Memory for associative integrations depends on emotion and age

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MEMORY FOR ASSOCIATIVE INTEGRATIONS DEPENDS ON EMOTION AND AGE

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A key feature of human memory is the ability to remember not only discrete pieces of information but also to form novel associations between them. A special type of association, called an “integration”, can be formed when the pieces are encoded as a single representation in memory (Wollen, Weber & Lowry, 1972; Murray & Kensinger, 2012). The work presented here investigates what neural mechanisms underlie the formation and subsequent retrieval of integrated mental images in younger adulthood (individuals aged 18-30), whether those mechanisms differ based on the emotional content of the integration, and whether older and younger adults generate and remember emotional integrations differently from one another. I show that younger adults utilize two different routes to form integrations, depending on their emotional content: a rapid, perceptually-supported route that allows for fast integration of emotional pairs but that leads to poor downstream memory for the associates, and a slow, conceptually-supported route for neutral pairs that takes more time but that leads to strong downstream memory. Conversely, older adults utilize slow, controlled processing of emotional integrations that leads to strong memory, but they fail to produce durable memory for non-emotional pairs due to age-related associative deficits. Together, these results highlight differences both within and between age groups in the formation and retrieval of emotional and non-emotional integrations, and suggest a circumstance – integration of emotional pairs – in which older adults can overcome previously reported age-related deficits.

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I. Introduction and Background Literature

Integration is one process by which two or more discrete pieces of information can be combined into a single mental representation (Diana, Yonelinas, & Ranganath, 2008; Graf & Schacter, 1989; Wollen, Weber, & Lowry, 1972). For example, one might integrate the representations of a casket, some family members, and a church together as a "funeral". The benefit of such integration is that retrieval of such a representation – the "funeral" – allows access to multiple related items or features simultaneously without having to separately retrieve the individual representations of a casket and a church. Integrations represent a "special" type of associative memory that differs from more traditional types of associative binding (e.g., simply remembering that "casket", "family" and "church" were presented simultaneously on a screen).

To date, numerous studies have explored both the behavioral (Dorfman, 1999; Graf & Schacter, 1989; Mandler, 1980; Wollen, Weber, & Lowry, 1972) and neural (Bader et al., 2010; Diana, Yonelinas, & Ranganath, 2008; Ecker, Zimmer, & Groh-Bordin, 2007; Haskins et al., 2008; Staresina & Davachi, 2006; 2008; 2010) bases for the formation and retrieval of such integrations. By and large, these investigations have focused on neutral information, but many of the integrations we utilize every day – such as the "funeral" example above – contain emotional information. To date, there has been little research investigating the effect that emotional information has on the formation of these integrations. The overarching goals of my dissertation research, therefore, were to: (1) Investigate the whether the encoding and retrieval of emotional and neutral integrations are supported by similar or dissociable neural mechanisms and (2) Investigate whether older (age 65+) and younger (age 18-30) adults form and retrieve emotional and neutral integrations differently from one another. These goals are addressed in the second and third chapters of this dissertation, respectively.

Though, as noted, there has been little investigation in the role that emotion plays in the integration process, some interactions between emotion and associative binding have been documented. It has been well established that emotional information is handled differently in memory from non-emotional information, with emotional information typically receiving a mnemonic benefit (reviewed by Hamann, 2001; Kensinger, 2009). The emotionality of an experience is typically characterized along two orthogonal dimensions: arousal (how exciting or calming an experience is) and valence (how pleasant or unpleasant; Russell, 1980). Although much of the prior work investigating emotion's effect on memory has focused on the dimension of arousal (Cahill et al., 1994; Cahill & McGaugh, 1995), there is evidence that valence can influence associative memory as well (Pierce & Kensinger, 2011). Moreover, valence and arousal may interact to influence both the subjective qualities of a memory (Sharot & Phelps, 2004; Talarico & Rubin, 2003; Zimmerman & Kelley, 2010) and also the way that the amygdala interacts with visual and prefrontal processes (Mickley Steinmetz, Addis, & Kensinger, 2010).

Although memory for emotional information is typically enhanced relative to neutral information, there has historically been disagreement over how emotion – and in particular, emotional arousal – affects the binding of associated neutral details. In some cases, emotion has been shown to enhance the binding of related details (Hadley & MacKay, 2006; MacKay & Ahmetzanov, 2005; McKay et al., 2006), while in others emotion has been shown to have no effect or to impair such binding (Jacobs & Nadel, 1998; Kensinger & Schacter, 2006; Payne et al., 2004). More recent accounts have sought to reconcile these inconsistencies. Mather (2007) proposed an "object based" framework, with arousal enhancing the binding of information encoded as an item feature but not of information encoded as a contextual detail (see also Kensinger, 2007, 2009). This framework can account for much of the extant data, but there are some exceptions, when arousal does not enhance memory for intra-item features (Guillet & Arndt, 2009) and when it does enhance memory for inter-item binding (Pierce & Kensinger, 2011).

Recognizing the need to account for these contradictory patterns, Mather and Sutherland (2011) proposed the "Arousal-Biased Competition" (ABC) model, describing how arousal may bias resources toward the most conspicuous or goal-relevant stimuli. Thus, if a single item (e.g., a snake) gains priority, then arousal will enhance the binding of the features of that item (e.g., its color, form). But if the pairing of items takes on importance (e.g., the snake and its owner) then arousal will enhance the binding of that association. In other words, it is not the *type* of detail (item vs. contextual or intra- vs. inter-item associations) that predicts the effect of arousal but the *goal relevance* of the detail (see related discussion by Levine & Edelstein, 2009). Although it is always the case that goal-relevant information will be prioritized, according to ABC, arousal exaggerates this prioritization; thus, arousal will enhance the binding of goal-relevant features and will impair the binding of features that are not goal relevant.

In this context, the effect of arousal on associative binding will depend critically on the way the to-be-bound pieces of information are initially processed or perceived. On the one hand, because integration requires that pieces of information be processed as a coherent whole, all features that are being bound into that representation may be goal-relevant. If true, then arousal may lead to a beneficial effect on the process of integration, possibly facilitating the creation of the mental representation. On the other hand, because arousing features can capture attention and become prioritized for processing, the presence of those arousing features may make it harder to attend to the other features present at the same time, thereby making the successful creation of an integrated image harder to achieve.

To directly investigate the effect that emotion would have on the creation of integrated representations, I conducted a study (Murray & Kensinger, 2012) that encouraged integrative mental imagery between verbal paired associates. I asked participants to study pairs of words and to either maintain separate mental images of the items (non-integration) or to create an integrated, interactive mental image of the two items (integration). Some pairs contained an emotional and a neutral word, and other pairs contained two neutral words. Each study pair was displayed for two, four, or six seconds, and after each pair participants were asked to report the vividness of the two individual images (non-integrated) or one unified image (integrated) they were able to generate.

Participants consistently rated their imagery success as being high for emotional pairs, regardless of the length of the encoding trial, but they reported little success in generating images for neutral pairs during short (two-second) encoding trials. These results are consistent with the prediction that arousal would facilitate the process of integration: when arousal was present, participants were able to create an image that integrated two distinct items, even with little time to do so.

Participants were then given a surprise cued recall test in which they were given a single studied word and asked to provide its paired counterpart. Because this was an associative task, I unsurprisingly found that pairs studied in the integration condition were better recalled than those studied in the non-integration condition. Conversely, on an item recognition test, performance was better in the non-integrated condition than in the integrated one.

The twist, however, was that the integration benefit was disproportionately *greater* for neutral pairs than for pairs containing an emotion word. Although participants had an easier time generating the integrated images for the emotional pairs, they showed *less* of a mnemonic benefit from integration of those pairs. At the broadest level, these data suggest that *forming* such integrated representations – actually assembling together the different perceptual and semantic features – and *remembering* those representations in long-term memory could be differentially affected by arousal. It is interesting to note that this distinction parallels one noted by Zimmerman and Kelley (2010); they reported that participants gave higher judgments-of-learning to emotional pairs than to neutral ones but actually remembered the emotional pairs less well. When reviewing this study, Madan and colleagues (2012) suggested that the participants might have applied less effort when forming associations of those emotional items, an explanation that is also consistent with my data. It may be the case that if information is more easily integrated – perhaps via processes implemented in visual processing regions – the mnemonic storage of that integration is less effortful and therefore less durable.

These behavioral results suggest a dissociation between the processes leading to integration with emotional items and with neutral items, but the basis for this dissociation is unknown. When engaged by emotional events, amygdala activity often modulates the processing within sensory regions (Compton, 2003; Mather et al., 2006; Vuilleumier et al., 2001; Vuilleumier et al., 2004) and also processing within the HC (Richardson, Strange, and Dolan, 2004; see Phelps, 2004 for review) and other medial temporal lobe regions (Dolcos, LaBar, and Cabeza, 2004; McGaugh, McIntyre, and Power, 2002). Emotion can also influence the allocation of elaborative processing resources (Anderson and Phelps, 2001; Libkuman, Stabler, and Otani, 2004). It is, therefore, possible that the facilitated integration I have previously reported could stem from emotion's modulation of binding processes (e.g., within the medial temporal lobes), of perceptual processes (e.g., within visual regions), or of conceptual processes (e.g., within prefrontal regions; see Compton, 2003, and Graf and Schacter, 1989 for a discussion of how these different processes may affect integration). Part of the second chapter of this dissertation will investigate these different possibilities by having participants perform a similar integration task while undergoing a functional MRI scan, which will help elucidate the neural mechanisms that underlie the formation of emotional and non-emotional integrations.

My previous investigation employed younger adults as participants, but there are several reasons to believe that older adults may integrate emotional pairs differently from younger adults. The question of how older adults can form novel associations in memory is a timely one: older adults represent an ever-increasing percentage of the population, particularly as the "baby boom" generation reaches older adulthood. It has been established that older adults are particularly deficient at forming novel associations between discrete pieces of information (an "age-related associative deficit"; Chalfonte &

Johnson, 1996; Cowan et al., 2006; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008). However, it has also been demonstrated that older adults can overcome this reported associative deficit by utilizing strategies that promote integration. In one study by Naveh-Benjamin, Brav, and Levy (2007), older adults were encouraged to utilize a semantic integration strategy to learn novel word pairs (i.e., putting the words together into a meaningful sentence). Using this strategy, older adults' associative memory performance was significantly better than in a condition that did not involve integration, and their associative memory performance for integrated pairs did not differ from the performance of younger adults.

Whether older adults will have similar success using an integrative mental imagery strategy, however, remains unknown. If integrative mental imagery relies primarily on perceptual processing, it may be difficult for older adults to find success. It is known that perceptual processing – particularly visual processing – declines in advancing age, and this decline is typically accompanied by what is assumed to be a compensatory increase in frontal processing (Davis et al., 2008). This so-called "posterior-anterior shift in aging" may lead older adults to fail at integration if it relies on perceptual processes; on the other hand, if successful integration relies more on frontal processes like elaboration on stimulus features then older adults may be well suited to generate integrative representations.

Moreover, there is good reason to expect that the presence of emotional information will interact with age in the formation of integrated representations. Although the regions of the brain that underlie emotion processing typically show little age-related change (Chow & Cummings, 2000; Raz, 2000), older adults tend to process emotional information differently than younger adults (Carstensen, Isaacowitz, & Charles, 1999; Leclerc & Kensinger, 2008). Specifically, it has been suggested that older adults seek more meaning from emotional events than younger adults do, possibly in service of chronically-active regulatory goals (reviewed by Mather & Carstensen, 2005). Older adults may also be more likely to process emotional information in elaborative or self-referential ways than younger adults (Gutchess et al., 2007). In my previous work with younger adults (Murray & Kensinger, 2012), I presented evidence that additional elaboration at encoding lead to stronger memory for the integration of non-emotional pairs; if older adults are committing those elaborative resources to emotional pairs, then we may see older adults show a benefit from integration for those emotional pairs similar to the benefit younger adults show for non-emotional pairs. The third chapter of this dissertation will investigate which of these possibilities is correct: do older adults succumb to age-related associative deficits during integration, or do they capitalize on age-related changes in emotion processing to successfully integrate and remember emotional pairs?

Together, the studies presented in this dissertation contribute to our understanding of the cognitive and biological mechanisms that support the formation and retrieval of integrated mental representations. As discussed, while many investigations have examined the effects of emotion on associative binding, we frequently utilize the types of integrations I have described in our everyday lives. Despite this, the mechanisms underlying such integrations have been relatively understudied. By investigating these mechanisms further – and by understanding how they may change with advancing age – we can better understand a common memory process about which little is currently known. Moreover, understanding how emotional and non-emotional information is integrated and remembered by older and younger adults can have implications for understanding the maintenance of cases wherein associative memory for emotional information goes awry, as in cases of major depression or generalized anxiety, as well as provide new directions for delineating ways to support cognitive and mnemonic processing in older age.

II. The Route to Integrative Associative Memory Depends on Emotion

A wealth of studies have investigated what brain regions are complicit in the formation and retrieval of associations in memory. By and large, these studies have offered support for a “dual-process” structure of the medial temporal lobes (see Brown & Aggleton, 2001 and Eichenbaum, Otto, & Cohen, 1994), with the hippocampus supporting associative binding and regions of surrounding parahippocampal gyrus supporting memory for individual items (see Diana, Yonelinas, & Ranganath, 2007 and Eichenbaum, Yonelinas, & Ranganath, 2007 for reviews). An important caveat, though, is most relevant to the present investigation: hippocampal processes may not be necessary for the formation and retrieval of integrated representations. Instead, other regions of the medial temporal lobes may be involved in those processes; the parahippocampal gyrus, in particular, is thought to be one of the first sites of integration of information from other sensory cortices (Bachevalier & Nemanic, 2008; Suzuki, 2010), suggesting that it may be a plausible candidate region for the formation of novel integration.

Evidence to suggest that integration creates an associative representation that can be retrieved by processes typically associated with item memory (e.g., parahippocampal gyrus) has come from two sets of data sampling patients with medial temporal lobe amnesia. Giovanello, Keane, and Verfaellie (2006) showed that patients with amnesia were better at differentiating between studied and rearranged pairs if the pairs formed compound words (e.g., correctly responding “old” to the studied words “blackmail” and “jailbird”, but “new” to the rearranged word “blackbird”) than if the pairs formed novel associations. Quamme, Yonelinas, and Ranganath (2007) presented similar findings: the researchers tested five amnesic patients, two of whom had undergone a left unilateral temporal lobectomy, damaging the hippocampus as well as the surrounding gyrus, and three of whom were believed to have lesions restricted to the hippocampus as a result of cerebral hypoxia following cardiac arrest. When given pairs of unrelated nouns to study, hypoxic patients with relatively spared parahippocampal gyrii later recognized the pairs more readily if the words had been combined into a compound word with a novel definition (e.g., “cloud-lawn” would be defined as, “A yard used for sky-gazing.”) than if the words were presented in a sentence (e.g., “The ___ could be seen from the ___”). The two patients with temporal lobectomies, whose damage extended into the parahippocampal gyrii, did not show any such benefit from integration. Together, these data suggest that the hippocampus may not be necessary for the formation and retrieval of integrated representations, but rather regions of the parahippocampal gyrus may play an important role in those processes.

Several recent neuroimaging investigations with healthy individuals have further examined what neural processes underlie the formation integrations. Recent investigation has revealed that the hippocampus may not be necessary for the formation and retrieval of integrations. In one study that parallels the previously presented patient data, Haskins et al. (2008) demonstrated that encoding two words, such as “slope” and “bread”, as a novel compound word (e.g., “slopebread”) disproportionately recruited perirhinal cortex – a region of parahippocampal gyrus – over encoding those two words as part of a sentence. Building on this evidence, Staresina and Davachi (2010) demonstrated that although the perirhinal cortex does indeed appear to be involved in creating integrated representations, it might be that the perirhinal cortex actually receives information that is *already* integrated in sensory processing regions. They showed that imagining fragmented objects as an integrated whole (e.g., viewing a fragmented picture of an avocado with a red border, and having to imagine a whole, red avocado) recruited activity in the ventral visual pathway, and that activity increased linearly with the level of fragmentation of the object. Thus, while more traditional associative binding may indeed recruit hippocampal activity, the process of forming novel integrated representations may rely on other regions of the medial temporal lobes (e.g., parahippocampal gyrus) or on regions outside of the medial temporal lobes (e.g., visual processing regions).

Extent data suggest, then, that the formation of novel integrations may rely on either the parahippocampal gyrus or visual processing regions, or some combination thereof (Haskins et al., 2008; Staresina & Davachi, 2006; 2008; 2010). Further, patient data suggest that the retrieval of integrations may recruit parahippocampal gyrus. The first aim of the present study, therefore, will be to use functional MRI to investigate what brain regions are active when healthy younger adults encode and retrieve novel integrated representations in memory.

As noted in the introductory chapter, these previous investigations into the neural correlates of integrated associations have typically used neutral stimuli: words like “slope” and “bread”, or pictures of avocados or elephants. However, we generate many integrations that contain both emotional and non-emotional content, such as the example of the features that make up a funeral. As described previously, there are several mechanisms through which emotion – via amygdala activity – may interact with the formation of novel integrations. First, the amygdala may modulate binding processes within other regions of the medial temporal lobes. Animal research has shown that the amygdala shares significant reciprocal connections with other regions of the medial temporal lobes (Canteras & Swanson, 1992; Krettek & Price, 1977; Pitkänen et al., 2000; Savander, LeDoux, & Pitkänen, 1997; Shi & Cassell, 1999), and the amygdala's role in the modulation of emotional memories – via interaction with other medial temporal lobe regions – has been well established (Cahill & McGaugh, 1998; Gallagher & Chiba, 1996; Kensinger & Schacter, 2006).

Second, the amygdala may modulate perceptual processes – particularly visual processes like those described by Staresina and Davachi (2010). Neuroimaging studies have shown that participants tend to exhibit greater activity in visual cortex and ventral visual stream when viewing emotional versus non-emotional images (Compton, 2003; Mather et al., 2006; Vuilleumier et al., 2001; Vuilleumier et al., 2004), likely because of modulation of visual processing by the amygdala. These data suggest that processing of emotional items within the visual cortex may be prioritized, leading these items to be attended to before neutral items (Öhman, Flykt, & Esteves, 2001; Öhman & Mineka, 2001), to hold attention longer (Knight et al., 2007; LaBar et al., 2000; Nummenmaa, Hyona, & Calvo, 2006), and to be associated with greater encoding activity in visual regions than non-emotional items (Bradley et al., 2003; Mather et al., 2006). As such, the presence of emotional information could facilitate processing within these visual regions, leading to the rapid generation of an integration like that described in my previous behavioral work (Murray & Kensinger, 2012).

Third, the amygdala may modulate conceptual processes, such as those governed by the prefrontal cortices. Emotional arousal can influence the way in which elaborative resources are deployed, which in turn will influence what stimuli or stimulus features may subsequently be elaborated on. It has been demonstrated that emotional information is detected rapidly and appears to draw attention (Öhman, Flykt, & Esteves, 2001), and the attention-grabbing features of emotional material are strong enough to overcome attentional impairments like the "attentional blink" (Anderson & Phelps, 2001). Thus, the amygdala may play a role in directing attention, possibly leading individuals to attend more to the emotional components of an integration than the non-emotional ones.

For these reasons, and based on my prior research demonstrating that integration with emotional items can be achieved faster than integration with neutral items – but that such integrations are also less durable over a delay (Murray & Kensinger, 2012) – I hypothesized that emotion would enhance the connection between visual activity and integrative ability but might reduce the reliance on medial temporal lobes or prefrontal processes for the integration process. To test this hypothesis, I had participants perform an integrative and a non-integrative mental imagery task followed by an associative recognition task, all while undergoing an fMRI scan. Here, I demonstrate that emotion affects the processes used to form and retrieve vivid integrations: imagining neutral integrations selectively recruits activity in lateral prefrontal cortex and right posterior parahippocampal gyrus, and this activity increases parametrically with self-reported integration success. Conversely, imagining negative integrations selectively recruits activity in cuneus – a region implicated in visual processing – and this activity also increases parametrically with self-reported integration success. Finally, I present connectivity analyses using psychophysiological interaction that suggest that amygdala engagement during the creation of integrations is related to disengagement of hippocampal and prefrontal processes, providing further evidence that emotion affects the neural processes supporting integration.

Methods

Participants

Participants were 20 younger adults (11 female) aged 18-30 (*M* = 24.4). Three participants (2 female) were excluded for excessive motion (greater than 5 degrees of translation or rotation in any of the three movement axes) for a final sample size of 17. Participants provided informed consent in a manner approved by the Boston College and Massachusetts General Hospital Institutional Review Boards, and were remunerated at $25 per hour. For each participant, anatomical MR data were collected prior to the encoding phase of the study, and functional MR data were collected during both the encoding and recognition phases.

Stimuli

Stimuli were 300 semantically unrelated verbal pairs generated pseudorandomly from negative and neutral words in the Affective Norms for English Words (Bradley & Lang, 1999) and Kučera and Francis (1967) series. Following randomization, pairs were hand-checked to ensure no pre-existing semantic relationship between the two referents. Negative words had a mean valence rating of 2.7 (on a scale from 1 = “extremely unpleasant” to 9 = “extremely pleasant”) and a mean arousal rating of 5.7 (1 = “extremely calming” to 9 = “extremely agitating”), and neutral words were matched to the negative words on frequency, word length, and imageability. 240 pairs were presented during encoding, with the remaining 60 pairs serving as new “lures” during recognition. At recognition, 120 of the studied pairs were presented as intact and 120 were presented as rearranged. At encoding and retrieval, half of the presented pairs in each condition – non-integrative and integrative imagery at encoding; intact, rearranged, and new pairs at recognition – contained a negative word paired with a neutral word (“negative” pairs) and half contained two neutral words (“neutral” pairs). Studied pairs at encoding and new pairs that appeared at retrieval were varied across participants.

Encoding and retrieval trials were jittered with a variable duration sensorimotor baseline task (Stark & Squire, 2001) in which arrows that randomly pointed to the left or right were presented for one second, and participants had to make a button press corresponding to the direction in which the arrow was pointing. The arrows were presented for the duration of the inter-trial interval (2 – 12s).

All stimuli were presented with a Macintosh Intel Core 2 Duo running MacStim 3 software (WhiteAnt Occasional Publishing) and rear-projected onto a screen at the back of the MR scanner as white, lowercase letters (48-point Lucida Grande font) on a black background. Participants viewed stimuli through a mirror mounted on the MR head coil. Responses were made using a 5-button MR-safe USB button box and recorded using the MacStim software. Trial sequences and timing were generated using the “optseq” program (Dale, 1999).

MRI Anatomical Scan

All imaging was performed on a 1.5T Siemens Avanto full-body magnetic resonance scanner (Erlangen, Germany) with all images acquired using a high-resolution 32-channel head coil. Anatomical images were collected using a multiplanar rapidly-acquired gradient echo (MP-RAGE) sequence in a sagittal orientation, with field of view = 256 x 256, matrix = 256 x 256, and slice thickness of 1.33 mm (no gap) to yield 1 x 1 x 1.33 mm voxel resolution (TR/TE = 2730/3.31 ms, flip angle = 40°).

MRI Functional Scan

Image acquisition. BOLD-weighted functional images were obtained using a T2*-weighted echoplanar imaging sequence, with 26 interleaved 3.12 mm (0.6 mm skip) slices oriented parallel to the long axis of the hippocampus acquired within each volume (TR/TE = 2000/40 ms, field of view = 256 mm, 64 x 64 mm acquisition matrix, flip angle = 90°). A total of 296 volumes were acquired during each of four encoding runs, and 196 volumes were acquired during each of four recognition runs. Where full-brain coverage was not available because of slice orientation, I ensured full coverage of the ventral temporal lobe and prefrontal cortex for each participant.

Procedure. Following the consenting procedure, participants practiced both the non-integrative and integrative imagery tasks outside of the scanner. Encoding was divided into four runs. In the first two runs participants were instructed to perform non-integrative mental imagery and in the latter two runs were instructed to perform integrative mental imagery. As described in Murray and Kensinger (2012), imagery order was not counterbalanced because previous testing indicated participants were unable to successfully perform non-integrative imagery after learning of integrative imagery. During each of the two non-integrative runs, participants viewed 60 word pairs (30 negative pairs and 30 neutral pairs, randomly intermixed) for five seconds each and were instructed to generate separate mental images for each item in as much vivid detail as possible. They were explicitly instructed not to imagine the items together or interacting in any way. After five seconds, the pair disappeared from the screen and participants were given two seconds to rate their imagery success on a scale from 1 (“no image for one or both items” or “I could only imagine the items together”) to 4 (“I could imagine each item, separately, in very vivid detail”). Pairs that the participant failed to rate within two seconds (fewer than 1% of all trials) were automatically given a rating of "1". During each of the two integrative runs, participants again viewed 60 word pairs and were instructed to generate a mental image that combined both items into a single mental representation. Pairs were again shown for five seconds, followed by the two-second rating period (1 = "no image generated" or "I could only imagine the items separately"; 4 = "extremely vivid image that incorporates both items") and one second of fixation. Under both encoding strategies, the five-second presentation time was specifically selected because it had been previously shown not to have a behavioral effect of emotion on successful image generation or on recognition performance. In this way, any neural activity revealed would not be confounded by different rates of imagery success or successful memory for emotional and neutral pairs.

Following the encoding runs, participants were removed from the scanner, given instructions and practice trials for a surprise recognition task, and then returned to the scanner. After a brief localizer scan, participants performed the recognition task. The recognition task was divided into four runs, each consisting of 30 pairs that were intact from study, 30 pairs that were rearranged from study, and 15 pairs that were new "lures". Rearranged pairs were always rearranged within encoding strategy, emotionality, and word position; that is, items studied in the non-integrative condition were always presented rearranged with other non-integrative items, neutral words initially presented with emotional words were rearranged to appear with different emotional words, and words that appeared in the left-hand position of a pair were rearranged to appear in the left-hand position of the new pair. Each pair appeared on the screen for four seconds, during which time participants made a button press to indicate whether the pair was intact, rearranged, or new. Pairs remained on the screen for the full four seconds, regardless of when the participant made a response, before the next test pair was presented. Test pairs were randomly jittered with the sensorimotor baseline task.

Imaging data preparation and analysis. Functional images were temporally and spatially preprocessed using the Statistical Parametric Mapping (SPM5) software (Wellcome Trust Centre for Neuroimaging). Slices in each volume were temporally synchronized to the first slice acquired, realigned using six motion parameters to correct for movement, and spatially normalized to the Montreal Neurological Institute anatomical template. Images were smoothed using a 7.6mm isotropic full-width half-maximum Gaussian kernel. Data were concatenated across the four runs (separately for the encoding and recognition phases) and regressors were added to all first-level analyses to correct for linear drift in the MR signal. Imaging data were prepared separately for the encoding runs and recognition runs, but the parameters were the same for both memory phases.

Statistical analyses were performed using the SPM5 general linear model (GLM). Event-related analyses were conducted. At encoding, separate regressors were entered for each combination of encoding strategy (non-integrative; integrative), emotionality (negative; neutral) and subsequent memory (hits, defined as correct subsequent identification of intact pairs *or* correct subsequent identification of both recombined pairs containing the referents of the encoded pair [Kirwan and Stark, 2004]; misses). Retrieval trials were divided by encoding strategy, emotionality, and accuracy (hits, defined by correct identification of an intact *or* recombined pair; misses). Parametric modulation regressors were modeled for each condition, representing participants' imagery success ratings (i.e., their 1-4 imagery ratings); all participants provided a sufficiently large number of each of the four ratings for this to be possible. At retrieval, if the items in a rearranged pair came from two encoding pairs that received different ratings, the lower rating was used as the parametric regressor value). Also modeled were nuisance regressors modeling linear drift in the MR signal for each run, and for retrieval runs I modeled a separate regressor representing all "new" trials.

Separately for encoding and retrieval, the eight conditions of interest were submitted to a repeated-measures ANOVA with encoding strategy, emotionality, and subsequent memory (encoding) or accuracy (retrieval) as factors. The four parametric modulation contrasts associated with correct memory also were submitted to a repeated-measures ANOVA with encoding strategy and emotionality as factors.

Psychophysiological interaction (PPI) analysis. All PPI analyses were conducted using the PPI toolbox built in to the SPM5 software. Volumes of interest (VOI) for the left amygdala seed region were defined functionally at the single-subject level by contrasting negative integration > neutral integration, and drawing a 6mm VOI around the peak voxel in left amygdala for each participant (Figure 1; see Table 2 for individual peak coordinates). For each subject, a PPI was run for the interaction between negative integration and neutral integration, weighting those conditions +1 and -1 respectively while weighting all other conditions 0. The contrast images generated from these PPIs were then submitted to a second-level one-sample *t*-test to show which regions were more positively – or less negatively – correlated with left amygdala for negative integration than neutral integration, and then submitted to a one-sample *t*-test to show which regions were more positively – or less negatively – correlated with left amygdala for neutral integration than negative integration.

To isolate the directionality of the correlations for negative a neutral integration, separate PPI analyses were run at the single-subject level for negative integration > baseline (i.e., weighting the negative integrative condition +1 and all other conditions 0) and for neutral integration > baseline. The same VOIs defined for the full interaction were used to define the seed regions for both of these analyses. The contrast images generated from these PPI analyses were then submitted to separate second-level one-sample *t*-tests to reveal left amygdala correlations with other brain regions during negative integration and neutral integration. To determine directionality, I inclusively masked these second-level baseline contrasts with the relevant contrast from the second-level interaction (i.e., negative > baseline and baseline > neutral were each masked with negative > neutral, and neutral > baseline and baseline > negative were each masked with neutral > negative). In this way, the results of the "vs. baseline" contrasts were constrained to only show activity in regions that were also active in the full interaction. For example, if a region reached threshold in the negative > neutral and negative > baseline contrasts but not the baseline > neutral contrast, then logically that region must be positively correlated with left amygdala for negative integration. These combined masks were thresholded at $p < 0.01$, unless otherwise noted.

Correction for multiple comparisons. I ran a Monte Carlo simulation (Slotnick, 2008) to determine the cluster extent threshold necessary to yield a corrected $P < 0.05$. This simulation indicated that a cluster extent of 8 voxels or greater, at an uncorrected threshold of $p < 0.001$, would have a corrected Type 1 error rate of $p < 0.05$. All reported analyses use this threshold, except where otherwise noted (i.e., regions for which I had an *a priori* hypothesis, such as visual regions during negative integration).

Results

Behavioral Results

Corrected recognition data (hits [saying "recombined" to a recombined pair or "intact" to an intact pair] minus false alarms [saying "intact" or "recombined" to a new pair]) for all successfully-imagined pairs (rated a "3" or "4" at encoding) were submitted to a 2 (encoding strategy: non-integrative, integrative) x 2 (emotionality: negative, neutral) repeated-measures ANOVA, which revealed that pairs studied integratively ($M_{\text{negative}} = 56.5\%$, $SE = 3.7\%$; $M_{\text{neutral}} = 55.8\%$, $SE = 3.6\%$) were better recognized than those studied non-integratively ($M_{\text{negative}} = 43.4\%$, $SE = 2.2\%$; $M_{\text{neutral}} = 44.8\%$, $SE = 2.5\%$), $F(1,16) = 24.25$, $p < 0.001$. No effect of emotion was observed, nor did emotion and encoding strategy interact. The absence of an emotion effect was unsurprising, as I specifically selected an encoding presentation time – five seconds – that had not shown previous behavioral effects on recognition memory (Murray and Kensinger, 2012). In this way, I could ensure that any neural effects of emotion would not be confounded with differences in encoding or retrieval success for emotional or neutral pairs.

Neuroimaging results

Parametric neuroimaging analyses. ***Parametric effects of integrative imagery success that precedes correct recognition.*** I used parametric modulation analysis to reveal which brain regions showed a linear increase in activity as a function of participants' ratings of mental imagery vividness and success. I restricted the analysis to pairs that were successfully recognized, to ensure that the activity revealed by the analysis was reflective of the integration process and not of other memory demands. I examined the regions that showed a significant interaction between emotion and encoding strategy in a second-level 2 X 2 ANOVA. Regions including the right posterior parahippocampal gyrus, left dorsolateral prefrontal cortex and right anterior prefrontal cortex showed disproportionate increases in activity during the integration of neutral pairs (see Figure 2; see Table 1 for all peak activations and voxel extents).

Reversing the interaction contrast, no regions were found to track selectively with increasing imagery success for negative integration at the corrected level. However, dropping the threshold to $p_{\text{uncorrected}} < 0.005$ revealed a region of cuneus (BA 17/18; 0, -66, 4, $k = 5$) that increased selectively for integration of negative pairs (Figure 2).

Confirming the dissociation between regions that tracked parametrically with successful integration of neutral items and of negative items, a conjunction analysis revealed no regions that showed a stronger parametric correspondence to both neutral integrative vs. non-integrative success and also negative integrative vs. non-integrative success, even when the threshold was dropped to $p_{\text{uncorrected}} < 0.005$.

Parametric effects of prior imagery success during successful recognition. I again used parametric modulation analysis to determine whether imagery vividness/success ratings would influence neural activity during successful retrieval differently for emotional and neutral pairs. In other words, how does the vividness of the integration created during encoding influence the activity corresponding to its successful retrieval? A second-level 2x2 ANOVA (encoding x emotion, for hits only) revealed a region of left posterior parahippocampal gyrus (-24, -36, 4, $k = 10$) whose parametric correspondence was strongest for neutral pairs that were studied integratively (Figure 3).

Though no regions showed the strongest parametric correspondence for negative integration at the corrected threshold, dropping the threshold to $p_{\text{uncorrected}} = 0.005$ revealed a region of cuneus (6, -80, 24, $k = 5$). A conjunction analysis revealed that only a region of left angular gyrus (-60 -52 32, $k = 15$) showed stronger parametric correspondence to both neutral integrative vs. non-integrative and negative integrative versus non-integrative retrieval.

Traditional imaging analyses. ***Effects of emotion and encoding strategy on subsequent memory.*** Though the above analyses focused on the successfully remembered pairs, I also were interested in examining how emotion would affect the processes leading to successful (vs. unsuccessful) memory for integrated pairs. For this analysis, parametric modulation analyses are less informative (because, among other reasons, the ratings of imagery success become largely unbalanced across conditions when analyzing subsequent misses). Instead, I conducted a standard, random-effects whole-brain analysis. In the full interaction (encoding x emotionality x subsequent memory), no regions selectively related to subsequent hits for neutral pairs studied integratively. However, a region of precuneus (BA 31; -16, -52, 24, $p < 0.001$, $k = 5$) selectively corresponded with subsequent memory during the integrative encoding of negative pairs, and dropping the significance threshold to 0.005 revealed a region of left amygdala (-10 6 -12, $k = 9$) as well.

As further evidence that the precuneus and amygdala were selectively active during the integrative encoding of negative but not neutral pairs, when I directly contrasted, for neutral pairs, integrative encoding trials that preceded subsequent correct memory to non-integrative encoding trials that preceded subsequent memory, this contrast revealed only a region of left parahippocampal gyrus (BA 36; -30 -54 -2, *k* = 20), with no voxels within visual processing regions or amygdala revealed, even if the significance threshold were lowered to $p_{\text{uncorrected}} < 0.005$.

Effects of emotion and encoding strategy on recognition performance. For the full interaction (encoding strategy x emotion x accuracy), no voxels survived, even at $p_{\text{uncorrected}} < 0.005$. Similarly, no voxels survived any of the two-way interactions (emotion x accuracy, encoding strategy x accuracy, or emotion x encoding strategy).

Connectivity analysis. ***Psychophysiological interactions (PPI) between left amygdala and other brain regions during negative and neutral integration.*** Because I had an *a priori* hypothesis that effects of emotion may be related to amygdala activity, I conducted PPI analyses, selecting the left amygdala as a seed region and observing what other regions were functionally coupled with it during the encoding conditions.

For neutral integration greater than negative integration, I found left amygdala activity correlated with bilateral HC (24 -16 -12, *k* = 47; -20 -22 -12, *k* = 31), left orbitofrontal cortex (-40 40 -20, *k* = 60) and medial orbitofrontal cortex (-4 56 -22, *k* = 15). For negative integration greater than neutral integration, I found left amygdala activity correlated with right parahippocampal gyrus (32 -14 -26, *k* = 10). By using these full interaction contrasts to mask PPIs generated from the individual conditions versus baseline (e.g., negative integration vs. baseline), I was able to infer the directionality of these correlations (Figure 4; see Methods). During negative integration, left amygdala activity was negatively correlated with bilateral HC (26 -16 -10, *k* = 19; -22 -20 -12, *k* = 17), right ventromedial prefrontal cortex (8 52 -26, *k* = 35), and bilateral orbitofrontal cortex (36 42 -12, *k* = 7; -28 36 -22, *k* = 5; -6 56 -22, *k* = 9). At the $p < 0.01$ threshold, no regions were positively correlated with left amygdala during negative integration. See Table 3 for all activations.

Interim Discussion and Conclusions

The aim of the present study was to test the hypothesis that the regions supporting integration would differ based on the emotional content of the integration. The results of this study revealed that emotion affects the neural processes that relate to participants' self-reported vividness and success in forming and retrieving integrations. During both encoding and retrieval, activity in visual processing regions supported the encoding and retrieval of emotional integrations, while activity in prefrontal cortex and parahippocampal gyrus supported the encoding and retrieval of neutral integrations. These data suggest that individuals have two distinct routes to integrative success, and the likelihood of their engagement depends on the emotional content to be integrated.

Staresina and Davachi (2010) suggested that integration could take place within the visual processing stream, before information even reaches the medial temporal lobes. Although there were several major differences between that paper and the present report (including the format and emotionality of stimuli used), our results offer support for the idea that visual processing regions can support integration. However, our results also suggest that when the integrations are supported by mental imagery, as in the present study, the contribution of visual processing regions is specific to integrations that contain emotional information. Together, these results indicate that emotional and neutral integrations rely on separable neural processes for successful encoding and retrieval. Indeed, parametric analyses offer strong support for this dissociation: not only is the integration of emotional pairs selectively associated with visual activity and the integration of neutral pairs selectively associated with prefrontal cortex and medial temporal lobe activity, but in each case activity in those regions increases as a function of encoding success.

Analyses using psychophysiological interaction as a method of functional connectivity revealed that the decreased reliance on prefrontal and medial temporal lobe activity for emotional integrations was likely related to amygdala engagement. These analyses revealed a disruptive, negative correlation between the amygdala and the medial temporal lobe and ventromedial prefrontal cortex/orbitofrontal cortex during negative integration: increases in left amygdala activity during negative integration were related to decreases in activity in those regions. This suggests that when participants encoded images that elicited an emotional reaction and amygdala activity, those frontal and temporal regions were less involved in the integration process. This result emphasizes that amygdala engagement may not only facilitate processing, as has often been described (e.g., Anderson and Phelps, 2001; Cahill and McGaugh, 1995; Hamann, 2001; Öhman, Flykt, and Esteves, 2001) but may also be connected to disruptions in encoding processes.

Taken together with my prior behavioral data (Murray and Kensinger, 2012) – which suggested a faster method of integration for emotional pairs than neutral ones, but a less durable maintenance of those traces – these neuroimaging data suggest that integrations formed using primarily visual processes, rather than additional prefrontal cortex and medial temporal lobe processes, may be created faster but may be less durable in memory. This hypothesis will be an important one for future research to test directly, by testing participants after delays of longer than the 30 minutes used here.

I believe that the current data present a compelling case that younger adults utilize two routes to successfully creating and remembering integrated associative representations: a visually-supported route for integrations containing emotional information and a frontally- and temporally-supported route for integrations that contain only neutral information. Moreover, successful downstream memory is supported by similar regions to those observed at encoding, with successful recognition of previously-integrated neutral pairs supported by a region of posterior parahippocampal gyrus and successful recognition of previously-integrated emotional pairs supported by the cuneus. Thus, these data inform the discussion about whether special types of associations – such as integrations – are supported by perceptual (e.g., visual) processes or conceptual (e.g., frontal/temporal) processes: the neural processes that support integration depend on the emotionality of information being integrated. These results are an important step in understanding why events that contain emotional information are often remembered differently than events that do not contain emotional information, particularly in cases where emotional information either impedes (Jacobs and Nadel, 1998; Payne et al., 2004) or facilitates (MacKay et al., 2004; MacKay and Ahmetzanov, 2005; Hadley and MacKay, 2006) the formation of novel associations.

It has been debated whether special types of associations, such as integrations, can be formed within visual processing regions (Staresina and Davachi, 2010) or whether the medial temporal lobes are required for their successful creation and retrieval (Giovanello, Keane, and Verfaellie, 2006; Quamme, Yonelinas, and Norman, 2007; Staresina and Davachi, 2006; 2008). Here I show that the answer depends on the emotional content of the integrated information. The encoding and retrieval of emotional integrations rely disproportionately on visual processing regions, specifically cuneus and precuneus, while neutral integrations rely heavily on prefrontal and medial temporal lobe regions. Moreover, I raise the possibility that amygdala activity during the integration of negative pairs may potentially have a disruptive effect on frontal and temporal processing, with increased activity in left amygdala negatively correlating with reduced activity in bilateral ventromedial prefrontal cortex/orbitofrontal cortex and bilateral hippocampus.

Although these data help to clarify the cognitive and neural mechanisms that support different types of integration in younger adults, there is reason to believe that these mechanisms will differ as individuals get older. Aging is accompanied by marked changes to both neuroanatomical structure and cognitive processing of emotional information, and this combination of changes would predict different performance for older adults on the integration task. I discuss these changes and predictions in the next chapter, and empirically test age-related differences in the integration of emotional and non-emotional pairs.

III. Age-Related Changes in Associative Memory for Emotional and Non-emotional Integrative Representations

As outlined in the first chapter of this dissertation, it is important to consider what age-related differences may exist in the formation and retrieval of novel integrations. To briefly recapitulate, we know that older adults are often shown to be particularly deficient at forming novel associations (Chalfonte & Johnson, 1996; Cowan et al., 2006; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008); indeed, one of the chief memory complaints in aging relates to forming associations between novel pieces of information, such as learning the name that goes with the face of a new acquaintance (Naveh-Benjamin, 2000; Sperling et al., 2003; Zelinski & Gilewski, 1988). Given this known age-related associative deficit, it may be reasonable to hypothesize that older adults may struggle to form novel integrations, which requires the use of associative information. However, we know that this associative deficit can be attenuated: Naveh-Benjamin and colleagues (2007) showed that the use of a semantic integration strategy at encoding lead older adults to perform as successfully as their younger counterparts on a test of associative memory.

If older adults can successfully integrate, there is reason to believe that emotion may interact with integration differently for older adults than for younger adults. Recall that my previous work demonstrated that when given sufficient time to encode, younger adults show a disproportionate associative memory benefit for non-emotional integrations than for emotional integrations. Timing differences from that behavioral study, along with the neural data presented in the previous chapter, suggest that younger adults may be engaging more conceptually elaborative processing of non-emotional information. Older adults, on the other hand, have been shown to naturally process emotional information in a more controlled fashion than younger adults do (see review by Mather & Carstensen, 2005). It has been suggested that older adults are chronic emotion regulators, and are constantly engaging in controlled processing of emotional information in service of their regulatory goals (Carstensen, Fung, & Charles, 2003; Carstensen, Isaacowitz, & Charles, 1999). It may also be the case that older adults find more self-relevance in emotional material, which facilitates increased conceptual or elaborative processing (Gutchess et al., 2007).

Although the neural data I presented in the previous chapter indicated that younger adults may rely on visual processing to support the integration of emotional pairs, it is possible that older adults may not – or cannot – utilize those same perceptual processes due to age-related neural changes. As discussed in the introductory chapter, Davis and colleagues (2007) describe a posterior-anterior shift in aging, wherein older adults show a shift away from perceptual processing of information and a shift towards more frontally-driven processing, possibly in compensation for degradation of perceptual systems. Thus, older adults may be unable to access the same rapid, facilitated perceptual processes for emotional integration that younger adults do, and may need to rely on more frontally- or conceptually-driven processing of those integrations. What effect this would have on both successful integration and subsequent memory, however, remains an open question that will be tested here.

Though no prior study to my knowledge has investigated memory for emotional integrations in older age, a recent study from Nashiro and Mather (2011) demonstrated that older adults did not exhibit an associative memory benefit for emotional information.

They observed an associative memory benefit for emotional picture-location judgments for younger adults, but they found no such enhancement for older adults: picture-location memory did not differ for those individuals regardless of the stimulus emotionality. These data may suggest that emotion would not benefit older adults' associative integration on a word-pair learning task; however, these data are also not entirely consistent with my previous behavioral work with younger adults (Murray & Kensinger, 2012). In that study, the integrative benefit conveyed by emotion was in the *creation* of an integrated representation whereas Nashiro and Mather revealed an emotional benefit in the maintenance of locations in memory. It is possible that older adults would demonstrate an effect of emotion on the *creation* of an integrated representation, even if downstream deficits in older adults' associative binding prevented them from maintaining that bound representation in memory. Alternately, it is possible that just as in Nashiro and Mather, older adults would show no integrative benefit for emotional pairs.

Thus, there are several possibilities for how older adults may perform on the integration task. First, it may be the case that age-related deficits in forming novel associations will prevent them from being able to integrate at all. Second, older adults may be able to integrate, but their integrative success may be specific to emotional pairs; older adults may naturally process emotional information more elaboratively, and that elaboration may benefit integrative memory in a similar fashion to the benefit shown by younger adults with non-emotional pairs. Finally, it may be possible that use of the integration strategy may facilitate memory for older adults for all pairs, similar to the benefit observed by Naveh-Benjamin, Brav, and Levy (2007). Experiment 1 tested these alternatives.

EXPERIMENT 1

Method

Participants

Participants were 24 older adults (17 female) aged 65-85 (*M* = 72.4) and 24 younger adults (14 female; $M_{\text{age}} = 19.7$) recruited from the greater Boston area through print and web-based advertisement. Younger adults recruited for this study did not participate in any of the studies reported in Murray and Kensinger (2012). Participants were pre-screened to exclude those with a history of psychiatric or neurological disorders and for current depression or high anxiety (see Table 4 for participant characteristics). Informed consent was obtained in a manner approved by the Boston College Institutional Review Board. Older adults also participated in a prior session of cognitive tasks to ensure that they were within age-adjusted normed ranges[1] (mean score on Mini-Mental State Exam [Short Form] = 28.9, *SE* = 0.16).

Stimuli

Stimuli were words selected from the Affective Norms for English Words (ANEW) series (Bradley & Lang, 1999), the Kučera and Francis (1967) word list, and word lists used by Kensinger and Corkin (2003). A total of 80 positive, 80 negative, and 200 neutral words were selected. Positive and negative words were selected from the

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[1] Tests administered in the cognitive task session were the Mini-Mental State Exam (Short Form; Folstein et al., 2010), Generative Naming (Spreen & Benton, 1977), modified Wisconsin Card Sorting Task (Nelson, 1976), Big 5 Personality (Goldberg, 1999), Geriatric Depression Scale (Sheikh & Yesavage, 1986), Future Time Perspective Scale (Lang & Carstensen, 2002), and the following tasks from the Wechsler Adult Intelligence Scale (Wechsler, 1997): Logical Memory 1 and 2, Visual Pairs 1 and 2, Verbal Pairs 1 and 2, California Verbal Learning Test, Digit Span, Digit Symbol Copy, Mental Arithmetic, and Mental Control.

ANEW database and were matched on arousal, with mean arousal ratings of 5.6 (1.0) and 5.9 (1.0) respectively (“1” considered to be extremely calming, “9” considered to be extremely arousing). The mean valence rating for positive and negative words was 7.9 (1.9) and 2.4 (1.7), respectively. Neutral words were selected from the ANEW, Kučera and Francis, and Kensinger and Corkin word lists (M_{valence} = 5.3 (0.5), M_{arousal} = 4.4 (1.0)) and were matched to the positive and negative words on frequency, length, and imageability. Words were pseudorandomly combined to form 40 word pairs that included a positive word and a neutral word, 40 word pairs that contained a negative word and a neutral word, and 40 word pairs that contained two neutral words. For all pairs that contained an emotion word, the emotion word was always the left-hand word in the pair. The remaining 120 words (40 positive, 40 negative, 40 neutral) were used as “new” lures on the cued recall test. Pairings of words were varied across participants, as well as what words appeared in each encoding condition.

All stimuli were presented on a Macintosh Intel Core 2 Duo computer running MacStim 3 software (WhiteAnt Occasional Publishing). Stimuli were presented at the center of the screen, as white text on a black background. All stimuli were presented in lowercase, with size 48 Lucida Grande font.

Procedure

The procedure was divided into an imagery practice phase, a study phase, and an associative cued recall test. As described in Murray and Kensinger, the order of imagery tasks during the study phase was not counterbalanced: participants always performed the non-integrative trials first and integrative trials second. This was done so that participants would better understand what qualified as “integrative” imagery (e.g., not just picturing the two words side-by-side), and also because pilot testing revealed that it was more difficult for both older and younger participants to generate non-integrative images after acclimating to integrative imagery than vice versa.

Imagery practice phase. Participants viewed ten pairs of words (e.g., “card + mouse”), and were asked to maintain separate mental representations of each item individually (“non-integrative” study). After each pair they were then to rate the vividness of their mental image on a 1-4 scale. They were given the heuristic that a “1” would indicate no success for that pair: they didn’t know what one of the words meant, they could not generate an image for one or both words, or they could only generate a combined mental image; a “2” would indicate that they could imagine both items, but not vividly (their images were “fuzzy” or “blurry”); a “3” would indicate that they could generate moderately detailed images for both items; a “4” would indicate that both items were imagined separately, clearly, and with vivid detail. Participants then viewed ten different pairs and were instructed to imagine the two words concatenated together in some way that merged them into a single image (e.g., “owl + office” could be imagined as an office full of owls in business suits; “integrative” study). Again, a 1-4 rating was made following each pair.

Study phase. Participants first viewed 60 pairs and were instructed to use the non-integrative imagery strategy as practiced. Older adults were shown the pairs for six seconds and younger adults were shown the pairs for four seconds; older adults received slower encoding times because of extensive evidence for age-related slowing of processing (e.g., Salthouse, 1996). Following each pair, participants were prompted to make their 1-4 rating of imagery success. Following non-integrative study, participants viewed 60 different pairs for six seconds and were instructed to imagine them using the integrative imagery strategy. Again, a 1-4 rating was collected after each pair was presented.

Of the 60 pairs within each study block, 20 pairs contained a negative word and a neutral word, 20 pairs contained a positive word and a neutral word, and 20 pairs contained two neutral words. These pairs were presented in random order. Following the study blocks, participants were given a 30-minute break, during which they performed several pencil-and-paper tasks.

Associative cued recall test. Participants were presented with a single word on the screen along with a number from 1 – 360 (corresponding to the trial number) and were given a pad of paper with lines numbered 1 – 360. They were told that for each word, they should first decide if the word was seen during the study phase. If they believed the item to be previously studied, they were to write down the word it had been presented with during the study phase on the corresponding line; if they could not recall the paired referent, they were instructed to either make a guess or leave the line blank. If they believed the item to be a new item that had not been previously studied, they were to write "NEW" on the corresponding line. The test was self-paced, and participants were instructed to press any key on the keyboard to move to the next test item after recording their response.

Results

Data Included in Analysis

Only pairs for which participants indicated successfully creating a vivid mental image – that is, those pairs rated either a "3" or "4" – were included in analysis. Younger adults rated 83.2% (*SD* = 9.6%) of non-integrative and 84.5% (*SD* = 11.1%) of integrative pairs as successfully imagined. There was no main effect of encoding (*F*(1,23) = 0.41, $p > 0.50$) nor emotion (*F*(1,23) < 0.01, $p > 0.95$) on younger adults' imagery success, nor did encoding and emotion interact (*F*(1,23) < 0.01, $p > 0.95$).

Older adults rated 77.6% (*SD* = 13.1%) of non-integrative and 73.5% (*SD* = 13.5%) of integrative pairs as successfully imagined. There was no effect of encoding (*F*(1,23) = 2.58, $p > 0.10$) nor emotion (*F*(1,23) = 1.70, $p > 0.20$), and encoding and emotion did not interact (*F*(1,23) = 0.88, $p > 0.35$).

Directly comparing the two age groups by including age (younger, older) as a between-subjects factor revealed no main effects of encoding (*F*(1,46) = 0.54, $p > 0.45$), emotion (*F*(1,46) = 1.05, $p > 0.30$), nor did any interactions reach significance (all *F'*s < 2.1, all *p*'s > 0.15).

Though I included in the design pairs that contained positive words as well as pairs that contained negative words, no difference was observed in cued recall memory for neutral words based on their pairing with positive or negative words for younger (*t*(23) = 1.08, $p > 0.25$) or older (*t*(23) = 0.88, $p > 0.35$) adults. As such, pairs containing either a negative or positive word were collapsed into a single "emotional" category for all analyses.

Item Recognition

Item recognition results were drawn from participants' written responses: "hits" were counted as all old words for which participants did not write "NEW", misses were counted as old words for which participants incorrectly wrote "NEW", and false alarms were counted as new words for which participants provided a response or left the response line blank. Corrected recognition scores were computed from each participant by subtracting false alarm rates from hit rates (Table 5). Although the results reported below are based on corrected recognition scores, the results do not differ if only hits are analyzed.

Older vs. younger adults. Corrected recognition scores were submitted to a 2 (age: younger adults, older adults) x 2 (encoding strategy: integrative, non-integrative) x 2 (emotion: emotional, neutral) mixed-factors ANOVA. A significant main effect of age was observed ($F(1,46) = 40.99$, $p < 0.001$, partial $\eta^2 = 0.47$), with younger adults demonstrating better corrected recognition ($M = 63.7\%$, $SD = 9.6\%$) than older adults ($M = 45.9\%$, $SD = 9.6\%$), as well as a main effect of encoding strategy, with non-integrative items recognized better than integrative items ($F(1,46) = 21.52$, $p < 0.001$, partial $\eta^2 = 0.32$). Age did not interact with any factors, nor did encoding strategy and emotion interact (all *F*'s < 1).

Associative Cued Recall

Cued recall performance was assessed for the right-hand words from each pair. These were all neutral words, divided by whether they were paired with an emotion word (positive or negative) or a second neutral word. Cued recall data were first submitted to a 2 (age group) x 2 (encoding strategy) x 2 (cue emotionality) mixed-factors ANOVA. Because age significantly interacted with both emotion and encoding strategy, the data were then analyzed separately for both older and younger adults in a 2 (encoding strategy: integrative, non-integrative) x 2 (emotion: emotional, neutral) repeated-measures ANOVA.

Older adults vs. younger adults. The omnibus ANOVA revealed a significant main effect of encoding ($F(1,46) = 15.53$, $p < 0.001$, partial $\eta^2 = 0.22$), with better recall performance for items studied integratively than non-integratively. Though no main effect of age was observed ($F(1,46) = 0.64$, $p > 0.43$), age group and emotion interacted significantly ($F(1,46) = 15.61$, $p < 0.001$, partial $\eta^2 = 0.25$). This was qualified by a significant three-way interaction between age, encoding strategy, and emotion ($F(1,46) = 7.95$, $p < 0.01$, partial $\eta^2 = 0.15$). As seen in Figure 5, and as just reported in the single-group ANOVAs, younger adults showed a disproportionately larger benefit from integration for neutral pairs, whereas older adults showed a disproportionately large benefit from integration for emotional pairs.

Older adults. A main effect of encoding was observed (integrative > non-integrative, $F(1,23) = 6.22$, $p = 0.02$, partial $\eta^2 = 0.21$), as well as a main effect of emotion (emotion > neutral, $F(1,23) = 4.46$, $p = 0.05$, partial $\eta^2 = 0.16$). Though the interaction between encoding and emotion did not reach significance, a trend was observed ($F(1,23) = 3.94$, $p = 0.06$, partial $\eta^2 = 0.15$), with participants demonstrating better memory for integrative emotional pairs than non-integrative emotional pairs and no difference between memory for integrative neutral and non-integrative neutral pairs (see Figure 5, right bars).

Younger adults. Younger adults demonstrated an effect of encoding strategy ($F(1,23) = 9.35$, $p < 0.01$, partial $\eta^2 = 0.29$), wherein cued recall was better for items that were studied integratively than for items that were studied non-integratively. A main effect of emotion was also observed, $F(1,23) = 11.50$, $p < 0.01$, partial $\eta^2 = 0.33$, with items from neutral pairs recalled better than items from emotional pairs. The interaction between emotion and encoding did not reach significance, but a trend was observed ($F(1,23) = 4.02$, $p = 0.06$, partial $\eta^2 = 0.15$). The nature of this trend was in the same direction as that reported in Murray and Kensinger (2012) and was in the opposite direction as the older adults' pattern: although younger adults received a numerical benefit from integration for emotional pairs, the benefit was disproportionately larger for neutral pairs (Figure 5, left bars).

Experiment 1: Discussion

Both older and younger adults showed a mnemonic benefit for item recognition when items were studied non-integratively than integratively. Critically, while no effect of emotion was observed on the item recognition test (for either age group in isolation, or when including age as a between-subjects factor), emotion and encoding strategy did have an effect on associated cued recall that differed as a function of age.

On the cued recall test, the younger adults' data generally replicated the findings of Murray and Kensinger (2012): though a numerical benefit from integration was observed for emotional pairs, a disproportionately larger advantage was observed for the integration of two neutral items. However, older adults showed a significant mnemonic benefit from integration for a neutral word only when it was integrated with an emotional word. The three-way interaction between age, encoding strategy, and emotion was significant, confirming that older adults do indeed show a mnemonic benefit from integration that is markedly different that of younger adults.

In Murray and Kensinger (2012), we argued that younger adults may rely on faster, less controlled binding processes for emotional pairs but must engage in more controlled, elaborative processing to successfully integrate neutral pairs, which leads to a downstream mnemonic benefit for the neutral pairs, similar to a levels-of-processing effect. The current results are consistent with that interpretation, but they clarify that this conclusion does not extend to older adults. As discussed previously, older adults are more likely than younger adults to elaborate on emotional information or process it in a controlled fashion (Mather & Carstensen, 2005) but they have difficulty with the spontaneous use of controlled or elaborative encoding strategies for neutral information (Buckner & Logan, 2002; Naveh-Benjamin, 2000). Thus, while younger adults may elaborate more on neutral integrations and less on emotional integrations, older adults may elaborate more on emotional integrations and less on neutral integrations. In both age groups, the integration that receives more elaborative processing at encoding may be the integration that is better remembered.

Experiment 1 alone cannot confirm that this is the case for older adults, though, because there is no experimental manipulation of degree of elaboration. Experiment 2 tests the hypothesis that older adults elaborate more on emotional pairs than neutral pairs by manipulating how long participants have to encode. In Experiments 2A and 2B of Murray and Kensinger (2012) we found that when encoding trials are speeded for younger adults, the integrative benefit for neutral pairs disappears. Younger adults also reported less success at imagining integrated neutral pairs at speeded encoding times. At longer encoding trials, the integrative benefit for neutral pairs reemerges, and becomes even larger as encoding time increases, suggesting that young adult participants need time to create salient neutral integrations. For older adults, I expect the opposite to be true: at short and moderate encoding times, there should be little or no benefit from integration for neutral pairs, because older adults have difficulty spontaneously elaborating on those pairs (Buckner & Logan, 2002; Naveh-Benjamin, 2000). I also expect that older adults will report lower rates of imagery success for neutral pairs at shorter encoding times. At long encoding times, I may see an integrative benefit emerge for neutral pairs if it is the case that older adults simply take longer to elaborate effectively on those pairs, or I may continue to see no benefit. For emotional pairs, I expect that speeding encoding will attenuate the integrative benefit because older adults will not have sufficient time to engage in controlled elaboration of those pairs. I expect that as encoding time increases, the integrative benefit for emotional pairs will reemerge as it did for younger adults with neutral pairs.

EXPERIMENT 2

Method

Participants

Participants were 24 older adults (19 female) aged 65-85 ($M = 75.2$; $M_{\mathrm{MMSE}} = 29.2$, $SE = 0.16$) that did not participate in Experiment 1, as well as 24 younger adults (15 female; $M_{\mathrm{age}} = 19.8$) who did not participate in Experiment 1 nor in any experiments from Murray and Kensinger (2012). Participant characteristics are available in Table 4.

Stimuli

The same stimuli used in Experiment 1 were used in Experiment 2. At encoding, pairs were presented for four, six, or eight seconds (for older adults), or for two, four, or six seconds (for younger adults). As in Experiment 1, older adults received slower presentation times to compensate for age-related slowing of processing (Salthouse, 1996). Under each encoding strategy (non-integrative and integrative), 20 pairs were presented at the “speeded” encoding time, 20 pairs were presented at the “moderate” encoding time, and 20 pairs were presented at the “long” encoding time. As described in Experiment 2A of Murray and Kensinger, stimulus emotionality (whether the pair contained an emotion word or not) varied across encoding presentation time: each presentation time contained between six to eight pairs of each emotion (positive + neutral, negative + neutral, neutral + neutral). Presentation time was blocked in groups of ten pairs of the same encoding speed, in order to reduce set-shifting demands, though participants were given no cue ahead of time for how long each pair would be displayed on-screen. Assignment of pairs to each presentation time block was counterbalanced across participants.

Procedure

Aside from the encoding time manipulation, the procedure for Experiment 2 was identical to Experiment 1.

Results

Data Included in Analysis

As in Experiment 1, only pairs for which participants indicated successfully creating a vivid mental image – that is, those pairs rated either a “3” or “4” – were included in analysis. The effect of emotion, encoding strategy, presentation speed, and age on the successful imagery of pairs is described below.

Item Recognition

Older adults vs. younger adults. Corrected recognition data were submitted to a 3 (presentation speed: speeded, moderate, extended) x 2 (age group) x 2 (encoding strategy) x 2 (emotion) mixed-factors ANOVA. This revealed main effects of encoding strategy (non-integrative > integrative; $F(1,46) = 69.26$, $p < 0.001$, partial $\eta^2 = 0.60$), encoding time (extended > moderate > speeded; $F(2,92) = 82.04$, $p < 0.001$, partial $\eta^2 = 0.64$), and age (younger adults > older adults, $F(1,46) = 563.34$, $p < 0.001$, partial $\eta^2 = 0.93$). Age did not interact with any factors, nor were any other interactions observed (all *F*'s < 1.7, all *p*'s > 0.20). The item recognition data for older and younger adults are displayed in Table 6.

Percentage of Qualified Pairs

It was hypothesized that for younger adults, integrating two neutral words would require more elaborative effort than integrating an emotional and a neutral word, while older adults would demonstrate more success at integrating an emotional word with a neutral word than they would to integrate two neutral words. To test this hypothesis, I examined what percentage of integrated pairs older and younger adults rated as a "3" or "4" as a function of encoding time and emotion.

Older adults vs. younger adults. The percentages of integrative pairs rated as a "3" or "4" were submitted to a 3 (presentation speed) x 2 (age) x 2 (emotion) mixed-factors ANOVA. The analysis revealed main effects of presentation speed (extended = moderate > speeded; $F(2,92) = 12.60$, $p < 0.001$, partial $\eta^2 = 0.22$) and emotion (emotional > neutral; $F(1,46) = 4.81$, $p = 0.03$, partial $\eta^2 = 0.10$). Critically, a three-way interaction was observed between emotion, presentation speed, and age ($F(2,92) = 4.08$, $p = 0.02$, partial $\eta^2 = 0.08$). As seen in Figure 6, extended encoding times lead to an increase in "successful" neutral pairs for younger adults and an increase in successful emotional pairs for older adults. This increase in integrative benefit emerges at both moderate and extended encoding times for younger adults but only at extended encoding times for older adults.

Older adults. Older adults demonstrated a significant main effect of presentation speed on the percentage of pairs successfully integrated, (extended > moderate = speeded; $F(2,46) = 4.47$, $p = 0.02$, partial $\eta^2 = 0.16$). Though no effect of emotion was observed ($F(1,23) = 2.25$, $p > 0.1$), emotion and presentation speed interacted significantly ($F(2,46) = 3.40$, $p = 0.04$, partial $\eta^2 = 0.13$). At extended encoding times, older adults rated more emotional pairs as successfully integrated than at moderate or speeded times; however, this was not the case for neutral pairs (see Figure 6).

Younger adults. Younger adults showed a significant main effect of presentation speed (extended = moderate > speeded; $F(2,44) = 11.50$, $p < 0.001$, partial $\eta^2 = 0.33$). No effect of emotion was observed ($F(1,23) = 2.85$, $p = 0.11$) and emotion and presentation speed did not interact, though there was a trend towards an interaction observed ($F(2, 46) = 2.83$, $p = 0.07$, partial $\eta^2 = 0.11$; see Figure 6).

Associative Cued Recall

Cued recall performance for neutral words that were paired with either emotional or other neutral words were submitted to a 3 (presentation time) x 2 (encoding strategy) x 2 (cue emotion) x 2 (age group) mixed-factors ANOVA. Because the four-way interaction was revealed to be significant, data were then analyzed separately for older and younger adults.

Older adults vs. younger adults. Main effects were observed for encoding strategy (integrative > non-integrative; $F(1,46) = 21.87$, $p < 0.001$, partial $\eta^2 = 0.32$), presentation time (extended > moderate > speeded; $F(2,92) = 16.99$, $p < 0.001$, partial $\eta^2 = 0.27$), and age group (younger > older; $F(1,46) = 7.66$, $p < 0.01$, partial $\eta^2 = 0.14$). Significant two-way interactions were observed between presentation time and encoding strategy ($F(2,92) = 4.71$, $p = 0.01$, partial $\eta^2 = 0.09$) and cue emotion and age group ($F(1,46) = 7.69$, $p < 0.01$, partial $\eta^2 = 0.14$). A significant three-way interaction was observed between encoding strategy, cue emotion, and age group ($F(1,46) = 5.40$, $p = 0.03$, partial $\eta^2 = 0.11$).

These interactions were all qualified by a significant four-way interaction between age group, encoding time, encoding strategy, and cue emotion ($F(2,92) = 6.11$, $p < 0.01$, partial $\eta^2 = 0.12$). The nature of this four-way interaction, seen in Figures 7A and B, is that: (1) Younger adults demonstrate a consistent mnemonic benefit from integration over non-integration when given a neutral word with an emotion word, but show a disproportionately larger benefit from integrating a neutral word with another neutral word as encoding time increases; (2) Older adults never demonstrate a mnemonic benefit from integration over non-integration when given two neutral words at any encoding trial length, but do show a mnemonic benefit – that increases as encoding time increases – from integrating a neutral word with an emotional word.

Older adults. Significant main effects of encoding strategy (integrative > non-integrative; $F(1,23) = 20.89$, $p < 0.001$, partial $\eta^2 = 0.48$), presentation time (extended > moderate = speeded, $F(2,46) = 7.27$, $p < 0.01$, partial $\eta^2 = 0.24$), and cue emotion (emotional > neutral; $F(1,23) = 4.29$, $p = 0.05$, partial $\eta^2 = 0.16$) were observed. Encoding strategy and cue emotion interacted significantly ($F(1,23) = 5.61$, $p = 0.03$, partial $\eta^2 = 0.20$) such that recall performance was equivalent for neutral words that were paired with either emotional or neutral words under non-integrative study ($M_{\text{emo}} = 11.2\%$, $SE_{\text{emo}} = 1.0\%$; $M_{\text{neu}} = 11.0\%$, $SE_{\text{neu}} = 1.3\%$), but a mnemonic benefit was observed for neutral words integrated with emotional words over neutral words integrated with other neutral words (M_{emo} = 20.2%, SE_{emo} = 1.9%; M_{neu} = 13.5%, SE_{neu} = 1.3%). These data are displayed in Figure 7A. No other interactions reached significance (all *F*'s < 2.10, all *p*'s > 0.13).

Younger adults. Younger adults demonstrated significant main effects of encoding strategy (integrative > non-integrative; $F(1,23) = 10.70$, $p < 0.01$, partial $\eta^2 = 0.32$) and presentation time (extended = moderate > speeded; $F(2,46) = 10.19$, $p < 0.001$, partial $\eta^2 = 0.31$). A significant interaction was observed between presentation time and encoding strategy ($F(2,46) = 3.53$, $p = 0.04$, partial $\eta^2 = 0.13$) and this was qualified by a significant three-way interaction between presentation time, encoding strategy, and cue emotion ($F(2,46) = 4.06$, $p = 0.02$, partial $\eta^2 = 0.15$). For pairs containing an emotion word, an integrative benefit was observed consistently across all three encoding speeds. For pairs containing two neutral words, no integrative benefit was observed when encoding trials were speeded, but one emerged during four-second encoding trials and increased in magnitude during six-second trials. These data are displayed in Figure 7B.

Experiment 2: Discussion

The aim of Experiment 2 was to directly test the hypothesis that the age-divergent pattern of results revealed in Experiment 1 was connected to age differences in how neutral and emotional pairs may be elaborated. The results of Experiment 2 were consistent with this interpretation. Younger adults appear to integrate emotional items quickly; even on speeded trials, they report high rates of encoding success and show some downstream mnemonic benefit from integration. Their integration of neutral pairs, however, requires time. When encoding time is limited, younger adults do not appear to have sufficient time to engage the controlled or elaborative effort required to successfully integrate neutral words with one another, and so they report lower success rates for integration. Yet when the time interval is sufficiently long for them to engage elaborative processes, they not only succeed at integration for neutral items, they also appear to create deeper representations that confer a larger mnemonic benefit than is conferred by the more automatic integrations created for emotional items.

Older adults showed a strikingly different effect of integration: they show no integrative benefit for neutral pairs after *any* encoding length, perhaps because of general deficits with associative binding (e.g., Castel & Craik, 2003; Light et al., 2004; Naveh-Benjamin, 2000). They do demonstrate a mnemonic benefit from integrating pairs containing an emotional word, and the magnitude of that benefit is tied to the length of the encoding epoch. Older adults show a larger integrative benefit when given more encoding time for emotional pairs, suggesting controlled or elaborative processing of emotional information that requires time to implement. Much the same way that younger adults require some sufficient amount of time to access the controlled processes necessary to integrate neutral pairs, older adults require sufficient time to successfully integrate emotional pairs.

The discrepancy between younger and older adults' performance, therefore, can be reconciled by considering the types of processes engaged by young and older adults. Younger adults may benefit from emotion's potential to enhance the intra-item binding processes that are required for integration (Hadley & MacKay, 2006; MacKay et al., 2004; MacKay & Ahmetzanov, 2005; Mather, 2007). This rapid binding may allow them to create an integration even when time is limited, but it may lead to a shallower representation that is not well maintained in memory. Older adults, in contrast, may not benefit from this facilitated binding. Nashiro & Mather (2011) also reported that older adults did not receive the same mnemonic benefit for intra-item binding as did younger adults. Instead, older adults may elaborate more on emotional information, using processes that require time to implement but that convey larger benefits to the retention of those representations in memory.

Interim Discussion and Conclusions

Across two experiments, I show that older adults demonstrate a significant mnemonic benefit for neutral words that were imagined as a single, integrated unit with emotional words. No such benefit is observed when they imagine two neutral words as a single, integrated unit. Age also appears affect the time needed to see a mnemonic advantage for integrating pairs containing an emotional word. For younger adults, this happens at the shortest duration, and for older adults this happens at the longest duration.

These results fit nicely with the argument that older adults are more likely than younger adults to gain emotional meaning from events (Carstensen, Fung, & Charles, 2003) and to process emotional information in a controlled fashion to serve emotion regulatory goals (Carstensen, Isaacowitz, & Charles, 1999; see review by Mather & Carstensen, 2005). The fact that older adults take time to integrate emotional pairs is consistent with this notion that they are processing emotional information in a more top-down fashion than younger adults. By contrast, younger adults may integrate emotional pairs through more rapid, prioritized processing (evidenced by that age group's ability to integrate successfully at very short encoding times).

The present results show that older adults do not benefit from facilitated integration of emotional information in the same way that younger adults do. It has been shown previously that older adults have facilitated processing of emotional information (e.g., on visual search or rapid serial visual presentation tasks), even on tasks that use these same types of emotional words (Mickley Steinmetz, Muscatell, & Kensinger, 2010). However, this facilitated detection of the stimuli does not seem to lead to the same rapid facilitation of integration in older adults as it does in younger adults. This lack of facilitated binding is consistent with the findings of Nashiro and Mather (2011), who found that older adults did not show enhanced picture-location binding for emotional images, and is consistent with their inability to show an enhanced creation of emotional integrations in the speeded condition in the present study.

The caveat to this previous point, though, is that older adults may still benefit from some facilitated processing as the result of the presence of emotional information even though that facilitation does not lead to *rapid integration* as it does in younger adults. Emotion may instead enhance other processes – for example, the ability to strategically retrieve information about the stimuli necessary for integration. This is likely a frontally driven process, and thus older adults may also exhibit different fronto-amygdalar connectivity than younger adults. Presently, though, this point is speculative, but highlights the need for follow-up imaging investigation.

These results also demonstrate a circumstance under which older adults are able to overcome the previously-reported associative deficit. When given a strategy to use (e.g., instructions and examples for how to integrate), this enables them to utilize the controlled mechanisms necessary for integration (see Naveh-Benjamin, Brav, & Levy, 2007, for evidence that providing older adults with encoding strategies can attenuate age-related deficits). This support appears sufficient to allow them to successfully *integrate* emotional or neutral pairs, as shown in Figure 6. However, when it comes to *retaining* those pairs in memory, older adults show a benefit only for the emotional ones. This is likely because the emotional information present in those pairs likely engenders some additional elaborative processing (e.g., in service to emotion regulatory goals, due to self-referential processing, etc.) that leads the memory trace for those pairs to be more durable.

In conjunction with the neural results presented in the second chapter of this dissertation, it appears that younger adults utilize two different routes to integrative success depending on the emotional content of the studied pairs: controlled, frontally-driven integration of neutral pairs, which takes time to complete, and a rapid, perceptually-driven integration of emotional pairs. By contrast, older adults appear to have utilized one route to integrative success: a slow, controlled integration of pairs. This integration succeeds for neutral and emotional pairs, but it produces a durable memory trace only for emotional pairs.

Thus, when instructed to create integrated mental images of emotional and neutral words, or of two neutral words together, younger and older adults show markedly different mnemonic effects when recall memory is tested. I suggest that this is a result of the two age groups elaborating on different types of information during integration: younger adults rely on more rapid integrative processes for emotional pairs and elaborate more on neutral pairs, while older adults elaborate more on emotional pairs. The elaborative processing, while time consuming for both age groups, results in a more durable memory representation. As such, the end result is that younger adults show a disproportionate associative mnemonic benefit for neutral words integrated with other neutral words, while older adults show a disproportionate associative mnemonic benefit for neutral words integrated with emotional words.

IV. General Conclusions and Open Questions

The goals of my dissertation research, as outlined in the first chapter of this document, were to investigate the neural basis for encoding and retrieving emotional and neutral integrations, and to investigate whether older and younger adults differed behaviorally during integration and retrieval of those integrations. The intention of these questions was to advance the understanding of how an ecologically common, but scientifically understudied, type of associative memory is formed and retrieved, as well as to further inform our theoretical understanding of how emotional information affects the associative binding of unrelated neutral information for both younger and older adults.

To the first goal, I have demonstrated that when younger adults integrate pairs containing an emotional referent, that integration is supported by shallow perceptual processes that track parametrically with subjective ratings of imagery success. Similar processes support the retrieval of those pairs. Moreover, amygdala activity may have a disruptive effect on frontal and temporal processes during emotional integration: psychophysiological interaction revealed that as amygdala activity increased during emotional integration, activity decreased in those other regions. These results, coupled with prior behavioral results (Murray & Kensinger, 2012) and those presented in the third chapter here, highlight an important disconnect between facilitated processes at encoding and successful subsequent memory. Although young adults can rapidly integrate emotional pairs – and do so with high levels of self-reported success – that facilitated integration does not translate into successful downstream memory. Rather, young adults demonstrate successful memory when integrations contain *no* emotional information, but that strong memory performance comes at the expense of encoding speed.

Related to the above, the neuroimaging results I present further inform discussion about the biological mechanisms that support the formation and retrieval of integrations in younger adults. It has been previously noted that, although the hippocampus has typically been shown to support associative memory (Aggleton and Brown, 1999; Eichenbaum, Yonelinas, and Ranganath, 2007), integrations represent a special type of association that may be supported by either parahippocampal gyrus (Haskins et al., 2008; Staresina & Davachi, 2006; 2008) or visual processing regions (Staresina & Davachi, 2010). My data suggest that either of these sets of regions may be complicit in both the formation *and* retrieval of such integrations; which set of regions depends on the content of the integration, with emotional integrations being supported at encoding and retrieval by visual processing regions and non-emotional integrations being supported at encoding and retrieval by parahippocampal gyrus.

To the second goal, I have shown that older and younger adults do indeed differ behaviorally form one another in the formation and retrieval of emotional and non-emotional integrations. Whereas younger adults demonstrate the rapid yet shallow encoding of emotional integrations and the slow yet durable encoding of non-emotional integrations described above, older adults demonstrate a quite different pattern of behavior. Older adults appear to engage in slower, more controlled processing of emotional pairs than their younger counterparts, and while younger adults show poor memory for emotional integrations, older adults show a marked benefit from integrating those pairs. These results highlight an age-related reversal in the type of information to which elaborative resources are delegated: non-emotional information in a younger cohort and emotional information in an older cohort. What remains unclear, however, is when in the lifespan this apparent reversal occurs, and why. A wealth of literature has suggested that as people get older and their future time perspective becomes increasingly limited, they prioritize emotional goals and well-being over other goals like knowledge seeking (Carstensen et al., 2000). This type of cognitive explanation would suggest that the shift from non-emotional to emotional elaboration may be a gradual shift that takes place across the lifespan. On the other hand, this shift may instead have a biological basis: as individuals grow older, gray matter volume declines and white matter integrity begins to degrade, and this process can be relatively rapid (Grieve et al., 2005). Among these declines are loss in structure and function to perceptual processing regions (Davis et al., 2008). If younger adults are utilizing perceptual processes to facilitate emotional integration, then relatively rapid loss of function in those perceptual regions – which, according to Davis and colleagues (2008), is accompanied by a compensatory increase in frontal processing – may also lead to a relatively rapid change in the way emotional pairs are processed. Although dichotomizing individuals into “younger” and “older” adults, as I have done here, is a useful first step, it will be important for future investigation to include individuals from across the entire lifespan to determine the nature of this reversal.

How older adults engage with emotional material during integration remains an open question, as well. As I have suggested previously, there are several possible alternatives for *how* older adults may elaborate on emotional material. On the one hand, older adults may chronically emotion regulate, as has been suggested by others (reviewed by Mather & Carstensen, 2005), and this regulation leads them to process that emotional information – and related neutral information – in a deeper fashion. On the other hand, older adults may be more apt than younger adults to process emotional information in a self-referential way (Gutchess et al., 2007), and self-referential processing typically leads to deeper encoding of information (Craik & Lockhart, 1972). Psychophysiological measures like electrodermal activity (which tracks autonomic arousal; Urry, 2010) or corrugator electromyography (which tracks stimulus valence; Bradley & Lang, 2007) could adjudicate between these two possibilities. If older adults are engaging emotion regulation processes during emotional integration – particularly negative integration – this might be reflected by reduced electrodermal and corrugator response, indicating a reduction in the felt emotion of those images relative to their younger counterparts. On the other hand, if older adults are not regulating but simply creating more elaborate or "more emotional" images, this should be reflected by increases in both of those measures.

Though associative deficits have frequently been reported in older adulthood (e.g., Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000), such a deficit is not apparent for integrated emotional pairs. These results not only highlight emotional differences between older and younger adults, but also indicate a potential boundary condition for the associative deficit: that is, this deficit can be attenuated or eliminated in older adults when they have access to strategies that promote integration (see also Naveh-Benjamin, Brav, & Levy for further evidence). Understanding such boundaries – and moreover, ways to attenuate cognitive deficits in older adulthood – is critical for understanding how to better support cognition in older age. Future investigation should explore other ways to attenuate such deficits. For example, it has been shown that older adults' performance is improved on a source-monitoring task – remembering after a long delay whether they had performed an action or simply imagined performing the action during an initial encoding session – when given cue-related retrieval support (Thomas & Bulevich, 2006). That is, when older adults are given strategies about what types of information to search memory for during the source judgment, they perform significantly better than when they must perform that memory search unassisted. Manipulating reward has also been shown to be effective at attenuating older adults' mnemonic deficits: older adults' recall and recognition memory are equivalent to that of their younger counterparts when they are given positive motivational feedback at encoding (i.e., feedback that an encoding judgment was made within a response deadline) or are told that certain items will be associated with monetary rewards at test (Mather & Schoeke, 2011). It is important to understand the support conditions that lead to successful associative and recall memory in older adulthood in order to promote continued cognitive success in that age group.

Additionally, it is critical to bear in mind the delay between encoding and retrieval used in my studies. In both sets of studies, I employed a relatively short delay – approximately 30 minutes – between those two phases of memory. However, the consolidation hypothesis (Müller and Pilzecker, 1900), suggests that after information is initially encoded it remains in a fragile state before being solidified into memory (see review by McGaugh, 2000). The consolidation process is relatively slow, and one proposed reason is to give any associated emotional response sufficient time to influence the consolidation process (McGaugh, 2000; Phelps, 2004). Indeed, there is robust evidence that arousal often enhances the consolidation of information, such that the beneficial effects of arousal are more likely to be apparent after longer delays than after shorter ones. This pattern of results has been shown not only in assessments of item memory (Sharot & Phelps, 2004) but also in tests of associative memory (Pierce & Kensinger, 2011). Thus, it is possible that even if emotional integrations are encoded shallowly and are maintained less well over relatively short delays (e.g., 30 min), they may have a shallower forgetting curve than neutral integrations, making them *more* durable over longer delays. Adjudicating between these alternatives – by assessing memory for integrations after multiple delays, or by disrupting consolidation through a retroactive interference task – would appear to be important for determining whether arousal primarily exerts its effects on integration through processes that occur as the image is initially formed or whether the effects continue as it is stored. It will therefore be informative for future research to examine how arousal affects the durability of integrations over different periods of consolidation.

General Conclusions

The body of work presented here represents steps forward in understanding how both older and younger adults handle a special type of association: integrative mental imagery. Younger adults appear to utilize different routes for integration depending on the emotionality of the integration, with emotional integrations supported by rapid visual processing and non-emotional integrations supported by slower, deliberative fronto-temporal processing. Older adults, on the other hand, exhibit slower, deliberative processing for emotional pairs and show little success at integrating non-emotional pairs, though the biological mechanisms underlying these processes are still unknown. In both age groups, slower and more controlled processing is related to strong memory over a 30-minute delay, resulting in an age-related interaction in the type of material that benefits from integration. This result not only inform the theoretical questions of how emotion affects the associative integration of non-emotional information, and how it does so in both older and younger adulthood, but also offers several avenues for fruitful future research.

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Table 1.

Chapter 2: Parametric Correspondence to Integration Vividness During Neutral Integration

Region	Laterality	x	y	z	*t*	*k*
DLPFC (BA9)	L	-32	46	30	3.88	14
Posterior HC/PHG (BA36)	R	44	-30	-12	3.86	9
Precentral gyrus (BA6)	L	-54	4	8	3.84	44
Primary motor area (BA6)	R	24	16	54	3.84	28
Anterior HC (BA34)	L	-12	-2	-22	3.77	16
Posterior insula (BA13)	R	50	-10	6	3.72	10
Anterior PFC (BA10)	R	24	62	16	3.47	8

Table 2.

Chapter 2: Peak Voxel Coordinates (MNI) for Each Participant's Amygdala VOI for Psychophysiological Interaction

Participant	x	y	z
1	-32	12	-28
2	-28	8	-28
3	-16	-2	-28
4	-16	-6	-26
5	-30	0	-28
6	-32	4	-28
7	-32	6	-28
8	-16	0	-20
9	-20	-6	-30
10	-16	2	-30
11	-28	0	-22
12	-34	8	-26
13	-24	4	-24
14	-26	-6	-24
15	-14	4	-24
16	-24	-8	-22
17	-28	8	-20

Table 3.

Chapter 2: Regions Significantly Correlated With Left Amygdala During Psychophysiological Interaction

Region	Lat.	x	y	z	t	k	Directionality
vmPFC	R	8	52	-26	4.61	35	Neg -
HC	R	26	-16	-10	3.56	19	Neg -
OFC	R	36	42	-12	3.27	7	Neg -
OFC	L	-28	36	-22	3.11	5	Neg -
OFC	L	-6	56	-22	3.06	9	Neg -
Striatum	R	26	-14	-4	3.01	19	Neg -
HC	L	-22	-20	-12	2.92	17	Neg -
Auditory Cortex	R	56	-26	2	2.83	28	Neu +
Auditory Cortex	R	66	-24	8	2.71	32	Neg -

Table 4.

Chapter 3: Participant Characteristics

Exp.	Measure	Age Group	Mean	SD	t	p
1	Beck Depression Inventory	Younger	2.74	0.49	n/a	
	Beck Anxiety Inventory	Younger	3.55	0.72	n/a	
	Geriatric Mood Scale	Older	0.88	0.12	n/a	
	Dysexecutive Questionnaire	Younger	18.24	2.80	n/a	
	Shipley Vocabulary	Younger	32.91	1.90	5.74	<0.001
		Older	35.50	1.13		
	Digit Symbol Copy	Younger	60.22	5.11	7.30	<0.001
		Older	51.08	3.40		
	VVIQ[a]	Younger	63.56	7.55	4.27	<0.001
		Older	71.90	5.88		
2	Beck Depression Inventory	Younger	2.10	0.44	n/a	
	Beck Anxiety Inventory	Younger	3.40	0.70	n/a	
	Geriatric Mood Scale	Older	0.66	0.14	n/a	
	Dysexecutive Questionnaire	Younger	15.07	2.01	n/a	
	Shipley Vocabulary	Younger	36.45	2.50	2.06	0.04
		Older	37.60	1.10		
	Digit Symbol Copy	Younger	58.49	5.67	10.04	<0.001
		Older	45.28	3.07		
	VVIQ	Younger	62.00	7.07	5.73	<0.001

Older	73.04	6.25

The Beck Depression Inventory and Beck Anxiety Inventory are from Beck, Epstein, Brown, and Steer (1988); the Dysexecutive Questionnaire is from Wilson et al. (1996); the Geriatric Mood Scale is from Sheikh and Yesavage (1986); the Shipley Vocabulary Test is from Shipley (1986); the Digit Symbol Copy is from Wechsler (1997); the Generative Naming (FAS) Word Fluency measure is from Spreen and Benton (1977); the Vividness of Visual Imagery Questionnaire (VVIQ) is from Marks (1973).

[a] I reversed the scoring scale so that a “1” would indicate low imagery and a “5” would indicate high imagery, to be consistent with the experimental task instructions; maximum possible imagery score = 80.

Table 5.

Chapter 3: Recognition Percentage (Standard Deviation) for Hits and False Alarms, Experiment 1

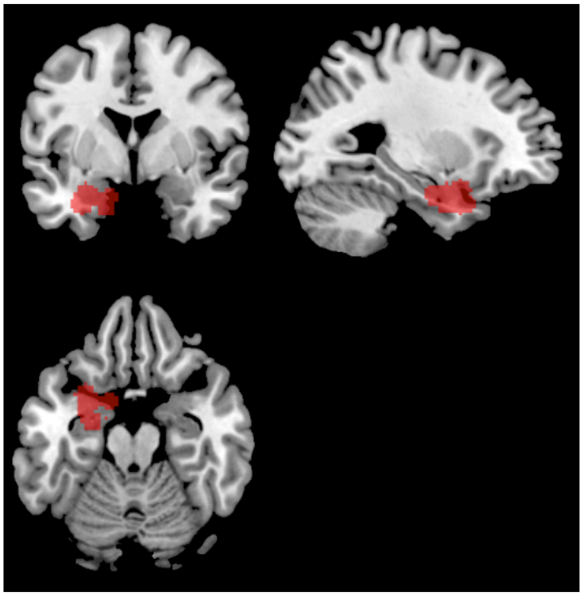
Group	Encoding strategy	Pair type	Hits	False Alarms
Younger Adults	Integrative	Emotional	68.2 (10.9)	6.4 (1.9)
		Neutral	66.2 (13.2)	6.8 (2.5)
	Non-integrative	Emotional	74.7 (12.0)	6.4 (1.9)
		Neutral	72.3 (11.4)	6.8 (2.5)
Older Adults	Integrative	Emotional	52.4 (13.0)	9.7 (1.8)
		Neutral	53.5 (14.7)	12.0 (2.2)
	Non-integrative	Emotional	60.9 (11.2)	9.7 (1.8)
		Neutral	60.0 (12.6)	12.0 (2.2)

Table 6.

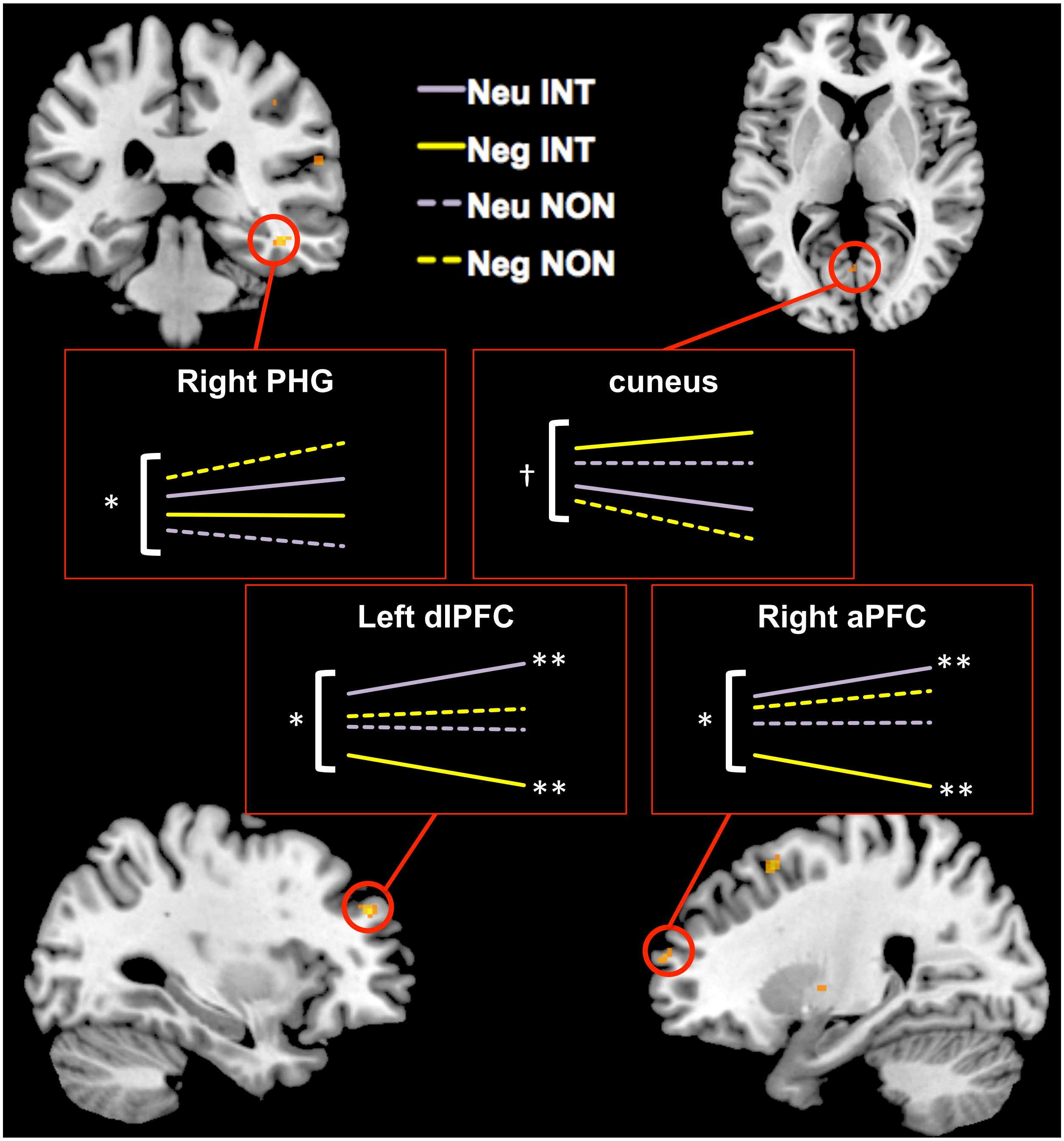
Chapter 3: Recognition Percentage (Standard Deviation) for Hits and False Alarms, Experiment 2

Group	Strategy	Pair type	Time	Hits	False Alarms
Younger Adults	Int	Emotional	Speeded	65.6 (13.0)	9.2 (1.2)
			Moderate	73.4 (10.4)	9.2 (1.2)
			Extended	79.4 (15.6)	9.2 (1.2)
		Neutral	Speeded	62.5 (13.7)	9.0 (1.3)
			Moderate	67.4 (13.1)	9.0 (1.3)
			Extended	77.3 (18.3)	9.0 (1.3)
	Non-int	Emotional	Speeded	72.1 (11.0)	9.2 (1.2)
			Moderate	77.9 (12.7)	9.2 (1.2)
			Extended	86.9 (10.7)	9.2 (1.2)
		Neutral	Speeded	70.7 (11.4)	9.0 (1.3)
			Moderate	78.6 (10.2)	9.0 (1.3)
			Extended	83.7 (12.4)	9.0 (1.3)
Older Adults	Int	Emotional	Speeded	48.7 (6.2)	9.9 (3.7)
			Moderate	54.7 (6.2))	9.9 (3.7)
			Extended	60.6 (6.0)	9.9 (3.7)
		Neutral	Speeded	50.3 (8.8)	9.8 (3.9)
			Moderate	56.5 (10.6)	9.8 (3.9)
			Extended	61.5 (7.4)	9.8 (3.9)

Non-int	Emotional	Speeded	57.1 (7.6)	9.9 (3.7)
		Moderate	60.6 (9.0)	9.9 (3.7)
		Extended	73.4 (7.2)	9.9 (3.7)
	Neutral	Speeded	55.8 (7.7)	9.8 (3.9)
		Moderate	60.9 (7.5)	9.8 (3.9)
		Extended	71.5 (6.6)	9.8 (3.9)

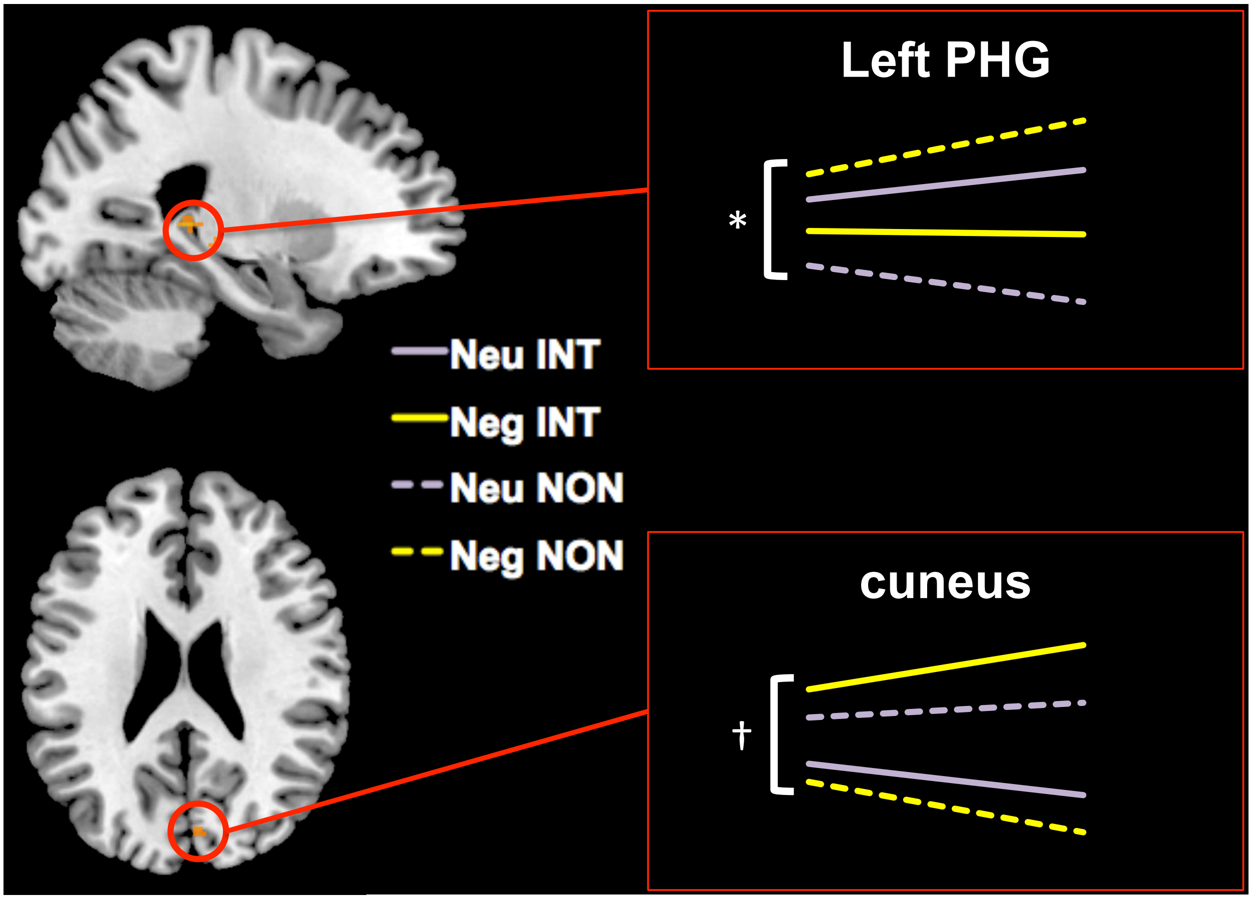


Chapter 2: Figure 1. Composite map of all participants' volumes of interest used for PPI analysis.

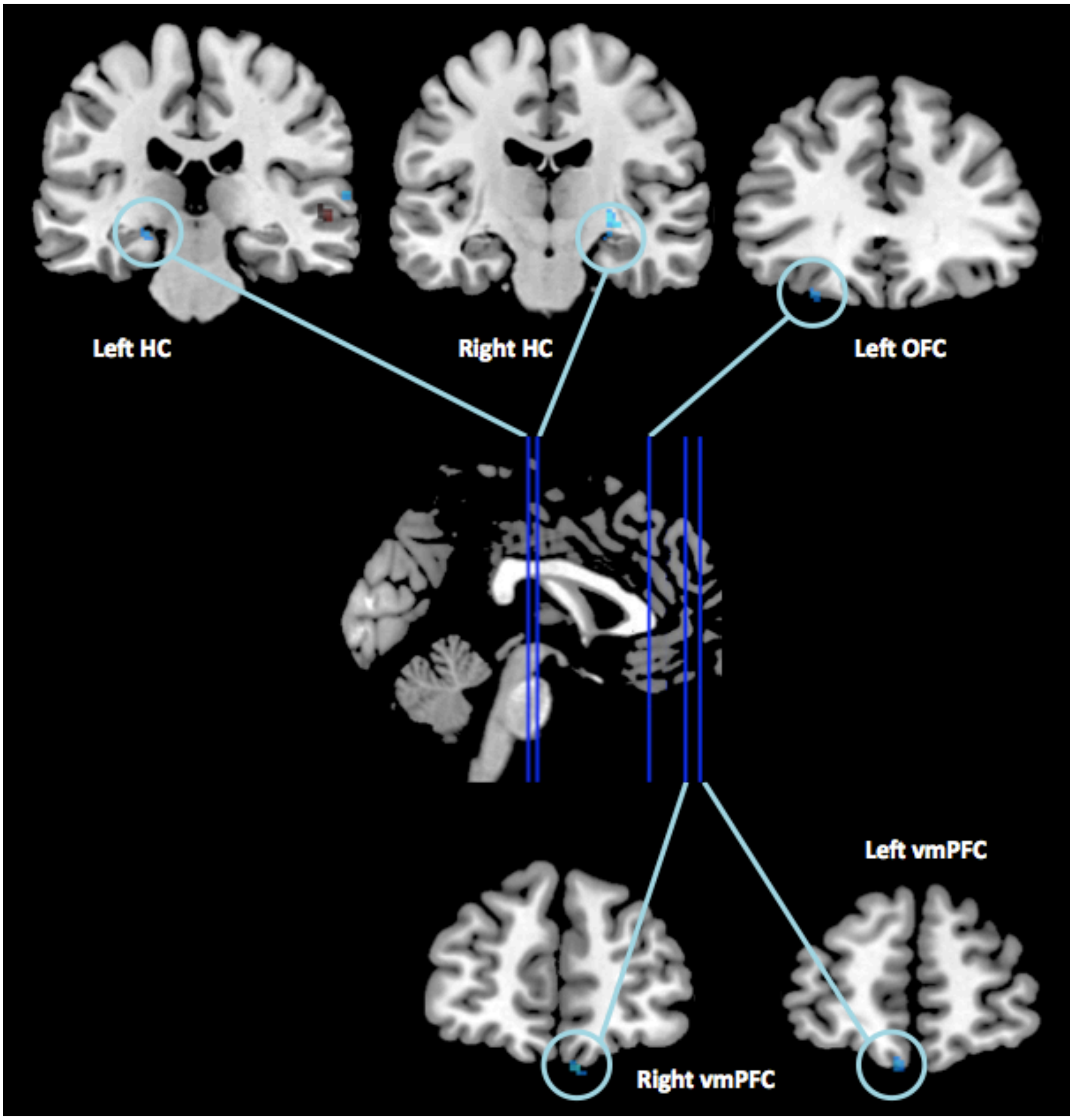


Chapter 2: Figure 2. Regions that show significant parametric increase during encoding as a function of successful integration. Right parahippocampal gyrus (44 -30 -16), left dorsolateral PFC (-32 46 30), and right anterior prefrontal cortex (24 62 16) all show selective parametric increase during neutral integration. Cuneus (0 -66 4) shows selective parametric increase during negative integration. Lines represent beta weights (slope) for

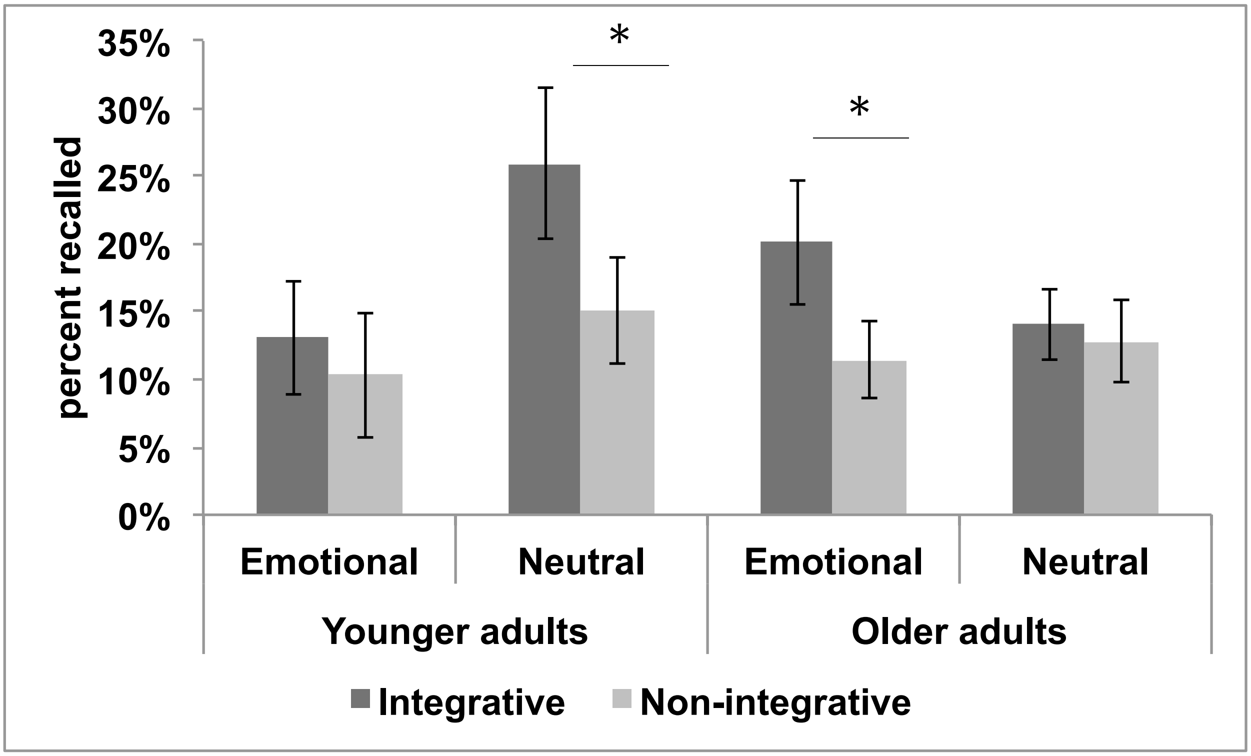
the parametric relation, extracted from the peak voxel within each cluster. Dashed lines represent weights from the non-integrative condition and solid lines represent weights from the integrative condition. † = full interaction is significant at $p_{\text{uncorrected}} < 0.005$; * = full interaction is significant at $p_{\text{corrected}} < 0.05$; ** = pairwise comparison (e.g., neutral integration > negative integration) is significant at $p_{\text{corrected}} < 0.05$.



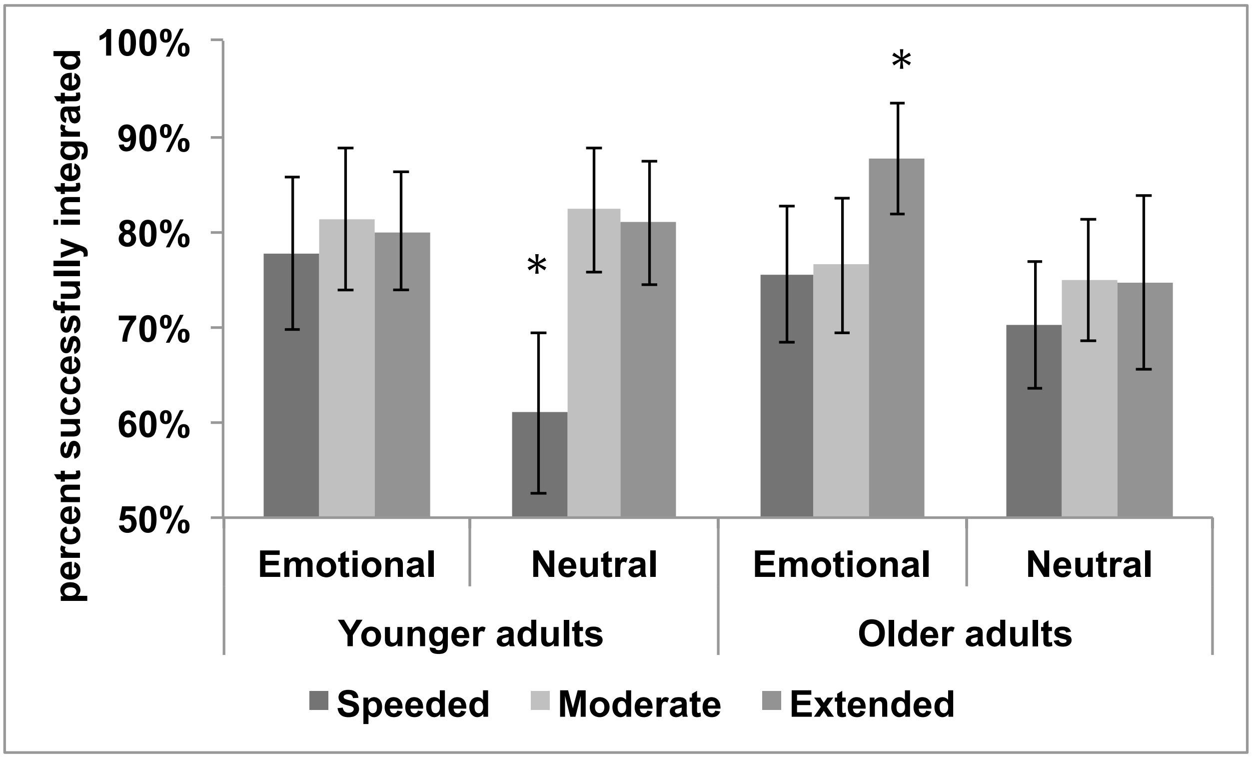
Chapter 2: Figure 3. Regions that show significant parametric increase during retrieval as a function of prior successful visual integration. Left parahippocampal gyrus (-24, -36, 4,) shows selective parametric increase during neutral integration. Cuneus (6 -80 24) shows selective parametric increase during negative integration. Lines represent beta weights for the parametric relation, extracted from the peak voxel within each cluster. Dashed lines represent weights from the non-integrative condition and solid lines represent weights from the integrative condition. † = full interaction is significant at $p_{\text{uncorrected}} < 0.005$; * = full interaction is significant at $p_{\text{corrected}} < 0.05$.



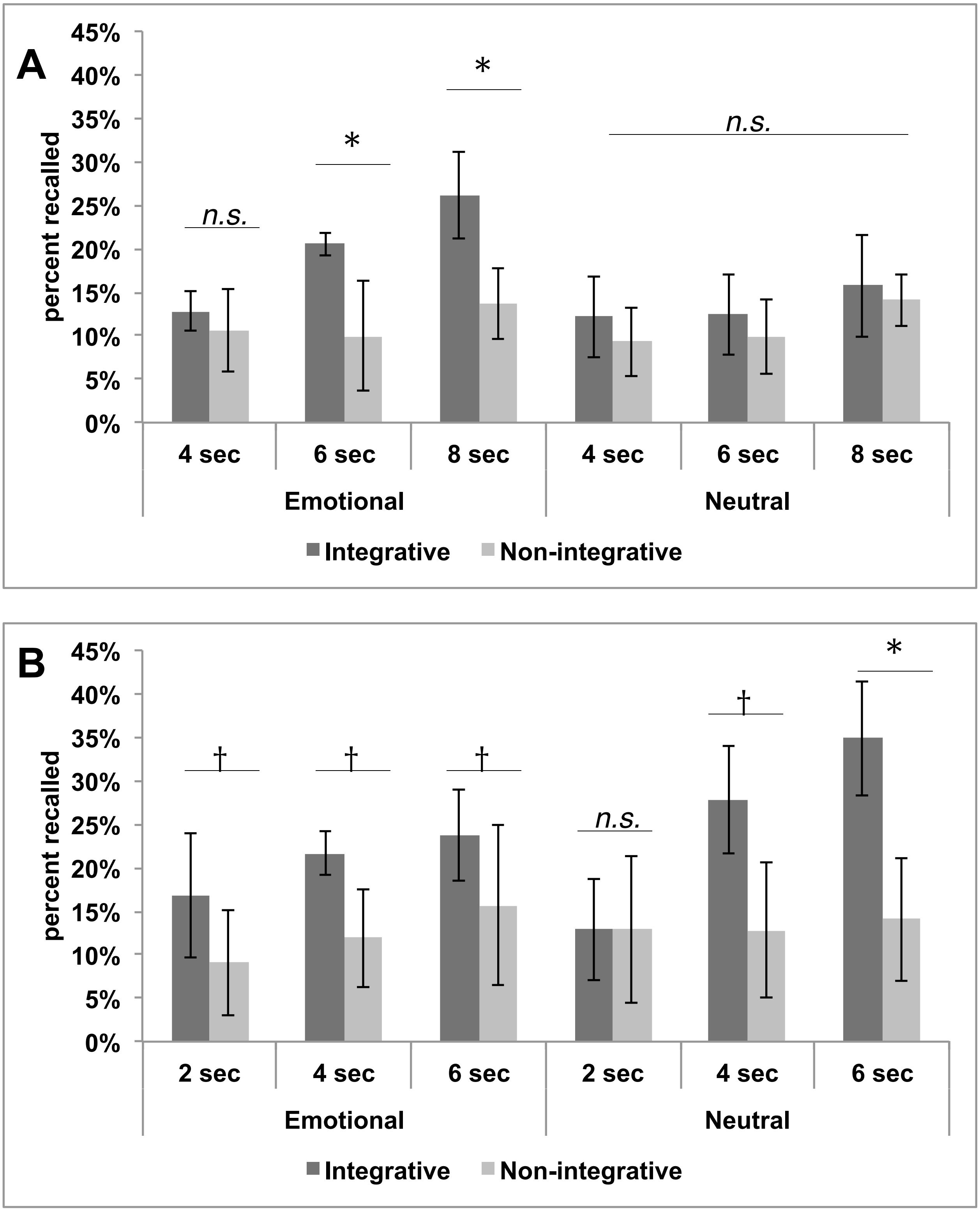
Chapter 2: Figure 4. Regions that show a significant negative correlation with amygdala activity during negative integration.



Chapter 3: Figure 5. Associative cued recall performance, Experiment 1. Younger adults show a significant benefit from integration (dark bars > light bars) for neutral pairs, whereas older adults show a significant benefit from integration for emotional pairs. Error bars represent 95% confidence interval around the mean (corrected for within-subject comparisons; Morey, 2008). Asterisks indicate significance within condition at a Bonferroni-corrected alpha level of $p < 0.0125$.



Chapter 3: Figure 6. Percentage of integrative pairs rated as a "3" or "4" at encoding. Younger adults (left bars) report no difference in successful integration of emotional pairs regardless of encoding speed, but report integrating significantly fewer neutral pairs when encoding is speeded. Older adults (right bars) report no difference in successful integration of neutral pairs regardless of encoding speed, but report integrating significantly more emotional pairs when encoding time is extended. Error bars represent 95% confidence interval around the mean (corrected for within-subjects comparisons; Morey, 2008). Asterisks indicate significance within condition at a Bonferroni-corrected alpha level of $p < 0.004$.



Chapter 3: Figure 7. Associative cued recall performance, Experiment 2. (A) Older adults do not show a mnemonic benefit from integration regardless of encoding speed,

nor do they show an integrative benefit for emotional pairs when encoding is speeded. However, a significant benefit from integration is seen when given six or eight seconds to encode. (B) Younger adults show a benefit from integration for all pairs, except for neutral pairs when encoding is speeded. The benefit from integration is disproportionately larger for neutral pairs than for emotional pairs when younger adults are given four or six seconds to encode. Error bars represent 95% confidence interval around the mean (corrected for within-subjects comparisons; Morey, 2008). Asterisks indicate significance within condition at a Bonferroni-corrected alpha level of $p < 0.008$; crosses (†) indicate significance at an uncorrected alpha level of $p < 0.05$.