

EMOTION,
AGING,
AND HEALTH

Edited by
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DEFAULT MODE NETWORK AND LATER-LIFE EMOTION REGULATION: LINKING FUNCTIONAL CONNECTIVITY PATTERNS AND EMOTIONAL OUTCOMES

BRUNA MARTINS AND MARA MATHER

Aging is marked by cognitive declines across modalities. Sensory processing becomes noisier, memories tougher to access, and complex tasks increasingly difficult to perform accurately (Goh, 2011; Li & Lindenberger, 2002). Lateral areas of the prefrontal cortex (PFC) involved in salience and executive processing lose volume with age (Cabeza, 2002; Fjell et al., 2009; Raz et al., 2005). In addition, older people show difficulty maintaining and manipulating information (Goh, An, & Resnick, 2012; Park & Reuter-Lorenz, 2009) and selectively inhibiting distractions (Lustig, Hasher, & Zacks, 2007) compared with younger adults.

However, despite structural declines in lateral brain regions, overall emotional experience tends to be less negative for older than younger adults. Self-reported well-being is lowest in midlife and increases after age 50 (Jeste et al., 2013), and older adults report less negative affect in daily life than do younger people (Stone, Schwartz, Broderick, & Deaton, 2010). Negative affect does

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tend to increase in the last decade of life before the terminal year (Schilling, Wahl, & Wiegering, 2013); however, when physical functioning is accounted for, negative affect is lower in late life than in midlife, even among those over age 85 (Windsor, Burns, & Byles, 2013). In this chapter, we focus on emotion regulation processes in healthy aging. Although we do not discuss physical health and its impact on emotion regulation, we caution that this remains an important area for future consideration.

Older adults show improvements relative to younger people in well-being, as well as in outcomes related to the regulation of emotions. Mood disorders indicating emotional dysregulation such as depression (Blazer, 2003; Piazza & Charles, 2006) and anxiety (Fiske, Wetherell, & Gatz, 2009) decrease in prevalence with age (Kessler et al., 2005). Subclinical mood symptoms such as ruminative thinking also tend to decrease across the lifespan (Sütterlin, Paap, Babic, Kübler, & Vögele, 2012). Thus, healthy older adults appear to manage their emotional well-being better than do younger adults. A possible mechanism for this difference may involve changes in emotion regulation brain networks.

Successful emotion regulation is associated with activity in lateral executive regions, as well as medial regions in younger adults (Buhle et al., 2014; Frank et al., 2014). While lateral brain structures and functions tend to decline with age, medial brain structures involved in self-related processing remain relatively intact in later life (Fjell et al., 2009; Gutches, Kensinger, Yoon & Schacter, 2007; Lalanne, Grolleau, & Piolino, 2010). These well-maintained medial areas of the PFC may help sustain emotion regulation function in late life despite declines in lateral PFC.

In this chapter, we discuss the functional connectivity of medial self-related brain circuits and suggest how this network connectivity may support emotion regulation in older adults. First, we provide background on emotional outcomes and self-related processing in later life. Next, we introduce the brain circuits contributing to emotion regulation and review age-related changes within these networks. Then we report connectivity changes in a network known as the *default mode network* (DMN)—a set of medial regions involved in internally directed or self-generated thought (Andrews-Hanna, Smallwood, & Spreng, 2014). We then compare DMN functional connectivity with attention and executive networks in older adults to connectivity in two different populations: (a) people with depression, a disorder marked by increased self-focus and negative functional outcomes; and (b) mindfulness practitioners trained to be aware of self-related processes, who generally show positive functional outcomes. On the basis of this review, we propose a model of how self-related processing and increased connectivity of the DMN with other networks may promote positive emotional outcomes in both healthy aging and mindfulness experts. Throughout the chapter, we graphically describe each component of the model in Figure 1.1, one pathway at a time.

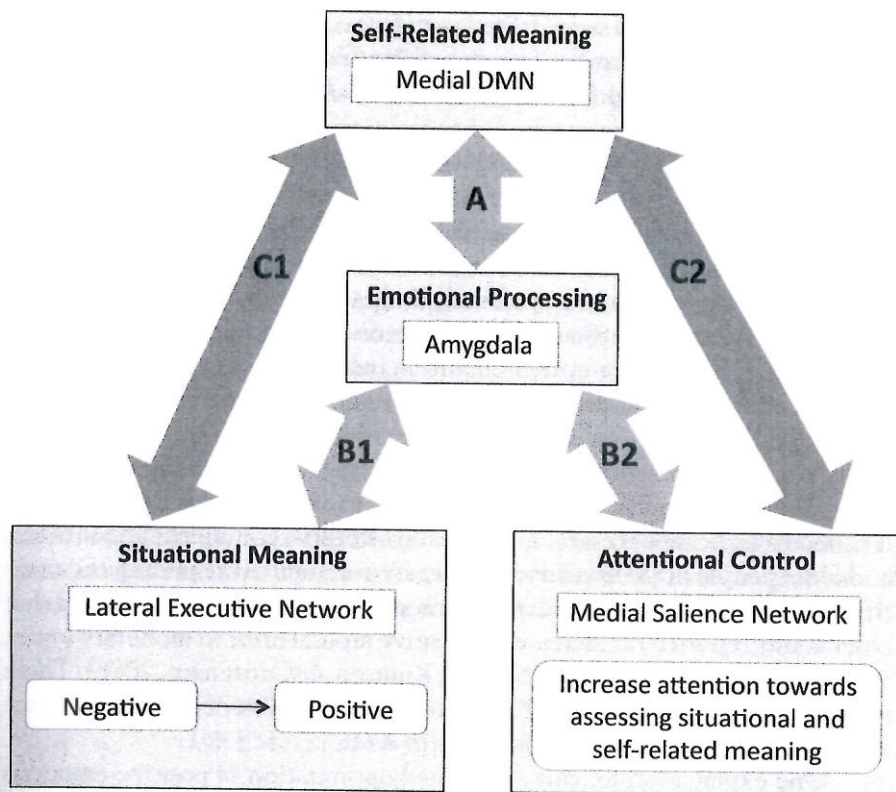


Figure 1.1. A model of brain network integration in emotion regulation in aging. (A) Default mode network (DMN) is more functionally connected to the amygdala for older adults; (B1) Lateral executive network–amygdala connectivity demonstrates no significant age differences; (B2) Medial salience network–amygdala connectivity is enhanced for older adults compared to younger adults; (C) Older adults and mindfulness experts show increased connectivity between DMN–executive and DMN–salience networks. Integration of situational and self-related processing in emotion regulation may drive positive outcomes in both populations. Note that the C-paths are weakened for depressed individuals.

POSITIVE EMOTION AND SELF-RELATED PROCESSING ARE PRIORITIZED IN LATER LIFE

Older adults show a preference to ignore negative and attend to positive information relative to younger adults, indicating a *positivity effect* (Mather & Carstensen, 2005). For instance, older adults more quickly detected items appearing in the same location as a previously seen positive image than a previously seen negative image, while younger adults did not show this difference by valence (Mather & Carstensen, 2003). Similarly, older adults preferred to

look at happy faces and away from angry faces; in contrast, younger adults demonstrated a gaze bias for fear-provoking faces (Isaacowitz, Wadlinger, Goren, & Wilson, 2006). Thus, older adults tend to disengage from negative information.

Older adults also appear to regulate their emotions during unavoidable interactions with negative stimuli more than do younger adults. In one study, younger and older adults either naturally viewed disgusting videos of surgical operations or were told to increase or decrease their emotional reactions during the films (Kunzmann, Kupperbusch, & Levenson, 2005). Younger adults showed no difference between the control condition (i.e., natural film viewing) and the increasing emotion condition, whereas older adults showed no difference between the control condition and the decreasing emotion condition. This suggests a tendency for older adults to focus away from negative content and for younger adults to amplify their negative emotions under natural viewing conditions. In another experiment, older and younger adults listened to audiotapes of strangers making offensive comments about them, and older people made fewer and less negative comments regarding the tapes than younger adults (Charles & Carstensen, 2008). Another study found that older adults reported no increase in negative arousal prior to monetary losses, while younger participants did (Nielsen, Knutson, & Carstensen, 2008). These studies suggest that older adults tend to naturally diminish negative affect once it is induced, even without instructions to do so.

One explanation for this age-related optimization of positive emotions is that older adults focus more on emotional outcomes and regulation of affect than do younger adults. Socioemotional selectivity theory argues that as perceived lifespan decreases, older adults tend to maximize positive affective experiences in the present moment, which in turn should support psychological and emotional well-being across the lifespan (Carstensen, Isaacowitz, & Charles, 1999; Charles & Carstensen, 2008; Lang & Carstensen, 2002). Greater focus on emotional well-being and maintenance of affect in later life may lead to differences in how new information is processed in relation to one's personal goals and self-relevance. In one study, older and younger adults were shown negative film clips of injustice situations and asked to either passively view, suppress their emotional reactions, or positively refocus their attention to a pleasant memory unrelated to the video (Phillips, Henry, Hosie, & Milne, 2008). Older adults reported lower levels of negative emotion after utilizing self-relevant distraction rather than an emotional suppression strategy, while younger adults showed no difference between conditions. Thus, it appears that for older adults, using self-relevant positive information as a distraction improves affect more than does suppressing emotions.

Older adults show a preserved capacity for processing the self-relevance of information, and thus boost later memory for that information (Gutchess

et al., 2007; Leshikar, Park, & Gutchess, 2014; Symons & Johnson, 1997). Older adults engage self-referential medial prefrontal cortical regions (MPFC) more during the encoding of positive information than negative, and this activity is predictive of later memory for the encoded information (Gutchess, Kensinger, & Schacter, 2007; Leclerc & Kensinger, 2008). In contrast, younger adults show greater MPFC activity during encoding of negative stimuli, and better memory for these negative items that are processed in relation to the self. Thus, self-referent information is not always better remembered but is selectively encoded based on valence. These findings suggest that older adults tend to selectively process positive information more self-referentially, whereas younger adults selectively process negative stimuli in relationship to the self through medial activation. Medial brain structures that process self-relevance decline across the lifespan at a slower rate than lateral central executive regions (Fjell et al., 2009) and may help boost positive associations in memory. We posit that by selectively increasing the self-relevance of positive but not negative emotional situations, older adults can increase well-being (Figure 1.1, Path A). Before discussing the functional connectivity of the self-related circuits, we review how functional connectivity can be used as a method for assessing networks.

AGE-RELATED CHANGES IN FUNCTIONAL CONNECTIVITY OF EMOTION REGULATION CIRCUITS

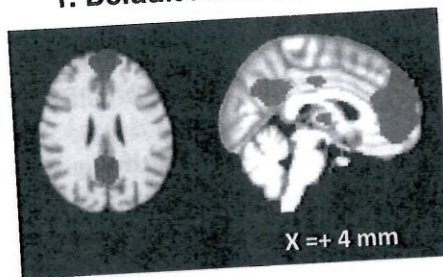
Functional Connectivity Methods for Quantifying Network Circuitry

While traditional functional magnetic resonance imaging methods identify regions activated in the brain by specific tasks, *functional connectivity* methods identify synchronization among regions in the brain in their spontaneous fluctuations in activity. Correlated temporal patterns among different regions identify networks (Friston, Frith, Liddle, & Frackowiak, 1993). Different networks associated with different functions, such as visuospatial processing or executive processing, can be identified from patterns of brain activity even while people are at rest (Laird et al., 2011; Mennes et al., 2010; Smith et al., 2009). In this chapter, we focus on three canonical networks in the brain: (a) a medial DMN, which includes regions in MPFC and posterior cingulate cortex and is more active during rest than during cognitive task performance; (b) a lateral executive network with key regions in dorsolateral PFC and posterior parietal cortex, activated during effortful goal-directed working memory tasks; and (c) a primarily medial salience network active in attentional control, including areas in the anterior insula, anterior cingulate cortex, and ventrolateral PFC (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Greicius, Krasnow, Reiss, & Menon, 2003; Raichle et al., 2001). Throughout the chapter, we aim to

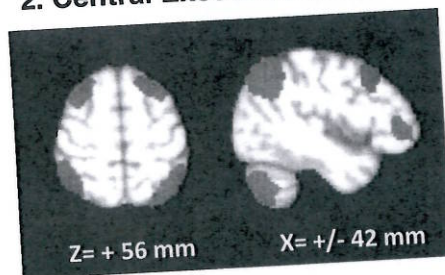
investigate the coupling between these three networks, as well as the functional connectivity within each. The anatomical representation of each network is provided in Figure 1.2. In Figure 1.1, we suggest how these three networks may function together to support emotion regulation processing in aging, and we review evidence from depressed patients and mindfulness practitioners that also supports this proposed mechanism. Activity in a brain region known as the amygdala is associated with fear learning and emotional responding (LeDoux, 2003), and in Figure 1.1 we review how connectivity of the amygdala with these networks of interest may influence emotion regulation.

Functional connectivity can be assessed both across regions of the same network (intranetwork connectivity) as well as between different networks (internetwork connectivity). For instance, recent evidence supports that the executive network coactivates with other networks depending on the goals at hand; for instance, it is coactive with the DMN during an autobiographical task that requires thinking about one's self, but not during an attentionally demanding planning task that does not rely on self-processing

1. Default Mode Network



2. Central Executive Network



3. Salience Network

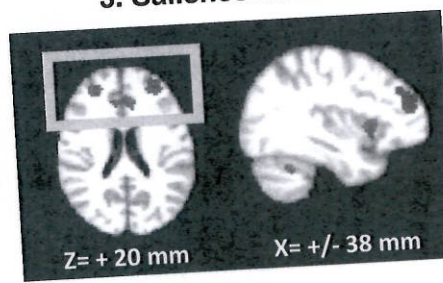


Figure 1.2. Regions of the default mode, executive, and salience networks. (1) Key regions of default mode network (DMN) include the medial prefrontal cortex (MPFC) and posterior cingulate cortex. (2) Executive network whose key regions include the dorsolateral prefrontal cortex and posterior parietal cortex. (3) Regions of the salience network including the ventrolateral prefrontal cortex, anterior insula, and anterior cingulate cortex (highlighted in grey box). Data from Shirer et al. (2012).

(Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). In the following sections, we review changes within the DMN, as well as internetwork changes between the DMN and the executive/salience networks in healthy older adults, depressed patients, and mindfulness practitioners.

Default Mode Network and Self-Related Processing

The DMN activates during unstructured cognitive processing, including daydreaming about self-relevant agendas at rest (Buckner, Andrews-Hanna, & Schacter, 2008; Mason et al., 2007). It comprises primarily medial structures, including the MPFC, the posterior cingulate cortex/precuneus, the inferior parietal lobule, and the hippocampus (Raichle et al., 2001; see Figure 1.2, Section 1, for DMN regions). During attention-demanding cognitive tasks, DMN activity decreases and activity in the salience network increases (Shulman et al., 1997; Figure 1.2, Section 3). Most cognitive tasks also yield anticorrelations between the DMN and the executive network, with the exception of tasks in which self-related processing promotes goal-directed task performance (Spreng et al., 2010). However, among older adults, DMN activity decreases less as cognitive task difficulty increases (Persson, Lustig, Nelson, & Reuter-Lorenz, 2007; Sambataro et al., 2010). A recent study indicated that these age differences in DMN activity carry over to emotion regulation (Martins, Ponzio, Velasco, Kaplan, & Mather, 2015). In this study, the posterior component of the DMN was activated during use of both self-reflective distraction and reappraisal emotion regulation strategies in older adults. In contrast, among younger adults, the posterior DMN activated only during self-reflective distraction. This suggests that the DMN is involved in a broader range of contexts in emotion regulation and self-reflective processing for older people (Martins et al., 2015; see also Spreng & Schacter, 2012; Figure 1.1, Path A).

Older Adults Show Greater Amygdala Connectivity With DMN and Other Networks During Uninstructed Emotion Regulation

Emotion regulation success is often quantified in terms of down-regulation of activity in the amygdala, which can be modulated by different emotion regulation processes (Ochsner, Silvers, & Buhle, 2012). One of the most effective emotion regulation strategies, *cognitive reappraisal*, involves trying to “see the silver lining” in a negative situation (Gross, 2002). During reappraisal use, the MPFC and the DMN promote self-reflective processes that determine the personal meaning of stimuli and monitor one’s emotional state (Ochsner et al., 2012; Figure 1.1, Path A). Activity in regions of the salience network directs attention toward the assessment of emotional and

situational meaning (Figure 1.2, Section 3), and lateral executive network regions alter and update meaning in working memory during reappraisal processing (Figure 1.2, Section 2).

Both younger and older adults demonstrate strong functional connectivity between the anterior DMN and the amygdala (Figure 1.1, Path A), as well as connectivity between lateral executive network regions and the amygdala when instructed to reappraise (Urry et al., 2006; Winecoff, Labar, Madden, Cabeza, & Huettel, 2011; Figure 1.1, Path B1). However, when processing negative stimuli in the absence of explicit emotional regulation instructions, older adults show greater functional connectivity between the anterior cingulate cortex (hub of the salience network; Figure 1.2, Section 3) and the amygdala than do younger adults (St. Jacques, Dolcos, & Cabeza, 2010; Figure 1.1, Path B2). In another study, older adults who recalled more positive faces from a set of positive, negative, and neutral video clips showed stronger resting MPFC–amygdala functional connectivity than did those who recalled more negative faces, but this effect was not found in younger adults (Sakaki, Nga, & Mather, 2013). This tighter coupling between MPFC and the amygdala in older adults was also found to predict the strength of bias in memory toward recalling positive items (Sakaki et al., 2013). It thus appears that older adults show stronger spontaneous functional connectivity between medial structures and the amygdala than do younger adults when processing emotional stimuli (Figure 1.1, Paths A and B2). In the next section, we investigate age-related changes in connectivity both within the DMN and between the DMN and the salience and executive networks (Figure 1.1, C paths).

DMN FUNCTIONAL CONNECTIVITY AND EMOTION REGULATION

Functional Connectivity Decreases Within the DMN for Older Adults

Within the DMN, functional connectivity decreases with age (Andrews-Hanna et al., 2007; Batouli, Boroomand, Fakhri, Sikaroodi, & Oghabian, 2009; Bluhm et al., 2008; Damoiseaux et al., 2008; Grady, Grigg, & Ng, 2012). In particular, connectivity between anterior and posterior DMN regions is weaker among older than younger adults during both resting state (Bluhm et al., 2008; Damoiseaux et al., 2008) and cognitive task performance (Sambataro et al., 2010). Older adults also demonstrate weaker functional connectivity within the DMN during performance of a self-reflective processing task (Grady et al., 2012). These studies demonstrate a decline of functional connectivity within the DMN with age, both at rest and during cognitive and self-related task performance.

Increased Connectivity Between DMN and Other Networks in Later Life

While DMN internal functional connectivity decreases with age, DMN connectivity with the salience and executive networks increases (Figure 1.1, B paths). Resting state connectivity of the DMN, salience, executive, visual, and somatomotor networks, and other networks reveal less segregation with increasing age (20–89 years; see Chan, Park, Savalia, Petersen, & Wig, 2014). This indicates that younger adults show greater differentiation between networks and that age leads to greater cohesion between networks. Internetwork connectivity was also assessed during task performance of an autobiographical planning task and a visuospatial task, and the relationships between the functional connectivity of the DMN, executive, and salience networks were assessed in younger and older adults (Spreng & Schacter, 2012). Older adults showed greater coupling between the DMN and the executive network for both visuospatial and autobiographical planning tasks. On the other hand, younger adults showed coupling between the DMN and the executive network for the autobiographical task, and between the salience and executive network for the visuospatial task (which requires attentional control). These findings suggest that the functional connectivity of the DMN to other networks increases in later life (Figure 1.1, C paths). However, whether these enhanced connections indicate facilitation of self-related processing in cognitive contexts remains speculative. Therefore, we draw from two other populations—depressed patients and mindfulness practitioners—and examine how changes in functional connectivity relate to differing emotional outcomes.

Default Mode Connectivity Increases With Rumination in Depression

Perseveration on negative self-related thoughts, or *rumination*, is among one of the cardinal symptoms of depression (Nolen-Hoeksema, 1991). Patients with major depressive disorder (MDD) attend more to and better remember negative than positive stimuli (Williams et al., 1996). Individuals with depression are faster to detect a dot in the same spatial location as a preceding negative face than following a neutral one (Joormann & Gotlib, 2007), indicating a negativity bias in spatial attention. In addition, depressed individuals show greater MPFC activity during tasks promoting negative self-focus than controls, and this activation correlates with rumination scores (Nejad, Fossati, & Lemogne, 2013). Resting state functional connectivity within the DMN is increased for depressed patients relative to controls (Berman et al., 2011) and is predictive of depressive episode duration (Greicius et al., 2007).

Depression is also associated with decreased connectivity between the DMN and the salience and executive networks. Anand et al. (2005) reported decreased connectivity between the MPFC and the amygdala for individuals

with MDD relative to healthy controls, both at rest and when viewing emotional images. Furthermore, greater dominance of DMN over executive network activity at rest correlates positively with maladaptive depressive rumination scores and correlates negatively with a measure of adaptive self-related reflection (Hamilton et al., 2011). In summary, depressed individuals show greater DMN intranetwork connectivity, and decreased internetwork connectivity between the DMN and other networks during both rest and task performance (weakened C paths in Figure 1.1). We next contrast these DMN connectivity patterns to those of mindfulness practitioners, who, like older adults, demonstrate positive functional outcomes.

Intranetwork and Internetwork Default Mode Connectivity is Enhanced for Mindfulness Practitioners

A central aim of mindfulness practice is to observe the present moment, and increase awareness of both self and situation, without judgment or attempts to change the status quo (Hayes, Strosahl, & Wilson, 1999; Kabat-Zinn, 2003). Mindfulness practice is associated with increases in well-being and can decrease stress (see the review by Rubia, 2009). For instance, mindfulness practice leads to decreased self-reported negative affect and to fewer ruminative and depressive symptoms (Chambers, Gullone, & Allen, 2009). Additionally, mindfulness meditators are better able to disengage from negative images, similar to what is seen among older adults (Ortner, Kilner, & Zelazo, 2007).

Meditators with extensive mindfulness experience show increased functional connectivity within the DMN. Meditation experts with more than 120 months of experience showed greater functional connectivity within the DMN than did novices both at rest and during meditation (Brewer et al., 2011). In addition, self-reported mindfulness in daily life is positively associated with resting state connectivity strength within the DMN (Prakash, De Leon, Klatt, Malarkey, & Patterson, 2013). In terms of internetwork connectivity, relative to novices, experienced mindfulness meditators¹ show increased DMN connectivity to executive network regions in the dorsolateral PFC both at rest and during meditation (Brewer et al., 2011; Farb et al., 2007; see Figure 1.1, Path C1), and increased posterior DMN functional connectivity to the anterior

¹It is important to note that mindfulness experience differed across the studies reviewed here, and the operational definition of a "mindfulness expert" is heterogeneous. Mindfulness experience included participants in mindfulness training studies who trained for 2 months according to a manualized mindfulness based stress reduction (MBSR) protocol relative to control participants, mindfulness practitioners with over 120 months meditation practice (Concentration, Loving-Kindness, and Choiceless Awareness meditation) who were selected as a special population, and one study reviewed utilized self-reported daily mindfulness scores as a continuous variable in their analyses.

cingulate cortex of the salience network (Figure 1.1, Path C2). These findings suggest that functional connectivity of the DMN with regions outside of the network also increase with mindfulness practice.

INTEGRATING SITUATION AND SELF: EMOTION REGULATION IN AGING, DEPRESSION, AND MINDFULNESS PRACTICE

Based on the literature on aging, depressed individuals, and mindfulness practitioners reviewed above, we now discuss the consistent relationships between functional connectivity of the DMN, executive, and salience networks across these three populations.

Older Adults Show Greater Corticolimbic Functional Connectivity During Uninstructed Reappraisal

Increased connectivity between brain regions involved in processing self and situation may promote older adults' strategies in natural emotion regulation settings. Connectivity between medial and limbic structures tends to be stronger for older than younger adults when viewing emotional stimuli without explicit emotion regulation instructions (Sakaki et al., 2013; St. Jacques et al., 2010). Older adults show spontaneous enhancement of these DMN-amygdala and salience network-amygdala circuits relative to younger adults, even without reminders or supporting cues. In our model of emotion regulation in aging, we propose that these networks regulate the amygdala by updating self-related meaning of reappraisals (see Ochsner et al., 2012; Figure 1.1, Path A). However, connectivity of executive regions and the amygdala during cued emotion regulation is similar across the lifespan (Winecoff et al., 2011; Figure 1.1, Path B1). Thus, it seems that younger adults are equally capable of regulating their emotions but are less likely to do so when not reminded. This motivational account fits the notion that older adults more readily recruit cognitive control mechanisms to regulate their emotions (Knight et al., 2007; Kryla-Lighthall & Mather, 2009; Mather & Carstensen, 2005; Mather & Knight, 2005) and maps well onto previous behavioral findings in which younger adults' memory biases resemble those of older adults when in an emotion-focus condition (Kennedy, Mather, & Carstensen, 2004; Mather & Johnson, 2000).

Older adults also appear to have stronger functional connectivity of the salience network and DMN with the amygdala than do younger adults (Sakaki et al., 2013; St. Jacques et al., 2010; Figure 1.1, Path B2). Given the role of regions in the salience network and DMN in utilization of reappraisal strategies (Ochsner et al., 2012), stronger connectivity between these networks and the amygdala may facilitate emotion regulation strategy use. Enhancement of

medial emotion regulation circuits may provide additional regulation routes to down-regulate the amygdala and compensate for gray matter loss in lateral executive network regions (Cabeza, 2002; Fjell et al., 2009; Raz et al., 2005).

Increased DMN Internetwork Connectivity May Represent Greater Self-Reflection in Aging

Changes in connectivity of networks involved in self-related processing, attentional control, and executive control of emotion may support improved emotion regulation in later life. Relating the self to the situation could represent a possible compensatory mechanism in aging, involving two stages. As previously mentioned, like younger adults, older adults may initially engage salience network–amygdala circuits to increase attention directed toward a stimulus and executive network–amygdala circuits to maximize the positivity of situational meaning (i.e., reappraising a sad situation as only being temporary). In a second stage of processing, older people may use enhanced DMN–executive network and DMN–salience network connections to increase awareness of the associations between positive interpretations and the self (and to dissociate negative interpretations from the self). Increased synchrony between the DMN and lateral executive network regions may result from the integration of self-related processing in more contexts in later life (Martins et al., 2015; Spreng & Schacter, 2012; Figure 1.1, C paths). An age-related increase in associating positive situations to the self and decreasing self-involvement in unalterable negative situations may be one route leading to age by valence interactions in emotional memory (Glisky & Marquine, 2009; Gutchess, Kensinger, & Schacter, 2007; Gutchess, Kensinger, Yoon, et al., 2007; Kensinger & Leclerc, 2009).

In addition, internetwork connectivity between the DMN and the salience and executive networks is also enhanced with mindfulness expertise. Given that both older adults and mindfulness experts show high levels of well-being and stronger functional connectivity across networks, a connection may exist between network connectivity and outcomes (Figure 1.1, C paths). It is possible that mindfulness experts also assess the self and situation closely, but accept rather than change these situations. It is not surprising that mindfulness and awareness of situational and self-related appraisals have been suggested as a first step in enacting reappraisal strategies (Garland, Gaylord, & Fredrickson, 2011). Regions overlapping with the DMN show activation during self-reflection, regardless of whether self-related processing is conscious or implicit (Rameson, Satpute, & Lieberman, 2010). However, the connection between situational context and positive emotions in older adults remains unknown, and clarifying the role of awareness of these contextual links is an important direction for future research. Furthermore, while the three populations investigated in this chapter demonstrate a consistent pattern in DMN

internetwork functional connectivity, differences between these special populations are multifactorial and could represent other variables unexplored in our review. Differing functional mechanisms may manifest in similar network patterns that differ in terms of their etiology. Future research should investigate direct relationships between outcomes in these populations and DMN networking in order to better clarify the mechanisms outlined here.

In contrast, depressed individuals failed to show enhanced connectivity between the DMN and other networks. We suggest that decreased internetwork connectivity further reduces the ability of self-processing to alter negative situations and/or the ability of situational appraisals to alter negative thoughts. Depression is associated with a decreased ability to assess situations, feelings, and emotions from a distanced perspective (Sheppard & Teasdale, 2000). Decreased DMN–executive network and DMN–salience network interactions may lead to processing the self separately from emotion regulation goals. Processing of negative situations separately from emotional self-assessment may also decrease feelings of self-efficacy and maintain feelings of hopelessness (Maier & Seligman, 1976).

Intranetwork Connectivity Cannot Predict Emotion Regulation Outcomes

The stronger connectivity found within the DMN for depressed patients and mindfulness practitioners was strikingly different from the decreased connectivity found within the DMN in aging populations. Ruminative symptoms correlate with increased internal connectivity of the DMN in depressed patients (Berman et al., 2011), and in parallel, with level of mindfulness meditation practice both in daily life and in the laboratory (Brewer et al., 2011; Prakash et al., 2013). Thus, stronger internal DMN connectivity is not in itself diagnostic of well-being; it tracks negative emotional outcomes for depressed patients and positive emotional outcomes in mindfulness expertise. This suggests that decreased DMN connectivity in older adult populations is unlikely in itself to impair emotion regulation. However, more research is needed to uncover which characteristics of these populations are consistently associated with DMN internal connectivity.

SUMMARY

Emotional resilience in later life poses an age-related enigma. Lateral executive structures decline, and yet older adults show improvements in emotional outcomes. Emotion regulation goals that shift with age and rely on brain regions that decline relatively little through the lifespan such as the

MPFC, help explain this puzzle (Mather, 2012). The DMN shows enhanced connectivity with the executive and salience network regions for both older adults and mindfulness experts, but not for depressed individuals. In contrast, the internal connectivity of the DMN increases for both depressed patients and mindfulness practitioners, but decreases in older adults. This shows that there is no consistent relationship between favorable emotional outcomes and DMN intranetwork connectivity. This remains an area to be investigated in future research.

We propose an emotion regulation mechanism in which the functional connectivity between the DMN and lateral executive/medial salience networks may represent the integration of successful reappraisal outcomes and self-related meaning. Taking stock of situational and self-related feelings and emotions is the first step toward emotion regulation (Garland et al., 2011). In the case of older adults, internetwork connectivity may link positive reappraisals to the self.

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MPFC, help explain this puzzle (Mather, 2012). The DMN shows enhanced connectivity with the executive and salience network regions for both older adults and mindfulness experts, but not for depressed individuals. In contrast, the internal connectivity of the DMN increases for both depressed patients and mindfulness practitioners, but decreases in older adults. This shows that there is no consistent relationship between favorable emotional outcomes and DMN intranetwork connectivity. This remains an area to be investigated in future research.

We propose an emotion regulation mechanism in which the functional connectivity between the DMN and lateral executive/medial salience networks may represent the integration of successful reappraisal outcomes and self-related meaning. Taking stock of situational and self-related feelings and emotions is the first step toward emotion regulation (Garland et al., 2011). In the case of older adults, internetwork connectivity may link positive reappraisals to the self.

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