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Emotion processing in the aging brain is modulated by semantic elaboration

Maureen Ritchey[a,b,*], Brandy Bessette-Symons[c], Scott M. Hayes[d,e], Roberto Cabeza[a,b]

[a] Center for Cognitive Neuroscience, Duke University, United States
[b] Department of Psychology & Neuroscience, Duke University, United States
[c] Department of Psychology, Ithaca College, United States
[d] Memory Disorders Research Center & Neuroimaging Center, VA Boston Healthcare System, United States
[e] Department of Psychiatry, Boston University School of Medicine, United States

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ABSTRACT

The neural correlates of emotion processing have been shown to vary with age: older adults (OAs) exhibit increased frontal activations and, under some circumstances, decreased amygdala activations relative to young adults (YAs) during emotion processing. Some of these differences are additionally modulated by valence, with age-related biases toward positive versus negative stimuli, and are thought to depend on OAs' capacity for controlled elaboration. However, the role of semantic elaboration in mediating valence effects in the aging brain has not yet been explicitly tested. In the present study, YAs and OAs were scanned while they viewed negative, neutral, and positive pictures during either a deep, elaborative task or a shallow, perceptual task. fMRI results reveal that emotion-related activity in the amygdala is preserved in aging and insensitive to elaboration demands. This study provides novel evidence that differences in valence processing are modulated by elaboration: relative to YAs, OAs show enhanced activity in the medial prefrontal cortex (PFC) and ventrolateral PFC in response to positive versus negative stimuli, but only during elaborative processing. These positive valence effects are predicted by individual differences in executive function in OAs for the deep but not shallow task. Finally, psychophysiological interaction analyses reveal age effects on valence-dependent functional connectivity between medial PFC and ventral striatum, as well as age and task effects on medial PFC-retrosplenial cortex interactions. Altogether, these findings provide support for the hypothesis that valence shifts in the aging brain are mediated by controlled processes such as semantic elaboration, self-referential processing, and emotion regulation.

Emotion processing is well-preserved relative to other cognitive functions in aging, with little structural decline in the amygdala (Grieve, Clark, Williams, Peduto, & Gordon, 2005; Soininen et al., 1994) as well as few changes in the ability to detect emotional information (LaBar, Mesulam, Gitelman, & Weintraub, 2000; Mather & Knight, 2006). However, there may be alterations in how older adults (OAs) prioritize emotional information relative to young adults (YAs), in that OAs tend to focus more on positively valenced information and less on negatively valenced information (e.g., Isaacowitz, Wadlinger, Goren, & Wilson, 2006; Kennedy, Mather, & Carstensen, 2004; Mather & Carstensen, 2003; Mather & Knight, 2005; but see Leclerc & Kensinger, 2008b; Mickley Steinmetz, Muscatell, & Kensinger, 2010). Complementing these behavioral findings, OAs tend to show different patterns of brain activity in response to emotional material when compared to YAs. These differences have been characterized as under-recruitment of the amygdala (e.g., Gunning-Dixon et al., 2003; Iidaka et al., 2002; Tessitore et al., 2005) and over-recruitment of frontal control regions (e.g., Leclerc & Kensinger, 2008a; St. Jacques, Dolcos, & Cabeza, 2010), a pattern that has been referred to as Fronto-amygdalar Age-related Differences in Emotion (FADE; St. Jacques, Bessette-Symons, & Cabeza, 2009).

Despite this gross characterization, amygdala findings have been mixed—although some studies report amygdala under-recruitment in aging (Fischer et al., 2005; Gunning-Dixon et al., 2003; Iidaka et al., 2002; Murty et al., 2009; Tessitore et al., 2005), others report no change (Leclerc & Kensinger, 2008a; Mather et al., 2004; St. Jacques et al., 2010; Wright, Wedig, Williams, Rauch, & Albert, 2006). This discrepancy has been linked to differences in emotion ratings between age groups: those studies that report rating differences tend to also report amygdala differences, whereas the others do not (St. Jacques et al., 2009). There may also be differences in responses to negatively versus positively valenced stimuli, with the latter eliciting enhanced activity in OAs relative to YAs

* Corresponding author at: Center for Cognitive Neuroscience, Duke University, Box 90999, LSRC Bldg., Durham, NC 27708, United States. Tel.: +1 919 668 2299; fax: +1 919 681 0815.
E-mail address: maureen.ritchey@duke.edu (M. Ritchey).

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(Mather et al., 2004). Frontal findings, however, have been fairly consistent: OAs tend to recruit greater activity in frontal regions such as the medial prefrontal cortex (PFC) (St. Jacques et al., 2010; Tessitore et al., 2005) and lateral PFC (Gunning-Dixon et al., 2003; Murty et al., 2009; Tessitore et al., 2005) during emotion processing relative to YAs. Taken together, these findings are consistent with the assumptions that amygdala responses map onto OAs' reported emotional experience, and that this experience may be affected by age-related increases in emotion control, mediated by the frontal lobes. At the neural level, these findings are also compatible with a general pattern of neural activity in aging, referred to as the Posterior-to-Anterior Shift in Aging (PASA). This shift has been hypothesized to reflect heightened recruitment of frontal control regions as compensation for reductions in processing in posterior brain regions, such as perceptual processing in visual cortex, that typically accompany aging (Grady et al., 1994). PASA has been identified in numerous functional neuroimaging studies of aging across multiple cognitive domains (e.g., Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Dennis & Cabeza, 2008).

Within the domain of emotion processing, increased recruitment of frontal regions may be indicative of enhanced semantic elaboration of positively valenced stimuli or down-regulation of responses to negatively valenced stimuli. Behavioral studies of emotion processing in OAs have been marked by shifts in valence processing, characterized both as positivity shifts (Mather & Carstenson, 2005; Mather & Knight, 2005) and negativity reductions (Charles, Mather, & Carstenson, 2003; St. Jacques et al., 2010). OAs exhibit attentional biases toward positive and away from negative information relative to YAs (Isaacowitz et al., 2006; but see Leclerc & Kensinger, 2008b; Mather & Carstensen, 2003) and retrieve more positive memories than negative whereas YAs tend to show the reverse pattern (Kennedy et al., 2004; Mather & Knight, 2005). Theories espousing positivity shifts have tended to emphasize enhanced elaboration and up-regulation of positively valenced stimuli as OAs attempt to maximize positive affect as they get older (socioemotional selectivity theory; reviewed by Mather & Carstenson, 2005).

In keeping with these theories, behavioral positivity shifts are correlated with individual differences in executive function (Mather & Knight, 2005), which are presumably supported by the frontal lobes (Miller & Cohen, 2001), and are eliminated under divided attention conditions (Mather & Knight, 2005). Within the frontal lobes, the medial PFC is a likely candidate for mediating age-related positivity shifts. Positive versus negative or neutral stimuli tend to elicit greater activations in medial PFC in young populations (Dolcos, LaBar, & Cabeza, 2004; Kensinger & Schacter, 2006), though medial PFC regions also may be more broadly involved in emotional experience (Phan, Wager, Taylor, & Liberzon, 2002) and control (Ochsner & Gross, 2005). OAs have been shown to over-recruit the medial PFC in response to positive versus negative stimuli relative to YAs (Gutchess, Kensinger, & Schacter, 2007; Leclerc & Kensinger, 2008a). A similar pattern has also been observed in lateral PFC (Gutchess et al., 2007). Enhanced medial PFC activation in response to positive stimuli may be attributable to self-referential processing. The medial PFC shows heightened activity when participants attend to stimuli that are self-relevant versus non-relevant (Gutchess et al., 2007; Kelley et al., 2002) and retrieve autobiographical memories (Cabeza et al., 2004; Levine et al., 2004). The capacity for self-referential processing appears to be intact in aging (Glisky & Marquine, 2009), and its association with the medial PFC has been replicated in OAs, in that both young and older adults show heightened activity in this region when evaluating whether adjectives describe one's self or another person (Gutchess et al., 2007). Altogether, these findings engender the interpretation that age-related over-recruitment of the frontal lobes during positive valence processing may reflect controlled, elaborative processes instantiated in the medial PFC (Kensinger & Leclerc, 2009).

In contrast to these positive valence effects, there is additional evidence that OAs over-recruit the PFC in response to negatively valenced stimuli. Reductions in attention to and memory for negative stimuli in OAs have been interpreted as the results of emotion regulation processes designed to mitigate negative emotion (as reviewed by Mather & Carstenson, 2005; St. Jacques et al., 2009). In keeping with this idea, heightened frontal responses to negative stimuli have been interpreted as indexing emotion regulation processes in OAs, evidenced by concomitant increases in emotional stability (Williams et al., 2006) and decreases in amygdala response to negative stimuli (Gunning-Dixon et al., 2003; Tessitore et al., 2005), as well as negative correlations between frontal and amygdala regions (St. Jacques et al., 2010; Urry et al., 2006). One of these studies also identified decreases in amygdala response to stimuli that normative ratings classify as negative but OAs' individual ratings classify as neutral, suggesting reductions in perceived negativity and corresponding amygdala response (St. Jacques et al., 2010). A recent study explicitly tested the neural consequences of reappraisal, an emotion regulation strategy, in both YAs and OAs, and showed that reappraisal was associated with increased frontal and decreased amygdalar activations (Winecoff, Labar, Madden, Cabeza, & Huettel, 2010). Finally, there is evidence that in addition to predicting behavioral valence shifts (Mather & Knight, 2005), individual differences in executive function modulate the degree to which OAs engage ventrolateral PFC while inhibiting negative responses to stigmatized individuals (Krendl, Heatherton, & Kensinger, 2009), as well as the degree to which OAs down-regulate amygdala activation during reappraisal (Winecoff et al., 2010).

Although OAs' dependency on medial and lateral PFC regions during emotional processing has been hypothesized to reflect controlled processes, direct evidence supporting this hypothesis is scarce. Divided attention studies have provided behavioral evidence for a relationship between controlled processes and age effects on emotional processing (Mather & Knight, 2005); however, there is no direct evidence tying these effects to age differences in medial and lateral PFC. In addition, divided attention impacts multiple aspects of controlled processing, leaving open the question of which core mechanisms drive age effects on emotional processing. One way to address these questions is to modulate the task demands on semantic elaboration, thus targeting a specific candidate mechanism for the described age effects. Semantic elaboration is likely to be a subcomponent of emotion regulation and appraisal (Ochsner et al., 2009). By definition, the emotion regulation strategy of reappraisal involves re-interpreting the affective meaning of an event or stimulus, and not surprisingly, compared with distraction, reappraisal involves increased recruitment of regions associated with semantic processing such as left lateral prefrontal and temporal regions (McRae et al., 2010). Furthermore, reappraisal of emotional pictures boosts subsequent memory for those pictures, thought to be driven by this regulation strategy's reliance on semantic processing (Dillon, Ritchey, Johnson, & LaBar, 2007). Self-referential processing also shares some features and substrates with semantic processing, in that both promote enhanced subsequent memory and left lateral PFC recruitment (Craik et al., 1999; Kelley et al., 2002). Although medial PFC involvement in self-referential processing may reflect a more specialized mechanism that is not exclusively driven by semantic functions (Glisky & Marquine, 2009; Kelley et al., 2002), enhancements in semantic processing may increase the likelihood that a stimulus may be interpreted as self-relevant and thus facilitate the recruitment of these other self-referential processes. Thus, because of these links to other higher-order functions, semantic elaboration may provide an access point by which one can test the influence of aging on emotional control.