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Testing the "Boundaries" of boundary extension: Anticipatory scene representation across development and disorder

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Abstract

Recent studies have suggested that *Boundary Extension* (BE), a scene construction error, may be linked to the function of the hippocampus. In this study, we tested BE in two groups with variations in hippocampal development and disorder: a typically developing sample ranging from preschool to adolescence and individuals with Down syndrome. We assessed BE across three different test modalities: drawing, visual recognition, and a 3D scene boundary reconstruction task. Despite confirmed fluctuations in memory function measured through a neuropsychological assessment, the results showed consistent BE in all groups across test modalities, confirming the near universal nature of BE. These results indicate that BE is an essential function driven by a complex set of processes, that occur even in the face of delayed memory development and hippocampal dysfunction in special populations.

KEYWORDS

down syndrome, memory development, hippocampus, prediction error, top-down influences

1 | INTRODUCTION

The visual system is constantly engaged in sensing the world: in our interaction with the environment, we can scan complex scenes and environments quickly and with little effort. Yet, due to saccadic eye movements, we process the world as a succession of distinct glances. How, then, does the brain construct a continuous representation of the space around us? When we explore the environment, the visual system intermittently scans scenes, and the brain expands on the fragmented visual information through top-down sources and predictions (e.g., Bar et al., 2006; Gilbert & Li, 2013; Nadel & Peterson, 2013). A striking example of this top-down influence is the *Boundary Extension* (BE) phenomenon, which occurs as a commission error in which observers remember seeing beyond the physical limits of a previously presented scene (Hubbard, Hutchinson, & Courtney, 2010; Intraub, 2010, 2012, 2014; Intraub, Bender & Mangels, 1992; Intraub, Gottesman & Bills, 1998; Intraub & Richardson, 1989).

By integrating top-down information with visual input, BE constitutes one of the mechanisms thought to be involved in combining discrete scene snapshots, making our interaction with the world a continuous and cohesive experience. Because this ability is such a fundamental aspect of our understanding of the environment, it is not surprising that developmental studies have demonstrated BE as early as three and four months of age (Quinn & Intraub, 2007). In fact, BE has been reported across the lifespan; for instance, Seamon, Schlegel, Hiester, Landau, and Blumenthal (2002) examined the developmental trajectory of BE from young children aged six years to older adults aged 84 years (6–7 years; 10–12 years; 18–21 years; 58–84 years) using a drawing test. On each trial participants studied a photograph for 15 s and then drew it from memory (see example in Figure 1). Across ages, all participants drew more background than was present in the original stimuli.

Despite providing a quantitative assessment of BE, the drawing task has several limitations, including the variability in drawing skills across age subgroups and between participants. To address this limitation, Kreindel and Intraub (2016) implemented a forced-choice recognition task to assess BE in young children aged 4–5 years, compared to adults. In this task, participants viewed a photograph of a scene for 15 s (Figure 2). The target photograph (either a close-up or wide-angle view) was then replaced with a pair of photographs including an

identical copy of the target photograph and a closer or wider view of the same scene. The participant was asked to select the one that matched the photograph previously presented. Both adults and young children made more errors on close-up trials (target photograph was a close-up view) than on wider-view trials (target photograph was a wide-angle view), erring by selecting photographs in which the object looked smaller and included more of the surrounding background than the target (see Figure 2 for more details). The BE asymmetry was present even in instances of increased spatial differences between the target and the test photograph (low-similarity). The recent results of Kreindel and Intraub (2016) helped to confirm that BE was present in young children using methods that control for the inherent measurement difficulties of drawing tasks, and further emphasized that BE occurs across a wide age-range.

Indeed, across the lifespan, through various modalities, and across populations, BE has been repeatedly observed (Chadwick, Mullally & Maguire, 2013; Chapman, Ropar, Mitchell, & Ackroyd, 2005; Czigler, Intraub, & Stefanics, 2013; Gottesman & Intraub, 1999; Hubbard et al., 2010; Intraub, 2002, 2010; Intraub, Bender, & Mangels, 1992; Intraub, Gottesman, & Bills, 1998; Intraub & Richardson, 1989; Park, Intraub, Yi, Widders, & Chun, 2007; Quinn & Intraub, 2007; Seamon et al., 2002). It has therefore been of great interest to find a group of adult patients who show attenuated BE. Mullally, Intraub, and Maguire (2012) found that amnesic patients with bilateral hippocampal damage (who in other tests, also exhibited impaired ability to imagine a spatially coherent scene), actually showed more veridical representations of scenes. This attenuation of prediction errors has been theoretically salient because these adults do not have damage to the lower or higher order visual systems, but display selective damage to the hippocampus (Clark & Maguire 2016; Mullally et al., 2012). These findings provide evidence suggesting that the hippocampus may be involved in formulating predictions that influence memory of visual scenes, and they intersect with an accumulating body of work showing interactions between the hippocampus and perceptual functions (e.g., Aly, Ranganath, & Yonelinas, 2013; Lee, Yeung, & Barense, 2012). Neuroimaging studies have provided further converging evidence for the involvement of the hippocampus and surrounding parahippocampal cortex in BE (Chadwick et al., 2013; Maguire, Intraub & Mullally, 2015; Maguire & Mullally, 2013; Park, Intraub, Yi, Widders, & Chun, 2007; although see Kim, Dede, Hopkins & Squire, 2015). Specifically, Chadwick et al. (2013) suggested that the hippocampus is responsible for the extrapolation of the scene beyond the stimulus view initiated when we first encounter a scene, a representation of the extended scene that is then processed within the visual and parahippocampal cortices, driven by a top-down process.

Based on the presence of BE across development, one might be tempted to assume that the continuity of this phenomenon also reflects continuity in the underlying neural support for predictive errors (i.e., implying that the hippocampus is online early and driving BE from 3 months of age). However, most current theoretical approaches to hippocampal development suggest a protracted trajectory, with infant memories being supported by cortical mechanisms and/or the earliest development of hippocampal subfields (Gómez & Edgin, 2015; Jabès & Nelson, 2014; Olson & Newcombe, 2014). Developmental neuroimaging studies and data from animal models show that the hippocampus has protracted development and might not be fully developed until late adolescence (Golarai et al., 2007; Krogsrud et al., 2014; Lee, Ekstrom, & Ghetti, 2014, although see Ofen Chai, Schuil, Whitfield-Gabrieli, and Gabrieli 2012 on the influence of frontal cortex), suggesting that young children, compared to adults, might be using different neural substrates or earliest developing subfields of the hippocampus for scene construction. There are also substantial behavioral shifts in episodic memory across development, with most data suggesting that long-term memory retention is not adult-like until seven years, with continued modifications through adolescence and well into adulthood, including increases in scene recognition and recall (Edgin, Spanò, Kawa, & Nadel, 2014; Golarai et al., 2007; Ofen, 2012). To date, only one study has reported BE in adolescents from 9 to 16 years (Chapman et al., 2005) using a "zoom task" in which participants could adjust the view to match the originally presented photograph. Therefore, in the current study, we aimed to expand on these previous investigations to determine if BE may fluctuate alongside known periods of hippocampal development (e.g., from preschool to adolescence) or in those with known hippocampal deficits (e.g., individuals with Down syndrome [DS]). We focused on the role of hippocampus in BE based on previous neuroimaging findings that demonstrated that the hippocampus is recruited during the generation of anticipatory scene structure, along with structures in the temporal and visual cortex (Chadwick, Mullally, & Maguire, 2013; Maguire, Intraub, & Mullally, 2015; Maguire & Mullally, 2013; Park et al., 2007).

In the present study we tested the development of BE in a sample of typically developing participants spanning four years of age to adolescence, using drawing tasks, the recognition test from Kreindel and Intraub (2016), and a more naturalistic boundary reconstruction task in three dimensions (Intraub, 2004; Intraub, Morelli, & Gagnier, 2015). We focused on the comparison between young children aged 4–7 years and adolescents aged 13–17 years, as these age groups are associated with substantial structural and functional changes in the hippocampus (Ghetti, DeMaster, Yonelinas, & Bunge, 2010; Lavenex & Banta Lavenex, 2013; Riggins, Geng, Blankenship, & Redcay, 2016). Given the extended development of the hippocampus, we would predict age-related changes in BE. Specifically, while we expected to replicate BE in young children across different test modalities found in Kreindel and Intraub (2016), it is possible that adolescents might show differences in the pattern and/or strength of BE. Consistent with Kreindel and Intraub's findings, we also expected to replicate BE in conditions of low-similarity between test items and the test photograph.

In this study, we also tested BE in individuals with DS (trisomy 21), a population with altered hippocampal development. Individuals with DS and representative animal models have been shown to display abnormal hippocampal functioning including delays in myelination (Ábrahám et al., 2012), altered neurogenesis, and impaired short and long-term plasticity in the dentate gyrus (Kleschevnikov et al., 2012; Witton et al., 2015). These dysfunctions at the microstructural level—accompanied by evidence of hippocampal volume reduction (Pinter, Eliez, Schmitt, Capone, & Reiss, 2001; White, Alkire, & Haier, 2003)—

are likely to contribute to the widely-observed phenotype in this population characterized by pervasive learning deficits in tasks tapping relational memory binding and allocentric navigation (Banta Lavenex et al., 2015; Edgin et al., 2010; Pennington, Moon, Edgin, Stredron, & Nadel, 2003). This phenotype has repeatedly been measured using a well-validated assessment of memory in this population, a spatial paired associates task (CANTAB Paired Associates learning; Edgin et al., 2010, 2014; Pennington et al., 2003; Spanò & Edgin, 2016; Visu-Petra, Benga, Tincas, & Miclea, 2007; van Hoogmoed, Nadel, Spanò, & Edgin, 2016).

Further, new work in the Tc1 mouse model, which is a direct model of the human condition given the insertion of a human chromosome 21, has suggested that these animals show impaired short-term plasticity (mossy fiber transmission tested via paired-pulse facilitation) in dentate gyrus-CA3 excitatory synapses, suggesting less developed input into the CA3 autoassociative network during short-term intervals of stimulation. Hippocampal differences in the Tc1 mouse related to memory deficits (Witton et al., 2015). Given this well-established profile of hippocampal dysfunction at both neurological and behavioral levels in this population (Banta Lavenex et al., 2015; Kleschevnikov et al., 2012; Witton et al., 2015), and evidence of attenuated BE in patients with hippocampal lesions (Maguire, Intraub, & Mullally, 2015; Mullally, Intraub, & Maguire, 2012), we hypothesized that individuals with DS may also demonstrate reduced BE compared to controls. Based on previous studies suggesting altered top-down influences of memory representations on implicit perceptual judgments in individuals with DS (Spanò, Peterson, Nadel, Rhoads, & Edgin, 2015), BE might be more attenuated for low similarity comparisons as individuals with DS cannot quickly access memory representations and may primarily rely on visual information.

We also expected to replicate deficits in a spatial paired associates learning task compared to controls (the CANTAB PAL); the paired associates test has repeatedly been shown to be impaired in DS and is often used as a valid behavioral marker of memory impairment in this group (Edgin et al., 2010, 2014; Spanò & Edgin, 2016). In total, comparisons across these two populations will add to our understanding of BE and its relation with hippocampal development.

2 | MATERIALS AND METHODS

2.1 | Participants

Twenty-eight typically developing children and adolescents from 4 to 17 years were recruited through a variety of means, including contact with public parent organizations, and the use of marketing lists (i.e., Experian and Craigslist). Participants were divided into two age subgroups to examine the developmental trajectory of BE: 14 young children ($M_{age}(SD) = 4.9$ (0.68); range = 4.08–6.50 years; 5 females) and 14 adolescents ($M_{age}(SD) = 14.6$ (1.3); range = 12.5–17 years; 7 females). IQ was not significantly different between the two groups ($t(26) = .9$, $p = .38$), nor was gender (X^2 (1, $N = 28$) = .58, $p = .35$). These age groups were chosen to represent periods in which we should see gains in hippocampal development. Prior to age seven, children show development in a number of memory functions, with imaging and neuroanatomical evidence to suggest that hippocampal CA fields are still undergoing change, and most studies have suggested greater maturity in the hippocampal response to memory recall after 14 years (Ghetti et al., 2010; Lavenex & Banta-Lavenex, 2013; Riggins et al., 2016).

In addition to these two age groups, we tested 14 participants with DS ranging in age from 11 to 24 years ($M_{age}(SD) = 18.2$ (4.4); 5 females), recruited through local and parent organizations and advertisement in Tucson and Phoenix areas. Exclusion criteria included the presence of mosaicism and autistic disorder diagnosis. We verified DS (trisomy 21) through karyotype report or medical records. The comparison sample included a group of 14 typically developing young children equivalent to the DS sample in mental age (MA, "MA-matched" controls). The MA group was drawn from young children in the typically developing group. Because DS is an intellectual disability, and there is a tendency for increased correlations between cognitive abilities in this group, the typical procedure for determining group effects is to match participants on scores from a standardized IQ test. In this study we matched participants based on their verbal raw score performance on the KBIT-II, an IQ measure often used in DS (e.g., Edgin et al. 2010; Spanò & Edgin, 2016). There were no significant differences between these two groups on their total verbal raw score on this standardized IQ assessment, the matching variable [$t(26) = -.45$, $p = .66$] (Table 1).

2.2 | Experimental measures

Three BE measures relying on different test modalities were employed in this study: a drawing paradigm, a visual recognition test, and a boundary reconstruction task. We also assessed object-location memory with a well-validated test of hippocampal function for the DS population (i.e., CANTAB Paired-Associates Learning; Edgin et al. 2010).

2.2.1 | Boundary extension measures

2.2.1.1 | Scene-memory drawing task

Participants were first presented with a sample photograph of two children on swings and were asked to describe the photograph and to use a finger to circle the entire photo (Kreindel & Intraub, 2016). If the participant did not correctly identify all the items included in the photograph, the participant was prompted to point all the items in the scene. Participants were then instructed to focus on the stimulus photograph, a basketball in a gym scene, for 15 s and take a mental picture of the photograph by pretending their eyes were like cameras. After 15 s the photograph was removed, and participants were presented with the same sheet with the empty square used in the object-drawing task and subsequently asked to draw from memory the original scene. The square of the answer sheet was identical to the frame of the basketball photograph. After completion, participants were asked to describe the items depicted in their drawings. BE was defined as reducing the area covered by the object and thus, including more of the surrounding background. Two outcome variables were used for this test: (a) the *proportion drawn*: the area of the object in the drawing divided by the area of the original object in the photograph (Intraub & Bodamer, 1993; Mullally et al., 2012; Seamon et al., 2002) and (b) the proportion of the

TABLE 1 Group comparisons on BE measures (Scene-memory Drawing, Recognition, and 3D Scene Memory Tasks) and neuropsychological outcomes (CANTAB PAL and KBIT-II)

	1 Adolescents (12.5–17 years)	2 Young Children (4.08–6.50 years)	3 Down Syndrome (11–24 years)	*T* [a] *(p)*	
				1 vs. 2	*2 vs. 3*
BE Measures					
Scene-memory Drawing Task: Proportion Drawn	0.52 (0.09)	0.51 (0.06)	0.31 (0.07)	−0.11(0.91)	−2.22 (0.04)
Recognition Task					
Proportion Errors on Close-up trials 13%	0.16 (0.05)	0.61 (0.06)	0.61 (0.07)	5.91 (<0.001)	0.00 (1.00)
Proportion errors on Wider-view trials 13%	0.05 (0.02)	0.26 (0.06)	0.36 (0.06)	3.49 (0.002)	1.10 (0.28)
Proportion Errors on Close-up trials 30%	0.08 (0.02)	0.53 (0.08)	0.59 (0.05)	5.3 (<0.001)	0.65 (0.52)
Proportion Errors on Wider-view trials 30%	0.01 (0.01)	0.14 (0.05)	0.26 (0.07)	2.21 (0.04)	1.33 (0.2)
3-D Scene Memory Task: Proportion of the Area Recreated	1.12 (0.03)	1.38 (0.14)	1.55 (0.20)	1.8 (0.095)	0.7(0.49)
Neuropsychological Measures					
CANTAB PAL: Mean Errors to Success	0.71 (0.16)	2.86 (0.46)	6.06 (0.59)	4.41 (<0.001)	4.27 (<0.001)
KBIT–II					
Verbal Raw Score	NA	32.07 (2.05)	30.36 (3.19)	NA	−0.45 (0.66)
Full IQ, Standardized Score	110.14 (3.23)	114 (2.79)	44.57 (1.45)	0.9 (0.38)	−22.68 (<0.001)

Standard Error is indicated in parenthesis. *T* values correspond to the test of group differences for each measure.

space covered by the drawn object calculated by dividing the area of the basketball drawn by the participant by the area of the empty square (see Figure 1). Drawings were digitized, and the number of pixels in the object were counted using Adobe Photoshop. Both variables were obtained by measuring the area in pixels.

2.2.1.2 | Object-drawing task

This test was included to control for possible differences in participants' use of space when simply drawing (without a memory load). Participants were presented with a sheet with a centered empty square outlined by black lines. The examinee was asked to indicate the edges of the square, and subsequently instructed to draw a "big, round happy face" within the square. The outcome variable used in this study was the proportion of the space covered by the drawn object calculated by dividing the area of the face drawn by the participant by the area of the empty square, both measured in pixels.

2.2.1.3 | Recognition task

To assess BE with a task less reliant on motor demands, a two-alternative forced-choice (2AFC) recognition test was used (Kreindel & Intraub, 2016). Compared to the drawing task, this test also allows for a rapid assessment of memory for visual scenes as the participant is asked to select the target immediately after presentation, whereas in the drawing task participant reproduces the scene as memory unfolds. In this test, participants were presented with a photograph of a scene for 15 seconds (the target). The target was then replaced with a pair of photographs, which included a copy of the target and either the closer-view or wider angle view of the scene. The participant was asked to select the photograph that matched the target (for more details see Kreindel & Intraub, 2016). A total of 40 trials were presented: on half of the trials the target photograph was the closer view ("close trials") and on the other half it was the wider-angle view ("wide trials"). Additionally, on half the trials we used a high similarity test pair (wider view showed 13% more of the scene than the closer view) and on half we used a low similarity test pair (wider view showed 30% more of the scene than the closer view). This variable was included to increase the chance that distractor selection would provide a sensitive enough forced choice to detect BE. In total, this test included three different versions of each scene: a close-up view and two wider-angle views (the high- and the low-similarity views). The position of the correct answer in the pair tests was also counterbalanced. Two counterbalancing orders were used (e.g.,

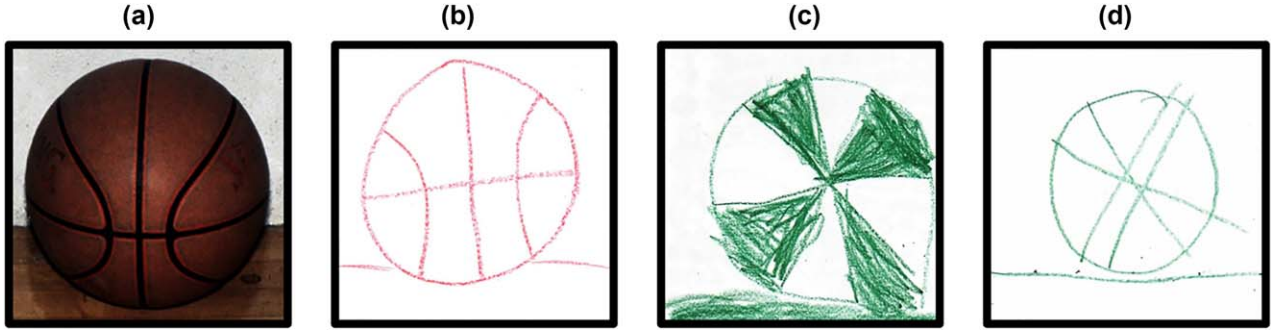

FIGURE 1 The target photograph (panel a), and examples of drawings representative of the three groups for the scene-memory drawing task: adolescents (panel b), young children (panel c), and individuals with DS (panel d) [Color figure can be viewed at wileyonlinelibrary.com]

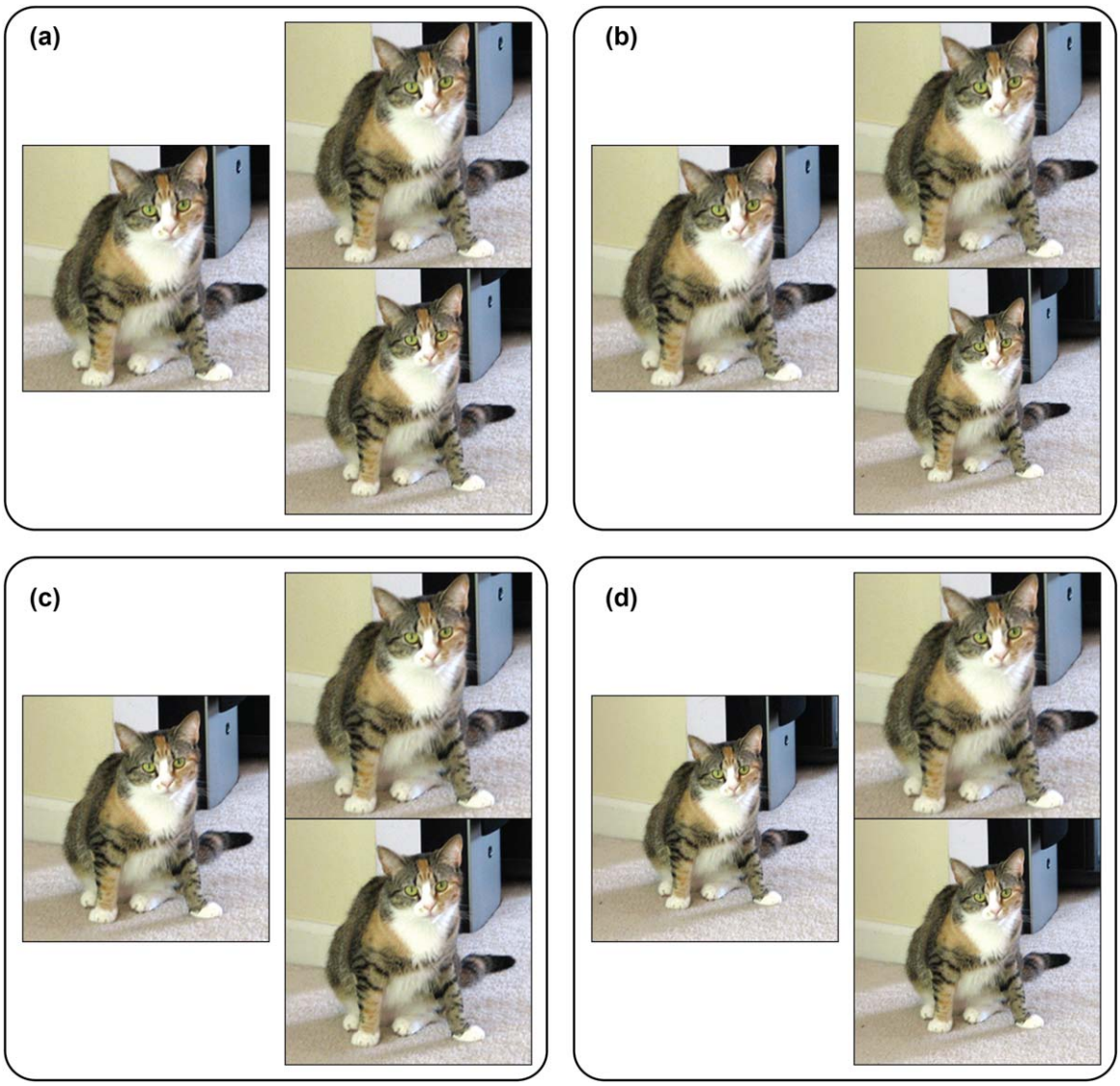

FIGURE 2 An example of the scenes in the recognition task. In this example, participants are presented with a close-up photograph of a cat inside a house for 15 s (close-up trial). The target object is then replaced with a pair of photographs which includes a copy of the original photograph and either a high-similarity photograph (the wider view shows only 13% more of the scene than the close-up, panel a) or a low-similarity photograph (the wider view shows 30% more of the scene than the close-up, Panel b). In the wide-angle trials, the target stimulus was a wide-angle photograph (either high-similarity [panel c] or low-similarity [panel d]) and the test pair included a copy of the same photograph and the close-up photograph. For display purposes, the close-up photograph in the figure is always shown on the top. The position of the target was counterbalanced [Color figure can be viewed at wileyonlinelibrary.com]

the close-up target in Order one became the wide-angle target in Order two and the wide-angle target in Order one became the close-up target in Order two).

Before proceeding to the 2AFC experiment, the examiner tested participants' perceptual ability to distinguish a closer from a wider view of the same scene and indicate the differences between two photographs—for example, the object looked smaller in the wider view. Participants then completed four practice trials for the 2AFC experiment, in which they were asked to select the photograph from a test pair that matched the target photograph after a 15 s exposure. If the participant did not select the correct matching photograph, the original photograph was presented again simultaneously with the test pair and the participant was, once again, asked to find the match for the target photograph. After the familiarization phase, participants were presented with the test stimuli. BE was defined as making more errors on close-up target trials (selecting the wider view at test) than on wider-view target trials (selecting the closer view at test). The outcome variables were the proportion of errors on wider-view target trials and close-up target trials for both high- and low-similarity conditions. Additionally, we calculated a *BE index* by subtracting errors on wide trials (selecting the closer view) from errors on close trials (selecting the wider view), divided by total errors.

2.2.1.4 | Guessing task

Following the protocol designed by Kreindel and Intraub (2016), our participants were also asked to complete the *guessing task* to test if BE

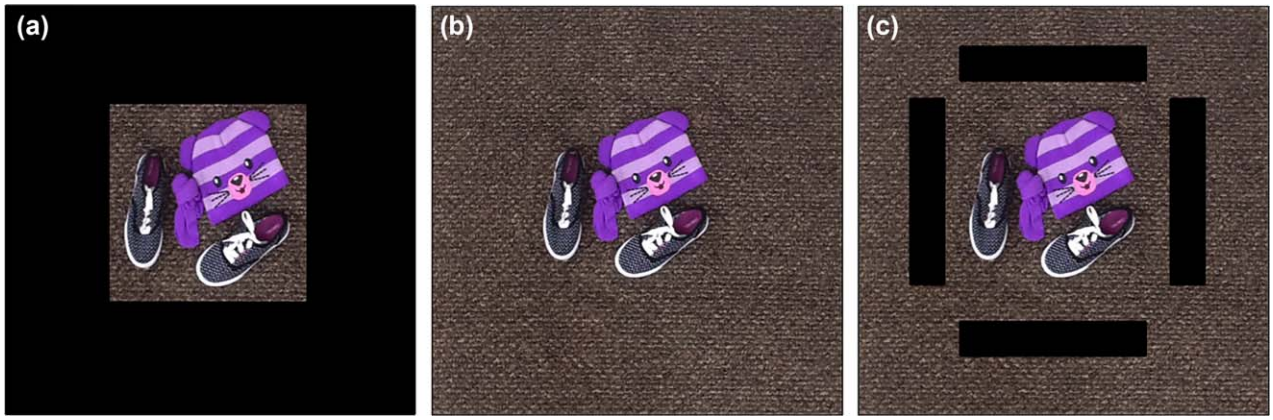

FIGURE 3 Protocol for the 3D scene memory task. (a) During the encoding phase, participants were presented with a scene within a window for 30 s and asked to remember the edges of the window (36" × 36"). After removal of the window (b), participants were asked to recreate the edges of the window from their memory with four wooden planks (c) [Color figure can be viewed at wileyonlinelibrary.com]

in the recognition task reflected a selection bias favoring the wider-angle view. Forty novel photographs were used to match a scene from the recognition task in terms of category and object size. The protocol was identical to the recognition task except that the target object was not shown and the participant had to guess, from a pair of photographs, which one the examiner was hiding.

2.2.1.5 | 3-D scene memory task

The reconstruction task was created in the Edgin laboratory based on a similar 3D exploration task (Intraub, 2004) (Figure 3). Participants were presented with a scene within a window and asked to remember the edges of the window. After 30 s, participants were asked to recreate the edges of the window from their memory with four wooden planks. A 36" × 36" window including a carpet layout with a hat, a pair of socks, and a pair of shoes was used. BE was defined by an increase in the reconstructed scene area relative to the original scene's window size. The outcome variables were (a) the area of the window created by the participant divided by the area of the original window (i.e., proportion of the area created) and (b) the proportion of the space covered by the window's area calculated by dividing the area of the window created by the participant by the area of the carpet (see Figure 3).

2.2.2 | Intelligence measure

2.2.2.1 | Kaufman brief intelligence test, second edition

The Kaufman brief intelligence test, second edition (KBIT-II) is a measure of verbal (i.e., verbal knowledge and riddles) and nonverbal (i.e., matrices) intelligence. The verbal scale includes two subtests: verbal knowledge, a vocabulary test in which children point to pictures matching words, and riddles, a test in which children respond to a question with one word. The nonverbal scale includes the subtest Matrices, which involve problem solving and understanding of relations. This instrument is suitable for individuals from 4 to 90 years old (Kaufman & Kaufman, 2004) and was used as a measure of general intelligence. Standard scores for the KBIT-II have a mean of 100, and a standard deviation of 15. The verbal scale raw scores were used to match individuals with DS and typically developing children.

2.2.3 | Memory measure

2.2.3.1 | CANTAB paired-associates learning

In this task, the participant was asked to learn associations between abstract visual patterns and hiding locations on a computer screen. Participants were first presented with six boxes, which opened up one at a time. A shape appeared in one of the boxes and the participant was asked to remember where the shape was hidden. After the presentation, the shape appeared in the middle of the screen and the examiner asked the participant to touch the box where the shape was hidden. Thus, this task required the subject to generate the spatial location associated with the stimulus. The task increased in difficulty from 1 to 8 shapes to be remembered.

Based on functional neuroimaging data in healthy adults and patients with mild cognitive impairment, the hippocampus is activated during both encoding and retrieval on this task (de Rover et al., 2011). CANTAB paired-associates learning (PAL) has been used as a benchmark measure for memory deficits in several patient groups. In individuals with DS, performance on this test demonstrates low levels of noncompletion, adequate test-retest reliability, and sensitivity to detect differences between individuals with DS and control participants without the confounding influence of deficits in language (Edgin et al., 2010, 2014; Pennington et al., 2003; Visu-Petra et al., 2007). Further, performance on this task has been shown to correlate with parent-reported memory skills and ERP assessments (Spanò & Edgin, 2016; van Hoogmoed, Nadel, Spanò, & Edgin, 2016). Given that this measure theoretically maps onto hippocampal function, we used this test as a benchmark of memory functions that might develop or are impaired in the groups in our investigation. We focused on mean errors to success as outcome measure.

2.3 | Procedures

Participants took part in a 1-hour testing session in a laboratory setting or in their home in a location with minimal distractions. Each participant completed the *object-drawing task* first and then the *scene-memory task*, followed by the *recognition task*, *the guessing task* and the *3-D scene memory task*. Lastly, each participant received the KBIT-II, a test

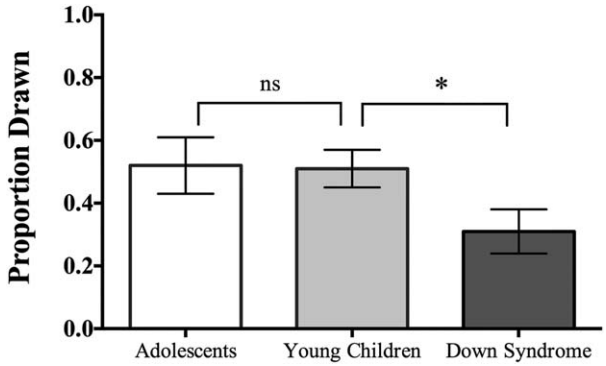

FIGURE 4 Mean proportion drawn for each age group in the scene-memory drawing task. Error bars show the 95 percent confidence intervals. In both comparisons, participants reduced the area covered by the object compared to the original picture and, as a result, included more of the surrounding background. The mean proportion was significantly reduced in individuals with DS compared to their controls, suggesting a greater BE in this task. N.B.: 1 corresponds to the size of the original object.

of general intellectual ability, and the CANTAB PAL, a task requiring the recollection of the association between a pattern and its specific location. Participants were compensated for their time. The University of Arizona Biomedical Institutional Review Board approved all study procedures.

3 | RESULTS

3.1 | Scene-memory drawing task

3.1.1 | Age-related differences

As shown in Figure 4, young children and adolescents reduced the area covered by the object compared to the original picture and included more of the surrounding background. To quantify the extent of BE, we compared the proportion of space filled by the object drawn by the participant in relation to the original object using one-sample *t* tests in both groups, separately. In younger children, the mean of the proportion of space filled by the drawn object ($M = 0.32$, $SD = 0.15$) was lower than the proportion of space filled by the original object (0.63), a statistically significant mean difference of 0.31, 95% CI [0.22–0.4], $t(13) = -7.7$, $p < .001$. The same pattern of results was found in the older group; the mean of the proportion of space filled by the object ($M = 0.33$, $SD = 0.2$) was lower than the proportion of space filled by the original object (0.63), which equated to a statistically significant mean difference of 0.30, 95% CI [0.18–0.42], $t(13) = -5.3$, $p < .001$. While both groups expanded the background when drawing, the *proportion drawn* was not statistically different between young children ($M = 0.51$, $SD = 0.24$) and adolescents ($M = 0.52$; $SD = 0.34$), $t(23.3) = -0.11$, $p = .91$.

3.1.2 | Comparisons with DS

Participants with DS showed similar results to their MA-matched controls: the mean of the proportion of space filled by the object ($M = 0.19$, $SD = 0.16$) was lower than the proportion of space filled by the original object (0.63), a statistically significant mean difference of 0.44, 95% CI [0.34–0.53], $t(13) = -10.1$, $p < .001$. Additionally, when we compared individuals with DS and MA group, the mean *proportion drawn* was significantly reduced in individuals with DS ($M = 0.31$, $SD = 0.07$) compared to their controls ($M = 0.51$; $SD = 0.24$), $t(26) = -2.22$, $p = .04$, suggesting greater BE in the DS group on this task.

3.2 | Object-drawing task

3.2.1 | Age-related differences

Young children and adolescents did not differ on the mean proportion of the space covered by the control object: young children ($M(SD) = 0.27$ (0.15)) and adolescents ($M(SD) = 0.37$ (0.25)); $t(21.2) = -1.22$, $p = .24$.

3.2.2 | Comparisons with DS

The mean proportion of the space covered by the control object was not different between participants with DS ($M(SD) = 0.23$ (0.20)) and their controls ($M(SD) = 0.27$ (0.15)); $t(23.7) = -0.7$, $p = .49$. Both comparisons indicate that participants drew objects of similar dimensions when not embedded in scenes.

3.3 | Recognition task

Group differences in the proportion of errors on close trials (trials on which the target was the closer view of the pair) and wide trials (trials on which the target was the wider view of the pair) were examined using a two-way repeated measures analysis of variance (ANOVA).

3.3.1 | Age-related differences

As shown in Figure 5, both younger children and adolescents show BE across high and low similarity conditions, making more errors on close trials (selecting the wider view) than on wide trials (selecting the closer view). A 2 (children vs. adolescents) × 2 (close trials vs. wide trials) × 2 (high-similarity vs. low-similarity) mixed measures ANOVA was conducted on the mean proportion of errors. The critical main effect of trial type (close trials vs. wide trials) was significant, $F(1, 26) = 17.82$, $p < .001$; participants erred more frequently on close trials (selecting the wider view) than on wide trials (selecting the closer view). More errors were made on high-similarity trials than on low-similarity trials, $F(1, 26) = 14.52$, $p = .001$, with no *similarity* × *age group* interaction, $F(1, 26) = 0.99$, $p = .33$, indicating that both groups were sensitive to the spatial differences between high- and low-similarity comparisons. While BE was observed in both groups, we found an interaction between the trial type and group, $F(1, 26) = 6.62$, $p = .02$, indicating reduced BE in adolescents compared to young children (see Figure 5). No significant three-way interaction was found (*age group* × *trial type* × *similarity*), $F(1, 26) = 1.26$, $p = .27$. Overall, young children made more errors than adolescents ($t(26) = -10.28$, $p < .001$). Together, these results provide evidence that both groups exhibited the pattern of error asymmetry defining BE. However, developmental differences

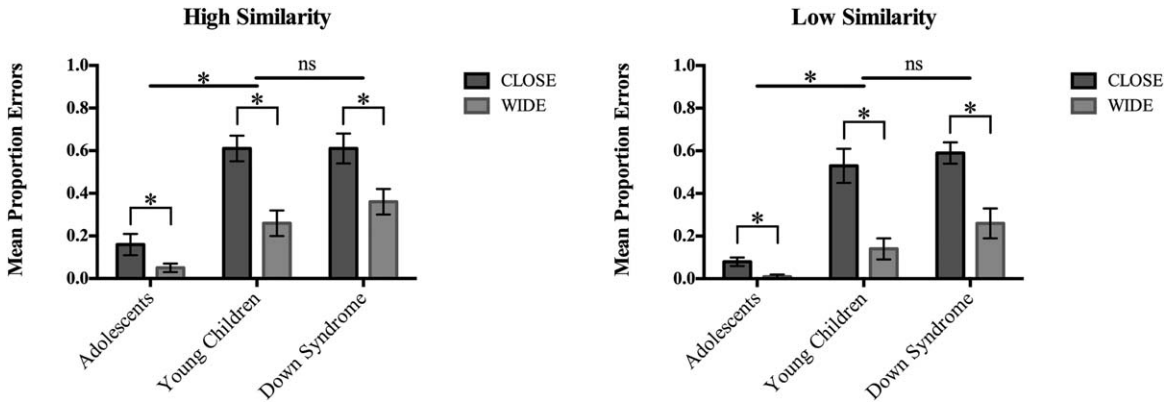

FIGURE 5 Mean proportion of errors on close trials (close-up was the target) and wide trials (wider-view was the target) in both conditions of similarity (high vs. low) for young children, adolescents and individuals with DS. Error bars show the 95 percent confidence interval around each mean. A greater proportion of errors on close trials indicates BE. * For the comparison between adolescents and young children, results showed a significant main effect of trial type and group × trials interaction in repeated measures ANOVA in both high- and low-similarity conditions. ns: In the DS-MA comparison, results showed a significant main effect of condition in both high- and low-similarity conditions, but no group × trials interactions. The MA group and young children in the typically developing group include the same individuals.

in the strength of the BE error were found, with greater BE in younger children than adolescents.

3.3.2 | Comparisons with DS

Participants with DS and the control group did not differ in the number of total errors on close ($p = .70$) or wide trials ($p = .20$) for both high and low similarity conditions, suggesting that participants with DS were not making more errors compared to controls. When we look at the proportion of errors (Table 1), both groups exhibited the same pattern of errors: a higher proportion of errors on close trials compared to wide trials. Similar to the previous group comparison, we performed a 2 X 2 X 2 mixed measures ANOVA, which revealed a main effect of the trial type, $F(1, 26) = 19.83$, $p < .001$. There was no interaction between the trial type and group, $F(1, 26) = 0.26$, $p = .62$, As shown in Figure 5, more errors were made on high-similarity trials than on low-similarity trials, $F(1, 26) = 8.30$, $p = .008$, with no similarity x group interaction, $F(1, 26) = 0.69$, $p = .41$. No significant three-way interaction was found (*group* × *trial type* × *similarity*), $F(1, 26) = 0.11$, $p = 0.74$. Thus, individuals with DS exhibited BE that was similar to that of MA-matched controls, and this effect was consistent across high and low similarity conditions (11/14 participants with DS presented BE in both conditions with 13% and 30% difference in zoom factor).

3.4 | Guessing task

3.4.1 | Age-related differences

When guessing, the wider view was selected by young children on 47% of the trials and by adolescents on 51% of the trials. A 2 (young children vs. adolescents) × 2 (close selections vs. wide selections) revealed that both groups selected wider and closer view equally when the participant was asked to guess which one the examiner was hiding, $F(1, 26) = 0.07$, $p = 0.79$, and that there was no *group x trial type* interaction, $F(1, 26) = 0.20$, $p = 0.66$.

3.4.2 | Comparisons with DS

The same analysis showed that individuals with DS and their MA-matched controls did not select wider view more often than closer view when guessing, $F(1, 26) = 0.52$, $p = 0.48$, and that there was no *group x trial type* interaction, $F(1, 26) = 1.67$, $p = 0.21$. Children with DS selected the wider view on 60% of the trials.

3.5 | 3-D scene memory task

3.5.1 | Age-related differences

In younger children, the proportion of space of the window created from memory ($M = 0.24$, $SD = 0.09$) was greater than that of the original window (0.17), a statistically significant mean difference of 0.07, 95% CI [0.14–0.12], $t(13) = 2.75$, $p = .016$. Similar results were found for adolescents: the proportion of the window's area created from memory ($M = 0.19$, $SD = 0.02$) was higher than that of the original window (0.17), a statistically significant mean difference of 0.02, 95% CI [0.01–0.03], $t(13) = 4.49$, $p = .001$. Additionally, we compared the proportion of the area created by the participant between the two groups by performing an independent *t* test. The proportion was calculated by dividing the area of the window created by the participant by the area of the original window. Results indicated that the groups were not different (Figure 6): younger children ($M = 1.38$ $SD = 0.53$) and adolescents ($M = 1.12$, $SD = 0.11$), $t(14.1) = 1.79$, $p = .10$.

3.5.2 | Comparisons with DS

Only 9 participants with DS completed this test. However, eight of the nine participants demonstrated BE. The proportion of space covered by the area of the window created from memory ($M = 0.27$, $SD = 0.10$) was greater than the original window (0.17), a statistically significant

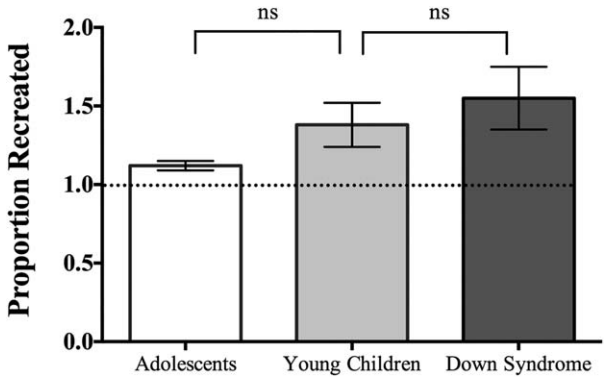

FIGURE 6 Mean proportion reconstructed for each group in the 3D scene memory task. Error bars show the 95 percent confidence intervals. In both comparisons, participants extended the boundaries of the window compared to the original window. No group differences emerged. N.B.: 1 corresponds to the size of the original window.

mean difference of 0.09, 95% CI [0.02–0.17], $t(8) = 2.7$, $p = .025$. When we compared the proportion of the areas between the participants with DS and the control group, no significant differences emerged between participants with DS ($M = 1.55$, $SD = 0.61$) and controls ($M = 1.38$, $SD = 0.53$), $t(21) = 0.70$, $p = .49$.

3.6 | Relation between BE and a paired associates memory task

3.6.1 | Age-related differences

To assess age-related differences in memory performance, we compared the performance of young children and adolescents on a behavioral measure of object-location memory (i.e., CANTAB PAL) by performing an independent samples *t* test. Results indicated significantly poorer performance, based on mean errors to succeed, in young children ($M = 2.86$, $SD = 1.72$) compared to the older group ($M = 0.71$, $SD = 0.61$), ($t(13.4) = 4.41$, $p < .001$). These results show expected shifts in memory function, with greater ability to recall the spatial location associated with an object cue, in adolescents. Additionally, we related performance on the CANTAB PAL to BE across different test modalities controlling for age. We used the following outcome variables: (a) BE index for the recognition task, (b) the proportion drawn for the drawing test, and (c) the proportion of the window created by the participant for the 3-D scene task. We found no statistically significant relation between mean errors to success on the PAL task and the three BE measures (BE index: $r(23) = -.02$, $p = .92$; proportion drawn: $r(25) = -.09$, $p = .65$; proportion created: $r(25) = .098$, $p = .63$).

3.6.2 | Comparisons with DS

Replicating a number of previous studies, we found that participants with DS made more errors ($M = 6.06$, $SD = 2.22$) on the PAL task compared to controls ($M = 2.86$, $SD = 1.72$), $t(26) = 4.27$, $p < .001$ (Table 1), demonstrating deficits in object-location binding. Despite impaired memory performance on this well-established behavioral indicator of memory in this population, individuals with DS show clear BE across several tasks. We also found a positive relation between paired associates memory errors and the BE index in DS ($r(14) = .61$, $p = .02$). These results show that reduced BE related to better performance on the object-location paired associates learning task. Performance on CANTAB PAL was not related to other BE outcome variables: proportion drawn: $r(14) = -.22$, $p = .45$ and proportion of space created: $r(9) = -.40$, $p = .29$).

4 | DISCUSSION

The current study examined BE across two populations with known variation in hippocampal function, including two separate developmental age groups (young children aged 4–7 years and adolescents aged 13–17 years) and a group of individuals with DS, an intellectual disability characterized by altered hippocampal development (Banta Lavenex et al., 2015; Edgin et al., 2010; Kleschevnikov et al., 2012; Pennington et al., 2003; Witton et al., 2015). The key finding is that in spite of well-replicated deficits in hippocampal development and function, individuals with DS exhibited robust BE as measured by three different paradigms (a forced-choice recognition test, a drawing task, and a 3D scene memory task). Like the typically developing populations tested, they automatically extrapolated the continuation of a scene beyond the boundaries of a given view. In line with our expectations, age-dependent changes in memory performance (i.e., CANTAB PAL) across typical development and specific memory deficits in the DS group were confirmed.

Our BE results replicate previous studies using similar paradigms. First, BE was consistently observed across test modalities in typically developing children and adolescents. In contrast to our predictions, individuals with DS demonstrated striking anticipatory representation across all the test modalities and showed greater BE on one out of the three tasks administered (i.e., the drawing task), compared to MA-matched controls. It is of interest that across groups, all participants exhibited BE on both high and low-similarity test conditions, indicating that BE was robust enough that even the low similarity test comparisons (a 30% difference in the spatial scope of test items) were sensitive to the error. A guessing control condition demonstrated that BE on the forced-choice task reflected a memory error, rather than a guessing bias. Converging evidence for BE was obtained in the drawing task (free recall) in which a drawing control demonstrated that differences observed could not be attributed to differences in drawing skill. Finally, BE was also observed in the 3D scene memory task, in which participants remembered boundary placement in real space.

The almost universal presence, but variability, in BE (as described in Maguire et al., 2015) may be the result of variation in an individual's ability to engage in various stages of processing associated with scene representation. These stages may reflect different mechanisms in the hippocampus as well as decision processes regarding the memory. BE has been often noted to reflect a two-stage process, including (a) the

mental construction of the scene and (b) a decision regarding the boundaries of the original image in which the participant must distinguish information that had been visually perceived from the constructed continuation of the view (Intraub, 2010, 2012; Intraub & Dickinson, 2008). Despite consistent observations of BE in the current study, we observed group differences in BE on some tasks, which can be explained by appealing to the second stage of this two-stage model.

First, in our typical development groups, young children exhibited greater BE than adolescents in the forced-choice recognition task. This is the first comparison across these age groups, and it is important to note that the observed difference mirrors that reported for typically-developing 4–5 year olds and young adults using the same task as Kreindel and Intraub (2016). They found that young children exhibited robust BE under conditions in which the adults did not (presentation of relatively wide-angle "scenic" scene—a factor known to reduce or eliminate BE in adults). There is no known research suggesting differences in scene construction across these age groups, but there is a well-established developmental trajectory (continual development at least to the age of 12 years) associated with discerning the difference between internally-generated and externally perceived information (e.g., Sussman, 2001; Foley & Johnson, 1985; Lindsay, 2008; Sluzenski, Newcombe, & Ottinger, 2004). Thus, it may be that young children accept more of the constructed continuation of the scene as actually having been perceived when remembering the stimulus (Johnson, Hashtroudi, & Lindsay, 1993). Kreindel and Intraub (2016) attributed adult's reduced BE, relative to 4–5 year olds, to more mature strategies during study and more refined decision processes at test than could be implemented by young children. In line with this finding, when presentation time for adults was reduced (limiting time to implement ancillary strategies) BE occurred for these pictures. We suggest that the difference between young children and adolescents in the current study reflects these developmental changes, and it is possible that adolescents are more likely to adopt these advanced strategies on the recognition task because of the lessened cognitive demands and cue availability. This finding may motivate inclusion of a wider range of age groups in future BE research.

Second, a group difference emerged between individuals with DS and controls in one of the three BE tasks—the drawing task. This is the only free recall task administered and it places greater demands on working memory. Here, in the absence of a test stimulus, the participant must utilize memory alone while simultaneously conducting source monitoring and drawing what they remember seing. This greater cognitive demand may have compromised the DS group's ability to monitor source, leading them to accept more of their constructed scene representation as having been viewed before. Indeed, Chapman et al. (2005) pointed out that compared with recognition-based tasks, drawing tasks, in general, tend to lead to greatest BE. The drawing task also takes more time than the forced-choice recognition or the 3D memory task (where participants point out the remembered location of the boundaries). Therefore, the extended time taken to complete the drawing task might cause the representation to continue to shift over time, leading to increased BE.

Despite these differences, BE was indeed observed across groups and test modalities, highlighting the presence of BE in a population with known hippocampal disruption. This finding, in combination with prior research suggesting BE in typically developing infants as young as 3–4 months old (Quinn & Intraub, 2007), supports the idea that BE reflects a fundamental, and perhaps, ecologically necessary anticipatory process. Based on these findings, we suggest that BE may be driven by a varied set of processes and due to the ecological relevance of this function it may be possible that some patient groups may demonstrate BE through alternate mechanisms. A highly practiced aspect of cognition, such as anticipating space beyond the current view, would be a strong candidate for reorganization. Indeed, work on patients with developmental amnesia, who possess hippocampal deficits from early childhood, has suggested that other markers of scene construction can be mediated by frontal cortex and semantic memory through reorganization of function across development (Mullally, Vargha-Khadem, & Maguire, 2014).

All together, these findings demonstrated that, given the necessity of this function, BE may be achieved via similar cortical mechanisms or perhaps through the use of the earliest developing subfields of the hippocampus, which may be less impacted than dentate gyrus in DS (Witton et al., 2015) and mature early on in typical development (Lavenex & Banta Lavenex, 2013). CA1 of the hippocampus, for instance, develops early and has been shown to learn environmental configurations with repetition (Nakashiba, Young, McHugh, Buhl, & Tonegawa, 2008), suggesting that BE in our young group might be supported by this structure. CA1 and the short-route connections may be the substructures that facilitate acquisition of statistical regularities (Schapiro, Turk-Browne, Norman, & Botvinick, 2016), and with time and greater exposure to the environment patient groups might be able to use intact cells in this structure to learn some regularities about scenes (expanded views being one possibility). Just as H.M. learned the layout of his home with practice in that environment (Corkin, 2002), so may patients acquire this fundamental skill out of the sheer need to navigate our visual world. However, once reorganized by other mechanisms, the nature of these effects, such as the available details, may differ. More work is needed to determine the neural mechanisms supporting BE in patient groups with hippocampal compromise and the nature of scene representations in these populations.

Despite their noted deficits in hippocampal structure and function, as well as other cognitive impairments, individuals with DS clearly demonstrated BE. These results may help to provide a greater understanding of the mechanisms underlying this phenomenon. One view, as noted by Maguire and Mullally (2013), has suggested that different subregions of the hippocampus may facilitate aspects of the scene construction process. For instance, BE has been proposed to reflect pattern completion (PC) mechanisms, in which the autoassociative networks in the hippocampus complete patterns and bias our scene construction based on past experience. Given the proposed competition in pattern separation (PS) and PC

in the hippocampus (Hunsaker & Kesner, 2013; Yassa & Stark, 2011 for reviews), those with DS could possibly demonstrate BE without the high fidelity PS afforded by the dentate gyrus.

The two-stage process described by Intraub and colleagues likely involves additional steps for scene storage and construction in the hippocampus. First, at encoding, scenes must be viewed and uniquely stored according to their features in hippocampus (PS). Second, at recall, the stimulus representation will trigger a reinstatement of the previous memory (PC), and finally, the participant compares the tested visual scene with the stored representation. The first two stages may involve slowly maturing hippocampal function, and the last stage is a decision process that may also have a protracted developmental course. In individuals with DS, it is possible that PS at encoding and the decision processes are largely impaired, but they might be able to reinstate a less detailed/erroneous memory during retrieval processes. DS has been posited to be associated with PS deficits and dentate gyrus underdevelopment, a set of neurological impairments that would cause the individual greater difficulty in creating orthogonal representations of similar inputs (Kleschevnikov et al., 2012; Smith, Kesner, & Korenberg, 2014; Witton et al., 2015). Therefore, individuals with DS might rely on PC to show BE: from repeated experience, they acquired memories of individual scene representations that are extended in space, and when a scene stimulus is encountered again these memories are reactivated, and perhaps erroneously for memories not identical to the target. However, we would predict that these memories would lack detail. Individuals with DS may have acquired enough understanding of the properties of the visual world to expand the boundaries, but this expansion may come without a detailed anticipation of what is contained in that expanded world. This explanation is speculative, and as suggested by us, as well as Maguire et al. (2015), more work is needed to determine how BE may map onto separate functions of hippocampal subregions, both in relation to subfield differences as well as differences across the anterior-posterior axis.

If participants with DS exhibit BE without utilizing the hippocampus in the same way as neurologically intact adults, another prediction is that they would not be able to engage in detailed scene imagination, even while exhibiting intact BE. Indeed, Spanò and Edgin (2016) have recently found that parents report impaired episodic memory in this population, partly because these memories lack details. Further, although the group with DS expanded the boundaries on the drawing task, they might not necessarily retain the visual details of the scene (e.g., some of the local features). While drawing skills—such as reproducing a vertical line, copying a square—are considered to be a strength in this population compared to other intellectual disabilities (Silverstein, Legutki, Friedman, & Takayama, 1982), the absence of detailed scene memory or imagination would be in line with previous work showing a focus on global vs. local visual details in this group (e.g., Bihrle, Bellugi, Delis, & Marks, 1989; Porter & Coltheart, 2006). Our current drawing task had a relatively simple scene background and did not lend to a close examination of the level of detail retained. However, future investigations should determine if BE may occur even when the scene background details are not well represented.

While we believe our results may help to inform the ongoing debate regarding these fundamental processes, the main limitation of our study is the absence of neuroimaging methods to characterize hippocampal dysfunction/development in these groups. This limitation led us to select the age-range in the typical childhood sample to allow for the strongest contrast in age, and thus hippocampal development. We compared an extended age range in the two typically developing groups, allowing for certainty in the changes in episodic memory measured across age. We are also certain that our group with DS shows memory impairments, based on established premise in the previous literature and our measurement of object-place binding deficits in this current investigation. Parent-reports, results of navigational studies, and numerous neuropsychological and neuroimaging studies (based on animals and humans) have pointed to a profile of hippocampal dysfunction (Banta Lavenex et al., 2015; Edgin et al., 2010; Kleschevnikov et al., 2012; Nadel, 1999, 2003; Pennington et al., 2003; Spanò & Edgin, 2016; Uecker, Mangan, Obrzut, & Nadel, 1993; Witton et al., 2015). Indeed, we make a strong claim that DS is one of the most well-characterized nonlesion conditions of hippocampal compromise in the literature.

In summary, our findings support the near-universal nature and presence of BE and lead us toward future investigations of the processes that underlie this anticipatory spatial error. These results indicate that BE is an essential function, likely driven by a complex set of processes, including functions of the hippocampus and decision processes across development. What was particularly striking was that DS participants exhibited BE that was equal to or greater than controls, although their memory for object-location associations was relatively poor. This finding suggests that the anticipatory projection of expected space that characterizes BE, might be a more basic function than object-location associations in memory for scenes. BE has been observed not only in DS but also in a study of children with Asperger's syndrome (Chapman et al., 2005) who exhibited greater BE than controls. To date, the only group that has shown reduced BE has been patients with selective and complete hippocampal damage (Mullally et al., 2012), suggesting that BE can be completed with partial hippocampal function or through reorganization. We suggest that it would be worthwhile to conduct more research on BE, particularly studies including neuroimaging, to understand how BE effects may be mediated by hippocampal or extrahippocampal mechanisms across development or in developmental disorders.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare in reference to this work.

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