RUNNING HEAD: Functional Neuroimaging Studies of Aging and Emotion

Functional Neuroimaging Studies of Aging and Emotion: Fronto-Amygdalar Differences during Emotional Perception and Episodic Memory

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Keyword: fMRI, affect, frontal cortex, amygdala, older adults, emotional regulation

In press at Journal of International Neuropsychological Society

Word Counts:

Abstract = 91

Manuscript = 2865

References = 46

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Abstract

Emotional processes are enhanced in aging, such that aging is characterized by superior emotional regulation. This article provides a brief review of the neural bases supporting this effect with a focus on functional neuroimaging studies of perception and episodic memory. The most consistent finding across these studies is that older adults show an alteration in the recruitment of the amygdala, but greater recruitment of the frontal cortex. These *Fronto-amygdalar Age-related Differences in Emotion* (FADE) may reflect emotional regulation strategies mediated by frontal brain regions that dampen emotion-related activations in the amygdala.

In the last decade, the number of empirical studies examining emotion and aging has risen substantially. Despite age-related declines in many cognitive domains (Dennis & Cabeza, 2008), healthy aging has less of an impact on emotion (Kensinger, 2008) and has been characterized by superior emotional regulation, the ability to exert control over emotional responses (Ochsner & Gross, 2005). According to socioemotional selective theory, aging is associated with motivational differences in allocating attention to emotional information. This leads to increases in mood and well-being, and potentially greater likelihood that positive events will be attended to and remembered (positivity shift; Mather & Carstensen, 2005). In sum, there are a substantial number of behavioral studies demonstrating that emotional processes are maintained and sometimes enhanced in aging. However, it is critical to also understand the neural mechanisms underlying the effects of aging on emotion in order to distinguish potential age-related differences in emotional regulation strategies and to dissociate memory encoding versus retrieval processes. The present article provides a brief review of the small, but growing literature on functional neuroimaging studies investigating the effects of aging on emotional perception and episodic memory. Although the field is complex, and sometimes contradictory due to many differences between studies (e.g., stimuli, particular contrast & task, etc.; see **Table 1**) there is a consistent pattern whereby aging is associated with alterations in amygdalar activity coupled with an increase in frontal activity, particularly in medial frontal regions associated with emotional regulation processes. Table 1 summarizes the results of age-related functional neuroimaging studies of emotional perception and episodic memory by showing both age-related differences and age-invariant activations elicited across a number of brain regions. We call this pattern *Fronto-amygdalar Age-related Differences in Emotion* (FADE). Before turning to the evidence supporting or opposing the FADE pattern we begin with an overview of the neural systems involved in emotional processing and the impact of aging.

Table 1 here

The Emotional Brain and Aging

The neural processing of emotionally salient events involves many brain regions (Phan et al., 2002) including automatic processes in the amygdala and controlled processes in the prefrontal cortex (PFC). The amygdala is critical for the detection of emotions and the generation of physiological responses. Furthermore, the amygdala optimizes perception and memory of emotional events through its dense connections with cortical and sub-cortical areas

(Amaral & Price, 1984), including the modulation of memory consolidation (LaBar & Cabeza, 2006). In contrast, the PFC exerts control over emotions (Ochsner & Gross, 2005), with medial and lateral sub-regions supporting different neural processes. First, medial PFC (Brodmann's Area 10), including nearby anterior cingulate cortex (ACC; Brodmann's Area 32, 24), coordinates the generation and regulation of affect (Phan, et al., 2002). Anterior medial PFC regions (particularly BA 10) are also associated with self-referential processes (Amodio & Frith, 2006), which refers to relating information to one's self. Medial PFC is part of the default network, which refers to a set of regions that tend to be deactivated during attention demanding tasks and activated during internally focused tasks, such as during rest (Gusnard et al., 2001). The default network is implicated in emotionally meaningful events (Cabeza & St Jacques, 2007) and malfunctions in depressed patients (Mayberg, 1997; Sheline, et al., 2009). Second, lateral PFC regions (Brodmann's Area 44/46, 46/9) are more generally related to controlled processes (Miller & Cohen, 2001) that contribute to emotional regulation (Ochsner & Gross, 2005).

Compared to structural and functional decline in other brain regions, the amygdala and some sub-regions of the PFC might be less vulnerable to aging. First, the structural integrity of the amygdala remains relatively preserved in aging (Good, et al., 2001; Grieve et al., 2005), as does the functional recruitment of this region to novelty (Wright, et al., 2008; Wright et al., 2006). Second, there is evidence for structural integrity of the medial PFC and ACC (Salat, Kaye, & Janowsky, 2001; also see Raz & Rodrigue, 2006; although see Petit-Taboue et al., 1998). In fact, older adults sometimes show less deactivation in medial PFC regions during cognitive tasks (Grady et al., 2006), which has been linked to their difficulty in disengaging default mode activity during these attention demanding tasks. One interpretation of this finding is that older adults chronically engage self-referential processes (Kensinger & Leclerc, 2009), which might interfere or benefit performance depending upon the particular cognitive task (Gutchess et al., 2007b). In contrast to the medial PFC, aging has a large impact on the structural integrity of the lateral PFC (Raz, et al., 2005). Functional neuroimaging studies have shown that lateral PFC regions are over-recruited in aging (Grady, 2008). In particular, greater age-related recruitment of the PFC is typically coupled with a reduction in the recruitment of posterior regions (Posterior-Anterior Shift in Aging, PASA; Dennis & Cabeza, 2008), a pattern of activation linked to compensation (Davis et al., 2008).

In sum, the relative preservation of the structure and function of the amygdala and specific frontal regions in older adults might underlie the maintenance and enhancement of emotional processes in aging.

Aging and Emotional Perception

Functional neuroimaging studies of age-related differences in emotional perception are generally consistent with the FADE pattern.   Below we discuss the findings relevant to the amygdala and frontal cortices, and the interaction between these regions.

One of the most consistent finding from functional neuroimaging studies of emotional perception is an age-related reduction in amygdala activation for negative stimuli (**see Table 1**). For example, in the first fMRI study of emotion and aging, Iidaka et al. (2002) found less left amygdala activity for negative faces in older adults when compared to young adults, and other studies have since replicated this finding (Fischer, et al., 2005; Gunning-Dixon, et al., 2003; Tessitore, et al., 2005; also see Erk et al., 2008). However, in the aforementioned studies (Gunning-Dixon, et al., 2003; Iidaka, et al., 2002; Tessitore, et al., 2005) older adults reported negative stimuli valence ratings that were less negative than the ones given by young adults and associated with the standardized ratings (Lang et al., 1997). Thus, one possible interpretation is that the age-related reduction in amygdala activity reflects an inability of the stimuli to elicit strong negative emotions in older adults rather than a deficit in amygdala function. Consistent with this idea, others and we have found that amygdala activity can be as strong in older as in young adults when stimuli were classified according to participants' own ratings (Leclerc & Kensinger, 2008a; Mather, et al., 2004; St Jacques et al., 2008; Wright, et al., 2006) or when there were no age-related differences in emotional ratings (Fischer, et al., 2005). Furthermore, we (St Jacques, et al., 2008) found that amygdala activity was indeed reduced for negative stimuli that older adults subjectively rated as neutral. Interestingly, age-invariant activity in the amygdala is typically observed for positive stimuli (Gutchess et al., 2007a; Leclerc & Kensinger, 2008b; Mather, et al., 2004; although see Williams, et al., 2006), and might reflect a shift in the preference of amygdala activation in aging (Mather, et al., 2004; also see Wright, et al., 2006, 2007). In sum, the function of the amygdala remains intact in aging. Below we discuss age-related findings in the frontal cortex and how this might interact with the amygdala findings.

In contrast with the amygdala, functional neuroimaging studies of emotional perception have generally found an age-related increase in the recruitment of the frontal cortex, especially in

medial PFC regions (**see Table 1**), although age-related increases in lateral PFC regions are also prevalent (Gunning-Dixon, et al., 2003; Gutchess et al., 2007a; Tessitore, et al., 2005). We and others (St Jacques, et al., 2008; Williams, et al., 2006) found an age-related increase in the recruitment of medial PFC during the perception of negative versus neutral pictures, while other studies have observed that the age-related increases in medial PFC recruitment are greater for positive versus negative stimuli (Gutchess et al., 2007a; Leclerc & Kensinger, 2008a). These apparent differences might be due to the dissociable effects of arousal and valence in dorsal versus ventral aspects of the medial PFC (e.g., Dolcos et al., 2004). For example, Leclerc and Kensinger (2008a) found age-invariant activity in dorsomedial regions reflecting emotional arousal, whereas, the age-related differences observed in ventromedial regions (specifically ventral ACC) reflected differences in positive versus negative valence. Future research is needed to tease apart potential age-related differences in the neural correlates subserving emotional arousal and valence.

In sum, consistent with the FADE pattern, emotional perception studies of aging converge on the observation of an age-related alteration in amygdala activation coupled with an increase in frontal cortex activation, which suggest that older adults engage more controlled processing during the perception of emotional stimuli. It is also critical to understand how the effects of aging on emotional processing ramify through cognitive operations, such as memory processes.

Aging and Emotional Episodic Memory

In young adults, memory is usually better for emotional than neutral stimuli. Although this enhancement for emotional memory is relatively preserved in healthy aging, there is an age-related alteration in the extent of the enhancement, especially for negative information. Only recently have functional neuroimaging studies begun to explore the neural bases of the age-related changes in emotional memory, and the available evidence is consistent with FADE. Below we discuss the age-related findings in the amygdala and PFC.

Despite differences in methodology, all three available functional neuroimaging studies of memory encoding show age-invariant amygdala activity coupled with age-related increases in PFC activity. For example, we (St Jacques et al., 2009) found that amygdala activity predicted subsequent memory of negative versus neutral pictures in both young and older adults, but that older adults recruited additional frontal activity to support memory formation as visual cortex

activity declined. Similarly, Murty et al. (In Press) found age-related increases in the recruitment of left DLPFC during the encoding of negative versus neutral picture blocks, but they did not observe age-related differences in the amygdala. Consistent with behavioral findings of preserved enhancement for emotional memory in aging, Murty et al. (In Press) suggested that the increased recruitment of the PFC might reflect compensation. Complementing these findings, Kensinger and Schacter (2008) observed age-invariant recruitment of the amygdala during successful memory encoding of objects, irrespective of the particular negative or positive valence, but older adults elicited greater medial PFC activity during successful encoding of positive objects. Furthermore, others and we have observed an age-related decrease in functional connectivity between the amygdala and the areas that typically support memory formation (i.e., hippocampus) but an age-related increase in functional connectivity with PFC areas involved in controlled processing (Murty, et al., In Press; St. Jacques et al., 2009). Currently, only one study (Murty, et al., In Press) has examined age-related effects during memory retrieval, where they found that older adults showed a reduction in the recruitment of the amygdala during memory retrieval of negative versus neutral blocks coupled with an age-related increase in right DLPFC.

In sum, the results of these initial fMRI studies suggest that aging leads to an increased reliance on controlled processes in the PFC that support and maintain enhanced memory for emotional materials.

The FADE Pattern

Evidence from age-related functional neuroimaging studies across both emotional perception and memory domains generally show a pattern of activity consistent with FADE, although some studies provide only partial support potentially due to methodological differences (Fischer, et al., 2005; Gutchess et al., 2007a; Iidaka, et al., 2002) and to focused region of interest analyses on the amygdala (Mather et al., 2004; Wright et al., 2006; 2007). Below we focus on the evidence that supports the FADE pattern and provide possible interpretations of this empirical regularity.

Although age-invariant activation in the amygdala was observed during both emotional perception and the encoding and formation of emotional memories, suggesting that the function of the amygdala remains intact in aging, the amount of amygdala activity elicited in older adults might differ depending upon the recruitment of controlled processes involving the frontal cortices. There are at least three potential interpretations of the increase in frontal recruitment

associated with the FADE pattern. First, the frontal increase could be an instance of the posterior anterior shift in aging (PASA), which is frequently observed in non-emotional domains (Dennis & Cabeza, 2008). Consistent with this interpretation, others and we have found that the increase in frontal activity is coupled with a decrease in the recruitment of posterior regions (St Jacques, et al., 2008, 2009; Tessitore, et al., 2005; also see Gunning-Dixon, et al., 2003; Iidaka, et al., 2002). Furthermore, in keeping with the compensatory account of PASA, we also found a significant correlation between the age-related increase in frontal activity and the reduction in visual cortex activity during emotional perception (St Jacques, et al., 2008) and that the age-related frontal increase was predictive of subsequent memory for negative stimuli (St Jacques, et al., 2009).

Second, age-related increases in medial PFC could reflect an augmentation of self-referential processes (Kensinger & Leclerc, In Press), which are processes previously associated with this region (Northoff & Bermpohl, 2004). One line of evidence supporting this interpretation is that medial PFC recruitment in older adults has been shown to vary as a function of valence (Kensinger & Schacter, 2008; Leclerc & Kensinger, 2008a). For example, Leclerc and Kensinger (2008a) found an age-related reversal in the medial PFC, such that older adults recruited this region more for positive stimuli and less for negative stimuli (although see Williams, et al., 2006). They suggested that older adults might interpret positive stimuli in a more self-relevant way. In keeping with this interpretation, a study directly interrogating age-related differences in self-referential processing for emotional stimuli found that older adults recruited medial PFC regions to a greater extent for self-related positive words (Gutchess et al., 2007a). Given that older adults tend to engage the default network more during cognitive tasks (Grady, et al., 2006), one possibility is that the positivity shift observed in perception and memory studies might result from an age-related increase in the tendency to interpret information in a self-relevant manner (cf. Kensinger & Leclerc, In Press).

Third, age-related frontal increases could reflect emotional regulation. Consistent with FADE, in many studies, the age-related increase in frontal activity was coupled with a reduction in amygdala activity during perception (Gunning-Dixon, et al., 2003; Tessitore, et al., 2005; also see Fischer, et al., 2005; Iidaka, et al., 2002; Samanez-Larkin, et al., 2007; St Jacques, et al., 2008; although see Williams, et al., 2006) and retrieval (Murty, et al., In Press) of negative stimuli. Thus, one possibility is that older adults' enhanced emotional regulation strategies lead

to the recruitment of PFC-mediated control processes that dampen amygdala responses for negative stimuli. For example, we examined age-related differences in the functional connectivity with the amygdala and found an age-related increase in the functional connectivity between the ventral ACC and the amygdala (St Jacques, et al., 2008). Importantly, we found a negative correlation between these regions during the perception of negative pictures that older adults subjectively rated as neutral and a subsequent decrease in amygdala activity, which suggests the engagement of emotional regulation. Urry et al. (2006) directly asked older adults to regulate emotions while viewing negative pictures and found that compared to passive viewing, when older adults were asked to decrease their emotional responses they recruited greater vmPFC activity coupled with a reduction in the recruitment of the amygdala. In fact, emotional well-being in aging has been associated with a shift from automatic processing to more controlled processing of emotions via the recruitment of medial PFC (Williams, et al., 2006).

In sum, age-related increases in frontal activity might reflect compensation, self-referential processing, or emotional regulation. It is important to note, however, that these accounts are not incompatible with each other. For example, emotional regulation can be seen as a form of compensation (cf. St Jacques, et al., 2008), and self-referential processing could be seen as an emotional regulation strategy (cf. Kensinger & Leclerc, In Press). Yet, not all forms of emotional regulation are beneficial for performance (i.e., compensatory) and self-referential processing is not necessarily an effective regulation strategy. Thus, understanding the specific contributions of each of these processes and their interactions is a major challenge for future research.

Conclusions

Functional neuroimaging studies examining age-related differences in the perception and memory for emotional information converge on findings consistent with FADE. Whether the increased recruitment of the PFC and alterations in the amygdala reflect more general patterns of age-related differences or motivational differences in self-referential processing and emotional regulation will be an important avenue for future research. Furthermore, empirical testing of the FADE pattern is needed to determine whether this empirical regularity will hold more generally across different methodologies. Many of the complexities of emotion and age interactions in the brain such as valence versus arousal effects, automatic versus controlled processing of emotions,

perception versus emotional experience, possible sex differences, and potential individual differences in brain volume have yet to be disentangled.   In fact, we have only just begun to understand the neural bases of age-related effects in emotion on perception and memory, and extending these findings to other cognitive domains such as working memory and decision-making, as well as to understanding pathological aging such as Alzheimer's disease, will be critical for a complete understanding of the emotional brain and aging.

Acknowledgements

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Table 1. *Results of Functional Neuroimaging Studies of Aging and Emotion*

				Ant		Med		DL		VL		Pos		Ins		PCC		DPC		VPC		Amy		HC		PHG		Temp		TO		Occ		BG		TH		CB	
Perception				L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
Author Year	**Stimuli**	**Contrast & Scanning Task**	**Behavior**																																					
St.Jacques 08	pictures	neg > neut; emotion rating	neg: Y > O, neut: Y = O			○							○										❖									●	●	○	○				
Mather 04*	pictures	neg vs baseline; emotion rating	neg: Y > O, neut: Y = O																				●	●															
		pos vs baseline; emotion rating	pos: Y = O, neut: Y = O																				❖	❖															
LeClerc 08	objects	neg > neut conj. pos > neut; semantic rating	RT: Y < O			❖														❖										❖							●	❖	
		neg > pos; semantic rating	RT: Y < O		●	●		●					●					●	●	●			●													●		
		pos > neg; semantic rating	RT: Y < O	❖	○	○						○	❖			○		○				●								○	○				○			
Gutchess 07	words	pos > neg; self/other rating		○				○				○	○	○				○	○									○	❖	○		○	○					○	○
		pos self > neg self; self rating				○		○				○	○					○										❖		○								
		(pos self>pos other)>(neg self>neg other); self/other rating				○		○				○	○															○										
Fischer 05	faces	neg(a) > neut; passive viewing	neg: Y = O											○									●																
Gunning-Dixon 03	faces	emotion (h,a,s,d,neut) > age discrimination; ratings	emot: Y > O; RT: Y > O					○		○													●																
Iidaka 02	faces	neg (a, s) > control; gender discrimination																●					●																
		pos (h) > control; gender discrimiation																●									●					●							
Tessitore 05	faces	neg (a, afr) > control; perceptual matching	RT: Y < O									○	○	○	○								●								●	●							
Williams 06*	faces	neg (f) > neut; passive viewing	neg: Y > O			○	○																●													●	●		
		pos (h) > neut; passive viewing	pos: O > Y			●	●																●													●	●		
Wright 06*	faces	neg (f) +novel > neut; passive viewing	neg: Y = O																				❖									●	●						
Wright 07*	faces	neg (f) + novel > neut; passive viewing	neg: Y = O																				❖	❖															
Episodic Memory																																							
Murty IP	pictures	neg > neut; semantic rating				○																	●																
		neg > neut; old/new recognition	Y > O			○	○											●					●																
St. Jacques 09	pictures	neg > neut; emotion rating	neg: Y > O, neut: Y = O			○	❖					●	●	●				●	●	❖	●	○	●		●		●	●			●	●	●						○
Kensinger 08	objects	neg & pos > neut; semantic rating	Y: neg > pos, O: pos >neg					❖											❖		❖																		
		neg > pos & neut; semantic rating	Y: neg > pos, O: pos >neg																								❖												
		pos > neg & neut; semantic rating	Y: neg > pos, O: pos >neg	❖	❖	○	○									○	❖								❖			❖	❖				❖					

● Young > Older; ○ Older > Young; ❖ Young = Older

Contrast: neg: negative, pos: postive, neut: neutral; h: happy, a: angry, s: sad, d: disgust, f: fear, afr: afraid

Behavior: Unless indicated, the behavioral results refer to subjective emotion ratings; RT = Response Time

Brain Regions: Frontal Cortex: Ant: Anterior, Med: Medial, DL: Dorsolateral, VL: Ventrolateral, Pos: Posterior, Ins: Insula; PCC: Posterior Cingulate Cortex; DPC: Dorsal Parietal Cortex, VPC: Ventral Parietal Cortex;
  Amy: Amygdala; HC: Hippocampus, PHG: Parahippocampal Gyrus; Temp: Temporal Cortex, TO: Temporal-Occipital Cortex; Occ: Occipital Cortex, BG: Basal Ganglia; TH: Thalamus; CB: Cerebellum

* Indicates Region of Interest (ROI) Analysis