

Socioemotional Functioning and the Aging Brain

Gregory R. Samanez-Larkin and Laura L. Carstensen

Abstract

Effective social and emotional functioning is essential to healthy relationships at any age. Although the understanding of socioemotional functioning in late life has increased in recent decades, most of the existing research relies on information reported by individuals on questionnaires or during interviews. Social neuroscience promises to uncover important and novel information that can greatly enhance this growing area of research. In particular, social neuroscience is allowing tests of hypotheses that cannot be tested well using traditional behavioral methods. This chapter identifies the important contributions that social neuroscience has made to our understanding of the socioemotional aspects of adult development and aging. It reviews studies that utilize a variety of methods to assess autonomic and central nervous system function from peripheral physiology to electrophysiology to fMRI. It argues that brain imaging introduces a way to tease apart findings that may reflect top-down processes from ones that are bottom-up, and that the neuroscience literature to date provides surprisingly consistent support for the postulates of socioemotional selectivity theory (SST) and a motivated basis for the positivity effect.

Keywords adult development, aging, emotion, motivation, social cognition, positivity effect, anticipation, memory, learning, reward, emotion regulation, individual differences, fMRI, ERP, psychophysiology, methods, (functional) connectivity, amygdala, caudate, anterior cingulate, medial prefrontal cortex, dorsolateral prefrontal cortex

Effective social and emotional functioning is essential to healthy relationships at any age. Although the understanding of socioemotional functioning in late life has increased in recent decades, most of the existing research relies on information reported by individuals on questionnaires or during interviews. Social neuroscience promises to uncover important and novel information that can greatly enhance this growing area of research. In particular, social neuroscience is allowing tests of hypotheses that cannot be tested well using traditional behavioral methods.

Throughout this chapter we identify the important contributions that social neuroscience has made to our understanding of the socioemotional aspects of adult development and aging.

A growing body of research suggests that the ability to regulate emotion remains stable and in some aspects may improve across the adult life span (Charles & Carstensen, 2007). Compared to their younger counterparts, older adults recover more quickly from negative emotional states, are less likely to respond to verbal slights with anger

(Charles & Carstensen, 2008), maintain positive emotional states longer than younger adults (Carstensen, Pasupathi, Mayr, & Nesselroade, 2000; Carstensen et al., 2011; Charles & Carstensen, 2008), report superior emotional control (Carstensen et al., 2011; Gross et al., 1997; Lawton, Kleban, Rajagopal, & Dean, 1992; Tsai, Levenson, & Carstensen, 2000), and display less physiological arousal when experiencing negative emotions (Levenson, Carstensen, Friesen, & Ekman, 1991; Tsai et al., 2000). A number of studies using a variety of experimental methods have found that older adults selectively attend to positive stimuli and are more likely to retrieve positive memories than negative ones (Charles, Mather, & Carstensen, 2003; Fernandes, Ross, Wiegand, & Schryer, 2008; Isaacowitz, Toner, Goren, & Wilson, 2008; Isaacowitz, Wadlinger, Goren, & Wilson, 2006a, 2006b; Kennedy, Mather, & Carstensen, 2004; Mather & Carstensen, 2003).

These somewhat surprising findings contribute to what is often called the “paradox of aging.” Despite age-related losses, emotional well-being remains relatively high in old age. An important question for neuroscientists is whether the positive profile of findings emerging in the literature reflects age-related changes in brain function, such as the relative structural preservation of select emotional processing regions or even the serendipitous benefits of brain deterioration, or is instead the result of motivational and experiential changes associated with adult development and aging. For example, could less robust brain activation *account* for a slowness to anger? Or does it reflect motivation on the part of older adults to maintain strong social bonds? Given the breadth and the depth of age-related loss (in the brain and elsewhere) it is easy to be drawn to explanations rooted in dysfunction associated with physical aging. We argue, however, that the existing literature better supports claims that top-down changes in motivation play a substantial—if not primary—role in functional changes observed in the aging brain.

We come to the subject matter from the perspective of socioemotional selectivity theory (SST; Carstensen, 1992, 2006). The theory contends that as people age and time horizons imposed by mortality shrink, people place increasingly greater priority on goals related to well-being and relatively less on emotionally riskier goals associated with expanding horizons, learning, and social exploration. Consequently social and cognitive resources are more likely to be allocated to the regulation of emotion

(Carstensen, 2006; Carstensen, Fung, & Charles, 2003). Strong preferences for social partners who are well known and meaningful are apparent among older adults, for example (Fredrickson & Carstensen, 1990; Fung, Carstensen, & Lang, 2001; Fung, Carstensen, & Lutz, 1999); and there is mounting evidence that attention and memory operate in support of well-being as well. Our research team has coined the term “positivity effect” to describe the developmental shift from a preference for negative information in youth to a preference for positive information at older ages (Carstensen, Mikels, & Mather, 2005). The effect is operationalized as a ratio representing the relative difference between younger and older adults. In some cases, it is driven by heightened attention to positive and in others by relatively reduced attention to negative material. This developmental pattern has been observed in memory across short periods of time, that is, across experimental sessions (Charles et al., 2003; Mather & Johnson, 2000), as well as in autobiographical memories that span many years (Kennedy et al., 2004). A preference for positive over negative is also evident in affective working memory (Mikels, Larkin, Reuter-Lorenz, & Carstensen, 2005) and in affective forecasting (Nielsen, Knutson, & Carstensen, 2008). In the last five years, the positivity effect has been widely replicated in independent laboratories (Comblain, D’Argembeau, & Van der Linden, 2005; Fernandes et al., 2008; Isaacowitz et al., 2008; Isaacowitz et al., 2006b; Kisley, Wood, & Burrows, 2007; Mather, Knight, & McCaffrey, 2005; Schlagman, Schulz, & Kvavilashvili, 2006; Spaniol, Voss, & Grady, 2008). Importantly, this preference for positive information is not impervious to context. SST maintains that chronically activated goals change with age, but of course there are circumstances when younger adults strive to regulate emotion and those when older adults pursue informational goals. Interestingly, when goals are explicitly instructed, age differences in positivity are eliminated (Löckenhoff & Carstensen, 2007). That is, all things being equal, older adults appear to focus on positive information but experimental conditions and instructions can and do eliminate age differences.

With the development of *in vivo* functional brain imaging techniques in humans, a growing body of research has focused on exploring age differences in cognitive function. Over the past couple of decades much progress has been made in the cognitive neuroscience of aging (Buckner, Head, & Lustig, 2006; Cabeza, Nyberg, & Park, 2005; Grady, 2008). Only relatively recently have studies

of emotional and social aspects of aging received attention by neuroscientists. In the last several years, especially, attention to the neural basis of emotional functioning in older adults has burgeoned. In this chapter, we review studies across a wide range of domains including the emotional processing of social stimuli; the anticipation of, exposure to, and memory for emotional stimuli; attention to emotion; and emotion regulation. The studies reviewed in this chapter utilize a variety of methods to assess autonomic and central nervous system function from peripheral physiology to electrophysiology to fMRI. We maintain that brain imaging introduces a way to tease apart findings that may reflect top-down processes from ones that are bottom-up and that the neuroscience literature to date provides surprisingly consistent support for the postulates of SST and a motivated basis for the positivity effect. After attempting to comprehensively review and synthesize the literature on socioemotional functioning in the aging brain, we identify existing gaps in the literature and discuss potential directions for future research.

Social and Emotional Processing in the Aging Brain

By far, the most common approach to the study of age differences in neural responses associated with social and emotional stimuli are based on responses to facial expressions. In fact, the first study exploring age differences in emotional responses using fMRI asked a group of younger and older adults to make gender discriminations while viewing images of the faces of young adults expressing negative emotions (Iidaka et al., 2002). While viewing these faces, older adults, compared to younger adults, showed significantly reduced activation in the amygdala. In contrast, older adults did show significant activation in one medial prefrontal region, the cingulate, while viewing negative faces, while younger adults did not. A similar reduction in subcortical activation and increased cortical activation while viewing negative social stimuli has been replicated in a number of other studies using emotional facial expressions. This age-related decrease in amygdala activation has been observed during the passive viewing of angry faces (Fischer et al., 2005), valence discrimination of negative (sad, angry, fearful, disgusted) facial expressions (Gunning-Dixon et al., 2003), and expression matching of fearful and angry faces (Tessitore et al., 2005). Alongside this reduction in amygdala activity, the same studies found an age-related increase in insula activity

(Fischer et al., 2005), an increase in lateral and dorsomedial frontal activation (Gunning-Dixon et al., 2003; Tessitore et al., 2005), and anterior cingulate activity in older but not younger adults (Gunning-Dixon et al., 2003).

In all of these studies which expose participants to mostly negative emotional facial expressions, older adults show a reduction in amygdala activation. Investigators commonly conclude that this is evidence of age-related amygdala dysfunction, although it is hard to fully reconcile this interpretation given the important role this subcortical region plays in emotional processing (Phelps, 2006; Sergerie, Chochol, & Armony, 2008; Zald, 2003) yet also the overwhelming behavioral evidence for intact emotional processing into old age (Carstensen et al., 2005). Subsequent experiments have shown that amygdala activation is relatively robust in older adults under certain conditions, raising questions about whether lesser activation in older adults reflected lesser salience of experimental tasks or stimuli as opposed to dysfunction. One study, for example, found similarly high levels of amygdala activation in younger and older adults (Wright, Wedig, Williams, Rauch, & Albert, 2006). In this study, participants were instructed to passively view but focus on the eyes of familiar and novel fearful faces while undergoing fMRI. Prior studies with young adults have shown that novelty also activates the amygdala (Dubois et al., 1999; Schwartz et al., 2003). When examining the combined effects of negative valence and novelty by contrasting the viewing of fearful novel faces with neutral familiar (pre-exposed) faces, the two age groups did not differ in amygdala sensitivity (Wright et al., 2006). Although this provides evidence that the amygdala can be equivalently activated in healthy younger and older adults, the authors did not test the independent effects of novelty and negative valence on amygdala activity in the two age groups. It is possible that the amygdala could be driven by the combination of negative valence and novelty in young but primarily novelty and not negative valence in the old. A follow up study found no age differences in amygdala responses when isolating the contrast of novel versus familiar in younger and older adults during the passive viewing of neutral faces (Wright et al., 2008). Although this result provides evidence for similar novelty responses in the amygdala, it does not address how the age groups differ in the processing of emotional valence. However, these studies do provide important evidence that the amygdala can be activated in older adults and does

not suffer from global functional decline in healthy aging.¹ In contrast to the view that the amygdala dysfunctions with age, it is possible that older adults show less reactivity in the amygdala during the processing of negative emotional stimuli as a result of changing goals and shifting priorities which reduce the salience of stimuli.

Although most of the early literature focuses on age-related reductions in subcortical amygdala activity, one study explored the potential role of cortical activations in regulatory processes in social emotional tasks (Williams et al., 2006). Although prior studies have reported an increase in prefrontal activity in older adults while viewing negative stimuli, Williams and colleagues documented an age group by valence interaction in the medial prefrontal cortex during the passive viewing of happy and fearful faces using fMRI. Activity in this region was greater in older adults while viewing negative faces, but lower than younger adults while viewing positive faces.² The authors interpreted these results as suggesting that older adults may be engaging in more regulation while viewing negative faces than positive faces. Additional temporal support for this interpretation was provided by electrophysiological findings. A similar pattern emerged in this medial prefrontal cortical area when examining event-related potentials (ERPs). Older adults had an increased late fronto-central ERP signal during the viewing of negative faces but a decreased early fronto-central signal during the viewing of positive faces. This pattern of results suggests that older adults may have a more controlled, regulatory response to negative social stimuli but a more free, unregulated response to positive social stimuli. Providing additional support for this interpretation, both the fMRI and ERP effects in the medial prefrontal cortex correlated with individual differences in emotional stability as assessed by neuroticism (Williams et al., 2006). Individuals with greater medial prefrontal fMRI responses and increased late ERP signals to negative stimuli also had higher levels of emotional stability.

In summary, a number of studies have examined neural responses to emotional, facial stimuli in younger and older adults. The common finding across studies is an age-related decrease in amygdala activation during the perception of negative faces and an age-related increase in a number of lateral and medial prefrontal cortical regions. Yet a combination of novelty and negative valence activates the amygdala equivalently in younger and older adults. Initial evidence from one study supports the

hypothesis that the increase in the medial prefrontal cortex may be playing a regulatory role even in passive viewing tasks and has linked this cortical increase to an individual difference measure of emotional stability. This interpretation of the subcortical decreases and cortical increases is consistent with the age-related positivity effect which suggests that relative positivity in older age is regulatory in nature.

Emotional Processing in the Aging Brain: Positivity Effects in Anticipation, Exposure, Memory, and Regulation *Anticipation of Emotional Stimuli*

A number of studies have appeared that examine age differences in the anticipation of cued emotional stimuli. One study examined neural activity using fMRI while participants viewed symbolic cues (smile, frown, or neutral icon) that deterministically signaled an upcoming positive, negative, or neutral emotional image from the IAPS picture database. Analyses focused on the anticipation of negative stimuli. The authors reported an age-related decrease in rostral anterior cingulate activity during the anticipation of negative stimuli (Erk, Walter, & Abler, 2008), and interpreted this result as in line with older adults' reduced focus on negative future events. Not only did the researchers report a reduction in cingulate activity during negative anticipation, they also report a reduction in amygdala activity during exposure to negative images (Erk et al., 2008). Within the older participants in the sample, an individual difference analysis showed that individuals with higher scores on the reappraisal subscale of the emotion regulation questionnaire (ERQ) showed reduced amygdala activation (Erk et al., 2008). This finding provides initial direct support that the age differences in amygdala activity during negative emotional processing may be associated with regulatory efforts.

Similar age differences in the processing of negative stimuli are found in other studies focusing on anticipation using incentive-based tasks with financial gains and losses. One particular study examined the physiological anticipation of gains and losses while younger and older participants played the Iowa Gambling Task (IGT). In the IGT, participants begin by randomly selecting cards from four decks in an attempt to learn over time which decks are better (i.e., yield higher overall positive earnings or points). Two decks have high gains but larger losses leading to a negative expected value over time and the other two decks have smaller gains and

smaller losses leading to a positive expected value over time. When reaching for *negative* expected value decks younger adults generate an anticipatory skin conductance response, whereas older adults generate a skin conductance response when reaching for decks with a *positive* expected value (Denburg, Recknor, Bechara, & Tranel, 2006). Important individual differences in learning emerge as well. A subset of older adults performs just as well as younger adults, but some perform much worse (Denburg, Tranel, & Bechara, 2005). What distinguishes these groups is that those who perform well have these positive anticipatory physiological markers (Denburg et al., 2006). The authors interpret these results as physiological evidence suggesting that older adults are more likely to learn in this task by seeking gains whereas younger adults learn by avoiding losses. The idea that this physiological guiding signal has been tuned over the adult life span from a focus on signaling the avoidance of negativity toward a focus on seeking positivity is consistent with SST.

A similar effect has been observed in a task that does not require learning revealing age differences in prefrontal and striatal activity using fMRI. When younger and older adults are shown explicit cues that signal a potential financial gain or loss of varying magnitudes, the age groups do not differ during the anticipation of gains in either self-reported positive affect or neural activation in the nucleus accumbens, caudate, or insula. However, when anticipating losses younger adults self-report more negative affect and show more sensitivity to loss magnitudes in the caudate and insula when compared to older adults (Samanez-Larkin et al., 2007). An age-by-valence-by-magnitude interaction in the caudate and insula suggests that these regions are not dysfunctional in old age, but instead that they respond selectively to gains and not losses in older adults. The only region where older adults showed a significant signal during loss anticipation was in a region of the medial prefrontal cortex, the anterior cingulate. In a follow-up study, the authors linked these anticipatory biases to subsequent learning performance. The individuals who showed reduced sensitivity in the insula during loss anticipation in the first task (that did not require learning) later performed worse (controlling for age) in a probabilistic loss-avoidance learning task (Samanez-Larkin, Hollon, Carstensen, & Knutson, 2008). Thus, although this reduction in anticipatory anxiety may contribute to higher well-being, there may be negative consequences especially in financial domains.

It will be important for future studies to pursue these individual differences in physiological responses and learning performance in order to further characterize the underlying explanatory variables. Are these anticipatory patterns of activity linked to regulatory efforts? If this positivity effect is goal-directed and part of regulatory efforts, the benefits of improved well-being may also come at a cost. The preliminary evidence suggests that a positivity effect in financial domains can have deleterious side effects. If older adults are sensitive to potential positive outcomes but less sensitive to potential negative consequences, this could put older adults at an elevated risk for financial scams (Denburg et al., 2007).

Exposure to Emotional Stimuli

Although age differences emerge during anticipation of rewards, younger and older adults show relatively similar responses to *actual* gains and losses on these tasks in the nucleus accumbens, caudate, and medial prefrontal cortex (Cox, Aizenstein, & Fiez, 2008; Samanez-Larkin et al., 2007). That is, older adults are not impervious to loss when it occurs but appear to respond little to the prospect of loss before it occurs. Initial evidence suggested that the error signal in the anterior cingulate is disrupted in older age (Nieuwenhuis et al., 2002), yet when behavioral performance is matched between groups the age differences in error signaling disappear (Eppinger, Kray, Mock, & Mecklinger, 2008). Nevertheless, even if older adults accurately represent and show similar physiological responses to gains, losses, and errors, there is evidence that older adults may differentially weight feedback information when making future decisions. For example, there is some evidence that older adults compared to younger adults learn better from positive than negative feedback (Denburg et al., 2006; Eppinger et al., 2008; Wood, Busemeyer, Kolling, Cox, & Davis, 2005).³

A number of other studies have explored age differences in responses to emotional images. One study which used electrophysiology asked younger, middle-aged, and older adults to view and make valence ratings on a set of positive, negative, and neutral IAPS pictures while measuring ERPs. An age-by-valence interaction emerged in a parietal brain region (Pz). There was a stronger signal during the evaluation of negative images in the young adults, but no age differences at the Pz for positive images (Kisley et al., 2007; Wood & Kisley, 2006). This Pz site has been linked to very early attention. The authors suggest that this is evidence that the

age-related positivity effect appears even at an early processing stage. However, it is important to note that such an early effect does not rule out a regulatory explanation of age-related positivity effects. Chronically activated goals in older adults could tune attentional resources and contribute to these early effects.

A similar positivity effect was reported in another study where younger and older adults viewed and made arousal ratings on positive, negative, and neutral IAPS pictures while undergoing fMRI. Again, an age-by-valence interaction emerged but this time in amygdala activity. Younger adults showed greater amygdala activation than older adults while viewing negative images. Older adults showed greater amygdala activation for positive compared to negative, whereas younger adults did not (Mather et al., 2004). This finding extends other work and provides additional evidence that the amygdala is not only activated by novelty but also by positive emotional stimuli. The authors interpret the results through the lens of socioemotional selectivity theory and suggest that the sensitivity of the amygdala may change with age and that this change may be related to a shift in emotional goals.

A similar age-by-valence interaction but with a complete age-related valence reversal was observed in the anterior cingulate using a different set of stimuli (matched in arousal across valence) while participants made nonemotional (relative physical size) judgments during picture viewing. This positivity effect (full valence reversal) emerged when participants didn't have to make an emotional judgment. The authors interpret their results as evidence for controlled processing differences during the viewing of positive and negative images (Leclerc & Kensinger, 2008). These authors have also observed age-by-valence interactions in the medial prefrontal cortex when exposed to emotional words (Leclerc & Kensinger, in press). In addition to the interactions in the medial prefrontal cortex, when exposed to emotional objects, consistent with several studies cited thus far, they also found that older adults had less amygdala activity when viewing negative compared to positive pictures (Leclerc & Kensinger, in press).

Nearly all of the studies reviewed thus far find age differences in activation of the amygdala and/or medial prefrontal cortex, but none of the studies has examined the interactions between these two regions. Are the age differences in responses in these regions related? A more recent study explored the functional connectivity of these regions that have previously shown age-by-valence interactions: the

amygdala and anterior cingulate. While younger and older adults viewed negative IAPS images and made valence ratings, older adults had greater levels of functional connectivity between the amygdala and anterior cingulate (St. Jacques, Dolcos, & Cabeza, 2010). The authors discuss a possible regulatory interpretation of their results in line with SST. They speculate that this subcortical structure, the amygdala, may be regulated during the viewing of negative stimuli by this cortical structure in the medial prefrontal cortex, the anterior cingulate. Previous studies in young adults show increases in the medial prefrontal cortex and decreases in the amygdala during successful regulation (Ochsner & Gross, 2005) lending support to this age-related regulatory hypothesis.

Emotional Memory

As cited in the introduction to this chapter, age-related positivity effects have also emerged in memory. Three recent studies have examined memory for emotional stimuli using functional neuroimaging. In one study, younger and older adults viewed and made valence ratings on a set of positive, negative, and neutral IAPS images while undergoing fMRI (St. Jacques, Dolcos, & Cabeza, 2009). In a surprise cued-recall test outside of scanner, the older adults showed a reduction in memory for negative relative to neutral images. Providing additional evidence that the amygdala is functionally intact in older age, the neuroimaging data revealed that both groups recruited greater amygdala activity during the successful encoding of negative relative to positive images. However, older adults showed higher levels of dorsolateral prefrontal activation during the successful encoding of negative images than the younger adults. Further functional connectivity analyses revealed a reduced coupling of the amygdala with the hippocampus and ventrolateral prefrontal cortex but an increased coupling between the amygdala and the dorsolateral prefrontal cortex (St. Jacques et al., 2009). Similar to the connectivity effects during picture viewing discussed above, this age-related shift in connectivity may suggest that older adults are engaging in less primary stimulus encoding (amygdala and hippocampus) and more regulation of the negative emotional stimuli (amygdala and dorsolateral prefrontal cortex). Importantly, although this interpretation is speculative and no direct evidence for differential regulatory efforts in the two age groups was provided in this particular study, this pattern of age-related differences in neural activity would be predicted by SST.

In another study using negative and neutral IAPS images that collected functional imaging data during both the encoding and retrieval phases, older adults show greater dorsolateral prefrontal activation during encoding and greater dorsolateral prefrontal and cingulate and less amygdala activity during retrieval when compared to younger adults. Replicating St. Jacques and colleagues (2009) but also extending the findings to the retrieval stage, in this study functional connectivity analyses revealed that older adults had reduced amygdala-hippocampal coupling and increased amygdala-prefrontal coupling during both encoding and retrieval (Murty et al., 2009).

Another memory study identified a common set of regions in both younger and older age groups that were activated during the successful encoding of emotional stimuli. Both younger and older adults showed significant amygdala and orbitofrontal activation during the successful encoding of all emotional stimuli (Kensinger & Schacter, 2008). However, older adults showed greater anterior cingulate activity than the younger adults during the successful encoding of positive object images (which were later correctly recognized outside of scanner) (Kensinger & Schacter, 2008). Nearby medial prefrontal regions showed a similar pattern during the successful encoding of verbal stimuli as well (Leclerc & Kensinger, in press). In this study, older adults showed greater activation during the encoding of positive relative to negative words. The older adults also showed a positivity effect in memory for the words (Leclerc & Kensinger, in press).

In summary, although a number of studies identified age differences in subcortical and mostly medial prefrontal regions during emotional anticipation and exposure, the studies focusing on emotional memory reveal both medial and dorsolateral prefrontal effects during both memory encoding and retrieval. These initial studies suggest that these prefrontal processes may mediate behavioral positivity effects in memory and provide potential evidence for the role of regulatory efforts at the encoding stage (St. Jacques, Bessette-Symons, & Cabeza, 2009).

Emotion Regulation

A number of possible regulatory suggestions and implications have been raised in the discussion of many of the studies reviewed thus far. Although initial regulatory evidence was provided above linking reappraisal (Erk et al., 2008) and emotional stability (Williams et al., 2006) to reductions in amygdala

activation and interactions in the medial prefrontal cortex, few studies have explicitly manipulated emotion regulation in older adults (Urry, van Reekum, Johnstone, & Davidson, 2009; Urry et al., 2006; van Reekum et al., 2007; Winecoff, LaBar, Madden, Cabeza, & Huettel, in press). In all four of the existing studies, older adults were instructed to intentionally decrease their emotional responses to negative pictures. In the decrease condition all four studies reported a significant reduction in amygdala activity from the control condition suggesting that (1) the amygdala can be activated by negative stimuli in older adults and (2) that amygdala activation to negative stimuli is reduced when older adults are regulating their emotional responses. In line with other studies where regulatory interpretations were speculative, when regulation was instructed these studies also found a coupling between the amygdala and both the medial (Urry et al., 2006; Winecoff et al., in press) and lateral prefrontal cortex (Winecoff et al., in press). Even more interesting, higher inverse coupling between the ventromedial prefrontal cortex and amygdala predicted more adaptive profiles of diurnal cortisol secretion in an individual difference analysis (Urry et al., 2006). The pattern of results across these studies is remarkably similar to the findings from studies without instructed regulation summarized above.

Summary and Conclusions

As described in this chapter, the growing body of research on socioemotional functioning in the aging brain reveals consistent age differences in patterns of activity in prefrontal and subcortical regions during emotional processing. The most informative and consistent findings that emerge across a wide range of studies are: (1) there is an age-related reduction in subcortical activation associated with exposure to negative affective stimuli and (2) it is often coupled with an increase in cortical activation. As reviewed above, initial evidence for reduced response to negative stimuli raised legitimate questions about the functional capacity of the aging brain. The pattern emerging in the literature, however, is inconsistent with an argument that the maintenance of well-being in old age is the serendipitous consequence of neural degradation. Rather, brain regions involved in both positive and negative emotional processing in young adulthood appear to be selectively responsive to positive material in older adults. The evidence to date suggests that older adults are effectively regulating emotional responses.

Cognitive Decline and Emotional Stability: A Paradox?

A similar age-related increase in cortical activation commonly emerges in the cognition and aging neuroimaging literature (Cabeza, 2002; Reuter-Lorenz & Lustig, 2005; Spreng, Wojtowicz, & Grady, 2010). Although there is still some unresolved debate about whether this increase in cortical activity is compensatory or the result of dedifferentiation, many studies suggest that this cortical activity is compensating for faulty age-related functioning in other regions. Are the age-related cortical increases in socioemotional tasks also due to declining functional capacity in subcortical regions?

In fact, one intriguing postulate is that age-related increases in emotional well-being are the result of functional declines in the amygdala (Cacioppo, Berntson, Bechara, Tranel, & Hawkley, 2011). However, as reviewed above, cognitive decline and neural atrophy explanations cannot account for many of the findings. Many of the studies reported above show age-by-valence interactions in the same brain regions (Gutchess, Kensinger, & Schacter, 2007; Leclerc & Kensinger, 2008, 2010, in press; Mather et al., 2004; Samanez-Larkin et al., 2007; Williams et al., 2006). These subcortical and cortical regions can be activated in some conditions, but in other conditions are not. Thus, the age differences cannot be *caused* by age-related structural or functional atrophy in these regions.

On the contrary, there is some evidence that cognitive decline or even amygdalar dysfunction would produce the opposite effects and lead to negativity biases. One recent study found greater amygdala activity in patients with mild Alzheimer's disease compared to age-matched controls (Wright, Dickerson, Feczko, Negeira, & Williams, 2007). This abnormal amygdala activity correlated with irritability and agitation/aggression symptoms. This effect could be either due to hyper-responsivity in the amygdala due to disease-related medial temporal pathology, or the result of unregulated amygdala reactivity due to damage to connections with control input from cortical regions projecting into the medial temporal lobe—or a combination of both. These results provide support for a relationship between cognitive decline, abnormal amygdala function, and negative affect (not positive affect). This speaks against cognitive decline or neural atrophy explanations of the positivity effect.

If the effects are not due to declining subcortical structures but instead subcortical activity is modulated through cortical control regions by motivation,

this may create a paradox. It is well known that older adults show difficulty in tasks that require lateral prefrontal resources (Hedden & Gabrieli, 2004; West, 1996). These same regions typically emerge in studies of emotion regulation (Ochsner & Gross, 2007). If older adults are suffering from cognitive decline in controlled frontal resources, how is it neurally possible that regulation improves with age? After all, there is well-documented structural decline in older adults in many regions implicated in both emotional control and basic emotional responding including the lateral prefrontal cortex, insula, and striatum (Raz, 2005; Raz et al., 2005).

However, this may not be a paradox at all. Motivation may compensate for structural decline. It has been demonstrated that even frontal regions that suffer from relatively steep age-related structural decline can be functionally activated in older adults under supportive conditions in cognitive tasks (Logan, Sanders, Snyder, Morris, & Buckner, 2002; Lustig & Buckner, 2004). In one of the emotional tasks reported in this chapter, the authors documented relatively smaller *structural* medial prefrontal volumes, but the age by valence *functional* interaction held when controlling for structural decline in this region (Williams et al., 2006). Thus, even though prefrontal regions suffer from age-related structural decline, these same regions may be selectively functionally recruited to meet the motivational demands of older adults (Kryla-Lighthall & Mather, 2009).

Although some studies provide evidence for lateral prefrontal activity contributing to differential emotional processing in old age (Murty et al., 2009; Samanez-Larkin, Robertson, Mikels, Carstensen, & Gotlib, 2009; St. Jacques et al., 2009), a large proportion of the studies find age differences in medial prefrontal regions. A variety of brain regions near the frontal midline including the anterior cingulate and dorso- and ventromedial prefrontal cortex show age differences in responses to positive and negative affective stimuli, age by valence interactions, and age differences in connectivity with the amygdala. See Table 34.1 for a list of studies, conditions, and coordinates and Figure 34.1 for a graphical depiction of age differences in medial prefrontal activity. Interestingly, the possibility that medial versus lateral prefrontal distinctions may play a role in age differences in cognition and emotion was suggested before virtually all of these studies were published (MacPherson, Phillips, & Della Sala, 2002).

To the extent that these medial prefrontal activations reflect regulation (Ochsner & Gross, 2005;

Table 34.1 Age Effects in the Medial Prefrontal Cortex During Socioemotional Processing.

Study	Condition	R	A	S
Gunning-Dixon et al., 2003	Negative Valence	0	8	44
Gutchess et al., 2007	Age × Valence (self)	11	39	35
Iidaka et al., 2002	Negative Valence	2	18	40
Kensinger & Schacter, 2008	Positive Valence	0	33	-10
	Positive Valence	-8	45	26
Leclerc & Kensinger, 2008	Age × Valence	0	39	-5
Leclerc & Kensinger, in press	Age × Valence	-4	39	9
Samanez-Larkin et al., 2007	Negative Valence	13	37	20
St Jacques et al., 2010	Amygdala Connectivity	-4	44	-2
Tessitore et al., 2005	Negative Valence	-10	31	40
Urry et al., 2006	Amygdala Connectivity	5	37	-12
	Amygdala Connectivity	-23	43	-10
Williams et al., 2006	Age × Valence	-20	37	37
	Age × Valence	8	46	35

See Figure 34.1 for an anatomical map of peak coordinates. Coordinates listed in Talairach space.

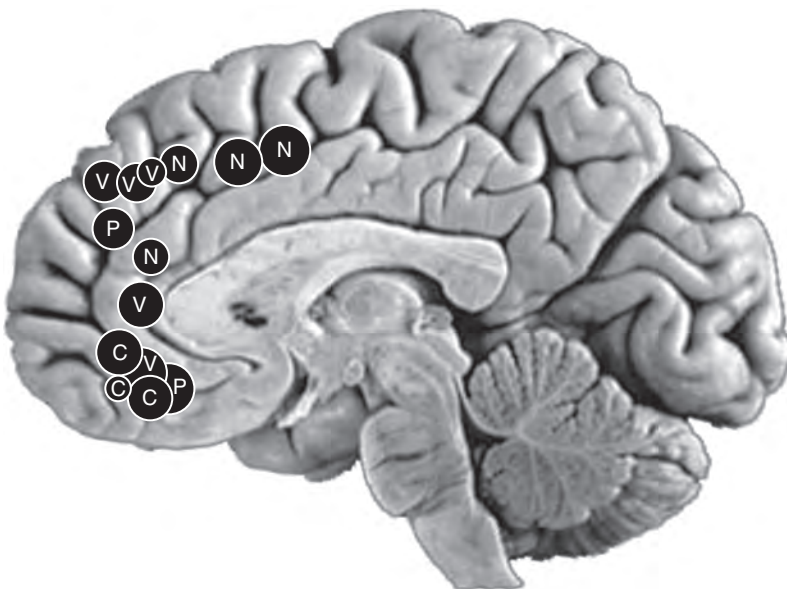


Fig. 34.1 Regions of the medial prefrontal cortex identified with fMRI showing age effects during socioemotional tasks. N = negative valence; P = positive valence; V = age by valence interaction; C = functional connectivity with the amygdala. For a list of all coordinates and studies, see Table 34.1. In the figure Talairach coordinates are projected onto the medial wall (L/R = 0). Marker diameter indicates distance from the midline (smaller markers = farther from midline).

Ochsner et al., 2004), these findings may offer evidence for important age differences in regulatory strategies. In older age, regulation may be more automatic and less cognitively effortful (Scheibe & Blanchard-Fields, 2009) due to chronically activated goals.⁴ Although it is certainly possible that age-related decreases in lateral prefrontal resources (Hedden & Gabrieli, 2004) may also contribute to this lateral to medial shift in regulatory, prefrontal processing, it is also possible that this shift occurs naturally as regulatory strategies change over the adult life span. Presently, neural differences in regulatory strategies have received very little attention in social neuroscience (Goldin, McRae, Ramel, & Gross, 2008; McRae et al., 2010). As this area continues to grow, it will be essential to explore how the neural mechanisms underlying regulatory strategies may change with age.

Future Directions in the Social Neuroscience of Aging

Although a number of studies that rely on simple perceptual judgment tasks suggest that older adults are impaired (Ruffman, Henry, Livingstone, & Phillips, 2008), a vast amount of behavioral research suggests that older adults function exceptionally well in social situations (Hess, 2006). In fact, across a range of domains, older adults display intact and in some cases superior social cognitive abilities (Blanchard-Fields, 2007; Blanchard-Fields & Heckman, forthcoming; Blanchard-Fields, Horhota, & Mienaltowski, 2008). An important detail to note is that often criterion measures for accuracy in the emerging perceptual studies are based on normative data collected from younger adults. Future studies should keep with the tradition of the social cognition and aging literature and not overweigh agreement with younger adult norms but instead focus on possible implications of age differences in behavior and underlying neural processes.

In fact, one of the only studies with non-facial social stimuli examining social cognition in the aging brain reveals both an age-related positivity effect in self judgments but remarkably similar social discrimination in the medial prefrontal cortex (Gutches et al., 2007). In this study younger and older adults evaluated positive and negative trait adjectives and decided whether the words applied to the self or a social other. When evaluating whether adjectives applied to the self, an age-by-valence interaction emerged in the dorsomedial prefrontal cortex. Activation in this region was greater for positive relative to negative adjectives in older but not

younger adults. The study also provided evidence for an intact self-versus-other representation in the medial prefrontal cortex in older adults. There were no significant age differences in the medial prefrontal cortex for self versus other judgments (Gutches et al., 2007).

Although this suggests that older adults may show similar neural activity discriminating the self and other, interesting age differences may emerge within self-relevant thought. In some contexts older adults may be less inwardly focused even when considering highly personal agendas (Mitchell et al., 2009). When compared to younger adults, older adults showed an attenuated difference between anterior and posterior medial prefrontal regions when asked to contemplate self-relevant agendas (i.e., hopes and aspirations, duties and obligations). The authors interpreted these findings as possible evidence for an age-related change from focusing primarily on specific personal details and instead focusing on a more broad (and potentially interpersonal) picture.

One important consideration in all social cognitive studies of healthy aging (or any group comparison for that matter) is that younger and older adults may interpret tasks or stimuli differently. Future studies will need to use stimuli that are comparably socially relevant for the age groups studied. For example, most of the studies exploring facial affect processing reported in this chapter did not include older faces. Older adults, then, are often processing age out-group faces. This detail may contribute to age differences in functional activity. In fact, when authors use both younger and older adult faces as stimuli important differences emerge. Although behavioral studies have not observed differences for in- or out-group faces in identification accuracy or memory in older adults (Ebner & Johnson, 2009), in a neuroimaging study within-group responses in the amygdala were larger than out-group responses (Wright et al., 2008). These effects held when controlling for valence ratings of neutral face stimuli and novelty recognition errors. This could be a confound in prior studies that didn't use old faces and reported age differences in amygdala function.

In addition to age differences in social salience, emotional perceptions of stimuli may vary across age. Investigators should consistently attempt to categorize stimuli based on the subjective ratings of individual participants (St. Jacques et al., 2010). However, also reporting any systematic age differences in perception may uncover important effects. Interestingly, in one study reported in this chapter

the rating data showed that older adults rated more negative pictures as neutral (St. Jacques et al., 2010). Many other studies have documented American, German, and Korean older adults rating the same stimuli more positively than younger adults (Grühn & Scheibe, 2008; Kwon, Scheibe, Samanez-Larkin, Tsai, & Carstensen, 2009; Mather & Knight, 2005; Smith, Hillman, & Duley, 2005).

Similarly, an interesting detail often overlooked in studies of emotion labeling of facial expressions is that although no age differences emerge in labeling happy, surprised, and neutral expressions, older adults more often disagree with young adult norms for anger, disgust, and sadness (Keightley et al., 2007). Meta-analyses of emotion recognition and aging suggest that older adults are especially “worse” at categorizing fear and anger (Isaacowitz et al., 2007; Ruffman et al., 2008). Although these are often characterized as “errors” by the authors, when the direction of this effect is more carefully explored interesting implications emerge. For example, when categorizing younger faces in one study, the older adults perceived the same faces as less angry and more sad than younger adults (Iidaka et al., 2002). This may have important social implications. If older adults systematically perceive high-arousal negative expressions, such as anger, in others as lower arousal expressions, such as sadness, they may take a less confrontational approach to the social interaction. However, this may also lead to miscommunication if the social partner feels misunderstood.

Future studies in social neuroscience should not ignore the wealth of evidence for age-related preservation and improvement in social cognitive function and should instead build upon this wealth of prior research and focus efforts on uncovering the functional implications of potential age differences (Hess, 2006).

Conclusions

In summary, the patterns of decreased subcortical but increased cortical responses to negative emotional stimuli in older adults suggest that regulatory neural processes are involved in the age-related positivity effect. The majority of the age differences in neural activity during negative processing and behavioral positivity effects cannot be explained by cognitive decline or neural atrophy theories. Both subcortical and cortical brain regions can be modulated in healthy older adults when necessary but appear to respond selectively to goal congruent stimuli. Future research should continue to directly manipulate and measure emotion regulation in

younger and older adults. Many studies speculate about the role of regulation, but direct measures of regulatory processing during the tasks are not always provided. Additionally, future research in social neuroscience should extend beyond examining age differences in the processing of facial affect and consider social cognition more broadly. Many of the original studies supporting socioemotional selectivity theory focused on age differences in social interactions as a function of limitations in future time perspective (Carstensen, 1992; Fredrickson & Carstensen, 1990; Lang & Carstensen, 1994). Understanding the neural correlates of social interaction and social understanding across the adult life span could make important contributions to the literature on socioemotional selectivity theory.

The expansiveness of this handbook suggests that research across areas in psychological neuroscience will continue to grow. In future years, emerging integrative research examining socioemotional processing in the aging brain will surely make novel and lasting contributions toward a more comprehensive understanding of the psychology of human aging.

Acknowledgements

During the preparation of this chapter, Gregory R. Samanez-Larkin was supported by National Institute on Aging pre-doctoral NRSA AG032804 and Laura L. Carstensen was supported by National Institute on Aging MERIT award AG08816. The authors thank Mara Mather and Ben Eppinger for comments.

Notes

- 1 An important methodological detail to acknowledge here is that small subcortical structures like the amygdala may be volumetrically smaller and poorly spatially normalized in older adults. Without careful methods this can bias between-group tests. The study described (Wright et al., 2006) documented smaller amygdala volumes in the older adults. Based on this finding, the authors used less spatial smoothing (7mm) and careful ROI definition methods to be sure that comparisons between groups in amygdala activity were reliable. It is important to consider that other studies showing reductions in amygdala activation in older adults use large smoothing kernels which may systematically reduce the signal in this small subcortical structure (Fischer et al., 2005; Gunning-Dixon et al., 2003; Tessitore et al., 2005). Like any group comparisons, careful methods in the study of adult development are vital for all investigators. Beyond the potential structural confounds described here, there are many other issues regarding subject selection, task design, and analyses that have been covered in recent reviews (D’Esposito, Deouell, & Gazzaley, 2003; Gazzaley & D’Esposito, 2005; Rugg & Morcom, 2005) with one review providing a summary of suggestions for studies using fMRI (Samanez-Larkin & D’Esposito, 2008).

- 2 Although Williams and colleagues documented an age-related reduction in medial prefrontal activity during the processing of positive stimuli, in the only other study using social stimuli that has attempted to isolate differences between the processing of positive and negative expressions in younger and older adults, the authors found similar ventromedial prefrontal and dorsal anterior cingulate (deactivation) activity that distinguished happy from other expressions (Keightley, Chiew, Winocur, & Grady, 2007). Thus, it does not appear that these regions cannot be modulated by positive emotional stimuli in old age.
- 3 Although recent studies have been interpreted as suggesting that the opposite is true, that older adults learn better from negative than positive feedback, (Eppinger & Kray, 2011; Frank & Kong, 2008; Haümmerner, Li, Müller, & Lindenberger, in press) it is important to note that none of these studies have actually provided evidence for a robust behavioral age-related shift toward a preference for negative over positive information from young adulthood to old age. Instead these studies provide little evidence for valence effects and more consistent evidence for a general age-related reduction in learning from probabilistic feedback (Mell et al., 2005, 2009; Samanez-Larkin et al., 2010, in press).
- 4 However, even if it is easier it is also important to note that regulation should still take some effort for older adults, as evidenced by reversals of the positivity effect when attention is divided (Knight et al., 2007; Mather & Knight, 2005).

References

- Blanchard-Fields, F. (2007). Everyday problem solving and emotion: An adult developmental perspective. *Current Directions in Psychological Science*, 16, 26–31.
- Blanchard-Fields, F. & Heckman, A. (forthcoming). Social cognition and aging. In D. Park & N. Schwarz (Eds.), *Cognitive aging: A primer* (2nd ed.). New York: Psychology Press.
- Blanchard-Fields, F., Horhota, M., & Mienaltowski, A. (2008). Social context and cognition. In S. Hofer & D. Alwin (Eds.), *Handbook on cognitive aging: Interdisciplinary perspectives* (pp. 614–628). Sage Press.
- Buckner, R. L., Head, D., & Lustig, C. (2006). Brain changes in aging: A lifespan perspective. In E. Bialystok & F. I. M. Craik (Eds.), *Lifespan cognition: Mechanisms of change*. Oxford University Press.
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, 17(1), 85–100.
- Cabeza, R., Nyberg, L., & Park, D. (2005). *Cognitive neuroscience of aging: Linking cognitive and cerebral aging*. New York, NY, US: Oxford University Press.
- Cacioppo, J. T., Berntson, G. G., Bechara, A., Tranel, D., & Hawley, L. C. (2011). Could an aging brain contribute to subjective well being?: The value added by a social neuroscience perspective. In A. Todorov, S. T. Fiske, & D. Prentice (Eds.), *Social neuroscience: Toward understanding the underpinnings of the social mind* (pp. 249–262). New York: Oxford University Press.
- Carstensen, L. L. (1992). Social and emotional patterns in adulthood: Support for socioemotional selectivity theory. *Psychology and Aging*, 7(3), 331–338.
- Carstensen, L. L. (2006). The influence of a sense of time on human development. *Science*, 312(5782), 1913–1915.
- Carstensen, L. L., Fung, H. H., & Charles, S. T. (2003). Socioemotional selectivity theory and the regulation of emotion in the second half of life. *Motivation and Emotion*, 27(2), 103–123.
- Carstensen, L. L., Mikels, J. A., & Mather, M. (2005). Aging and the intersection of cognition, motivation and emotion. In J. E. Birren & K. W. Schaie (Eds.), *Handbook of the psychology of aging* (Sixth ed.). Academic Press.
- Carstensen, L. L., Pasupathi, M., Mayr, U., & Nesselroade, J. R. (2000). Emotional experience in everyday life across the adult life span. *Journal of Personality & Social Psychology*, 79(4), 644–655.
- Carstensen, L. L., Turan, B., Scheibe, S., Ram, N., Ersner-Hershfield, H., Samanez-Larkin, G. R., Brooks, K. P., Nesselroade, J. R. (2011). Emotional experience improves with age: Evidence based on over 10 years of experience sampling. *Psychology and Aging*.
- Charles, S. T. & Carstensen, L. L. (2007). Emotion regulation and aging. In J. J. Gross (Ed.), *Handbook of emotion regulation*. New York: Guilford Press.
- Charles, S. T. & Carstensen, L. L. (2008). Unpleasant situations elicit different emotional responses in younger and older adults. *Psychology and Aging*, 23(3), 495–504.
- Charles, S. T., Mather, M., & Carstensen, L. L. (2003). Aging and emotional memory: The forgettable nature of negative images for older adults. *Journal of Experimental Psychology: General*, 132(2), 310–324.
- Comblain, C., D'Argembeau, A., & Van der Linden, M. (2005). Phenomenal characteristics of autobiographical memories for emotional and neutral events in older and younger adults. *Experimental Aging Research*, 31(2), 173–189.
- Cox, K. M., Aizenstein, H. J., & Fiez, J. A. (2008). Striatal outcome processing in healthy aging. *Cognitive, Affective and Behavioral Neuroscience*, 8(3), 304–317.
- D'Esposito, M., Deouell, L. Y., & Gazzaley, A. (2003). Alterations in the BOLD fMRI signal with ageing and disease: A challenge for neuroimaging. *Nature Reviews Neuroscience*, 4(11), 863–872.
- Denburg, N. L., Cole, C. A., Hernandez, M., Yamada, T. H., Tranel, D., Bechara, A., et al. (2007). The orbitofrontal cortex, real-world decision making, and normal aging. *Annals of the New York Academy of Sciences*, 1121, 480–498.
- Denburg, N. L., Recknor, E. C., Bechara, A., & Tranel, D. (2006). Psychophysiological anticipation of positive outcomes promotes advantageous decision-making in normal older persons. *International Journal of Psychophysiology*, 61(1), 19–25.
- Denburg, N. L., Tranel, D., & Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia*, 43(7), 1099–1106.
- Dubois, S., Rossion, B., Schiltz, C., Bodart, J. M., Michel, C., Bruyer, R., et al. (1999). Effect of familiarity on the processing of human faces. *NeuroImage*, 9, 278–289.
- Ebner, N. C. & Johnson, M. K. (2009). Young and older emotional faces: Are there age-group differences in expression identification and memory? *Emotion*, 9(3), 329–339.
- Eppinger, B. & Kray, J. (2011). To choose or to avoid: Age differences in learning from positive and negative feedback. *Journal of Cognitive Neuroscience*, 23(1), 41–52.
- Eppinger, B., Kray, J., Mock, B., & Mecklinger, A. (2008). Better or worse than expected? Aging, learning, and the ERN. *Neuropsychologia*, 46(2), 521–539.
- Erk, S., Walter, H., & Abler, B. (2008). Age-related physiological responses to emotion anticipation and exposure. *Neuroreport*, 19(4), 447–452.

- Fernandes, M., Ross, M., Wiegand, M., & Schryer, E. (2008). Are the memories of older adults positively biased? *Psychology and Aging, 23*(2), 297–306.
- Fischer, H., Sandblom, J., Gavazzeni, J., Fransson, P., Wright, C. I., & Backman, L. (2005). Age-differential patterns of brain activation during perception of angry faces. *Neuroscience Letters, 386*(2), 99–104.
- Frank, M. J. & Kong, L. (2008). Learning to avoid in older age. *Psychology and Aging, 23*(2), 392–398.
- Fredrickson, B. L. & Carstensen, L. L. (1990). Choosing social partners: How old age and anticipated endings make us more selective. *Psychology and Aging, 5*, 335–347.
- Fung, H. H., Carstensen, L. L., & Lang, F. R. (2001). Age-related patterns in social networks among European-Americans and African-Americans: Implications for socioemotional selectivity across the life span. *International Journal of Aging and Human Development, 52*(3), 185–206.
- Fung, H. H., Carstensen, L. L., & Lutz, A. M. (1999). Influence of time on social preferences: Implications for life-span development. *Psychology and Aging, 14*(4), 595–604.
- Gazzaley, A. & D'Esposito, M. (2005). BOLD functional MRI and cognitive aging. In R. Cabeza, L. Nyberg, & D. Park (Eds.), *Cognitive neuroscience of aging: Linking cognitive and cerebral aging* (pp. 107–131). New York, NY: Oxford University Press.
- Goldin, P. R., McRae, K., Ramel, W., & Gross, J. J. (2008). The neural bases of emotion regulation: Reappraisal and suppression of negative emotion. *Biological Psychiatry, 63*(6), 577–586.
- Grady, C. L. (2008). Cognitive neuroscience of aging. *Annals of the New York Academy of Sciences, 1124*, 127–144.
- Gross, J. J., Carstensen, L. L., Pasupathi, M., Tsai, J. L., Goettestam Skorpen, C., & Hsu, A. Y. C. (1997). Emotion and aging: Experience, expression, and control. *Psychology and Aging, 12*(4), 590–599.
- Grühn, D. & Scheibe, S. (2008). Age-related differences in valence and arousal ratings of pictures from the International Affective Picture System (IAPS): Do ratings become more extreme with age? *Behavior Research Methods, 40*, 512–521.
- Gunning-Dixon, F. M., Gur, R. C., Perkins, A. C., Schroeder, L., Turner, T., Turetsky, B. I., et al. (2003). Age-related differences in brain activation during emotional face processing. *Neurobiology of Aging, 24*(2), 285–295.
- Gutchess, A., Kensinger, E. A., & Schacter, D. (2007). Aging, self-referencing, and medial prefrontal cortex. *Social Neuroscience, 2*(2), 117–133.
- Haümmerner, D., Li, S., Muüller, V., & Lindenberger, U. (in press). Life span differences in electrophysiological correlates of monitoring gains and losses during probabilistic reinforcement learning. *Journal of Cognitive Neuroscience*.
- Hedden, T. & Gabrieli, J. D. (2004). Insights into the aging mind: A view from cognitive neuroscience. *Nature Reviews Neuroscience, 5*(2), 87–96.
- Hess, T. M. (2006). Adaptive aspects of social cognitive functioning in adulthood: Age-related goal and knowledge influences. *Social Cognition, 24*(3), 279–309.
- Iidaka, T., Okada, T., Murata, T., Omori, M., Kosaka, H., Sadato, N., et al. (2002). Age-related differences in the medial temporal lobe responses to emotional faces as revealed by fMRI. *Hippocampus, 12*(3), 352–362.
- Isaacowitz, D. M., Löckenhoff, C. E., Lane, R. D., Wright, R., Sechrest, L., Riedel, R., et al. (2007). Age differences in recognition of emotion in lexical stimuli and facial expressions. *Psychology and Aging, 22*(1), 147–159.
- Isaacowitz, D. M., Toner, K., Goren, D., & Wilson, H. R. (2008). Looking while unhappy: Mood-congruent gaze in young adults, positive gaze in older adults. *Psychological Science, 19*(9), 848–853.
- Isaacowitz, D. M., Wadlinger, H. A., Goren, D., & Wilson, H. R. (2006a). Is there an age-related positivity effect in visual attention? A comparison of two methodologies. *Emotion, 6*(3), 511–516.
- Isaacowitz, D. M., Wadlinger, H. A., Goren, D., & Wilson, H. R. (2006b). Selective preference in visual fixation away from negative images in old age? An eye-tracking study. *Psychology and Aging, 21*(1), 40–48.
- Keightley, M. L., Chiew, K. S., Winocur, G., & Grady, C. L. (2007). Age-related differences in brain activity underlying identification of emotional expressions in faces. *Social Cognitive and Affective Neuroscience, 2*(4), 292–302.
- Kennedy, Q., Mather, M., & Carstensen, L. L. (2004). The role of motivation in the age-related positivity effect in autobiographical memory. *Psychological Science, 15*(3), 208–214.
- Kensinger, E. A. & Schacter, D. L. (2008). Neural processes supporting young and older adults' emotional memories. *Journal of Cognitive Neuroscience, 20*(7), 1161–1173.
- Kisley, M. A., Wood, S., & Burrows, C. L. (2007). Looking at the sunny side of life: Age-related change in an event-related potential measure of the negativity bias. *Psychological Science, 18*(9), 838–843.
- Knight, M., Seymour, T. L., Gaunt, J. T., Baker, C., Nesmith, K., & Mather, M. (2007). Aging and goal-directed emotional attention: Distraction reverses emotional biases. *Emotion, 7*(4), 705–714.
- Kryla-Lighthall, N. & Mather, M. (2009). The role of cognitive control in older adults' emotional well-being. In V. Berntson, D. Gans, N. Putney, & M. Silverstein (Eds.), *Handbook of theories of aging, 2nd Edition* (pp. 323–344): Springer Publishing.
- Kwon, Y., Scheibe, S., Samanez-Larkin, G. R., Tsai, J. L., & Carstensen, L. L. (2009). Replicating the positivity effect in picture memory in Koreans: Evidence for cross-cultural generalizability. *Psychology and Aging, 24*(3), 748–754.
- Lang, F. R. & Carstensen, L. L. (1994). Close emotional relationships in late life: Further support for proactive aging in the social domain. *Psychology and Aging, 9*, 315–324.
- Lawton, M. P., Kleban, M. H., Rajagopal, D., & Dean, J. (1992). Dimensions of affective experience in three age groups. *Psychology and Aging, 7*(2), 171–184.
- Leclerc, C. M. & Kensinger, E. A. (2008). Age-related differences in medial prefrontal activation in response to emotional images. *Cognitive, Affective and Behavioral Neuroscience, 8*(2), 153–164.
- Leclerc, C. M. & Kensinger, E. A. (2010). Age-related valence-based reversal in recruitment of medial prefrontal cortex on a visual search task. *Social Neuroscience, 5*(5), 560–576.
- Leclerc, C. M. & Kensinger, E. A. (in press). Neural processing of emotional pictures and words: A comparison of young and older adults. *Developmental Neuropsychology*.
- Levenson, R. W., Carstensen, L. L., Friesen, W. V., & Ekman, P. (1991). Emotion, physiology, and expression in old age. *Psychology and Aging, 6*(1), 28–35.
- Löckenhoff, C. E. & Carstensen, L. L. (2007). Aging, emotion, and health-related decision strategies: Motivational manipulations can reduce age differences. *Psychology and Aging, 22*(1), 134–146.

- Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-recruitment and nonselective recruitment: Dissociable neural mechanisms associated with aging. *Neuron*, *33*(5), 827–840.
- Lustig, C. & Buckner, R. L. (2004). Preserved neural correlates of priming in old age and dementia. *Neuron*, *42*(5), 865–875.
- MacPherson, S. E., Phillips, L. H., & Della Sala, S. (2002). Age, executive function and social decision making: A dorsolateral prefrontal theory of cognitive aging. *Psychology and Aging*, *17*(4), 598–609.
- Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K. N., et al. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, *15*(4), 259–263.
- Mather, M. & Carstensen, L. L. (2003). Aging and attentional biases for emotional faces. *Psychological Science*, *14*(5), 409–415.
- Mather, M. & Johnson, M. K. (2000). Choice-supportive source monitoring: Do our decisions seem better to us as we age? *Psychology and Aging*, *15*(4), 596–606.
- Mather, M. & Knight, M. R. (2005). Goal-directed memory: The role of cognitive control in older adults' emotional memory. *Psychology and Aging*, *20*, 554–570.
- Mather, M., Knight, M. R., & McCaffrey, M. (2005). The allure of the alignable: Younger and older adults' false memories of choice features. *Journal of Experimental Psychology: General*, *134*(1), 38–51.
- McRae, K., Hughes, B., Chopra, S., Gabrieli, J. D. E., Gross, J. J., & Ochsner, K. N. (2010). The neural bases of distraction and reappraisal. *Journal of Cognitive Neuroscience*, *22*(2), 248–262.
- Mell, T., Heekeren, H. R., Marschner, A., Wartenburger, I., Villringer, A., Reischies, F. M. (2005). Effect of aging on stimulus-reward association learning. *Neuropsychologia*, *43*(4) 554–563.
- Mell, T., Wartenburger, I., Marschner, A., Villringer, A., Reischies, F. M., & Heekeren, H. R. (2009). Altered function of ventral striatum during reward-based decision making in old age. *Frontiers in Human Neuroscience*, *3*, 34.
- Mikels, J. A., Larkin, G. R., Reuter-Lorenz, P. A., & Carstensen, L. (2005). Divergent trajectories in the aging mind: Changes in working memory for affective versus visual information with age. *Psychology and Aging*, *20*(4), 542–553.
- Mitchell, K. J., Raye, C. L., Ebner, N. C., Tubridy, S. M., Frankel, H., & Johnson, M. K. (2009). Age-group differences in medial cortex activity associated with thinking about self-relevant agendas. *Psychology and Aging*, *24*(2), 438–449.
- Murty, V. P., Sambataro, F., Das, S., Tan, H. Y., Callicott, J. H., Goldberg, T. E., et al. (2009). Age-related alterations in simple declarative memory and the effect of negative stimulus valence. *Journal of Cognitive Neuroscience*, *21*(10), 1920–1933.
- Nielsen, L., Knutson, B., & Carstensen, L. L. (2008). Affect dynamics, affective forecasting, and aging. *Emotion*, *8*(3), 318–330.
- Nieuwenhuis, S., Ridderinkhof, K. R., Talsma, D., Coles, M. G., Holroyd, C. B., Kok, A., et al. (2002). A computational account of altered error processing in older age: Dopamine and the error-related negativity. *Cognitive, Affective and Behavioral Neuroscience*, *2*(1), 19–36.
- Ochsner, K. N. & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences*, *9*(5), 242–249.
- Ochsner, K. N. & Gross, J. J. (2007). The neural architecture of emotion regulation. In J. J. Gross (Ed.), *Handbook of emotion regulation* (pp. 87–109). New York: Guilford Press.
- Ochsner, K. N., Knierim, K., Ludlow, D. H., Hanelin, J., Ramachandran, T., Glover, G., et al. (2004). Reflecting upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience*, *16*(10), 1746–1772.
- Phelps, E. A. (2006). Emotion and cognition: Insights from studies of the human amygdala. *Annual Review of Psychology*, *57*, 27–53.
- Raz, N. (2005). The aging brain observed in vivo: Differential changes and their modifiers. In R. Cabeza, L. Nyberg, & D. Park (Eds.), *Cognitive neuroscience of aging: Linking cognitive and cerebral aging* (pp. 19–57). New York: Oxford University Press.
- Raz, N., Lindenberger, U., Rodrigue, K., Kennedy, K. M., Head, D., Williamson, A., et al. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex*, *15*(11), 1676–1689.
- Reuter-Lorenz, P. A. & Lustig, C. (2005). Brain aging: Reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology*, *15*(2), 245–251.
- Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: Implications for neuropsychological models of aging. *Neuroscience and Biobehavioral Reviews*, *32*(4), 863–881.
- Rugg, M. D. & Morcom, A. M. (2005). The relationship between brain activity, cognitive performance, and aging: The case of memory. In R. Cabeza, L. Nyberg, & D. Park (Eds.), *Cognitive neuroscience of aging: Linking cognitive and cerebral aging* (pp. 132–154). New York: Oxford University Press.
- Samanez-Larkin, G. R. & D'Esposito, M. (2008). Group comparisons: Imaging the aging brain. *Social Cognitive and Affective Neuroscience*, *3*(3), 290–297.
- Samanez-Larkin, G. R., Gibbs, S. E. B., Khanna, K., Nielsen, L., Carstensen, L. L., & Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nature Neuroscience*, *10*(6), 787–791.
- Samanez-Larkin, G. R., Hollon, N. G., Carstensen, L. L., & Knutson, B. (2008). Individual differences in insular sensitivity during loss anticipation predict avoidance learning. *Psychological Science*, *19*(4), 320–323.
- Samanez-Larkin, G. R., Kuhn, C. M., Yoo, D. J., & Knutson, B. (2010). Variability in nucleus accumbens activity mediates age-related suboptimal financial risk taking. *Journal of Neuroscience*, *30*(4), 1426–1434.
- Samanez-Larkin, G. R., Robertson, E. R., Mikels, J. A., Carstensen, L. L., & Gotlib, I. H. (2009). Selective attention to emotion in the aging brain. *Psychology and Aging*, *24*(3), 748–754.
- Samanez-Larkin, G. R., Wagner, A. D., & Knutson, B. (in press). Expected value information improves financial risk taking across the adult life span. *Social Cognitive and Affective Neuroscience*.
- Scheibe, S. & Blanchard-Fields, F. (2009). Effects of regulating emotions on cognitive performance: What is costly for young adults is not so costly for older adults. *Psychology and Aging*, *24*(1), 217–223.
- Schlagman, S., Schulz, J., & Kvavilashvili, L. (2006). A content analysis of involuntary autobiographical memories: Examining the positivity effect in old age. *Memory*, *14*(2), 161–175.

- Schwartz, C. E., Wright, C. I., Shin, L. M., Kagan, J., Whalen, P. J., McMullin, K. G., et al. (2003). Differential amygdalar response to novel versus newly familiar neutral faces: A functional MRI probe developed for studying inhibited temperament. *Biological Psychiatry*, *53*, 854–862.
- Sergerie, K., Chochol, C., & Armony, J. L. (2008). The role of the amygdala in emotional processing: A quantitative meta-analysis of functional neuroimaging studies. *Neuroscience and Biobehavioral Reviews*, *32*(4), 811–830.
- Smith, D. P., Hillman, C. H., & Duley, A. R. (2005). Influences of age on emotional reactivity during picture processing. *Journals of Gerontology: Series B: Psychological and Social Sciences*, *60B*, 49–56.
- Spaniol, J., Voss, A., & Grady, C. (2008). Aging and emotional memory: Cognitive mechanisms underlying the positivity effect. *Psychology and Aging*, *23*(4), 859–872.
- Spreng, R. N., Wojtowicz, M., & Grady, C. L. (2010). Reliable differences in brain activity between young and old adults: A quantitative meta-analysis across multiple cognitive domains. *Neuroscience and Biobehavioral Reviews*, *34*(8), 1178–1194.
- St. Jacques, P., Bessette-Symons, B., & Cabeza, C. (2009). Functional neuroimaging studies of aging and emotion: Fronto-amygdalar differences during emotional perception and episodic memory. *Journal of the International Neuropsychological Society*, *15*, 819–825.
- St. Jacques, P., Dolcos, F., & Cabeza, R. (2010). Effects of aging on functional connectivity of the amygdala during negative evaluation: A network analysis of fMRI data. *Neurobiology of Aging*, *31*(2), 315–327.
- St. Jacques, P., Dolcos, F., & Cabeza, R. (2009). Effects of aging on functional connectivity of the amygdala for subsequent memory of negative pictures. *Psychological Science*, *20*(1), 74–84.
- Tessitore, A., Hariri, A. R., Fera, F., Smith, W. G., Das, S., Weinberger, D. R., et al. (2005). Functional changes in the activity of brain regions underlying emotion processing in the elderly. *Psychiatry Research*, *139*(1), 9–18.
- Tsai, J. L., Levenson, R. W., & Carstensen, L. L. (2000). Autonomic, subjective, and expressive responses to emotional films in older and younger Chinese Americans and European Americans. *Psychology and Aging*, *15*(4), 684–693.
- Urry, H. L., van Reekum, C. M., Johnstone, T., & Davidson, R. J. (2009). Individual differences in some (but not all) medial prefrontal regions reflect cognitive demand while regulating unpleasant emotion. *NeuroImage*, *47*(3), 852–863.
- Urry, H. L., van Reekum, C. M., Johnstone, T., Kalin, N. H., Thurow, M. E., Schaefer, H. S., et al. (2006). Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. *Journal of Neuroscience*, *26*(16), 4415–4425.
- van Reekum, C. M., Johnstone, T., Urry, H. L., Thurow, M. E., Schaefer, H. S., Alexander, A. L., et al. (2007). Gaze fixations predict brain activation during the voluntary regulation of picture-induced negative affect. *NeuroImage*, *36*(3), 1041–1055.
- West, R. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin*, *120*, 272–292.
- Williams, L. M., Brown, K. J., Palmer, D., Liddell, B. J., Kemp, A. H., Olivieri, G., et al. (2006). The mellow years?: Neural basis of improving emotional stability over age. *Journal of Neuroscience*, *26*(24), 6422–6430.
- Wincoff, A., LaBar, K., Madden, D., Cabeza, R., & Huettel, S. (in press). Cognitive and neural contributors to emotion regulation in aging. *Social Cognitive and Affective Neuroscience*.
- Wood, S., Busemeyer, J., Kolling, A., Cox, C. R., & Davis, H. (2005). Older adults as adaptive decision makers: Evidence from the Iowa Gambling Task. *Psychology and Aging*, *20*(2), 220–225.
- Wood, S., & Kisley, M. A. (2006). The negativity bias is eliminated in older adults: age-related reduction in event-related brain potentials associated with evaluative categorization. *Psychology and Aging*, *21*(4), 815–820.
- Wright, C. I., Dickerson, B. C., Feczko, E., Negeira, A., & Williams, D. (2007). A functional magnetic resonance imaging study of amygdala responses to human faces in aging and mild Alzheimer's disease. *Biological Psychiatry*, *62*(12), 1388–1395.
- Wright, C. I., Negeira, A., Gold, A. L., Britton, J. C., Williams, D., & Barrett, L. F. (2008). Neural correlates of novelty and face-age effects in young and elderly adults. *NeuroImage*, *42*(2), 956–968.
- Wright, C. I., Wedig, M. M., Williams, D., Rauch, S. L., & Albert, M. S. (2006). Novel fearful faces activate the amygdala in healthy young and elderly adults. *Neurobiology of Aging*, *27*(2), 361–374.
- Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews*, *41*(1), 88–123.