

Object-Based Mental Rotation and Visual Perspective-Taking in Typical Development and
Williams Syndrome

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Abstract

This study examined Object-based (OB) rotation and Visual Perspective-Taking (VPT) abilities in Williams Syndrome (WS) compared to typically-developing (TD) 5-10 year-olds. Extensive difficulties with both types of imagined rotation were observed in WS; WS performance was in line with the level of ability observed in TD 5 year-olds. However, an atypical pattern of errors on OB and VPT tasks was observed in WS compared to TD groups. Deficits in imagined rotations are consistent with known atypical cortical development in WS. Such difficulties in updating the position of the self following movement in WS may have implications for large-scale spatial navigation.

Keywords: Williams Syndrome, Mental Rotation, Visual Perspective-Taking, Development, Visuospatial

Object-based mental rotation and visual perspective-taking in typical development and Williams syndrome

Williams syndrome (WS) is a rare genetic disorder resulting from a hemizygous deletion of approximately 28 genes, at locus 7q11.23 (Osborne, 2012). A distinctively uneven cognitive profile associated with WS has been well documented, with a discrepancy between stronger verbal abilities and relatively weaker visuospatial processing (Jarrod, Baddeley, & Hewes, 1998).

Difficulties on both on small- and large-scale visuospatial tasks have been consistently reported in WS, including deficits on spatial construction tasks (e.g., Hoffman, Landau, & Pagani, 2003), mental rotation (Farran et al., 2001), coding of spatial frames of reference (Nardini, Atkinson, Braddick, & Burgess, 2008), and large-scale environmental route learning (Farran et al., 2010). The pattern of visuospatial deficits in WS has, in part, been attributed to impairments identified in dorsal stream structure and function; the dorsal stream deficit hypothesis (Atkinson et al., 2003). However, deficits in dorsal stream functioning are not specific to WS (Atkinson & Braddick, 2011) and atypical dorsal stream processing may be fractionated in WS, with some processes less affected than others (Stinton, Farran, & Courbois, 2008). The dorsal stream deficit hypothesis may therefore not wholly explain the idiosyncratic pattern of visuospatial impairments in this disorder. As such, a more detailed examination of the specific cognitive difficulties typically expressed in WS, such as mental rotation, and how this relates to known underlying deficits in cortical functioning is therefore required.

Object-Based (OB) vs. Visual Perspective-Taking (VPT) Mental Rotation

In the field of visuospatial research, a distinction has been made between performance on tasks that require object-based (OB) mental rotation and those requiring body-based (egocentric)

visual perspective-taking (VPT) transformations (Hegarty & Waller, 2004; Zacks, Mires, Tversky, & Hazeltine, 2000). These two types of imagined rotation differ in the spatial frames of reference that are mentally manipulated. In OB mental rotation, the imagined position of an object or array can be mentally rotated relative to either an environment-centred (based on relationships between features within an environment) or an object-centred frame of reference (centred on the relationship between features within the rotating object), whilst one's body-based frame of reference does not move. This allows an individual to imagine what an object would look like at alternative orientations, without the need for actual or imagined self-movement. In contrast, during VPT tasks, an individual imagines their own rotation or movement within or around an array or environment relative to their own body-based (egocentric) frame of reference. VPT transformations therefore involve spatial updating of the location of the self within a fixed environment. This would therefore allow an individual to imagine what a scene would look like from an alternative viewpoint.

Development of OB Rotation and VPT Abilities

Piaget and Inhelder (1971) suggested that children develop the ability to solve VPT and OB mental rotation tasks at different ages, with the ability to perform OB tasks by 7-8 years and successful performance on VPT tasks developing later at 9-10 years when children can inhibit egocentric responding (i.e., continuing to give an answer to a rotation task that is identical to that of their current position). However, later research has suggested that performance on VPT tasks in children differs depending on the way in which such tasks are framed (for a review, see Newcombe & Frick, 2010). For instance, Newcombe and Huttenlocher (1992), found that 3 and 4 year-olds could succeed on VPT tasks when given questions that were related to identifying the locations of specific items from non-occupied perspectives, rather than asking participants to match alternative viewpoints from a range of pictures.

Using a reaction time test, Marmor (1975) found that children as young as 5 years are able to succeed on OB mental rotation tasks, and by 8 years are able to perform almost at an adult level. In line with adult data (e.g., Shepard & Metzler, 1971; Zacks, Ollinger, Sheridan, & Tversky, 2002), reaction times were found to be slower for an increased angle of rotation for 5- and 8-year-olds. Together, these studies suggest that OB and VPT abilities emerge earlier than originally thought, with both becoming available at approximately four years.

Roberts and Aman (1993) argued, however, that children below the age of 7 years are not fully competent on VPT tasks. That is, when determining left-right directions from non-occupied positions they tend to respond in line with their stationary egocentric left-right reference frames. In children aged 7-8 years, who were more able to correctly determine left-right directions from a non-occupied position, a linear increase in reaction time was found with greater angularity between real and imagined viewpoints. This is in contrast to typical adults, who do not demonstrate an angular discrepancy effect in VPT tasks (Wraga, Creem, & Proffitt, 2000; Zacks et al., 2000), and indicates that children may use a different technique, such as graduated imagined rotation of the self, whilst adults may be more able to use the relationships between items in the array and external landmarks to support a more automatic updating of their body-based frame of reference (Wraga et al., 2000).

Neurological Distinction between OB Rotation and VPT

Despite high correlations between performance on OB and VPT transformation tasks in adults (Hegarty & Waller, 2004), a measurable distinction between these transformation types has been demonstrated by neuroimaging data. That is, OB and VPT tasks are associated with increased activity in two dissociable yet overlapping neural systems (e.g., Zacks et al., 2000; Zacks et al., 2002). Zacks, Vettel, and Michelon (2003) showed that rotations of an array (OB) were associated with increased right interparietal sulcus activity and a decrease in activity in left

temporo-parietal junction and superior temporal sulcus, whilst imagined rotations of the self (VPT) were associated with increased activation of left parieto-temporo-occipital junction and superior temporal sulcus. More recently, when comparing a VPT with an OB task, Lambrey, Doeller, Berthoz, and Burgess (2012) found significantly greater activation of the parieto-occipital sulcus, including the retrosplenial cortex, and areas such as the left anterior hippocampus in VPT than OB rotation tasks. These areas are thought to be involved in transforming between egocentric to allocentric spatial representations (Vann, Aggleton, & Maguire, 2009), which may be important for successful imagined self-rotations. Thus, this region may be associated with an ability to update egocentric spatial locations (supported by the posterior parietal lobe) within an allocentric frame of reference (supported by hippocampal and medial temporal lobe structures) during VPT tasks (Lambrey et al., 2012).

Neuroimaging research in WS has found a number of structural and functional abnormalities in cortical regions associated with visual-spatial processing. In particular, impairment of the superior parietal lobule has been identified in WS (Eckert et al., 2005), a region associated with OB rotation (e.g. Podzebenko, Egan, & Watson, 2002). Furthermore, atypical metabolism and function of the anterior hippocampus (Meyer-Lindenberg et al., 2005), and decreased parieto-occipital grey-matter concentration (Boddaert et al., 2006) have also been identified. Given the role of these cortical regions in the spatial updating of one's viewpoint following actual and imagined rotation (Vann et al., 2009), individuals with WS are likely to show poor performance on associated tasks. Therefore, although atypical dorsal stream functioning may go some way to explaining mental rotation difficulties in WS (Atkinson et al., 2003; Stinton et al., 2008), atypical processing and functioning of more widespread structures and their intercortical connectivity may further explain the specific pattern of spatial deficits observed in this disorder.

OB and VPT Abilities in WS

To date, only a handful of studies of visuospatial abilities in WS have included tests of OB mental rotation. For instance, Farran, Jarrold, and Gathercole (2001) found that individuals with WS had significantly poorer mental rotation abilities than TD children matched for non-verbal ability, and that this was associated with their poor performance on a Block Design type task. Similarly, Vicari, Bellucci, and Carlesimo (2006) report that although no difference was evident between individuals with WS and mental-age-matched TD 6 year-olds on tasks requiring mental visualisation of objects, the WS group scored significantly below the TD 6 year-olds on tasks that required spatial manipulation and rotation of images. Research into VPT abilities in WS and how performance across different spatial transformation tasks compares with that of TD individuals is also limited. In one study, Farran et al. (2010) asked individuals with WS to state whether a picture of an animal placed between themselves and the examiner would appear the right-way-up or upside-down from the viewpoint of the examiner. Results yielded chance performance in the WS group, although questions only examined imagined self-rotation by 180°.

In one study that examined the use of different spatial reference frames in TD and WS, Nardini et al. (2008) found that although TD 5 year-olds and individuals with WS were able to use body- and environment-based frames of reference to locate a hidden object within an array following actual movement of the self, difficulties were observed on tasks that followed the movement of the array, requiring an array-based frame of reference. The authors conclude that difficulties with using an array-based frame of reference in WS may be related to difficulties in mental rotation. Detailed examination of performance on both OB and VPT tasks, which require imagined, rather than actual movement in WS, may provide further insight into the specific pattern of difficulties, and subsequently allow clearer conclusions to be drawn as to the nature of different aspects of visuospatial processing in this group.

The aim of the present study was to examine performance on OB and VPT tasks in individuals with WS compared to TD children between 5 and 10 years of age, and to examine changes in performance with increasing degrees of rotation across groups. OB rotation tasks can either require an individual to imagine the rotation of a single object, or the rotation of an array of objects, and these are likely to rely on shared underlying mechanisms (Lambrey et al., 2012). Similarly, VPT tasks can be separated into those that require the individual to imagine a displacement of the self to an unoccupied viewpoint around an array, or to imagine the rotation of the self within an array. Despite the overlapping underlying mechanisms involved in the two types of OB rotation and two VPT rotations, there may be different levels of difficulty and ranges in sensitivity across such tasks. As such, the current study used four separate rotation tasks (two OB and two VPT tasks) with the purpose of examining this range of abilities across each group and to provide a more detailed understanding of the specific difficulties in mental transformation in WS compared to TD children.

Method

Participants

Sixty-eight typically developing (TD) children were recruited from three London primary schools. Twenty-one participants with Williams Syndrome (WS) were recruited from the records of the Williams Syndrome Foundation, UK. All WS participants had received a positive diagnosis of WS, based on a “fluorescence in situ hybridisation” (FISH) test for deleted Elastin gene on chromosome 7. All TD participants were tested in a quiet room within their schools, whilst WS participants were tested either at their home or in a testing room at the University. Written informed consent was obtained from the parents of all participants.

Due to difficulties in concentration, one TD and one WS participant were subsequently excluded from the analyses. For analyses of performance across development, participants were

separated into four TD age-groups; 5 years (N=16, mean= 5.53, SD= .37), 6 years (N=17, mean= 6.71, SD= .30), 8 years (N=18, mean= 8.30, SD= .43), and 10 years (N=16, mean= 10.08, SD= .33) and compared to the WS group (N=20, mean age= 24.38, SD=10.58). Verbal and Non-verbal abilities were assessed using the British Picture Vocabulary Scale-III (BPVS-III; Dunn, Dunn, Styles, & Sewell, 2009) and the Ravens Coloured Progressive Matrices (RCPM; Raven, Raven, & Court, 2003), respectively.

Visual Perspective-Taking (VPT) Path

The VPT path task was conducted to examine body-based rotation abilities. In this task, participants were sat in front of a 2D map-like route presented on an A4 piece of paper on a table in front of them (Figure 1a), and asked to imagine walking the route from start to finish. Along the route were 20 decision points, with 10 left turns, and 10 right turns. The route consisted of 5 turns at no imagined rotation (0°), 10 turns in which the participant must imagine themselves at 90° from their actual vantage point, and 5 turns at 180° (imagining looking directly behind their actual view). At each turn the participant stated whether they would turn their body to the left or the right to continue down the path. Given that young children and some individuals with WS have difficulties distinguishing their left from right sides (Landau & Hoffman, 2005), each participant was given a sticker on one hand (randomised left and right across participants) so that instead of declaring a left or right turn, they stated whether they would turn to their 'sticker' or 'no-sticker' side. This was similar to a method used by Newcombe and Huttenlocher (1992) with TD 3 and 4 year olds, that significantly improved performance on such tasks.

Object-Based (OB) Monkey Mental Rotation

The OB monkey task was used to examine the ability to mentally rotate a single image, based on the classic mental rotation paradigms used by Shepard and Metzler (1971).

Participants were asked to view two cartoon monkeys above a horizontal line and one monkey below the line at varying degrees of rotation from upright (Figure 1b). Stimuli were presented on a 14" laptop computer screen. Participants were asked to choose which of the two monkeys on the top matched the one underneath. The incorrect monkey was always a mirror-image of the correct monkey so that verbal coding could not be used to solve the task (e.g., red hand is next to the tail). Participants indicated their response by pressing either the designated left or right button on the keyboard in front of them.

The monkey task consisted of six practice trials (to indicate whether the participant understood the task) and 32 experimental trials (4 x 0° trials, 8 x 45° trials, 8 x 90° trials, 8 x 135° trials, and 4 x 180° trials). For counterbalancing, half of the trials included a target monkey with the red hand to the right, and half with the target as the mirror image (red hand to the left).

Visual Perspective-Taking (VPT) Circle

The VPT circle task was based on Newcombe and Huttenlocher (1992) and was used to examine ability to imagine the self rotating around an array. In contrast to Newcombe and Huttenlocher (1992), a circular board was used instead of a square board to present the array of objects. This controlled for the use of a frame of reference based on aligning the four sides of the board with the walls of the room or edges of the table (Kelly & McNamara, 2010).

Participants were positioned in front of one of two white 13" circular arrays (i or ii) of four 3D coloured clay objects (see Figure 1ci and cii). Array i) contained a pig, a tree, a house, and a football. Array ii) contained a snail, a car, a traffic cone and a shoe. Participants were first asked to name each object to demonstrate that they knew the correct word for each and that each object was equally recognisable.

Throughout the task, the participant was asked to imagine looking at the array from different viewpoints and asked a series of questions about the position of the different objects

from the imagined perspectives. For each imagined rotation condition, participants were asked “imagine you are standing here and looking this way (a red arrow was placed on the table to indicate imagined direction of gaze), which object is a) closest to you, b) furthest away from you, c) to your left and d) to your right. Questions were presented in blocks for each rotation, but the order of questions varied randomly for each trial.

All participants were tested on both arrays (i and ii, separately) to measure mental rotation abilities at a variety of imagined displacements (45° , 90° , 135° and 180° , collapsed across clockwise and anti-clockwise rotations). Two different arrays of objects were used as opposed to one array so that all orientations could be measured without introducing a high cognitive load of having too many objects on one array. Array i therefore allowed for imagined self-rotations of 90° and 180° , and Array ii, for rotations of 45° and 135° . The order of presentation of the two arrays (i or ii first) was counterbalanced across participants.

The test consisted of 32 trials (16 trials for each array): four 0° (control), eight 90° rotation trials, four 180° rotation trials, eight 45° rotation trials and eight 135° rotation trials. Therefore, this differed from the task used by Newcombe and Huttenlocher (1992) by including a greater number of angles of rotation, allowing for an analysis of the changes in the number of errors with increased rotation from 0° . In addition, comparable to the VPT path task, one hand of each child was marked with a sticker in order that they did not have to use the terms ‘left’ and ‘right’, which could have introduced a confound. Instead, participants referred to their ‘sticker side’ and ‘non-sticker side’.

Object-Based Circle

Participants were positioned in front of one of two separate arrays of four coloured shapes (see Figure 1di), with a central red arrow pointing towards one of the shapes (e.g. a blue moon). The participant was asked to imagine that the whole array was turned until the red arrow

was pointing upwards and the object (e.g. the blue moon) it was pointing to was at the top. They were then asked to indicate in turn (using array 1dii) where the other three objects would have moved to, given this rotation. For example, the participant was asked “If I were to turn the circle of shapes around so that the red arrow is now pointing upwards and the blue moon is at the top, can you point the blue arrow to show me where the yellow square has moved to?” Participants then moved the blue arrow on the blank circular board (Figure 1dii) to the required position.

Across the two arrays, participants could be tested on the same degrees of mental rotation as in the VPT circle (45° , 90° , 135° , and 180° , collapsed across clockwise and anti-clockwise rotations). This test consisted of 24 trials: three at 0° (control), six at 45° rotations, six 90° rotation trials, six 135° rotations, and three 180° rotation trials. The 0° control condition was used to determine whether the participant understood the instructions. A pilot study showed that it was important to first demonstrate an actual rotation of the board so that the participant could grasp the concept of the whole array rotating. This was done by briefly rotating one array to 45° clockwise and then anticlockwise whilst the experimenter said, “Look at what happens when I turn the circle, all the shapes move around”. This small degree of rotation was chosen so that participants could not use their memory for the final location of shapes on experimental trials for this array.

- FIGURE 1 HERE-

All participants completed the BPVS-III and RCPM before any mental rotation measures. Participants then received either the VPT path task or OB monkey task (counterbalanced across participants), followed by the two circle tasks. The OB circle task was always conducted before the VPT circle as participants who are given a perspective-taking task first, have been found to make fewer errors on subsequent object-based tasks of similar content, but not vice-versa

(Pellizzer, Bâ, Zanello, & Merlo, 2009). All tasks were completed on the same day, with breaks given where necessary. Total testing time was approximately 45 minutes. However, when shorter testing sessions were required, two sessions were used (session 1: BPVS-III, RCPM; session 2: other tasks) spaced less than one month apart (mean = 16.28 days [sd= 16.99]).

Results

BPVS-III and RCPM

Analysis of variance (ANOVA) was conducted separately for BPVS and RCPM scores, each with group (5 levels; 5y, 6y, 8y, 10y, and WS) as a between-subjects factor (see Table 1). This demonstrated an uneven cognitive profile in WS, characteristic of the disorder (Jarrold et al., 1998), with nonverbal abilities at a level no different from TD 5 and 6 year-olds and verbal abilities at the level of TD 8 and 10 year-olds.

-TABLE 1 HERE -

Visual Perspective-Taking (VPT) Path

Given the different number of trials across each degree of rotation within the VPT path task, total correct responses for each rotation were converted to percentage scores for analysis across groups. For mean percentage correct for each rotation across groups, see Figure 2a.

To examine whether the performance in each group differed from chance (50%) on rotation trials, one-sample t-tests were conducted on the data (Bonferroni-adjusted level for multiple comparisons = .013). On 90° trials, all groups except 5 year-olds scored significantly above chance (6 years, $t(15) = 7.000, p < .001$; 8 years, $t(16) = 8.752, p < .001$; 10 year, $t(15) = 8.137, p < .001$; WS, $t(18) = 4.624, p < .001$), and on 180° trials the 5 year-olds [$t(13) = -5.591, p < .001$] and WS groups [$t(18) = -3.541, p = .002$] scored significantly below chance, indicating

the consistent use of a disadvantageous strategy at this angle of rotation. Ten year-olds were the only group to score significantly above chance on 180° trials, $t(15) = 2.449, p = .027$.

A mixed ANOVA, with group as a between-participant factor (5 levels: 5y, 6y, 8y, 10y, and WS) and rotation as within-participant factor (3 levels: 0°, 90°, and 180°) was conducted on the data. There was a significant main effect of group, $F(1, 77) = 10.604, p < .001$, partial $\eta^2 = .355$, with Tukey post-hoc tests showing that the WS group scored below 8- and 10- year-olds ($p = .010$ and $p < .001$, respectively), and 5 year-olds scored below 6, 8 and 10 year-olds ($p = .033, p = .001$ and $p < .001$, respectively). A significant main effect of rotation was also found, reported as a linear contrast, $F(1, 77) = 216.197, p < .001$, partial $\eta^2 = .737$, on account of reduced accuracy with increased rotation from upright.

There was also a significant group by rotation interaction, $F(8, 154) = 3.735, p = .003$, partial $\eta^2 = .162$. To further examine the effect of rotation in each group, repeated measures ANOVAs were conducted. A significant effect of rotation was found for all groups, reported as linear contrasts. As shown in Table 2, rotation had increasingly less impact on accuracy with age in the TD groups, with the weakest effect in TD 10 year-olds and a similar effect of rotation observed in the WS group as TD 5 and 6 year-olds.

- FIGURE 2 HERE-

-TABLE 2 HERE-

OB Monkey Mental-Rotation

To examine differences across groups on number of correct responses in the monkey mental rotation task for each degree of rotation from upright, data were collapsed across equivalent clockwise and anti-clockwise degrees of rotation (e.g. collapsed all 45° and -45° rotation trials). As the total number of trials differed for each degree of rotation, the mean

percentage of correct responses for each rotation was calculated. Following difficulties in completing the task correctly, one TD 6 year-old was excluded from the analyses. For percentage of correct scores for each degree of rotation in each group, see Figure 2b.

To examine whether performance in each group differed from chance (50%), one-sample t-tests were conducted. Results yielded significant above-chance performance (Bonferroni-adjusted level for multiple comparisons = .013) in each TD group for 45° trials [5 years, $t(15)=3.651, p=.002$; 6 years, $t(15)=5.705, p<.001$; 8 years, $t(16)=17.599, p<.001$; and 10 years, $t(15)=14.346, p<.001$], and 90° trials [5 years, $t(15)=3.651, p=.002$; 6 years, $t(15)=5.705, p<.001$; 8 years, $t(16)=17.599, p<.001$; and 10 years, $t(15)=14.346, p<.001$]. However, only 8 and 10 year-old TD children performed significantly above chance on 135° [$t(16)=9.414, p<.001$ and $t(15)=9.925, p<.001$, respectively] and 180° trials [$t(16)=3.781, p=.002$ and $t(15)=7.064, p<.001$, respectively]. In contrast to VPT path results, the WS group did not score significantly differently from chance on any rotation trials ($p>.013$ for all), despite performing reliably above chance on 0° control trials $t(19)=3.040, p=.007$, demonstrating an ability to understand the task.

A two-way mixed ANOVA was conducted with a between-participant factor of group (5 levels: 5y, 6y, 8y, 10y, and WS) and within-participant factor of rotation (5 levels: 0°, 45°, 90°, 135°, and 180°). Results showed a significant main effect of group, $F(4, 80) = 14.603, p<.001$, partial $\eta^2 = .422$, with post-hoc Tukey tests showing that the WS group scored significantly below all TD groups ($p<.01$ for all). In addition, 5 and 6 year-olds scored below 10 year-olds ($p=.015$ and $p=.023$, respectively), and no differences were found between any other TD groups ($p>.05$ for all).

There was also a significant main effect of rotation, $F(4, 320) = 19.920, p<.001$, partial $\eta^2 = .199$. Bonferroni-corrected post-hoc tests showed a greater percentage correct at 0° compared to 45°, 135° and 180° ($p<.01$ for all). A greater percentage correct was also found

for 45° trials compared to 135° and 180° ($p < .01$ for both), and for 90° compared to 135° and 180° ($p < .01$ for both). No other significant differences were found ($p > .05$).

A significant group by rotation interaction was also found, $F(16, 320) = 2.492, p = .002$, partial $\eta^2 = .111$. To examine this pattern further, repeated measures ANOVAs for the effect of rotation in each group were conducted. As shown in Table 2, the interaction was due to a main effect of rotation in the younger TD and the WS groups only, although significant differences between levels of rotation did not remain following pairwise comparisons in the WS group.

Visual Perspective-Taking Circle

On control trials from own vantage point (no rotation), almost all participants performed perfectly, with only four participants making one error each (two 6 year-olds, one 10 year-old and one participant with WS). One WS and one TD 5 year-old were unable to pass the control phase and were therefore not included in subsequent analyses.

Correct responses could be divided into near-far trials (naming objects nearest and furthest following imagined rotations) and left-right trials (naming objects to the left and right of the self following imagined rotations). To examine differences in performance on near-far compared to left-right trials, t-tests were conducted for WS and TD groups separately. In both groups, participants showed significantly stronger performance on near-far than left-right trials; TD, (Mean near-far = 92.86%, Mean left-right = 74.24%), $t(65) = 5.527, p < .001$; and WS, (Mean near-far = 59.77%, Mean left-right = 33.45%), $t(18) = 5.257, p < .001$. This could suggest that near-far trials are easier than left-right trials. However, we suggest that responses on near-far trials could have been based on an alternative strategy that does not require mental rotation. That is, participants might have made allocentric spatial judgements based on their understanding of distances between the target object and direction arrow, rather than using mental rotation. To ensure that the data entered into analysis was a pure measure of mental

rotation, all subsequent analyses on this task examined the effect of rotation on left-right trials only, as these could not be completed by an alternative strategy; these trials required the use of left-right body coordinates following imagined rotation of the self.

Left-right trials were divided by degree of rotation (4 levels: 45°, 90°, 135° and 180°), with data collapsed across equivalent clockwise and anti-clockwise degrees of rotation (e.g. imagined rotations -90° to the left and 90° to the right) for analysis. For percentage correct on left-right trials across groups on the VPT circle task, see Figure 2c.

Data showed that 8 and 10 year-olds scored highly across the task and were not affected by rotation, demonstrating ceiling performance on 0°, 45° and 90° trials. In comparison, the 5 and 6 year-olds showed a decline in performance with increased rotation, and the WS group showed very poor performance on all rotation trials above 45°.

To examine whether the performance in each group differed from chance (25%), one-sample t-tests were conducted on the data (Bonferroni-adjusted level for multiple comparisons = .013). Results indicate that, similar to performance on the OB monkey task, all TD groups scored significantly above chance on 45° trials [5 years, $t(14) = 4.840, p < .001$; 6 years, $t(16) = 7.486, p < .001$; all 8 and 10 year-olds scored 100% correct]. The WS group also scored significantly above chance on 45° trials, $t(18) = 5.112, p < .001$. On 90° trials, only 6, 8, and 10 year-olds scored significantly above chance, [6 years, $t(16) = 4.915, p < .001$; 8 years, $t(17) = 18.222, p < .001$; all 10 year-olds scored 100% correct]. Only 8 and 10 year-old TD children performed significantly above chance on 135° [$t(17) = 11.251, p < .001$ and $t(15) = 7.889, p < .001$, respectively] and 180° trials [$t(17) = 5.234, p < .001$ and $t(15) = 4.472, p < .001$, respectively]. Scores in the WS group however, were not significantly different from chance for 90°, 135° or 180° trials ($p > .013$ for all).

The data did not meet assumptions for normality for any variables in TD or WS groups (Kolmogorov-Smirnov, $p < .01$). Therefore, data for each group were analysed using non-

parametric tests. Kruskal-Wallis test was carried out on percentage correct for left-right responses with a participant factor of group (5 levels: 5, 6, 8, 10 and WS) collapsed across all rotation trials and also for each degree of rotation separately. There was a significant difference across groups on percentage correct on all rotation trials ($H(4) = 50.618, p < .001$). No significant difference was found across groups on 0° trials ($H(4) = 4.000, p = .406$), suggesting that all groups understood the task.

Bonferroni-corrected Mann-Whitney post-hoc tests revealed that on 45° trials, the 5-year, 6-year, and WS groups performed more poorly than the 8 and 10 year-old groups ($p < .05$ for all). All other comparisons at 45° were not significant ($p > .05$). On 90° trials, 5 year-olds scored below 8 and 10 year-olds ($p = .001$), 6 years below 10 year-olds ($p < .005$), and WS below 6, 8 and 10 year-olds ($p < .001$ for all). On 135° trials, 5 and 6 year-olds and WS groups performed significantly below 8 and 10 year-olds ($p < .005$ for all). On 180° trials, results demonstrated that 5 year-olds performed more poorly than 8 year-olds ($p < .005$), and WS were reliably below 8 and 10 year-olds ($p < .001$).

To examine the effect of rotation across each group, Friedman's ANOVAs with a within-participant factor of degree of rotation (5 levels: $0^\circ, 45^\circ, 90^\circ, 135^\circ, 180^\circ$) were conducted for all groups together, and then for each group separately (Table 2). This demonstrated a significant main effect of rotation for each group.

Types of errors on VPT circle task.

The different types of errors made on the VPT circle task were analysed to examine differences in strategies used and whether specific aspects of the tasks were more difficult for some groups. Errors were separated into three categories, 'egocentric' (an answer from own vantage point), 'reversal' (switching left and right), and 'miscellaneous' errors (all other errors). Mean number of each error-type on left-right trials across groups were analysed. Results from

one-way ANOVAs showed a significant difference across groups on all types of error; ‘egocentric’ (5-years $M=2.20$ [3.63]; 6-years $M=1.47$ [3.54]; 8-years $M=0$; 10-years $M=0$; WS $M=3.95$ [2.84]), $F(4, 84) = 7.452, p < .001$; ‘reversal’ (5-years $M=3.67$ [3.31]; 6-years $M=3.53$ [3.28]; 8-years $M=1.22$ [1.70]; 10-years $M=1.13$ [1.93]; WS $M=2.95$ [2.64]), $F(4, 84) = 3.668, p = .009$; and ‘miscellaneous’ (5-years $M=1.13$ [2.10]; 6-years $M=.47$ [.62]; 8-years $M=0$; 10-years $M=0$; WS $M=2.53$ [2.32]), $F(4, 84) = 10.016, p < .001$. Tukey-corrected post-hoc tests showed that the WS group made a significantly greater number of egocentric errors than 6, 8 and 10 year-olds ($p < .05$ for all), and significantly more ‘miscellaneous’ errors than all TD groups ($p < .05$ for all). There were no differences across groups in number of reversal errors. However, one-way ANOVAs of the proportion of error-type by all participants who made errors found a significant difference across groups in proportion of egocentric errors made (5 years = 21.2% [31.1%]; 6 years = 16.1% [32.5%]; 8 years = 0.0%; 10 years = 0.0%; WS = 42.1% [28.2%]), $F(4, 58) = 4.629, p = .003$; reversal errors (5 years = 66.1% [40.9%], 6 years = 78.4% [36.8%], 8 years = 100%, 10 years = 100%, WS = 31.2% [28.2%]), $F(4, 58) = 9.799, p < .001$; and miscellaneous errors (5 years = 12.7% [26.3%], 6 years = 5.6% [7.0%], 8 years = 0.0%, 10 years = 0.0%, WS = 26.7% [24.1%]), $F(4, 58) = 4.301, p = .004$. Tukey-corrected post-hoc tests showed that this was due to the WS group making a significantly higher proportion of Egocentric and Miscellaneous errors than 6, 8 and 10 year-olds ($p < .05$ for all), and significantly smaller proportion of Reversal errors than all TD groups ($p < .05$ for all).

Object-Based Circle

On control trials from own vantage point (no rotation), all participants performed faultlessly, except for one participant with WS who made one error. This showed that all groups understood the task.

Responses could be divided into far trials and left-right trials. For consistency with the analysis performed on VPT circle task data, only responses to left-right trials were analysed. For left-right transformation trials, participants were asked to point a blue arrow in the correct direction of a shape that was situated either to the left or right of the shape that the red arrow was pointing to, e.g. when the red arrow pointed to the yellow square, only the responses to the position of the blue moon (left) and green circle (right) were analysed (see Figure 1di). To examine the effect of rotation on correct responses, data were collapsed across equivalent clockwise and anti-clockwise degrees of rotation in the same way as for the VPT circle. For percentage correct across groups on the VPT circle task, see Figure 2d.

A mixed ANOVA with group (5 levels; 5, 6, 8, 10 and WS) as a between-participant factor and rotation (5 levels: 0°, 45°, 90°, 135°, and 180°) as within-participant factor was conducted. There was a significant main effect of group, $F(4, 79) = 14.917, p < .001$, partial $\eta^2 = .430$. Tukey-corrected post-hoc tests found 5 year-olds and WS scored significantly more poorly than 8 and 10 year-olds ($p < .01$ for all), and 6 year-olds scored below 10 year-olds ($p = .001$). There were no other significant group differences ($p > .05$).

There was also a significant main effect of rotation, reported as a linear contrast, $F(1,79) = 137.240, p < .001$, partial $\eta^2 = .635$. A significant group by rotation interaction was also found, $F(16, 316) = 3.171, p < .001$, partial $\eta^2 = .138$, demonstrating that, similar to the pattern observed for other rotation tasks, the effect of rotation differed across groups. Results of repeated-measures ANOVAs for each group (Table 2) show that, in contrast to all TD groups, for whom no significant detriment to performance on 180° trials was found compared to other levels of rotation, a different pattern of performance was seen in WS.

Types of errors on OB circle task.

To examine errors on the OB circle task, errors were categorised into three distinct types, by the same method used in the VPT circle task. Mean number of each type of error on left-right trials was calculated from the data and one-way ANOVAs were conducted to examine the differences in mean number of each type of error across groups. In line with the VPT circle, there was a significant difference in the number of each error type across groups: ‘egocentric’ (5 years $M = .73$ [1.39]; 6 years $M = .82$ [1.74]; 8 years $M = .89$ [1.78]; 10 years $M = .50$ [1.32]; WS $M = 2.18$ [1.94]), $F(4, 83) = 2.606$, $p = .042$; ‘reversal’ (5 years $M = 3.33$ [2.32]; 6 years $M = 3.29$ [2.44]; 8 years $M = 1.94$ [1.86]; 10 years $M = 1.06$ [1.53]; WS $M = 3.00$ [1.50]), $F(4, 83) = 3.949$, $p = .006$; and ‘miscellaneous’ (5 years $M = 4.20$ [2.68]; 6 years $M = 2.29$ [2.66]; 8 years $M = 1.89$ [2.45]; 10 years $M = 1.13$ [1.46]; WS $M = 3.88$ [1.99]), $F(4, 83) = 5.803$, $p < .001$. Tukey-corrected post-hoc tests found that the WS group made significantly more egocentric and miscellaneous errors than 10 year-olds ($p < .05$ for both), 5 and 6 year-olds made more reversal errors than 10 year-olds ($p < .05$ for both) and 5 year-olds made more miscellaneous errors than 8 and 10 year-olds ($p < .05$ for both).

In contrast to the differences in error types in the VPT circle however, results showed that for all participants who made errors in each group, no significant difference across groups was found in the proportion of each error type. This indicates that, unlike on the VPT circle, no group had a preponderance to make a specific type of error more than any other group on this task.

Relationships between Age and Mental Rotation

In the TD group (collapsed across groups), when controlling for BPVS scores, age was significantly correlated with performance on the VPT path, $r(59) = .384$, $p = .002$; VPT circle, $r(59) = .320$, $p = .012$; and OB circle, $r(59) = .267$, $p = .038$, but not for the OB monkey task

($p > .05$). When controlling for RCPM scores, age was only correlated with performance on the two VPT tasks; VPT path, $r(58) = .370, p = .004$; VPT circle, $r(58) = .280, p = .030$.

In contrast to the pattern observed across TD children, in the WS group, performance on the OB monkey task was found to correlate significantly with chronological age, even when controlling for BPVS raw score, $r(14) = .591, p = .016$, and when controlling for RCPM, $r(14) = .741, p = .001$. Thus, older individuals with WS performed at a higher level on this OB mental rotation task than younger individuals, irrespective of performance on measures of verbal and non-verbal abilities. No significant relationship was seen between chronological age and any of the other tasks in the WS group ($p > .05$ for all).

Mental Rotation and Verbal and Non-Verbal Abilities

In the TD group (collapsed across groups), when controlling for age, all mental rotation tasks except VPT path, $r(57) = .220, p = .093$, were positively correlated with RCPM scores; OB monkey, $r(57) = .371, p = .004$; VPT circle, $r(57) = .401, p = .002$; OB circle, $r(57) = .392, p = .002$. Also when controlling for age, results showed a significant relationship between BPVS raw score and OB monkey, $r(57) = .296, p = .023$.

In the WS group, a significant positive correlation was found between performance on RCPM and OB circle task scores, $r(17) = .69, p = .003$, even when controlling for age, $r(14) = .659, p = .006$. No other correlations were found between RCPM and rotation tasks for the WS group ($p > .05$ for all).

Similar to TD groups, a significant positive correlation was found in the WS group between BPVS raw score and performance on the OB monkey task, $r(19) = .59, p = .007$, although this did not remain when controlling for chronological age $r(16) = .38, p = .118$. No other correlations were found between BPVS and rotation tasks ($p > .05$ for all).

Discussion

The aim of this study was to examine object-based (OB) mental rotation and visual perspective-taking (VPT) abilities in individuals with WS compared to TD children between 5 and 10 years. In line with previous studies (e.g., Newcombe & Huttenlocher, 1992), the results indicate a significant improvement in both OB rotation and VPT ability between the ages of 6 and 8 years, suggestive of similar developmental progression for both abilities in typical development.

The percentage of correct responses on the OB monkey task was seen to decline with rotation in TD 5 and 6 year-old children, but not for 8 and 10 year-olds, who showed near-ceiling performance on this task. A similar pattern was observed in the OB circle task, with no effect of rotation seen above 45° in 8 and 10 year-olds, due to consistently good performance across the task in older children. These findings therefore provide a clear picture of changes in mental rotation performance with age in typical development.

In contrast to OB mental rotation, a decline in performance with rotation on VPT tasks is often not reported in typical adults (e.g. Wraga et al., 2000; Zacks et al., 2000). However, such a decline has been identified in TD children (Roberts & Aman, 1993). Although Roberts and Aman (1993) examined reaction times, the present study demonstrates that a decline in performance with increased imagined rotation can also be observed in relation to accuracy on VPT tasks. On the two VPT tasks, TD children under 8 years exhibited difficulties in determining left-right body coordinates (despite having eliminated any requirement to understand the terms 'left' and 'right') with increased misalignment from actual viewpoint. In contrast, 10 year-olds (on the VPT path) and 8 and 10 year-olds (on VPT circle) showed no difference in accuracy between 90° and 180° rotations, a pattern similar to that observed in typical adults. This contributes to the literature in TD children, indicating that between 8 and 10 years of age, children may develop a more appropriate strategy for performing imagined

transformations of the self to different locations, to be more in-line with strategies observed in typical adults (Wraga et al., 2000; Zacks et al., 2000).

The results from the WS group data in this study were also in line with that of previous findings (Farran & Jarrold, 2004; Farran et al., 2001; Vicari et al., 2006), demonstrating poor performance on both tasks requiring OB mental rotation in this group. In particular, when required to imagine the rotation of a single image (OB monkey task), despite demonstrating an understanding of the task on trials in the upright position, as a group, participants with WS scored significantly below all TD groups on all rotation trials. Moreover, performance in the WS group was significantly below all TD groups even on 0° trials, suggesting that difficulties in visual matching in WS may have contributed somewhat to these results. That said, given an effect of rotation was still identified in this group, this suggests, similar to the pattern observed in TD 5 and 6 year-olds, some individuals with WS found the task increasingly more difficult with escalating degrees of rotation, i.e., they were able to use mental rotation.

This study also provided insight into VPT abilities in WS compared to TD 5-10 year-olds. Two VPT tasks were conducted to examine the ability to perform imagined movement of the self around a circular array and the ability to determine left-right body coordinates following imagined self-rotations to either 90° or 180° from actual viewpoint. Participants with WS performed poorly on both VPT tasks, indicative of profound difficulties at all angles of imagined self-rotation, with performance at chance on rotations above 90° on the VPT circle task. This is in line with previous research that indicated chance performance in WS when asked to imagine the perspective of another individual at 180° from own viewpoint (Farran et al., 2010). The current results extend these findings, demonstrating difficulties in this group at even lesser degrees of imagined self-rotation. On the VPT path task, scores in the WS group were not significantly different to that of TD 5 year-olds, albeit at a level above chance on trials requiring imagined rotation of the self by 90°. On this task, at imagined self-rotations of 180°, both TD 5

year-olds and participants with WS yielded scores significantly below chance, indicating that not only do young TD children and individuals with WS have profound difficulties in imagining turning the self by 180°, they demonstrated a similar preponderance to select an egocentric option (choosing the left or right that corresponded to their actual viewpoint). Similarly, when asked to imagine the rotation of the self around an array of objects (VPT circle), performance in the WS group fell to chance level on trials that required imagined rotations greater than 45°, indicative of profound difficulties with such activities.

The pattern of performance in individuals with WS both on OB and VPT tasks was in line with that of TD children of comparable non-verbal ability. At first glance, this is unsurprising, given that individuals with WS have often been found to perform at a similar level to TD 4-6 year-olds on a number of cognitive tasks including spatial (Nardini et al., 2008) and numerical abilities (Ansari, Donlan, & Karmiloff-Smith, 2007). However, in the current study, despite a similar level of performance in the WS group as 5 and 6 year-olds on most tasks, individuals with WS demonstrated an atypical pattern of performance.

The observed pattern of performance in WS on OB and VPT tasks in this study may, therefore, reflect that of a divergent developmental trajectory rather than what could be simply accounted for by developmental delay. This was reflected in part by the types of errors made on the VPT circle task compared to TD groups. On the VPT circle task, egocentric errors were the most prominent error type in individuals with WS, compared to left-right reversal errors making up the majority of errors in TD children. This prominence was not identified in the OB circle task, suggesting that imagined rotations of the self may present additional egocentric difficulties in WS that are not seen with imagined rotations of objects in a similar array.

The specific pattern of difficulties identified in the WS group may relate to difficulties in updating their egocentric position within an allocentric frame of reference as required for successful self-rotations (Burgess, Spiers, & Paleologou, 2004). Updating the location of the

self during imagined rotations is thought to rely on the successful translation between egocentric parietal representations and allocentric hippocampal spatial codes (Lambrey et al., 2012; Vann et al., 2009). The profound difficulty in updating one's egocentric location on the VPT task in WS is therefore consistent with atypical processing in anterior hippocampal (Meyer-Lindenberg et al., 2005) and parietal-occipital regions (Boddaert et al., 2006) in this group. In addition, difficulties in updating the imagined location of the self may explain why individuals with WS were more likely to make egocentric than left-right reversal errors (as seen in TD children), in the current study.

The large proportion of egocentric errors in WS is similar to findings that indicate young children interpret VPT instructions egocentrically and have difficulty in rotating this frame of reference in order to complete these tasks (Epley, Morewedge, & Keysar, 2004). Epley and colleagues also suggested that adults initially interpret instructions egocentrically, but have a superior ability to inhibit an egocentric response and adjust to using an appropriate strategy quickly and effectively. Difficulties in inhibition have been reported in individuals with WS (Menghini, Addona, Costanzo, & Vicari, 2010), and as such, failures in self-rotation in WS may also reflect difficulties in suppressing an egocentric response.

On the OB circle task, only the WS group demonstrated performance on 180° that was significantly below any other rotation trial. This may have, like in the VPT circle task, reflected a different pattern of performance than seen in typical development. For instance, whereas some TD children may have been able to use an alternative strategy to support performance on 180° trials such as a verbal or 'flipping' strategy, individuals with WS did not demonstrate the ability to do so.

Further examination into individual differences in performance on these tasks in WS found that OB rotation abilities as measured on the monkey task increased with chronological age, even when controlling for verbal or non-verbal abilities. This is contrasted with our

findings in TD children, for whom OB mental rotation of a single image was positively related to verbal ability. Thus, TD children who were able to apply verbal strategies during these tasks may have further supported their performance on the monkey task.

In line with our findings of age in WS and OB mental rotation, in a study examining development trajectories of spatial reference frames in WS, Nardini et al. (2008) found that older WS participants aged 26-42 were the only WS group in their study to score above chance on a task requiring the ability to use an array-based spatial frame of reference (i.e. OB mental rotation). Although this difference in ability between younger and older WS individuals remained marginal, this finding, alongside the present results, indicates that some older individuals with WS may have developed strategies to successfully complete OB rotation tasks that are independent of verbal or non-verbal development. However this was only shown (in the present study) on a task involving the mental manipulation of a single object and no such relationship was evident between WS age and mental manipulation of multiple items in an array (OB circle). It could be inferred from this that difficulties resulting from having an additional cognitive load of more than one object to mentally transform do not remediate with age in this group and is more associated with level of non-verbal cognition, as shown in the relationship between RCPM performance and OB array rotation. In the WS group, age-related factors such as experience with tasks or games requiring mental rotation may have facilitated performance. Future studies should therefore include, not only a greater age-range of individuals with WS, but also examine age-related differences in spatial performance. Assessments of experience with mental rotation tasks would also be beneficial. In addition, the use of tasks that examine performance across comparable degrees of rotation would allow clearer comparison of performance across different tasks in individuals with WS.

The ability to update self-to-object representations is important for successful large-scale spatial navigation, and performance on such environmental learning tasks has been found to be

associated with the ability to imagine the self rotating (Kozhevnikov, Motes, Rasch, & Blajenkova, 2006). Difficulties in large-scale environmental learning have been reported in WS, particularly in relation to developing an understanding of the spatial relationships between locations in space and their relationship to the self, following movement (Farran et al., 2010). The profound deficits on small-scale VPT tasks in WS therefore suggest that such strategies may not be available to support performance on navigational activities in the same way as TD children and adults.

Conclusion

The results of this study identified extensive difficulties in performing mental transformations both of objects and the self in individuals with WS. As a group, individuals with WS performed in line with what could be expected based on non-verbal ability, often demonstrating performance at a level similar to TD 5 and 6 year-olds. However, a different pattern of errors was observed in the WS group compared to TD individuals, indicative of divergent rather than simply arrested or delayed development. When asked to imagine the rotation of a single image, performance in WS was positively correlated with chronological age, suggesting that some older individuals with WS may have developed successful techniques by which to mentally rotate objects.

Findings suggest that poor performance on VPT in WS is related to difficulties in inhibiting a prepotent egocentric response. However, it is likely that deficits in imagined rotations of the self are related to atypical processing in cortical regions associated with the translation of egocentric and allocentric spatial frames of reference required for successful updating of the position of the self following both imagined and actual movement. Given the relationship between visual perspective-taking and successful large-scale navigation in typical individuals, difficulties in imagined self-rotation are likely to be implicated in poor performance

observed during large-scale spatial tasks in WS. Specific implications of difficulties in VPT for large-scale navigation in WS and the possible reliance on atypical navigation strategies in this group are an area for further investigation.

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