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Issue: *The Year in Cognitive Neuroscience***The emotion paradox in the aging brain**

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This paper reviews age differences in emotion processing and how they may relate to age-related changes in the brain. Compared with younger adults, older adults react less to negative situations, ignore irrelevant negative stimuli better, and remember relatively more positive than negative information. Older adults' ability to insulate their thoughts and emotional reactions from negative situations is likely due to a number of factors, such as being less influenced by interoceptive cues, selecting different emotion regulation strategies, having less age-related decline in prefrontal regions associated with emotional control than in other prefrontal regions, and engaging in emotion regulation strategies as a default mode in their everyday lives. Healthy older adults' avoidance of processing negative stimuli may contribute to their well-maintained emotional well-being. However, when cardiovascular disease leads to additional prefrontal white matter damage, older adults have fewer cognitive control mechanisms available to regulate their emotions, making them more vulnerable to depression. In general, although age-related changes in the brain help shape emotional experience, shifts in preferred strategies and goal priorities are also important influences.

Keywords: emotion regulation; aging; fMRI; ventromedial prefrontal cortex; amygdala

Introduction

Emotions prepare the body for action, guide decisions, and highlight what should be attended to and remembered. However, it can be difficult to turn off or ignore emotions. When negative emotions last for a long time and are maintained even when no longer appropriate, disorders such as chronic depression or anxiety ensue. As emotions are central to everyday function and well-being, it is important to understand how aging affects the experience and regulation of emotion. Recent research reveals intriguing findings about emotion and aging and raises questions about which aspects of these age-related changes in emotional processing can be accounted for by age-related changes in the brain, and which are more influenced by other factors, such as changes in other body systems, increased experience, or shifts in goals. In this paper, I review various types of age differences in emotion experience and regulation, and discuss relevant changes in the brain.

The paradox of emotional well-being in aging

In old age, physical health and strength typically decline. The death of a spouse or close friends is more likely than earlier in life. Cognitive agility decreases and it is harder to remember information. Social networks shrink. This picture sounds depressing. Yet, on average, adults' emotional well-being is somehow maintained or even improved as they age.¹ For instance, older adults move out of highly negative emotional states faster than younger adults do and maintain the absence of negative affect more consistently.^{2,3} Middle-aged and older adults are less physically and emotionally reactive to interpersonal stressors than younger adults.⁴ When older adults experience interpersonal tensions, they engage less in destructive conflict strategies, such as yelling, arguing, or name calling,⁵ and generally find tense interpersonal situations less stressful than younger adults do.⁶

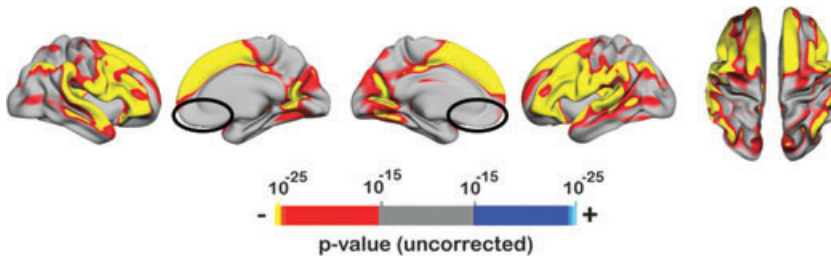


Figure 1. Fjell *et al.*¹⁰ assessed cortical thickness across six different samples with a total of 883 participants. Negative correlations between age and cortical thickness were seen in the superior, middle, and inferior frontal gyri, but not in the anterior cingulate cortices or in ventromedial prefrontal cortex. The frontal regions that showed little relationship with age are circled in the image. Figure is adapted from Fjell *et al.*¹⁰

What might explain older adults' pattern of lower reactivity to negative situations and more ephemeral negative emotional experience? There are two obvious potential answers to this puzzle. One is that older adults are better than younger adults at regulating their emotions and so can more easily defuse negative feelings and situations. The other is that older adults do not experience negative feelings and situations as intensely as younger adults do and so have less need to defuse them. In this paper, I will review behavioral and brain data to critically examine both of these putative explanations for the paradox of emotion in aging.

Aging affects dorsal and lateral PFC more than ventromedial PFC

To answer the question of whether older adults differ from younger adults in their abilities to regulate emotions, it is important to consider whether there are age-related declines in the brain regions associated with emotion regulation abilities. Research indicates that effective emotion regulation relies on the prefrontal cortex (PFC). Both the ventromedial PFC and the adjacent anterior cingulate cortex (ACC) play important roles in controlling one's own emotion. For instance, close family members rated ventromedial PFC lesion patients as more irritable, emotionally labile, apathetic, and emotionally impoverished than did family members of nonventromedial PFC lesion patients.⁷ Across both the ACC and the PFC, ventral regions are more critical for emotional processing, whereas dorsal regions are more critical for cognitive executive functions.⁸

Although the PFC is especially vulnerable to decline in normal aging, this vulnerability varies by

subregion. In particular, the ventromedial PFC develops earlier in childhood than other regions⁹ and maintains its cortical thickness throughout the adult life span¹⁰ (Fig. 1). The ACC also maintains its cortical thickness in normal aging, whereas lateral and superior regions of PFC thin dramatically. Findings that cortical thickness declines more in aging in dorsal than ventral ACC and PFC (Fig. 1) suggest that some of the neural circuitry critical for emotion regulation is well preserved in aging. However, as reviewed in the following sections, emotion regulation processes do not remain constant, but instead change in a variety of ways with age.

Older adults use different emotion regulation strategies than younger adults do

Which emotion regulation strategies people favor shifts with age; older adults are more likely to select strategies that involve ignoring things that might elicit negative emotion and are less likely to directly engage with emotionally negative stimuli, problems, or situations. For instance, a study that used random-digit dialing to ask over a thousand younger, middle-aged, and older Americans about their emotion regulation strategies¹¹ found that self-reported suppression increased with age (although the age increase was only significant for women), whereas self-reported rumination, reappraisal, and active coping all decreased with age for both genders (self-reported suppression also increased across age cohorts in a Spanish sample¹²).^a When attempting to deal with everyday problems,

^aIn contrast with these findings of greater suppression across older cohorts, a study in Hong Kong found no age

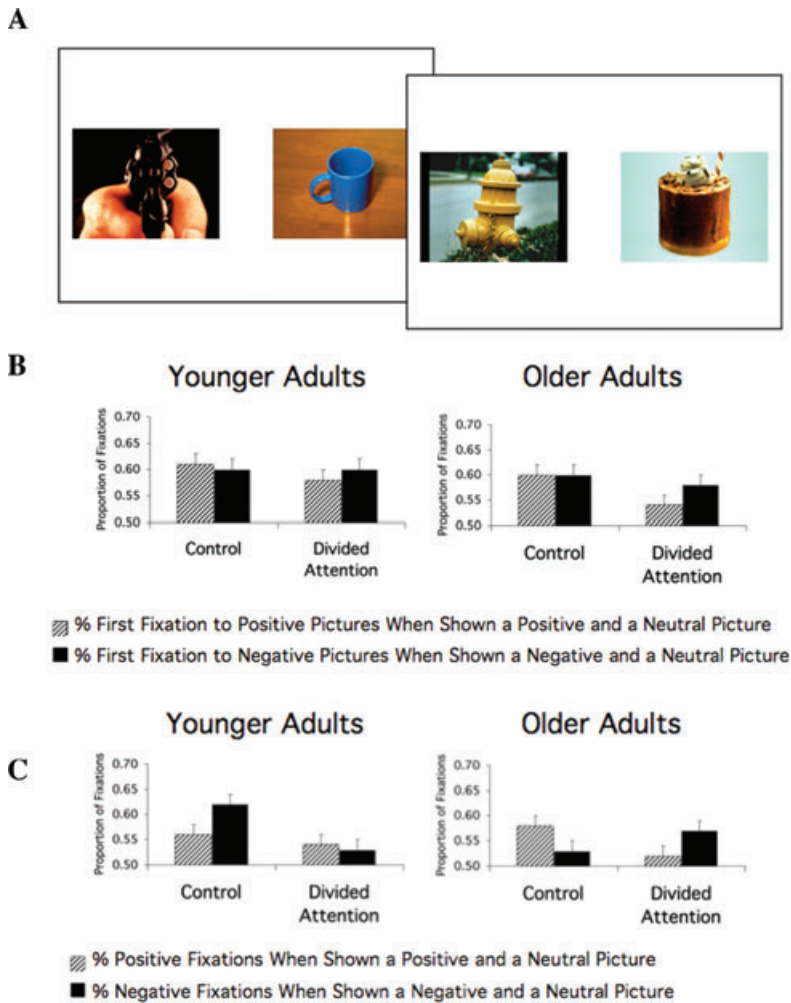


Figure 2. In a study by Knight *et al.*,¹⁷ younger and older adults’ eye movements were measured while they looked at pairs of pictures for six seconds each. (A) An example negative–neutral pair and an example neutral–positive pair are shown. Divided attention participants were distracted by a concurrent listening task while they looked at the pictures whereas control participants just looked at the pictures. (B) Participants’ first fixation was more likely to be on an emotional picture than on a neutral picture, regardless of age. However, age differences emerged in the remaining time the pictures were shown, with older adults showing a positivity effect in the control condition but a negativity effect in the divided attention condition. Figure is from Mather.¹⁹

older adults are more likely to endorse strategies that involve withdrawing from the situation and attending selectively to things other than the situation itself.¹⁴ When shown negative and neutral stimuli

together, older adults tend to look away from the negative images^{15–18} (Fig. 2). Furthermore, older adults show this negativity avoidance more when induced into a negative mood whereas younger adults showed mood-congruent looking.²⁰ These findings suggest that older adults are more likely than younger adults to ignore stimuli that might increase negative moods, and that their selective attention serves as an emotion regulation strategy.

The emotion regulation strategies people select may shift with age because of changes in which ones are easiest to implement.²¹ Different aspects of

differences in suppression and greater reappraisal among middle-aged than younger adults.¹³ But in this study the younger adults were university students and the middle-aged adults were recruited from local insurance companies, which may have led to group differences unrelated to age.

emotion regulation tap different PFC circuits.²² For instance, effortful regulation often involves lateral PFC regions, whereas automatic regulation is more likely to involve ventral ACC or medial PFC.^{23,24} An example of an effortful regulation strategy is when people reinterpret situations or contexts of stimuli to change their emotional meaning. During this type of reappraisal, people reliably activate dorsal PFC.²⁵ Thus, older adults may avoid using reappraisal to regulate emotions because it relies on regions of PFC particularly affected by aging.

Older adults are more effective than younger adults at avoiding negative distraction

Older adults' reliance on emotion regulation strategies that involve self-directed selective attention and suppression is surprising when considering that, compared with younger adults, older adults tend to be more susceptible to distraction.^{26,27} But recent research reveals an interesting pattern—although they are more easily distracted than younger adults by neutral stimuli, older adults are less easily distracted by emotional (especially negative) stimuli. For instance, a study with over 400 participants recruited via random digit dialing found that those in their 20s, 30s, and 40s were slower to name the ink color of emotional words than of neutral words, but this effect diminished with age and eventually reversed by the 70s.^{28, b} In another emotional Stroop study, younger and older adults showed similar impairment in naming the color of negative words, but younger adults were also slower in naming the color of neutral words following negative words, whereas older adults did not show this sustained effect of negative information.³⁰ When participants were asked to indicate whether a face was fearful or happy, while ignoring the words “FEAR” or “HAPPY” superimposed on the face,³¹ older adults did not perform significantly worse than younger adults on measures of conflict adaptation and interference reduction (these measures were assessed by comparing trials that had been preceded by congruent versus incongruent trials—people tend to adapt to the congruency on one trial, affecting their perfor-

mance on the next trial). But when asked to indicate whether a face was male or female while ignoring the words “MALE” or “FEMALE,” older adults exhibited poorer performance than the younger adults.

Although the studies described above show that older adults experience less interference from emotional stimuli than from neutral stimuli, they either did not distinguish positive from negative stimuli in their reported results or only compared negative stimuli to neutral stimuli. However, a couple of studies suggest that older adults' superior distraction avoidance is specific to negative stimuli, not positive stimuli. For instance, when asked to identify a target digit printed on top of a distractor face, younger adults were most distracted by angry faces, whereas older adults were most distracted by happy faces.³² In another study, when asked to indicate whether two digits placed on either side of a word were both odd or even, younger adults were slower when distractor words were negative than when they were neutral or positive.³³ In contrast, older adults showed no significant reaction time differences based on the valence of the distractors. In a surprise recognition memory test 10 minutes later, younger adults showed the best recognition of the negative distractors whereas older adults showed the best recognition of the positive distractors (Fig. 3), suggesting age differences in which distractor items were attended enough to be encoded successfully.

The increasing ability with age to avoid negative distraction seems to extend to everyday life as well. In a sample of older adults between the ages of 70 and 97 who reported on their daily stressors, such as arguments, health-related problems, and how much

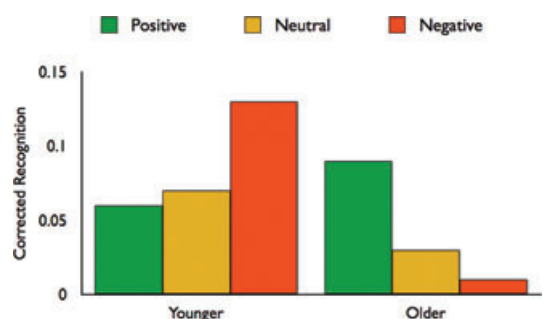


Figure 3. Corrected recognition (hits–false alarms) for positive, neutral, and negative words that were presented previously as irrelevant distracting items between two task-relevant digits. Figure is adapted from data presented in Thomas and Hasher.³³

^bNote that another study testing 36 younger and 36 older adults found conflicting results.²⁸ The reason for the discrepancy is not clear.

they experienced cognitive interference (e.g., “Did you think about something you didn’t mean to?”), the incidence of stressful events in the past 24 hours predicted cognitive interference less with increasing age.³⁴

What are the brain regions involved in ignoring negative distraction? There is evidence that, in younger adults, compared with avoiding distraction from neutral stimuli, avoiding distraction from emotional stimuli is more associated with activity in lateral inferior frontal gyrus,^{35–37} and that suppressing emotional reactions to stimuli yields activity in inferior frontal gyrus as well.²² Activity in the inferior frontal gyrus during presentation of emotionally distracting images also predicts better working memory performance for the target nonemotional memoranda,³⁵ suggesting that activity in this region helps diminish emotional interference. Consistent with the possibility that this region plays a critical role in avoiding emotional interference, patients with PFC brain lesions involving the inferior frontal gyrus (including Brodmann areas 44, 45, and 47) were more distracted by task-irrelevant emotional images than were patients with ventromedial PFC lesions.³⁸ In addition, resolving emotional interference engages regions of the ACC that are more ventral than the dorsal ACC regions engaged while resolving nonemotional interference.^{39,40}

However, the precise brain regions involved in ignoring negative distractions may change with age. For example, one fMRI study suggests that the inferior frontal gyrus is differentially involved in emotional interference for younger and older adults.⁴¹ In this study, younger and older adults were scanned as they completed a task in which they either judged the valence (negative vs. positive) or the substance (metal vs. fruit) of a central word. Some trials of each type involved congruent and others involved incongruent flanking words. The behavioral findings were consistent with those described earlier, with older adults showing more interference from incongruent words in the substance judgment task than younger adults, but less interference than younger adults in the valence judgment task. Although it did not achieve a significant interaction, there was a parallel pattern in a region of left inferior frontal gyrus; older adults showed significantly greater activity during incongruent trials than control trials in the substance but not the valence task and vice versa for younger adults. Unfortunately, from

these data we cannot be sure whether more activity in this region indicates less efficient processing or more effective involvement of this region in avoiding emotional distraction. In this study, although older adults were overall better at avoiding emotional distraction than younger adults, both younger and older adults showed more distractibility from incongruent distractors that were negative than from those that were positive. No analyses by valence were reported for the fMRI data.

Whereas older adults did not have difficulty avoiding distraction from positive incongruent stimuli in the study just described, another fMRI study⁴² was more consistent with the behavioral studies described earlier in which older adults were worse at avoiding positive distraction. In this study, older adults showed greater distractibility from irrelevant positive faces than from irrelevant neutral faces when attention to the central face location was high, whereas younger adults did not show differential distractibility for positive versus neutral faces. This age by distractor type interaction in reaction type was paralleled by an interaction in the ACC, such that older adults showed greater ACC activity during happy distractors shown under high attention than during neutral distractors, but younger adults did not. Furthermore, greater ACC signal during processing happy faces than neutral faces was associated with a measure of emotional stability in the older adults. No significant ACC engagement was seen in conditions with fearful or sad distractor faces. The greater ACC activation among older adults on trials with distracting positive faces may reflect both greater subjective salience of the positive distractors and the increased regulation demands imposed by this affective conflict.

In summary, older adults are often better than younger adults at ignoring emotionally negative distraction. These findings are striking given the back-drop of age-related impairments in avoiding distraction by neutral stimuli.^{26,27} As suggested earlier, such findings raise the possibility that brain regions necessary for resolving interference from emotional stimuli may decline less with age than other brain regions. However, one additional critical piece of the picture is that older adults tend to be *more* distracted than younger adults by positive stimuli (although not always⁴¹). Thus, if their enhanced ability to ignore negative stimuli is due to relative preservation of certain PFC or ACC circuits, those

circuits must be specialized for dealing with interference from negative stimuli rather than emotional stimuli more broadly. Another possibility raised in the following section is that the negativity avoidance effects seen among older adults are the result of a greater chronic focus on emotion regulation goals.

Downregulating negative affect may be more of a default mode for older adults than for younger adults

In the previous sections we reviewed evidence that, compared with younger adults, older adults favor different emotion regulation strategies and are more adept at avoiding emotional distraction. Another important factor to consider is how likely they are to focus on regulating emotion in the first place. Socioemotional selectivity theory (SST) posits that as perceived time left in life becomes more limited, people shift motivational priorities to focus more on regulating emotions (and in particular, experiencing more positive, and less negative, emotions) and less on other goals such as information seeking.⁴³ Indeed, in their self-reports, older adults are more likely than younger or middle-aged adults to endorse statements such as, “I try hard to stay in a neutral state and to avoid emotional situations,” which indicate a focus on controlling emotions.⁴⁴ Their responses to problems presented in vignettes involve more impulse control than those of younger adults⁴⁵ and are more emotion-focused.^{14,46}

In addition to age differences in self-reports about emotion regulation, in laboratory studies involving emotional stimuli, older adults often selectively attend to and remember positive stimuli compared with negative stimuli more than younger adults do.^{47,48} In contrast, it seems that younger adults need reminders to get them to focus on regulating emotion—younger or middle-aged adults’ memories become more consistent with emotion regulation goals (and more emotionally similar to older adults’ memories) when they are reminded of their emotions by being asked to rate or think about their current emotions.^{49,50} The “cognitive-control model” extension of SST posits that older adults’ positivity effect results from older adults’ chronic activation of emotion regulation goals.^{47,51–53} Because, compared with younger adults, older adults focus more on regulating emotions when processing new stimuli, they should be more likely to engage cognitive control resources in the service of

the emotional goals. Consistent with the cognitive-control model, older adults with higher cognitive control abilities are more likely to show positivity effects (i.e., relatively more attention to, and better memory for, positive compared with negative information than younger adults) than those with lower cognitive control abilities.^{52,54} Furthermore, reducing the availability of cognitive resources for emotion regulation by having participants engage in a concurrent task that demands cognitive control reverses older adults’ positivity effect in attention¹⁷ and memory.^{52, c}

Also consistent with the role of top-down processes, in eye-tracking studies positivity effects in attention are not evident in the first eye fixation but emerge after that. For instance, when an emotional picture is shown next to a neutral picture, both younger and older adults’ first fixation tends to be on the emotional stimulus,¹⁷ consistent with findings reviewed earlier that older adults detect emotionally arousing stimuli as effectively as younger adults. However, compared with younger adults, fewer of older adults’ remaining fixations during the six-seconds display time are devoted to the negative stimuli and more are devoted to the positive stimuli (Fig. 2). Older adults also show attentional biases away from negative faces in a dot probe task,¹⁸ and in this type of task, the attentional bias against angry faces takes about a second to emerge.⁵⁶ Furthermore, eye-tracking analyses over a 4-s duration show that older adults show the strongest attentional biases against angry faces and toward happy faces in the later portions of the trial.⁵⁷ Of particular relevance for the emotion regulation account of the positivity effect, older adults’ attentional biases away from angry faces is mediated by how much they endorse everyday use of emotion suppression strategies.⁵⁶

Emotional stimuli also influence subsequent visual processing differently for younger and older adults. An event-related potential (ERP) study in which a face was displayed for 400–800 ms and then a checkerboard pattern was flashed for 100 ms over

^cIn contrast, distraction from a secondary task that requires little cognitive control (hearing one word at the beginning of a picture presentation period and immediately indicating whether it was a word or a non-word) does not influence older adults’ positivity effect in attention.⁵⁴

the face found that younger adults showed enhanced early visual processing of the checkerboard (as indicated by greater P1 response) when the faces were angry, happy, or sad than when they were neutral.⁵⁸ Although there was no overall main effect of age on the P1 amplitude, there were age differences in the influence of emotion. Older adults showed no emotional advantages and actually showed smaller P1 amplitudes when faces were angry than when they were neutral. This suggests that older adults withdrew their attention from angry faces, reducing subsequent visual processing of probes appearing over those faces.

A study examining age differences in binocular rivalry effects for emotional faces also revealed that older adults suppress processing of angry faces and enhance processing of happy faces.⁵⁹ In this study, a picture of a house was presented to one eye and a picture of a face was presented to the participant's other eye on each trial. Under these conditions, people perceive the two images alternating, as they compete in the brain for perceptual dominance. As seen in previous studies of binocular rivalry, for younger adults both happy and angry faces dominated perception for longer durations than neutral faces. But for older adults, the angry faces were perceived for less time than the neutral faces whereas the happy faces were perceived for longer than the neutral faces. Although people have limited voluntary control over binocular rivalry dominance, paying attention to one stimulus increases its dominance.^{60,61} These age differences in binocular rivalry in addition to the ERP P1 findings described earlier indicate that older adults' suppression of processing angry faces impacts even basic visual perception.

Another indication of age differences in whether positive or negative stimuli are attended more deeply come from ERP studies that assessed the late positive potential while younger and older adults studied pictures.^{62,63} The late positive potential is a positive deflection in the brain electrophysiological response to a stimulus occurring about 400 ms after stimulus onset. It is greater in response to stimuli with motivational relevance than in response to neutral stimuli⁶⁴ and is increased both by automatic and directed attention.⁶⁵ Younger adults showed the largest late positive potentials to negative stimuli, whereas older adults showed either similar late positive potentials to negative and positive stimuli⁶² or the greatest response to positive stimuli.⁶³ Older

adults subsequently recalled fewer negative pictures than younger participants did, but similar numbers of positive and neutral pictures, and the difference in the ERP amplitude for positive versus negative pictures was marginally significantly related to the difference in number of positive versus negative pictures recalled.⁶³

Older adults show greater PFC activity for emotional than neutral stimuli

The studies reviewed in the previous section show that older adults tend to process positive stimuli more deeply while ignoring negative stimuli, at least when they have cognitive control resources available. If such effects result from a more chronic focus on emotion regulation among older adults than younger adults, they should be associated with additional recruitment of prefrontal control regions. Even if older adults tend to use different strategies than younger adults, PFC should still be involved.

Indeed, in fMRI studies contrasting brain activity while processing negative faces or pictures versus neutral faces or pictures, older adults tend to show more dorsolateral and ventrolateral PFC activity and less amygdala activity than younger adults.^{66–73} Findings of greater PFC and reduced amygdala responses among older adults than younger adults when viewing negative stimuli may reflect more effective spontaneous emotion regulation. Consistent with this possibility, in a study in which older adults were asked to diminish their affective response to negative stimuli, those with a negative correlation between ventromedial PFC and amygdala had steeper, more normative declines in stress hormones during the day, suggesting that PFC–amygdala interactions may contribute to effective emotion and stress regulation.⁷⁴

While older adults generally show more PFC activity for negative than neutral pictures or faces in studies that involve passive viewing or simple ratings of the pictures, when tasks instruct participants to deeply process presented stimuli, older adults show a larger increase in PFC activity in response to positive stimuli than negative stimuli compared with younger adults (Fig. 4).^{75,76} This suggests that PFC control regions may be recruited either to more deeply process positive stimuli or to diminish emotional responses to negative stimuli, and that recruitment for one or the other purpose varies depending on the task context.

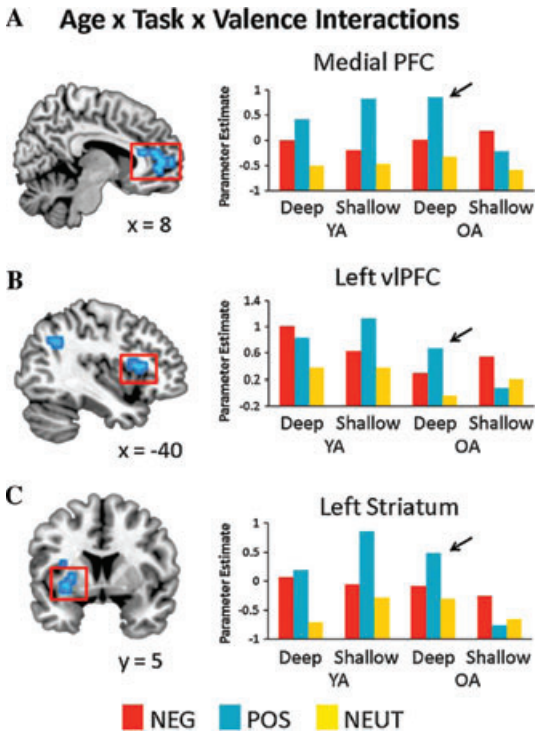


Figure 4. Interactions of age, task, and valence on activity in (A) medial prefrontal cortex, (B) left ventrolateral prefrontal cortex, and (C) striatum, all indicating a greater difference between positive than negative trials during deep versus shallow processing in older adults. Figure is from Ritchey *et al.*⁷⁶

As reviewed earlier, ventromedial PFC maintains its cortical thickness in normal aging, whereas lateral and dorsal regions show clear decline (Fig. 1). This raises the question of whether ventromedial PFC plays a more important role in emotion regulation for older adults than for younger adults. As shown in Figure 5A, older adults’ greater activation in PFC when processing negative stimuli does not tend to occur in ventromedial PFC. Instead, the activations tend to be in more dorsal regions of PFC. While the peak regions activated more for older adults for positive than negative stimuli also extend into dorsal PFC, they show more overlap with ventromedial PFC. Thus, when compared with younger adults, older adults’ greater PFC activity for negative than neutral stimuli is not centered in ventromedial PFC, whereas their greater PFC activity for positive than negative stimuli is more likely to be seen in ventromedial PFC (Fig. 5B).

Whether or not people remember information can help indicate how deeply they processed it. But

there are many different types of processing that can enhance later memory for new information. For instance, when seeing a picture of a forest scene, someone might focus on trying to identify the types of tree shown, whereas someone else might think about how the picture makes them feel happy and relaxed. Both types of associations should increase the likelihood of remembering the picture, but be associated with different patterns of brain activity during encoding. Interestingly, a number of studies have revealed age differences in the patterns of brain activity associated with successful encoding of emotional stimuli. For instance, in a study in which participants rated whether objects would fit in a file drawer, there was an interaction of item valence and age group on later recognition, such that older adults were as effective as younger adults at remembering positive items but less effective at remembering negative and neutral items.^{77,78} Successful recognition of positive items was more associated with ventromedial PFC for older adults than younger adults.⁷⁸ Also, during encoding of positive information, the ventromedial PFC and amygdala were more strongly correlated with hippocampal activity for older adults than for younger adults.⁷⁷ Medial PFC is activated by thinking about one’s relationship to external stimuli,⁷⁹ and so one potential explanation for older adults’ greater ventromedial PFC activity while processing positive stimuli is that they are thinking more about how the positive stimuli relate to themselves than younger adults do.⁸⁰

Age differences have also been found in brain regions associated with encoding of fearful faces,⁸¹ as successful encoding of fearful faces was more associated with amygdala and hippocampus in younger adults than older adults and more associated with insula and dorsolateral PFC in older adults than younger adults.

In another study,⁸² brain activity during memory encoding of negative stimuli differed by age group, with older adults showing less functional connectivity than younger adults between the amygdala and hippocampus but more functional connectivity between the amygdala and dorsolateral PFC. As expected based on previous studies, younger adults showed a larger advantage in memory for negative stimuli than older adults did. Thus, across studies, there are contrasting patterns of older adults’ amygdala connectivity during memory encoding for

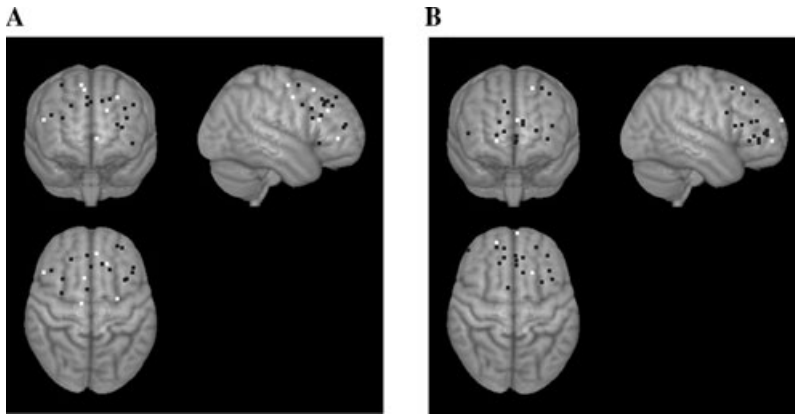


Figure 5. Across fMRI studies reviewed by Nashiro, Sakaki, and Mather,⁵³ peak activations are shown for age differences in prefrontal involvement while processing (A) negative stimuli and (B) positive stimuli. Peak activations that were greater for older than younger are shown in black; those greater for younger are shown in white. On average, the contrasts in which older adults showed greater activity than younger adults for negative stimuli tended to yield more dorsal peak activity foci (mean MNI $Z = 25.7$) than the contrasts in which older adults showed greater activity than younger adults for positive stimuli (mean MNI $Z = 18.5$; comparison of negative and positive $t(29) = 2.33, P < .05$). [Correction added after online publication. 03/26/2012: the previous symbol was changed from $>$ to $<$.] Figures are from Nashiro *et al.*⁵³

positive stimuli⁷⁷ (ventromedial PFC) and negative stimuli⁸² (dorsolateral PFC).

Elucidating how the PFC–amygdala connectivity changes with age is important, as preservation of this connectivity is associated with well-being. A study in which older adult participants (aged 64–89) simply viewed a series of positive, negative, and neutral pictures while in an fMRI scanner reveals that PFC–amygdala connectivity during memory encoding relates to well-being in everyday life.⁸³ Participants with high life satisfaction showed stronger correlations in activity between the orbitofrontal cortex, ventromedial PFC, hippocampus, amygdala, and thalamus during viewing positive pictures than during viewing negative pictures, whereas these differences in functional connectivity were weaker for those lower in life satisfaction. Thus, emotion-processing and memory-encoding regions showed more coordinated activity during viewing positive than negative pictures for those high in life satisfaction.

The findings reviewed in this section reveal that, compared with younger adults, older adults show a greater increase in PFC and decrease in amygdala activity when just asked to view negative stimuli compared with neutral stimuli, but that when asked to deeply process stimuli, they show a greater increase in PFC activity for positive over negative stimuli.⁵³ In these contexts in which there are no instructions to regulate emotions, older adults tend to

engage more dorsal PFC cognitive control regions (possibly to diminish the emotional impact of negative stimuli) and more ventromedial PFC (possibly to engage more deeply with self-relevant aspects of positive stimuli). Furthermore, those who show more coordination of PFC regions with memory encoding regions when processing emotional information appear to be more likely to have high levels of well-being in everyday life.

When instructed to regulate, age differences depend on type of strategy and the specific instructions given

The findings reviewed in the two previous sections suggest that older adults tend to engage in emotion regulation as a default mode whereas younger adults need to be reminded of their emotions to activate emotion regulation goals. They also indicate that older adults select different emotion regulation strategies than younger adults. However, they do not address the question of whether older adults are generally better than younger adults at regulating emotion when emotion regulation is the top priority for both age groups.

Laboratory studies that instruct people to up- or downregulate their emotions using a specific strategy while viewing emotional film clips or pictures reveal different patterns of findings across types of regulation strategies. One consistent pattern is that older adults are not impaired at suppressing the

expression of emotion when instructed to do so.^{84–86} Furthermore, older adults also show less cost of suppressing emotional expression in terms of memory for the stimuli shown during suppression trials.⁸⁷ The findings of a reduced cost of suppression for older adults suggest that they use different strategies than younger adults when trying to suppress their outward emotional expressions, but that these strategies do not involve ignoring the emotion elicitor.

In contrast, studies that instruct participants to reappraise emotional stimuli reveal mixed findings, which may result from the different reappraisal instructions given. For instance, when attention deployment is controlled so that participants must attend to an aversive stimulus, older adults are worse than younger adults at diminishing their negative reactions by reappraising the meaning of those stimuli.⁸⁸ However, when attention deployment is not controlled, older adults are better than younger adults at diminishing their negative reactions when given reappraisal instructions.⁸⁹ One possibility is that, when attention deployment is not controlled, older adults will try to ignore the negative stimuli rather than reappraise them, despite the instructions.

Other studies suggest that older adults are better than younger adults at implementing some types of refocusing or reappraisal strategies (e.g., focusing away from a negative stimulus by thinking about a positive memory⁸⁶) but worse at others (e.g., thinking of themselves as an emotionally detached and objective third party⁹⁰).

These differences across studies suggest that focusing on nonemotional aspects of a negative effect-inducing situation is not an effective strategy for older adults, whereas focusing on something else works well for them. This may relate to age-related increases in distractibility;²⁷ ignoring one aspect of a situation while attending to another may be more challenging than ignoring the whole situation while attending to something unrelated.

In the study that involved a detachment reappraisal strategy,⁹⁰ participants were scanned during the task and, in general, younger and older adults both showed greater PFC but less amygdala activity during “reappraise” trials than during “experience” trials. Thus, when people are trying to regulate emotion using a detached reappraisal strategy, younger and older adults show similar patterns

of brain activity. However, one age difference that emerged was that for the negative reappraise versus experience contrast, younger adults showed a larger difference in activity in the left lateral inferior frontal gyrus than older adults did. For older adults, but not younger adults, activity in this region was related to regulation success on negative trials. That age differences emerged in the left inferior frontal cortex is intriguing given that this region may be recruited to help avoid negative distraction as discussed earlier. Across all participants in this study (controlling for age), higher scores on a composite score from a battery of cognitive tests testing response speed, memory, and executive function predicted less amygdala activation when down-regulating negative affect. Thus, higher cognitive function was associated with more effective emotion regulation when instructed to do so, both for younger and for older adults.

More striking age differences in PFC activity were seen in another fMRI reappraisal study in which gaze was controlled while participants reappraised the meaning of negative pictures.⁸⁸ In this study, older adults showed less ventrolateral and dorsomedial PFC activity than younger adults while reappraising negative images. Thus, it seems that the less that older adults are able to use attention redeployment strategies, the more that age differences emerge.

Another interesting age difference is that, when asked to downregulate negative reactions after watching a disgusting video, older adults showed less cost in terms of their concurrent working memory performance than did younger adults.⁹¹ Participants were told to use whatever emotion regulation strategy they had available, thus it could be that the emotion regulation strategies employed by older adults were less cognitively taxing than the strategies employed by younger adults.

In summary, previous studies comparing younger and older adults’ effectiveness at implementing specific emotion regulation strategies when instructed to do so reveal mixed findings.⁹² Older adults are as good as younger adults at suppressing facial expression of their emotions and experience less cost of this strategy in terms of what they remember. Reappraisal or refocusing success varies widely, with some studies finding that younger adults do better and other studies finding that older adults do better. These differences likely stem from differences in reappraisal instructions. In particular, older adults

do well when cued to direct their attention to something else entirely⁸⁶ or to reappraise the meaning of negative stimuli,⁸⁹ but not when they are asked to be emotionally detached⁹⁰ or to focus on nonemotional aspects of the emotion-eliciting event.⁸⁹

At the outset of this paper, I noted that there are two obvious potential explanations for the paradox of emotional well-being in aging. The first is that older adults are better at regulating their emotions. However, as should now be clear, neither younger nor older adults are consistently better than the other group at regulating emotion. Instead, the story is more nuanced. Older adults excel at some modes of regulating emotion (such as avoiding attending to negative stimuli) but not at others (such as certain types of reappraisal). In addition, the research reviewed here suggests that, in their everyday lives, older adults favor different emotion regulation strategies and focus more of their cognitive resources on regulating emotion than younger adults do. These age-related shifts in strategy selection and resource allocation may shape well-being more than age-related changes in emotion regulation skill level.

Age differences in the initial emotional sensation

The other potential explanation for the paradox of emotional well-being in aging mentioned at the outset of this paper was that negative stimuli and emotions may be less potent for older adults than for younger adults, and therefore older adults experience less negative affect. There are at least a couple of ways that negative stimuli might feel less potent for older adults. The first is due to declines in interoceptive processes. Part of what determines initial emotional sensations are cues from brain regions that perceive body sensations, such as heartbeats, breath, gastrointestinal sensations, and flushing of the skin. These contribute to people's interoception of their own body states and help shape the feeling and intensity of emotions.^{93,94} With age, people are less aware of visceral sensations such as esophageal pain,⁹⁵ rectal distension,⁹⁶ gastric distension,⁹⁷ and heartbeats.⁹⁸ Multiple factors may contribute to this reduced perception of bodily states. Brain regions critical for interoception, such as the insula, decline in volume with age⁹⁹ and the specificity of neural representations decreases in the somatosensory cortex.¹⁰⁰ Changes in signal transmission in afferent

fibers and changes in neurotransmitter quantity and metabolism may also contribute to the age-related declines in interoception.^{101,102} Unfortunately, existing research provides little information about how age differences in interoception may relate to emotional experience and general well-being, but it is an important question for future research.

The second way that negative stimuli might feel less potent is if the amygdala's preferential processing of negative arousing stimuli declines with age. This is the explanation for the positivity effect put forward in the "aging-brain model,"¹⁰³ in which age-related declines lead the amygdala to activate less in response to negative stimuli, which in turn diminishes the arousal response to those stimuli and impairs later memory for them.

Certainly, as already reviewed, compared with younger adults, older adults do typically show less amygdala activity in response to negative stimuli.^{67,68,71,104} However, reduced amygdala response is not necessarily an indication of poor function. Studies of emotion regulation indicate that people show less amygdala response to negative stimuli when they are asked to diminish their emotional response to those stimuli along with greater prefrontal activity,^{22,105} and so older adults' pattern of greater PFC and reduced amygdala activity when told to observe negative stimuli may reflect spontaneous (uninstructed by the experimenter) emotion regulation. Furthermore, the amygdala is one of the regions showing the most declines in volume in Alzheimer's disease,¹⁰⁶ yet patients with Alzheimer's disease show hyperactive amygdala responses to novel fearful faces relative to healthy older adults.¹⁰⁷ Thus, diminished responses might not be the pattern expected from an amygdala in decline.

Other data also suggest that age differences in amygdala function reflect shifts in processing strategies more than declines in functional capacity. For instance, fMRI studies that included positive as well as negative and neutral pictures reveal an age by valence interaction in the amygdala (e.g., Fig. 6) such that, unlike younger adults, older adults showed the most amygdala activity in response to positive rather than negative pictures.^{69,104} (See also Ref. 83.) Thus, older adults' decreased amygdala response is selective to negative stimuli and does not extend to positive stimuli—a pattern indicating that the amygdala maintains the capacity to respond to emotionally arousing stimuli.

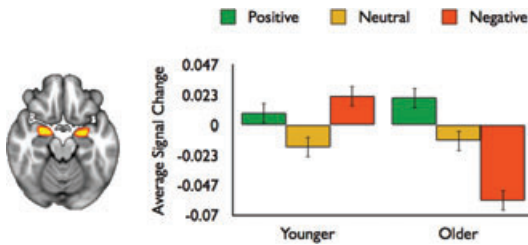


Figure 6. Average signal change in the amygdala for younger and older adults while viewing positive, neutral, or negative pictures. Figure is adapted from Mather *et al.*¹⁰⁴

Another interesting pattern across studies noted by Kensinger and Leclerc⁸⁰ is that older adults showed as much of an increase as younger adults in amygdala activity in response to novel fearful compared with familiar neutral faces in studies in which faces were presented rapidly (at a 200-ms rate),^{108,107} but showed less amygdala response to negative stimuli than younger adults in studies in which faces were presented more slowly.^{67,68,71} Thus, age-related declines in negative affect are unlikely the result of impairments in amygdala initial responsiveness to negative stimuli, but rather arise because of how older adults subsequently respond.

Behavioral data also indicate that younger and older adults show similar responses to arousing negative stimuli initially, but then diverge. For instance, older adults show at least as much of an advantage as younger adults in detecting emotional or threatening stimuli.^{109,110} Indeed, within one study, older adults showed as much of an advantage as younger adults in detecting angry faces in a matrix of happy or neutral faces but were more efficient than younger adults at detecting happy or neutral faces in a matrix of angry faces, indicating they were less distracted by nontarget angry faces than other types of nontarget faces.¹¹¹ Thus, older adults' enhanced ability to avoid distraction from negative stimuli does not stem from impairments in being able to detect those stimuli.

These brain and behavioral data showing similar rapid responses to potentially threatening stimuli among younger and older adults argue against the idea that older adults' shifts away from attending to negative stimuli are due to declines in amygdala function and the ability to monitor and quickly notice negative stimuli. Instead, the age differences emerge in later processing, when strategic processes have more influence.

In summary, there are age-related declines in the types of interoceptive sensation that contribute to emotional experience. Such declines may decrease the intensity of some negative emotions, making the task of regulating emotion less challenging for older adults than for younger adults. However, another aspect of initial emotional experience—detecting negative stimuli—still seems intact in normal aging and the amygdala still responds to emotionally arousing stimuli that are positive or that are negative but displayed too rapidly for strategic processes to diminish responding.

Late-life depression is often associated with PFC damage

So far, this review has focused on the general pattern of well-maintained emotional well-being in late life. However, some people do get unhappier with age, and some even experience an episode of major depression for the first time late in life. In this section, I review how depression in late life might relate to the neural systems already discussed.

In the U.S. population, the incidence of depression in the past 12 months decreases across age cohorts, with the highest incidence among those 18–29 and the lowest among those greater than 65.¹¹² In addition, the likelihood of experiencing one's first episode of major depression is lower among those older than 65 than in the other age groups. However, among those older adults experiencing major depression, it appears that for at least half of them, this is their first episode of depression.¹¹³

Late-onset depression differs in many ways from early-onset depression. It seems to be less genetically determined¹¹⁴ and is associated with frontostriatal abnormalities, executive control deficits, and the presence of vascular disease. This syndrome is known as "vascular depression," and the hypothesis is that cerebrovascular disease leads to damage in white matter tracts connecting frontal regions with striatum, amygdala, and hippocampus.^{115–118} According to the vascular depression hypothesis, this damage impairs basic emotion regulation functions and leads to depression that is less amenable to antidepressant treatment. For instance, patients over the age of 60 who were still depressed after a 12-week treatment with escitalopram, a selective serotonin reuptake inhibitor antidepressant, initially had more white matter abnormalities in multiple frontal brain regions than patients who responded to the

antidepressants,^{119,120} and nonresponders also initially had lower semantic fluency performance than responders.¹²¹ Also, suggesting a link between PFC function and vascular depression are findings that repetitive transcranial magnetic stimulation to the left dorsolateral PFC led to greater remission from depression among patients with clinically defined vascular depression than did sham stimulation.¹²²

Analysis of a large sample of older depressed patients indicated that a vascular depression profile could be distinguished from other types of depression by a high probability of having deep white matter MRI hyperintensities, executive dysfunction, and late-life onset of the depression.¹²³ This subtype was nearly perfectly identified by the presence of deep white matter hyperintensities, although including executive dysfunction as a measure increased the accuracy of class membership identification. In addition, a meta-analysis of 30 studies revealed that late-life onset of depression was associated with more frequent and intense white matter abnormalities than earlier-onset depression.¹²⁴

Impaired ACC function has been identified as a key feature of depression in younger adults,¹²⁵ which may be due to the role of the ACC in integrating ventral and subcortical networks with dorsal cognitive networks in ways that support the experience and regulation of emotion.¹²⁶ Older depressed patients who did not respond to antidepressant treatment had smaller dorsal and rostral ACC volume than those who did remit.¹²⁷ Thus, in older adults, preservation of the ACC may be an important determinant in recovery from depression.

In summary, depression in later life is often associated with white matter damage in frontostriatal and limbic regions and with decline in executive function. These associations suggest that age-related vulnerability to PFC decline, especially in PFC white matter, affects emotion regulation abilities. Older adults who, because of vascular disease or other risk factors, show the most decline in executive function, also are likely to be those who lose the ability to regulate emotion successfully and thus become more vulnerable to depression.

Conclusions

Knowing about the declines expected in cognitive function and physical health for older adults might lead one to predict significant declines in well-being and emotion regulation. But a paradox of aging

is that the frequency of negative affect and incidence of depression actually decrease. What might explain this surprising pattern? This review highlights the fact that age-related changes in emotion cannot be explained simply by which brain regions decline most structurally with age, although such brain changes may help shape emotion regulation strategies. In addition, other obvious explanations, such as the ideas that older adults are more skilled at regulating emotions or experience negative stimuli less intensely, also are insufficient to explain the full pattern of age-related changes. Instead, it is important to consider age-related shifts in preferred strategies and priorities and how these interact with the strengths and vulnerabilities of the aging brain to better understand how emotional experience changes with age.

Compared with younger adults, older adults pay attention to different types of emotional stimuli and prefer to regulate their emotions in different ways. In their attention and memory, older adults often show a positivity effect, in which they favor positive relative to negative stimuli more than younger adults do. Despite age impairments in ignoring neutral distractions, older adults are even better than younger adults at ignoring distracting negative stimuli. Furthermore, with age preferred emotion regulation strategies shift to favor suppression over rumination or reappraisal. When viewing emotional stimuli, older adults often show an increase in prefrontal activity (relative to viewing neutral stimuli) that is greater than that shown by younger adults.

How do these findings relate to the fact that that ventromedial prefrontal brain regions, supporting the types of emotion processing strategies older adults excel at and prefer, decline less structurally than dorsal and lateral prefrontal brain regions (Fig. 1)? Ventromedial PFC has been linked to many aspects of emotion regulation, and older adults have been shown to engage it more when deeply processing positive stimuli than younger adults. However, not all of the age changes in emotion processing can be explained by a greater reliance on ventromedial PFC among older adults. In younger adults, lateral left inferior frontal gyrus is associated with ignoring negative distraction, which is something that older adults excel at despite significant age-related declines in cortical thickness in this region. Older adults often show greater increases in dorsal PFC activity when viewing negative stimuli (relative

to neutral stimuli) compared with younger adults (Fig. 5A), again despite the fact that there are age-related declines in this region. Thus, older adults appear to recruit a variety of prefrontal regions when confronted with negative stimuli—including prefrontal subregions that show significant age-related structural decline as well as those that do not.

This pattern of findings can be explained by the idea that, in addition to age-related changes in brain circuitry underlying emotional processing, there are age-related changes in emotional goals that lead older adults to focus more on regulating emotions. Older adults therefore are more likely to recruit prefrontal resources to regulate emotions than younger adults are. Some emotion regulation strategies, such as reappraisal, may be more difficult for older than younger adults to successfully implement. But unless specifically asked to use such strategies, older adults may be able to downregulate negative affect more effectively than younger adults by focusing more of their resources on this goal and by using strategies that work well for them, such as selectively attending to or ignoring stimuli.

In conclusion, the brain shows many changes with age, and in cognition, these changes mostly result in declines in function. This is not the case for emotional processing. Understanding how some emotional functions can be well-maintained despite declines in brain function should not only advance theories about emotion, but should also help clinicians design interventions to support effective emotional processes throughout life.

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Conflicts of interest

The author declares no conflicts of interest.

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