The Affective Neuroscience of Aging

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Abstract

Although aging is associated with clear declines in physical and cognitive processes, emotional functioning fares relatively well. Consistent with this behavioral profile, two core emotional brain regions, the amygdala and ventromedial prefrontal cortex, show little structural and functional decline in aging, compared with other regions. However, emotional processes depend on interacting systems of neurotransmitters and brain regions that go beyond these structures. This review examines how age-related brain changes influence processes such as attending to and remembering emotional stimuli, regulating emotion, and recognizing emotional expressions, as well as empathy, risk taking, impulsivity, behavior change, and attentional focus.

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INTRODUCTION

Aging is a multifaceted process that involves interacting brain regions and neurotransmitter systems that are not uniformly affected by aging. As should be expected given the variability in vulnerability to aging among brain regions and systems, some everyday abilities decline more than others in normal aging. Emotion is a fascinating domain within the study of aging because emotional functions show less decline in normal aging than many other processes, and in some cases, are as or more effective in older adults than in younger adults. In this article, I first review brain regions and neurotransmitter systems that play important roles in emotion and how these fare in aging. I then review age differences in various emotional tasks and processes and what is known about how they relate to age-related brain changes.

THE FATE OF EMOTION-RELATED BRAIN REGIONS AND MONOAMINERGIC NEUROTRANSMITTER SYSTEMS IN NORMAL AGING

Prefrontal Cortex

In the 1990s, a frontal theory of aging emerged, accounting for older adults' cognitive deficits by the greater decline in prefrontal than in other brain regions in aging (West 1996). But when it came to affect, the prefrontal theory of aging did not make sense. For instance, after a tamping iron destroyed part of the lower middle section of the prefrontal cortex (in the ventromedial prefrontal

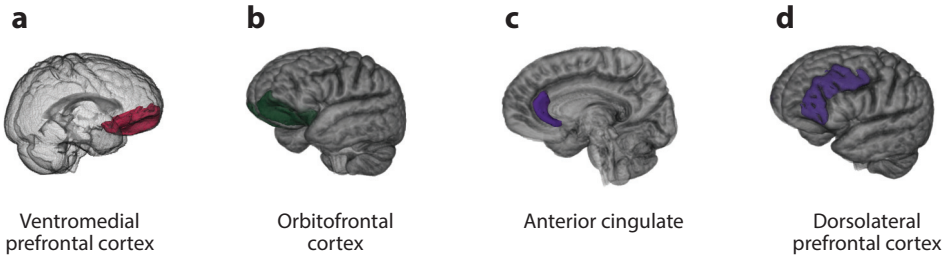

Figure 1

Subdividing the prefrontal cortex is not simple, and boundaries are not always agreed upon. However, in terms of understanding the aging and emotion literature, several subregions are important. (*a*) First, the ventromedial prefrontal cortex (vmPFC) is the medial portion of the prefrontal cortex from the lower half of the prefrontal cortex, demarcated at the genu (or "knee" in Latin) of the corpus callosum. (*b*) The orbitofrontal cortex is the "floor" of the frontal cortex, which is found just above the eye orbits. (*c*) The anterior cingulate cortex is the medial portion of the prefrontal cortex that is adjacent to the corpus callosum. The vmPFC overlaps with the medial part of the orbitofrontal cortex and typically includes the ventral portion of the anterior cingulate (Clark et al. 2008). (*d*) Although the dorsolateral prefrontal region is often defined as the middle frontal gyrus covering the lateral part of Brodmann areas 9 and 46 (e.g., Murray & Ranganath 2007), some studies examining age differences in anatomical volume define it more broadly to include superior, middle, and inferior frontal gyri spanning from the most dorsomedial point of the cortex down to the lateral orbital sulcus (e.g., Lövdén et al. 2013).

cortex or vmPFC; see **Figure 1*a***) of the famous lesion patient Phineas Gage, he lost the ability to control his emotions. Yet despite age-related prefrontal decline, emotional control impairments are not associated with normal aging.

Indeed, a striking contrast exists between the emotional behavior of older adults and that of patients with vmPFC lesions. In many cases, vmPFC damage is associated with impulsive aggression, violence, and anger (Grafman et al. 1996). Older adults, on the other hand, tend to be less prone to outbursts or feelings of anger than younger adults (Birditt & Fingerman 2005, Charles & Carstensen 2008, Phillips et al. 2006), and partner aggression is lower among older than younger adults (O'Leary & Woodin 2005). Another characteristic of vmPFC lesions in patients is the loss of ability to maintain secure attachments (Damasio et al. 1990). In contrast, deficits in attachment processes are not associated with aging—instead, attachment anxiety is lower among older than younger adults (Chopik et al. 2013).

Phillips & Della Sala (1998) were the first to propose that the frontal theory of aging needed to be revised to accommodate such discrepancies. They proposed that dorsolateral prefrontal regions subserving fluid intelligence decline more in normal aging than do orbitofrontal regions associated with emotional contributions to social behavior and decision making (see **Figure 1*b***). They subsequently tested a modified version of their theory with vmPFC as the critical preserved region using a battery of tasks selected to tap either vmPFC or dorsolateral PFC (dlPFC) and found that age-related impairments were significantly more pronounced on the dlPFC tasks (MacPherson et al. 2002).

Subsequent findings that vmPFC declined in volume significantly less than dlPFC supported this hypothesis regarding differential rates of decline. For instance, an analysis aggregating across six different samples with a total of 883 participants found that highly significant negative correlations existed between age and cortical thickness in the superior, middle, and inferior frontal gyri but not in the anterior cingulate cortices or in vmPFC (**Figure 2**; Fjell & Walhovd 2010).

Thus, the pattern of emotion-related findings and the structural data make a compelling case for relatively preserved vmPFC in aging. However, it should be noted that researchers using the

vmPFC: ventromedial prefrontal cortex

dlPFC: dorsolateral prefrontal cortex

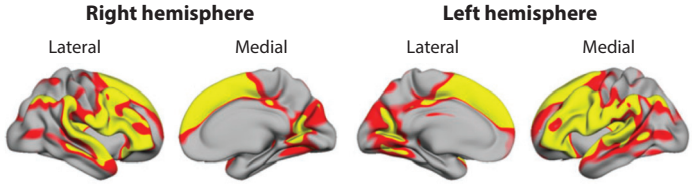

Figure 2

Brain regions shown in yellow are those that exhibited the largest decline in cortical thickness with age across a sample of 883 participants ranging in age from 18 to 94 (Fjell et al. 2009b).

Iowa Gambling Task, delay discounting, or facial emotion recognition as part of task batteries to assess ventromedial-dorsolateral distinctions in aging sometimes concluded that vmPFC functions are also significantly impaired in aging (Baena et al. 2010, Lamar & Resnick 2004). As addressed in later sections, it is problematic to assume that these particular tasks depend on vmPFC.

Amygdala

The amygdala abuts the anterior end of the hippocampus (**Figure 3**) and is a collection of nuclei that have somewhat distinct roles but together play a key role in emotion. In particular, the amygdala helps detect potentially emotionally relevant stimuli—relevant because they are novel, pose a threat, or are goal relevant—and then modulates other brain systems to enhance attention and memory for those stimuli. It is clearly involved in anxiety and fear but also plays a part in positive affect and motivation.

Findings regarding the structural integrity of the amygdala suggest that it is better maintained in aging than are most other regions, although findings are not entirely consistent. In some structural magnetic resonance imaging (MRI) studies, the amygdala shows no significant differences in volume across the adult lifespan, in the context of decline in other structures (Jernigan et al. 2001, Jiang et al. 2014, Li et al. 2014, Shen et al. 2013). A postmortem study also showed no significant decrease in volume with age (Brabec et al. 2010). Some studies reveal age-associated declines in amygdala volume that are less marked than in other brain regions (Good et al. 2001, Grieve et al.

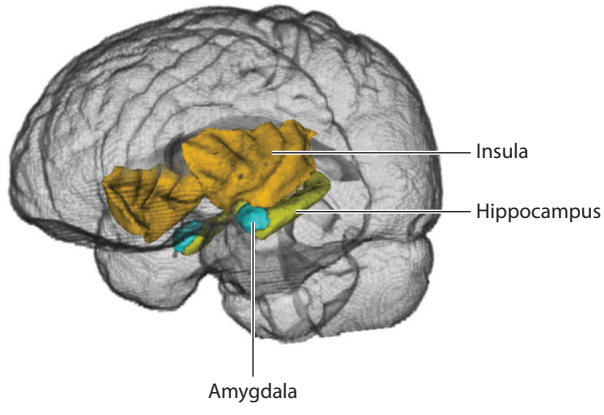

Figure 3

Locations of the left amygdala, hippocampus, and insula; the right amygdala, hippocampus, and insula are shown in the background.

2005, Kalpouzos et al. 2009, Long et al. 2012), whereas others show notable negative associations between amygdala volume and age (Allen et al. 2005b, Curiati et al. 2009, Fjell et al. 2013b, Mu et al. 1999, Walhovd et al. 2005).

There are also conflicting findings among longitudinal studies. Amygdala and hippocampal volumes showed similarly significant declines when assessed using an automated program (FreeSurfer; Fjell et al. 2009a) that held up when those who converted to Alzheimer's disease three to four years later were excluded (Fjell et al. 2013a). In contrast, in two studies using hand tracing, no longitudinal amygdala decline was detected (Cherbuin et al. 2011, Frodl et al. 2008).

Differences across studies may have to do with methods used to assess amygdala volume (e.g., FreeSurfer may not be accurate for the amygdala; Morey et al. 2009) or differences in the people assessed. On balance across the cross-sectional and longitudinal studies, the evidence suggests there is some decline in the amygdala but that it is often less pronounced than that found in other regions such as the hippocampus, a region involved in memory processes adjacent to the amygdala.

One issue to keep in mind is that for the amygdala, bigger is not necessarily better. Greater amygdala volume can be associated with having had stressful experiences (Tottenham et al. 2010), and stressed people show reduced amygdala gray matter density after a stress-reduction program (Hölzel et al. 2009). On the other hand, among both younger and older adults, greater amygdala volume is associated with the size and complexity of one's social network (Bickart et al. 2011).

Furthermore, the intrinsic integrity of a brain region will have little impact without connections to other brain regions. Initial findings regarding the effects of aging on amygdala connectivity are intriguing. Resting-state functional MRI reveals that the functional connectivity density of an amygdala-based network increases with age, in contrast with age-related functional connectivity density decreases in nodes of other networks (such as the default mode network and dorsal attention network; Tomasi & Volkow 2012).

Prefrontal-amygdala functional connectivity may reflect PFC regulation of anxiety and other emotional responses. Among older adults, amygdala connectivity with vmPFC (see **Figure 1**) during processing of emotion stimuli is associated with more positive memories (Sakaki et al. 2013), less negative evaluation of pictures (St. Jacques et al. 2010), and a more normative decline in cortisol over the course of a day (Urry et al. 2006). Thus, for older adults, medial PFC-amygdala functional connectivity during rest seems to be associated with more positive emotions or stress profiles, and thus far, there is no evidence for declines in functional connectivity for the amygdala (instead, the reverse is seen; Tomasi & Volkow 2012).

The role of structural connectivity in older adults' emotional well-being is less clear. Among younger adults, trait anxiety scores have been linked with the structural integrity of the uncinate fasciculus, a white matter tract that connects the amygdala to ventrolateral PFC. Some studies find that better structural integrity predicts lower anxiety, whereas others report the opposite relationship (for a review, see Clewett et al. 2014). The uncinate fasciculus shows decreased white matter intensity in normal aging (Burzynska et al. 2010, Davis et al. 2009). If this plays a causal role in anxiety, one should see increased prevalence of anxiety with age that is not accounted for by other risk factors. This is not the case: In population-based studies, there is no positive association with age and anxiety (Beekman et al. 1998, Schaub & Linden 2000). Consistent with this, in a study that examined the relationship of anxiety to the amygdala-ventral PFC in those aged 19 to 85 (with connectivity assessed for all of ventral PFC rather than just the uncinate fasciculus), better white matter structural integrity of the amygdala-ventral PFC pathway was not associated with lower anxiety either across the whole group or when age was accounted for (Clewett et al. 2014). One interesting possibility is that amygdala-vmPFC structural connectivity may promote negative emotional processing among younger adults but positive emotional processing among older adults (Ford & Kensinger 2014).

Functional neuroimaging indicates that, in older adults, the amygdala still activates robustly to novel salient stimuli, such as novel faces (Wright et al. 2007, 2008). As I review in the later section on age-related positivity effects, other studies have found age-related shifts in the type of emotional stimuli to which the amygdala activates most strongly. In this section, the evidence reviewed indicates that the amygdala shows relatively little decline in structure or function in normal aging.

Insula

The insula is a cortical area found within the sulcus separating the temporal lobe from the parietal and frontal lobes that receives interoceptive sensory information from the internal milieu of the body and helps regulate autonomic nervous system activity. It is involved in many aspects of emotion, including pain sensation, self-related and empathic feelings, and risk and uncertainty processing.

Findings regarding adult age differences in insula volume vary. Cross-sectional studies using manual tracing find a moderate negative association with age that is not always significant (Allen et al. 2005a, Raz et al. 2010). Allen and colleagues argued that findings of more marked insula decline from voxel-based morphometry studies (Good et al. 2001, Tisserand et al. 2004) may result from data-smoothing artifacts at the border of the insula.

There have not been many longitudinal studies of insular volume, but findings from two studies using similar tracing methods differed somewhat. In one study, there was a significant decline between the first and second assessment but not between the second and third assessment (Raz et al. 2010); in the other, the insula showed substantially more shrinkage longitudinally but was also identified as the brain region with the most individual differences in longitudinal change across those studied (Persson et al. 2014). This high degree of individual difference in change may also help explain differences in findings across studies.

Consistent with the structural declines seen in the insula, older adults are less aware of visceral sensations than are younger adults (for a review, see Mather 2012). Older adults are also less vulnerable to pain associated with visceral pathology even though they are more vulnerable to neuropathic pain (Gagliese 2009). Research is needed to test whether there are direct relationships between age-related declines in structure and in sensation.

The insula also serves as the hub in a resting-state network known as the salience network. The salience network responds to behaviorally relevant stimuli and facilitates dynamic interactions among other large-scale networks (Menon & Uddin 2010). Resting-state functional MRI (fMRI) studies reveal age-related declines in functional connectivity within the salience network (He et al. 2014, Meier et al. 2012, Onoda et al. 2012) and between the frontoinsular cortex and other resting-state networks (He et al. 2014).

Thus, in summary, current evidence indicates the insula is a region that shows moderate age-related decline with notable individual differences.

Dopaminergic Influences

To understand emotional processing, it is important to also consider the role of neurotransmitter systems. Two that have critical roles in emotional processing and that have been identified as showing significant age-related changes are dopamine and norepinephrine. These two neurotransmitters have similar structures and interacting effects on cognition. However, they also have distinct roles.

Dopamine has received much attention for its effects on reward processing and is also important for learning, attention, and movement control. Midbrain dopamine neurons typically activate

briefly following unpredicted rewards. This response codes a prediction error, or the difference between obtained and predicted reward value (Schultz 2013). These signals provide powerful tools to support learning about various states, rules, and sequences in the world.

LC: locus coeruleus

Aging affects the dopaminergic system (for a review, see Li & Rieckmann 2014). Dopaminergic neurons and dopamine transporters decrease in density, and positron emission tomography markers of dopamine system function show associations between these declines and executive function among older adults (Bäckman et al. 2010). Genes associated with dopaminergic system function are more strongly associated with individual differences in working memory and executive functions in late than in early life, suggesting that age-related decline in dopamine function makes genetic variation more influential (Colzato et al. 2013, Li et al. 2013, Nagel et al. 2008, Störmer et al. 2012).

Noradrenergic Influences

The locus coeruleus (LC) is a small nucleus in the brainstem that is the primary source of the brain's noradrenaline. Its neurons fire at different rates, depending on whether one is alert or drowsy, and respond rapidly to arousing stimuli, such as loud noises and threatening stimuli. Although the LC is small, its neurons have particularly long axons and so can infuse large regions of the brain with noradrenaline whenever arousal increases.

The literature on age-related structural changes in the LC is mixed. For instance, in one study, postmortem counts of LC neurons decreased 40% across a 60-year period (Vijayashankar & Brody 1979), whereas in another study using different methods, younger and older nondemented adults showed no difference in LC neuron count or size (Mouton et al. 1994). A key factor is that both Alzheimer's and Parkinson's diseases target the LC, and in these disorders, LC damage occurs long before symptoms are marked enough to lead to a diagnosis (e.g., Braak et al. 2011).

Individual differences in both LC structure and noradrenaline levels are associated with cognitive function. In a postmortem study, neuronal density in the LC was more strongly correlated with cognitive decline in the few years right before death than was neuronal integrity in the ventral segmental area, substantial nigra, or dorsal raphe nucleus (Wilson et al. 2013). In vivo, LC integrity (as assessed by structural imaging optimized to show the LC neuromelanin deposits) is correlated with verbal IQ scores (Clewett et al. 2015). In addition, higher levels of cerebrospinal fluid noradrenaline are associated with poorer cognitive performance (Wang et al. 2013).

RELATIONS BETWEEN EMOTIONAL PROCESSING IN AGING AND BRAIN FUNCTION

In the previous sections, I outlined how key brain regions and neurotransmitter systems contributing to emotional functioning fare in normal aging. In the next sections, I turn to the question of how specific aspects of emotional behavior might relate to these age-related changes in the brain.

Positivity Effect

In 2003, we reported an age-by-valence interaction in attention (Mather & Carstensen 2003) and memory (Charles et al. 2003). Relative to younger adults, older adults focused more on positive and less on negative stimuli, a pattern that became known as the age-related positivity effect (Mather & Carstensen 2005). Many subsequent (but not all) studies found similar effects, and a recent meta-analysis of 100 studies indicated that the age-by-valence interaction is a reliable effect in memory and in attention (Reed et al. 2014).

Older adults' positivity effect could help maintain better moods (e.g., Isaacowitz et al. 2009b) and thereby help explain how longitudinal studies show that levels of negative affect tend to decrease whereas positive affect either tends to increase slightly or shows less decrease than negative affect with increasing age, at least until individuals are in their 70s (Carstensen et al. 2011, Charles et al. 2001, Gruenewald et al. 2008). But does the positivity effect actually result from emotion-regulation processes? Or is it just a serendipitous side effect of age-related decline in brain mechanisms (in particular the amygdala) that support noticing and remembering negative, potentially threatening information (Cacioppo et al. 2011)?

As reviewed previously, the amygdala does not show marked decline among healthy older adults, either in structure or function. Furthermore, it is relatively more responsive to positive than negative stimuli in older adults compared with younger adults (Erk et al. 2008, Ge et al. 2014, Kehoe et al. 2013, Leclerc & Kensinger 2011, Mather et al. 2004, Waldinger et al. 2011; but see Moriguchi et al. 2011 for no age-by-valence effects in the amygdala). Thus, the amygdala does not stop responding to emotional stimuli in later life, but instead shifts the valence to which it is most responsive.

Other findings regarding the positivity effect also do not fit an amygdala decline account. The amygdala draws attention to emotionally salient stimuli and helps create more long-lasting memory traces of those stimuli. Like younger adults, older adults show an advantage in noticing and detecting potentially threatening or arousing stimuli (Hahn et al. 2006, Knight et al. 2007, LaBar et al. 2000, Leclerc & Kensinger 2008b, Mather & Knight 2006), suggesting intact amygdala detection functionality. When stimuli are presented in pairs and looking patterns are assessed, the positivity effect in visual attention does not emerge until after the first look or detection of the stimuli, at a point when controlled processes can exert an influence (Isaacowitz et al. 2009a, Knight et al. 2007), suggesting that a key component of the age-related positivity effect is that older adults are more likely to disengage from negative stimuli. Consistent with this, younger adults are significantly slower to disengage from negative than positive distractors, whereas older adults are slightly better at disengaging from negative than positive distractors (Hahn et al. 2006) or no-longer-relevant stimuli (Ashley & Swick 2009).

Also arguing against the amygdala-decline account are findings that the age-by-valence positivity effect interactions in memory and pleasantness ratings are stronger for low- than high-arousal emotional words (Kensinger 2008, Streubel & Kunzmann 2011). Likewise, younger and older adults showed similar amygdala activation in response to high-arousal negative stimuli, but for low-arousal negative stimuli older adults showed decreased amygdala activity compared with younger adults, along with increased activity in the anterior cingulate cortex (Dolcos et al. 2014). Greater anterior cingulate cortex activity was associated with less negative ratings of low-arousal negative pictures for older but not for younger adults (for similar links between vmPFC/anterior cingulate activity and rating intensity, see also Ge et al. 2014). Thus, across studies, older adults' memory, ratings, and amygdala activity resembles that of younger adults more when stimuli arousal is high than when it is low.

The positivity effect modulation by arousal fits with a regulation account of the age difference, as once someone has reacted to a stimulus, emotion regulation tends to be more difficult and less successful for higher-arousal stimuli (Sheppes 2014). Thus, if older adults generally attempt to regulate their responses to emotional stimuli after processing them, the biggest age differences should be seen for those stimuli that offer the highest opportunity for modulation by regulatory strategies: negative or positive stimuli that are not so arousing.

Consistent with a regulatory account, compared with younger adults, older adults tend to show a greater increase in prefrontal activation for emotional than neutral stimuli (for reviews,

see Mather 2012, Nashiro et al. 2012a, St. Jacques et al. 2009). In particular, vmPFC and adjacent anterior cingulate cortex seem to play an especially important role in maintaining older adults' well-being. Greater activity in these regions (in tandem with less activity in the amygdala) during processing negative emotional stimuli has been linked with greater positivity, better emotional stability, and a better diurnal stress profile among older adults (Dolcos et al. 2014, Sakaki et al. 2013, Urry et al. 2006, Williams et al. 2006). Likewise, there are links between well-being and responses in these regions during processing of positive stimuli. During a cueing task, older adults were more distracted than younger adults by task-irrelevant positive faces (but not by sad or fearful faces) and showed greater activity in anterior cingulate in response to the distracting positive faces than did younger adults (Brassen et al. 2011). This anterior cingulate activity was associated with greater emotional stability.

Across studies, it seems clear that activity in these medial frontal cortex regions is associated with age differences in positivity, but it is not as clear when older adults will show greater or less activity than younger adults. Whereas studies using the International Affective Picture System images or emotional faces have found greater medial PFC activation to negative than positive stimuli among older compared with younger adults (Leclerc & Kensinger 2011, Williams et al. 2006), studies using words or object images have found age-related reversals in vmPFC regions in the opposite direction: Older adults show more medial PFC activity during processing positive than negative stimuli and vice versa for younger adults (Leclerc & Kensinger 2008a, 2010, 2011). Medial PFC could be employed both to engage more deeply with positive stimuli (for instance, by relating it to oneself) and to reinterpret or to distract oneself from negative stimuli. Thus, it may vary across stimuli sets (and also depend on orienting instructions) whether the desire to disengage from negative stimuli or to engage with positive stimuli is the stronger driving motivation during the session.

Behavioral studies provide further support for the notion that older adults engage prefrontal resources in order to help increase positivity and/or diminish negativity of attention and memory by showing that higher executive function is associated with higher positivity among older adults but not younger adults (Isaacowitz et al. 2009b, Knight et al. 2007, Mather & Knight 2005, Petrican et al. 2008, Sasse et al. 2014, Simón et al. 2013; but see Foster et al. 2013 for conflicting findings).

Why might older adults be more likely than younger adults to deploy cognitive resources to regulate emotions? Socioemotional selectivity theory posits that everyone has some sense of time left in life and that as time is perceived as more limited, people prioritize emotional goals more (Carstensen et al. 2006), which in turn should lead to more focus on regulating emotion when confronted with emotional stimuli (Kryla-Lighthall & Mather 2009). One prediction from this perspective that has not received support is that one's perceived time left in life should predict the positivity effect (Demeyer & De Raedt 2013, Foster et al. 2013). However, individual differences in depression and optimism likely also influence perceived time left in life and should be associated with a lower positive-to-negative ratio in attention and memory. This opposing correlation could obscure the effects of any concurrent lifespan changes. Thus, manipulations of time perspective provide a cleaner way to examine if there is a relationship between time perspective and the positivity effect. Indeed, studies manipulating time perspective have shown that shifting to a more limited time perspective increases positivity in emotion perception (Kellough & Knight 2012) and memory (S.J. Barber, P.C. Opitz, B. Martins, M. Sakaki, and M. Mather, manuscript in preparation).

In summary, the age-related positivity effect cannot be accounted for by age-related amygdala decline. The effect is often associated with age-related differences in how medial PFC responds to positive versus negative stimuli, which is consistent with a regulatory account.

Emotion Regulation

The aging and emotion regulation literature can be confusing because researchers who focus on everyday outcomes and behaviors portray older adults as being better at regulating emotions, yet in the laboratory, when they are given a structured emotion-regulation task, there is no clear evidence of greater emotion-regulation skill among older adults (for reviews, see Mather 2012, Mather & Ponzio 2015, Silvers et al. 2013). How can we reconcile these different perspectives? First, insofar as older adults focus more on emotional goals, they should allocate more resources to regulate emotions throughout their everyday lives, which should improve emotional outcomes. In other words, older adults may be chronic emotion regulators, whereas younger adults are more sporadic (e.g., Mather & Johnson 2000). Second, different emotion-regulation strategies rely on different brain regions, and older adults may compensate for lateral prefrontal declines by shifts in their go-to or preferred emotion-regulation strategy. Thus, laboratory-based experiments may fail to capture the regulatory strategies that older adults use in their everyday lives. Indeed, there is an age difference in preferences such that with greater age, people tend to prefer distraction more and reappraisal less (Scheibe et al. 2015).

Reappraisal (involving changing one's interpretation of an emotional stimulus) is a cognitively demanding strategy that, in younger adults, tends to recruit dorsal and lateral PFC regions as well as the posterior parietal lobe but does not typically recruit the vmPFC (Buhle et al. 2013). In two neuroimaging studies, older adults activated left ventrolateral PFC less than younger adults when reappraising to diminish the impact of negative emotional pictures (Opitz et al. 2012, Winecoff et al. 2011). Across two regulation strategies (reappraisal and distraction), older adults showed less dlPFC activity for regulation trials than younger adults showed (Allard & Kensinger 2014). Thus, one pattern now seen across a few studies is less lateral PFC activity during instructed emotion regulation for older than younger adults. Also, older adults are less effective than younger adults at disengaging brain regions associated with the default mode network during reappraisal (Martins et al. 2014).

On the one hand, older adults' preference for using distraction rather than reappraisal is surprising given that selective attention shares some dlPFC mechanisms with working memory, and declines in working memory are one hallmark of aging. Also, older adults are less effective at avoiding being distracted by external salient stimuli (Madden et al. 2014). Yet voluntary attention shifting, or top-down attention, shows little influence of age (Greenwood et al. 1993, Madden 2007). Parietal cortex plays a key role in top-down attention, and fewer age differences tend to be seen in functional activity in parietal cortex than in other regions during cognitive tasks (Spreng et al. 2011). Well-maintained voluntary control over attention selection may make distraction an attractive emotion-regulation option for older adults. In particular, older adults do well at using expectations or cues to guide subsequent attention (Madden 2007), which suggests that preparing to implement distraction when given a cue that something emotional is about to occur would be a particularly effective strategy for older adults. In contrast, without an external cue, proactive control is likely a computationally costly strategy for lateral PFC (Braver et al. 2014) and so may not be effective for older adults.

Recognizing Others' Emotions

Emotions are conveyed in many ways, but faces are often the most specific and clear signal of emotions. Both face identity (Germine et al. 2011) and emotion-recognition abilities (Ruffman et al. 2008) decline with age. One question is whether the age-related declines in recognizing emotions are just a function of some of the general declines in face processing. For instance, brain

imaging studies reveal that older adults show less neural specialization for faces in the ventral visual cortex (Goh et al. 2010) and declines in the contributions of fusiform face area to identifying and remembering faces (Dennis et al. 2008, Grady et al. 2000). In addition, the white matter tracts passing through the right fusiform gyrus are more reduced in their structural integrity among older adults than white matter more generally, and the integrity of these tracts is associated with the ability to discriminate two similar faces (Thomas et al. 2008).

However, the emotion deficits cannot be explained simply by declines in general face-processing abilities because aging has a different impact on the ability to recognize different emotions (Ruffman et al. 2008). Older adults tend to be worse than younger adults at identifying fear and sadness and sometimes also anger. In contrast, they show little impairment at recognizing happiness, surprise, and disgust. Indeed, they sometimes are better than younger adults at recognizing disgust.

What might explain the finding that older adults show no impairment and instead even better disgust recognition than younger adults? The recognition and experience of disgust is more closely linked with the insula than any other brain region. Thus, older adults' ability to recognize others' disgust expressions suggests age-related maintenance or even increased insular involvement in face processing. Consistent with this, older adults showed more insular cortex activity than younger adults during successful encoding of fearful faces (Fischer et al. 2010) and during rating emotions (Keightley et al. 2007). However, it is hard to reconcile better insula function in late life with the age-related declines seen in the insula (as described in the insula section above).

A more plausible possibility is that age-related shifts in general face-processing strategies cause the selective enhancement in disgust recognition. Compared with younger adults, older adults are less likely to look at someone's eyes and more likely to look at their mouth or nose (Circelli et al. 2013, Firestone et al. 2007, Heisz & Ryan 2011, Murphy & Isaacowitz 2010, Sullivan et al. 2007, Wong et al. 2005) and are worse than younger adults at detecting configural changes in the eye region than in the mouth/nose region of the face (Chaby et al. 2011, Slessor et al. 2013). The age difference in top-bottom bias is seen for both neutral and emotional faces but not for scenes (Circelli et al. 2013).

Research with younger adults indicates that fear, sadness, and anger are more recognizable from the top half of the face, whereas happiness and (especially) disgust are more recognizable from the bottom half of the face (Calder et al. 2000). Surprise showed no strong top-bottom bias (Calder et al. 2000). These differences correspond with the pattern of impairment/lack thereof for older adults' emotion recognition. Indeed, among older adults, looking more at the top half of a face predicted better recognition of anger, fear, and sadness, whereas looking more at the bottom half of a face predicted better recognition of disgust, and happiness and surprise showed no significant relationship (Wong et al. 2005).

If intact perception of facial disgust expressions is due to a general shift in face-processing mechanisms and not to a stronger influence of brain regions specialized for perceiving disgust, then perception of disgust should not be selectively maintained in aging in other sensory modalities. This appears to be the case, as aging is associated with impairments in perceiving which emotion others express verbally, and disgust is as impaired as the other emotions (e.g., Lambrecht et al. 2012).

These age-related shifts in face processing may stem from changes in the brain networks involved in face processing. A network of brain regions contributes to perceiving and interpreting eye gaze, including the superior temporal sulci, the medial prefrontal cortex, and the amygdala. Existing research does not provide sufficient information to indicate whether a particular component of this network involved in processing eye gaze is particularly affected in aging. The one fMRI study to compare younger and older adults while they categorized emotion from pictures of eyes had a small sample and did not find the typical behavioral impairments among the older adults (Castelli et al. 2010).

In summary, aging is associated with declines in recognizing facial expressions of some emotions more than others and a slight improvement in recognizing disgust. These shifts do not appear to be due to selective declines in brain regions more involved in perceiving one emotion than another (if such segregation exists; for arguments against it, see Lindquist et al. 2012) but instead are due to changes in how older adults process faces. Such face-processing changes may be due to age-related changes in the structure and function of face-processing regions, but clear brain linkages have yet to be established.

Empathy

To successfully navigate the social world, it is important not just to recognize what emotions others are experiencing, but also to be able to predict how the emotion will influence their actions. To make such predictions, we rely on both the capacity to personally share (and thereby simulate) the emotions of others and the ability to understand how the perspective of others may differ from our own. These affective and cognitive aspects of empathy rely on dissociable neural circuits and so may be affected differently by aging.

Current models suggest that the insula is involved in simulating the feelings of others via embodied representations of their emotional states (e.g., Bernhardt & Singer 2012). On the other hand, the cognitive aspects of empathy (requiring theory of mind) rely on a neural network including the medial prefrontal cortex, posterior superior temporal sulcus, temporoparietal junction, and temporal pole (Bzdok et al. 2012).

Self-reported assessments of empathy show either no age-related differences in empathy (Diehl et al. 1996, Eysenck et al. 1985) or declines (Chen et al. 2014, Phillips et al. 2002, Schieman & Van Gundy 2000). When emotional and cognitive empathy are distinguished using separate subscales, cognitive but not affective empathy is lower among older than younger adults (Bailey et al. 2008, Beadle et al. 2012; but see Khanjani et al. 2015). A limitation of these studies is their cross-sectional design. A study that examined both cross-sectional and longitudinal age effects found that older cohorts tended to report less empathy but that there was no decline in self-reported empathy in individuals over a 12-year period, suggesting that cross-sectional findings of age differences in empathy may be due to cohort rather than age effects (Grühn et al. 2008). Considered together, these self-reported findings provide little clear evidence of age-related decline in empathy.

Going beyond self-report measures by using measures of emotion perception, emotion congruency with the speaker, and sympathetic body and facial responses, one study found that older adults tended to be more perceptive and empathic for a more self-relevant social loss theme than for a life transition theme, and older adults performed as well as or better than younger adults for this theme (Richter & Kunzmann 2011). Thus, as in other domains, older adults perform quite well when given self-relevant contexts (Hess 2005).

Theory-of-mind tests tap some of the processes needed for cognitive empathy. As outlined in the previous section, older adults are less likely to attend to eyes than are younger adults. They also tend to be impaired at a common theory-of-mind test using pictures of eyes (Bailey et al. 2008, Khanjani et al. 2015, Phillips et al. 2002, Slessor et al. 2007), although their impairment also extends to inferring age and gender based on eyes (Slessor et al. 2007), so it does not seem to be emotion specific. Likewise, when given stories testing the ability to make theory-of-mind inferences about the beliefs of others, older adults are impaired, but they tend to be similarly impaired at making inferences about physical or mechanical causation (German & Hehman 2006, Happé et al. 1998, Slessor et al. 2007; but see Maylor et al. 2002 for conflicting findings). These studies suggest that age-related impairments in cognitive empathy likely stem from broader impairments in cognitive function (Moran 2013). Consistent with this, older adults showed less activation in the dorsomedial

PFC than did younger adults while performing three different mentalizing tasks (Moran et al. 2012), whereas there were no consistent age differences in activity within the regions typically associated with cognitive empathy.

Another fMRI study compared younger, middle-aged, and older adults' responses to brief animations of hands or feet in painful or nonpainful situations and in dyads or alone (Chen et al. 2014). Across age groups, there was a significant effect of social context, with greater activity in the medial prefrontal cortex, posterior superior temporal sulcus, posterior cingulate cortex, and fusiform gyrus in the dyad trials. In contrast, in the right anterior insula, the response to seeing others in pain (compared with no pain) decreased across age groups, with older adults showing no significant effect. However, such changes were not significantly associated with insular gray matter changes (Chen et al. 2014), suggesting that structural volume in itself is not a strong predictor. Older adults also showed less insula activation in comparison with younger adults when offered unfair divisions of money in an ultimatum game study (Harlé & Sanfey 2012). These findings suggest that insula is less involved in interpreting social situations among older than younger adults.

In summary, initial evidence suggests that older adults show less involvement of the insula in situations in which one might simulate the feelings of others, and some evidence also suggests that although they show similar cognitive-empathy brain networks, decreased involvement of brain regions such as dlPFC that support executive function more generally may contribute to declines in making inferences about the mental states of others. Self-reported empathy scales do not necessarily reflect these changes.

Iowa Gambling Task

As mentioned previously, research using behavioral tasks to discriminate dlPFC from either ventromedial or orbital PFC in contributing to age differences has yielded mixed results (Baena et al. 2010, Lamar & Resnick 2004, MacPherson et al. 2002). A key issue that has not been fully appreciated is that the tasks used to tap vmPFC function also rely on other regions in the PFC and elsewhere. In this and the next section, I focus on the two decision tasks that have received the most attention in the aging literature and discuss what can and what cannot be gleaned from the current findings about the neural underpinnings.

The Iowa Gambling Task demonstrated that patients with vmPFC lesions have deficits in decision making that relate to impaired integration of emotional signals (Bechara et al. 1996). When given this gambling task, patients with vmPFC lesions are less likely to learn to avoid decks of cards that typically yield positive outcomes but occasionally lead to a large loss. Yet the vmPFC's role in making decisions and the underlying mechanisms of the Iowa Gambling Task have been the subjects of much debate (e.g., Buelow & Suhr 2009, Maia & McClelland 2004).

Despite uncertainty about what processes it taps, the Iowa Gambling Task has been the most highly utilized task to probe for adult age differences in decision making, and across studies, older adults are more impaired at avoiding the risky decks in this task (Mata et al. 2011). But does this impairment reflect vmPFC impairment? Not necessarily. Patients with dlPFC lesions also show deficits on the Iowa Gambling Task (Fellows & Farah 2005a), which suggests that impairments in working memory that allow ongoing information to be updated and integrated may contribute to declines in performance on the task among some older adults.

Indeed, there are indications that older adults' impairments on the task relate to impairments in learning from the decks over time. First of all, older adults' deficits tend to be stronger in later blocks than in initial ones (Denburg et al. 2005, Zamarian et al. 2008), with impairments sometimes seen in the later blocks even when there is no overall main effect of age (Baena et al. 2010, Isella et al. 2008). This pattern suggests a learning deficit. Also, older adults show more

recency effects and more rapid forgetting in the task (Wood et al. 2005). Thus, impairments in memory processes may account for the age impairments in this task seen in some studies.

The Iowa Gambling Task has also revealed an emotional difference across age groups even when performance is equivalent. Whereas younger adults weighted previous losses more heavily than previous wins in their card deck choices, older adults weighted wins and losses evenly (Wood et al. 2005). In addition, healthy younger adults typically produce larger anticipatory skin conductance responses before selecting from a "bad" than a "good" deck in the task (Bechara et al. 1996). In contrast, older adults who completed the task successfully showed the opposite pattern, with larger anticipatory skin conductance responses before selecting from a good than a bad deck (Denburg et al. 2006). These findings indicate that the emotional nature of decision strategies in this task shift with age to focus more on the positive than on the negative outcomes, a shift seen in other contexts as well, such as during decision search (Löckenhoff & Carstensen 2007, Mather et al. 2005), deciding among risky gambles (Mather et al. 2012), and anticipating wins or losses (Nielsen et al. 2008).

Delay Discounting

Would you prefer $10 now or $15 in a month? Given evidence that vmPFC lesions lead to impulsive behavior (Berlin et al. 2004), one might think that vmPFC should help people be more patient and wait for delayed rewards instead of taking less valuable immediate rewards. But although patients with vmPFC lesions are less likely than controls to think about distant future events, they do not show differences in how much they value present versus future monetary rewards on a delay discounting task (Fellows & Farah 2005b). Thus vmPFC seems to influence how likely one is to think about one's own distant future rather than how much one values rewards in the future.

Older adults typically show less delay discounting than younger adults (Eppinger et al. 2012, Green et al. 1994, Reimers et al. 2009), although such differences can be reduced by controlling for income levels (Green et al. 1996). In addition, the animal literature shows consistent decreases in delay discounting with age (e.g., Roesch et al. 2012, Simon et al. 2010), although a critical difference is that delay discounting tasks for animals require the animal to learn about the delays and rewards via repeated experience. With humans, most delay discounting tasks simply describe the amount of money and delay in text format on each trial and do not present outcomes until the end of the session. One interesting finding is that when two options differ only in delay (and not in reward amount), older rats are impaired at learning to avoid the longer delay option, but that when the two options differ in reward amount (and not in delay), they are not impaired (Roesch et al. 2012). Thus, learning about differences in time duration may be more impaired in aging than is learning about differences in amount (cf. Zanto et al. 2011).

Among healthy participants between the ages of 63 and 93, those with greater structural thickness in the vmPFC exhibited less delay of gratification (Drobetz et al. 2014). Likewise, in rats trained in the delay discounting task before lesioning, orbitofrontal lesions resulted in less impulsive choices of a smaller-sooner reward over a larger-later reward than did sham lesions (Winstanley et al. 2004). Thus, the orbitofrontal cortex may help integrate information about the delay into the representation of value for an option. Failure to integrate that information makes the delayed option seem more attractive, and older adults may be impaired at this integration of time delay information into value estimations.

However, in initial functional neuroimaging studies with humans, there was no indication that vmPFC changes are associated with delay discounting changes in aging. For instance, in two fMRI studies, there were no significant age differences in medial PFC regions associated with temporal

discounting (Eppinger et al. 2012, Samanez-Larkin et al. 2011). Furthermore, in a study of 123 older adults, functional connectivity between fronto-insular seed regions and PFC did not differ for those older adults with high versus low delay discounting (Han et al. 2013). Thus, further work is needed to evaluate the role of vmPFC in age differences in delay discounting.

Studies also suggest a role for other neural systems. For instance, the same study with the negative structural correlation with vmPFC found that greater dlPFC cortical surface area predicted greater delay of gratification (Drobetz et al. 2014). Also, younger adults showed significantly greater striatal activation when choosing immediate over delayed choice options, whereas older adults showed no significant difference (Eppinger et al. 2012, Samanez-Larkin et al. 2011), suggesting that age-related reductions in dopaminergic reward sensitivity may be involved. In the next section, we review age-related changes in dopaminergic influences over reward processing.

Reward Processing

Dopaminergic coding of reward prediction error seems to be disrupted in older adults. Older adults show reduced prediction error–related activity in the vmPFC and ventral striatum (a region that encompasses the nucleus accumbens and is involved in reward processing) in tasks requiring learning about which response to make to specific stimuli (Eppinger et al. 2013, Samanez-Larkin et al. 2014). Older adults also show impairments on behavioral reward learning tasks (e.g., Mell et al. 2005), especially those involving more computationally demanding model-based strategies (Worthy et al. 2014). Both the prediction error signal in the ventral striatum and probabilistic reward learning performance are enhanced when older adults receive the dopamine precursor levodopa (Chowdhury et al. 2013).

Age-related impairments may be specific to situations in which reward prediction errors support learning, because in other contexts older and younger adults show similar influences of reward. In older adults, striatal regions still respond robustly to rewarding outcomes (e.g., Samanez-Larkin et al. 2014, Schott et al. 2007, Vink et al. 2015). Recognition and source memory are enhanced by positive compared with negative feedback (Eppinger et al. 2010, Mather & Schoeke 2011) and by reward anticipation (Spaniol et al. 2014) in older adults as much as in younger adults. Task reaction times are also speeded up by potential rewards as much for older as younger adults (Vink et al. 2015).

Emotion and Behavior Change

Why do we have emotions, in particular negative emotions? One overarching potential function of emotions is to trigger behavior change (Frijda & Parrott 2011, Oatley & Johnson-Laird 1987). Yet emotions often enhance learning associations (Mather 2007). Thus, strong emotion during learning a contingency (e.g., whenever I select this option, I get a reward) could impair later behavior change that requires suppressing the learned association.

Reversal learning research indicates that orbitofrontal brain regions are critical for updating knowledge about choice outcomes and so should support flexible behavior. Yet although orbitofrontal lesions alone impair performance, when there is a concurrent amygdala lesion, orbitofrontal lesions no longer impede learning contingency reversals (Stalnaker et al. 2007). This suggests that orbitofrontal cortex facilitates flexible updating by opposing amygdala stabilization of the prior contingency. Consistent with the notion that orbitofrontal cortex works against amygdala-strengthening emotional associations, orbitofrontal activity is greater during reversal of emotional than neutral outcomes, with negative functional connectivity seen between orbitofrontal cortex and amygdala (Nashiro et al. 2012b). Older adults show effects of emotion that are similar

to those of younger adults both in an fMRI reversal task (Nashiro et al. 2013b) and when updating simple associations between stimuli (Nashiro et al. 2013a), suggesting that prefrontal-amygdala interactions mediating flexible updating remain intact in later life.

Being able to flexibly change behavior may also depend on the LC and the noradrenaline it releases (Aston-Jones & Cohen 2005). Not much is known yet about how age-related changes in the LC-noradrenaline system might relate to the likelihood of exploring new options versus remaining fixated on current choices, but it is an interesting avenue for future research, especially given findings of less exploratory behavior (Mata et al. 2013) and less information seeking during decision making (Mather 2006) among older than younger adults.

Arousal and Cognitive Selectivity

As outlined in the recent Glutamate Amplifies Noradrenergic Effects model (Mather et al. 2015), the LC increases the selectivity of processing through a variety of mechanisms, including shunting blood flow and metabolic resources to highly active regions and away from other regions. At local synapses, norepinephrine interacts with the brain's primary excitatory neurotransmitter, glutamate, to amplify activity at the most highly active neurons while inhibiting activation elsewhere. These modulatory effects of the LC are especially potent in moments of high emotional arousal, when people tend to focus on whatever is most salient and ignore the rest. Thus, noradrenaline prepares the brain for targeted action by supporting processing in brain regions that are most highly active at that moment. This model accounts for findings that arousal increases the selectivity of attention and memory, favoring salient and high-priority items (e.g., Lee et al. 2014, Sakaki et al. 2014). Initial evidence indicates that older adults show similar enhancement of bottom-up salience under arousal (Sutherland & Mather 2015) but that arousal does not increase selectivity for older adults; instead, it broadly enhances processing of both low- and high-priority items (T.H. Lee, S.G. Greening, A. Ponzio, D. Clewett, and M. Mather, manuscript in preparation).

CONCLUSIONS

Emotion processes depend on interacting systems of neurotransmitters and specific brain regions. Changes with age in these systems vary in nature and in degree.

The amygdala and the vmPFC, two brain regions that play key roles in emotion processing, show less structural and functional decline with age in comparison with many other brain regions. In addition, they show shifts in processing that support favoring positive over negative stimuli in attention and memory. Although older adults do perform differently than younger adults on tests that have previously been identified with the vmPFC, such as facial emotion expression recognition and the Iowa Gambling Task performance, the differences in performance are better explained by factors other than age-related vmPFC decline, such as a reduced focus on eyes during face processing and declines in dlPFC working memory and learning processes.

The insula shows both structural and functional decline in aging that initial evidence suggests may be linked to age-related changes in empathic processes. Yet despite the role of the insula in feelings of disgust, older adults tend to recognize disgusted facial expressions as well or better than younger adults, potentially due to their greater focus on noses and mouths rather than eyes when looking at faces.

Age-related decline in the dopaminergic system is associated with impaired reward prediction error computation, but when new learning is not involved, reward anticipation and response are well maintained in aging.

The noradrenergic system is vulnerable to pathology that slowly progresses throughout the lifespan and may trigger a compensatory release of noradrenaline. Older adults often show as much of an arousal response to emotional stimuli as younger adults, but this arousal seems to have less of a targeted effect on cognitive processing.

In general, shifts in the relative efficacy of different brain systems may contribute to changes in the strategies older adults use to cope with difficult emotional situations and to maintain effective emotional processing. The relative lack of decline in core emotion-related brain regions likely plays a key role in explaining older adults' well-maintained emotional functioning, in particular the ability to maintain positive affect and minimize negative affect in everyday life.

SUMMARY POINTS

1. Amygdala and vmPFC structure and function are relatively well maintained in healthy aging.
2. Increased vmPFC activity (along with decreased amygdala activity) in older adults confronted with negative stimuli is associated with better everyday emotional outcomes.
3. Age-related declines in lateral PFC may be related to shifts in preferred emotion-regulation strategies.
4. Selective sparing of recognition of facial disgust along with declines in recognition of fear, sadness, and anger is better accounted for by changes in general face-processing strategies than by aging effects on specific brain regions.
5. Although reward-learning processes are impaired among older adults, responses to rewarding outcomes are maintained.
6. Potential age-related decreases in insular contributions to interoception and simulating the emotions of others deserve further examination.
7. For both older and younger adults, emotion interferes with updating associations via amygdala-PFC interactions.

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