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Remembering things without context: Development matters

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Abstract

Spatial context supports memory retrieval in adults. To understand the development of these effects, context effects on object recognition were tested in neurotypical children ages 3 years to adulthood ($n = 3–6$ years = 34, $n = 10–16$ years = 32, $n = \text{college age} = 22$) and individuals with Down syndrome (DS) ages 10–29 years ($n = 21$). Participants engaged in an object recognition task; objects were presented in scenes and either remained in that same scene or were removed at test. In some groups (<4.5 years and with DS) context effects were present even though object recognition was poor. After 4.5 years, children demonstrated memory flexibility, while later in adolescence context effects reemerged, showing nonlinearity in the development of these effects.

Keywords

context; object recognition; development; hippocampus; medial temporal lobe; executive function; Down syndrome

Context provides a scaffold for memories, facilitating encoding and serving as a cue for retrieval. For example, stable visual-spatial contexts can facilitate successful object identification and episodic memory (Nadel, 2008; Hayes, Nadel, & Ryan, 2007; Tsivilis, Otten, & Rugg, 2001; Bar & Aminoff, 2003; Bar, 2004). Context-dependent memory effects have been demonstrated in infants (Rovee-Collier, Hayne, & Colombo, 2001; Mast, Fagen, Rovee-Collier & Sullivan, 1980), for verbal and visual material in adults (Smith & Vela, 2001), and in rodents (Dellu et al. 1997; Dix & Aggleton 1999). Hayes, Nadel, and Ryan (2007) reported decrements in recognition memory performance when objects were presented in backgrounds that differed from the original learning context (i.e., a visually rich, two-dimensional scene). In several studies, young adults showed 12–15% poorer recognition performance under multiple encoding and retrieval conditions (e.g., incidental vs. intentional encoding), leading the authors to suggest that the binding of objects to context was obligatory and automatic in adults.

Infants, too, appear to show context-dependent memory, as measured by deferred imitation paradigms, displaying poorer recall when event sequences are learned and tested in different environments (Hayne, Boniface, & Barr, 2000). Further, visual recognition memory for objects is impaired when a background color shifts between learning and test in young

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infants (Robinson & Pascalis, 2004). Some have assumed that context dependent responses in infants and adults reflect continuity in this behavior and its neural basis across development (Rovee-Collier & Giles, 2010; Richmond, Sowerby, Colombo & Hayne, 2004). Available brain data, however, raise serious questions about this position. The structures known to support context processing include the hippocampus and parahippocampal gyrus in the medial temporal lobe (Hayes, Nadel, & Ryan, 2007; Nadel, Willner, & Kurz, 1985; Aminoff, Kveraga & Bar, 2013), and recent evidence suggests protracted development of these regions. Critical pathways in the hippocampus continue to develop until at least 6 years of age (Jabès, Banta Lavenex, Amaral, & Lavenex, 2010). Other recent work suggests an extended course of development in the parahippocampal cortex, with refinement continuing through adulthood (Golarai et al., 2007). Despite substantial development in the neural structures supporting context, few developmental studies have examined context effects across a significant age-range.

An interesting and revealing exception is a set of studies utilizing the Visual Paired Comparison (VPC) procedure. Tests of VPC performance have shown that context modulates performance in both infants and adults (Robinson & Pascalis, 2004; Richmond, Sowerby, Colombo & Hayne, 2004), consistent with the idea that the processes underlying this effect are the same across development. However, recent evidence shows that while hippocampal damage disrupts VPC performance in adults, neonatal hippocampal lesions have no immediate impact on task performance (Zeamer, Heuer, & Bachevalier, 2010). These data suggest that the VPC task can be solved in more than one way, and call into question the idea that context effects in this task reflect the same mechanisms in infants and adults.

One possibility consistent with Zeamer et al. (2010) supposes that in infants and young children objects and contexts are processed in a unitized, and hence inflexible, manner that relies mostly on cortical representations of environmental stimuli. As medial temporal lobe systems mature and connections between MTL structures and other cortical networks strengthen, neural representations of objects in scenes become more relational, reflecting the processing of configurations of elements in the scenes made possible by involvement of the MTL. Both unitized and relational representations of objects in contexts could support the context effects that have been reported in the literature, but they would do so by invoking different processes and different underlying neural systems. If this is the case, we would expect the following to occur during the developmental course of context effects: 1) the presence of context effects may vary across different developmental periods as the source of these effects changes, and 2) context effects may be independent from episodic memory performance (i.e., are demonstrated across children with very different levels of memory performance) because they tap different neural systems. Alternatively, if context effects come online early and are mediated by the same neural system across development, there should be developmental constancy in these effects and consistent relations with episodic memory performance.

To explore these possibilities and to better understand context effects across development, we examined their developmental course using the “object-in-scene” paradigm described in Hayes et al. (2007). Study 1 tested children ages 10 years to young adulthood, a time period

during which development of the medial temporal lobe continues, including refinements in hippocampus and parahippocampal cortex (Golarai et al., 2007; Ghetti, DeMaster, Yonelinas, & Bunge, 2010; DeMaster, Pathman, & Ghetti, 2013). Protracted development of, and refinement in, the function of medial temporal lobe structures may alter context effects across this age range. Study 2 examined this context effect in young children, ages 3 to 6 years, a time period known to be important for the development of episodic memory, the function most closely associated with the medial temporal lobe (Yim, Dennis, & Sloutsky, 2013; Drummey & Newcombe, 2002; Sluzenski, Newcombe, & Kovacs, 2006; Rajan, Cuevas, & Bell, 2013; Lavenex, & Lavenex, 2013). Finally, Study 3 tested this effect in a population with medial temporal lobe dysfunction: individuals with Down syndrome (DS). DS, a syndrome resulting from the triplication of chromosome 21, has been consistently linked to deficits on hippocampal-dependent tasks of explicit memory (Pennington, Moon, Edgin, Stedron & Nadel, 2003). Neurologically, this population shows reductions in hippocampal volume (Pinter et al., 2001), and recently, differences in hippocampal myelination, particularly in the dentate gyrus, have been reported (Ábrahám et al., 2012). Mouse models of DS exhibit a phenotype consistent with hippocampal impairment, including disruptions in neurogenesis in the dentate gyrus and impaired long-term potentiation (Rueda et al., 2005; Siarey, Stoll, Rapoport, & Galdzicki, 1997). Thus, this group's performance on the object-in-scene task could illuminate any role played by the hippocampal formation in context effects. In total, this research aims to provide a comprehensive view of the development of context effects across two critical periods in typical development (i.e., the preschool years and adolescence), as well as the development of these effects in a population with known hippocampal impairment.

Study 1

Method

Participants—All experimental procedures were approved by the University of Arizona Institutional review board. The participants in Study 1 included older children and adolescents ranging from 10 to 16 years who were recruited through a variety of means, including contact with public parent organizations and the use of marketing lists (i.e., Experian and Craigslist). This group included 32 participants (17 females, 15 males; mean (SD) age, 12.88 (1.73) years). The mean (SD) KBIT-II IQ of the sample was 103.63 (13.92) (95% confidence interval 98.82–108.43), the sample included 13 (40.6%) non-Hispanic white children, 15 (46.9%) Hispanic children, and 4 (12.5%) children of other ethnicities, reflecting a sample largely representative of the average population IQ and demographic background of the Arizona region. Since the stimuli in the study were modified from those used in Hayes et al. (2007), an additional 22 undergraduate students (mean age = 19.68, 12 females, 10 males) were recruited for replication from the university of University of Arizona undergraduate participant study pool.

Materials—Using Adobe Photoshop Version 6.0, images of household objects were centered on a white background or in the forefront of a scene and edited to appear naturalistic (i.e., each object was placed carefully as to appear integrated in the scene). The stimuli fell into three experimental conditions (Figure 1):

1. SCENE.SCENE: the same object-scene conjunction was shown during encoding and recognition.
2. SCENE.WHITE: at encoding an object was displayed within a scene, and then displayed on a white background at recognition, thus constituting a context shift.
3. WHITE.WHITE: the same image of an object on a white background was shown during encoding and recognition. This condition served as a baseline measure of how children's memory for objects alone may change, regardless of context.

Object in scene test: Stimuli were individually presented with E-prime, each preceded by a fixation cross. At encoding, participants were specifically instructed to look at the objects and remember them. Set size varied as a function of age to limit floor and ceiling effects. The adolescents saw 20 stimuli in each of the three conditions. Adult participants saw 40 stimuli in each of the SCENE.SCENE and SCENE.WHITE conditions, and 20 in the WHITE.WHITE condition. All stimuli were presented for 3 sec, with a 2 sec ISI.

After 5 minutes delay, participants performed a recognition test. Participants pressed a green “□” button positioned in the keyboard to designate ‘yes’ responses (i.e., they saw the object before) and a red “X” button for ‘no’ responses. During the recognition phase, lure images were presented ($n = 20$ for SCENE and OBJECT lures). Across the studies in this report we present the results of absolute levels of performance (percentage correct or false alarms) across experimental conditions. The inclusion of lure objects also allowed for some analyses to be completed with a signal detection approach (i.e., d' prime discriminability index values that take into account response bias; Banks, 1970; Wixted, 2007). In line with previous investigations using this paradigm (Hayes et al., 2007), we analyzed absolute levels of performance and only examined d' prime values when false alarm rates differed across age-levels. While this test was administered as part of a larger neuropsychological battery in all three studies, we present only the results of this measure in Study 1.

IQ: The *Kaufman Brief Intelligence Test, Second Edition (KBIT-II)* is a standardized IQ scale (Kaufman & Kaufman 2004) that was administered to control for general cognitive function. The outcome measure of interest was the entire IQ standard score, which includes verbal and non-verbal subtests.

Results

We replicated the findings of Hayes et al. (2007) in undergraduate young adults with the current study's stimuli. Consistent with the results of that study, accuracy was significantly lower in the SCENE.WHITE condition (71.8%) than in the SCENE.SCENE (81.8%, paired samples test $t(21) = 3.20, p < 0.01$) condition, showing roughly the same amount of a “context shift” decrement as previous studies. False alarm rates did not differ between scenes and objects (object 5.0%, scene 7.7%, paired samples $t(21) = 1.37, p > 0.15$).

Results in the older children and adolescent group are presented in Table 1. In Table 1 the results are presented for younger (<13 years, $n = 17$) and older (≥ 13 years, $n = 15$) children separately. This grouping was set according to the median point for age in this sample (12.92 years), and is an age grouping corresponding to the age-ranges tested in recent

studies demonstrating developmental changes in memory during adolescence (Golarai et al., 2007; Ghetti, DeMaster, Yonelinas, & Bunge, 2010; DeMaster, Pathman, & Ghetti, 2013). There were no statistically significant differences in gender distribution (younger group: 52.9% male, older group: 46.0% male, $X^2(1, 32) = 0.54, p = 0.46$) or IQ (mean (SD) IQ young sample = 107.47 (13.93); mean (SD) IQ older sample = 99.27 (11.52), $F(1, 30) = 3.24, p = 0.08$) across age groups. However, given the marginal difference in IQ, we tested the Pearson correlation between IQ and each experimental condition. All r values were less than 0.20 and none reached significance ($p > 0.42$ for all).

First, using repeated measures ANOVA, we tested the interaction of age group and the main conditions of interest (SCENE. SCENE and SCENE. WHITE). There was a significant effect of condition, $F(1, 30) = 4.16, p = 0.05$ (mean (SD) SCENE. SCENE = 0.86 (0.11), mean (SD) SCENE.WHITE 0.81 (0.16), and a significant interaction of condition and age group, $F(1, 30) = 4.16, p = 0.05$. The between subjects effect of age did not reach significance $F(1, 30) = 1.42, p = 0.24$. Table 1 shows posthoc tests of the differences between conditions within each age-group, examined with paired samples t -tests, and age group differences on each individual condition using ANOVA. Starting with the older group (13 years), we find a pattern similar to the results reported in previous studies and replicated here with undergraduates. Specifically, accuracy was significantly lower in the SCENE.WHITE condition than in the SCENE.SCENE condition (paired samples $t(14) = -2.23, p = 0.04$). False alarm rates did not differ between scenes or objects (paired samples $t(14) = -1.23, p = 0.24$). Therefore, just as demonstrated in undergraduates, children older than 13 years show context effects on object recognition.

The pattern in younger children in this age range (10–13 years) is quite different. Unlike the robust effect found in Hayes et al. (2007), replicated here in young adults, and present in older children, the younger group showed no difference between the SCENE.WHITE condition and the SCENE.SCENE condition (paired samples $t(16) = 0.00, p = 1.00$). False alarm rates did not differ between scenes or objects (paired samples $t(16) = 1.43, p = 0.17$).

Table 1 also shows the differences across age groups for each task condition. Across age, there was no difference in recognition in the WHITE.WHITE condition or the SCENE.WHITE condition, but younger children performed more poorly on the SCENE.SCENE condition than older children ($p = 0.007$). Increasing expertise in encoding and retaining detailed spatial scenes may make possible the benefit of context on object recognition in older children and adults. The apparent absence of context effects between 10–13 years of age stands in contrast with previous literature showing context effects in infants. Study 2 examines context effects across another critical period for the development of episodic memory, ages 3 to 6 years. Will very young children also fail to show context effects on this paradigm or will we find results consistent with the previous literature? We assessed context effects on object recognition as well as performance on neuropsychological tasks that could help explain the underlying processes relating to any developmental transitions.

Study 2

Method

Participants—In study 2, we tested 43 participants aged 3 to 6 years, a critical period for the development of episodic memory. Participants were recruited through contact with public parent organizations, preschools, and the use of marketing lists (i.e., Experian and Craigslist). To eliminate biased responses (due to only responding to one button), we excluded participants with d' prime = 0 on the WHITE.WHITE condition, the condition with the strongest performance overall. A d' prime = 0 demonstrates no ability to discriminate between seen and unseen pictures. Nine participants were excluded, leaving a sample of 34 (15 female; 19 male) children ages 3–6 years (mean (SD) age = 4.72 (0.71)). Age groups were established with a median split (median = 4.58), at the middle point of the theoretically important transition period of 3 to 6 years ($n < 4.5$ years = 16; $n > 4.5$ years = 18). KBIT-II IQ did not significantly differ across the age groups (mean (SD) IQ young sample = 109.88 (9.40); mean (SD) IQ older sample = 110.35 (9.45), $F(1, 24) = 0.01$, $p = 0.91$). The total sample included 20 (58.8%) non-Hispanic white children, 7 Hispanic children (20.6%), and 7 (20.6%) children of other ethnicities. The d' prime exclusions were not statistically more likely to occur in the younger vs. older sample (27.3% younger vs. 14.3% older, $X^2(1, 43) = 1.10$, $p = 0.30$). Finally, there was no difference in gender distribution across age groups (younger group: 68.8% male, older group: 44.4% male, $X^2(1, 34) = 2.03$, $p = 0.15$).

Materials—The materials were the same as Study 1. However, the number of stimuli was reduced in each condition to limit floor effects. In this younger sample, 15 pictures were used in each condition; these were randomly presented for 3 sec with a 2 sec ISI. During the recognition phase, each stimulus shown at encoding and 20 scene and object lures were presented. Participants completed a customized battery of neuropsychological measures (Edgin et al., 2010), including:

IQ and vocabulary knowledge: The materials and the procedure were the same as Study 1. In study 2 we focused on the subtest “verbal knowledge”, a measure of receptive vocabulary. The outcome measure of interest was the raw score on this subtest. KBIT-II raw scores were also used to determine the IQ and mental age (MA) matches of children in study 2 and 3.

Spatial paired associates: The CANTAB Paired-Associates Learning (PAL) task assesses the learning of associations between non-verbalizable stimuli (patterns) and the location where each pattern appears within a circular spatial array on a touch-screen computer. The participant is asked to remember the spatial location associated with each pattern and to touch that place in response to the presentation of the pattern (1–8 patterns are displayed per trial). This task has a recollective component, requiring memory for the originally presented spatial location, and impairments on it are an early indicator of Alzheimer’s disease (Swainson et al., 2001). Based on functional neuroimaging data in adults the hippocampus is activated during both acquisition and retrieval on this task (de Rover et al., 2011). The outcome measure from this task is the mean errors to success.

Inhibitory control and working memory: The Modified DOTS task (Davidson, Amso, Anderson, & Diamond, 2006) is a measure of inhibitory control and working memory involving three phases: 1) in the congruent location phase, participants press a box on a touch screen directly under a presented stimulus (i.e., a cat); 2) in the incongruent location phase (e.g., measure of inhibitory control), participants press a box in spatial conflict with the presented stimulus (i.e., across the screen, as cued by a frog), and 3) a combined phase (e.g., measure of working memory) for which the rules alternate randomly. The measures of interest are the percentage of correct responses for each phase.

Results

Using repeated measures ANOVA we tested the interaction of age group and the main conditions of interest (SCENE.SCENE and SCENE.WHITE). There was a significant effect of condition, $F(1, 32) = 12.91, p = 0.001$ (mean (SD) SCENE.SCENE = 0.78 (0.15), SCENE.WHITE 0.71 (0.18), and a significant interaction of condition and age group, $F(1, 32) = 4.03, p = 0.05$. The overall effect of age did not reach significance, $F(1, 32) = 0.01, p = 0.91$. Table 2 shows posthoc tests of the differences between conditions in each age-group using paired samples t-test and age group differences on each individual condition in this young child sample using ANOVA. The youngest sample of children (< 4.5 years) did show a benefit of context on object recognition, with significantly lower accuracy in the SCENE.WHITE condition relative to the SCENE.SCENE condition ($t(15) = -3.80, p = 0.002$). While false alarm rates were quite high, they did not differ between scenes or objects ($t(15) = 0.99, p = 0.34$).

Reflecting the significant condition by age group interaction, children > 4.5 years did not show a benefit of context on object recognition, with no difference in accuracy between the SCENE.WHITE condition relative to the SCENE.SCENE condition ($t(17) = -1.17, p = 0.26$). False alarm rates did not differ between scenes and objects ($t(17) = -0.05, p = 0.97$). While the benefit of maintaining the learning context was apparent in the youngest children, older children (>4.5 years to 13 years (from Study 1)) did not show this pattern.

Though younger and older children did not differ in hit rates across any condition, false alarms, for both object and scene stimuli, were less in the older children (Object FA $p = 0.04$; Scene FA $p = 0.05$). In order to compare age-related changes in performance across the conditions we calculated d'prime values, which adjust for age differences in false alarms and response bias, and tested the relation between d'prime values and age group using ANOVA. Across age, d'prime values for the SCENE.WHITE condition improved significantly, suggesting older children were better able to detect objects that had been removed from their scene context (M (SEM) d'prime older: 1.43 (0.13), M (SEM) d'prime younger: 0.98 (0.15), ($F(1, 32) = 5.16, p = 0.03$). D'prime values for the other conditions did not significantly differ across ages ($F(1,32) < 2.00, p > 0.15$ for both).

Older children become better able to recognize objects on their own and at the same time seem to lose their sensitivity to context shifts. This increasing ability to remember objects separate from contexts could relate to a number of cognitive processes, including associative memory, object labeling (i.e., deeper conceptual processing), or executive functions (i.e. the ability to examine the items in memory with flexibility or inhibit the background and focus

solely on the object). To assess some of the cognitive components that might drive better detection of objects removed from context, we examined the relation between d' prime values for the SCENE.OBJECT condition and scores on the tests of vocabulary knowledge, inhibitory control, working memory, and the paired associates learning measure. Age was also entered into the model to control for associations solely driven by age-related change. With linear regression, the model ($F(5, 28) = 6.32, p < 0.001, r^2 = 0.53$) had one statistically significant predictor - the CANTAB PAL mean errors to success ($\beta = -0.35, p = 0.04$), suggesting that as children were better able to recognize the object removed from context they were also less likely to make errors on the paired associates task. All other variables, including the executive measures and vocabulary, did not contribute significantly to the model. As children across this age-range lose context dependent effects their memory improves dramatically. Objects that appear separate from their original encoding context are better remembered, and there is a large reduction in false alarms. Better memory for removed objects is related to performance on the CANTAB PAL, a measure requiring the recollection of an object's association with a spatial location. In total, these results seem to suggest that the importance of context for object recognition follows a u-shaped developmental trajectory - present in the youngest children, disappearing in the school years, and appearing again in older adolescents and adults.

In Study 3, we tested the presence of context dependent effects in a population with known hippocampal dysfunction, DS. The hippocampus plays a central role in supporting configural representations of spatial context (Nadel, 2008), suggesting that developmental changes in context effects could be altered in populations with hippocampal dysfunction. Given the pattern in Study 2, we expected that children with DS would demonstrate poor episodic memory but would also show the context effects, a finding that would highlight the differences in the source of context-dependent memory effects across age and in individuals with memory disorders.

Study 3

Method

Participants—The participants in Study 3 included 25 individuals with DS ranging from 10 to 29 years. After excluding 4 participants who demonstrated d' prime = 0 on the WHITE.WHITE condition, the final sample consisted of 21 individuals (9 males, 12 females; mean (SD) age, 16.96 (5.33) years). All had IQ scores in the range of intellectual disability ($IQ < 70$), with an average IQ score of 45.05 (SD: 6.00, 95% CI 42.32–47.78). This sample included 14 (66.7%) non-Hispanic white children, 5 Hispanic children (23.8%), and 2 (9.5%) children of other ethnicities. Three of the participants were aged above 25 years, an age period associated with greater risk for Alzheimer's disease in this group. However, no parent showed concerns regarding dementia in their children, and none of these subjects met diagnostic cut-offs for dementia on a well known questionnaire assessment for the condition, the dementia scale for intellectual disability (DMR (Evenhuis, 1999); findings were not reported in detail here because it was used as a screening tool only for older participants. To put some findings in context, we compare the performance in the group of individuals with DS to the sample collected in Study 2 on episodic recall on the paired

associates measure (CANTAB PAL). The groups had equivalent raw scores on the total KBIT-II verbal scale (DS $M(SD) = 30.14 (13.21)$, 95% CI 24.49–35.79; typical $M(SD) = 31.26 (9.29)$, 95% CI 28.14–34.38, $t(53) = -0.37$, $p = 0.71$, Cohen's $d = -0.09$) and nonverbal scale (DS $M(SD) = 14.43 (3.26)$, 95% CI 13.04–15.82; typical $M(SD) = 14.47 (5.85)$, 95% CI 12.5–16.44, $t(53) = -0.03$, $p = 0.98$, Cohen's $d = -0.02$). To examine the processes that may change across higher and lower functioning individuals with DS or with age, we split the sample into participants with mental age equivalents on the KBIT-II that were above or below the median nonverbal mental age of the entire sample (4.8 years), and by a median split in age (15.67 years).

Materials—The materials and the procedure were the same as Study 2.

Results

Table 3 shows the performance on the CANTAB PAL in the group with DS as compared to the typically developing sample from Study 2. The group was significantly impaired on this measure in comparison to the MA matched children (independent samples $t(52) = 2.83$, $p = 0.007$). These data replicate a number of other studies in showing that individuals with DS have difficulty remembering abstract objects in specific locations, a marker of hippocampal impairment.

However, as shown in Table 3, individuals with DS did show context effects in both MA level samples (greater than ($n = 9$) and less than 4.8 years ($n = 12$)). Using repeated measures ANOVA we tested the interaction of mental age group and the main conditions of interest (SCENE. SCENE and SCENE. WHITE), showing a clear difference between experimental conditions, reflecting a decreased in performance after the context shift ($F(1,19) = 11.46$, $p = 0.003$). However, there was no interaction of MA level and condition ($F(1,19) = 0.15$, $p = 0.71$), and no effect of MA ($F(1,19) = 0.008$, $p = 0.93$). Examining differences in chronological age, we used repeated measures ANOVA to test the interaction of age group (< 15.67 years ($n = 11$) and > 15.67 years ($n = 10$)) and the SCENE.SCENE and SCENE. WHITE conditions. Again, there was a main effect of experimental condition ($F(1,19) = 11.82$, $p = 0.003$). However, there was no interaction of age level and condition ($F(1,19) = 0.59$, $p = 0.45$), and no main effect of age ($F(1,19) = 1.44$, $p = 0.25$). False alarm rates did not significantly differ between scenes and objects ($t(21) = 1.20$, $p = 0.25$). As shown in Table 3, higher MA related to better executive functioning ($p < 0.01$ for both working memory and inhibitory control) and vocabulary ($p = 0.05$), but the level of MA did not relate to context-dependent memory effects or the spatial paired associates measure ($p = 0.84$).

False alarms were numerous in both MA groups, and they did not differ across MA levels ($p > 0.10$ for both). In summary, individuals with DS show difficulties on a spatial paired associates measure and substantially impaired object recognition, with high false alarm rates. However, despite their impaired memory performance, they show clear context effects for object recognition.

Discussion

The results of this study suggest that the interaction of context with memory for objects changes during development in a non-linear fashion. Context effects were present in the youngest children, participants with atypical development (e.g., individuals with DS, who have medial temporal lobe impairment), older children, and adults. However, children between 4.5 and 6 years and 10–13 years of age showed no context effects. Other studies have shown similar transitions across development; Pattwell et al. (2011) showed reduced contextual fear responses in adolescent compared to adult mice. In humans Robinson and Pascalis (2004) also reported a transition to flexible responding on a contextual VPC task at 18 and 24 months of age. The developmental discontinuity shown in the current study strongly suggests that the context effects we observe in our young participants and in adults reflect different underlying mechanisms. It also reminds us that we should not take surface similarity between behaviors at different ages as proof that these behaviors are mediated by the same processes across the life-span.

The continuity of memory function across development has been debated, with some suggesting the neural systems for memory are in place early in development (Rovee-Collier & Giles, 2010), while others suggest a protracted developmental course (Nadel & Zola-Morgan, 1984; Moscovitch, 1984; Ribordy, Jabès, Banta Lavenex, & Lavenex, 2013). In the latter view, multiple systems support memory and these systems may have distinct developmental trajectories. One interesting possibility builds on the notion that the brain pathways leading to explicit memory, largely within the temporal lobe, comprise a hierarchy of representational systems, beginning with simple representations at the start of the so-called “ventral stream” (Ungerleider & Mishkin, 1982), and building through ever more complicated representations of objects, scenes and episodes (Nadel & Peterson, 2013). Could context effects on object memory reflect the engagement of different representational levels in children and adults, reflecting a developmental progression across the entire hierarchy?

Some time ago, Nadel and Willner (1980) suggested that contextual effects would be mediated by different neural substrates as a function of the nature of the representations required, with hippocampus only in play when configural context representations are involved. The distinguishing feature of a configural representation is that it reflects the relations among a set of entities, while maintaining the individual identity of each entity. This feature provides the basis for the flexibility associated with hippocampal representations. Configural representations are to be contrasted with unitized representations, in which features are fused, rather than flexibly related to one another. Such unitized representations have been linked to the parahippocampal region as well as neocortical structures (Staresina & Divachi, 2010). Our results could well be explained by shifts in the kind of representations engaged during the encoding of our object-scene stimuli across developmental stages. Specifically, young children and those with DS may process objects in context in a unitized fashion, but after 4.5 years the hippocampus allows for the configural processing of objects in scenes.

Our data suggest there are three ‘stages’ to explain: (1) at the youngest ages we tested, and in the participants with DS, objects and scenes were likely bound together at encoding into a unitized representation, causing poorer memory when objects did not reappear in the original background scene; (2) sometime between 4–5 years of age, children develop the ability to remember items and scenes as separate, but associated. This ability conveys new found flexibility in the use of their memory representations (i.e., such as demonstrated on the paired associates measure); and (3) still later in development, there appears to be refinement in children’s ability to recognize scene-item pairs as previously viewed. This refinement allows for the reemergence of context effects in later adolescence; effects that are very reliably measured in adulthood in studies employing these same paradigms (Hayes et al., 2007).

The transition to more flexible use of memories in typically developing children likely reflects an increasing ability to represent items and context configurally. This transition observed around 4.5 years in the typically developing sample parallels the time course of late developing hippocampal circuits (Ribordy et al. 2013). Here, the pattern observed in the group with DS can help us to understand the transition between developmental stages. No matter the mental age of the individuals with DS, they showed context effects and high rates of false alarms, very much mirroring the pattern of results in our youngest group of children. These individuals never make the transition to flexible encodings, but they show robust context effects, presumably reflecting unitized object-scene representations that are not dependent on the hippocampus. It is informative that there are executive function and vocabulary differences between high and low functioning individuals with DS, but no shift to flexible learning across mental or chronological age (which is absent in all participants with DS) or differences in the PAL task. These facts taken together suggest that a functional hippocampus is necessary for memory flexibility on this task.

What accounts for the second transition we observed? Our results suggest that the re-emergence of context dependency in later development is related to better scene recognition per se. In older children the benefit of context seemed to relate to an increase in the ability to recognize repeated object-scene conjunctions. Essentially, children are becoming experts at retaining the details of these scenes, and this expertise allows for increased levels of performance in comparison to the condition in which the object is removed. These data parallel some other recent findings in the literature. In one example, Chai, Ofen, Jacobs, and Gabrieli (2010) examined recognition memory for scenes with high and low complexity, showing development through adulthood for scenes with high levels of complexity only. Differences in activation in the parahippocampal gyrus were found for high complexity scenes, and this activity was associated with retrieval success. Golarai and colleagues have also reported developmental change in the parahippocampal place area in late adolescence (Golarai et al., 2007). Volumes of the right fusiform gyrus and the left parahippocampal place area increased across age, as measured by an expansion of the activated region into the surrounding cortex. This increased volume correlated with better memory retention for scenes and faces.

These late developments in scene recognition differ from the developmental trajectory of memory for objects without background context. Golarai et al. (2007) also showed that

object recognition, independent of scene processing, developed earlier and was not related to changes in brain activation across this age-range. Our data also suggest little change when objects must be recognized on their own; late developing change was observed for scenes only. Thus, the ability to recognize complex item-context configurations appears to increase across age, and here it seems to account for the transition to context-dependent responding in later childhood.

Some study limitations should be noted. The findings in the current study stem from cross-sectional comparisons during important developmental transition periods. Ideally, longitudinal data would eliminate any cohort differences. However, we present data from broadly representative children and we show few differences in background variables (i.e., IQ and gender) across the age cut-offs. Also of note is the later development to flexible responding reported here, compared to that seen in other investigations (Robinson & Pascalis, 2004). The difference in the age-transition period presented in our youngest group may reflect the complexity of the task. Robinson and Pascalis (2004) assessed context effects with a single trial design and the ‘visual paired comparison’ task, which involves memory for highly distinctive stimuli. We used explicit recognition across 75 trials; this number of trials may cause a substantial cognitive load, and invoke the need for pattern separation among a number of similar stimuli and their contexts. This latter ability may require a more fully developed hippocampal circuit. Future work should vary the pattern separation demands of similar tasks to determine if such demands influence the emergence of memory flexibility.

In summary, the findings of the current investigation suggest that context-dependent memory effects, at least for object recognition, are not constant across age. Our findings suggest instead that context effects may be driven by different representations and processes in young children and individuals with DS, as compared to older children and adults. More work is needed to further characterize the nature and brain bases of these representations at these different age-points. Although we are far from a complete understanding of the ways context affects memory, one thing seems clear: behaviors that appear similar or the same in young children and adults need not be the same at all.

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Figure 1.
Object in Scene Task

Figure 2.
Spatial Paired Associates Performance in Participants With and Without Down Syndrome

Table 1

Mean Recognition Hit and False Alarm Rates (Standard Error) in Study 1 for Younger and Older Adolescent Typically Developing Children

Mean (SE) Measures	younger (<13 yr) (N = 17)	older (13 yr) (N = 15)	F^a	p
SCENE.SCENE correct	81.47 (0.03)	91.67 (0.02)*	8.51	0.007
WHITE.WHITE correct	87.94 (0.02)	85.33 (0.03)	0.41	0.53
SCENE.WHITE correct	81.47 (0.03)	80.67 (0.05)*	0.02	0.89
False alarms: Object	0.06 (0.004)	0.07 (0.01)	1.66	0.21
False alarms: Scene	0.07 (0.01)	0.06 (0.004)	0.78	0.39

* Only in older children (13 yr) did SCENE.SCENE differ from SCENE.WHITE ($t(14) = -2.23$, $p = 0.04$), with a significant condition by age-group interaction, $F(1, 30) = 4.16$, $p = 0.05$, suggesting that context dependent responses reliably found in young adults comes on line in adolescence.

^a: F values in Table 1 correspond to the test of age group differences for each condition.

Table 2

Mean Recognition Hit and False Alarm Rates (Standard Error) in Study 2 for Younger and Older Typically Developing Children: Preschool to Early School Age

Mean (SE) Measures	younger (< 4.5 yr) (N = 16)	older (>4.5 yr) (N = 18)	<i>F</i> ^a	<i>p</i>
SCENE.SCENE correct	81.88 (0.04)*	77.83 (0.04)	0.59	0.45
WHITE.WHITE correct	83.75 (0.04)	80.39 (0.05)	0.31	0.58
SCENE.WHITE correct	68.94 (0.04)*	74.17 (0.04)	0.73	0.40
False alarms: Object	25.00 (0.06)	12.44 (0.03)	4.87	0.04
False alarms: Scene	27.81 (0.07)	12.33 (0.02)	4.11	0.05

* Only in younger children <4.5 yr did SCENE.SCENE differ from SCENE.WHITE $t(15) = -3.80$, $p = 0.002$, with a significant condition by age-group interaction, $F(1, 32) = 4.03$, $p = 0.05$, and d' prime values showed increasing ability to remember objects in the SCENE.WHITE condition across 3 to 6 years ($p = 0.03$).

^a: F values in Table 2 correspond to the test of age group differences for each condition.

Table 3

Mean Recognition Hit and False Alarm Rates (Standard Error) and Neuropsychological Outcome in Study 3 for Children with Down syndrome across Mental Age

Mean (SE) Measures	DS (MA 4.8 yr) (N = 12)	DS (MA >4.8 yr) (N = 9)	F^a	p
Object recognition task				
SCENE.SCENE correct	76.33 (0.06)*	77.00 (0.07)*	0.005	0.95
WHITE.WHITE correct	73.17 (0.04)	69.67 (0.07)	0.21	0.65
SCENE.WHITE correct	65.25 (0.06)*	63.11(0.07)*	0.06	0.81
False alarms: Object	46.50 (0.08)	26.89 (0.07)	2.94	0.10
False alarms: Scene	49.83 (0.09)	32.33 (0.08)	1.88	0.19
Neuropsychological measures				
CANTAB PAL mean errors to success	6.21 (0.83)	5.91 (1.21)	0.04	0.84
Inhibitory control proportion correct trials	55.36 (0.11)	92.63 (0.04)	9.03	0.008
Working memory proportion correct trials	49.23 (0.04)	74.03 (0.07)	9.70	0.006
Vocabulary raw score	14.67 (1.92)	21.78 (3.06)	4.24	0.05

* Results showed a significant main effect of condition in repeated measures ANOVA ($F(1,19) = 11.46$, $p = 0.003$), but no interaction.

^a: F values in Table 3 correspond to the test of age group differences for each condition.