




Dissociable Cognitive Systems for Recognizing Places and Navigating through Them: Developmental and Neuropsychological Evidence

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Recent neural evidence suggests that the human brain contains 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, 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. However, converging behavioral data — for instance, whether scene categorization and visually guided navigation abilities develop along different timelines and whether there is differential breakdown under neurologic deficit — would provide even stronger support for this two-scene-systems hypothesis. Thus, here we tested scene categorization and visually guided navigation abilities in 131 typically developing children between 4 and 9 years of age, as well as 46 adults with Williams syndrome, a developmental disorder with known impairment on “action” tasks, yet relative sparing on “perception” tasks, in object processing. We found that (1) visually guided navigation is later to develop than scene categorization, and (2) Williams syndrome adults are impaired in visually guided navigation, but not scene categorization, relative to mental age-matched children. Together, these findings provide the first developmental and neuropsychological evidence for dissociable cognitive systems for recognizing places and navigating through them.

Key words: development; dorsal stream; navigation; scene perception; Williams syndrome

Significance Statement

Two decades ago, Milner and Goodale showed us that identifying objects and manipulating them involve distinct cognitive and neural systems. Recent neural evidence suggests that the same may be true of our interactions with our environment: identifying places and navigating through them are dissociable systems. Here we provide converging behavioral evidence supporting this two-scene-systems hypothesis — finding both differential development and breakdown of “scene categorization” and “visually guided navigation.” This finding suggests that the division of labor between perception and action 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 cognitive and neural 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 and Milner, 1992). Interestingly, recent fMRI evidence in human adults suggests that this division of labor between perception and action systems is not limited to object processing but also extends to scene processing (Dilks et al., 2011; Kamps et al., 2016; Persichetti and Dilks, 2016, 2018, 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 without bumping into the cabinets or table) (Persichetti and Dilks, 2018; Dilks et al., 2022).

While the fMRI studies above provide neural evidence that identifying places and navigating through them may be

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Table 1. WS adults, MA children, and 4-year-old children participant characteristics for the primary experiments

	WS adults (<i>N</i> = 19)		MA children (<i>N</i> = 19)		4-year-olds (<i>N</i> = 19)	
	Mean (\pm SEM)	Range	Mean (\pm SEM)	Range	Mean (\pm SEM)	Range
Furnished rooms						
Chronological age (yr)	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						
Chronological age (yr)	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

dissociable systems, a stronger test of this hypothesis would ask whether these systems develop along different timelines in typical development, providing converging behavioral data for dissociable cognitive systems. Given previous work in object processing suggesting that visually guided action develops later than visual perception (Bertenthal, 1996; Atkinson et al., 2003; Dilks et al., 2008), we predicted that a similar developmental dissociation will be found in scene processing, with the visually guided navigation system developing later than the scene categorization system. Some initial neural and behavioral 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 5–8 years of age (Kamps et al., 2020). Behavioral studies likewise find protracted childhood development of locomotion, obstacle avoidance, and boundary-based spatial memory abilities (Pryde et al., 1997; Berard and Vallis, 2006; Julian et al., 2019). By contrast, the limited available evidence suggests scene categorization develops early; for example, scene recognition memory matures faster than face or object recognition memory (Golarai et al., 2007). Critically, however, no study has compared the development of visually guided navigation and scene categorization directly.

To further test the idea of dissociable cognitive systems for scene processing, 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 functions alongside remarkably preserved ventral stream functions (at least for object processing) (Atkinson et al., 1997; Paul et al., 2002; Meyer-Lindenberg et al., 2004; Landau et al., 2006; Dilks et al., 2008). 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 (TD) control participants.

To study the development and breakdown of these scene processing abilities, 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 and Dilks, 2018). They are: (1) 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 (2) 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. 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 36 adults with WS (23 females) participated in the primary experiments. Additional groups of 10 TD 4-year-olds (5 females; mean age = 53 months, range = 46–60 months), 19 TD 7-year-olds (10 females; mean age = 90 months, range = 84–95 months), and 10 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 and 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 nonverbal component specifically because nonverbal IQ is particularly susceptible to impairment in WS (Table 1). Matching of the raw nonverbal 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 with nonverbal 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 and Dilks, 2018) (Fig. 1). However, 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 and 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



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.”

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 and 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 and Dilks, 2018), and in all other aspects of the design, stimuli, and procedure. Immediately before 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 ~ 24 degrees visual angle on 11.97 inch \times 8.36 inch 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, 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 cognitive 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 (Fig. 2). A linear trend analysis revealed a

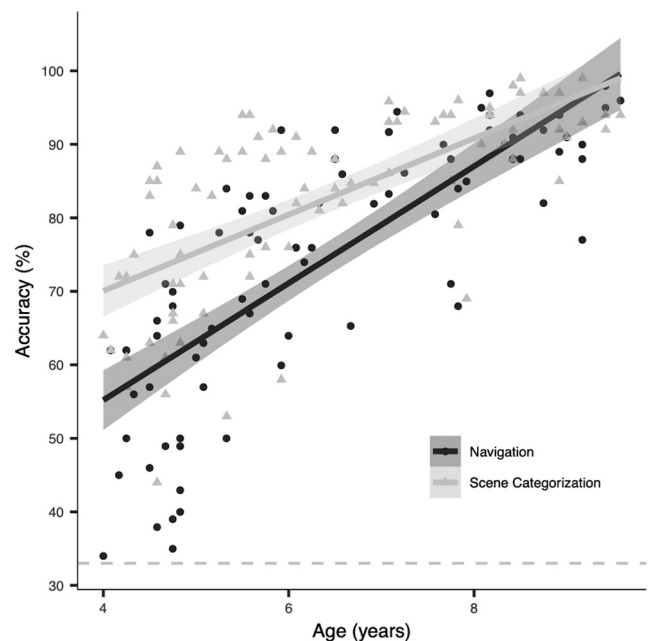


Figure 2. Average performance of TD children on the visually guided navigation and scene categorization tasks. The rate of development over age was significantly different between the visually guided navigation task and the scene categorization task, providing developmental evidence for dissociable visually guided navigation and scene categorization systems. Each black circle represents a participant’s performance on the visually guided navigation task. Each gray triangle represents a participant’s performance on the scene categorization task. Gray dotted line indicates chance performance. Shaded regions around the regression line represent a 95% CI.

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 because of floor or ceiling effects (McKone et al., 2012). Although all

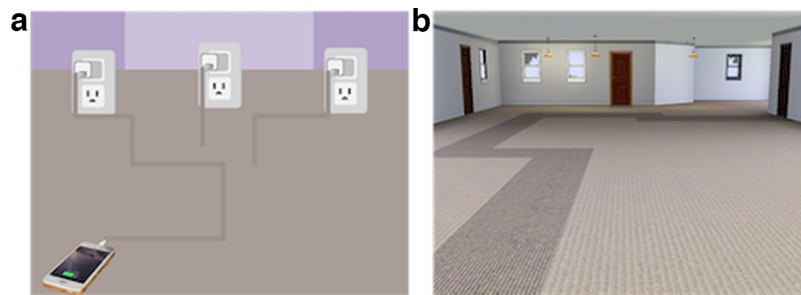


Figure 3. Example stimuli used in the follow-up “phone task” experiment. For the phone task (**a**), participants were asked to judge what outlet the phone was connected to via a complete wire. For the visually guided navigation task (**b**), participants were asked to judge which door they could leave 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.

children performed above floor on both tasks (one-sample t tests; all t values > 22.67 , p values $< 1e-16$, d values > 2.43) and below ceiling on both tasks (one-sample t tests; all t values > 12.78 , p values $< 1e-16$, both d values > 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 scene 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 (Fig. 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 navigation task 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 because of 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 because of 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, 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 (Fig. 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 (Fig. 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 processing, not scene categorization?

A final alternative explanation for our findings is that the scene categorization task might be solved using object processing, and may not involve scene processing at all. We addressed this alternative explanation in two ways. First, 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” (see Fig. 6 for exemplars of “empty room” stimuli). For comparison, participants again performed a visually guided navigation task on the same “empty room” stimuli. If children were simply using an object processing strategy to solve the scene categorization task in the furnished rooms experiment, then we should see no difference between the development of scene categorization and visually guided navigation in the empty rooms task, since they both now require scene processing. Contrary to this prediction, however, 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. Importantly, this pattern of performance was no different from how participants performed on the “furnished rooms” experiment ($F_{(1,119)} = 0.11$, $p = 0.74$, $\eta_p^2 = 0.001$). A

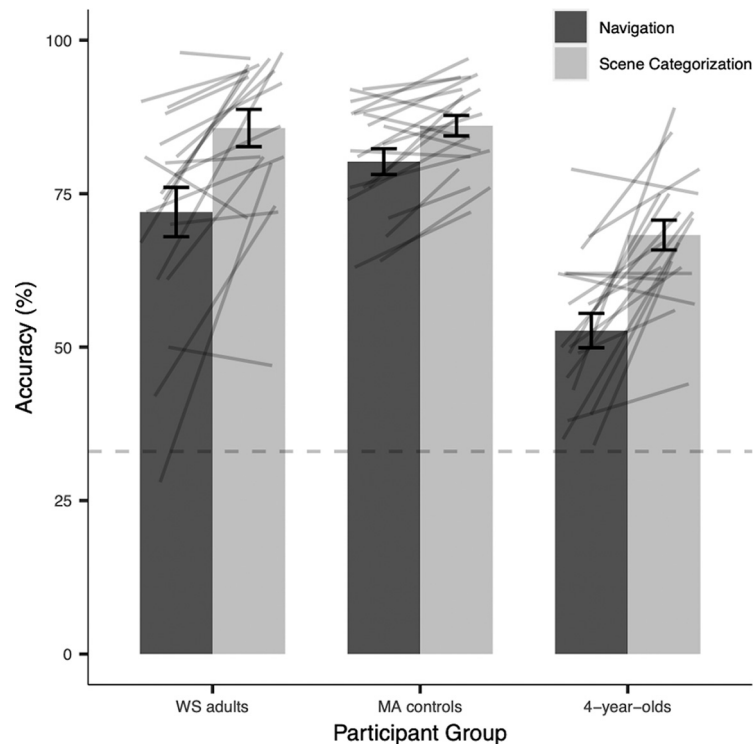


Figure 4. Average performance of WS adults, MA controls, and 4-year-olds on the visually guided navigation and scene categorization tasks. WS adults performed disproportionately worse on the visually guided navigation task than the categorization task, relative to MA controls, providing causal evidence 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 dissociable visually guided navigation and scene categorization systems, with the visually guided navigation system arising later in development than the scene categorization system. Gray dotted line indicates chance performance. Each solid gray line connects a participant's performance on the visually guided navigation task to the same participant's performance on the scene categorization task. Error bars depict the standard error of the mean.

permutation F test also failed to reveal a significant group \times trail type interaction ($p = 0.75$), and an additional Bayes factor (BF) hypothesis testing found evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.164$; $\text{BF} < 0.33$ supports the null hypothesis). Together, the similar performance between the furnished rooms and empty rooms experiments reveals that the differential development of visually guided navigation and scene categorization cannot be explained by an “object processing” strategy, but rather by two dissociable cognitive systems processing scene information. However, while performance on the scene categorization task in the furnished rooms requires “scene content” information (i.e., object information relevant for scene categorization; for example, a bed equals bedroom) and performance on the scene categorization task in the empty rooms requires spatial layout information, both kinds of information are represented within scene processing, not object processing.

Second, if children are using object processing to perform the scene categorization task specifically, then they should perform significantly better in the furnished rooms experiment than in the empty rooms experiment. However, a linear trend analysis did not reveal a significant effect between developmental trends for the “furnished rooms” and “empty rooms” scene categorization tasks ($F_{(1,119)} = 2.76$, $p = 0.10$, $\eta_p^2 = 0.02$). A permutation F test also failed to reveal a significant group \times trail type interaction ($p = 0.10$), and an additional BF hypothesis testing found marginal evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.720$; $\text{BF} < 0.33$ supports the null hypothesis). Together, the similar performance between the furnished rooms and empty rooms scene categorization tasks again suggests that children are using scene processing, not object processing, to perform the scene categorization task.

The visually guided navigation system is disproportionately impaired in WS

If visually guided navigation and scene categorization are dissociable cognitive systems, then these systems may be differentially impaired in a case of neurologic 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) \times 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 from MA controls on the scene categorization task ($t_{(36)} = 0.37$, $p = 0.72$, $d = 0.12$) (Fig. 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 nonverbal IQ, but as a consequence (because of their uneven cognitive profile), showed higher performance than MA controls on verbal IQ. It is possible then that WS adults may indeed be impaired on both the categorization and visually guided navigation tasks, but nevertheless perform better on the categorization task because of 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) \times

2 (task: visually guided navigation, scene categorization) mixed-model ANOVA, we found a significant interaction ($F_{(1,30)} = 8.27$, $p = 7.00 \times 10^{-3}$, $\eta_p^2 = 0.22$), with the WS adults performing worse than MA controls on the visually guided navigation task, relative to the scene categorization task ($t_{(30)} = 4.45$, $p = 1.00 \times 10^{-3}$, $d = 1.57$). 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 because of 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) \times 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 because of 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 TD 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 TD individuals, suggesting that WS individuals use 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) \times 3 (trial type: left, center, right) mixed-model ANOVA revealed a significant main effect of trial type ($F_{(2,72)} = 33.46$, $p < 1 \times 10^{-10}$, $\eta_p^2 = 0.48$), with both groups showing greater accuracy on center trials than right trials (pairwise comparisons, both p values < 0.01), and no difference between center trials and left trials (pairwise comparisons, both p values > 0.08) (Fig. 5). Critically, however, we failed to find a significant group \times 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 (Fig. 5). A permutation F test also failed to reveal a significant group \times trial type interaction ($p = 0.36$), and an additional BF hypothesis testing found evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.278$; $\text{BF} < 0.33$ supports the null hypothesis).

Critically, an even stronger test of the hypothesis that WS adults and TD children use qualitatively similar cognitive 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 (Dilks et al., 2008; Landau and Ferrara, 2013). We therefore next compared the WS adults with a younger group of TD 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) \times 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 BF hypothesis testing found marginal evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.342$; $\text{BF} < 0.33$ 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 \times trial type interaction: $F_{(2,72)} = 0.67$, $p = 0.52$, $\eta_p^2 = 0.02$) (Fig. 5). A permutation F test also failed to reveal a significant group \times trial type interaction ($p = 0.48$), and an additional BF hypothesis testing found evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.230$; $\text{BF} < 0.33$ supports the null hypothesis). Together, these results suggest that WS and TD children do not use qualitatively different cognitive mechanisms to solve the visually guided navigation task.

But what about the scene categorization task? Could the WS adults be using a qualitatively different cognitive mechanism than the MA controls to solve the scene categorization task, although they perform similarly? To address this possibility, we compared each group's pattern of performance across the three trial types of the scene categorization task (i.e., kitchen, bedroom, living room). We used the groups matched on the hardest task (i.e., visually guided navigation) to bring performance on the scene categorization task down from ceiling (see Restriction of range?). A 2 (group: WS adults, MA controls) \times 3 (trial type: bedroom, kitchen, living room) mixed-model ANOVA failed to

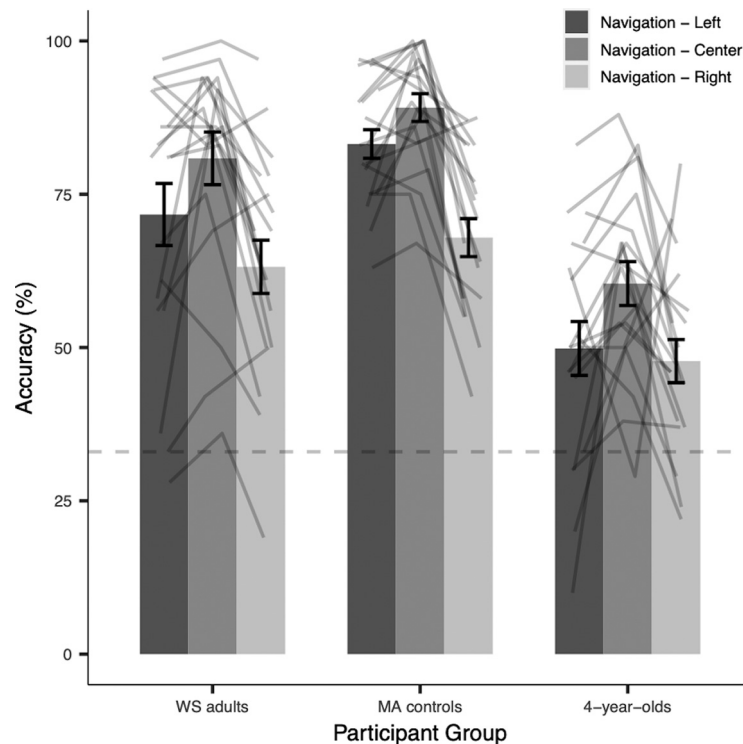


Figure 5. Patterns of performance of WS adults, MA controls, and 4-year-olds on each trial type of the visually guided navigation task. All three groups showed a similar pattern of performance, with higher accuracy on center trials than right trials and no difference between center trials and left trials, supporting the idea that all three groups used similar cognitive mechanisms to solve the task. Gray dotted line indicates chance performance. Each solid gray 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. Error bars depict the standard error of the mean.

reveal a significant group \times trial type interaction ($F_{(2,72)} = 1.05$, $p = 0.36$, $\eta_p^2 = 0.03$). A permutation F test also failed to reveal a significant group \times trial type interaction ($p = 0.35$), and an additional BF hypothesis testing found evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.323$; $\text{BF} < 0.33$ supports the null hypothesis). Thus, the WS profile cannot be explained by using a qualitatively different cognitive mechanism than MA controls to solve the scene categorization task, and instead arises from disproportionate impairment to the visually guided navigation system specifically. Of course, caution should be taken in interpreting the lack of significant differences between WS and TD groups on these measures, as it is always possible that differences between groups could be found using another measure. Nonetheless, 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 processing, rather than scene categorization?

Finally, we addressed the alternative explanation that WS individuals might have solved the scene categorization task using object processing, not scene processing, in two ways. First, 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) \times 2 (group: WS adults, MA controls) \times 2 (task: visually guided navigation, scene categorization) mixed-model ANOVA revealed a significant group \times 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 \times group \times task interaction ($F_{(1,68)} = 0.19$, $p = 0.67$, $\eta_p^2 = 0.003$), suggesting that the strength of the group \times 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 (Fig. 6). A permutation F test also failed to find a significant experiment \times group \times task interaction ($p = 0.67$), and an additional BF hypothesis testing found evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.018$; $\text{BF} < 0.33$ supports the null hypothesis). Thus, our findings cannot be explained by an “object processing” strategy.

Second, if the WS participants are using object processing to perform the scene categorization task, then they should perform significantly better in the furnished rooms experiment than in the empty rooms experiment. However, we found no significant difference in scene categorization performance between furnished rooms and empty rooms ($t_{(32.89)} = 0.69$, $p = 0.50$, $d = 0.23$). A permutation F test also failed to find a significant experiment \times group \times task interaction ($p = 0.49$), and an additional BF hypothesis testing found marginal evidence in favor of the null hypothesis ($\text{BF}_{10} = 0.388$; $\text{BF} < 0.33$ supports the null hypothesis), again revealing that WS adults are using scene processing, not object processing, to perform the scene categorization task.

Discussion

The present results provide behavioral evidence (developmental and neuropsychological) for the hypothesis that visually guided navigation and scene categorization are dissociable cognitive systems (Table 1). This “two-scene-systems” proposal dovetails with the classic division of labor found in object

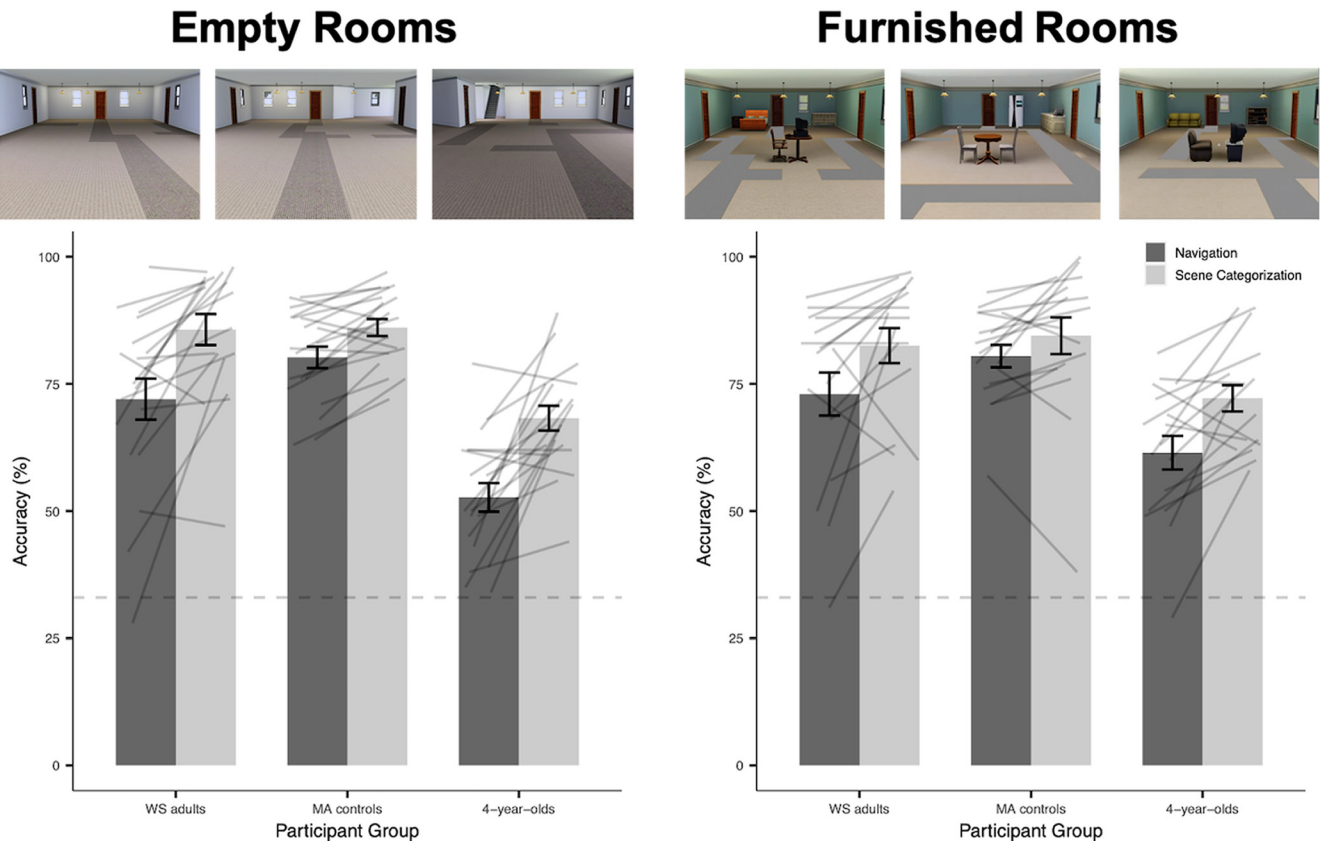


Figure 6. Average performance of WS adults, MA controls, and 4-year-olds on empty room versus furnished room stimuli. Across both empty room stimuli (left panel) and furnished room stimuli (right panel; the same data as those presented in Fig. 2), WS adults performed disproportionately worse on the visually 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 on 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. Gray dotted lines indicate chance performance. Each solid gray line connects a participant's performance on the visually guided navigation task to the same participant's performance on the scene categorization task. Error bars depict the standard error of the mean.

processing between dorsal systems for action and ventral systems for perception (Goodale and 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 current behavioral evidence that visually guided navigation ability matures later than scene categorization ability suggests that a similar developmental dissociation must be present at the level of the brain, with cortical regions supporting visually guided navigation maturing later than those supporting scene categorization. Although testing for developmental changes in the neural correlates of these tasks is beyond the scope of the present work, a parsimonious prediction is that the OPA undergoes protracted developmental change relative to the PPA. Three lines of initial evidence are consistent with this prediction. First, the tasks used here have been shown to differentially activate the OPA and PPA by adulthood (Persichetti and Dilks, 2018). Second, a similar pattern of protracted developmental change across childhood was found for another task ("boundary-based spatial memory") shown to depend on OPA by adulthood (Julian et al., 2016) compared with a control task that does not depend on OPA ("landmark-based spatial memory") (Julian et al., 2019). Third, and perhaps most directly, a recent developmental fMRI study found

that OPA is still developing sensitivity to navigationally relevant information across this same age range (Kamps et al., 2020), while no developmental changes were observed in the PPA. Nevertheless, future work will be required to test this linking hypothesis between brain and behavior directly. Indeed, both visually guided navigation and scene categorization abilities likely depend on brain regions beyond the OPA and PPA, respectively, and so it is possible that the behavioral results observed here originate from developmental changes in cortical regions beyond the OPA and PPA.

The idea of a late developing visually guided navigation system may seem surprising, given that humans begin navigating early in life (e.g., crawling ~6–9 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 and Spelke, 1994), and infants understand whether it is safe to locomote over a "visual cliff" (Gibson and 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 (including OPA) 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 regions are damaged in WS, and therefore whether these various navigational impairments result from damage to the same or different brain regions. Although the current work does not directly test the neural correlates underlying the disproportionate impairment of visually guided navigation compared with scene categorization in WS, it is still possible to speculate about the neural underpinnings of these two systems. For example, our findings suggest that WS adults have an underdeveloped OPA, since the visually guided navigation task used here has been shown to selectively activate OPA in TD adults (Persichetti and Dilks, 2018), and WS adults have reduced gray 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 and Dilks, 2016), one possibility is that the spatial reorientation and boundary-based spatial memory impairments result from an underdeveloped 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 information 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) (Oliva and Torralba, 2001, 2002; Oliva, 2014). Importantly, however, 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 (the neural correlate of scene categorization in adult humans) responses to scene boundaries are weaker in WS adults compared with TD adults. Notably, however, that study did not (1) compare WS adults to MA controls, (2) determine whether these dampened neural responses were specific to PPA versus also found in OPA, nor (3) 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.

Furthermore, 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

(Dilks et al., 2008; Landau and Ferrara, 2013). 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 ~4 years, consistent with many previous studies (Dilks et al., 2008; Landau and Ferrara, 2013).

Finally, the finding of impaired visually guided navigation ability with spared scene categorization ability in WS individuals is evidence for a single dissociation between the scene categorization and visually guided navigation systems. The claim that visually guided navigation and scene categorization are truly independent systems will require finding a complementary case to WS — that is, impaired scene categorization ability with spared visually guided navigation ability. Without such evidence, it could still be the case that a single mechanism (e.g., for scene processing in general) underlies both kinds of scene processing ability, and that visually guided navigation is simply a more difficult or complex case than scene categorization (despite our best efforts to rule out those possibilities here). Importantly, although the work presented here is not a double dissociation, we present consistent evidence across developmental and neuropsychological approaches, providing strong initial evidence for the hypothesis that these systems are cognitively dissociable, and setting the stage for future discovery of a case of impaired scene categorization, coupled with spared visually guided navigation.

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 cognitive systems.

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