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Dissociable systems for recognizing places and navigating through them: developmental and neuropsychological evidence

By

Rebecca J. Rennert

B.S., Georgetown University, 2018

Advisor: Daniel D. Dilks, PhD

An abstract of
A thesis submitted to the Faculty of the James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of
Masters of Arts
in Psychology, 2023.

Abstract

Dissociable systems for recognizing places and navigating through them: developmental and neuropsychological evidence

By Rebecca J. Rennert

Recent neuroimaging studies in adult humans suggest that scene processing depends on dissociable systems for scene categorization (i.e., recognizing a place as a particular kind of place, for example, a kitchen) – including the parahippocampal place area (PPA) – and visually guided navigation (e.g., finding our way through a kitchen, not running into the kitchen walls or banging into the kitchen table) - including the occipital place area (OPA). A stronger test of this hypothesis would ask whether there is differential development of these systems in a typically developing (TD) population, and whether there is differential breakdown under neurological deficit. Here we tested scene categorization and visually guided navigation abilities in 131 TD male and female children between 4 and 9 years of age, as well as 46 male and female adults with Williams syndrome (WS) – a developmental disorder involving cortical thinning in and around OPA. We found that i) visually guided navigation is later to develop than scene categorization, and ii) WS adults are impaired in visually guided navigation, but not scene categorization, relative to mental-age matched children. These findings provide the first developmental and neuropsychological evidence for dissociable scene processing systems for recognizing places and navigating through them.

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Signficiance statement

Two decades ago Milner and Goodale showed us that identifying objects and manipulating them involve distinct neural processes and recent fMRI evidence suggests the same may be true of our interactions with our environment: identifying places and navigating through them are neurally dissociable. Here we provide the strongest test of this two-scene-systems hypothesis and find both differential development and breakdown of “scene categorization” and “visually guided navigation”. This finding suggests that the division of labor between action and perception systems is a general organizing principle for the visual system, not just a principle of the object processing system in particular.

Introduction

Milner and Goodale’s classic work showed that recognizing objects and manipulating them involve distinct processes in human adults, with visual perception (e.g., recognizing a cup) supported by the “ventral stream,” and visually guided action (e.g., reaching out and grasping a cup) supported by the “dorsal stream” (Goodale & Milner, 1992). Interestingly, recent fMRI evidence in human adults suggests that this division of labor between systems for perception and action is not limited to object processing, but also extends to *scene* processing (Dilks et al., 2011; Kamps et al., 2016; Persichetti & Dilks, 2016; Persichetti & Dilks, 2018; Persichetti & Dilks, 2019). In particular, it has been proposed that the more ventral parahippocampal place area (PPA) supports scene categorization (i.e., recognizing a place as a particular kind of place; for example, a kitchen), while the more dorsal occipital place area (OPA) supports visually guided navigation (i.e., finding one’s way through an immediately visible place, for example, moving through a kitchen, not bumping into the walls or smashing into the kitchen table) (Persichetti & Dilks, 2018; Dilks et al., 2022).

While the fMRI studies above provide initial evidence for dissociable scene processing systems, a stronger test of this hypothesis would ask whether these systems develop along different timelines in typical development. Given previous work in object processing suggesting that visually guided action develops later than visual perception (Atkinson et al., 2003; Bertenthal, 1996; Dilks et al., 2008), we predicted that a similar developmental dissociation will be found in scene processing, with visually guided navigation developing later than scene categorization. Some initial evidence is consistent with this prediction. For example, OPA undergoes protracted development across childhood, with responses to first-person perspective motion (i.e., mimicking the visual experience of walking through a scene) still emerging from 5 to 8 years old (Kamps et al., 2020). Behavioral studies likewise find protracted development of locomotion, obstacle avoidance, and boundary-based spatial memory abilities well into childhood (Berard & Vallis, 2006; Julian et al., 2019; Pryde et al., 1997). By contrast, scene categorization appears to develop early. For example, scene recognition memory matures faster than face or object recognition memory (Golarai et al., 2007). Critically, however, no study to date has compared the development of visually guided navigation and scene categorization directly.

To further test the idea of dissociable scene processing systems, we also explored how these systems break down in the case of Williams syndrome (WS). WS is a genetic, developmental disorder involving impaired dorsal stream processing alongside remarkably preserved ventral stream processing (at least for previous work focusing exclusively on object processing) (Atkinson et al., 1997; Meyer-Lindenberg et al., 2004; Paul et al., 2002; Dilks et al., 2008; Landau et al., 2006). WS also involves cortical thinning in the posterior parietal lobe, including the OPA (Meyer-Lindenberg et al., 2006). Thus, if visually guided navigation and scene categorization are dissociable, then WS adults will show greater impairment on a visually guided navigation task than on a scene categorization task, relative to typically developing control participants.

To study the development and breakdown of these scene processing abilities, typically developing (TD) children and WS adults performed two tasks, previously shown to differentially activate the scene categorization system (including PPA) and the visually guided navigation system (including OPA) in adults (Persichetti & Dilks, 2018). They are: i) a scene categorization task, in which participants viewed images of rooms and were asked to categorize the scene as a bedroom, kitchen, or living room; and ii) a visually guided navigation task, in which participants looked at these same pictures, but instead indicated which path they would follow to exit the room along a complete path on the floor. Note that these two tasks are performed on exactly the same stimuli in the same participants, allowing a powerful within-subjects comparison of performance on the two tasks, and ensuring that any differences are unlikely to be explained by low-level visual properties or global attention.

Materials and Methods

Participants

Eighty-seven TD children (46 females; range = 48-115 months) and thirty-six adults with WS (23 females) participated in the primary experiments. Additional groups of ten typically developing 4-year-olds (5 females; mean age = 53 months, range = 46-60 months), nineteen typically developing 7-year-olds (10 females; mean age = 90 months, range = 84-95 months), and ten WS adults (3 females) were also recruited for three control experiments. The WS adults were recruited through the Williams Syndrome Association (WSA), and all had been positively diagnosed by a geneticist and the FISH test, confirming a deletion in the characteristic WS region of chromosome 7 (Ewart et al., 1993). We collected data from WS adults for the primary experiment during the 2016 WSA Convention. Once the control experiments were designed, we collected data from WS adults for the control experiments during the 2018 and 2022 WSA Conventions. All adult participants and legal guardians of child participants gave informed consent.

Participants were tested on a standardized intelligence test, the Kaufman Brief Intelligence Test (KBIT) (Kaufman, 1990). This test yields an overall IQ score, as well as scores for two components, Verbal and Non-verbal (Matrices). The Verbal subtest requires participants to match words or descriptions to pictures, and the Matrices subtest requires participants to judge which objects or patterns “go together.” Each WS adult was individually matched to a TD control participant (selected from the original group of TD 4 to 9-year-olds) based on the non-verbal component specifically because nonverbal IQ is particularly susceptible to impairment in WS. Matching of the raw non-verbal scores between the WS and mental-age matched (MA) groups was done as closely as possible ($t_{(18)} = 0.08$, $p = 0.94$, $d = 0.02$), with a mode of 0 points difference (maximum difference = 1, $N = 4$). Given the known relative strength of language abilities in WS compared to non-verbal abilities, the WS group unsurprisingly had significantly higher raw verbal scores than the MA children ($t_{(15)} = 6.94$, $p <$ 1e-5, $d = 1.73$).

Experimental design, stimuli, and procedure

Participants performed two tasks: a scene categorization task and a visually guided navigation task, as previously used in an adult fMRI study (Persichetti & Dilks, 2018) (*Figure 1*). However, in order to make the tasks more understandable and accessible to children, the scene categorization task was referred to as the “rooms” game, while the visually guided navigation task was referred to as the “doors” game. During the scene categorization task, participants were asked to imagine standing in the room, but had to indicate what kind of room they were standing in (i.e., a “bedroom”, “kitchen”, or “living room”). Participants responded by verbal report. During the visually guided navigation task, participants were asked to imagine that they were walking on a continuous path through the room, and had to indicate whether they could leave through the door on the left, center, or right wall. To aid understanding, younger children were told that the ground was “lava,” and that only the paths on the ground were safe to walk on. The visually guided navigation task was designed in this way to simulate real-world navigation through the environment, similar to walking on a sidewalk, and not the grass, or on a clear path through a cluttered space. Furthermore, although our visually guided navigation task did not actually require participants to navigate through the environment (by design), we were confident that having participants simply look at pictures of places and imagine navigating through the rooms would be sufficient to recruit systems involved in visually guided navigation because the task has previously been shown to activate OPA in adults (Persichetti & Dilks, 2018). Indeed, many fMRI studies have used similarly “passive” tasks to elicit activation in dorsal regions responsible for the control of actions directed at objects (Chao and Martin, 2000; Okada et al., 2000; Johnson-Frey et al., 2005). Participants responded by pointing in the direction of the door out of which they would exit, ensuring that performance on the task was not contaminated by difficulty mapping egocentric directions to words for “left” and “right”.

The two tasks were matched on difficulty in TD adults (Persichetti & Dilks, 2018), and in all other aspects of the design, stimuli, and procedure. Immediately prior to the testing session, all participants first completed a short training phase of nonspeeded practice trials for each task, during which they were given feedback about whether or not their response was correct (participants were not given feedback during the testing session). Participants advanced from the training phase after responding correctly to at least 10 practice trials and after the experimenter was satisfied that they understood the task instructions. For the testing phase, both tasks were performed on the same set of 36 images. Stimuli were identical to those used in Persichetti and Dilks (2018) and were presented at a size of approximately 24 degrees visual angle on 11.97” x 8.36” LCD screen using custom software written for the Matlab Psychophysics Toolbox (Brainard, 1997). Participants completed 6 blocks of each task (12 blocks in total), and the order of blocks was pseudorandomized and counterbalanced across participants. An instruction screen appeared at the start of each block indicating which game/task (i.e., “doors”/visually guided navigation or “rooms”/scene categorization) would come next. Each block consisted of 12 experimental trials, and each trial consisted of a stimulus presented for 500 ms, followed by a fixation screen, during which the participant gave a nonspeeded 3AFC response. The next trial began only after the participant had responded and was ready to start again. For both tasks, the experimenter recorded participant responses via button press. Finally, in order to verify that participants understood and were paying attention to the task, the testing phase was evenly interspersed with 12 “catch” trials (6 for each task, 1 per block), in which images were presented for 2000 ms, rendering the task trivially easy, and therefore assessing basic task understanding and attentiveness.

Results

The visually guided navigation system develops later than the scene categorization system in typical development

If visually guided navigation and scene categorization are indeed dissociable systems, then these systems may develop along independent timelines in typical development. To test this hypothesis, we compared scene categorization and visually guided navigation abilities in TD children between 4 and 9 years of age (*Figure 2)*. A linear trend analysis revealed a significant interaction between the developmental trajectories for the visually guided navigation task and the scene categorization task ($F_{(1,86)} = 44.1$, $p <$ 1e-8, $\eta_p^2 = 0.34$), with performance on the visually guided navigation task improving significantly more with age than on the scene categorization task. To give a numerical value for the rate of development with age, we calculated regression slopes for each task: regressing task performance on individuals' age gave a slope for visually guided navigation (B = 7.95) that was steeper than the slope for scene categorization (B = 5.19). Thus, visually guided navigation and scene categorization develop differentially, with visually guided navigation developing later than scene categorization.

Restriction of range?

We next addressed the possibility that these results could be driven by a restriction of range effect, which can produce false interactions due to floor or ceiling effects (McKone et al., 2012). Although all children performed above floor on both tasks (one sample t-tests; all *t*'s > 22.67, *p's* < 1e-16, *d's* > 2.43) and below ceiling on both tasks (one sample t-tests; all *t*'s > 12.78, *p's* < 1e-16, both *d's* > 1.37), the oldest children (i.e., the 8 to 9-year-olds) still performed close to ceiling, and the distribution of accuracy scores in the older group differed significantly from the normal distribution (Shapiro-Wilk normality test, W = 0.92, $p = 0.007$), consistent with the possibility of a restriction of range. For example, perhaps the near-ceiling performance of the older kids on the categorization task is actually driving the interaction of task and age. To rule out this possibility, we therefore dropped all of the older children from the analysis, and instead compared the performance on the visually guided navigation task and the scene categorization task for only the youngest children (i.e., the 4 to 5-year-olds), who clearly performed far from ceiling (*Figure 2*). A linear trend analysis again revealed a significant interaction between developmental trends for the visually guided navigation task and the scene categorization task ($F_{(1,42)} = 37.97$, $p <$ 1e-6, $\eta_p^2 = 0.48$), with performance on the visually guided improving significantly more with age than on the scene categorization task, even within our youngest participants. Thus, the finding that visually guided navigation is later to develop than scene categorization is not due to a restriction of range effect.

Attention or task understanding?

The visually guided navigation task might appear slower to develop than the scene categorization task because younger children simply paid less attention during the visually guided navigation task, or did not understand the task instructions. We addressed these possibilities in two ways. First, even the youngest (i.e., 4 to 5-year-old) children performed above chance on the visually guided navigation task ($t_{(41)} = 12.44$, $p <$ 1e-15, $d = 1.92$). On average, children performed at 82% and 85% accuracy on the visually guided navigation task and the scene categorization task, respectively. Second, we compared performance on several additional, slower catch trials designed to probe task understanding specifically. A linear trend analysis did not reveal a significant interaction between developmental trends for the visually guided navigation catch trials and the scene categorization catch trials ($F_{(1,86)} = 0.96$, $p = 0.33$, $\eta_p^2 = 0.01$). Thus, our results are not due to children not paying attention to, or not understanding, the visually guided navigation task.

Executive function?

Executive function develops considerably across childhood; thus, the slow development of visually guided navigation could be entirely driven by immature executive function abilities. For example, despite our best efforts to match task demands across the two tasks, immature executive function (e.g., inhibitory processing) could disproportionately affect the navigation task, since this task requires ignoring two possible wrong answers to select a correct one, while the categorization task does not. To address this concern, we recruited an additional group of 4-year-old children (N = 10) to perform a follow-up "phone" task in which participants viewed an image of a phone, wires, and three outlets, and answered which of three outlets the phone was connected to via a complete wire (*Figure 3A*). In this way, the phone task was closely matched to the visually guided navigation task in terms of executive function (and inhibitory processing in particular), but crucially did not involve visually guided navigation (*Figure 3B*). A paired-sample t-test revealed significantly stronger performance on the phone task than the visually guided navigation task ($t_{(9)} = 2.90$, $p = 0.02$, $d = 0.92$), ruling out the possibility that performance on the visually guided navigation task is explained by immature inhibition (since in that case, 4-year-olds would do equally poorly on both tasks), and consistent with the hypothesis of a slow-developing visually guided navigation system.

Object recognition, not scene categorization?

A final alternative explanation for our findings is that the scene categorization task can potentially be solved by recognizing the objects in the room (e.g., a "bed"), and then inferring the scene category (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). To address this alternative explanation, we created a second scene categorization task in which a brand-new group of participants (N = 34) was asked to judge the category of empty rooms (i.e., containing no objects whatsoever) that differed based on their spatial layout (i.e., the arrangement of the walls, floor, and ceiling). The categories of the “empty room” scene categorization task were now the “boring room”, “hallway room”, or “stairs room”. For comparison, participants again performed a visually guided navigation task on the same “empty room” stimuli. A linear trend analysis again revealed a significant interaction between developmental trends for the “empty rooms” visually guided navigation and scene categorization tasks ($F_{(1,33)} = 15$, $p < 0.001$, $\eta_p^2 = 0.31$), with performance on the visually guided navigation task improving significantly more with age than on the scene categorization task. Thus, our findings cannot be explained by an “object recognition” strategy.

The visually guided navigation system is disproportionately impaired in Williams syndrome

If visually guided navigation and scene categorization are dissociable cognitive systems, then these systems may be differentially impaired in a case of neurological insult caused by altered genetics. To test this prediction, we next tested adults with WS, who we predicted will show greater impairment on a visually guided navigation task than a scene categorization task, relative to MA controls. Consistent with this prediction, a 2 (group: WS adults, MA controls) x 2 (task: visually guided navigation, scene categorization) mixed-model ANOVA revealed a significant interaction ($F_{(1,36)} = 4.48$, $p = 0.04$, $\eta_p^2 = 0.11$), with the WS adults performing worse than MA controls on the visually guided navigation task ($t_{(36)} = 2.09$, $p = 0.04$, $d = 0.68$), but no different than MA controls on the scene categorization task ($t_{(36)} = 0.37$, $p = 0.72$, $d = 0.12$) (*Figure 4)*. These results suggest that WS adults are more impaired on the visually guided navigation task than the scene categorization task, relative to MA controls.

Importantly, the WS adults were matched to individual MA controls on *non-verbal* IQ , but as a consequence (due to their uneven cognitive profile), showed higher performance than MA controls on *verbal* IQ. It is possible then that WS adults may in fact be impaired on *both* the categorization and visually guided navigation tasks, but nevertheless perform better on the categorization task due to their relatively superior linguistic processing. To address this possibility, we found pairs of individual MA controls and WS adults (N=16 pairs) who were closely matched based on the *verbal* component of the KBIT-2 ($t_{(15)} = 0.86$, $p = 0.41$, $d = 0.21$; with a mode of 0.63 points difference). When we reran the critical 2 (group: WS adults, MA controls) x 2 (task: visually guided navigation, scene categorization) mixed-model ANOVA, we found a significant interaction ($F_{(1,30)} = 8.27$, $p = 7.00\text{e-}3$, $\eta_p^2 = 0.22$), with the WS adults performing worse than MA controls on the visually guided navigation task, relative to the scene categorization task ($t_{(30)} = 4.45$, $p = 1.00\text{e-}3$, $d = 1.57$). Thus, the WS profile cannot be explained by superior language processing (relative to MA controls), and instead arises from disproportionate impairment to the visually guided navigation system.

Restriction of range?

We next considered the possibility that these effects could be driven by a restriction of range effect (McKone et al., 2012). To address this concern, we found pairs of individual MA controls and WS adults who were closely matched based on their accuracy during the visually guided navigation task (where performance was on average further from ceiling than that for the categorization task). If the relative impairment of WS adults on the visually guided navigation task observed above is due to ceiling effects, then this impairment should disappear in this subset of individuals who scored further from ceiling overall (McKone et al., 2012). Rejecting this alternative prediction, when we reran the critical 2 (group: WS adults, MA controls) x 2 (task:

visually guided navigation, scene categorization) mixed-model ANOVA, we again found a significant interaction ($F_{(1,36)} = 5.21$, $p = 0.028$, $\eta_p^2 = 0.13$), with the WS adults performing disproportionately worse on the visually guided navigation task than the scene categorization task, relative to MA controls ($t_{(18)} = 3.86$, $p = 0.001$, $d = 0.88$). Thus, the observed interaction is not driven by ceiling effects.

Attention or task understanding?

The reduced accuracy of WS adults on the visually guided navigation task did not reflect a failure of the WS adults to understand or pay attention during the task, since the WS adults (like the MA controls) performed well above chance overall (WS = 72%, MA = 81%). Furthermore, there was no difference in the performance of WS adults on the scene categorization and visually guided navigation catch trials ($t_{(18)} = 1.05$, $p = 0.31$, $d = 0.24$). Accordingly, our results are not likely explained by WS failing to understand or pay attention during the visually guided navigation task.

Executive function?

But is the WS adults' impaired performance on the visually guided navigation task due to a possible impairment in executive function? To rule out this possibility, we recruited an additional group of WS individuals (N = 10) to perform the phone task (where inhibitory processing is now matched to the visually guided navigation task). A paired-sample t-test revealed significantly stronger performance on the phone task than the visually guided navigation task ($t_{(9)} = 2.86$, $p = 0.02$, $d = 0.29$), ruling out the possibility that WS adults' impaired performance on the visually guided navigation task is explained by impaired inhibitory control.

Does WS reflect typical cognition?

Given that WS is a genetic, developmental disorder, it has been argued that WS cannot be used as a neuropsychological model of the typical system, since genetic and developmental differences could lead to qualitatively different underlying systems between WS and typically developing individuals (Karmiloff-Smith, 1997). By contrast, our hypothesis is that despite their *quantitatively* worse performance relative to MA controls, WS individuals will nevertheless perform the visually guided navigation task *qualitatively* similar to typically developing individuals—suggesting that WS individuals employ a qualitatively similar mechanism. To test this hypothesis, we compared each group's pattern of performance across the three visually guided navigation trial types (i.e., left, center, and right). A 2 (group: WS adults, MA controls) x 3 (trial type: left, center, right) mixed-model ANOVA revealed a significant main effect of trial type ($F_{(2,72)} = 33.46$, $p <$ 1e-10, $\eta_p^2 = 0.48$), with both groups showing greater accuracy on center trials than right trials (pairwise comparisons, both p's < 0.01), and no difference between center trials and left trials (pairwise comparisons, both p's $> .08$) (*Figure 5*). Critically, however, we failed to find a significant group x trial type interaction ($F_{(2,72)} = 0.97$, $p = 0.38$, $\eta_p^2 = 0.03$), indicating that these patterns did not qualitatively differ between the two groups (*Figure 5*). A permutation F-test also failed to reveal a significant group x trail type interaction ($p = 0.36$), and an additional Bayes Factor hypothesis testing found evidence in favor of the null hypothesis ($BF_{10} = 0.278$; Bayes Factor < 0.33 supports the null hypothesis).

Critically, an even stronger test of the hypothesis that WS adults and typically developing children employ qualitatively similar cogntive systems would evaluate whether the WS pattern of performance (i.e., with lower performance on the visually guided navigation task than the categorization task) is found at earlier stages of typical development. This finding would support the idea that the WS cognitive profile arises from developmental arrest of systems that typically mature later in development – that is, qualitatively similar underlying mechanisms that did not fully mature (Landau & Ferrara, 2013; Dilks et al., 2008). We therefore next compared the WS adults with a younger group of typically developing 4-year-olds. Like the WS adults, 4-year-olds were significantly more accurate on the scene categorization task than the visually guided navigation task ($t_{(18)} = 4.77, p < 0.001, d = 1.36$). Further, a 2 (group: WS adults, 4-year-olds) x 2 (task: visually guided navigation, scene categorization) mixed-model ANOVA did not reveal a significant interaction ($F_{(1,36)} = 0.15, p = 0.70, \eta_p^2 = 0.004$), and a permutation F-test corroborated this result ($p = 0.69$). An additional Bayes Factor hypothesis testing found marginal evidence in favor of the null hypothesis ($BF_{10} = 0.342$; Bayes Factor < 0.33 supports the null hypothesis). Importantly, WS adults and 4-year-olds did not show evidence of qualitatively different patterns of performance across the visually guided navigation trial types (group x trial type interaction: $F_{(2,72)} = 0.67, p = 0.52, \eta_p^2 = 0.02$) (*Figure 5*). A permutation F-test also failed to reveal a significant group x trial type interaction ($p = 0.48$), and an additional Bayes Factor hypothesis testing found evidence in favor of the null hypothesis ($BF_{10} = 0.230$; Bayes Factor < 0.33 supports the null hypothesis). Of course, caution should be taken in interpreting the lack of signficant differences between WS and TD groups on these meaures, as it is always possible that differences between groups could be found using another measure. Nonetheless, taken together, we find no evidence against the hypothesis that WS involves qualitatively different underlying mechanisms that are less developed relative to their mental age, consistent with the idea that WS is a valid neuropsychological model of typical cognitive systems more generally.

Object recognition, rather than scene categorization?

Finally, to address the alternative explanation that WS individuals solved the task by recognizing objects, rather than categorizing scenes, a new group of participants was asked to judge the category of empty rooms that differed based on their spatial layout (i.e., the arrangement of the walls, floor, and ceiling). A 2 (experiment: furnished rooms, empty rooms) x 2 (group: WS adults, MA controls) x 2 (task: visually guided navigation, scene categorization) mixed-model ANOVA revealed a significant group x task interaction ($F_{(1,68)} = 5.43$, $p = 0.02$, $\eta_p^2 = 0.07$), with WS adults showing weaker performance on the visually guided navigation task than the scene categorization task, relative to the MA controls – but critically did not reveal a significant experiment x group x task interaction ($F_{(1,68)} = 0.19$, $p = 0.67$, $\eta_p^2 = 0.003$), suggesting that the strength of the group x task interaction effect (revealing greater impairment of the visually guided navigation system than the scene categorization system) did not differ between furnished and empty rooms tasks (*Figure 6*). A permutation F-test also failed to find a significant experiment x group x task interaction ($p = 0.67$), and an additional Bayes Factor hypothesis testing found evidence in favor of the null hypothesis ($BF_{10} = 0.018$; Bayes Factor < 0.33 supports the null hypothesis). Thus, our findings cannot be explained by an "object recognition" strategy.

Discussion

The present results provide converging developmental and neuropsychological evidence for the hypothesis that scene processing involves dissociable cognitive systems for visually guided navigation and scene categorization. This "two-scene-systems" proposal dovetails with the classic division of labor found in object processing between dorsal systems for action and ventral systems for object perception (Goodale & Milner, 1992), and suggests that the division between systems for action and perception constitutes a general organizing principle for the visual system more generally, operating across cognitive domains. This work also lends additional support to the idea that the dorsal action system may be later to mature than the ventral perception system, both for object and scene processing.

The finding that visually guided navigation ability undergoes protracted development across childhood closely mirrors recent evidence that OPA is still developing sensitivity to navigationally-relevant information across this same age range (Kamps et al., 2020), as well as evidence that boundary-based spatial memory and obstacle avoidance are still developing late into childhood (Berard & Vallis, 2006; Julian et al., 2019; Pryde et al., 1997). Nevertheless, the idea of a late developing visually guided navigation system may seem surprising, given that humans begin navigating early in life (e.g., crawling around 9 months) and show remarkably sophisticated navigational ability within the first few years. For example, young children can use boundaries to recover their orientation after becoming disoriented (Hermer & Spelke, 1994), and infants understand whether it is safe to locomote over a ‘visual cliff’ (Gibson & Walk, 1960). How then can we reconcile these observations with the hypothesis that visually guided navigation undergoes protracted development? One possibility is that these tasks rely on different systems. For example, the reorientation task may involve spatial memory systems in the hippocampus, while the visual cliff task may depend on basic depth perception in early visual cortex. A second possibility is that these tasks *do* rely on the same visually guided navigation system, and that despite development extending well into childhood (as detected here), the foundations of this system are nevertheless intact early, and sufficient to support these early navigational behaviors.

The finding that WS individuals are impaired in visually guided navigation is consistent with studies showing deficits on other navigation tasks in WS, including reorientation (Lakusta et al., 2010; Ferrara et al., 2019) and boundary-based spatial memory (Julian et al., 2019).

However, it is unclear precisely which neural systems are damaged in WS, and therefore whether these various navigational impairments result from damage to the same or different systems. Our findings suggest that WS adults have an under-developed OPA, since the visually guided navigation task used here has been shown to selectively activate OPA in typically developing adults (Persichetti & Dilks, 2018), and WS adults have reduced grey matter and sulcal depth in parietal cortex near the typical location of OPA (Meyer-Lindenberg et al., 2006). Given that OPA represents the egocentric distance and direction of environmental boundaries during navigation (Dilks et al., 2011; Julian et al., 2016; Persichetti & Dilks, 2016), one possibility is that the spatial reorientation and boundary-based spatial memory impairments result from an under-developed OPA as well. However, another possibility is that these impairments affect neural systems beyond OPA, such as the hippocampus (Doeller et al., 2008), which also may be dysfunctional in WS (Meyer-Lindenberg et al., 2006). Notably, it is unlikely that such damage affected performance on the visually guided navigation task here, since our task tested perception rather than memory.

In contrast to their impaired visually guided navigation ability, WS adults showed relatively spared scene categorization ability. Indeed, WS adults successfully categorized rooms based on both the spatial layout of the boundary walls and the objects within the rooms. The ability of WS adults to use either spatial layout or scene content infromation for scene categorization strengthens the claim that this system is intact, given evidence from both computer vision and adult fMRI studies suggesting that scene categories are represented by two independent, yet complementary descriptors: spatial boundary (i.e., the external shape, size, and scope of the space) and scene content (i.e., the internal features of the scene encompassing objects, textures, colors, and materials) (Epstein and Kanwisher, 1998; Oliva & Torralba, 2001;

Oliva & Torralba, 2002; MacEvoy and Epstein, 2011; Oliva, 2014). This finding also suggests that WS individuals do not have a deficit in boundary perception per se; rather, WS adults may be impaired in using boundaries for navigation (reflecting an impaired navigation system), despite a spared ability to use boundaries for scene categorization (reflecting an intact scene categorization system). Importantly, however, note that our results cannot yet establish whether the scene categorization system is *fully* spared in WS, or whether this system might also show some (relatively subtle) impairment as well. For example, supporting this second possibility, one recent study (Ferrara et al., 2019) found that PPA responses to scene boundaries are weaker in WS adults compared with typically developing adults. Notably, however, that study did not i) compare WS adults to MA controls, ii) determine whether these dampened neural responses were specific to PPA versus also found in OPA, nor iii) establish whether the response to scene boundary information reflected the use of such information for navigating versus categorizing scenes. Thus, future work will be required to establish whether the scene categorization system is fully spared in WS. In any case, our results do at least establish a relative impairment of WS adults in using boundary information for navigating versus categorizing scenes.

Finally, our study broadly supports a recent hypothesis about the nature of WS itself, which argues that the uneven WS cognitive profile emerges from developmental arrest of those cognitive abilities that are late emerging in typical development (Landau & Ferrara, 2013; Dilks et al., 2008). Consistent with the predictions of this hypothesis, we found that the visually guided navigation system, which is late developing in typical development, is likewise arrested in WS (resulting in weaker performance in WS, relative to MA controls), unlike the scene categorization system, which is earlier developing in typical development and relatively spared in WS. Although the precise age at which this developmental arrest occurs is not yet established, our results suggest that it may be around 4-years-old, consistent with many previous studies (Landau & Ferrara, 2013; Dilks et al., 2008).

In conclusion, here we found that visually guided navigation is later to develop than scene categorization, and is disproportionately impaired in WS. Future work will ask whether it is possible to find the complementary case of impaired scene categorization ability, but spared visually guided navigation ability, and thus evidence of a double dissociation. In any case, the present single dissociation provides the first developmental and neuropsychological evidence for dissociable scene categorization and visually guided navigation systems.

References

Atkinson, J., Braddick, O., Anker, S., Curran, W., Andrew, R., Wattam-Bell, J., & Braddick, F. (2003). Neurobiological Models of Visuospatial Cognition in Children With Williams Syndrome: Measures of Dorsal-Stream and Frontal Function. *Developmental Neuropsychology*, *23*(1–2), 139–172. https://doi.org/10.1080/87565641.2003.9651890

Atkinson, J., King, J., Braddick, O., Nokes, L., Anker, S., & Braddick, F. (1997). A specific deficit of dorsal stream function in Williams' syndrome. *NeuroReport*, *8*(8), 1919–1922.

Berard, J. R., & Vallis, L. A. (2006). Characteristics of single and double obstacle avoidance strategies: A comparison between adults and children. *Experimental Brain Research*, *175*(1), 21–31. https://doi.org/10.1007/s00221-006-0529-0

Bertenthal, B. I. (1996). Origins and early development of perception, action, and representation. *Annual Review of Psychology*, *47*, 431. http://dx.doi.org/10.1146/annurev.psych.47.1.431

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.

Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, *12*(4), 478–484. https://doi.org/10.1006/nimg.2000.0635

Dilks, D. D., Hoffman, J. E., & Landau, B. (2008). Vision for perception and vision for action: Normal and unusual development. *Developmental Science*, *11*(4), 474–486. https://doi.org/10.1111/j.1467-7687.2008.00693.x

Dilks, D. D., Julian, J. B., Kubilius, J., Spelke, E. S., & Kanwisher, N. (2011). Mirror-Image Sensitivity and Invariance in Object and Scene Processing Pathways. *Journal of Neuroscience*, *31*(31), 11305–11312. https://doi.org/10.1523/JNEUROSCI.1935-11.2011

Dilks, D. D., Kamps, F. S., & Persichetti, A. S. (2022). Three cortical scene systems and their development. *Trends in Cognitive Sciences*, *26*(2), 117–127. https://doi.org/10.1016/j.tics.2021.11.002

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences*, *105*(15), 5915–5920. https://doi.org/10.1073/pnas.0801489105

Epstein, R. A. (2008). Parahippocampal and retrosplenial contributions to human spatial navigation. *Trends in Cognitive Sciences*, *12*(10), 388–396. https://doi.org/10.1016/j.tics.2008.07.004

Epstein, R. A., & Vass, L. K. (2014). Neural systems for landmark-based wayfinding in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1635), 20120533. https://doi.org/10.1098/rstb.2012.0533

Ewart, A. K., Morris, C. A., Atkinson, D., Jin, W., Sternes, K., Spallone, P., Stock, A. D., Leppert, M., & Keating, M. T. (1993). Hemizygosity at the elastin locus in a developmental disorder, Williams syndrome. *Nature Genetics*, *5*(1), 11–16. https://doi.org/10.1038/ng0993-11

Ferrara, K., Landau, B., & Park, S. (2019). Impaired behavioral and neural representation of scenes in Williams syndrome. *Cortex*, *121*, 264–276. https://doi.org/10.1016/j.cortex.2019.09.001

Gibson, E. J., & Walk, R. D. (1960). The "visual cliff". *Scientific American*, *202*, 64–71.

Golarai, G., Ghahremani, D. G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J. L., Gabrieli, J. D. E., & Grill-Spector, K. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience*, *10*(4), 512–522. https://doi.org/10.1038/nn1865

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–25. https://doi.org/10.1016/0166-2236(92)90344-8

Gregory, E., Landau, B., & McCloskey, M. (2011). Representation of object orientation in children: Evidence from mirror-image confusions. *Visual Cognition*, *19*(8), 1035–1062. https://doi.org/10.1080/13506285.2011.610764

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature*, *370*(6484), 57–59. https://doi.org/10.1038/370057a0

Johnson-Frey, S. H., Newman-Norlund, R., & Grafton, S. T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral cortex (New York, N.Y. : 1991)*, *15*(6), 681–695. https://doi.org/10.1093/cercor/bhh169

Julian, J. B., Ryan, J., Hamilton, R. H., & Epstein, R. A. (2016). The Occipital Place Area Is Causally Involved in Representing Environmental Boundaries during Navigation. *Current Biology*, *26*(8), 1104–1109. https://doi.org/10.1016/j.cub.2016.02.066

Julian, J. B., Keinath, A. T., Marchette, S. A., & Epstein, R. A. (2018). The neurocognitive basis of spatial reorientation. *Current Biology : CB*, *28*(17), R1059–R1073. https://doi.org/10.1016/j.cub.2018.04.057

Julian, J. B., Kamps, F. S., Epstein, R. A., & Dilks, D. D. (2019). Dissociable spatial memory systems revealed by typical and atypical human development. *Developmental Science*, *22*(2), e12737. https://doi.org/10.1111/desc.12737

Kamps, F. S., Lall, V., & Dilks, D. D. (2016). The occipital place area represents first-person perspective motion information through scenes. *Cortex*, *83*, 17–26. https://doi.org/10.1016/j.cortex.2016.06.022

Kamps, F. S., Julian, J. B., Battaglia, P., Landau, B., Kanwisher, N., & Dilks, D. D. (2017). Dissociating intuitive physics from intuitive psychology: Evidence from Williams syndrome. *Cognition*, *168*, 146–153. https://doi.org/10.1016/j.cognition.2017.06.027

Kamps, F. S., Pincus, J. E., Radwan, S. F., Wahab, S., & Dilks, D. D. (2020). Late Development of Navigationally Relevant Motion Processing in the Occipital Place Area. *Current Biology*, *30*(3), 544-550.e3. https://doi.org/10.1016/j.cub.2019.12.008

Karmiloff-Smith, A. (1997). Crucial differences between developmental cognitive neuroscience and adult neuropsychology. *Developmental Neuropsychology*, *13*(4), 513–524. https://doi.org/10.1080/87565649709540693

Kaufman, A. S. & Kaufman, N. L. (Ed.) (1990). *Manualforthe Kaufman Brief Intelligence Test*. American Guidance Service.

Lakusta, L., Dessalegn, B., & Landau, B. (2010). Impaired geometric reorientation caused by genetic defect. *Proceedings of the National Academy of Sciences*, *107*(7), 2813–2817. https://doi.org/10.1073/pnas.0909155107

Landau, B., Hoffman, J. E., & Kurz, N. (2006). Object recognition with severe spatial deficits in Williams syndrome: Sparing and breakdown. *Cognition*, *100*(3), 483–510. https://doi.org/10.1016/j.cognition.2005.06.005

Landau, B., & Ferrara, K. (2013). Space and language in Williams syndrome: Insights from typical development. *Wiley Interdisciplinary Reviews. Cognitive Science*, *4*(6), 693–706. https://doi.org/10.1002/wcs.1258

McKone, E., Crookes, K., Jeffery, L., & Dilks, D. D. (2012). A critical review of the development of face recognition: Experience is less important than previously believed. *Cognitive Neuropsychology*, *29*(1–2), 174–212. https://doi.org/10.1080/02643294.2012.660138

Meyer-Lindenberg, A., Kohn, P., Mervis, C. B., Kippenhan, J. S., Olsen, R. K., Morris, C. A., & Berman, K. F. (2004). Neural Basis of Genetically Determined Visuospatial Construction Deficit in Williams Syndrome. *Neuron*, *43*(5), 623–631. https://doi.org/10.1016/j.neuron.2004.08.014

Meyer-Lindenberg, A., Mervis, C. B., & Berman, K. F. (2006). Neural mechanisms in Williams syndrome: A unique window to genetic influences on cognition and behaviour. *Nature Reviews. Neuroscience*, *7*(5), 380–393. https://doi.org/10.1038/nrn1906

Oliva, A., & Torralba, A. (2001). Modeling the Shape of the Scene: A Holistic Representation of the Spatial Envelope. *International Journal of Computer Vision*, *42*(3), 145–175. https://doi.org/10.1023/A:1011139631724

Oliva, A., & Torralba, A. (2002). Scene-Centered Description from Spatial Envelope Properties. In H. H. Bülthoff, C. Wallraven, S.-W. Lee, & T. A. Poggio (Eds.), *Biologically Motivated Computer Vision* (pp. 263–272). Springer. https://doi.org/10.1007/3-540-36181-2_26

Oliva, A. (2014). Scene Perception. In L.M. Chalupa & J.S. Werner (Eds.), The New Visual Neurosciences. Cambridge: MIT Press.

Okada, T., Tanaka, S., Nakai, T., Nishizawa, S., Inui, T., Sadato, N., Yonekura, Y., Konishi, J. (2000). Naming of animals and tools: a functional magnetic resonance imaging study of categorical differences in the human brain areas commonly used for naming visually presented objects. *Neurosci. Lett., 296,* 33–36.

Paul, B. M., Stiles, J., Passarotti, A., Bavar, N., & Bellugi, U. (2002). Face and place processing in Williams syndrome: Evidence for a dorsal-ventral dissociation. *NeuroReport*, *13*(9), 1115–1119.

Persichetti, A. S., & Dilks, D. D. (2016). Perceived egocentric distance sensitivity and invariance across scene-selective cortex. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *77*, 155–163. https://doi.org/10.1016/j.cortex.2016.02.006

Persichetti, A. S., & Dilks, D. D. (2018). Dissociable Neural Systems for Recognizing Places and Navigating through Them. *The Journal of Neuroscience*, *38*(48), 10295–10304. https://doi.org/10.1523/JNEUROSCI.1200-18.2018

Persichetti, A. S., & Dilks, D. D. (2019). Distinct representations of spatial and categorical relationships across human scene-selective cortex. *Proceedings of the National Academy of Sciences*, *116*(42), 21312–21317. https://doi.org/10.1073/pnas.1903057116

Pryde, K. M., Roy, E. A., & Patla, A. E. (1997). Age-related trends in locomotor ability and obstacle avoidance. *Human Movement Science*, *16*(4), 507–516. https://doi.org/10.1016/S0167-9457(96)00064-4

Furnished Rooms	**WS adults (N=19)**		**MA children (N=19)**		**4-year-olds (N=19)**	
	M (± SEM)	**Range**	**M (± SEM)**	**Range**	**M (± SEM)**	**Range**
Chronological Age (years)	28.58(1.82)	19-46	6.71(0.22)	5.75-8.5	4.54(0.07)	4.00-5.08
Matrices KBIT (raw score)	25.31(1.72)	14-42	25.16(1.81)	14-43	16.05(1.06)	20-35
Verbal KBIT (raw score)	71.44(2.68)	50-92	49.42(2.83)	34-71	27.05(0.90)	9-31

Empty Rooms	**WS adults (N=19)**		**MA children (N=19)**		**4-year-olds (N=19)**	
	M (± SEM)	**Range**	**M (± SEM)**	**Range**	**M (± SEM)**	**Range**
Chronological Age (years)	27.69(1.42)	19-44	7.07(0.12)	6.17-8.00	4.61(0.08)	4.00-5.00
Matrices KBIT (raw score)	24.00(2.29)	14-32	23.41(1.90)	14-33	14.59(0.70)	8-20
Verbal KBIT (raw score)	69.50(2.37)	59-78	49.41(2.41)	34-71	30.19(1.51)	19-42

Table 1. Williams syndrome (WS) adults, mental-age matched (MA) children, and 4-year-old children participant characteristics for the primary experiments.

Figure 1. Example stimuli used in the scene categorization and visually guided navigation tasks for the primary experiment. For the scene categorization task, participants were asked to judge whether the room is a bedroom, kitchen, or living room. The answers for the stimuli above, from left to right, are “bedroom,” “kitchen,” and “living room.” For the visually guided navigation task, participants were asked to judge which door they could leave out of along a complete path on the floor. The answers for the stimuli above, from left to right, are “left,” “center,” and “right.”

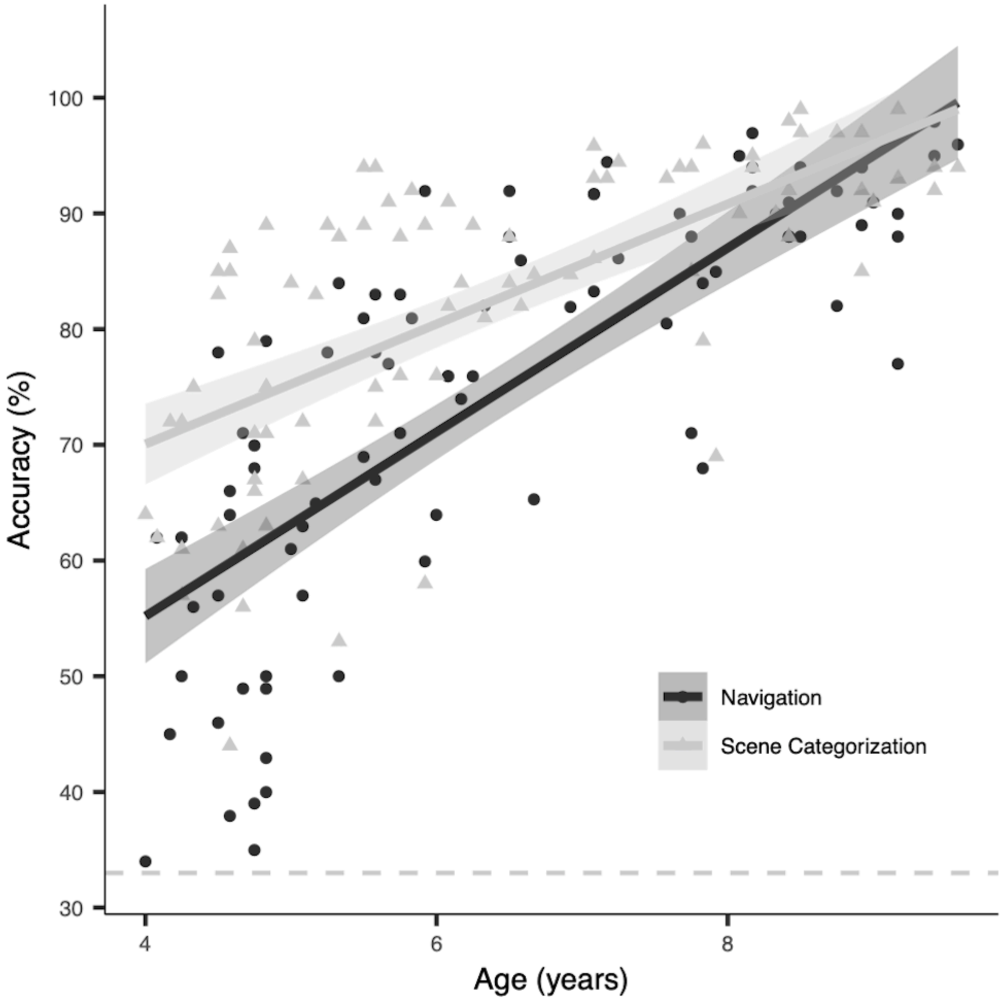

Figure 2. Average performance of typically developing children on the visually guided navigation and scene categorization tasks. The rate of development over age was significantly different between the visually guided navigation task and the scene categorization task, providing developmental evidence for independent visually guided navigation and scene categorization systems. Each black circle represents a participant's performance on the visually guided navigation task and each grey triangle represents a participant's performance on the scene categorization task. The grey dotted lines indicate chance performance. Shaded regions around the regression line indicate a 95% confidence interval.

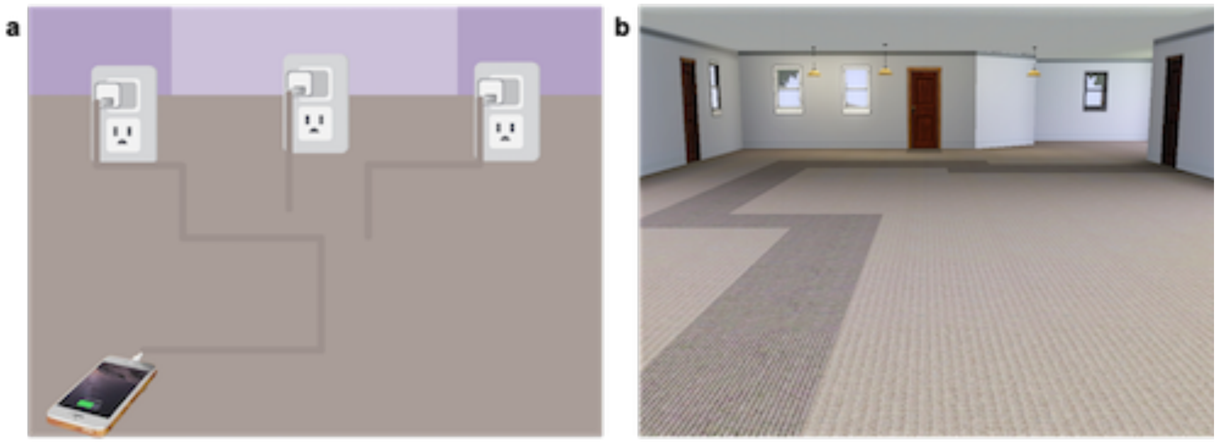

Figure 3. Example stimuli used in the follow-up “phone task” experiment. For the phone task (a), participants were asked to judge what outlet the phone was connected to via a complete wire. For the visually guided navigation task (b), participants were asked to judge which doors they could leave out of along a complete path on the floor. These tasks are matched on virtually every aspect except only one (b) involves visually guided navigation.

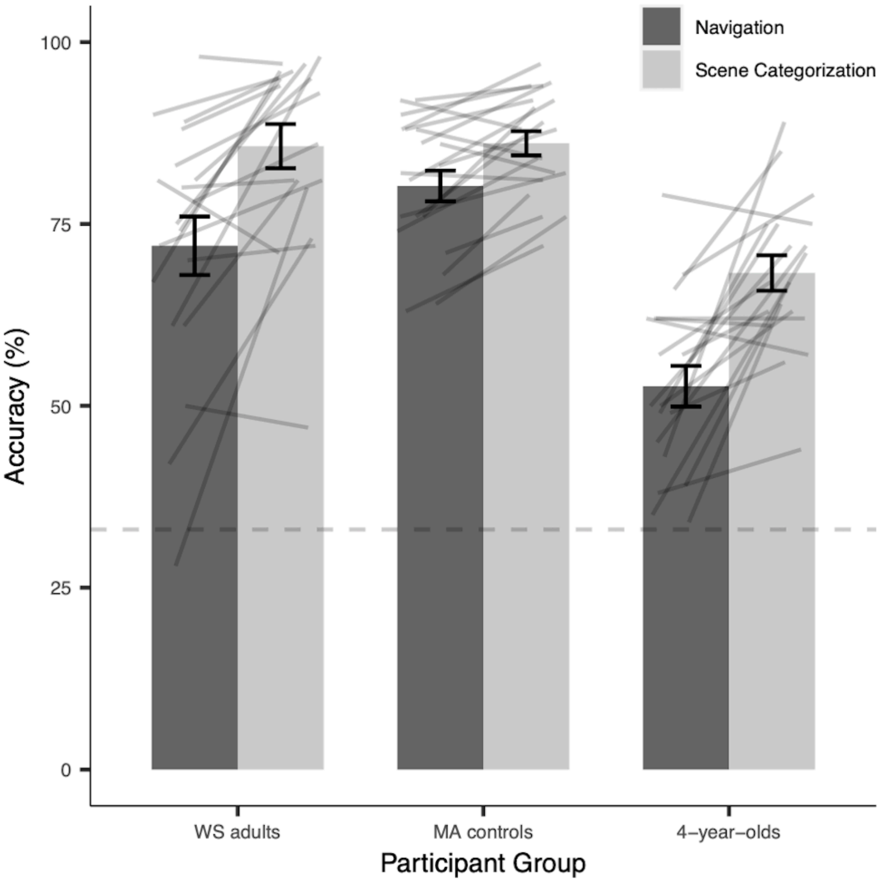

Figure 4. Average performance of WS adults, MA controls, and 4-year-olds on the visually guided navigation and scene categorization tasks. WS adults performed disproportionately worse on the visually guided navigation task than the categorization task, relative to MA controls, providing causal evidence for the dissociation between these systems. Further, 4-year-olds performed disproportionately worse on the visually guided navigation task than the scene categorization task, relative to MA controls (who were 7 years old on average), providing developmental evidence for independent visually guided navigation and scene categorization systems, with the visually guided navigation system arising later in development than the scene categorization system. The grey dotted line indicates chance performance. Each solid grey line connects a participant's performance on the visually guided navigation task to the same participant's performance on the scene categorization task.

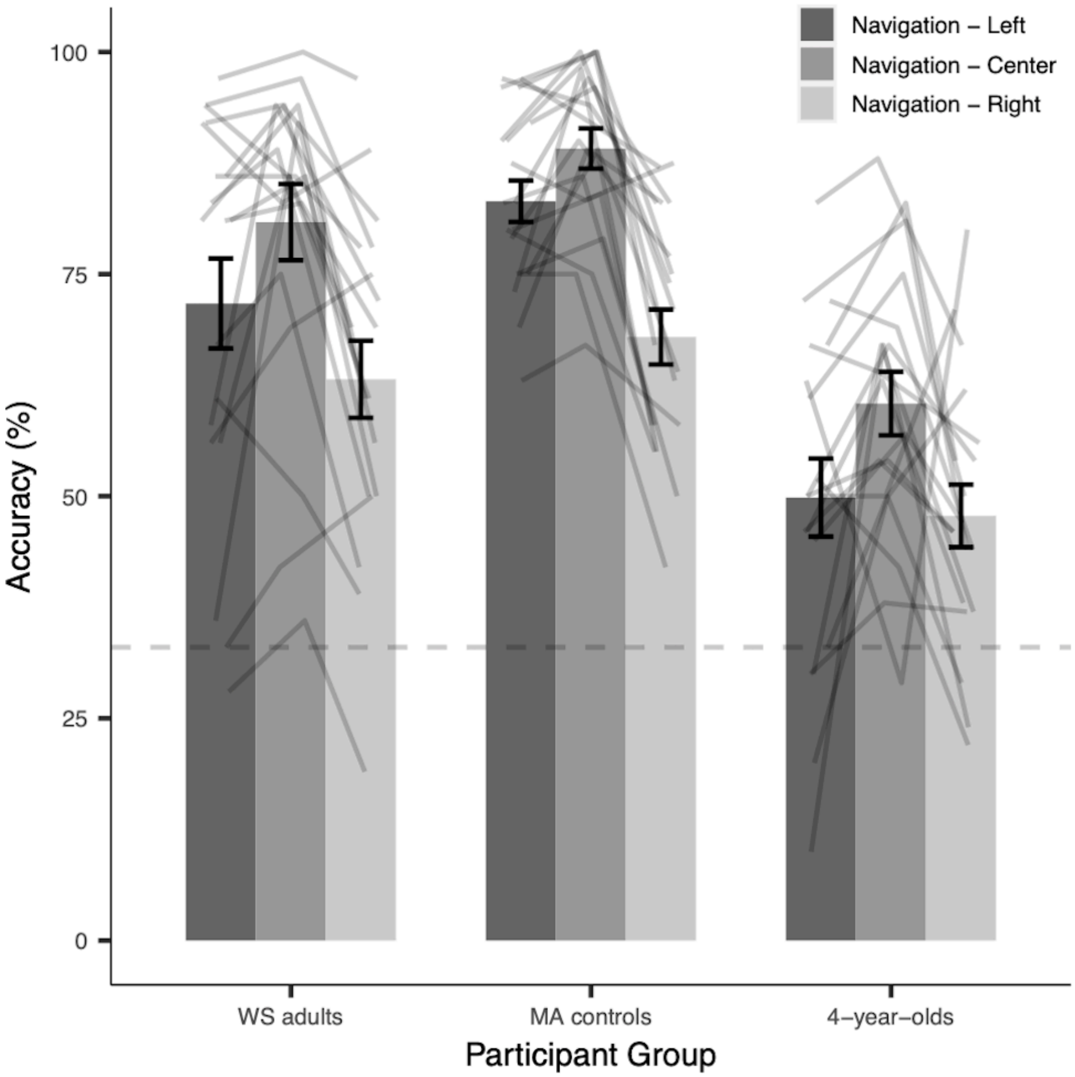

Figure 5. Patterns of performance of WS adults, MA controls, and 4-year-olds on each trial type of the visually guided navigation task. All three groups showed a similar pattern of performance, with higher accuracy on center trials than right trials and no difference between center trials and left trials, supporting the idea that all three groups employed similar cognitive mechanisms to solve the task. The grey dotted line indicates chance performance. Each solid grey line connects a participant's performance on the left trials to the same participant's performance on the center trials, and then to the same participant's performance on the right trials.

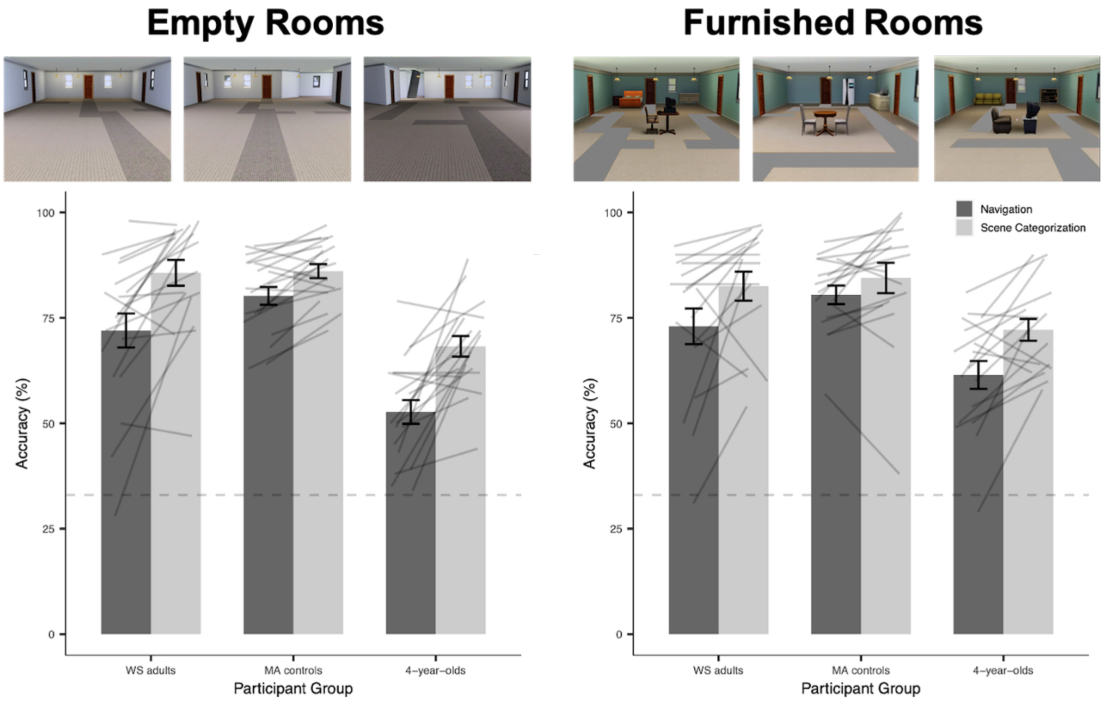

Figure 6. Average performance of WS adults, MA controls, and 4 year olds on furnished room versus empty room stimuli. Across both empty room stimuli (a) and furnished room stimuli (b; the same data as those presented in Figure 2), WS adults performed disproportionately worse on the visually guided navigation task than the scene categorization task, relative to MA controls, and no differences were found between the Empty Rooms and Furnished Rooms tasks, indicating that WS adults' performance on the scene categorization task was not driven by object categorization ability. Likewise, 4-year-olds performed disproportionately worse on the visually guided navigation task than the scene categorization task, relative to MA controls, and no differences were found between the Empty Rooms and Furnished Rooms tasks, indicating that the 4-year-olds' performance on the scene categorization task was not driven by object categorization ability. The grey dotted lines indicate chance performance. Each solid grey line connects a participant's performance on the visually guided navigation task to the same participant's performance on the scene categorization task.