City Research Online

City, University of London Institutional Repository

This is the accepted version of the paper.

This version of the publication may differ from the final published version.

Permanent repository link: http://openaccess.city.ac.uk/18749/

Link to published version: http://dx.doi.org/10.1002/aur.1924

City Research Online: http://openaccess.city.ac.uk/   publications@city.ac.uk

Spatial navigation from same and different directions: The role of executive functions, memory and attention in adults with Autism Spectrum Disorder

Melanie Ring[1,1,2], Sebastian B. Gaigg[1], Olivier de Condappa[2,3], Jan M. Wiener[2] and Dermot M. Bowler[1]

[1]Autism Research Group, Department of Psychology, School of Social Sciences, Rhind Building, City, University of London, London, EC1V 0HB, UK

[2]Wayfinding Lab, Psychology Research Centre, Bournemouth University, Poole, BH12 5BB, UK

[1]Correspondence concerning this article should be addressed to Melanie Ring, Autism Research Group, Department of Psychology, School of Social Sciences, Rhind Building, City, University of London, Northampton Square, London, EC1V 0HB, United Kingdom. Email: Melanie.ring.1@city.ac.uk or +44(0)20 7040 8380.

[2] Melanie Ring is now based at Department of Child & Adolescent Psychiatry, Medical Faculty of the Technical University Dresden, Dresden, Germany.

[3] Olivier De Condappa is now based at School of Applied Social Sciences, Health and Life Sciences, De Montfort University, The Gateway, Leicester, LE1 9BH, UK.

Acknowledgements

Lay summary

Navigating an environment is difficult for people with ASD independent of whether they are travelling in the same or in a different direction from that which they originally studied. The present study suggests that flexibility in alternating travel directions, difficulties in remembering landmarks as well as reduced attention to landmarks while learning a route play a role in the navigation difficulties in ASD. Guidance at route learning might help autistic individuals to improve their ability to navigate in their environments.

Abstract

To resolve some of the inconsistencies in existing research into spatial navigation in Autism Spectrum Disorder (ASD), we tested two large age- and ability-matched groups of ASD and typically developing (TD) participants for their spatial navigation abilities in a route learning task, which has been shown to shed light on the strategies participants employ when navigating complex environments. Participants studied a route through a virtual maze by watching a short video of a first-person perspective navigating a maze. The maze included four four-way intersections that were each marked with two unique landmarks in two corners of the intersection. At test, static images of the intersections, either as seen during the video or as approached from a different direction, were presented and participants had to indicate in which direction they would need to travel (straight, left or right) in order to follow the originally studied route. On both types of test trials, the ASD group performed worse and their difficulties were related to reduced cognitive flexibility. Eye-movement data and follow-up item-memory tests suggested that navigation difficulties may have been related to differences in attention during encoding and less spontaneous use of landmarks as cues for navigation. Spatial navigation performance was best predicted by memory for landmarks as well as by executive functions. The results are discussed in relation to theories of underlying navigation-related brain regions. More research is needed to disentangle the influence of executive functions, memory and attention on spatial navigation.

Keywords: spatial navigation, autism, memory, executive function, task support, eye movements

Introduction

Individuals with an Autism Spectrum Disorder (ASD) show difficulties in interactions and communication with others, as well as restricted and repetitive behaviours, interests and activities (American Psychiatric Association, 2013). In addition, ASD is associated with a characteristic profile of strengths and difficulties across various domains of cognition, including memory (Boucher & Bowler, 2008; Boucher et al., 2012; Bowler et al., 2011) and executive functions (Hill, 2004a & b). These domains have attracted considerable attention in ASD because they can shed light on the aetiology of ASD by analogy with other groups of individuals, such as patients with amnesia (Boucher & Warrington, 1976) or frontal lobe damage (Minshew et al., 1992) or typically developing older adults (TD OA; ageing analogy - Bowler, 2007), and because impairments in memory and/or executive functions have consequences for an individual's adaptive functions in their own right (e.g., Gilotty et al., 2002; Henry et al., 2014; Jones et al., 2011; Panerai et al., 2014; Williams et al., 2014). The present paper aims to address some unresolved questions concerning the interacting effects of memory and executive difficulties in a functional domain that remains relatively under-researched in ASD - spatial navigation.

Two different forms of navigation are of interest in the context of this study. *Egocentric* navigation describes navigation where the route is encoded in relation to the navigator's own body or point of view (Hartley et al., 2004) and is regulated through the caudate nucleus (Bohbot et al., 2004). In contrast, *allocentric* navigation operates independently of a single viewpoint and requires the formation of an abstract cognitive map of the environment in which the relationships among locations and landmarks are encoded (Bohbot et al., 2004). Neuroimaging studies point to the importance of the (right) human hippocampus for allocentric navigation (Bohbot et al., 2004) and studies in humans with medial temporal lobe lesions show impairments in allocentric navigation leaving performance

on an egocentric condition intact (Feigenbaum & Morris, 2004; Goodrich-Hunsaker et al., 2010).

There are different conceptualizations of memory difficulties in ASD, all leading to the prediction that allocentric navigation should be impaired in particular in ASD individuals. For example, the *relational binding account* (Bowler et al., 2011) suggests that similar to other forms of relational memory, such as memory for the spatio-temporal context of an item presentation (e.g. Bennetto et al., 1996; Bigham et al., 2010; Bowler et al., 2004, 2014; Cooper et al., 2015; Minshew & Goldstein, 1993; Poirier et al., 2011; Ring et al., 2015, 2016), allocentric navigation involves associating different elements (or items) of information and should, therefore, pose particular difficulties for individuals with ASD. In addition, relational memory processes are thought to be supported by the hippocampus, which has also been shown to support successful spatial navigation through the environment (Burgess et al., 2002; Eichenbaum, 2004; Opitz, 2010).

A parallel view would suggest that allocentric navigation involves the processing of complex information and should, therefore, pose particular difficulties for ASD individuals because of a relation to executive dysfunction (Minshew et al., 1992; Minshew et al., 1994; Minshew et al., 1995; Minshew & Goldstein, 1998; Williams et al., 2015). Particular difficulties in executive functions in ASD have been reported previously in planning tasks (e.g. Hughes et al., 1994; Robinson et al., 2009) and tasks assessing mental flexibility (e.g. Rumsey & Hamburger, 1988, 1990; Hughes et al., 1994; Ozonoff et al., 2004).

Finally, as a combination of both of these accounts the ageing analogy suggests that there might be parallel between ASD individuals' cognitive functions and that of TD OA (Bowler, 2007), who have recently presented particular difficulties in allocentric navigation (Wiener et al., 2012), in flexibly switching between different navigation strategies (Harris et al., 2012), as well as a bias towards the use of egocentric extra-hippocampal navigation

strategies (Wiener et al., 2013). Overall, irrespective of whether memory difficulties in ASD are conceptualised as an impairment of relational memory processes (implicating primarily hippocampal processes) and/or executive functions (implicating primarily frontal lobe processes), the prediction is that ASD individuals experience disproportionate difficulties with allocentric navigation.

The results of the few previous studies that have investigated spatial navigation in ASD, however, report mixed findings. Some studies found no differences between groups (Edgin & Pennington, 2005; Caron et al., 2004), some studies found an overall navigational deficit in ASD independent of whether conditions probed allocentric or egocentric skills (Lind et al., 2013), and a few studies found specific allocentric navigational difficulties as predicted (Prior & Hoffmann, 1990; Lind et al., 2014; Ring et al., under revised review). Only three of these earlier studies compared allocentric and egocentric conditions within one study (Lind et al., 2013, 2014; Ring et al., submitted). Since executive functions have been found to play an important role in spatial navigation (Moffat et al., 2007), they may be a relevant factor in explaining some of the inconsistencies found in previous spatial navigation studies in ASD.

Indeed, when looking at memory in ASD, Maister et al. (2013) found that executive functions were related to reduced autobiographical memory in that only ASD children with poor set shifting abilities reported fewer episodic details in their autobiographical memories, whereas ASD children with good set shifting abilities performed similarly to TD children. In addition, Goddard et al. (2014) reported that set shifting abilities were a significant predictor for autobiographical memory, again showing that autobiographical memory difficulties may at least in part be corollary of executive dysfunction rather than memory problems per se.

The current study investigates the effects of executive functions on spatial navigation in ASD individuals more closely by using a route-learning paradigm previously developed

for the use in TD OA (Wiener et al., 2013) systematically comparing allocentric and egocentric spatial navigation and by additionally measuring executive functions by means of the Intradimensional/Extradimensional (IED) shift task from the CANTAB. In the current navigation paradigm, participants were asked to study a route through a maze including four four-way intersections, each of which marked with two pictures of animals that served as landmarks for navigation. At test, participants were presented with static images of the intersections asking them to indicate the original travel direction. Importantly, egocentric and allocentric trials presented here, differed only in the way the images of the intersections were presented to the participant, i.e. as being approached from the same (egocentric) or a different direction as at study (allocentric). Further, a potential preference for extra-hippocampal egocentric navigation strategies by the ASD individuals was tested. Finally, to gain some additional information about attentional processes during task performance, participants' eye movements were measured throughout the task and item memory (i.e. memory for the landmarks that typically guide navigation) was examined after the navigation task. We predicted specific difficulties with allocentric navigation for ASD participants, a preference for egocentric navigation strategies, and executive function difficulties that may play a role in the navigation difficulties in ASD individuals for both types of navigation.

Methods

Participants

Thirty-seven ASD (30 men, M_{age} = 42.61 years, age range: 26-64 years) and 31 TD (25 men, M_{age} = 40.71 years, age range: 21-64 years) adults were matched on gender, X^2 = 0.00, p = .96, chronological age (CA), Verbal (VIQ), Performance (PIQ) and Full-scale Intelligence Quotient (FIQ) as measured by the third edition of the Wechsler Adult Intelligence Scale (WAIS-III[UK]; The Psychological Corporation, 2000; see Table 1).

Individuals were selected from a panel of participants with whom the Autism Research Group at City, University of London is in regular contact. All participants were native English speakers and ASD compared to TD individuals showed significantly higher scores on the AQ (Baron-Cohen et al., 2001; Table 1). All TD individuals scored below, and all except five individuals with ASD scored above 26 on the AQ, which is suggested as a sensitive cut-off value when using the AQ for screening purposes (Woodbury-Smith et al., 2005). All ASD participants had been diagnosed by experienced clinicians according to DSM-IV-TR criteria (American Psychiatric Association, 2000) and 32 individuals were available to complete the Autism Diagnostic Observation Schedule (ADOS; Lord et al., 1989) carried out by individuals trained to research reliability standards on this instrument. Out of these 32 individuals, eight scored just below the total ADOS cut-off score. None of the ASD participants scored below threshold on ADOS and AQ. All participants were nevertheless included in the sample since all had received a clinical diagnosis of an ASD, which was our main inclusion criterion. TD individuals were included in the study if they did not report a personal or family history of a psychological or neurodevelopmental disorder or taking psychotropic medication. All participants were reimbursed for their time and travel expenses according to standard university fees. This study was approved by City, University of London's ethics committee (name: Route learning and route retracing in adults with Autism Spectrum Disorders; approval number: PSYETH(UPTD) 12/13 43), and the procedures used adhere to the guidelines set out by the British Psychological Society.

[Insert Table 1 here]

Materials

A virtual environment displaying a tunnel bounded by brown brick walls to the right and left and a grey floor and ceiling programmed in Vizard 3.0 was adapted from Wiener et al. (2013). In a 38-second video, participants were passively transported along a route through the environment turning either right or left at each of four, four-way intersections, each marked with two pictures of animals (e.g. dog, snake, panda), serving as landmarks hanging from the ceiling of the maze in two opposite corners of the intersection (see Figure 1 top left for a schematic drawing of the route). At test, participants saw twelve static images of the intersections in random order, with some intersections shown from the same direction of travel as encountered during study whilst others were shown from a different direction of travel. Same and different direction images could be distinguished only in terms of the positions of the animal landmarks marking the intersections (see Figure 1 for examples). Different direction images never presented the intersection as coming from the direction in which the training route continued. For example, in the original route Intersection 1 was marked with the picture of a dog in the near right-hand corner and the picture of a butterfly in the far left-hand corner of the intersection as seen from the participants' direction of travel. The same arrangement was presented for a same direction trial. The two different direction trials either presented the dog picture in the near left and the butterfly in the far right-hand corner of the intersection or the butterfly in the near right-hand corner and the dog in the far left-hand corner.

[Insert Figure 1 here]

To measure the extent to which possible inflexible responses on the navigation task may be related to difficulties with executive functions, cognitive flexibility was tested using

the *IED* from the Cambridge Neuropsychological Test Automated Battery (CANTAB). This task presented participants with pairs of pink shapes and white lines on top and measured rule learning based on reward and rule changes. Participants' response perseveration at Stage 8, presenting the extradimensional shift, i.e. a shift in reward from the pink shapes to the white lines, was of particular interest. The number of times participants continued to choose the pink shapes over the white lines because they had previously been correct and rewarded (perseverative mistakes) was measured. The IED has been shown to be sensitive to frontal lobe damage (Owen et al., 1993), and ASD individuals have previously shown more perseverative errors on the extradimensional shift of the task (Hughes et al., 1994; Ozonoff et al., 2004), making the IED a good control task. Only 36 ASD (29 men, M_{age} = 43.00 years, age range: 26-64 years) and 25 TD (21 men, M_{age} = 42.68 years, age range: 21-64 years) individuals were available for the task, who were, however, still matched in terms of gender, X^2 = 0.12, p = .73, CA, VIQ, PIQ and FIQ, t_{max} < 0.33, p_{min} > .74, Cohen's d_{max} < 0.09, 95% CI_{max}(-0.43, 0.59).

Procedure

In a practice task, participants studied twice a video presenting a virtual route including two four-way intersections and were then presented with one same and one different direction trial at test. Participants received corrective feedback and more practice if needed and were given the chance to ask questions. The main experiment was then presented in Tobii studio version 3.1.6 and a Tobii TX300 recorded eye movements during study and test with a sampling rate of 240 Hz. Each study and test phase started with a five-point calibration procedure, thus allowing participants to readjust their seating position and take breaks between blocks. Participants took part in six study-test blocks. Each study block presented them with the same virtual route that included four, four-way intersections at which

the route turned either right or left. During each test the same 12 static images (4 same, 8 different direction images) of the intersections were presented in a new random order. Participants were told that the test images showed the intersections they had travelled through in the video but that some of them would now be presented as if approached from another direction (although never from the opposite direction so that no U-turns would be required). Participants were told that their task would be to indicate in which direction they would need to travel to follow the original route they had studied. The test images remained on the screen until participants gave a verbal response after which the next trial started. No feedback was provided at test.

After the last test block, free and cued recall tests followed. First, participants were asked to name all the animals they could remember and the experimenter noted down their answers. Next, participants were asked to complete an empty map (see Figure 1 top right) with the route they had studied, starting at an arrow pointing in the direction of travel and to label the empty boxes placed at the corners of the intersections with the names of the animals they had seen as the landmarks.

Scoring

Two behavioural measures were calculated from the data. Participants' responses were scored as a percentage of correct trials for each block to obtain an *accuracy score*. *Strategy scores* were derived from participants' responses on two of the different direction trials for each block. These trials were the same for every participant. Only on these two trials, each of the three directions corresponded to a different strategy as explained with reference to Figure 2.

[Insert Figure 2 here]

When looking at Figure 2, at study the first intersection was marked by Landmark A in the near right-hand corner and Landmark B in the far left-hand corner of the intersection, the intersection was approached from the front (grey arrow) and the route turned left. In the *different direction* trial presented at test, the same intersection was now approached from the right in relation to the original travel direction (black arrow) and was marked with Landmark A in the near left-hand corner and Landmark B in the far right-hand corner of the intersection (see Figure 1 bottom middle for the actual image). Using a *Configuration strategy,* the participant would have encoded the original relationship between the two landmarks and the travel direction and would give the correct answer to go straight at this intersection following the original travel direction. If a participant used only one of the landmarks as a cue, for example turn left at Landmark A or B, the answer would be to turn left (dotted arrow), leading to an incorrect answer and a score for the *Associative Cue strategy*. A third possibility is that the participant used one of the landmarks as a beacon making them turn away from Landmark A or turn towards Landmark B leading to a right turn (dashed arrow), an incorrect answer and a score for the *Beacon strategy*.

Eye movements

Eye movements were measured at study, i.e. while participants were watching the route video (encoding). Fixations were defined as lasting a minimum of 100ms (Hannula et al., 2007) and we inspected total fixation duration (i.e. sum of the duration of all fixations) and number of fixations on the front animal (AOI1) and the landmark animal presented at the back of the intersection (AOI2) at encoding as extracted using Tobii studio version 3.3.0. For follow-up analyses, we defined three additional AOIs representing the three directions participants could choose to inspect if potential differences between groups in fixation number and duration on the landmarks may have been related to the fact that one group may

have spent longer time/more fixations inspecting one of the travel directions. Five ASD and 3 TD individuals were excluded from the final eye-movement analyses as the Tobii software revealed that the validity of their data was below 70% on more than three blocks. Therefore, the final sample for eye-movement data consisted of 32 ASD (27 men, M_{age} = 40.72 years, age range: 26-64 years) and 28 TD (23 men, M_{age} = 41.54 years, age range: 21-64 years) individuals, still matched on gender, X^2 = 0.05, p = .82, CA, VIQ, PIQ and FIQ, t_{max} < 0.90, p_{min} > .37, Cohen's d_{max} < 0.24, 95% CI_{max}(-0.28, 0.74).

Results

The data were analysed with Chi-Squared tests for nominal data, bivariate correlations, linear regression analyses, independent samples t-tests and repeated measures ANOVAs. Greenhouse Geisser correction (GGC) was used when the Sphericity assumption was violated and Bonferroni corrected post-hoc tests were applied in case of significant differences. The level of significance was set to .05 and Cohen's d and partial Eta-Squared are reported as effect size measures.

Behavioural data

Accuracy

The data, presented in Figure 3, were analysed with a 2 (Group [ASD, TD]) x 2 (Trial type [egocentric, allocentric]) x 6 (Block [1, 2, 3, 4, 5, 6]) repeated measures ANOVA. A main effect of *Group*, $F(1,66)$ = 5.35, p < .05, Cohen's d = 0.56, 95% CI(0.07, 1.04), indicated higher accuracy for the TD compared to the ASD group. Significant main effects of *Trial type*, $F(1,66)$ = 136.55, p < .0001, Cohen's d = 1.49, 95% CI(1.11, 1.86), and *Block*, $F(3.53,232.66)$ = 10.06, p < .0001, η_p^2 = .13, GGC, showed higher accuracy for egocentric compared to allocentric trials, and a gradual increase in accuracy from Blocks 1 to 6. No

interactions were significant, $F_{max} < 1.76$, $p_{min} > .14$, $\eta_p^2{}_{max} < .03$, suggesting that the ASD group experienced similar difficulties in allocentric and egocentric navigation vis-a-vis the comparison group.

[Insert Figure 3 here]

Strategy

Strategy scores are presented in Figure 4 and were analysed with three separate 2 (Group [ASD, TD]) x 6 (Block [1, 2, 3, 4, 5, 6]) repeated measures ANOVAs. For the *Associative Cue strategy*, a non-significant trend of a Group x Block interaction, $F(5,330) = 1.91$, $p = .09$, $\eta_p^2 = .03$, was found. No main effects were significant, $F_{max} < 1.38$, $p_{min} > .24$, $\eta_p^2{}_{max} < .03$. For the *Beacon* and *Configuration strategies*, however, significant main effects of Block$_{Beacon}$, $F(4.24,279.61) = 6.68$, $p < .0001$, $\eta_p^2 = .09$, GGC, and Block$_{Configuration}$, $F(3.78,249.69) = 9.19$, $p < .0001$, $\eta_p^2 = .12$, GGC, showed a decrease in the use of the *Beacon* and an increase in the use of the *Configuration strategy* from Blocks 1 to 6. No other main effects or interactions were significant, $F_{max} < 1.46$, $p_{min} > .23$, $\eta_p^2{}_{max} < .03$.

[Insert Figure 4 here]

Eye-movement data

Encoding (fixations on landmarks, while studying the route)

The data, presented in Table 2, were analysed with 2 (Group [ASD, TD]) x 2 (AOI [AOI1, AOI2]) x 6 (Block [1, 2, 3, 4, 5, 6]) repeated measures ANOVAs.

Total Fixation Duration

A significant main effect of *Group*, $F(1,58) = 5.90$, $p < .05$, Cohen's $d = 0.63$, 95% CI(0.10, 1.14), showed that TD as opposed to ASD individuals fixated longer on the landmark animals while watching the video. In addition, both groups fixated the animal presented at the back of the intersection (AOI2) for longer than the front animal (AOI1), $F(1,58) = 4.92$, $p < .05$, Cohen's $d = 0.25$, 95% CI(-0.11, 0.61). It is worth noting here, that both landmarks were presented for similar time durations. No interactions were significant, $F_{max} < 1.87$, $p_{min} > .10$, $\eta_p^2{}_{max} < .04$.

When running follow-up tests to inspect if ASD compared to TD individuals looked longer at the three different directions, no significant between-group differences were found, $F_{max} < 1.2$, $p_{min} > .33$, $\eta_p^2{}_{max} < .02$.

Number of Fixations

Similarly to fixation durations, significant main effects of *Group*, $F(1,58) = 5.48$, $p < .05$, Cohen's $d = 0.61$, 95% CI (0.08, 1.12), and *AOI*, $F(1,58) = 9.38$, $p < .01$, Cohen's $d = 0.32$, 95% CI(-0.04, 0.68), showed more fixations on the landmarks for the TD compared to the ASD group and fewer fixations on the front (AOI1) compared to the back animal (AOI2) overall. No main effect of Block or interactions were significant, $F_{max} < 1.35$, $p_{min} > .24$, $\eta_p^2{}_{max} < .03$.

[Insert Table 2 here]

Free and cued recall item-memory

The TD group recalled significantly more animals than the ASD group in free, $t(66) = 2.70$, $p < .01$, Cohen's $d = 0.66$, 95% CI(0.16, 1.14), and cued recall tests, $t(66) = 2.33$, $p <$

.05, Cohen's d = 0.57, 95% CI(0.07, 1.05). TD participants also had better recall of the animals' positions along the route, $t(65.99)$ = 1.97, p = .05, Cohen's d = 0.47, 95% CI(-0.02, 0.95), compared to the ASD group. There were, however, no significant between-group differences in the recall of turns along the route when cued with the map, $t(66)$ = 0.98, p = .33, Cohen's d = 0.24, 95% CI(-0.24, 0.72); see Table 3).[4]

[Insert Table 3 here]

Executive Functions

ASD (M = 11.67, SD = 11.15) compared to TD individuals (M = 5.76, SD = 7.14) showed significantly more perseverative errors on Stage 8 of the IED from the CANTAB, $t(58.70)$ = 2.52, p < .05, Cohen's d = 0.61, 95% CI(0.08, 1.12).

Relations between spatial navigation, item memory and executive functions

To investigate the relations between spatial navigation, eye-movement data, performance on item and executive functions tests, we ran bivariate correlation analyses. Table 4 shows only non-significant correlations of small effect size between fixation duration and number of fixations on the landmark animals at encoding and allocentric or egocentric navigation performance. However, there were positive correlations between memory for animals and allocentric navigation of medium (ASD group) to large (TD group) effect size, which were significant in the TD group and for both groups in total, indicating that the better participants remembered the animal landmarks, the better they performed on allocentric navigation trials. Correlations between item memory and egocentric navigation were only

---

[4] Inspecting the data presented below only for the 36 ASD individuals and 25 TD individuals that took part in the IED from the CANTAB, the directions of the effects stayed the same. However, the main effect of group in the accuracy analysis as well as the difference in memory for animal positions (p = .14) missed significance (p = .108), which could be caused by the reduced sample size.

small and not significant. There were also negative correlations between perseverative errors on the IED and egocentric navigation, which were small in the ASD and large and significant in the TD group and for both groups in total. Negative correlations between perseverative errors on the IED and allocentric navigation were medium sized for both groups and (marginally) significant, indicating the more perseverative errors participants made, the worse their overall navigation performance was.

We then investigated the predictive value of item memory and executive functions as well as interaction terms of these factors with group for spatial navigation performance. When entering these variables into a multiple linear regression using the forward method to predict allocentric navigation, the best model significantly explained 21.3% of total variance, $R^2 = .21$, $F(2,58) = 7.84$, $p < .01$, and included *perseverative errors*, $\beta = -.30$, 95% CI(-0.01, -0.00), $p < .05$, as well as *cued recall for animals*, $\beta = .28$, 95% CI(0.04, 0.58), $p < .05$, as significant predictors. The best model to predict egocentric navigation significantly explained 11.8% of total variance, $R^2 = .12$, $F(1,59) = 7.89$, $p < .01$, and it included *perseverative errors* as the only significant predictor, $\beta = -.34$, 95% CI(-0.01, -0.00), $p < .01$.

Discussion

The aim of this study was to systematically compare allocentric and egocentric spatial navigation using a task that offers the same level of complexity for both conditions and has been used previously in the TD ageing population. As well as navigational accuracy, we investigated whether participants showed a preference for a certain navigational strategy. In addition, the role of attention (as measured through eye movements) during encoding, executive functions (measured through the IED from the CANTAB) and memory for landmarks was investigated.

Contrary to predictions of a specific allocentric navigation deficit in ASD, ASD adults showed difficulties in same and different direction trials in this study. . There are two factors that may be able to explain the discrepancies in results for the current and past navigation studies. First, previous studies that used a virtual pool environment, where participants were asked to find a hidden platform in a computer-based version of the Morris Water Maze (Edgin & Pennington, 2005; Ring et al., under revised review) presented the navigation environment in an aerial view, which may have made the formation of an abstract navigation map easier. These tests are, therefore, less realistic in terms of the real life navigation requirements than 3-D environments. Such an environment is the island navigation task used by Lind et al. (2013, 2014), where participants were asked to find target objects that were initially marked by clearly visible flags and then hidden to probe memory dependant spatial navigation. Lind et al. (2013, 2014) observed that a group of ASD participants were less effective at finding the hidden objects despite having no difficulties reaching them when they were initially marked by the clearly visible flags. Although this study demonstrated navigation difficulties in ASD, the design of this paradigm does not clearly distinguish between egocentric and allocentric contributions to performance. While participants navigated their way toward the flags initially to find the objects, they did not have to rely extensively on memory but simply navigate toward the visible goal. And when the objects were subsequently hidden, participants might have relied on a combination of egocentric and allocentric memory at different points in the routes they took. The current findings, therefore build on studies such as those by Lind et al., (2013) suggesting that both egocentric and allocentric spatial navigation might pose difficulties for individuals with ASD in ecologically valid virtual environments, possibly due to difficulties with executive functions and/or the effective control of attention during route learning (see below for further discussion). Also, contrary to predictions, ASD individuals did not show a specific preference for an egocentric

navigation strategy similar to TD OA (see Wiener et al., 2013). However, as the task continued, ASD individuals showed a tendency for an increased use of the associative cue strategy, which has been reported to depend on brain regions outside the hippocampus, i.e. the striatum (Featherstone & McDonald, 2005). It is possible that the fronto-hippocampal system is not as severely affected in ASD as it is in TD OA. However, what might also explain the difference in strategy-use between ASD individuals and TD OA is the fact that Wiener et al. (2013) only screened their participants for mild cognitive impairments resulting from ageing but did not match their participants on cognitive ability, whereas our TD and ASD groups were well-matched on age and cognitive abilities.

There are two likely explanations for these surprising results. First, from a memory point of view, difficulties in spatial navigation performance can occur because of relational binding processes that are inherent in this particular navigation task (Rubin et al., 2014) and which are particularly difficult for ASD individuals (Bowler et al., 2011). Future studies should use a specific measure of relational binding especially binary – the relation between two items or an item and its context (Halford, 1992) – and ternary relations – associations among three pieces of information – to establish their specific role in the navigation difficulties in ASD reported in this paper.

A second explanation is related to increased perseveration in the ASD group in the current study which together with the counterbalanced presentation of allocentric and egocentric trials may have had a knock-on effect on egocentric trials, decreasing performance overall for the ASD group. The notion of decreased cognitive flexibility is in line with previous research on the topic (Dichter et al., 2010; Hughes et al., 1994; Ozonoff et al., 2004; Van Eylen et al., 2011). Indeed, when looking at the relevance of executive functions for egocentric and allocentric navigation performance in the current study, perseverative errors in

the IED task were a significant predictor, again emphasizing the relevance of the influence of executive functions in memory and navigation performance in ASD (see Maister et al., 2013).

A third important factor to consider is attention at encoding, as indicated by a number of previous studies (see Cooper et al., 2017; Gaigg et al., 2008, 2015; Loth et al., 2011; Ring et al., 2017). In the current study, ASD compared to TD individuals looked for a significantly shorter time and less often at the two landmarks marking the intersections, which may in part explain their later difficulties in remembering the landmarks on the item tests. The use of cues in the environment is, however, necessary for successful (allocentric) navigation (Bohbot et al., 2004). It is, therefore, possible that ASD individuals had difficulties in selecting the relevant information to focus on during the task, which is in fact a common feature of the disorder (see Boucher & Warrington, 1976; Bowler et al., 1997, 2008, 2009; Gaigg et al., 2008; Lopez & Leekam, 2003; Maister et al., 2013; Minshew & Goldstein, 2001; Minshew et al., 1997; Smith et al., 2007; Tager-Flusberg, 1991). Therefore, the question arises whether ASD individuals' navigation performance might be improved by the provision of task support (Bowler et al., 1997), such as specific instructions to encode the landmarks and to use them as cues for navigation. In addition, explicitly telling participants about the different pieces of information that need to be taken into account and related to one another might enhance task performance. Differences in the pattern of correlations between groups gave a hint that the two groups might have performed the task differently. Whereas ASD individuals' egocentric and allocentric navigation performance related to cued recall to the same extent (small effect size for both, $z = -0.24$, $p = .41$), there was a large and significant difference ($z = -2.23$, $p = .01$) between the correlation coefficients between cued recall and TD individuals' egocentric (negative and small correlation) and allocentric (positive and large correlation) navigation performance. This indicates that whereas TD

individuals were using two different processes for egocentric and allocentric navigation, ASD individuals might have relied on the same process for both conditions.

It is worth noting that virtual maze paradigms can only be simplifications of real-world navigation demands. However, they are useful to test and generate hypotheses. The current paradigm for example has shown that individuals with ASD do not spontaneously attend to cues in the environment for maze navigation. We would expect a similar finding in real world navigation where cues are all around and depending on them is vital to find the path to the desired location. Another finding from this study that can be transferred to real world navigation is that difficulties occur in ASD in environments that change their orientation rapidly. This can be the case at busy crossroads that can seem disorienting. These hypotheses should be followed up in real world navigation, e.g. by using portable eye-tracking devises and asking participants to navigate real roads coming from different directions.

In a more general context, regarding potential underlying brain mechanisms, the parietal lobes, the hippocampus and the PFC have been shown to be involved in spatial navigation (Moffat, 2009) and all three brain regions were previously reported to form part of the default mode network underlying functions such as Theory of Mind (ToM), autobiographical memory and episodic future thinking (Spreng et al., 2008). Lind et al. (2013) previously found support for the disturbance of the default network in ASD by reporting that difficulties in spatial navigation were related to problems in ToM and episodic memory. Difficulties in perspective-taking in ASD (Hamilton et al., 2009; Rehfeldt et al., 2007) may have also played a role in the difficulties with different-direction trials in the current study, as De Condappa and Wiener (2016) recently suggested, but to shed more light on these issues is a task for future research.

To conclude, the present study provides further support for the idea that adults with ASD experience difficulties in spatial navigation. It extends previous literature by highlighting the important roles of cognitive flexibility, item memory and attention for successful spatial navigation. The data also present evidence for the task support hypothesis as ASD individuals did not spontaneously use cues as effectively as TD individuals to enhance their task performance. More research is needed to disentangle the roles of executive functions, ToM and relational binding in spatial navigation, to investigate if spatial navigation can be improved in ASD by providing the right task support and to find out more about the underlying brain bases of this capacity.

References

American Psychiatric Association (2000). *Diagnostic and statistical manual of mental disorders- DSM-IV-TR (4th ed., text revision)*. Washington, DC: Author.

American Psychiatric Association (2013). *Diagnostic and statistical manual of mental disorders (Fifth ed.)*. Washington, DC: Author.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders, 31*(1), 5-17. doi:10.1023/A:1005653411471

Bennetto, L., Pennington, B. F., & Rogers, S. J. (1996). Intact and impaired memory functions in autism. *Child Development, 67*(4), 1816-1835. doi:10.2307/1131734

Bigham, S., Boucher, J., Mayes, A., & Anns, S. (2010). Assessing recollection and familiarity in autistic spectrum disorder: Methods and findings. *Journal of Autism and Developmental Disorders, 40*(7), 878-889. doi: 10.1007/s10803-010-0937-7

Bohbot, V. D., Iaria, G., & Petrides, M. (2004). Hippocampal function and spatial memory: Evidence from functional neuroimaging in healthy participants and performance of patients with medial temporal lobe resections. *Neuropsychology, 18*(3), 418-425. doi:10.1037/0894-4105.18.3.418

Boucher, J. & Bowler D. M. (Eds.). (2008). *Memory in autism: theory and evidence.* Cambridge: Cambridge University Press.

Boucher, J., Mayes, A. & Bigham, S. (2012). Memory in autistic spectrum disorder. *Psychological Bulletin, 138*(3), 458-496. doi:10.1037/a0026869

Boucher, J., & Warrington, E. K. (1976). Memory deficits in early infantile autism: Some similarities to the amnesic syndrome. *British Journal of Psychology, 67*(1), 73-87. doi:10.1111/j.2044-8295.1976.tb01499.x

Bowler, D. M. (2007). *Autism spectrum disorder. Psychological theory and research.* Chichester: Wiley.

Bowler, D. M., Gaigg, S. B., & Gardiner, J. M. (2008). Effects of related and unrelated context on recall and recognition by adults with high-functioning autism spectrum disorder. *Neuropsychologia, 46*(4), 993-999. doi: 10.1016/j.neuropsychologia.2007.12.004

Bowler, D. M., Gaigg, S. B., & Gardiner, J. M. (2009). Free recall learning of hierarchically organised lists by adults with Asperger's syndrome: Additional evidence for diminished relational processing. *Journal of Autism and Developmental Disorders, 39*(4), 589-595. doi: 10.1007/s10803-008-0659-2

Bowler, D. M., Gaigg, S. B., & Gardiner, J. M. (2014). Binding of multiple features in memory by high-functioning adults with autism spectrum disorder. *Journal of Autism and Developmental Disorders, 44*(9), 2355-2362. doi:10.1007/s10803-014-2105-y

Bowler, D. M., Gaigg, S. B., & Lind, S. (2011). Memory in autism: Binding, self and brain. In I. Roth & P. Rezaie (Eds.), *Researching the autism spectrum: Contemporary perspectives* (p. 316-346). Cambridge: Cambridge University Press.

Bowler, D. M., Gardiner, J. M. & Berthollier, N. (2004). Source memory in adolescents and adults with Asperger's syndrome. *Journal of Autism and Developmental Disorders, 34*(5), 533-542. doi:10.1007/s10803-004-2548-7

Bowler, D. M., Matthews, N. J., & Gardiner, J. M. (1997). Asperger`s syndrome and memory: Similarity to autism but not amnesia. *Neuropsychologia, 35*(1), 65-70. doi: 10.1016/S0028-3932(96)00054-1

Burgess, N., Maguire, E. A., & O`Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron, 35*(4), 625-641. doi:10.1016/S0896-6273(02)00830-9

Cambridge Neuropsychological Test Automated Battery (CANTAB). Testmanual

Caron, M.-J., Mottron, L., Rainville, C., & Chouinard, S. (2004). Do high-funcioning persons with autism present superior spatial abilities? *Neuropsychologia*, 42(4), 467-481. doi: 10.1016/j.neuropsychologia.2003.08.015.

Cooper, R. A., Plaisted-Grant, K. C., Baron-Cohen, S., & Simons, J. S. (2017). Eye movements reveal a dissociation between memory encoding and retrieval in adults with autism. *Cognition, 159.* 127-138.

Cooper, R. A., Plaisted-Grant, K. C., Hannula, D. E., Ranganath, C., Baron-Cohen, S., & Simons, J. S. (2015). Impaired recollection of visual scene details in adults with autism spectrum conditions. *Journal of Abnormal Psychology, 124*(3), 565-575. doi: 10.1037/abn0000070

Craik, F. I. M. & Anderson, N. D. (1999). Applying cognitive research to problems of aging. In D. Gopher & A. Koriat (Eds.) *Attention and performance XVII: Cognitive regulation of performance: Interaction of theory and application. Attention and performance* (pp. 583-615). Cambridge: The MIT Press.

De Condappa, O., & Wiener, J. M. (2016). Human place and response learning: Navigation strategy selection, pupil size and gaze behavior. *Psychological Research, 80*(1), 82-93. doi: 10.1007/s00426-014-0642-9

Dichter, G. S., Radonovich, K. J., Turner-Brown, L. M., Lam, K. S. L., Holtzclaw, T. N., & Bodfish, J. W. (2010). Performance of children with autism spectrum disorders on the Dimension Change Card Sort Task. *Journal of Autism and Developmental Disorders, 40*(4), 448-456. doi: 10.1007/s10803-009-0886-1

Edgin, J. O., & Pennington, B. F. (2005). Spatial cognition in autism spectrum disorders: Superior, impaired, or just intact? *Journal of Autism and Developmental Disorders, 35*(6), 729-745. doi:10.1007/s10803-005-0020-y

Eichenbaum, H. (2004). Hippocampus: Cognitive processes and neural representations that underlie declarative memory. *Neuron, 44*(1), 109-120. doi:10.1016/j.neuron.2004.08.028.

Featherstone, R. E., & McDonald, R. J. (2005). Lesions of the dorsolateral striatum impair the acquisition of a simplified stimulus-response dependent conditional discrimination task. *Neuroscience, 136*(2), 387-395. doi: 10.1016/j.neuroscience.2005.08.021

Feigenbaum, J. D., & Morris, R. G. (2004). Allocentric versus egocentric spatial memory after unilateral temporal lobectomy in humans. *Neuropsychology, 18*(3), 462-472. doi:10.1037/0894-4105.18.3.462

Gaigg, S. B., Bowler, D. M., Ecker, C., Calvo-Merino, B., & Murphy, D.G. (2015). Episodic recollection difficulties in ASD result from atypical relational encoding: behavioural and neural evidence. *Autism Research, 8*(3), 317-327. doi: 10.1002/aur.1448

Gaigg, S. B., Bowler, D. M., & Gardiner, J. M. (2014). Episodic but not semantic order memory difficulties in autism spectrum disorder: Evidence from the Historical Figures Task. *Memory,* doi:10.1080/09658211.2013.811256

Gaigg, S. B., Gardiner, J. M., & Bowler, D. M. (2008). Free recall in autism spectrum disorder: The role of relational and item-specific encoding. *Neuropsychologia, 46*(4), 986-992. doi:10.1016/j.neuropsychologia.2007.11.011

Gaigg, S. B., Rogers, C., & Bowler, D. M. (2012, May). *How flexible is the episodic memory system in ASD?* Paper presented at the International Conference on Innovative Research in Autism, Tours, France.

Gilotty, L., Kenworthy, L., Sirian, L., Black, D. O., & Wagner, A. E. (2002). Adaptive skills and executive function in autism spectrum disorders. *Child Neuropsychology, 8*(4), 241-248. doi: 10.1076/chin.8.4.241.13504

Goddard, L., Dritschel, B., Robinson, S., & Howlin, P. (2014b). Development of autobiographical memory in children with autism spectrum disorders: Deficits, gains, and predictors of performance. *Development and Psychopathology, 26*(1), 215-228. doi: 10.1017/S0954579413000904

Goodrich-Hunsaker, N. J., Livingstone, S. A., Skelton, R. W., & Hopkins, R. O. (2010). Spatial deficits in a virtual water maze in amnesic participants with hippocampal damage. *Hippocampus, 20*(4), 481-491. doi: 10.1002/hipo.20651

Halford, G. S. (1992). *Children's understanding: The development of mental models*. Hillsdale, N. J.: L. Erlbaum.

Hamilton, A. F. de C., Brindley, R., & Frith, U. (2009). Visual perspective taking impairment in children with autistic spectrum disorder. *Cognition, 113*(1), 37-44. doi: 10.1016/j.cognition.2009.07.007

Hannula, D. E., Ryan, J. D., Tranel, D., & Cohen, N. J. (2007). Rapid onset relational memory effects are evident in eye movement behaviour, but not in hippocampal amnesia. *Journal of Cognitive Neuroscience, 19*(10), 1690-1705. doi: 10.1162/jocn.2007.19.10.1690

Harris, M. A., Wiener, J. M., & Wolbers, T. (2012). Aging specifically impairs switching to an allocentric navigational strategy. *Frontiers in Aging Neuroscience, 4*:29. doi: 10.3389/fnagi.2012.00029.

Hartley, T., Trinkler, I., & Burgess, N. (2004). Geometric determinants of human spatial memory. *Cognition, 94*(1), 39-75. doi:10.1016/j.cognition.2003.12.001.

Henry, J. D., Terrett, G., Altgassen, M., Raponi-Saunders, S., Ballhausen, N., Schnitzspahn, K. M., & Rendell, P. G. (2014). A virtual week study of prospective memory function in autism spectrum disorders [Special Issue]. *Journal of Experimental Child Psychology, 127*, 110-125. doi: 10.1016/j.jecp.2014.01.011

Hill, E. L. (2004a). Evaluating the theory of executive dysfunction in autism. *Developmental Review, 24*(2), 189-233. doi:10.1016/j.dr.2004.01.001

Hill, E. L. (2004b). Executive dysfunction in autism. *Trends in Cognitive Sciences, 8*(1), 26-32. doi:10.1016/j.tics.2003.11.003

Hughes, C., Russell, J., & Robbins, T. W. (1994). Evidence for executive dysfunction in autism. *Neuropsychologia, 32*(4), 477-492. doi:10.1016/0028-3932(94)90092-2

Jones, C. R., Happé, F., Pickles, A., Marsden, A. J., Tregay, J., Baird, G., … Charman, T. (2011). 'Everyday memory' impairments in autism spectrum disorders. *Journal of Autism and Developmental Disorders, 41*(4), 455-464. doi: 10.1007/s10803-010-1067-y.

Lind, S. E., Bowler, D. M., & Raber, J. (2014). Spatial navigation, episodic memory, episodic future thinking, and theory of mind in children with autism spectrum disorder: Evidence for impairments in mental simulation? Frontiers in Psychology, 5:1411. doi: 10.3389/fpsyg.2014.01411

Lind, S. E., Williams, D. M., Raber, J., Peel, A., & Bowler, D. M. (2013). Spatial navigation impairments among intellectually high-functioning adults with Autism Spectrum Disorder: Exploring relations with theory of mind, episodic memory and episodic future thinking. *Journal of Abnormal Psychology, 122*(4), 1189-1199, doi:10.1037/a0034819.

Lopez, B., & Leekam, S. R. (2003). Do children with autism fail to process information in context? *Journal of Child Psychology and Psychiatry, 44*(2), 285-300. doi: 10.1111/1469-7610.00121

Lord, C., Rutter, M., Goode, S., Heemsbergen, J., Jordan, H., Mawhood, L., & Schopler, E. (1989). Autism diagnostic observation schedule: A standardized observation of communicative and social behaviour. *Journal of Autism and Developmental Disorders, 19*(2), 185-212. doi:10.1007/BF02211841

Loth, E., Gómez, J. C., & Happé, F. (2011). Do high-functioning people with autism spectrum disorder spontaneously use event knowledge to selectively attend to and remember context-relevant aspects in scenes? *Journal of Autism and Developmental Disorders, 41*(7), 945-961. doi: 10.1007/s10803-010-1124-6

Maister, L., Simons, J. S., & Plaisted-Grant, K. (2013). Executive functions are employed to process episodic and relational memories in children with autism spectrum disorders. *Neuropsychology, 27*(6), 615-627. doi:10.1037/a0034492

Minshew, N. J., & Goldstein, G. (1993). Is autism an amnesic disorder? Evidence from the California Verbal Learning Test. *Neuropsychology, 7*(2), 209-216. doi: 10.1037/08944105.7.2.209

Minshew, N. J., & Goldstein, G. (1998). Autism as a disorder of complex information processing. *Mental Retardation and Developmental Disabilities Research Reviews, 4*(2), 129-136. doi: 10.1002/(SICI)1098-2779(1998)4:2<129::AID-MRDD10>3.0.CO;2-X

Minshew, N. J., & Goldstein, G. (2001). The pattern of intact and impaired memory functions in autism. *Journal of Child Psychology and Psychiatry, 42*(8), 1095-1101. doi: 10.1111/1469-7610.00808

Minshew, N. J., Goldstein, G. Muenz, L. R., & Payton, J. B. (1992). Neuropsychological functioning in nonmentally retarded autistic individuals. *Journal of Clinical and Experimental Neuropsychology, 14*(5), 749-761. doi:10.1080/01688639208402860

Minshew, N. J., Goldstein, G., & Siegel, D. J. (1995). Speech and language in high-functioning autistic individuals. *Neuropsychology, 9*(2), 255-261. doi: 10.1037/0894-4105.9.2.255

Minshew, N. J., Goldstein, G., & Siegel, D. J. (1997). Neuropsychologic functioning in autism: Profile of a complex information processing disorder. *Journal of the International Neuropsychological Society, 3*(4), 303-316.

Minshew, N. J., Goldstein, G., Taylor, H. G., & Siegel, D. J. (1994). Academic achievement in high-functioning autistic individuals. *Journal of Clinical and Experimental Neuropsychology, 16*(2), 261-270. doi: 10.1080/01688639408402637

Moffat, S. D. (2009). Aging and spatial navigation: What do we know and where do we go? *Neuropsychology Review, 19*(4), 478-489. doi: 10.1007/s11065-009-9120-3

Moffat, S. D., Kennedy, K. M., Rodrigue, K. M., & Raz, N. (2007). Extrahippocampal contributions to age differences in human spatial navigation. *Cerebral Cortex, 17*(6), 1274-1282. doi: 10.1093/cercor/bhl036

Mottron, L., Morasse, K., & Belleville, S. (2001). A study of memory functioning in individuals with autism. *Journal of Child Psychology and Psychiatry, 42*(2), 253-260. doi:10.1017/S0021963001006722

Naveh-Benjamin, M. (2000). Adult age differences in memory performance: test of an associative deficit hypothesis. *Journal of Experimental Psychology: Learning, Memory and Cognition, 26*(5), 1170-1187. doi:10.1037/0278-7393.26.5.1170

Opitz, B. (2010). Neural binding mechanisms in learning and memory. *Neuroscience and Biobehavioural Reviews, 34*(7), 1036-1046. doi: http://dx.doi.org/10.1016/j.neubiorev.2009.11.001

Owen, A. M., Roberts, A. C., Hodges, J. R., Summers, B. A., Polkey, C. E., & Robbins, T. W. (1993). Contrasting mechanisms of impaired attentional set-shifting in patients with frontal lobe damage or Parkinson's disease. *Brain, 116*(5), 1159-1175. doi: 10.1093/brain/116.5.1159

Ozonoff, S., Cook, I, Coon, H., Dawson, H., Joseph, R. M., Klin, A., McMahon, W. M., Munson, J. A., Penningtin, B. F., Rogers, S. J., Spence M. A., Tager-Flusberg, H., Volkmar, F. R., & Wrathall, D. (2004). Performance on Cambridge Neuropsychological Test Automated Battery subtests sensitive to frontal lobe function in people with autistic disorder: Evidence from the collaborative programs of excellence in autism network. *Journal of Autism and Developmental Disorders*, *34*(2), 139-150. doi:10.1023/B:JADD.0000022605.81989.cc

Panerai, S., Tasca, D., Ferri, R., Genitori D'Arrigo, V., & Elia, M. (2014). Executive functions and adaptive behaviour in autism spectrum disorders with and without intellectual disability. *Psychiatry Journal,* 941809. doi: 10.1155/2014/941809

Poirier, M., Martin, J., Gaigg, S. B., & Bowler, D. M. (2011). Short-term memory in autism spectrum disorder. *Journal of Abnormal Psychology, 120*(1), 247-252. doi:10.1037/a0022298

Prior, M., & Hoffmann, W. (1990). Brief report: neuropsychological testing of autistic children through an exploration with frontal lobe tests. *Journal of Autism and Developmental Disorders, 20*(4), 581-590. doi:10.1007/BF02216063

Rehfeldt, R. A., Dillen, J. E., Ziomek, M. M., & Kowalchuk, R. K. (2007). Assessing relational learning deficits in perspective-taking in children with high-functioning autism spectrum disorder. *Psychological Record, 57*(1), 23-47.

Ring, M., Bowler, D. M. & Gaigg, S. B. (2017). An eye-movement study of relational memory in adults with Autism Spectrum Disorder. *Journal of Autism and Developmental Disorders*.

Ring, M., Gaigg, S. B., Altgassen, M., Barr, P. & Bowler, D. M. (under revised review). Allocentric versus egocentric spatial memory in adults with Autism Spectrum Disorder.

Ring, M., Gaigg, S. B., & Bowler, D. M. (2015). Object-location memory in adults with autism spectrum disorder. *Autism Research*, *8*(5), 609-619. doi: 10.1002/aur.1478

Ring, M., Gaigg, S. B., & Bowler, D. M. (2016). Relational memory processes in adults with autism spectrum disorder. *Autism Research*, *9*(1), 97-106. doi: 10.1002/aur.1493

Robinson, S., Goddard, L., Dritschel, B., Wisley, M., & Howlin, P. (2009). Executive functions in children with autism spectrum disorders. *Brain and Cognition, 71*(3), 362-368. doi: 10.1016/j.bandc.2009.06.007

Rubin, R. D., Watson, P. D., Duff, M. C., & Cohen, N. J. (2014). The role of the hippocampus in flexible cognition and social behavior. *Frontiers in Human Neuroscience, 8*:742. doi: 10.3389/fnhum.2014.00742

Rumsey, J. M., & Hamburger, S. D. (1988). Neuropsychological findings in high-functioning men with infantile autism, residual state. *Journal of Clinical and Experimental Neuropsychology, 10*(2), 201-221. doi: 10.1080/01688638808408236

Rumsey, J. M., & Hamburger, S. D. (1990). Neuropsychological divergence of high-level autism and severe dyslexia. *Journal of Autism and Developmental Disorders, 20*(2), 155-168. doi: 10.1007/BF02284715

Smith, B. J., Gardiner, J. M., & Bowler, D. M. (2007). Deficits in free recall persist in Asperger's syndrome despite training in the use of list-appropriate learning strategies. *Journal of Autism and Developmental Disorders, 37*(3), 445-454. doi: 10.1007/s10803-006-0180-4

Spreng, R. N., Mar, R. A., & Kim, A. S. N. (2008). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience, 21*(3), 489-510. doi: 10.1162/jocn.2008.21029

Tager-Flusberg, H. (1991). Semantic processing in the free recall of autistic children: Further evidence for a cognitive deficit. *British Journal of Developmental Psychology, 9*(3), 417-430. doi: 10.1111/j.2044-835X.1991.tb00886.x

The Psychological Corporation (2000). *Wechsler Adult Intelligence Scale III UK edition (WAIS-III^{UK}; 3rd ed.).* London, UK: Author.

Toichi, M., & Kamio, Y. (2003). Long-term memory in high-functioning autism: Controversy on episodic memory in autism reconsidered. *Journal of Autism and Developmental Disorders, 33*(2), 151-161. doi:10.1023/A:1022935325843

Van Eylen, L., Boets, B., Steyaert, J., Evers, K., Wagemans, J., & Noens, I. (2011). Cognitive flexibility in autism spectrum disorder: Explaining the inconsistencies? *Research in Autism Spectrum Disorders, 5*(4), 1390-1401. doi: 10.1016/j.rasd.2011.01.025

Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *The Journal of Neuroscience, 33*(14), 6012-6017. doi:10.1523/JNEUROSCI.0717-12.2013

Wiener, J., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: Effects of cognitive aging. *Frontiers in Aging Neuroscience, 4*:7, doi: 10.3389/fnagi.2012.00007

Williams, D. M., Jarrold, C., Grainger, C., & Lind, S. E. (2014). Diminished time-based, but undiminished event-based, prospective memory among intellectually high-functioning adults with autism spectrum disorder: Relation to working memory ability. *Neuropsychology, 28*(1), 30-42. doi: 10.1037/neu0000008

Williams, D. L., Minshew, N. J., & Goldstein, G. (2015). Further understanding of complex information processing in verbal adolescents and adults with autism spectrum disorders. *Autism, 19*, 859-867. doi: 10.1177/1362361315586171

Woodbury-Smith, M. R., Robinson, J., Wheelwright, S., & Baron-Cohen, S. (2005). Screening adults for Asperger syndrome using the AQ: A preliminary study of its diagnostic validity in clinical practice. *Journal of Autism and Developmental Disorders, 35*(3), 331-335. doi: 10.1007/s10803-005-3300-7

Table 1. *Descriptive statistics for autism spectrum disorder (ASD) and typically developing (TD) individuals.*

Measure	ASD (30m, 7f)		TD (25m, 6f)				Cohen's	
	M	*SD*	*M*	*SD*	*t*(66)	*p*	*d*	CI
Age (years)	42.61	12.5	40.71	13.8	0.60	.55	0.14	-0.33, 0.62
VIQ[a]	111	16.1	115	14.2	0.92	.36	0.22	-0.26, 0.70
PIQ[b]	107	16.2	110	12.8	0.74	.46	0.18	-0.30, 0.66
FIQ[c]	110	16.2	114	13.7	0.87	.39	0.21	-0.27, 0.69
AQ[d]	33.51	6.7	13.58	5.6	13.22	.00	3.22	2.47, 3.90
ADOS-C[f]	2.77 (1-6)	1.4						
ADOS-RSI[g]	6.03 (1-13)	2.9						
ADOS-Total[h]	8.63 (3-17)	3.5						
ADOS-Im[i]	1.19 (0-2)	0.7						
ADOS-SB[j]	1.38 (0-5)	1.2						

Note. [a]Verbal IQ (WAIS-III[UK]). [b]Performance IQ (WAIS-III[UK]). [c]Full-scale IQ (WAIS-III[UK]). [d]AQ- Autism-Spectrum Quotient. [e]ADOS- Communication subscale. [f]ADOS- Reciprocal Social Interaction subscale. [g]ADOS Total score- Communication+Reciprocal Social Interaction. [h]ADOS- Imagination/ Creativity subscale. [i]ADOS- Stereotyped Behaviours and Restricted Interests. ADOS scores range in brackets.

Table 2. *Total fixation duration and number of fixations during encoding for the two groups on the two landmarks presented at each intersection along the route - AOI1 (front object) and AOI2 (back object) across the six experimental blocks.*

		ASD (27m, 5f)		TD (23m, 5f)	
		AOI1	AOI2	AOI1	AOI2
Measure		*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*
Total Fixation Duration in s					
Block	**1**	8.72 (3.80)	10.27 (4.91)	10.33 (2.67)	11.57 (3.59)
	2	8.42 (3.64)	9.79 (4.03)	10.17 (2.66)	10.55 (3.29)
	3	8.21 (3.37)	9.18 (4.05)	9.92 (2.93)	10.16 (3.06)
	4	7.91 (3.54)	8.70 (4.06)	10.60 (2.83)	10.78 (3.10)
	5	8.03 (4.04)	8.92 (4.25)	10.24 (3.38)	11.11 (3.76)
	6	8.66 (4.38)	8.58 (4.32)	9.77 (3.45)	10.69 (3.20)
Number of Fixations					
Block	**1**	29.13 (12.24)	33.78 (15.14)	33.68 (7.48)	37.79 (11.11)
	2	29.56 (9.92)	34.03 (13.08)	34.46 (7.04)	36.54 (15.56)
	3	29.41 (9.66)	32.75 (13.25)	35.00 (10.46)	36.71 (11.61)
	4	27.69 (9.82)	30.47 (13.01)	36.32 (9.17)	37.75 (12.99)
	5	27.91 (14.01)	31.13 (14.58)	33.89 (13.76)	39.54 (12.52)
	6	30.06 (14.92)	29.38 (14.53)	31.75 (9.42)	36.43 (11.05)

Table 3. *Means (M) and Standard deviations (SD) for free and cued recall item tests for autism spectrum disorder (ASD) and typically developing (TD) individuals.*

	ASD (30m, 7f)	TD (25m, 6f)
	M (*SD*)	*M* (*SD*)
Free recall test		
Animals (out of 8)	0.72 (0.18)	0.82 (0.14)
Cued recall		
Turns along the route (out of 4)	0.90 (0.25)	0.95 (0.19)
Animals (out of 8)	0.71 (0.18)	0.80 (0.13)
Animal positions (out of number of animals)	0.57 (0.39)	0.74 (0.32)

Table 4. *Bivariate correlations between navigation performance on egocentric and allocentric trials, fixation duration and total number of fixations on the landmark animals at encoding, item memory for the landmark animals placed along the route and perseverative errors on the IED of the CANTAB as a measure of executive functions for individuals with autism spectrum disorder (ASD) and typical development (TD).*

	ASD Ego[a]	TD Ego[a]	z (p)[c]	ASD Allo[b]	TD Allo[b]	z (p)[c]	Total Ego[a]	Total Allo[b]
Total Fix[d]	.02 (.89)	.10 (.62)	0.28 (.39)	-.02 (.93)	-.20 (.31)	- 0.68 (.25)	.11 (.39)	.00 (.99)
Fix Count[e]	.05 (.76)	.18 (.36)	0.47 (.32)	-.03 (.86)	-.05 (.80)	- 0.07 (.47)	.15 (.23)	.04 (.75)
Free recall	.28 (.10)	-.09 (.64)	- 1.46 (.07)	.32 (.06)	.07 (.72)	-1.03 (.15)	.23 (.06)	.28*
Cued recall	.23 (.18)	-.00 (.99)	- 0.91 (.18)	.28 (.09)	.53**	1.20 (.11)	.21 (.08)	.41**
IED[f]	-.22 (.21)	-.60**	- 1.72 (.04)	-.33 (.05)	-.42*	- 0.40 (.34)	-.34**	-.38**

Note. [a]Accuracy for egocentric/same direction trials. [b]Accuracy for allocentric/different direction trials. [c]Significane of the difference between the correlation coefficients for the two groups. [d]Total fixation duration on the landmark animals at encoding. [e]Total number of fixations on the landmark animals at encoding. [f]Perseverative errors at the extradimensional shift Stage 8 of the IED of the CANTAB. **significant at $p < .01$. *significant at $p < .05$. For all other correlations, p-level in brackets.

Figure legends

Figure 1. Top left: schematic drawing of the route including the two landmarks at each intersection. Top middle: the first intersection serves as an example to display the directions of different direction trials. The arrows indicate the other two directions from which the intersections are approached in different direction trials. The black line displaying the route shows the directions for same direction trials. Top right: a schematic drawing of the empty map used for the cued recall route and item test following the navigation test procedure. Bottom: Example of test images from the first intersection. Bottom left: same direction test image of the first intersection. The correct answer would be to turn left at this intersection. Bottom middle: different direction test trial coming from the right (dashed arrow in top middle image). The correct answer would be to continue straight on. Bottom right: different direction test image coming from the opposite direction (dotted arrow in top middle image). The correct answer would be to turn right.

Figure 2. Schematic drawing to display the three different strategies for the different direction trials that distinguish between all three strategies and the directions that follow these strategies.

Figure 3. Accuracy for the two groups for same (egocentric) and different direction (allocentric) trials for the six blocks of the experiment.

Figure 4. Strategy use for TD (top left) and ASD (top right) groups for the different direction (allocentric) trials that distinguish between the three strategies (associative cue, beacon and configuration) for the six blocks of the experiment.
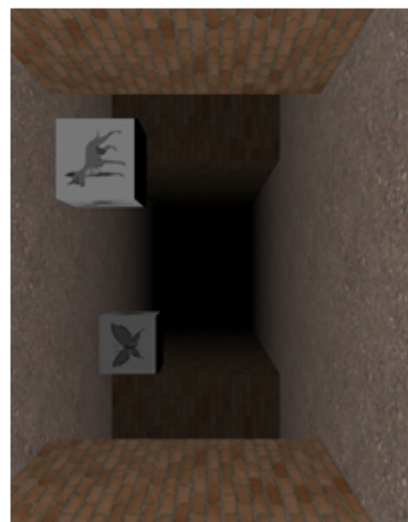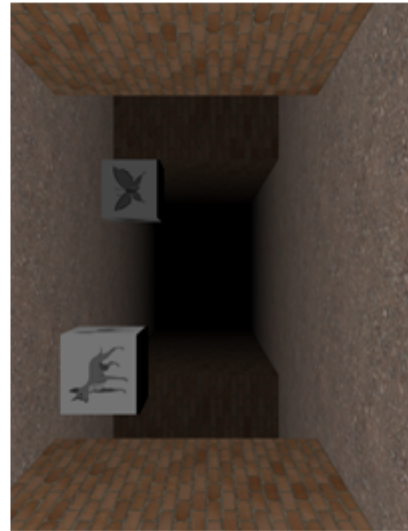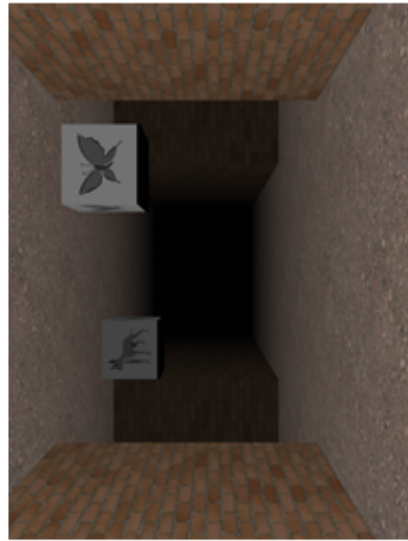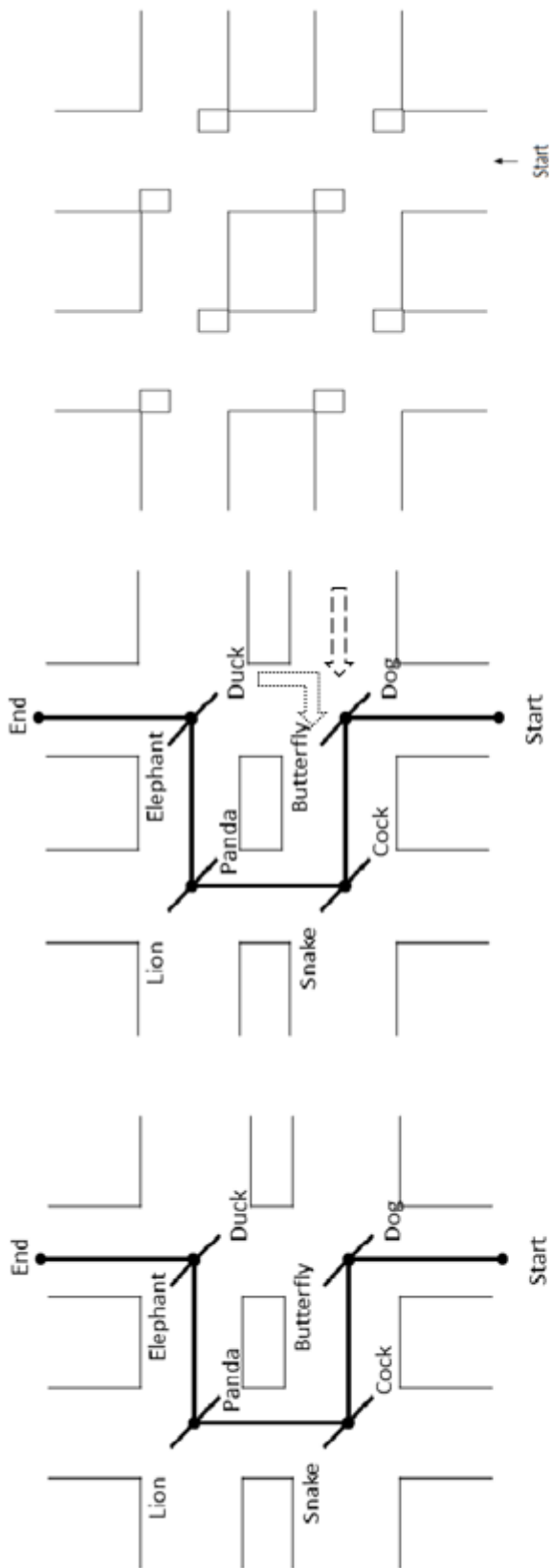
Figure 1

Figure 2

Original travel direction

Associative cue- "turn left at A or B"

Beacon- "turn towards B"

Configuration- relation between goal and landmarks

Figure 3

Figure 4