelligence Scale (WAIS-III) – vocabulary subtest
Leclerc et al. (2008)	• None mentioned	• None mentioned
Leclerc et al. (2010): Study 1	• Verbal intelligence • Processing speed	• Shipley Institute of Living Scale – vocabulary subtest • Wechsler Adult Intelligence Scale (WAIS-III) – digit/symbol substitution subtest
Leclerc et al. (2010): Study 2	• Verbal intelligence • Verbal fluency • Processing speed • Working memory	• Shipley Institute of Living Scale – vocabulary subtest • Controlled Oral Word Association Test (FAS) • Wechsler Adult Intelligence Scale (WAIS-III) – digit/symbol substation subtest • Wechsler Adult Intelligence Scale (WAIS-III) – backward digit span subtest
Leclerc et al. (2011)	• Subclinical dementia and mild cognitive impairments • Verbal intelligence • Processing speed	• Mini-Mental State Examination • Shipley Institute of Living Scale – vocabulary subtest • Wechsler Adult Intelligence Scale (WAIS-III) – digit/symbol subtest

Study (Continued)	Cognitive Processes (Continued)	Cognitive Assessments (Continued)
Murty et al. (2009)	• Subclinical dementia and mild cognitive impairments • Verbal intelligence • Processing speed • Executive function • Memory function	• Mini-Mental State Examination • Wechsler Adult Intelligence Scale Revised (WAIS-R) • Trail Making Test: Parts A and B • Word Fluency, Category Fluency, and Number/Letter Sequencing Tests • Wechsler Memory Scale-Revised: logical memory immediate and delayed recall subtests
Paradiso et al. (1997)	• Verbal intelligence • Performance intelligence	• Wechsler Adult Intelligence Scale – verbal and performance scales
Paradiso et al. (2003)	• Verbal intelligence • Performance intelligence • Prosopagnosia • Visual discrimination	• Wechsler Adult Intelligence Scale – verbal and performance scales • Benton Facial Recognition Test • Benton Visual Form Discrimination Test
Ritchey et al. (2011)	• Verbal intelligence • Verbal fluency • Working memory • Cognitive reasoning	• Wisconsin Card Sorting Test • Controlled Oral Word Association Test (FAS) • Wechsler Adult Intelligence Scale (WAIS-III) – mental arithmetic subtest • Wechsler Memory Scale (WMS-III) – mental control subtest & backward digit span subtest
Roalf et al. (2011)	• Subclinical dementia and mild cognitive impairments • Verbal intelligence	• Mini-Mental State Examination • Wechsler Adult Intelligence Scale Revised (WAIS-R)
St. Jacques et al. (2009 & 2010)	• None mentioned	• None mentioned
Tessitore et al. (2005)	• None mentioned	• None mentioned
Wright et al. (2006)	• Subclinical dementia and mild cognitive impairments • Verbal intelligence	• Mini-Mental State Examination • Boston Naming Test • National Adult Reading Test
Zsoldos et al. (2016)	• Subclinical dementia and mild cognitive impairments	• Mini-Mental State Examination

Table S2. Overall neural reference space for affect across age, k-threshold corrected at *p*<.01.

Region	*x*	*y*	*z*	*k*
R Parahippocampal Gyrus	**24**	**-3**	**-27**	**2345**
R Parahippocampal Gyrus	24	-3	-27	
R Middle Frontal Gyrus	45	24	21	
R Declive	30	-54	-15	
R Inferior Frontal Gyrus	39	15	24	
R Inferior Frontal Gyrus	36	27	-3	
R Inferior Frontal Gyrus	27	24	-9	
R Fusiform Gyrus	39	-42	-21	
R Precentral Gyrus	45	6	27	
R Parahippocampal Gyrus	21	-39	-9	
R Sub-Gyral	18	30	-6	
R Inferior Occipital Gyrus	24	-87	-9	
R Lingual Gyrus	18	-72	-6	
R Precentral Gyrus	42	18	3	
R Claustrum	33	15	-3	
R Parahippocampal Gyrus	24	-30	-21	
R Claustrum	21	27	3	
R Culmen	30	-48	-27	
R Precentral Gyrus	27	9	24	
R Precentral Gyrus	45	-3	33	
R Fusiform Gyrus	36	-69	-18	
R Lentiform Nucleus	27	-15	-12	
L Parahippocampal Gyrus	**-24**	**-3**	**-24**	**769**
L Parahippocampal Gyrus	-24	-3	-24	
L Fusiform Gyrus	-39	-66	-18	
L Parahippocampal Gyrus	-24	-33	-15	
L Fusiform Gyrus	-36	-57	-12	
L Declive	-27	-60	-12	
L Fusiform Gyrus	-45	-57	-15	
L Parahippocampal Gyrus	-24	-54	-3	
L Parahippocampal Gyrus	-27	-42	-15	
L Lingual Gyrus	-18	-45	-6	
L Thalamus	-21	-27	3	
L Culmen	-18	-45	-15	
L Middle Frontal Gyrus	**-42**	**18**	**24**	**282**
L Middle Frontal Gyrus	-42	18	24	
L Middle Frontal Gyrus	-30	15	21	
L Precentral Gyrus	-39	3	33	

Notes. *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm3; L = left, R = right.

Table S3. Meta-analytic contrasts comparing [younger > older] > [older > younger] for affect, valence, and arousal.

Region	*x*	*y*	*z*	*k*	*p*
Affect Overall					
L Parahippocampal Gyrus	**-27**	**-27**	**-18**	**399**	**<.01**
L Parahippocampal Gyrus	-27	-27	-18		<.01
L Lingual Gyrus	-18	-63	-3		<.01
L Uncus	-18	-3	-33		<.01
L Amygdala	24	-9	-24		<.01
L Caudate	**-12**	**-12**	**30**	**216**	**<.01**
L Caudate	-12	-12	30		<.01
L Caudate	-15	3	12		<.01
L Thalamus	-6	-6	21		<.01
R Mid-Cingulate Gyrus	6	9	27		<.01
R Thalamus	9	-6	18		<.01
Negative Affect					
L Parahippocampal Gyrus	**-27**	**-27**	**-21**	**266**	**<.01**
L Parahippocampal Gyrus	-27	-27	-21		<.01
L Parahippocampal Gyrus	-24	-9	-24		<.01
L Parahippocampal Gyrus	-24	-36	-12		<.01
L Lentiform nucleus	**-15**	**6**	**6**	**279**	**<.01**
L Lentiform nucleus	-15	6	6		<.01
Thalamus	-3	-6	21		<.01
R Parahippocampal Gyrus	**27**	**-3**	**-27**	**191**	**<.01**
R Parahippocampal Gyrus	27	-3	-27		<.01
R Claustrum	27	15	-15		<.01
R Parahippocampal Gyrus	12	0	-21		<.01
Positive Affect					
L Caudate	**-9**	**21**	**6**	**280**	**<.01**
L Caudate	-9	21	6		<.01
R Thalamus	6	-3	21		<.01
High Arousal Affect					
L Lentiform Nucleus	**-15**	**6**	**6**	**258**	**<.01**
L Lentiform Nucleus	-15	6	6		<.01
L Thalamus	-6	-6	21		<.01
L Caudate	-12	-12	30		<.01
Low Arousal Affect					
L Uncus	**-15**	**-3**	**-33**	**983**	**<.05**
L Uncus	-15	-3	-33		<.05
L Superior Temporal Gyrus	-51	12	-18		<.05
L Superior Temporal Gyrus	-33	3	-30		<.05
L Inferior Frontal Gyrus	-45	36	-9		<.05
L Middle Frontal Gyrus	-21	39	-3		<.05
L Inferior Frontal Gyrus	-33	39	-3		<.05
L Parahippocampal Gyrus	-18	0	-21		<.05
L Medial Frontal Gyrus	-9	51	6		<.05
L Inferior Frontal Gyrus	-36	27	-18		<.05
L Inferior Frontal Gyrus	-42	45	-12		<.05
R Culmen	**12**	**-39**	**-18**	**1156**	**<.05**
R Culmen	12	-39	-18		<.05
R Transverse Temporal Gyrus	36	-33	9		<.05

R Parahippocampal Gyrus	27	-51	-9	<.05
R Insula	39	-15	9	<.05
R Superior Temporal Gyrus	51	-12	3	<.05
R Superior Temporal Gyrus	42	-51	15	<.05
L Parahippocampal Gyrus	-27	-48	-9	<.05
L Parahippocampal Gyrus	-21	-39	-12	<.05
R Middle Temporal Gyrus	33	-54	30	<.05
L Culmen	-12	-48	-15	<.05

Notes. *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm^3; L = left, R = right. *P*-values are k-thresholded.

Table S4. Meta-analytic contrasts comparing [older > younger] > [younger > older] for affect, valence, and arousal.

Region	*x*	*y*	*z*	*k*	*p*
Affect Overall					
L Medial Frontal Gyrus	**0**	**57**	**18**	**557**	**<.02**
L Medial Frontal Gyrus	0	57	18		<.02
R Inferior Frontal Gyrus	27	30	-3		<.02
R Anterior Cingulate	12	42	0		<.02
R Medial Frontal Gyrus	9	42	15		<.02
R Claustrum	27	15	-15		<.02
L Anterior Cingulate	-12	36	18		<.02
Negative Affect					
R Superior Frontal Gyrus	**21**	**45**	**36**	**675**	**<.05**
R Superior Frontal Gyrus	21	45	36		<.05
R Medial Frontal Gyrus	9	42	18		<.05
R Anterior Cingulate	12	39	-3		<.05
R Medial Frontal Gyrus	6	47	18		<.05
R Inferior Frontal Gyrus	27	33	0		<.05
R Medial Frontal Gyrus	3	36	39		<.05
Positive Affect					
Nothing significant					
High Arousal Affect					
L Medial Frontal Gyrus	**0**	**57**	**15**	**378**	**<.01**
L Medial Frontal Gyrus	0	57	15		<.01
R Inferior Frontal Gyrus	27	30	-3		<.01
R Anterior Cingulate	12	42	0		<.01
R Claustrum	27	15	-15		<.01
L Medial Frontal Gyrus	-3	45	21		<.01
L Caudate	**-9**	**21**	**6**	**257**	**<.01**
L Caudate	-9	21	6		<.01
R Caudate	9	15	15		<.01
R Cingulate	3	0	21		<.01
L Caudate	-12	3	9		<.01
R Cingulate	6	9	36		<.01
L Thalamus	-9	-15	15		<.01
Low Arousal Affect					
L Anterior Cingulate	**-12**	**36**	**18**	**333**	**<.02**
L Anterior Cingulate	-12	36	18		<.02
L Inferior Frontal Gyrus	-15	30	-3		<.02
L Middle Frontal Gyrus	-24	39	33		<.02
L Anterior Cingulate	-9	45	0		<.02

Notes. *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm^3; L = left, R = right. No regions were significant for positive affect at any threshold. *P*-values are k-thresholded.

Table S5. Exploratory analyses of older adult positive affect, k-threshold corrected.

Region	*x*	*y*	*z*	*k*	*p*
Between-Age Older Adult Positive Affect (OA>YA)					
L Caudate Head (cluster)	**-10**	**23**	**5**	**5093**	**<.02**
L Caudate Head	-10	23	5		<.02
L Anterior Cingulate	-7	36	14		<.02
L Posterior Cingulate	-3	-41	17		<.02
L Putamen	-25	-2	-7		<.02
L Medial Frontal Gyrus	-4	42	25		<.02
R Superior Frontal Gyrus	19	52	2		<.02
R Medial Frontal Gyrus	19	60	-7		<.02
R Postcentral Gyrus	28	-29	33		<.02
R Caudate Tail	25	-38	22		<.02
R Thalamus (Pulvinar)	9	-32	17		<.02
R Caudate Body	13	2	23		<.02
R Posterior Cingulate	3	-43	24		<.02
L Cingulate Gyrus	0	-43	32		<.02
L Anterior Cingulate	-3	18	16		<.02
R Anterior Cingulate	3	24	10		<.02
R Anterior Cingulate	4	29	-1		<.02
R Insula	40	-43	18		<.02
R Caudate Body	22	-8	19		<.02
R Medial Frontal Gyrus	19	49	13		<.02
R Paracentral Lobule	10	-30	41		<.02
R Medial Frontal Gyrus	12	47	21		<.02
R Superior Frontal Gyrus	12	57	17		<.02
L Thalamus	-18	-23	5		<.02
Within-Age Older Adult Positive Affect (OA>OA)					
L Medial Temporal Gyrus	**-51**	**-42**	**9**	**744**	**<.05**
L Medial Temporal Gyrus	-51	-42	9		<.05
L Medial Temporal Gyrus	-51	-33	3		<.05
L Medial Temporal Gyrus	-57	-48	0		<.05
L Medial Temporal Gyrus	-42	-68	21		<.05
L Medial Temporal Gyrus	-36	-72	18		<.05
L Superior Temporal Gyrus	-48	-33	12		<.05

Notes. *BA* = Brodmann Area; *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm^3; L = left, R = right. *P*-values are k-thresholded. The within-age analysis includes any within-age (OA>OA) study-level contrasts where positive affect was the target. We also examined a meta-analytic contrast of [OAOA Positive Affect > (OAOA Negative Affect + OAOA Neutral Affect)] but there were no regions of activation that survived k-threshold correction.

Table S6. Coordinates for younger > older adult affective experience and perception, k-threshold corrected at *p*<.01.

Region	*BA*	*x*	*y*	*z*	*k*
Affective Experience					
L Parahippocampal Gyrus (cluster)	**27**	**-23**	**-31**	**-8**	**683**
L Parahippocampal Gyrus	27	-23	-31	-8	
L Parahippocampal Gyrus	18	-25	-57	3	
L Hippocampus		-27	-32	-1	
L Parahippocampal Gyrus	28	-20	-23	-9	
L Fusiform Gyrus	19	-22	-66	-4	
L Amygdala		-27	-4	-17	
L Superior Temporal Gyrus	38	-37	5	-18	
L Hippocampus		-33	-12	-17	
L Superior Temporal Gyrus	38	-46	4	-10	
L Insula	13	-34	-19	12	
L Posterior Cingulate	30	-23	-70	6	
L Hippocampus		-27	-41	1	
L Lingual Gyrus	18	-12	-57	6	
L Thalamus		-27	-24	4	
L Putamen		-25	4	-5	
L Insula	13	-31	-13	17	
L Caudate Body (cluster)		**-16**	**-9**	**23**	**361**
L Caudate Body		-16	-9	23	
R Cingulate Gyrus	24	7	5	23	
L Caudate Body		-16	8	17	
L Cingulate Gyrus	24	-3	-6	28	
L Caudate Body		-6	8	16	
L Anterior Cingulate	33	-3	18	16	
L Caudate Body		-13	11	9	
L Anterior Cingulate	24	-4	15	23	
Affective Perception					
R Parahippocampal Gyrus (cluster)	**35**	**20**	**-30**	**-7**	**570**
R Parahippocampal Gyrus	35	20	-30	-7	
R Lingual Gyrus	19	22	-62	1	
R Parahippocampal Gyrus	19	21	-48	-4	

Notes. *BA* = Brodmann Area; *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm^3; L = left, R = right.

Table S7. Coordinates for older > younger adult affective perception, k-threshold corrected at *p*<.05.

Region	*BA*	*x*	*y*	*z*	*k*
Affective Perception					
R Medial Frontal Gyrus (cluster)	**10**	**18**	**44**	**5**	**2134**
R Medial Frontal Gyrus	10	18	44	5	
R Middle Frontal Gyrus	9	35	45	36	
R Superior Frontal Gyrus	10	26	44	20	
R Middle Frontal Gyrus	11	28	37	-1	
L Medial Frontal Gyrus	9	-4	42	25	
R Middle Frontal Gyrus	8	41	37	44	
R Middle Frontal Gyrus	10	23	57	18	

Notes. *BA* = Brodmann Area; *x, y, z* = coordinates in Montreal Neurological Institute (MNI) space; *k* = cluster size in mm^3; L = left, R = right. Nothing was significant for OA>YA Affective Experience at *p*<.01, .02, or .05.

Table S8. Coactivation correlation matrix for younger>older adult affect, FDR-corrected for multiple comparisons.

Region	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. R Amygdala	.49	.80	.49	.49	-.13	.40	.48	.40	.38	-.06	-.05	.23	-.02	.07	.28	.18
2. R Hippocampus		.48	.12	.30	-.05	.17	.62	-.02	.30	.22	.21	-.26	.09	.17	.25	-.05
3. R Parahippocampal			.48	.65	-.05	.35	.42	.17	.50	.02	-.11	.21	-.08	-.02	.09	.12
4. R Parahippocampal				.30	.30	.73	.42	-.02	.72	.02	.05	.37	.09	.17	.09	-.05
5. R Inferior Frontal					-.05	.17	.42	.59	.50	.02	.05	.21	.09	.17	.42	.30
6. R Culmen						-.02	.02	-.02	.28	.62	.05	.37	-.08	.35	.09	.12
7. R Parahippocampal							.26	-.19	.32	.05	.10	.10	.13	-.19	-.05	-.02
8. R Hippocampus								.26	.63	-.15	.15	-.03	.18	.26	.18	.02
9. R Inferior Frontal									.09	-.17	.10	.44	.13	.41	.48	.54
10. R Parahippocampal										-.13	.21	.21	.24	.32	.03	.06
11. R Parahippocampal											-.03	.15	-.20	.04	.18	.02
12. L Parahippocampal												-.02	.78	.44	.32	.21
13. L Amygdala													.02	.27	.02	.37
14. L Parahippocampal														.31	.05	.09
15. L Parahippocampal															.48	.35
16. L Fusiform																.25
17. L Superior Temporal																

Note: Table continued on next page. Red indicates $p<.05$ with multiple corrections. Orange indicates $p<.01$ with multiple corrections.

Table S8 (continued). Coactivation correlation matrix for younger>older adult affect, FDR-corrected for multiple comparisons.

Region	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1. R Amygdala	.07	.07	.18	.02	-.06	.12	.12	.02	.18	.02	-.26	-.09	.07	-.06	-.26
2. R Hippocampus	-.21	-.02	-.05	.12	.22	.02	.02	.12	.12	.12	-.21	-.02	.17	.02	-.21
3. R Parahippocampal	-.02	-.02	.30	-.05	.02	.02	.22	-.05	-.05	-.05	-.21	-.02	-.02	.02	-.21
4. R Parahippocampal	.17	-.02	.12	-.05	.22	.22	.22	.12	.12	.12	-.02	-.02	-.02	.22	-.02
5. R Inferior Frontal	.17	-.02	.30	.12	.02	.22	.22	-.05	-.05	.30	-.02	-.02	.17	.22	-.21
6. R Culmen	-.02	.17	-.05	.12	.22	.22	.02	-.05	-.23	-.05	-.02	-.21	-.21	.02	-.02
7. R Parahippocampal	.01	.21	.17	-.02	.04	-.17	.26	-.02	.17	-.02	-.19	.01	.01	.04	-.19
8. R Hippocampus	-.17	-.17	.22	.22	.08	.31	.31	.22	.22	.22	-.17	.05	.26	.08	-.17
9. R Inferior Frontal	.21	.01	.17	.35	-.17	.47	.04	-.02	-.02	.35	.01	-.19	.21	.04	-.19
10. R Parahippocampal	.09	-.15	.28	.06	.37	.37	.37	.28	.06	.28	.09	.09	.09	.37	.09
11. R Parahippocampal	-.17	.26	.18	.02	.09	-.15	-.15	-.18	-.18	-.18	-.17	-.17	-.17	-.15	-.17
12. L Parahippocampal	.10	.10	-.11	.21	.33	.15	-.03	.05	-.11	.21	-.07	-.24	-.07	-.03	-.07
13. L Amygdala	.44	-.07	.05	-.11	-.03	.15	-.03	-.11	-.26	.05	-.07	-.24	-.24	-.03	-.07
14. L Parahippocampal	.31	-.05	-.08	.09	.18	.18	-.01	.09	-.08	.25	-.05	-.22	-.05	.01	-.05
15. L Parahippocampal	.21	.01	-.02	.35	.47	.47	.04	.17	.17	.35	.01	.01	.01	.04	.01
16. L Fusiform	.13	.13	-.08	.42	-.01	.37	-.01	-.08	.09	.25	-.05	-.22	.13	-.01	-.22
17. L Superior Temporal	.17	.35	.30	.30	.02	.22	.22	-.23	-.23	-.05	-.21	-.21	-.21	-.18	-.21
18. L Hippocampus		.21	-.02	-.21	.04	.04	-.17	-.02	-.02	.17	.01	-.19	-.19	.04	.01
19. L Superior Temporal			.35	.17	.04	-.17	.04	-.02	.17	-.02	.01	.01	.01	.04	-.19
20. L Posterior Insula				.12	.02	.02	.62	.47	.47	.30	.17	.54	.35	.22	.17
21. L Agran. Retrolimbic					.16	.42	.22	-.05	-.05	.12	-.02	-.21	.17	.02	-.21
22. L Hippocampus						.08	.08	.22	.22	.22	.04	.26	.04	.31	.04
23. L Lingual							.08	.22	.02	.42	.26	-.17	.26	.31	.04
24. L Thalamus								.22	.22	.22	.04	.26	.26	.08	.04
25. R Mid-Cingulate									.65	.65	.54	.54	.54	.42	.54
26. L Caudate Body										.47	.17	.73	.54	.22	.17
27. L Caudate Body											.54	.35	.73	.62	.17
28. L ant. Mid-Cingulate												.21	.41	.47	.60
29. L Mid-Cingulate													.41	.26	.21
30. L Caudate														.69	.01
31. L Caudate															.04
32. R Mid-Cingulate															

Note: Table continued from previous page. Red indicates $p<.05$ with multiple corrections. Orange indicates $p<.01$ with multiple corrections.

Table S9. Coactivation correlation matrix for older>younger adult affect, corrected for multiple comparisons.

Region	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. R Anterior Cingulate	.43	.26	.02	.59	.75	.61	.75	.89	.07	.07	.07	.20	.34	.20	.07	.13	.44	.74	.44	.23
2. R Anterior Cingulate		.20	.20	.70	.43	.53	.43	.36	.03	.19	.28	.14	.28	.36	.03	.09	.38	.09	.38	.19
3. L Superior Frontal			.02	.37	.02	.07	.02	.20	.87	.27	.07	-.03	.07	.43	.07	.13	.13	.44	.74	.23
4. L Caudate Body				.15	.02	.07	.02	.20	-.20	.07	.61	-.03	.61	.20	.61	.13	.13	.13	.13	.23
5. R Medial Frontal					.37	.47	.37	.50	.23	.30	.23	.30	.23	.50	.23	.06	.33	.33	.60	.16
6. R Middle Frontal						.88	.75	.66	-.20	-.13	.07	.43	.34	-.03	-.20	.13	.74	.44	.13	.23
7. R Caudate Head							.61	.53	-.17	-.07	.12	.53	.41	.03	-.17	.18	.85	.18	.18	.28
8. R Superior Frontal								.66	-.20	-.13	.07	.20	.34	-.03	-.20	.13	.44	.44	.13	.59
9. R Medial Frontal									.03	.00	.28	.14	.53	.14	.28	.09	.38	.66	.38	.19
10. L Superior Frontal										.15	-.17	-.22	-.17	.28	.12	-.15	-.15	.18	.52	-.12
11. L Medial Frontal											.37	-.19	-.07	.57	.15	.00	.00	.25	.50	.10
12. L Anterior Cingulate												.03	.41	.28	.41	.18	.18	.18	.18	.28
13. R Anterior Insula													.28	.14	-.22	.09	.66	.09	.09	.19
14. L Caudate Body														.03	.12	.18	.52	.18	.18	.28
15. R Medial Frontal															.28	.09	.09	.38	.66	.19
16. L Anterior Cingulate																-.15	-.15	.18	.18	-.12
17. R Inferior Frontal																	.25	.25	.25	.35
18. R Inferior Frontal																		.25	.25	.35
19. R Medial Frontal																			.63	.35
20. R Medial Frontal																				.35
21. R Mid Frontal																				

Note: Red indicates $p<.05$ with multiple corrections. Orange indicates $p<.01$ with multiple corrections.

Table S10. Graph theory metrics for the younger > older adult functional network across affect.

Region	*x*	*y*	*z*	*Eigenvector centrality*	*Betweenness centrality*	*Local efficiency*
R Amygdala	29	0	-25	.000	.108	.667
R Hippocampus	34	-8	-19	.000	.002	.833
R Parahippocampal Gyrus	22	0	-11	.000	.006	.733
R Parahippocampal Gyrus	23	-30	-12	.000	.037	.417
R Inferior Frontal Gyrus	35	6	-13	.000	.168	.350
R Culmen	24	-44	-11	.000	.000	.000
R Parahippocampal Gyrus	20	-30	-7	.000	.000	.000
R Hippocampus	33	-20	-11	.000	.000	.333
R Inferior Frontal Gyrus	30	14	-20	.000	.120	.100
R Parahippocampal Gyrus	33	-33	-13	.000	.000	.417
R Parahippocampal Gyrus	21	-48	-4	.000	.000	.000
L Parahippocampal Gyrus	-23	-31	-8	.000	.037	.000
L Amygdala	-27	-4	-20	.000	.037	.000
L Parahippocampal Gyrus	-20	-23	-9	.000	.000	.000
L Parahippocampal Gyrus	-25	-57	3	.000	.103	.000
L Fusiform Gyrus	-22	-66	-4	.000	.105	.167
L Superior Temporal Gyrus	-37	5	-18	.000	.000	.000
L Hippocampus	-33	-12	-17	.000	.000	.000
L Superior Temporal Gyrus	-46	4	-10	.000	.000	.000
L Posterior Insula	-34	-19	12	.232	.017	.500
L Agranular Retrolimbic Area	-23	-70	6	.000	.000	.000
L Hippocampus	-27	-41	1	.000	.000	.000
L Lingual Gyrus	-12	-57	6	.000	.034	.000
L Thalamus	-27	-24	4	.056	.000	.000
R Mid-Cingulate	7	5	23	.479	.032	.635
L Caudate Body	-16	9	23	.397	.006	.800
L Caudate Body	-16	8	17	.421	.004	.800
L Anterior Mid-Cingulate	-4	15	23	.277	.013	.722
L Mid-Cingulate	-3	-6	28	.264	.000	1.000
L Caudate	-6	8	16	.373	.000	.833
L Caudate	-13	11	9	.253	.000	.833
R Mid-Cingulate	10	8	33	.167	.000	1.000

Notes. *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; L = left, R = right.

Table S11. Graph theory metrics for the older > younger adult functional network across affect.

Region	*x*	*y*	*z*	*Eigenvector centrality*	*Betweenness centrality*	*Local efficiency*
R Anterior Cingulate	11	46	-1	.949	.189	.567
R Anterior Cingulate	14	39	9	.217	.000	.000
L Superior Frontal Gyrus	-29	60	5	.169	.000	1.000
L Caudate Body	-13	27	8	.042	.154	.000
R Medial Frontal Gyrus	11	47	7	.315	.189	.167
R Middle Frontal Gyrus	25	43	-2	.996	.000	.767
R Caudate Head	20	29	2	1.000	.162	.536
R Superior Frontal Gyrus	21	44	-14	.792	.079	.600
R Medial Frontal Gyrus	10	38	-6	.869	.277	.567
L Superior Frontal Gyrus	-15	60	9	.137	.000	1.000
L Medial Frontal Gyrus	-4	42	22	.020	.000	.000
L Anterior Cingulate	-7	36	14	.007	.000	.000
R Anterior Insula	33	18	5	.326	.019	.833
L Caudate Body	-3	14	11	.224	.245	.000
R Medial Frontal Gyrus	8	49	18	.124	.079	.333
L Anterior Cingulate	-7	35	-2	.007	.000	.000
R Inferior Frontal Gyrus	40	26	1	.000	.032	.417
R Inferior Frontal Gyrus	38	35	0	.000	.004	.833
R Medial Frontal Gyrus	15	60	-5	.484	.139	.333
R Medial Frontal Gyrus	12	60	12	.314	.133	.700
R Medial/Mid Frontal Gyrus	8	57	20	.136	.000	.000

Notes. *x*, *y*, *z* = coordinates in Montreal Neurological Institute (MNI) space; L = left, R = right.