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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

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Humans have the effortless ability to perceive the local visual environment, or “scene”. In a brief glance, we can recognize both what kind of scene it is (e.g., city or a beach), and how to navigate through that scene without running into obstacles. Recent functional magnetic resonance imaging (fMRI) evidence suggests that these remarkable human visual scene processing abilities may be supported by two functionally distinct systems with distinct neural bases: one for visually-guided navigation (i.e., how do I get around this place?), including the occipital place area (OPA), and the second for scene categorization (i.e., what kind of place it is), including the parahippocampal place area (PPA). Importantly, however, fMRI data are only correlational, and a stronger test of the hypothesis of independent visually-guided navigation and scene categorization systems would ask i) are these two systems *causally* dissociable (where one system can be impaired while the other spared), and further, ii) do these systems arise along *different timelines* in typical development? Here we tested visually-guided navigation and scene categorization abilities in adults with Williams syndrome (WS; a genetic developmental disorder involving cortical thinning in and around the posterior parietal lobe, potentially including OPA, but not PPA), as well as typically developing four- and seven-year-old children. Indeed, we found that i) WS adults show greater impairment on visually-guided navigation than scene categorization, relative to mental-age matched control participants; and ii) visually-guided navigation matures more slowly than scene categorization in typically developing children. These findings provide the first causal and developmental evidence for dissociable systems for categorizing scenes and navigating through them.

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1. INTRODUCTION

It has been well established that object processing is supported by two distinct systems: a dorsal system supporting visually-guided action (e.g., reaching for an object) and a ventral system supporting object perception (e.g., identifying an object) (Goodale & Milner 1992; Ungerleider & Mishkin, 1982). Some of the strongest causal evidence for functionally independent action and perception systems has been found in patients with neurological damage in one system, coupled with sparing of the other system. For example, Patient DF, who had damage to her ventral stream pathway (James et al., 2003), showed substantial impairments in her ability to perceptually discriminate orientations of a slot (a classic object perception task); however, her dorsal stream pathway was not damaged, and accordingly her ability to reach out and "post" paper through the same slot at various orientations was unaffected (Milner & Goodale 1995). Complementing this classic case, patients with dorsal stream damage and ventral stream preservation, including individuals with Williams syndrome (WS), were able to accurately report the orientation of a slot, but showed great impairments in executing visually-guided movements toward the slot (Dilks et al., 2008)– precisely the opposite pattern of impairment from that found in DF. As individuals with WS have a genetic developmental disorder involving cortical thinning in the dorsal stream (Meyer-Lindenberg et al., 2006), these findings are consistent with the two-stream hypothesis– damage to the dorsal stream impaired the action system, and an intact ventral stream spared the perception system. Similar results are found among patients with object ataxia (Perenin & Vighetto, 1988). Further, the two-systems hypothesis for object processing has been explored in typical development, with evidence suggesting that the dorsal system is later developing than the ventral system (Atkinson et al., 2003; Bertenthal, 1996; Csibra et al.,1998; de Haan et al., 2002; Diamond et al., 1989; Diamond & Goldman-Rakic,1989; Dilks et al., 2008; Gilmore & Johnson,1997a,1997b; Johnson et al., 2001; Munakata,1997). These findings provide classic evidence of a double dissociation supporting the two visual systems hypothesis for visually-guided action and perception in object processing.

Mirroring this well known division of labor in object processing between systems for visually-guided action and perception, our lab has recently proposed that the scene processing system can likewise be divided into systems for action and perception (Dilks et al., 2011; Kamps et al., 2016a, 2016b; Persichetti and Dilks, 2016; Persichetti and Dilks, 2018). In particular, functional magnetic resonance imaging (fMRI) studies in adults suggest that one scene-selective region in the dorsal stream, the occipital place area (OPA), supports visually-guided navigation (i.e., how can I get from here to the other side of the room?), while a second scene-selective region in the ventral stream, the parahippocampal place area (PPA), supports scene categorization (i.e., what kind of room am I in?). Perhaps the strongest neural evidence for this proposal comes from a recent study by Persichetti and Dilks (2018), who reported a double dissociation between OPA and PPA in adults, with OPA responding significantly more when participants performed a visually-guided navigation task than a scene categorization task, while PPA showed the opposite pattern of results, providing striking evidence for the two-streams-for-scene processing hypothesis.

Importantly, however, fMRI data are only correlational, and a stronger test of the hypothesis of independent visually-guided navigation and scene categorization systems would further provide causal evidence for the dissociation between these systems. That is, if visually-guided navigation and scene categorization are independent systems, then it should be possible to find cases of impairment of one ability (visually-guided navigation) coupled with sparing of the other ability (scene categorization). We sought causal evidence for the two-systems-for-scene-processing hypothesis by studying adults with WS. Given their cortical thinning of the dorsal stream, potentially including OPA, we predict that WS adults will perform significantly worse on a visually-guided navigation task than a scene categorization task, relative to typically-developing children matched on mental age.

Furthermore, if the visually-guided navigation and scene categorization systems are independent systems, then these systems would develop at different rates, even in typical development. We sought developmental evidence for the idea that visually-guided navigation and scene categorization systems develop independently by studying visually-guided navigation and scene categorization abilities in typically-developing children. As mentioned above, previous work on object processing found that the dorsal “action” system is slower to develop than the ventral “perception” system (Dilks et al., 2008). We therefore predicted that, analogously, the visually-guided navigation system (which includes the more dorsal OPA) will develop later than the scene categorization system (which includes the more ventral PPA). The development of scene processing is less explored than the development of object processing, and no studies to our knowledge have compared the development of visually-guided navigation and scene categorization abilities directly. However, some evidence suggests that visually-guided navigation undergoes protracted development, whereas scene categorization develops earlier. For example, performance on locomotion and obstacle avoidance tasks, which potentially involve OPA, is thought to mature slowly, with performance still improving from across middle childhood (ages 5-to-8-years old) (Pryde et al., 1997). Additionally, 7-year-olds show reduced use of anticipatory locomotor strategies (e.g., anticipating whether or not they will be able to step over an obstacle) compared to adults (Berard & Vallis, 2006). By contrast to the late-developing performance seen on tasks related to visually-guided navigation, scene categorization ability is generally thought to follow a relatively early developing trajectory– maturing even earlier than other ventral stream abilities like face recognition (Carey & Diamond, 1977; Golarai et al., 2007;

Weigelt et al., 2014), with adult-like performance on scene memory tasks by 5-to-6-years old (Weigelt et al., 2014).

However, critically, no study has compared these abilities directly on closely matched tasks. Through two psychophysical experiments, we combine causal and developmental evidence providing powerful support for the two-systems-for-scene-processing hypothesis.

2. METHODS

2. 1. Participants

Nineteen WS adults (13 females), 19 typically developing mental-age matched (MA) controls (average age = 7-years-old) (12 females), and 19 typically developing 4-year-olds (11 females) participated in the study. Participant characteristics are presented in Table 1. The WS adult participants were recruited through the Williams Syndrome Association and displayed the hemizygous microdeletion characteristic WS region of chromosome 7q11.23 (Ewart et al., 1993). Child participants were recruited through the Emory Child Study Center. All adults and legal guardians of child participants gave informed consent.

Each participant was tested on the Kaufman Brief Intelligence Test (KBIT; Kaufman & Kaufman, 1990). The standardized intelligence test calculates a composite IQ score as well as scores for two subtests: verbal and non-verbal. The verbal portion tests for participants' knowledge of word meanings and verbal language abilities. The nonverbal portion tests for problem solving through matrices requiring participant to judge which objects "go together" or which pattern "comes next."

Each WS participant was individually matched with a typically-developing MA control participant on the non-verbal subtest of the KBIT because non-verbal ability is known to be impaired in WS, while verbal/language ability is known to be relatively intact (Jarrold, Baddeley, & Hewes, 1998). This ensured that differences in non-verbal abilities could not explain any differences in performance between the visually-guided navigation and scene categorization tasks. Non-verbal raw scores between WS and MA groups were matched as closely as possible with 13 out of 19 exact matches and 6 out of 19 with maximum difference of ± 1.

2. 2. Design, stimuli, and procedure

Participants performed two tasks: a visually-guided navigation task and a scene categorization task (Figure 1A). In the visually-guided navigation task, the participants were asked to imagine they are standing in the room, and they were told to follow a complete path on the ground in order to walk out of one of the doors (i.e., either the left, center, or right door). To make the task more understandable to children, the children were told that the ground was "lava", the only safe spots to walk on were the paths on the ground and jumping across path breaks was not allowed. After stimulus presentation, the participant pointed to which door they would walk to exit. Response via pointing ensured that participants did not have difficulty mapping space to language– for example, mistakenly saying the word "left", when meaning the right direction. For the scene categorization task, the participants were asked again to imagine standing in the room, but now to verbally respond whether they were standing in a bedroom, living room, or kitchen. Both the visually-guided navigation and scene categorization tasks used the same set of stimuli (36 room images) and were matched on task demands as well as all aspects of design and procedure. The room stimuli were created using The Sims 3 software (The Sims Studio, 2010). Each task was be presented using software written using MATLAB Psychophysics Toolbox (Brainard, 1997). The participants viewed stimuli presented at a size of approximately 24 degrees visual angle on a 11.97" x 8.36" LCD screen.

The study session consisted of a training and testing phase. In the training phase participants completed a set of non-speeded, practice trials for each task. Each trial consisted of the room stimulus presentation. Depending on which task they were completing, they were given feedback about whether or not their response was correct to ensure instructions for each task were understood. After responding correctly to 10 trials in a row, participants advanced to the testing phase, during which no feedback was given. The testing phase consisted of 12 blocks in total (6 of each task). The order of blocks was counterbalanced across participants, and experimental trials were randomized within each block. Prior to each block, an instruction screen appeared, indicating which task (visually-guided navigation or scene categorization) would follow. In each block, 12 experimental trials were presented. Each trial consisted of a 500 ms stimulus (room image) presentation followed by a fixation screen, during which participants gave a non-speeded 3-alternative forced choice (3AFC) response. Following the participant response, the experimenter recorded the response via keypress, and then the next trial was presented. One room image per block was presented for a longer 2000 ms and functioned as a catch trial to assess participant attentiveness throughout the task. These 12 catch trials (6 per task, 1 per block) were easy trials that ensured participants understood and paid attention during the experiment.

3. RESULTS

3. 1. WS adults show greater impairment on visually-guided navigation than scene categorization, relative to MA controls.

If independent systems exist for visually-guided navigation and scene categorization, we predict that WS adults will show greater impairment on the visually-guided navigation task than the scene categorization task, relative to MA controls. To test this prediction for causally dissociable systems, we compared visually-guided navigation and scene categorization abilities in WS adults and MA controls (Figure 2).

We found that WS adults performed significantly less accurately on the visually-guided navigation task than the scene categorization task ($t_{(18)} = 3.95$, $p = 0.001$). However, in MA controls, there was only a marginally significant difference in performance between the visually-guided navigation and scene categorization tasks ($t_{(18)} = 2.03$, $p = 0.06$). Most importantly, a 2 (group: WS adults, MA controls) x 2 (task: navigation, scene categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 5.01$, $p = 0.03$), indicating that the WS adults performed significantly worse on the visually-guided navigation task than scene categorization, relative to MA controls. These findings suggest that the visually-guided navigation system is selectively impaired in WS, while the scene categorization system is spared, providing the first causal evidence for dissociable visually-guided navigation and scene categorization systems.

However, perhaps the WS adults' reduced accuracy on visually-guided navigation task was due to difficulty understanding directions or paying attention during the task, and not a selective impairment to the visually-guided navigation system. This alternative explanation is unlikely given that WS adults' performance on the visually-guided navigation task, while impaired, was nevertheless well above chance levels of 33% accuracy on both the visually-guided navigation and scene categorization tasks, demonstrating they were not randomly guessing during the task. To address the possibility directly, however, we analyzed the WS adults' performance on the catch trials that were interspersed throughout both tasks to assess their attentiveness and understanding. These catch trials involved longer presentations of stimuli (2000 ms versus 500 ms), and they were therefore trivially easy for both WS adults and MA children, allowing us to probe task understanding directly. We found that the WS adults' performance on the visually-guided navigation task catch trials was not significantly different than the performance on the scene categorization task catch trials ($t_{(18)} = 1.05$, $p = 0.31$), indicating that WS adults indeed understood the visually-guided navigation task just as well as they understood the scene categorization task.

Another possible alternative explanation for WS adults' reduced performance on the visually-guided navigation task is that this reduction in performance can be explained by more general spatial deficits in WS. For example, perhaps WS individuals have impairments in their more general ability distinguish between left and right, as found in previous studies of WS (Landau & Hoffman, 2007). Critically, confusing left and right would result in worse performance on the visually-guided navigation task, even if the visually-guided navigation system itself was completely spared in WS. To rule out this possibility, we analyzed the WS adults' performance on center trials only, where mistaking directions (e.g., pointing left when meaning right) could not affect performance (Figure 3). After excluding left and right trials, center trials consisted of just 33% of total visually-guided navigation trials; therefore, we selected a random 33% of scene categorization trails, for comparison. Here the WS adults still showed the same pattern of results as before: a 2 (group: WS adults, MA controls) x 2 (task: navigation, categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 9.36$, $p = 0.004$), with WS adults still performing disproportionately worse on the visually-guided navigation task than the scene categorization task, relative to MA controls. The consistency in results supports the idea that the visually-guided navigation system itself is impaired in WS, and that our results are not attributable to a more general impairment in discriminating left versus right.

A final alternative explanation is that the scene categorization task can be solved entirely by recognizing the particular objects in the room (e.g., a "bed"), and thus the category of the room in turn (e.g., only bedrooms have beds), rather than by directly recognizing the scene per se (e.g., recognizing the scene as a whole to be a bedroom). In this case, our findings might not reflect a dissociation *within* scene processing (i.e., between visually-guided navigation and scene categorization), but rather a more general dissociation between object and scene processing, with scene recognition operating entirely in the service of navigation. Previous neuroimaging work in adults found that PPA responds strongly to the scene categorization task, suggesting that this task indeed draws on scene recognition abilities in particular (Persichetti and Dilks, 2018). Further, numerous studies have failed to find evidence that object and scene recognition develop differentially across these age groups. Nevertheless, the possibility remains that participants in the present behavioral study solved the task using an alternative "object recognition" strategy. Thus, to ensure that our experiment is tapping into the scene categorization system in particular, and not the object perception system, we devised a version of the same experiment, where the room stimuli contained no objects, and could only be distinguished by their layouts (i.e., of the walls) (Figure 1B). We tested a new group of WS adults (N=17) and MA controls (N=17) (Table 2). In this new experiment, we found very similar results to our initial paradigm (Figure 4). Specifically, comparing the old "room content experiment" with the new "room layout experiment", a 2 (group: WS adults, MA controls) x 2 (task: navigation, categorization) x 2 (experiment: content, layout) failed to find a significant group x task x experiment interaction ($F_{(1,68)} = 0.40$, $p = 0.53$), indicating that both experiments show the same pattern of results. However, we still see a significant group x task interaction ($F_{(1,68)} = 5.96$, $p = 0.02$), revealing disproportionate impairment on visually-guided navigation compared to scene categorization in WS, across both experiments. Therefore, our findings cannot be explained by an alternative "object recognition" strategy, and rather reflect a dissociation within scene processing between visually-guided navigation and scene categorization.

3. 2. The visually-guided navigation system is later developing than the scene categorization system in typical development.

If visually-guided navigation and scene categorization are independent systems, then we hypothesize that these systems develop at different timelines in typical development. To test this prediction for developmentally dissociable systems, we compared visually-guided navigation and scene categorization abilities in typically developing 4-year-olds and 7-year-olds controls (the MA controls from Experiment A) (Figure 2).

We found that the 4-year-olds performed significantly less accurately on the visually-guided navigation task than the scene categorization task ($t_{(18)} = 4.79$, $p < 0.001$). However, as reported above, in MA controls, there was only a marginally significant difference in performance between the visually-guided navigation and scene categorization tasks ($t_{(18)} = 2.03$, $p = 0.06$). Critically, a 2 (group: 4-year-olds, MA controls) x 2 (task: navigation, categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 7.71$, $p = 0.009$), indicating that the 4-year-olds performed disproportionately worse on visually-guided navigation than scene categorization, relative to MA controls. These findings therefore suggest that the visually-guided navigation system is later developing than the scene categorization system in typical development, with the visually-guided navigation system “catching up” with the scene categorization system around 7-years-old.

But perhaps the 4-year-olds’ decreased accuracy on the visually-guided navigation task was due to difficulty understanding instructions or paying attention during the task, and not a later developing visually-guided navigation system. This alternative explanation is unlikely given that the 4-year-olds’ performance on the visually-guided navigation task, was nevertheless well above chance levels of 33% accuracy on both the visually-guided navigation and scene categorization tasks, demonstrating they were not randomly guessing during the task. However, to test this possibility directly, we analyzed the 4-year-olds’ performance on the catch trials that were included throughout both tasks to assess their attentiveness and understanding. These catch trials involved longer presentations of the stimuli (2000 ms versus 500 ms), and they were therefore trivially easy for both 4-year-olds adults and MA children, allowing us to probe task understanding directly. We found that the 4-year-olds' performance on the visually-guided navigation task catch trials was not different from their performance on the scene categorization task catch trials ($t_{(18)} = 0.66$, $p = 0.52$), indicating that the 4-year-olds understood the visually-guided navigation task just as well as they understood the scene categorization task.

Another alternative possibility is that the reduced performance on visually-guided navigation among 4-year-olds was driven by later development of the more general ability to distinguish left from right, rather than later development of the visually-guided navigation in particular. To address this possibility, we analyzed 4-year-olds' performance on center trials only, where mistaking directions (e.g., pointing left when meaning right) could not affect performance (Figure 3). After excluding left and right trials, center trials consisted 33% of total visually-guided navigation trials; therefore, we selected a random 33% of scene categorization trails. Here a 2 (group: 4-year-olds, MA controls) x 2 (task: navigation, categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 9.77$, $p = 0.004$), with 4-year-olds still showing the same pattern of results as before, performing disproportionately worse on the visually-guided navigation task than the scene categorization task, relative to MA controls. The consistency in results supports our findings of that the later development of the visually-guided navigation system that we observed is not explained by a more general deficit in ability to discriminate left from right.

A final alternative explanation is that the scene categorization task can be solved entirely by recognizing the particular objects in the room (e.g., a "bed"), and thus the category of the room in turn (e.g., only bedrooms have beds), rather than by directly recognizing the scene per se (e.g., recognizing the scene as a whole to be a bedroom). In this case, our findings might not reflect a dissociation *within* scene processing (i.e., between visually-guided navigation and scene categorization), but rather a more general dissociation between object and scene processing, with scene recognition operating entirely in the service of navigation, as previously described. Thus, to ensure that our experiment is tapping into the scene categorization system in particular, and not the object perception system, we devised a version of the same experiment, where the room stimuli contained no objects, and could only be distinguished by their layouts (i.e., of the walls) (Figure 1B), again as previously described. We tested a new group of 4-year-olds (N=17) and 7-year-olds (N=17) (Table 2). In this new experiment, we found very similar results to our initial paradigm (Figure 4). Specifically, comparing the old "room content experiment" with the new "room layout experiment", a 2 (group: 4-year-olds, MA controls) x 2 (task: navigation, categorization) x 2 (experiment: content, layout) failed to find a significant group x task x experiment interaction ($F_{(1,68)} = 0.61$, $p = 0.44$), indicating that both experiments show the same pattern of results. However, we still see a significant group x task interaction ($F_{(1,68)} = 10.54$, $p = 0.002$), revealing disproportionately worse performance on visually-guided navigation compared to scene categorization in 4-year-olds, across both experiments. Therefore, our findings cannot be explained by an alternative "object recognition" strategy, and rather reflect a dissociation within scene processing between visually-guided navigation and scene categorization.

4. DISCUSSION

The current study explored whether the hypothesized two-systems-for-scene-processing for visually-guided navigation and scene categorization are causally and developmentally dissociable. To investigate our hypothesis, we studied the visually-guided navigation system's susceptibility to damage in WS and the developmental profiles of both systems in typically developing children. We demonstrated that WS adults show greater impairment of visually-guided navigation than scene categorization, relative to controls matched on mental age. We also found that visually-guided navigation and scene categorization develop along two different timelines in typical development. Specifically, visually-guided navigation was found to develop later than scene categorization, where 4-year-olds perform disproportionally worse on the visually-guided navigation task than scene categorization task, relative to 7-year-olds. Control analyses eliminated the possibilities that these findings are explained by i) lack of understanding or attention during tasks, ii) impairments in or later development of the ability to distinguish left or right, or iii) an alternative "object recognition" strategy. Taken together then, these findings provide the first causal and developmental evidence for dissociable visually-guided navigation and scene categorization systems.

Our results challenge the widely held notion that scene processing serves navigation only (Cheng and Newcombe, 2005; Epstein and Kanwisher, 1998; Ghaem et al., 1997; Rauchs et al., 2008; Rosenbaum et al., 2004; Spelke et al., 2010). Contrastingly, we found strong causal and developmental evidence suggesting a division of labor within scene processing, with functionally independent systems for visually-guided navigation (which includes the more dorsal OPA) and scene categorization (which includes the more ventral PPA). The idea that action and perception are dissociable within scene processing coincides with the vast literature showing the same division of labor for object processing between the dorsal system for visually-guided action and ventral system for object perception (Atkinson et al., 2003; Dilks et al., 2008; Milner & Goodale 1995). Thus, our findings support the idea that this division of labor between action and perception in the dorsal and ventral systems respectively is a general organizing principle encompassing both scene and object perception systems.

Similar to evidence suggesting that the dorsal stream is slower to develop than the ventral stream in object processing (Atkinson et al., 2003; Bertenthal, 1996; Csibra et al.,1998; de Haan et al., 2002; Diamond et al., 1989; Diamond & Goldman-Rakic,1989; Dilks et al., 2008; Gilmore & Johnson,1997a,1997b; Johnson et al., 2001; Munakata,1997), in this study we found that the visually-guided navigation is later to develop than the scene categorization system. Furthermore, just as the dorsal stream was hypothesized to be selectively impaired in WS (Atkinson et al., 1997, 2003; Dilks et al., 2008), here we found that the corresponding visually-guided navigation system is selectively impaired in WS. Therefore, our findings support an emerging developmental hypothesis that the dorsal stream in general (rather than just object-specific systems in the dorsal stream) is later developing than the ventral stream.

In contrast to the general assumption that all “visuospatial” abilities are damaged in WS, we found that scene categorization ability in WS is relatively spared (relative to mental-age matched controls). The claim that this system is spared was strengthened by our finding that WS were able to categorize scenes based on both two key scene ‘descriptors’ established in the computational vision literature as fundamental for successful scene recognition, namely “scene content” (i.e., the objects, textures, and colors that make up a scene) and “scene layouts” (i.e., the shape, size, and scope of the boundaries that make up the space) (Greene and Oliva, 2009; Li et al., 2010; Oliva and Schyns, 1997; Oliva and Torralba, 2001; Walther et al., 2011).

Furthermore, our findings support the hypothesis that the impaired visually-guided navigation ability in WS may stem from developmental arrest of later maturing systems housed in the dorsal stream, corresponding to similar developmental arrest in WS found in dorsal stream object processing for action (Dilks et al., 2008). On the visually-guided navigation task, we found that WS adults performed similarly to typically developing 4-year-old children, with both groups exhibiting disproportionately worse performance on the visually-guided navigation task, relative to the scene categorization task, compared to MA controls. These results are consistent with the idea that slower developing cognitive systems may be more susceptible to breakdown than faster developing systems, whereby the development of visually-guided navigation in WS is arrested at the developmental point when the dorsal stream is lagging behind the ventral stream.

Intriguingly, given that WS is caused by a genetic deletion, these results further suggest that the vulnerability of the dorsal stream may have a genetic basis. For example, individuals with other neurogenetic syndromes including Fragile X syndrome, Turner syndrome, and velocardiofacial syndrome are shown to have selective visuospatial deficits on tasks that may be activating the dorsal stream (Bearden et al., 2001; Kogan et al. 2004; Romans et al., 1998). While genetics directly affecting behavior is a bold suggestion, potentially involving many downstream effectors, the idea that genetics may, in part, modulate specific aspects of cognition nevertheless opens many doors to future research.

Our findings also suggest that the scene categorization system is earlier developing than the visually-guided navigation system. Indeed, 4-year-olds are able to use both content and layouts of a scene to recognize what kind of place they are in, suggesting that their scene categorization abilities are intact very early. These findings are consistent with other reports of these abilities following a relatively early-developing trajectory and maturing even earlier than other ventral stream abilities like face recognition (Carey & Diamond, 1977; Golarai et al., 2007; Weigelt et al., 2014), with adult-like performance on scene memory tasks by 5-to-6-years-old (Weigelt et al., 2014).

However, the idea that visually-guided navigation matures later in development than scene categorization may seem counterintuitive. As infants start crawling around 8.5-months and walking at around 12-months (Bayley, 1969; Frankenburg et al., 1992), why then does it take up to 7 years for visually-guided navigation to catch up to scene categorization? We suggest that although infants learn to locomote very early on, their abilities to plan paths through cluttered environments may be relatively unsophisticated early in infancy and childhood. For example, refined navigation abilities, including locomotor ability and obstacle avoidance, were found to be adult-like in children only after the age of 8-years-old (Berard & Vallis, 2006; Pryde et al., 1997). Our experiments support the idea that this later developing visually-guided navigation ability is linked complex navigational functions carried out by the adult OPA, such as calculating navigational affordances (Bonner & Epstein, 2017) and detecting potential of paths in a scene (Patai & Spiers, 2017).

How do we know for sure if the WS adults and children are *really* navigating during our computer tasks? Can these two-dimensional stimuli presentations truly emulate the physical experience of real-world navigation? While Persichetti and Dilks (2018) used these same exact room image stimuli in neuroimaging, reporting a double dissociation between OPA and PPA in adults, with OPA responding significantly more when participants performed a visually-guided navigation task than a scene categorization task, it is still possible in our paradigm that participants did not perform the task using a navigation strategy, per se. Instead, participants may have used another strategy to solve the task that does not have to do with navigation. To address this limitation, we have planned a future experiment testing real-world visually-guided navigation in three-dimensional space. In this experiment, visually-guided navigation of WS adults, 4-year-olds, and 7-year-olds (or MA controls) will be directly tested in an obstacle-course type setup, where we will study path efficiency (e.g., length, speed, avoidance of obstacles) as a proxy for visually-guided navigation ability. Here, we expect WS adults to perform worse on this visually-guided navigation task, compared to MA controls, consistent with our findings of impaired visually-guided navigation system relative to scene categorization. Additionally, we expect 4-year-olds to also perform worse on this visually-guided navigation task compared to 7-year-olds, consistent with our findings of the later developing visually-guided navigation system. This real-world navigation task will provide supporting evidence that there are visually-guided navigation deficits in WS, alongside slow development 4- versus 7-year-olds.

Future work will also directly explore the development of OPA – putatively involved in visually-guided navigation, and PPA – putatively involved in scene categorization – using fMRI in typically and atypically developing individuals. Given the pattern of findings found here using psychophysical methods, we predict analogously that OPA will reach adult-like selectivity for scenes (i.e., 2-to-4 times greater responses to scenes than objects) later in development than PPA, and further that OPA will be less selective in WS compared to controls, while PPA will look similar between WS and control participants. Complementary neural evidence for the present finding would thus provide a direct link between the present findings and previous findings using fMRI in adults. Further, such studies could directly establish that damage to OPA in particular leads to the visually-guided navigation deficit observed in WS.

Finally, while here we find evidence of a single dissociation between visually-guided navigation and scene categorization in WS, the strongest evidence for the independence of these systems would reveal precisely the opposite case: that is, a case of an impaired scene categorization system, coupled with a spared visually-guided navigation system.

In conclusion, we have demonstrated that two visual scene processing systems for visually-guided navigation and scene categorization are supported through causal and developmental evidence. First, we have shown that selective impairment in visually-guided navigation system in WS compared to MA controls, suggesting that this system is more susceptible to breakdown than scene categorization. Second, we have shown that the visually-guided navigation system undergoes protracted development across childhood, further supporting the two-systems-for-scene-processing hypothesis. These findings provide the first causal and developmental evidence for dissociable processing systems for recognizing places and navigating through them.

Table 1

Participant characteristics for WS adults, MA controls, and 4-year-olds (room content experiment)

	WS adults (N = 19)			**MA controls (N = 19)**			**4-year-olds (N = 19)**		
	M	SE	Range	M	SE	Range	M	SE	Range
Chronological Age	28.57	1.82	19 - 46	6.80	0.22	5.58 - 8.41	4.54	0.07	4 - 5.08
Verbal KBIT (raw score)	71.43	2.67	50 - 92	47.52	2.91	30 - 71	27.05	0.89	20 - 35
Verbal KBIT (standard score)	80.25	2.38	64 - 98	116.10	2.98	97 - 138	108.57	1.66	93 - 119
Non-verbal KBIT (raw score)	25.31	1.72	14 - 42	25.21	1.74	14 - 43	16.05	1.06	9 - 31
Non-verbal KBIT (standard score)	74.47	4.16	48 - 115	111.84	4.04	76 - 149	110.94	3.03	89 - 145
KBIT composite IQ	76.43	3.32	59 - 107	116.15	3.65	87 - 147	111.47	2.23	93 - 132

Table 2

Participant characteristics for WS adults, MA controls, and 4-year-olds (room layout experiment)

	WS adults (N = 17)			**MA controls (N = 17)**			**4-year-olds (N = 17)**		
	M	SE	Range	M	SE	Range	M	SE	Range
Chronological Age	27.68	1.41	19 - 44	7.06	0.12	6.16 - 8	4.62	0.08	4 - 5
Verbal KBIT (raw score)	69.50	2.36	59 - 78	49.41	2.41	34 - 71	30.20	1.61	19 - 42
Verbal KBIT (standard score)	77.87	2.13	70 - 86	117.00	3.05	96 - 142	111.93	2.80	91 - 129
Non-verbal KBIT (raw score)	24.00	2.29	14 - 32	23.41	1.90	14 - 33	14.50	0.74	8 - 20
Non-verbal KBIT (standard score)	73.12	5.75	42 - 88	103.76	4.30	78 - 125	104.75	2.64	82 - 124
KBIT composite IQ	71.87	4.23	51 - 82	112.29	2.70	89 - 127	110.00	2.67	92 - 131

Figure 1. Example stimuli used in visually-guided navigation and scene categorization tasks for (A) room layout experiment and (B) rooms content experiment. For the visually-guided navigation task, participants were asked to point to which door they could leave out of following a complete path on the ground. The answers for both sets of stimuli above from left to right are pointing to the “left”, “center”, and “right” door. For the scene categorization task, participants were asked to judge which room they viewed. The answers for stimuli set (A), from left to right are “bedroom”, “kitchen”, and “living room”. The answers for stimuli set (B), from left to right are “boring”, “hallway room”, and “stairs room”. Stimuli set B were blurred to match visually-guided navigation and scene categorization task demands to those of stimuli set A.

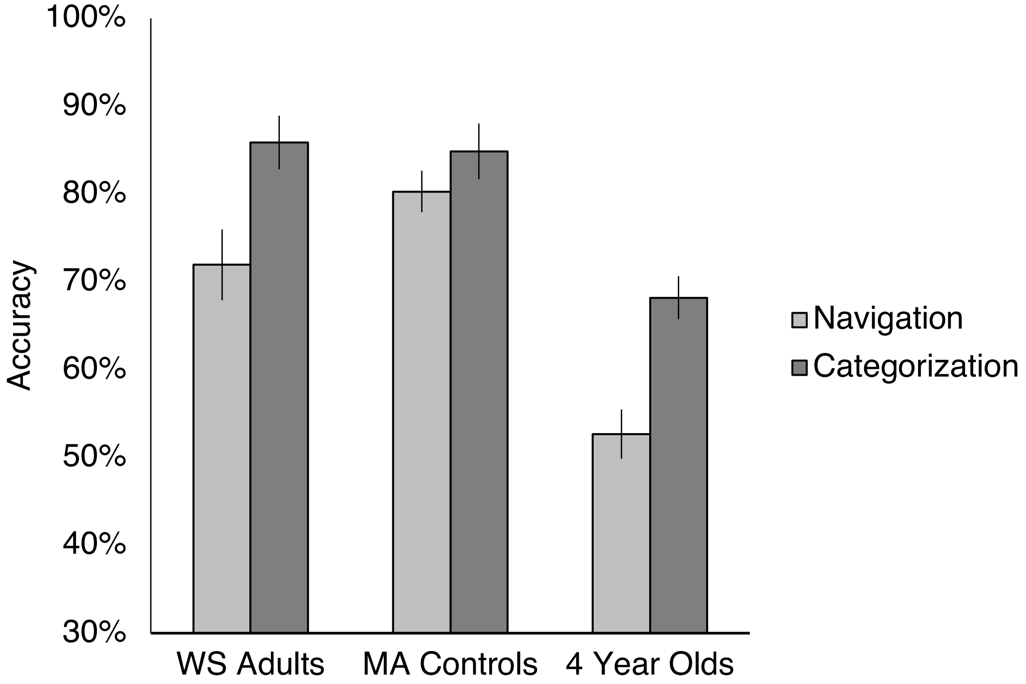

Figure 2. Average performance of WS adults, MA controls, and 4-year-olds on the visually-guided navigation and scene categorization tasks. WS adults performed disproportionately less accurately on the visually-guided navigation task than the scene categorization task, relative to MA controls. Specifically, a 2 (group: WS adults, MA controls) x 2 (task: navigation, scene categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 5.01$, $p = 0.03$), indicating that the visually-guided navigation system is selectively impaired in WS, while the scene categorization system is spared and providing causal evidence for the dissociation between these two systems. Further, 4-year-olds performed disproportionately less accurately on the visually-guided navigation task than 7-year-olds (MA controls). Critically, a 2 (group: 4-year-olds, MA controls) x 2 (task: navigation, categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 7.71$, $p = 0.009$), providing developmental evidence for independent visually-guided navigation and scene categorization systems, with visually-guided navigation system maturing later in development than the scene categorization system. Error bars indicate standard error.

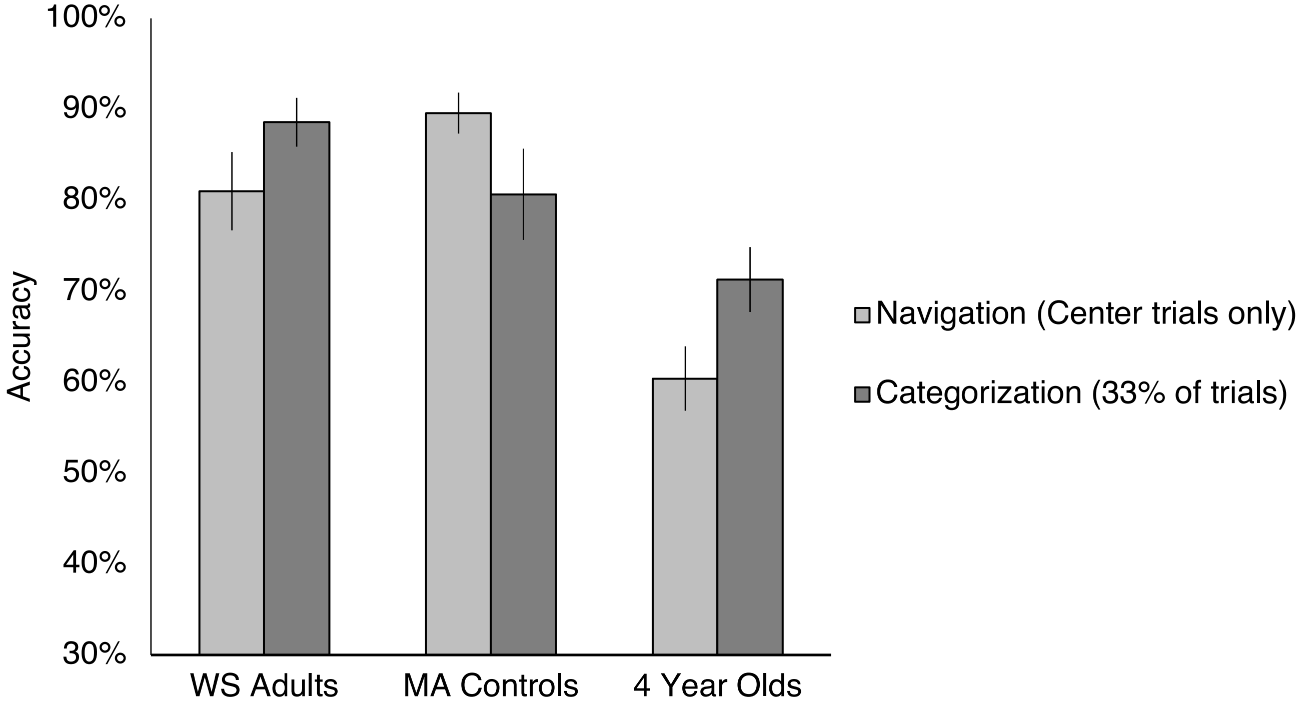

Figure 3. Average performance of WS adults, MA controls, and 4-year-olds on the center trials only of the visually-guided navigation task and 33% of scene categorization trials. This is a control analysis to ensure that reduced accuracy on the visually-guided navigation task in WS adults and 4-year-olds cannot be explained by impairments in distinguishing left vs right or later developing ability to distinguish left and right, respectively. Comparing WS adults and MA controls, a 2 (group: WS adults, MA controls) x 2 (task: navigation, categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 9.36$, $p = 0.004$), with WS adults still performing disproportionately less accurately on the visually-guided navigation task than the scene categorization task, relative to MA controls. Further, comparing 4-year-olds and MA controls, a 2 (group: 4-year-olds, MA controls) x 2 (task: navigation, categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,36)} = 9.77$, $p = 0.004$), with 4-year-olds still showing the same pattern of results as before, performing disproportionately less accurately on the visually-guided navigation task than the scene categorization task, relative to MA controls. Error bars indicate standard error.

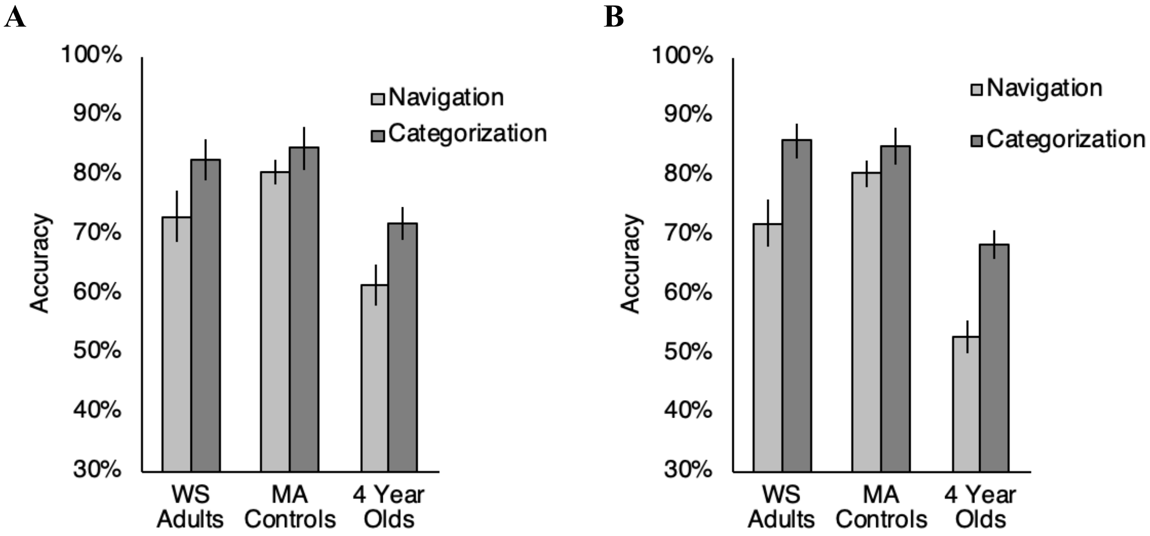

Figure 4. Average performance of WS adults, MA controls, and 4-year-olds on the visually-guided navigation and scene categorization tasks in the (A) room content experiment (reproduced from Figure 2 above) and (B) room layout experiment. We found disproportionate impairment on visually-guided navigation compared to scene categorization in WS, relative to MA controls, across both experiments. Specifically, comparing the room content experiment with the room layout experiment, a 2 (group: WS adults, MA controls) x 2 (task: navigation, categorization) x 2 (experiment: content, layout) failed to find a significant group x task x experiment interaction ($F_{(1,68)} = 0.40$, $p = 0.53$). Further, in 4-year-olds we that the visually-guided navigation system is later developing than scene categorization in typical development. Specifically, comparing the room content experiment with the room layout experiment, a 2 (group: 4-year-olds, MA controls) x 2 (task: navigation, categorization) x 2 (experiment: content, layout) failed to find a significant group x task x experiment interaction ($F_{(1,68)} = 0.61$, $p = 0.44$). These findings indicate that the pattern of results for both experiments are similar and serve as replicates. Error bars indicate standard error.

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