

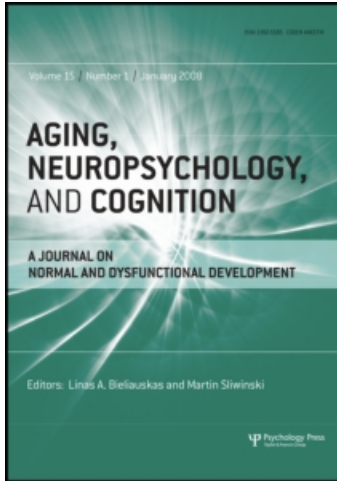
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Probing the Brain Substrates of Cognitive Processes Responsible for Context Effects on Recognition Memory¹

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ABSTRACT

Context effects on episodic recognition memory involve separable contributions of target-context binding, additive familiarity, and configural constancy. Here we examine whether these factors reflect contributions of processes attributed to different brain substrates. First, we challenged frontal and medial temporal lobe-based cognitive capacities in healthy young adults, employing divided attention tasks at encoding and retrieval, and extended retrieval delay, respectively. Target-context binding effects were specifically attenuated by delay, but not by divided attention. In a second experiment, older adults were identified by neuropsychological testing as having different levels of frontal and medial temporal lobe-dependent cognitive functions. Consistent with Experiment 1, older adults with low medial temporal lobe function exhibited reduced target-context binding effects, but levels of frontal function did not modulate binding effects. These findings indicate that unlike source memory, context effects on memory are associated with the integrity of medial temporal lobe-based processes but not with the integrity of frontal lobe-based processes. Our findings also emphasize the importance of discriminating between functional subgroups in the attempt to characterize memory processes in older adults.

Keywords: Aging; Frontal lobe; Medial temporal lobe; Context effect; Source memory; Association.

¹Portions of this study were carried out as part of a PhD dissertation by Tal Raz at Bar Ilan University, Ramat Gan, Israel.

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INTRODUCTION

The importance of contextual factors in memory retrieval processes is recognized in many memory models (e.g., Dennis & Humphreys, 2001; Howard, Fotedar, Datey, & Hasselmo, 2005; Murnane & Phelps, 1993, 1994; Raaijmakers & Shiffrin, 1981). The impact of context may be seen in the effects of contextual change or constancy on memory for studied materials – i.e., *context effects* (CEs). Such effects are widely found when target memory is tested by free recall (e.g., Godden & Baddeley, 1975; Parker & Gellatly, 1997), and cued recall (e.g., Nicolas & Carbonnel, 1996; Smith, Glenberg, & Bjork, 1978), but somewhat less consistently in recognition memory (CE reported, e.g., by Hollingworth, 2006 and Russo, Ward, Geurts, & Scheres, 1999, but not found, e.g., by Fernandez & Glenberg, 1985; Godden & Baddeley, 1980; Murnane & Phelps, 1993, 1994).

To account for the diversity of CEs findings, we have proposed that CEs reflect several memory-related cognitive processes. In an earlier study (Vakil, Raz, & Levy, 2007) we demonstrated the complex effects of reinstatement or change of local encoding context (i.e., a discrete stimulus presented in conjunction with a memory target; in that study, hats and faces, respectively) on visual object recognition memory. Relative to recognition of targets presented alone, three forms of context reinstatement yielded three levels of effects on recognition. Exact repetition of studied target-context pairs yielded the best target recognition, arguably because the context stimulus specifically cued memory for its accompanying target. This effect is in keeping with the ICE (Item, Context, Ensemble) theory (Murnane, Phelps, & Malmberg, 1999), which posits that CEs emerge when an ensemble representation is created in addition to the separate memories for item (target) and context. Old context stimuli accompanying different targets at test than at study also benefited recognition, albeit slightly (but significantly) less so. It is possible that such old context stimuli served to activate memories of the encoding episode as a whole, inducing recollective processes, and so indirectly cued the old targets. Alternatively, the increase in the number of correct ‘old’ judgments in such cases may result from the additive familiarity of target and context stimuli, as would be predicted by the global activation approach (Murnane & Phelps, 1994). The flip side of this benefit is a memory deficit: the presence of old encoding context together with a new (foil) stimulus was found to increase the probability of a false alarm, relative to foil accompaniment by new context or no local context. Finally, the effect on probe memory of a new context stimulus relative to no local context were interpreted as being caused by global similarity (i.e., the same presentation array) between encoding and retrieval formats. So, in that study, old faces were better remembered when topped with any hat, and conversely, a new face was significantly more likely to be misidentified as old if it was hatted (as were all the faces at study) than if it was bare-headed.

Accordingly, CEs may be seen as reflecting various mnemonic processes, which might have different brain substrates. The formation of associative or relational memory requires the contributions of the diencephalon and the medial temporal lobe structures, especially the hippocampus (Eichenbaum & Cohen, 2001; Prince, Daselaar, & Cabeza, 2005; Squire, Stark, & Clark, 2004). One interpretation of the advantage of exact target-context repetitions relative to other conditions is that it involves hippocampal-dependent associative binding between the target and context stimuli. Binding-based CEs may thus be seen as an indirect expression of associative learning: a type of cued recognition which does not require explicit retrieval of the associative relationship between target and context, but is nevertheless dependent on it.

Successful performance of memory tasks which are especially complex because of interference, or because of overlap in characteristics of relevant and irrelevant representations, may additionally require the contribution of prefrontal cortex processes (Moscovitch, 1994a; Vakil, 2005). For example, frontal lobe volume is correlated with semantic clustering that promotes retrieval success and avoidance of response bias (Kramer et al., 2005), and mid-ventrolateral prefrontal damage produces deficits in the active selection, comparison and judgment during retrieval (Thaiss & Petrides, 2003). Notably, source memory (which may best be described as explicit memory for encoding context) is considered to be especially dependent on frontal lobe function, being differentially impaired relative to item memory in the elderly (Glisky, Rubin, & Davidson, 2001; Hashtroudi, Johnson, & Chrosniak, 1989; Spencer & Raz, 1994, 1995) and in patients with frontal-lobe damage (Duarte, Ranganath, & Knight, 2005; Janowsky, Shimamura, & Squire, 1989; Swick, Senkfor, & Van Petten, 2006). Furthermore, numerous neuroimaging studies have identified prefrontal activations associated with the encoding and retrieval of source memory information (e.g., Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins, Foley, Schacter, & Wagner, 2002; Mitchell et al., 2008; Rugg, Fletcher, Chua, & Dolan, 1999).

It might therefore be expected that frontal lobe disorders would lead to a diminution of CEs. However, it has been demonstrated that patients with closed-head injuries who exhibit general declarative memory impairments, including deficits in direct source recollection, nevertheless benefit from context reinstatement at retrieval (Vakil, Biederman, Liran, Groswasser, & Aberbuch, 1994; Vakil, Golan, Grunbaum, Groswasser, & Aberbuch 1996a; Vakil, Openheim, Falck, Aberbuch, & Groswasser, 1997). Similarly, patients with Parkinson's disease who displayed impaired intentional content learning showed intact incidental learning of contextual information (Vingerhoets, Vermeule, & Santens, 2005). Furthermore, elderly individuals, whose source memory may be more impaired than their item memory

relative to younger people (e.g., Spencer & Raz, 1995), can nevertheless benefit equally from context reinstatement (Naveh-Benjamin & Craik, 1995; Vakil, Melamed, & Even, 1996b). These findings accord with studies that demonstrate that in healthy younger individuals, recognition is modulated by contextual reinstatement even when the contextual stimuli themselves are not recognized (Levy, Rabinyan, & Vakil, 2008), and that young adults used contextual contingencies when making recognition judgments even if they were not able to verbalize such contingencies (Manier, Apetroaia, Pappas, & Hirst, 2004). Thus, there seems to be a dissociation between the effects of frontal lobe dysfunction on direct and indirect measures of contextual memory. However, the aforementioned studies are somewhat incomplete, since they only measured the effects of repeated vs. completely new context or no context on target memory – an effect which may result from the additive familiarity of old target and old context. They did not assess whether such CEs remain intact in patient populations when original vs. recombined target-context pairs are presented at test, a manipulation that indicates the strength of target-context binding in memory. Neither did they assess the effects, relative to no local context, of the presence of new local context, which can potentially cause more misses by association, and may require more frontal lobe-based processes, e.g., monitoring, to achieve accurate recognition (Lundstrom, Ingvar, & Petersson, 2005).

Accordingly, the present study attempts to further characterize the contributions of medial temporal lobe- and frontal lobe-based cognitive processes to CEs. We employed an experimental paradigm maximizing target-context specificity and interactivity, which an earlier recognition memory study had shown to elicit robust complex CEs (Vakil et al., 2007). In that paradigm, participants view photographs of trial-unique male faces portrayed as wearing distinctive trial-unique hats (yielding specificity), the instructed task being to rate the compatibility of the faces and the hats (yielding interactive processing). Participants were instructed to remember the faces for a subsequent memory test, but not instructed to remember the hats (yielding attentional inequality and a target-context relationship).

At test, we compared the CE benefit to recognition of exact target-context repetitions ('Repeat condition') with CE benefit to memory for targets recombined with contexts which were seen previously but paired with different targets ('Re-pair condition'). A further characterization of CEs was attempted by using two different 'context-negative' conditions. In the 'New' condition, targets were accompanied by contexts that had not been seen at study. This condition is not completely neutral, since the presence of the novel contextual stimulus preserves the stimulus array structure and the global similarity between encoding and retrieval presentations, in that the face seen at study topped by a hat is once again seen topped by a hat,

even though it is a novel hat. This effect of global contextual similarity in presentation array emerges in comparison with the ‘None’ condition, of faces without hats. This type of contextual reinstatement is of the kind usually found in source memory studies, in which the context is not the specific stimulus paired with the probe, but a more general feature (e.g., speaker’s voice, font color) characteristic of many of the stimuli in the experiment.

The effects of context reinstatement on the evaluation of new (foil) stimuli (correct rejection vs. false alarms) are another index of memory for contextual information. If the presentation of previously seen context stimuli biases the observer to misjudge new targets as having been previously seen, one may infer that those context stimuli were remembered. The additive familiarity of target and context influences the memory judgment. We therefore included conditions in which foils were accompanied by old context, new context, or no local context stimuli. In a final stage of the experiment, we administered a two-alternative forced choice recognition test for a set of stimuli which had served as contexts during encoding but which did not appear in the first test stage. This provided an indication of the strength of the direct explicit memory for contextual material.

The current study includes two CE experiments, one employing a simulation of frontal- and medial temporal lobe functional decline through cognitive manipulations, and another involving the participation of older adults with different levels of frontal lobe and medial temporal lobe function. In the first experiment, we simulated medial temporal lobe functional decline by introducing a one-week delay between study and test (Mayes, Meudell, & Som, 1981; Shimamura & Squire, 1991). In another group of participants, we simulated frontal lobe impairment by divided attention (Craik, 1982; Craik, Routh, & Broadbent, 1983; Moscovitch, 1994b; Troyer & Craik, 2000; Troyer, Winocur, Craik, & Moscovitch, 1999), induced by having participants perform a simultaneous perceptual judgment at both study and test. We assessed the effects of these manipulations on CE relative to baseline full-attention, immediate test condition. We further compared those effects with the effects of the same manipulations on direct recognition memory for the context stimuli. Based on our previous studies (Vakil et al., 1994, 1996a, 1997), we predicted that the simulation of frontal lobe functional decline relative to baseline would yield impaired direct memory for contexts but preserved CE across all conditions. Furthermore, we predicted that simulated medial temporal lobe functional decline would diminish CE in the Repeat relative to the Re-pair conditions, due to the impairment in associative binding for which medial temporal lobe structures – especially the hippocampus – are crucial (Mayes et al., 2004). Additionally, delay was predicted to impair direct memory for contexts.

EXPERIMENT 1

Methods

Participants

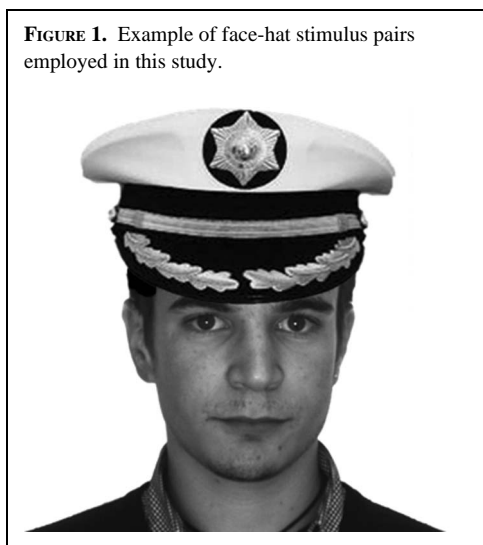
Participants were 57 young adults (22 males; mean age 22.2, range 18–32) self-reportedly in good health, with normal or adjusted-to-normal vision. All were undergraduate students at Bar-Ilan University, some of whom took part in the experiment to fulfill academic requirements, and others who volunteered in return for payment. Written informed consent was obtained from all participants for a protocol approved by the Bar Ilan University Institutional Review Board.

Participants were randomly assigned to one of two conditions: divided attention and immediate test (DivAttn, $n = 27$); or full attention and test after a retention delay of one week (Delay, $n = 30$). The data on the full attention and no delay condition are taken from a parallel group of 28 young adults, previously published in Vakil et al. (2007).

Materials

Stimuli consisted of 64 monochrome photographs of hat-topped but otherwise full faces of adult males, each 7×10 cm in size, and 60 monochrome photographs of hats, 3×3 cm in size. The hats were characteristic of types of work, e.g., police, firefighter, cook, or of cultural characters or types, e.g., Napoleon, Peter Pan, a witch; examples are provided in Figure 1. Each hat was correctly identified by at least 80% of 30 raters (not experimental participants) in a separate pretest. These stimuli were randomly paired to form 32 face-hat study pairs, and an additional 32 faces and 28 hats

FIGURE 1. Example of face-hat stimulus pairs employed in this study.



supplemented them to form the various test-pair combinations. Two different combination sets were created in this manner and each set formed the target pairs for half the participants. These two sets did not yield different accuracy rates or response times, so they were combined for all subsequent analyses. The order of presentation of stimuli in both study and test phases was randomized over participants.

Seven types of face-hat photo pairs or face-only photos were presented at test, each forming a different test condition:

- A. Eight of the originally studied pairs (Target Old, Context Old-Same [TOCO-S]; 'Repeat' condition).
- B. Eight pairs in which a studied target face was presented in the context of a hat that had been seen at study with a different face (Target Old, Context Old-Different [TOCO-D]; 'Re-pair' condition).
- C. Eight pairs in which a studied target face was presented in the context of a new hat that had not been seen at study (Target Old, Context New [TOCN]; 'New' condition).
- D. Eight studied target faces unaccompanied by any hat (Target Old [TO]; 'None' condition).
- E. Eight new unstudied faces presented in the context of a hat that had been seen at study with a different face (Target New, Context Old [TNCO]).
- F. Twelve pairs of new, unstudied faces and hats (Target New, Context New [TNCN]).
- G. Twelve new unstudied faces unaccompanied by any hat (Target New [TN]).
- H. For a separate test of direct memory for context, 8 studied hats which did not appear in the other trial types were paired with 8 unstudied foil hats (Context Direct).

Procedure

In the encoding phase, 32 face-hat pairs were presented to participants on a computer screen by SuperLab (Cedrus, Inc.) for 4 seconds each, who were instructed to rate face-hat compatibility by verbal response, using a scale of 1–5. They were also instructed to remember the faces for a subsequent memory test. Each participant performed four training trials before beginning the experiment.

At test, participants were told that they would see studied and unstudied faces, accompanied by the same or different studied and unstudied hats. They were instructed to indicate by key press, as quickly and accurately as

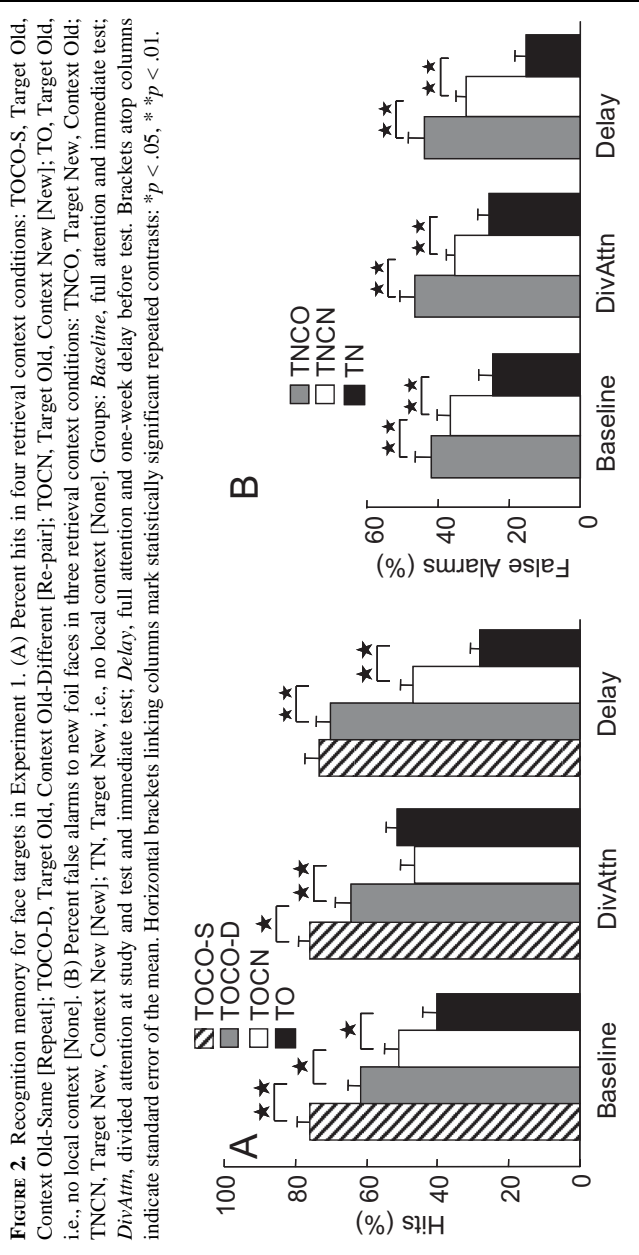
possible, if the face had been seen at study (Old) or not (New), irrespective of the hat now accompanying it. Participants were instructed to guess if unsure. They were then shown 64 face-hat pairs or face-only photos (types A–G above) in pseudo-random order. The rate of presentation of test trials was self-paced, with the response triggering the following trial.

For the Delay group, the encoding and test phases were separated by one week. For the DivAttn group, the encoding session was followed immediately by the test session. The DivAttn group simultaneously performed a distractor task during both encoding and retrieval stages (also used by Russo & Parkin, 1993, and by Vakil & Hoffman, 2004, to simulate frontal-lobe impairment). Before beginning the experiment, the participants in the DivAttn condition performed 10 training trials in which they were familiarized with tone stimuli at three frequencies (100 Hz, 150 Hz, and 200 Hz delivered via external speakers). While performing the memory tasks, participants heard a random sequence of those three tones at a pseudo-random SOA of 6–9 seconds, uncorrelated with the appearance of the visual stimuli of the memory task. They were asked to verbally classify each tone as high, medium, or low. Participants were instructed that the two tasks were of equal importance and that they were to concentrate equally on both of them.

After the face recognition test, a separate test was administered for recognition of context hats alone. Participants were shown eight pairs of photos of hats (type H, above), consisting of a studied context hat and an unstudied foil, and asked to indicate by key press which of the two hats had appeared at study – i.e., a two-alternative forced choice direct appraisal of recognition memory for the context hats. If they were unsure they were instructed to guess. For the DivAttn group, this test was also done simultaneously with the tone-classification distractor task.

Results

Performance of the DivAttn and Delay conditions participants was compared with the performance of an immediate test + full attention baseline group ($n = 28$) from an earlier study (Vakil et al., 2007). We examined CE on hits and false alarms separately for the various context types (portrayed in Figure 2a, and 2b, respectively). For hits, we performed a 3×4 mixed design, repeated measures ANOVA, with three groups (Baseline, DivAttn, or Delay) as the between-subjects factor and four context types (TOCO-S [Repeat], TOCO-D [Re-pair], TOCN [New], TO [None]) as the within-subjects factor. This analysis revealed a significant main effect of Context Type, $F(3, 246) = 74.91$, $p < .01$, no Group main effect, $F(2, 82) = .907$, $p < .1$, and a significant Context Type \times Group interaction $F(6, 246) = 4.57$, $p < .01$. To explore the sources of the interaction, we conducted separate repeated measures ANOVAs for each group, followed by repeated



contrasts. As previously reported (Vakil et al., 2007), in the baseline condition there was a significant main effect of Context Type, $F(3, 81) = 22.47, p < .01$. Repeated contrasts revealed statistically significant differences between Repeat and Re-pair conditions, $F(1, 27) = 17.19, p < .01$, between Re-pair and New conditions, $F(1, 27) = 5.17, p < .05$, and between New and None conditions, $F(1, 27) = 4.73, p < .05$. In the Delay group, there was a significant main effect of Context Type, $F(3, 87) = 45.56, p < .01$. Repeated contrasts revealed statistically significant differences between Re-pair and New conditions, $F(1, 29) = 27.20, p < .01$, and between New and None conditions, $F(1, 29) = 20.08, p < .01$; the difference between Repeat and Re-pair conditions was not significant, $F(1, 29) = 0.7, p > .1$. In the DivAttn condition, there was a significant main effect of Context Type, $F(3, 78) = 16.9, p < .01$. Repeated contrasts revealed statistically significant differences between Repeat and Re-pair conditions, $F(1, 26) = 5.91, p < .05$, and between Re-pair and New conditions, $F(1, 26) = 11.75, p < .01$; the difference between New and None conditions was not significant, $F(1, 26) = 1.70, p > .2$.

To assess the effect of context reinstatement on the generation of false alarms, we performed a 3×3 mixed design, repeated measures ANOVA, with three groups (Baseline, DivAttn, or Delay) as the between-subjects factor and three context types (TNCO, TNCN, TN) as the within-subjects factor. This analysis revealed a significant main effect of Context Type, $F(2, 164) = 41.52, p < .01$. The Group main effect was not significant, $F(2, 82) = 1.06, p > .1$, nor was the Context Type \times Group interaction, $F(4, 164) = 1.08, p > .1$. Repeated contrasts revealed that across groups, false alarm rates differed between Foil + Old context (TNCO) and Foil + New context (TNCN) conditions, $F(1, 82) = 13.59, p < .01$, and between Foil + New context and Foil + None context (TN) conditions, $F(1, 82) = 34.38, p < .01$.

For the purpose of studying CEs, the preceding data regarding separate measures of hits and false alarms are of primary importance, as context reinstatement affects responses to each type of probe independently. However, to complete the picture we also examined overall memory accuracy as reflected by corrected hits, i.e., hits minus false alarms for parallel context conditions of targets and foils. Thus, we examined Repeat Hits minus TNCO foils, Re-pair Hits minus TNCO foils, New Context Hits minus TNCN foils, and No Context (None condition) Hits minus No Context foils. For the Baseline group, the mean corrected hit scores were: Repeat 33.9% (SEM 5.3%), Re-pair 19.6% (SEM 5.7%), New 14.3% (SEM 4.3%), None 15.8% (SEM 5.2%). In the Delay group, the mean corrected hit scores were: Repeat 29.6% (SEM 5.1%), Re-pair 26.3% (SEM 5.5%), New 14.7% (SEM 4.2%), None 12.68% (SEM 5.0%). In the Divided Attention group, the mean corrected hit scores were: Repeat 29.6% (SEM 5.4%), Re-pair 18.1% (SEM 5.8%), New 11.1% (SEM 4.5%), None 25.8% (SEM 5.3%). A 3×4 mixed model repeated measures ANOVA revealed significant effect of Context

condition, $F(3, 246) = 10.7$, $p < .01$, no effect of group, $F(2, 82) < 1.0$, and a non-significant interaction, $F(6, 246) = 1.61$, $p > .1$.

In the direct recognition test for context hats, the DivAttn group correctly endorsed 85.2% of the previously presented context hats, and the Delay group endorsed 76.7% (in contrast with the baseline group performance of 80.6%). A one-way ANOVA indicated that these differences were not significant, $F(2, 82) = 1.44$, $p > .1$.

Discussion

This experiment revealed differential effects of various context types on recognition under conditions of delay and divided attention. While the significant contribution of binding to CE on hits (Repeat [TOCO-S] > Re-pair [TOCO-D]) which obtained for the baseline group was preserved in the DivAttn group, it was attenuated and not significant in the Delay group. In contrast, the contribution of preserved presentation array (New [TOCN] > None [TO]) seen in the baseline group was intact (and even slightly amplified) in the Delay group. To the extent that the delay manipulation simulates the attenuation of memory caused by medial temporal lobe functional decline, these findings indicate that it specifically affects binding-based CEs, perhaps reflecting associative memory processes especially dependent on the hippocampus (see below).

As predicted, the delay condition group also performed more poorly than the baseline group in direct memory for contexts (although this difference failed to reach statistical significance). Unexpectedly, the DivAttn was numerically (but not statistically) superior to the baseline group in direct memory for contextual stimuli, contrary to our prediction. Additionally, the effect of global study-test similarity, i.e., preserved presentation array CE (New [TOCN] > None [TO]) was not found in the DivAttn group; the reasons for these specific findings are unclear.

It is further noteworthy that the one week delay had the greatest impact (vs. baseline) on the None (TO or TN) conditions, in which no local context information is available. Hits dropped from 40.2 to 27.9%, and false alarms from 24.4 to 15.3%. It may be suggested that under conditions of greater forgetting, we rely more on contextual information – which generally benefits our overall performance, but sometimes impairs it. This notion is not unlike the ‘outshining’ principle (Smith & Vela, 2001), which states that CE are more likely to be found when retrieval memory demands are higher. This proposal must be tempered by the fact that the overall memory performance of the delay group was only numerically and not significantly weaker than the other two conditions; a study contrasting immediate and longer-delay remembering may highlight this effect more clearly.

Having seen the effects of divided attention and delay on CEs, we then attempted to determine whether this pattern of CEs changes yielded by

cognitive simulation of medial temporal and frontal lobe functional decline would also be found in persons with actual functional decline related to those brain areas. For that purpose, we tested CEs using the same task in older adults characterized as having high or low frontal or medial temporal lobe functions, using the methods of Glisky and colleagues (Davidson & Glisky, 2002; Glisky & Kong, 2008; Glisky, Polster, & Routhieaux, 1995; Glisky et al., 2001). Once again, we anticipated that low medial temporal lobe function, but not diminished frontal lobe function, would diminish binding-based CE. In contrast, following upon the results of Experiment 1, we predicted that the low frontal lobe function group would show intact binding-based and associative familiarity based CEs, but might not exhibit effects of preserved presentation array.

EXPERIMENT 2

Methods

Participants

Fifty-four older adults (14 male) between the ages of 65–95 ($M = 75.8$), without known history of psychiatric illness, dementia or neurological disorders that might impair their cognitive abilities, participated in the study. They averaged 11.6 years of education. It should be noted that many members of this age cohort in Israel had their schooling interrupted by wars and migration. All participants had normal or adjusted to normal vision. They were all in good age-appropriate general health, and capable of independent daily living. Participants were recruited through the cultural events coordinators in a senior housing facility and in a local community center, and volunteered to participate without compensation. An additional four persons were excluded after requesting to end their participation during the course of the study. Written informed consent was obtained from all participants for a protocol approved by the Bar Ilan University Institutional Review Board.

Materials

Neuropsychological assessments

For the initial procedure of characterizing participants on the basis of frontal lobe-based and medial temporal lobe-based functions, we administered nine neuropsychological tests that are assumed to assess the integrity of those functions (Davidson & Glisky, 2002; Glisky & Kong, 2008; Glisky et al., 1995, 2001). The *frontal lobe* assessments were: (1) Wisconsin Card Sorting Test (Hart, Kwentus, Wade, & Taylor, 1988); (2) Verbal Fluency (Benton & Hamsher, 1976), using the Hebrew letters *bet*, *gimel*, and *shin*; (3) the Arithmetic subtest of the Wechsler Adult Intelligence Scale-Revised

(WAIS-R; Wechsler, 1981); (4) the Mental Control subtest of the WAIS-R (Wechsler, 1981); and (5) the Backwards Digit Span of the Wechsler Memory Scale-Revised (WMS-R; Wechsler, 1987). The *medial temporal lobe* assessments were: (1–3) Logical Memory I, Verbal Pair Associates I, and Visual Pair Associates II subtests from WMS-R, and (4) the delayed recall measure (repetition 8) of the Hebrew version of the Rey Auditory Verbal Learning Test (Rey AVLT-H; Vakil & Blachstein, 1997).

Experimental test of recognition memory

As in Experiment 1.

Procedure

Participants were told that they were about to participate in an experimental study of memory which would include various short tests examining different forms of memory. Participants were tested in their homes. The overall testing time was on the order of 1.5 hours. The tests were administered in the following order: (1) *Rey AVLT-H, trials 1–7*; (2) *Visual Pair Associates I*; (3) *Face-hat recognition task* – as in Experiment 1; (4) *Rey AVLT-H, trial 8*; (5) *Visual Paired Associates II*; (6) *Verbal Fluency*; (7) *Logical Memory I*; (8) *Wisconsin Card Sorting Test*; (9) *Mental Control*; (10) *Verbal Paired Associates I* (11) *Backward Digit Span*; (12) *Arithmetic*; (13) *Verbal Paired Associates II*.

Assignment of participants to high/low medial temporal lobe and frontal lobe function groups

To achieve an optimal blend of the neuropsychological test scores to assess level of medial temporal lobe-based and frontal-lobe based functions, we used a slightly modified version of the factor weightings prepared by Glisky and Kong (2008), which were based on factor analysis using a sample of 227 older adults. There were two differences between the current weightings (Table 1) and those reported by Glisky and Kong. First, we applied the factor weighting they reported for the Long-Delay Cued Recall measure from the California Verbal Learning Test (Delis, Kramer, Kaplan, & Ober, 1987) to the delayed recall measure (repetition 8) of the Hebrew version of the Rey Auditory Verbal Learning Test (Rey AVLT-H; Vakil & Blachstein, 1997), which is the closest normed Hebrew equivalent of the CVLT. Additionally, the factor weightings reported by Glisky and Kong also included the Faces I subtest of the Wechsler Memory Scale-III, which we did not administer. However, the Faces I element had the appreciably lowest weighting of all tests on the Medial Temporal Lobe function factor, so we used the other factor weightings as reported with no further adjustments.

TABLE 1. Weightings of Test Scores on Frontal Lobe (FL) and Medial Temporal Lobe (MTL) Factor Scores

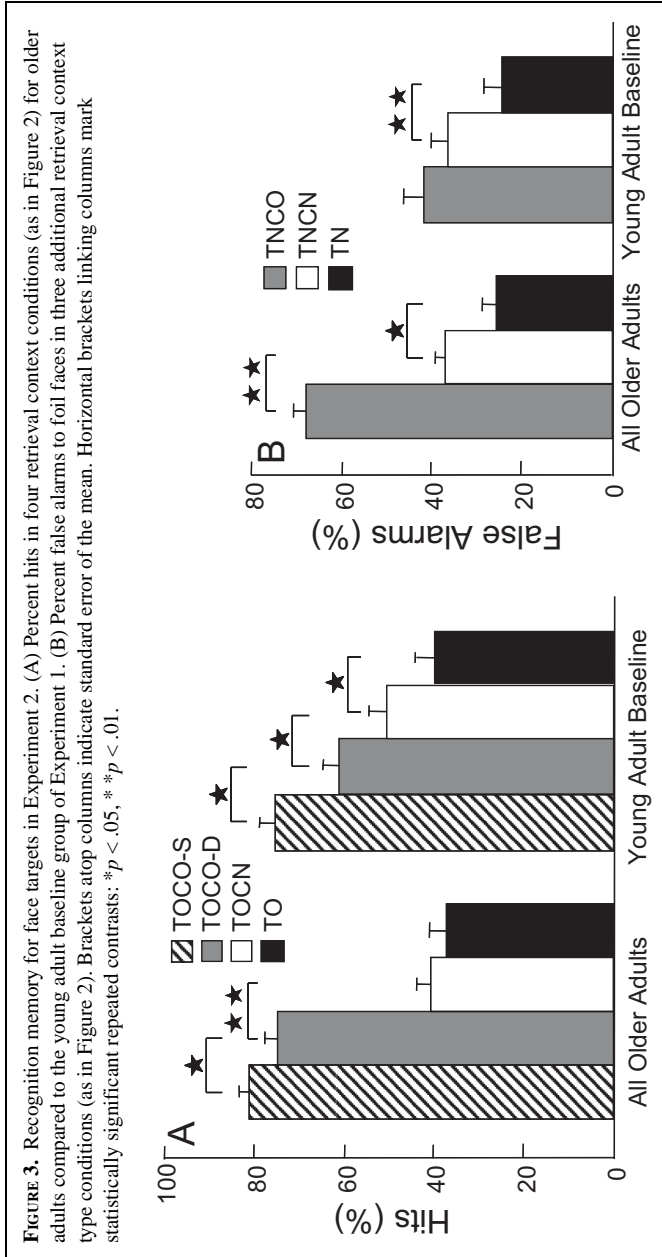
<i>FL Factor weighting</i>	
Wisconsin Card Sorting Test	0.425
Backward Digit Span	0.564
A verbal fluency (FAS) test	0.560
Mental Arithmetic	0.594
Mental Control	0.630
<i>MTL Factor weighting</i>	
Logical Memory I	0.536
Visual Paired Associates II	0.493
Verbal Paired Associates I	0.732
CVLT Long-Delay Cued Recall	0.624

Factor scores for each participant were then calculated using those test weightings, as follows: participants' scores on each of the nine tests were transformed into z scores. These z -scores were weighted and averaged. We considered one resulting average z -score to represent a composite estimate of frontal lobe (FL) function and the other a composite estimate of medial temporal lobe (MTL) function. Using those factor scores, and in accordance with the procedure used by Glisky and colleagues (Davidson & Glisky, 2002; Glisky et al., 1995, 2001), we then divided the participants into high and low MTL functional groups ($n = 27$ each) as well as into high and low FL functional groups ($n = 27$ each). Some overlap in frontal and medial temporal lobe functionality is to be expected in healthy aging. The weighted mean Z -scores employed for frontal lobe function and medial temporal lobe functional categories show a correlation of $r(52) = .49, p < .001$ in this group.

Results

Our initial examination focused on the older adult group as a whole relative to the young adult baseline group reported in Experiment 1. We compared group levels of CEs on hits and false alarms (Figure 3a and 3b, respectively) for the various context types.

For hits, we conducted a mixed-design repeated measures ANOVA, with the within-subjects factor of Context (four levels: TOCO-S [Repeat], TOCO-D [Re-pair], TOCN [New], TO [None]), and between-subjects factor of Age (Old and Young). This revealed a significant main effect of Context, $F(3, 240) = 66.04, p < .01$, no effect of Age, $F(1, 80) = .194, p > .1$, and a significant interaction, $F(3, 240) = 4.89, p < .01$. Within-subjects contrasts indicated that the interaction was marginal in the Repeat vs. Re-pair comparison, $F(1, 80) = 3.26, p = .075$, significant in the Re-pair vs. New comparison, $F(1, 80) = 22.89, p < .01$, and not significant in the New vs. None comparison, $F(1, 80) = 1.21, p > .10$. In other words, the differences between the



younger and older adults are primarily in the stronger impact of old contextual stimuli on endorsement of probes by the older adults, along with some loss in older adults of specific binding effects of old contextual stimuli accompanying their original pair members.

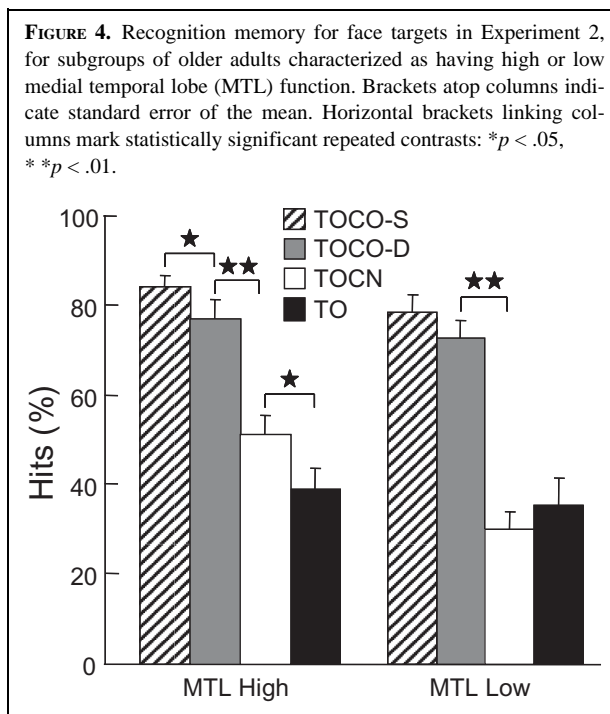
To further characterize the pattern of performance of older adults, we conducted a one-way repeated measures ANOVA and repeated contrasts comparing hit rates in the four context conditions. This confirmed the significant effect of Context, $F(3, 159) = 63.39, p < .01$, and revealed a significant difference between Repeat and Re-pair conditions, $F(1, 53) = 6.37, p < .05$, and between Re-pair and New conditions, $F(1, 53) = 63.92, p < .01$; the difference between New and None conditions was not significant, $F(1, 53) = 0.68, p > .1$.

The unexpected finding that overall hit rates did not differ between younger and older adults (i.e., no main effect of Age) may be a result of older adults' general tendency to more readily endorse probes as old when accompanied by old contextual stimuli. This may be seen in the false alarm rates (Figure 3b), which we examined with a mixed-design repeated measures ANOVA with the three context types (TNCO, TNCN, TN) as the within-subjects factor, and Age (Old and Young) as the between-subjects factor. We found a significant main effect of Context, $F(2, 160) = 58.03, p < .01$, a significant main effect of Age, $F(1, 80) = 7.20, p < .01$, and a significant interaction, $F(2, 160) = 13.49, p < .01$. Within-subjects contrasts indicated that the interaction was significant in the TNCO vs. TNCN comparison, $F(1, 80) = 20.74, p < .01$, and not significant in the TNCN vs. TN comparison, $F(1, 80) = 0.04, p > .1$. This indicates that the older adults had a strong bias towards endorsing foil probes especially when accompanied by old contextual stimuli (26% higher false alarm rate than young adults), which might explain their relatively high hit rate for the Repeat and Re-pair categories. We completed the characterization of the older adults group by conducting a one-way repeated measures ANOVA and repeated contrasts comparing the false alarm rates in the three context conditions. This confirmed the significant effect of Context, $F(2, 106) = 83.94, p < .01$, and revealed significant differences between both TNCO and TNCN conditions, $F(1, 53) = 82.45, p < .01$, and between TNCN and TN conditions, $F(1, 53) = 14.38, p < .01$.

In direct memory for contextual stimuli, the younger adults' correct recognition rate of 80.6% was significantly greater than older adults correct recognition rate of 61.5%, $F(1, 79) = 12.38, p < .01$ (data was missing for one young adult participant).

We then examined whether there would be differences in CEs within the older adults group based on level of medial temporal lobe (MTL) or frontal lobe (FL) function. We conducted mixed-design repeated measures ANOVAs, with the within-subjects factor of Context (four levels: TOCO-S [Repeat], TOCO-D [Re-pair], TOCN [New], TO [None]), and between-subjects factor of function Group (high and low, separately for MTL and FL function).

For the MTL groups comparison, there was a significant main effect of Context, $F(3, 156) = 64.83, p < .01$, a significant main effect of Group, $F(1, 52) = 5.83, p < .05$, and a marginal interaction, $F(3, 156) = 2.21, p = .089$. Because of the possible interaction, which was in consonance with our predictions, we examined the effect of Context for each group separately, using repeated measures ANOVAs. For the High MTL group (Figure 4), there was a main effect of context, $F(3, 78) = 27.10, p < .01$. Repeated contrasts revealed significant differences in hit rates between TOCO-S [Repeat] and TOCO-D [Re-pair] conditions, $F(1, 26) = 4.28, p < .05$, between TOCO-D [Re-pair] and TOCN [New] conditions, $F(1, 26) = 15.10, p < .01$, and between TOCN [New] and TO [None] conditions, $F(1, 26) = 6.03, p < .05$. In contrast, for the Low MTL group, while there was a significant main effect of Context, $F(3, 78) = 40.56, p < .01$, hit rates in the TOCO-S [Repeat] and TOCO-D [Re-pair] conditions did not differ significantly, $F(1, 26) = 2.30, p > .1$. Only the difference between TOCO-D [Re-pair] and TOCN [New] conditions was significant, $F(1, 26) = 72.44, p < .01$; the difference between TOCN [New] and TO [None] conditions was not significant, $F(1, 26) = 0.85, p > .1$. High and Low MTL function groups did not differ significantly in direct recognition of contextual stimuli, $F(1, 52) = 0.31, p > .1$.



In contrast, for the FL groups comparison, mixed-design repeated measures ANOVA yielded a significant main effect of Context, $F(3, 156) = 62.65$, $p < .01$, but no main effect of Group, $F(1, 52) = 0.41$, $p > .1$, and no interaction, $F(3, 156) = 0.38$, $p > .1$. Similarly, High and Low FL function groups did not differ significantly in direct recognition of contextual stimuli, $F(1, 52) = 0.18$, $p > .1$.

Comparisons of False Alarm CEs between each of the two MTL and FL function groups yielded no group effects and no interactions, all p values $> .1$.

As in Experiment 1, to round out the characterization of the performance of the participant group divisions, we also examined overall memory accuracy as reflected by corrected hits, i.e., hits minus false alarms for parallel context conditions of targets and foils. Thus, we examined Repeat Hits minus TNCO foils, Re-pair Hits minus TNCO foils, New Context Hits minus TNCN foils, and No Context (None condition) Hits minus No Context foils. For the MTL axis, the mean corrected hit scores for Low MTL were: Repeat 9.1% (SEM 4.7%), Re-pair 3.2% (SEM 4.6%), New -4.4% (SEM 3.5%), None 8.5% (SEM 5.2%). For High MTL, the mean corrected hit scores were: Repeat 17.0% (SEM 4.7%), Re-pair 10.0% (SEM 4.6%), New 11.1% (SEM 3.5%), None 14.0% (SEM 5.2%). A mixed model repeated measures ANOVA revealed a trend towards effect of context condition, $F(3, 156) = 2.30$, $p = .08$, a significant effect of group, $F(1, 52) = 4.96$, $p < .05$, and no interaction, $F(3, 156) < 1.0$. For the FL axis, the mean corrected hit scores for Low FL were: Repeat 10.4% (SEM 4.7%), Re-pair 1.9% (SEM 4.5%), New 4.1% (SEM 3.8%), None 9.3% (SEM 5.2%). For High FL, the mean corrected hit scores were: Repeat 15.7% (SEM 4.7%), Re-pair 11.4% (SEM 4.5%), New 2.6% (SEM 3.8%), None 13.1% (SEM 5.2%). A mixed model repeated measures ANOVA revealed a trend towards effect of context condition, $F(3, 156) = 2.30$, $p = .08$, no effect of group, $F(1, 52) = 1.01$, $p > .3$, and no interaction, $F(3, 156) < 1.0$. Thus, in terms of corrected hits as well as basic hit rates, the MTL group distinction is more predictive of context-dependent memory strength than the FL group division.

Discussion

As anticipated, in this experiment older adults with low medial temporal lobe function exhibited reduced target-context binding effects (i.e., the difference between CE caused by same [Repeat/TOCO-S condition] and different old contexts [Re-pair/TOCO-D condition]). In contrast, in older adults with higher medial temporal lobe based function, target-context binding context effects were extant, showing a profile comparable to young adults (Figure 4). However, the level of frontal lobe-based function had no impact on target-context binding effects. Furthermore, it is instructive that all older adults showed CE effects based on additive familiarity (i.e., Re-pair/TOCO-D vs. TOCN), as well as increased false alarms for TNCO vs. TNCN,

despite older adults' direct context memory scores being significantly lower than those of younger participants. The results of this experiment are in consonance with earlier findings (Naveh-Benjamin & Craik, 1995; Vakil et al., 1996b), that older adults may benefit from context reinstatement even when impaired in direct memory for context stimuli. The current results extend those earlier findings, in that we here see that a subset of older adults identified as having lower levels of medial temporal lobe function may be impaired specifically in binding-based context reinstatement effects.

An additional expression of age differences regarding context effects is the greatly increased false alarm rate for all older adult groups, which in this case was limited to the TNCO condition. The older adults seemingly found it difficult to ignore the additive familiarity contributed by the old contexts, leading them to incorrectly endorse a large percentage of foils accompanied by them. In contrast, in the absence of old context (TNCN and TN conditions), the older adults were not especially prone to false alarms. This finding may be related to reports that older adults are especially prone to memory errors when accuracy depends on specific recollections (Gallo, Cotel, Moore, & Schacter, 2007; Jacoby, 1999). Such 'recollect-to-reject' processes may be necessary to avoid false alarms induced by the presence of an old context, but not when a probe is presented alone. The present finding also accords with a recent report that older adults committed more false alarms than young adults when novel objects were presented in familiar but task-irrelevant contexts (Gutchess et al., 2007).

Contrary to our prediction, the global context effects of preserved presentation array (TOCN-New vs. TO-None) for hits depended not on level of FL function but on level of MTL function. Furthermore, all older adults exhibited significant preserved presentation array effects on false alarms (TNCN vs. TN). It is possible that the aspect of presentation array is differently processed by older adults; further studies are required to clarify this point.

It is instructive that the pattern of results initially seen in the analysis of the entire older adult group masked the profile of results revealed by comparing different subgroups. These findings emphasize the importance of examining subgroups of older adults when attempting to characterize the effects of aging on cognitive performance, especially in memory functions.

GENERAL DISCUSSION

In a pair of experiments, we addressed the question of the dependence of memory CEs on manifold processes – target-context binding, additive familiarity, and configural similarity – putatively associated with various brain areas. The findings of both experiments generally converge to suggest that while CEs may be modulated by medial temporal lobe function-related factors,

frontal lobe function-related factors do not seem to impact on CEs as they do on direct memory for source/context information.

The results reported here suggest a number of interesting functional dissociations. Impairment of medial temporal lobe-dependent processes, whether simulated by delay or identified in actuality by neuropsychological testing, led to a loss of binding-based contextual benefit to recognition. At the same time, CEs based on additive familiarity (benefit in Re-pair vs. TOCN and increased false alarms in TNCO vs. TNCN) remained intact under such impairments. The difference between intact additive and diminished binding-based benefits may be understood in the context of a current debate regarding the role of the hippocampus in single-item vs. associative recognition processes. Some researchers (e.g., Brown & Aggleton, 2001) have proposed that extrahippocampal medial temporal areas, such as the perirhinal cortex, subserve familiarity-based recognition processes for individual stimuli, and that the hippocampus is uniquely important in memory for configural (Rudy & Sutherland, 1995) or relational associations between stimuli (Eichenbaum & Cohen, 2001; see Squire et al., 2004, for an alternative view).

If what we have here described as impairment to medial temporal lobe function primarily reflects hippocampal processes, the divergence between binding- and additive familiarity-based CEs may be related to the proposed functional distinction within the medial temporal lobes. The additional contribution of the present study to this question lies in the fact that in the CE paradigm the effects of binding and additive familiarity are expressed indirectly, via the influence of the presence or absence of the contextual stimuli on the recognition judgment for targets or foils. Arguably, such effects may provide a 'purer' measure of associative memory strength than in paradigms where explicit associative judgments are rendered, in that the effect is automatic and not modulated by strategic processes (see below regarding frontal lobe contributions). This distinction reinforces our contention that CEs are reflective of a combination of cognitive processes that may be instantiated in various brain substrates. It should be remembered, though, that the characterizations of medial temporal lobe-based function presented in this study are based on behavioral indices, and are at best speculatively suggestive regarding brain integrity.

The findings of the current research do not provide insight into the neural basis of the CE yielded by global encoding-retrieval format similarity (the same presentation array) that characterizes the TOCN (New) and TNCN conditions compared to the TO (None) and TN conditions. In Experiment 1 the DivAttn group did not show that effect on hit rate (though it did impact on the parallel false alarm rate), implicating an FL aspect. Since that is the type of CE most structurally similar to standard source memory paradigms (in which one feature such as font color or speaker voice maps onto a large number of stimuli), that finding might be considered consonant with the

importance of frontal lobe processes for source memory. However, in Experiment 2, the level of older adults' FL function did not affect that effect on hit rates, which was instead modulated by level of MTL function (again, only on hit rates, while all older adults exhibited the effect on false alarms). Further research may better identify the brain substrates of processes that track and are influenced by such global contextual effects.

Employing a paradigm comparable to the one we employed, Kan, Giovanello, Schnyer, Makris and Verfaellie (2007) describe the performance of amnesic patients with medial temporal lobe damage on an associative recognition task employing word pairs. In their study, a studied word (six study presentations for amnesic patients) was presented at test either with its studied pair, a word previously paired with another studied word, or an unstudied word, to be discriminated from new foils. Patients showed no difference between hit rates for memory probes presented together with their original studied pair word or together with a word studied with a different probe. Matched controls (who received a single study presentation) exhibited a higher hit rate for studied words presented with their accompanying study pair words than with other previously presented words. This finding is in consonance with our report of Repeat > Re-pair hit rate difference limited to high MTL factor older adults.

Dennis et al. (2008) examined the neural correlates of successful encoding of item and source memory information in older and younger adults. They report that successful encoding was accompanied by less activation of prefrontal cortices and the hippocampus in older adults than in younger participants. Because Dennis and colleagues employed different study-test delays for older and younger participants, and used a direct test of associative binding rather than context effects, it is difficult to compare results of their study with ours. It is interesting to consider, though, whether the weaker levels of encoding activation they report might be indicative of changes in functional integrity of those areas, which could lead to differential functional profiles between older adults of the type we have reported.

In an eye movement study of the viewing of studied face-scene pairings, Hannula, Ryan, Tranel, and Cohen (2007) found that in contrast to healthy participants, who exhibited disproportionate viewing of the face originally studied with the scene compared to other equally familiar faces in the test display, hippocampal amnesics did not. Thus, hippocampal damage may impair even indirect measures of relational binding between stimuli, which is in consonance with our findings about MTL-based function and CEs.

The current findings are also relevant to an understanding of the role of frontal lobe processes in source memory and CE. Recent neuroimaging studies suggest that various frontal lobe areas play a number of roles in direct source memory retrieval. These include: holding the source characteristics relevant to the task in working memory, classifying or selecting recollections, and

providing general anticipatory set before source memory retrieval (Dobbins & Han, 2006; Simons, Owen, Fletcher, & Burgess, 2005a; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005b). Notably, these are strategic functions external to the actual retrieval of context information. The current findings that neither binding-based nor additive familiarity-based CEs are affected by aging-related declines in frontal lobe-dependent processes or by divided attention, as well as earlier reports (Naveh-Benjamin & Craik, 1995; Vakil et al., 1994, 1996a, 1997) that indirect memory for context as expressed in CEs is not impaired by frontal lobe damage, support making a distinction between having access to source/contextual information and making direct conscious judgments regarding source information. The conclusions that can be drawn from the manipulations we employed must be tentative, as divided attention did not impair direct memory for contextual stimuli in this paradigm, nor was there an effect of low and high frontal lobe function in older adults on direct memory for context. We did not therefore observe the dissociation between direct and indirect memory for context observed in the study of neuropsychological patients (Vakil et al., 1994, 1996a, 1997). Possibly, the task was too easy due to the fact that the hats employed were very unique and distinguishable. In future studies it will be beneficial to make this task more difficult. Nevertheless, the findings reported here do hint to differences in frontal and medial temporal contributions to memory for context, which are expressed in indirect as well as in direct memory measures.

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