Enhanced Spatial Navigation Skills in Sequence-Space Synesthetes

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Individuals with sequence-space synesthesia (SSS) perceive sequences like months, days and numbers in certain spatial arrangements. Several cognitive benefits have been associated with sequence-space synesthesia, such as enhanced mental rotation, more vivid visual imagery and an advantage in spatial processing. The current study aimed to further investigate these cognitive benefits, focusing on spatial navigation skills, to explore if the previously reported cognitive benefits are reflected in enhanced navigational performance. Synesthetes were distinguished from controls by means of a questionnaire, a consistency test and drawings. A virtual Morris Water Maze (MWM) task with two allocentric and two egocentric navigation conditions was used to assess spatial navigation abilities. For the allocentric tasks, participants had to use object cues to find a hidden platform and for the egocentric tasks, they had to use their own position as a reference. Results showed that synesthetes performed significantly better compared to controls on the allocentric and egocentric tasks that reflected real life situations more accurately. Further analyses revealed that specifically synesthetes with the ability to mentally rotate their spatial arrangements seemed to learn faster on the allocentric task. Results add to the existing literature concerning the cognitive benefits of SSS and are consistent with the previously found mental rotation advantage.

Keywords: sequence-space synesthesia, cognitive benefits, spatial navigation, allocentric, egocentric, virtual Morris Water Maze task

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Synesthesia is a phenomenon in which sensory stimulation leads to automatic and involuntary additional experiences. Many forms of synesthesia have been reported some of which are common, like perceiving coloured letters (grapheme-colour synesthesia), and some very rare, like tasting words (lexical-gustatory synesthesia). The current study focused on one of the more common forms: sequence-space synesthesia (SSS; Jonas & Price, 2014). Individuals with SSS perceive months, days of the week, numbers or other sequences in certain spatial arrangements. For instance, months might be seen in a circular form, days in a U-shaped alignment or numbers on a spiralling line (Jonas & Price, 2014). These additional visuospatial associations in SSS have previously been associated with several cognitive benefits. Sequence-space synesthetes seem to show a memory advantage (Simner, Mayo, & Spiller, 2009), they perform better on mental rotation tasks (Brang, Miller, McQuire, Ramachandran, & Coulson, 2013; Havlik, Carmichael, & Simner, 2015), they report stronger visual imagery (Havlik et al., 2015; Price, 2009; Rizza & Price, 2012), they demonstrate higher visuospatial working memory accuracy and show an advantage in spatial processing (Hale, Thompson, Morgan, Cappelletti, & Cohen Kadosh, 2014). The current study aimed to further investigate these cognitive benefits of SSS, specifically focusing on spatial navigation skills, since the previously reported benefits might be reflected in enhanced navigational performance.

Characteristics of sequence-space synesthesia

Some sequence-space synesthetes have a synesthetic percept of only one sequence, whereas others see more than a dozen different sequences (Eagleman, 2009). Visualizing numbers and time units, like days, months and years are most common, but all kinds of sequences can elicit visuospatial impressions, even the alphabet, temperatures, or shoe sizes (Eagleman, 2009). The specific sequences that elicit visuospatial impressions comprise just one of the many aspects that can vary among individuals with SSS. For instance, the perceived sequences can take many different shapes of varying complexity (Jonas & Price, 2014), from simple lines, bent lines, and zigzag lines to circles, squares, and triangles (Eagleman, 2009) and even elaborate three-dimensional landscapes (Brang et al., 2013). Some synesthetes experience the shapes in mental space (associators), others experience the shapes outside of their body (projectors; Jonas & Price, 2014). For some, the forms are fixed, while others are able to apply spatial transformations, like mentally rotating them and zooming in or out in order to see them from multiple viewpoints (Jonas & Price, 2014). Some synesthetes additionally experience detailed visual content, such as colour or texture (Jonas & Price, 2014). Spatial forms might also be seen in two or three dimensions or in first person or third person perspective (Eagleman, 2009).

For each sequence-space synesthete, the perceived spatial arrangements and characteristics are likely to be unique and can even be different for the different sequences that he or she is able to visualize (Jonas & Price, 2014). For example, the spatial form for months might be seen from different viewpoints with the passage of time, whereas the form for the alphabet might not involve spatial transformations because it does not change over time (Jonas & Price, 2014). Moreover, the spatial arrangements often involve personal importance, like distortions of date lines to mark personally significant events (Price & Pearson, 2013) or important months occupying more space than others (Brang et al., 2013). Despite these various manifestations of SSS, it is common for all sequence-space synesthetes that seeing, hearing or thinking about particular sequences, as a whole or in parts, automatically elicits additional visuospatial experiences that are consistent over time (Cohen Kadosh, Gertner, & Terhune, 2012; Price & Pearson, 2013).

Cognitive benefits and costs of sequence-space synesthesia

Previously, it has been shown that visuospatial associations in SSS are beneficial for several cognitive tasks. Sequence-space synesthetes with time forms (e.g., months or years) outperform non-synesthetes in tests that assess recall of dates of public events and content of events in their own life. Synesthetes subsequently reported that events were retrieved from spatial locations within their visuospatial forms (Simner et al., 2009). It seems that the additional experiences in SSS lead to richer encoding and retrieval opportunities during memory tasks (Rothen, Meier, & Ward, 2012). Moreover, sequence-space synesthetes perform better than controls on mental rotation tasks (Brang et al., 2013; Havlik et al., 2015), they report stronger visual imagery than controls (Havlik et al., 2015; Price, 2009; Rizza & Price, 2012) and demonstrate higher visuospatial working memory accuracy (Hale et al., 2014). Furthermore, SSS has been linked to increased spatial processing. This was demonstrated with a task comprising spatial stimuli (i.e., several circles differing in size), where participants were required to make judgements about the overlapping order (i.e., leftmost circle on the bottom and rightmost on the top, or the other way around; Hale et al., 2014), as well as by means of a questionnaire about cognitive styles (Mealor, Simner, Rothen, Carmichael, & Ward, 2016).

However, the consistent and automatic synesthetic experiences have some costs as well. Sequence-space synesthetes respond more slowly on target detection tasks when the spatial relationship between items of presented sequences, like months (Smilek, Callejas, Dixon, & Merikle, 2007) and numbers (Gertner, Henik, & Cohen Kadosh, 2009), is incongruent with their own visuospatial percept of those sequences. This suggests that SSS "impairs the ability to represent items of sequences in a flexible manner according to task demands" (Gertner et al., 2009, p. 366). Furthermore, it has been shown that synesthetes with number forms are slower in doing simple calculations (Ward, Sagiv, & Butterworth, 2009). Perhaps because they are relying on their visuospatial forms when solving these arithmetic problems instead of using rote retrieval (i.e., a memorization strategy based on repetition), which is more optimal in this case (Hale et al., 2014).

Sequence-space synesthesia and spatial navigation

The association of SSS with the previously reported benefits leads to the expectation that sequence-space synesthetes might have enhanced spatial navigation skills. Mental rotation, spatial processing, memory, and imagery are involved in spatial navigation (Harris, Wiener, & Wolbers, 2012). Evidence from patient studies support the role of memory and imagery in spatial navigation. Patients suffering from representational neglect are affected in memory and spatial imagery performance (Chersi & Burgess, 2015) and it has been shown that they experience deficits in navigation when they have to re-orient themselves (Guariglia, Piccardi, Iaria, Nico, & Pizzamiglio, 2005). So, when memory and imagery performance are affected, spatial navigation abilities are likely to be affected. Thus it is quite plausible that when memory and imagery performance are enhanced, as is reported for sequence-space synesthetes, spatial navigation abilities are enhanced as well.

Guariglia et al. (2005) used a human version of the Morris Water Maze (MWM) task in real space to test spatial navigation skills in patients with mental representation disorders. The original MWM task was developed for rats and required them to find a platform by using various cues while moving around in a pool (Morris, 1981). In the human version of the task used by Guariglia et al. (2005), participants had to explore a room and find a target location. This task only required target place learning from different starting positions. The current study used a computerized version of the MWM task similar to the one used by Ring, Gaigg, Altgassen, Barr and Bowler (2018) that was adapted from Feigenbaum and Morris (2004). In this version of the task, a virtual pool was presented on a touchscreen and participants were required to find a hidden platform by moving over the screen. Over trials they had to work out and learn the shortest possible path from the starting point to the platform. For some conditions, they had to make use of object cues (allocentric) and for other conditions they had to use their own position as a reference (egocentric) in order to find the platform.

Differentiating between allocentric and egocentric conditions is relevant because normally when navigating in an environment both allocentric and egocentric strategies can be used. When using an allocentric strategy – also called place strategy or spatial memory strategy – one uses cognitive maps (i.e., mental representations of an environment) by thinking about landmarks and their positions relative to each other (e.g., Di Tore, Corona, & Sibilio, 2014; Iaria, Petrides, Dagher, Pike, & Bohobot, 2003; Konishi & Bohobot, 2013). When using an egocentric strategy – also called response or route strategy – one navigates by following a learned sequence of self-movements, such as a series of left and right turns at precise decision points from a given starting position (e.g., turn right after the park; e.g., Bohobot, Lerch, Thorndycraft, Iaria, & Zijdenbos, 2007; Chersi & Burgess, 2015; Di Tore et al., 2014; Konishi & Bohobot, 2013). The MWM task involved two allocentric and two egocentric conditions of which the first conditions (i.e., Allocentric 1 and Egocentric 1) were more similar to navigation in daily environments.

Previous studies have demonstrated that the virtual version of the MWM task is sensitive to detect differences in spatial navigation between certain groups. Ring et al. (2018) demonstrated that individuals with autism spectrum disorder (ASD) have difficulties in allocentric navigation, particularly when the task required them to change position while the platform and objects kept the same locations (i.e., the Allocentric 1 condition). Feigenbaum and Morris (2004) also found impairment on this allocentric navigation task in patients who had undergone right temporal lobectomy (RTL). Using this virtual MWM task, the current study set out to investigate whether such differences in navigational performance exist between sequence-space synesthetes and non-synesthetes.

Besides comparing spatial navigation skills between the two groups, individual differences among sequence-space synesthetes were examined when assessing spatial navigation abilities in order to see if some specific synesthetic features contributed to performance. Specifically, the ability to mentally rotate spatial forms was expected to enhance performance in at least the allocentric condition, in which the display had to be mentally rotated in order to find the platform. Further influences of synesthetic features on navigational performance were explored as well. Individual differences among sequence-space synesthetes have previously been shown to influence performance on visuospatial tasks. For example, synesthetes who are able to project forms into space (i.e., projector synesthetes) are shown to perform best on mental rotation tasks (Havlik et al., 2015).

The current study aimed to further investigate the cognitive benefits of SSS. More specifically, do sequence-space synesthetes have enhanced spatial navigation skills? Knowing whether sequence-space synesthetes outperform non-synesthetes at spatial navigation tasks and knowing whether individual differences among synesthetes are associated with enhanced performance may reveal information about the cognitive processes involved in SSS. This study therefore contributes to a better understanding of SSS at a cognitive level and may extend our knowledge about the cognitive processes involved in allocentric and egocentric navigation strategies.

Methods

Participants

Participants with SSS were recruited through poster advertisements and via the SONA Radboud research participation system. Age- and sex-matched control participants were recruited via the SONA system as well. Based on an online screening questionnaire about synesthetic experiences, 23 potential synesthetes and 22 controls were invited to take part in the study. After the tasks in the lab, one potential synesthete was not included in the synesthete group (due to insufficient responses at the consistency task and a drawing without typical synesthetic characteristics) and one potential control participant appeared to be a synesthete. The groups that were taken into account in analysis comprised 23 individuals with SSS (20 women, M_{age} = 23.22 years, age range 18-25 years with three exceptions (34, 38 and 44 years)) and 21 controls (19 women, M_{age} = 21.57 years, age range 18-25 years). An independent samples t-test indicated no significant age difference between groups ($t(26) = 1.15$, $p = .263$). Because of unequal variances between groups (Levene's test was significant), the degrees of freedom were adjusted accordingly. Of those included in the synesthete group, 13 reported having spatial forms for numbers, 21 for days and 23 for months. All participants were educated at university level. Informed consent was obtained before filling out the online screening questionnaire and again in the lab before taking part in the experiment. Participation was voluntary and compensated with 15 euros or 1.5 credit points. The study was approved by the Ethics Committee of the Faculty of Social Sciences (ECSS) at Radboud University Nijmegen.

Tasks and procedure

General procedure

Before participating in the study, all participants filled out a self-report questionnaire about synesthetic experiences. In the lab, by means of a consistency test, drawings, and additional questions, sequence-space synesthetes were distinguished from control participants. Participants were asked to select locations on a computer screen for numbers, days, and months, yielding a consistency score of the placement of items, and to draw their visuospatial experiences (synesthetes) or intuitive representations (controls) of those sequences on paper. Then participants performed a virtual MWM task to assess spatial navigation skills. During allocentric and egocentric navigation tasks, participants were asked to find a hidden platform by moving over a touchscreen. For the allocentric tasks, they had to use object cues to find the platform and for the egocentric tasks, they had to use their own position as a reference to find the platform. Performance on these different tasks was assessed between groups and individual differences in the manifestation of SSS were taken into account in further analyses. We now describe each task in detail.

Screening questionnaire

An online SSS self-report questionnaire was developed in LimeSurvey and used as a screening tool to find participants for our study. The questions were based on descriptions of SSS in the literature and comprised some general screening questions (e.g., "Is the synesthetic experience automatically elicited when thinking of this sequence?") and some detailed questions about the perceived spatial forms (e.g., "Do you see this arrangement from a fixed perspective or are you able to rotate the form and adopt multiple viewpoints?"). When participants reported to have SSS for numbers, days and/or months, detailed questions followed about the spatial forms of each of those sequences separately. These questions covered all the characteristics of SSS as mentioned in the theoretical background. The complete questionnaire can be found in the Supplementary Materials (available in the online version). Filling out the questionnaire took about 10 to 20 minutes. Participants who reported having SSS received an invitation to participate in the study at Radboud University. Control participants filled out the questionnaire as well. They could just simply answer the first question ("Do you think you have sequence-space synesthesia?") with "no" and the specific questions about SSS did not appear. Before filling out the questionnaire, all participants were provided with a description of SSS and some examples of visuospatial forms to familiarize all of them with SSS prior to completing the questionnaire.

Consistency test

Because the screening questionnaire was based on self-report, participants' subjective reports of SSS were verified in the lab. Participants were asked again about the details of their spatial forms and performed a consistency test. The consistency test (Rothen, Jünemann, Mealor, Burckhardt, & Ward, 2016), written in E-prime 2.0, was obtained from Rothen et al. (2016) and adapted to the current study. Numbers 0-9, 50 and 100 ($N = 12$), days ($N = 7$) and months ($N = 12$) were centrally presented on a white background with font style Courier New and font size 18 in bold black. These stimuli were presented on a 24" BenQ screen with display resolution set to 1920x1080, controlled by a Dell computer running Windows 7.

Participants were comfortably seated in front of the screen at normal viewing distance. Stimuli were presented one by one in random order and participants had to select a location for each stimulus on the screen by making a mouse click. SSS participants were instructed to imagine the screen as the space in which they experienced the spatial arrangements of the sequences and choose locations that best fit their synesthetic experience. When a presented stimulus did not induce a synesthetic experience, they could press the space bar and the next stimulus appeared. There were five practice trials to get familiar with the task. Control participants were asked to find an intuitive location for each stimulus. They were instructed to try to choose the same location every time the stimulus reappeared, but they were not allowed to choose the same location for every single stimulus. Control participants did not have the opportunity to press the space bar. Afterwards they were asked if they had used a certain strategy for placing the different stimuli.

Each stimulus was presented for 1 s in the centre of the screen, then a cross appeared and participants could choose a location for the stimulus. All stimuli were presented three times resulting in a total of 93 (= 31x3) trials. Completing this task took about 15 minutes. The three chosen locations for each item formed a triangular area and we used the mean surface of all these areas together as the consistency score of each participant, according to the procedure described by Rothen et al. (2016).

Drawings

After the consistency test, SSS participants were asked to draw their spatial forms on a piece of paper and control participants were asked to draw a representation of numbers, days and months. Sequence-space synesthetes could use coloured pencils if they experienced additional colours with their spatial forms. It was verified whether control participants really associated those locations with the sequences or whether they just chose the same locations as remembered from the consistency test. These drawings were used as a control measure for the consistency test because control participants could achieve high consistency scores as well when adopting a certain strategy, for example placing items of a particular sequence in a straight line from left to right. Besides giving more confidence in distinguishing real sequence-space synesthetes from controls, these drawings were for some SSS participants an easier method to express their visuospatial experiences. This was especially relevant for those who perceived sequences with high visual content like colours because the consistency test was only a purely spatially-based estimate (Jonas & Price,

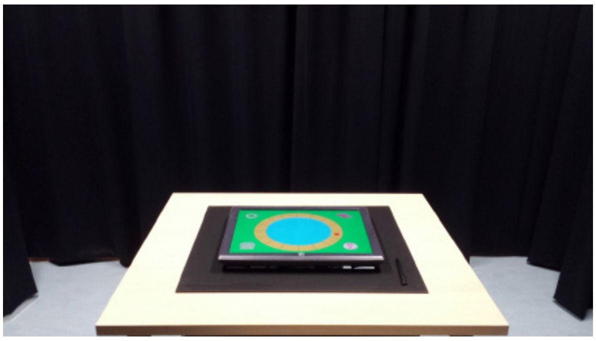

Fig. 1. Experimental set-up.

2014). This task took an additional 5 to 15 minutes, depending on the complexity of the drawings.

Morris Water Maze task

Finally, after the consistency test and drawings, participants performed a computerized version of the Morris Water Maze (MWM) task (Ring et al., 2018) to assess spatial navigation abilities. This task was written in Microsoft Visual Basic 6 and presented on a 19” ELO touchscreen with display resolution set to 1280x1024, controlled by a Dell computer running Windows XP. The screen was placed on a square table at comfortable height such that participants could easily reach the screen while standing. The table was surrounded by black curtains hanging from the ceiling to the ground and formed a 9 m2 separate area inside the room (Fig. 1). This prevented participants from using environmental cues, like doors and features on the wall, to guide navigation. There was enough space around the table such that participants could easily walk around the screen as instructed during the task. Lights were turned off to further reduce the influence of cues in the room.

On every trial, a virtual swimming pool environment was presented on the touchscreen. The display consisted of a blue circular area surrounded by an orange wall, representing water and the border of the pool, respectively. The green area outside the pool represented grass. There were four object cues (life ring, towel, chair, beach ball) around the pool, one in each corner of the screen (Fig. 2). Participants were instructed to find a hidden platform in the pool by moving over the touchscreen. They always had to start at the red dot that was presented in a fixed randomized order at the orange border. While searching for the platform, they used a touchscreen sensitive pen because this pen moved more easily over the screen than their finger and was therefore more accurate in registering the path that was taken. Participants were not allowed to lift the pen from the screen while searching for the platform and they were not allowed to cross the border of the pool. The platform, presented as a brown box, appeared once they passed the right location.

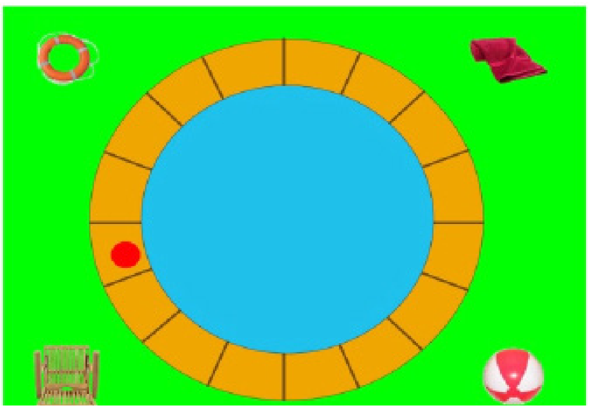

Fig. 2. Example of display.

Participants were asked to work out and learn the shortest possible path from the starting point to the hidden platform over several trials. There were three practice trials to get familiar with the task and to learn how to move properly over the screen. After these practice trials, participants had to perform five tasks, each consisting of 16 trials. The first task was always a place learning block and then two allocentric and two egocentric navigation blocks followed. These allocentric and egocentric blocks could be presented in any possible order, making a total of 16 different task orders. It was made sure that every order was performed by at least one synesthete and one control participant. For the allocentric tasks, participants had to use the object cues to find the platform and for the egocentric tasks, they had to use their own position as a reference. Importantly, participants had to figure out ‘the rule’ for finding the platform themselves.

Place learning

Place learning was used as a control condition to ensure that participants were able to perform the task properly and to check whether they showed learning over trials. There were no systematic manipulations during this condition. The objects, platform and participant kept the same positions (Fig. 3A).

Allocentric conditions

The two allocentric conditions were used to measure the strength of allocentric processing. In the first allocentric condition (Allocentric 1), the objects and platform stayed in the same location, but the participant changed position. The participant had to move to another side of the screen after every trial. This happened in a fixed randomized order. This condition was the original allocentric condition as developed by Feigenbaum and Morris (2004; Fig. 3B). In the second allocentric condition (Allocentric 2), the participant stayed in the same position, but the objects and platform changed in a fixed randomized order. The platform moved along with the objects, so they kept the same positions relative to each other. Participants did not see the platform and objects rotating, they only saw the new rotated order. This condition was added to the task by Ring et al. (2018; Fig. 3C).

Egocentric conditions

The two egocentric conditions were used to measure the strength of egocentric processing. In the first egocentric condition (Egocentric 1), the platform and participant stayed in the same location, but the objects rotated in a fixed randomized order. Participants did not see the objects rotating, they only saw the new rotated order. This condition was the original egocentric condition as developed by Feigenbaum and Morris (2004; Fig. 3D). In the second egocentric condition (Egocentric 2), the objects stayed in the same location, but now the platform and participant changed position in a fixed randomized order. The platform moved along with the participant, so platform and participant kept the same positions relative to each other. This condition was added to the task by Ring et al. (2018; Fig. 3E).

For each trial, participants had 60 seconds to find the platform. When a participant could not find the platform within these 60 seconds, a time out message appeared together with the platform. Every trial was followed by a distractor task. Participants had to 'pop' ten blue bubbles that appeared one by one at random locations on a black screen. After this distractor task, a black screen appeared with a yellow dot at one of the four sides of the screen, indicating on which side the participant had to stand for the upcoming trial.

After performing this virtual MWM task, participants were asked about their strategy for solving the task in order to control for the use of allocentric strategies in the allocentric conditions and egocentric strategies in the egocentric conditions. Additionally, they were asked about their navigational strategies in daily life. Performing the MWM task took about 30 minutes.

Data analysis

Consistency test

The three chosen locations for each item of the consistency test formed a triangular area and the mean surface in pixels across all these areas was our measure of consistency. The lower the score, the higher a participant's consistency of placing the items. Since sequence-space synesthetes always have the same spatial association for certain sequences, they were expected to consistently choose the same locations for the presented items. Controls do not have these spatial associations, therefore they were expected to choose these locations less consistently. However, because a substantial amount of control participants obtained high consistency scores by using certain strategies for placing the items, we eventually did not use a synesthesia cut-off score as in Rothen et al. (2016) to classify sequence-space

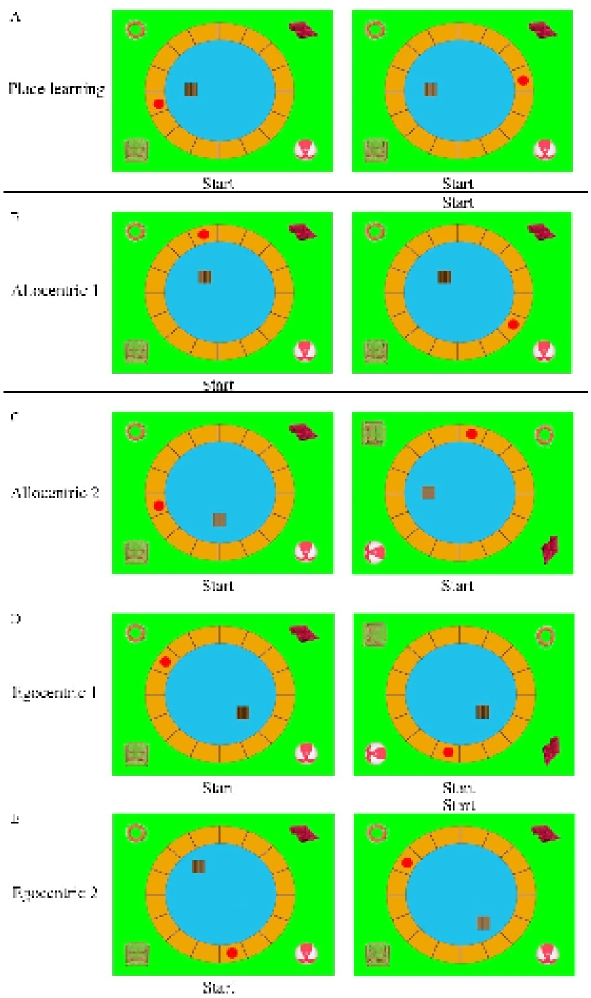

Fig. 3. Two example trials of each condition (A-E). 'Start' indicates the position of the participant relative to the screen. The platform was not visible for participants during the task, only after they passed the right location.

synesthetes and controls. Using only a cut-off score would have led to incorrect classification of participants.

Drawings

Instead of the consistency test, drawings and participants' descriptions of their synesthetic experiences – both from the questionnaire and questions in the lab – gave more confidence in correctly distinguishing sequence-space synesthetes from controls. Drawings were compared with the spatial forms generated by the consistency test and a comparison was made between drawings from synesthetes and controls. In addition to the drawings, synesthetes were asked how they perceived their visuospatial forms (e.g., projection vs. association, fixed perspective vs. multiple viewpoints). These subjective reports were compared to the answers given earlier (i.e., one up to five months prior to testing) in the self-report questionnaire. Controls were asked whether they always perceived the sequences like their drawings or whether the drawn locations were intuitive and not automatically elicited when thinking of those sequences.

Also, a complexity score was created for synesthetes based on the drawings and descriptions of their forms. For each sequence, ten complexity features were chosen, and one point was given for each feature that was present. The total score was divided by the number of sequences the synesthete perceived (i.e., one, two or three), so the score could range between zero and ten points. This score was used as a covariate in the analyses of the MWM task. An overview of the complexity features is presented in the Supplementary Materials (Table S9).

Morris Water Maze task

For the MWM task, four dependent measures were used to assess performance: (1) the length of the path taken to find the platform (Path Length), (2) the time needed to find the platform (Time to Target), (3) the percentage of time spent in the quadrant containing the platform, and (4) the angle of the path taken heading towards the platform after the first movement on the screen. We focused in our analyses on Time to Target and Path Length since these variables captured performance most directly and were straightforward to interpret. Moreover, these variables showed a clear learning effect over trials in contrast to the other two measures (Fig. S1 in the Supplementary Materials). For more details on why these latter measures were not included in further analyses, see General Discussion. Path Length was calculated as the difference between the shortest possible path and the actual path that was taken in order to enable comparison between trials. This measure was then transformed from pixel into mm. Time to Target was measured in milliseconds. Because of a very high variation in the data, both Path Length and Time to Target were square root transformed. Due to this transformation, the variation became less extreme for trials with long search times and path lengths (i.e., the first few trials). Data were analysed using repeated measures ANOVAs. As in Ring et al. (2018), these analyses were done for the Allocentric 1 and Egocentric 1 conditions and for the Allocentric 2 and Egocentric 2 conditions. These analyses were done separately for conditions 1 and 2, because the first conditions were the original conditions of the MWM task developed by Feigenbaum and Morris (2004) – and reflected real life situations more accurately (see General Discussion) – and the second conditions were the added conditions developed by Ring et al. (2018). Individual differences in the manifestation of SSS were used as between-subject factors in further exploratory analyses.

Additionally, there were several measures to control for correct performance. It was counted how often participants left the pool area, how often they lifted the pen from the screen, when they were timed out (i.e., when they could not find the platform within 60 seconds), and how much time they needed to complete the distractor task. Control measures were analysed using repeated measures ANOVAs.

Results

Data of the consistency test were analysed using t-tests and data of the MWM task using repeated measures ANOVAs. If the sphericity assumption was violated, Greenhouse-Geisser correction (GG) was applied. The significance level for all analyses was set to $\alpha = .05$.

Consistency test

When taking the consistency scores for numbers, months and days together, an independent-samples t-test indicated that sequence-space synesthetes performed significantly more consistently than controls ($t(22) = -2.18$, $p = .040$, $\Delta = .49$). Also for numbers and months separately – but not for days – sequence-space synesthetes performed significantly

Table 1. Descriptive statistics of the consistency scores of both groups for numbers, months and days together and separately.

	SSS		Con		
	M	***SD***	***M***	***SD***	***N* SSS/Con**
Total	2320	2125	6477	8495	23/21
Numbers	1335	1119	5125	8176	13/21
Months	2317	1985	7651	11473	23/21
Days	2456	4066	5969	12417	21/21

more consistently: for numbers ($t(21) = -2.09$, $p = .049$, $\Delta = .46$) and for months ($t(21) = -2.10$, $p = .048$, $\Delta = .46$). Because of unequal variances between groups (Levene's test was significant), the degrees of freedom were adjusted, and Glass's delta was used for determining the effect size. The descriptive statistics of both groups are summarized in Table 1 and the spreading of the individual consistency scores for numbers, months and days together are shown in Figure 4. Despite the significant difference in consistency between groups, this figure shows a clear overlap in the consistency scores between synesthetes and controls. A few examples of generated figures of performance of both sequence-space synesthetes and control participants are presented in the Supplementary Materials (Fig. S8 and S9).

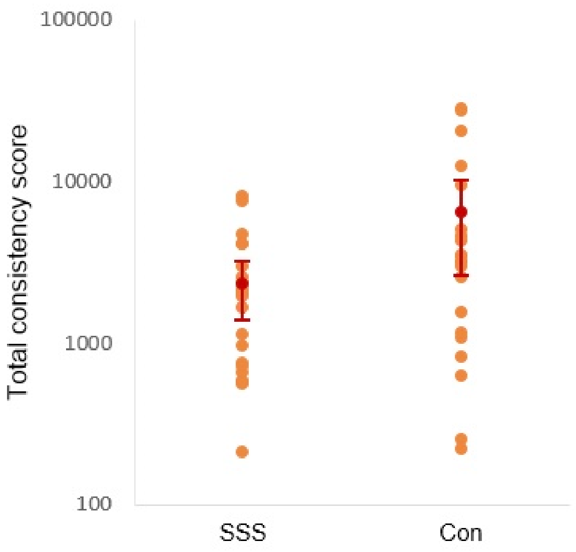

Fig. 4. Spreading of the individual consistency scores of both groups for numbers, months and days together. The red dot indicates the mean and error bars represent the 95% confidence interval. The scale of the y-axis is logarithmic.

Drawings

A comparison of drawings revealed some striking differences between sequence-space synesthetes and controls. Synesthetes showed a tendency to connect items of a sequence within a form (e.g., months connected as blocks in a circle), whereas controls just wrote the items down in isolation (e.g., months scattered on locations where they could remember them). For months, around 70% of the synesthetes connected items within a form, for days around 67% and for numbers around 54%. None of the control participants did this. In terms of complexity, drawings made by synesthetes were characterized by more elaborate and complex forms compared to those of controls. For months, around 65% of the synesthetes drew a circle, oval, square or a similar closed form while for days around 43%. For numbers, around 62% of the synesthetes drew a line with bends, corners or zigzags. None of the control participants did this. Most of them arranged the items of a sequence in rows or columns. For months, around 62% of the control participants did this, for days around 71% and for numbers around 67%. A detailed overview of the characteristics of each sequence for both groups can be found in the Supplementary Materials (Table S7 and S8) as well as a few examples of drawings made by sequence-space synesthetes and control participants (Fig. S10 and S11).

Morris Water Maze task

All analyses presented here focus on performance measured by the time needed to find the platform and the length of the path taken to find the platform. The results of the other two measures (i.e., Percentage of Time in Target Quadrant and Path Angle) are presented in the Supplementary Materials (Table S4 and S5 and Fig. S3 and S4). The complete tables with descriptive and inferential statistics for Time to Target and Path Length are presented in the

Supplementary Materials as well (Table S2 and S3). For Time to Target, not more than 2% of the trials per condition were outliers, and for Path Length this was not more than 3% (see Supplementary Materials for how outliers are dealt with).

Place learning

Data were analysed using a repeated measures ANOVA among the between-subjects factor group (SSS, controls) and the within-subjects factor trial (16 trials). For performance measured by Time to Target, a significant main effect was found for trial, $F(7.26, 304.98) = 20.21$, $p < .0001$, $\eta_p^2 = .33$, GG, meaning that the time needed to find the platform decreased over trials. There was no significant main effect for group or a significant group x trial interaction, which indicates similar learning over trials for both groups. Similar results were found for performance measured by Path Length (Table S1 and Fig. S1 in the Supplementary Materials).

Allocentric 1 and Egocentric 1

Data were analysed using a repeated measures ANOVA among the between-subjects factor group (SSS, controls) and the within-subjects factors trial (16 trials) and condition (allocentric, egocentric). For performance measured by Time to Target, significant main effects were found for trial, $F(6.40, 268.77) = 45.33$, $p < .0001$, $\eta_p^2 = .52$, GG, and for condition, $F(1, 42) = 6.44$, $p = .015$, $\eta_p^2 = .13$, showing that the time needed to find the platform decreased over trials and that it took more time to find the platform in the allocentric condition ($M = 47.47$, $SD = 15.67$) compared to the egocentric condition ($M = 41.71$, $SD = 14.02$) for most trials, suggesting that the allocentric condition was more

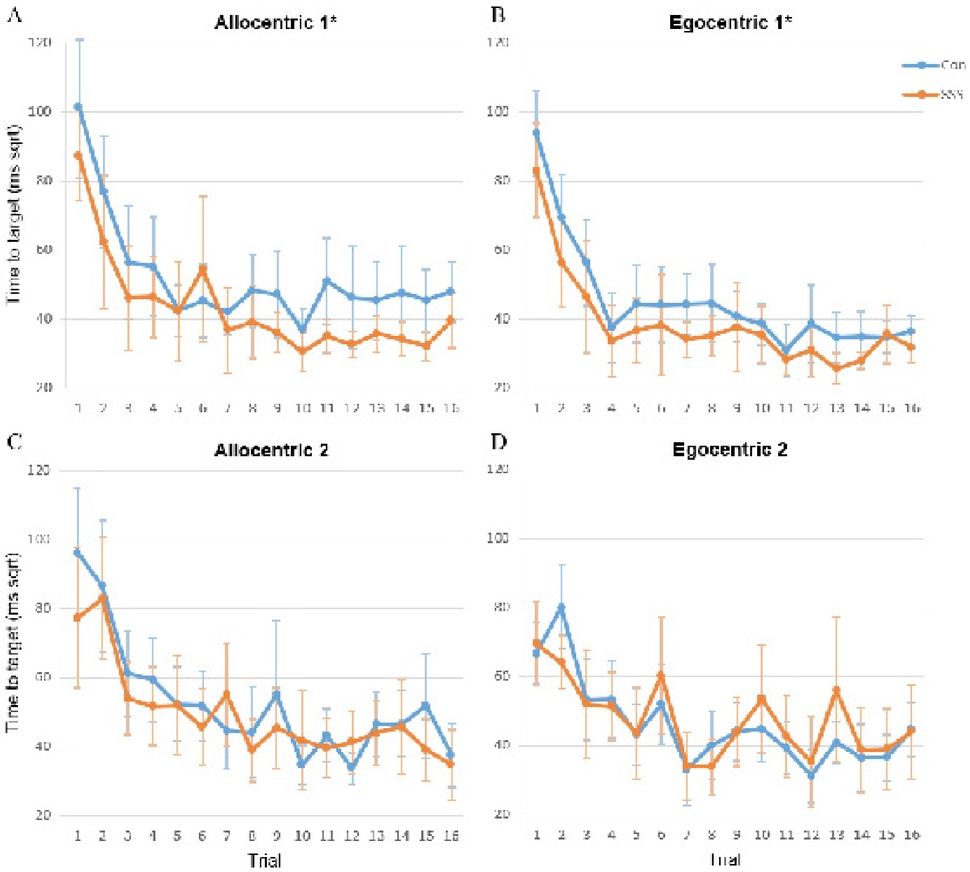

Fig. 5. Graphs showing the performance over trials measured by the time needed to find the platform in the Allocentric 1 and Egocentric 1 conditions (A and B) and the Allocentric 2 and Egocentric 2 conditions (C and D). The orange lines show the performance of sequence-space synesthetes, blue lines show the performance of control participants. Error bars reflect the 95% confidence interval. *Synesthetes performed significantly better in the Allocentric 1 and Egocentric 1 conditions compared to controls. The peaks in the learning curves can be explained by the fact that the starting point (red dot) appeared on the same location for every participant in a particular trial. For instance, the starting point in the 7th trial of Egocentric 2 was already close to the location of the platform, resulting in generally shorter times to find the platform. Likewise, the starting point in the 6th trial of Egocentric 2 was relatively far away from the platform, resulting in generally longer times to find the platform.

difficult. Importantly, a significant main effect of group, $F(1, 42) = 4.46$, $p = .041$, $\eta_p^2 = .01$, indicated that sequence-space synesthetes performed better at both conditions ($M = 40.83$, $SD = 13.17$) compared with controls ($M = 48.70$, $SD = 11.36$). There was no significant group x condition interaction. Figures 5A and B show performance over trials for both groups for the Allocentric 1 and the Egocentric 1 conditions, respectively. Similar results were found for performance measured by Path Length, except that the main effect of group was marginally significant (Table S2 and Fig. S2 in the Supplementary Materials).

Allocentric 2 and Egocentric 2

Data were analysed using a repeated measures ANOVA among the between-subjects factor group (SSS, controls) and the within-subjects factors trial (16 trials) and condition (allocentric, egocentric). For performance measured by Time to Target, significant main effects were found for trial, $F(6.07, 255.11) = 26.37$, $p < .0001$, $\eta_p^2 = .39$, GG, and for condition, $F(1, 42) = 4.17$, $p = .048$, $\eta_p^2 = .09$, showing that the time needed to find the platform decreased over trials and that it took more time to find the platform in the allocentric condition ($M = 51.00$, $SD = 16.12$) compared to the egocentric condition ($M = 46.94$, $SD = 18.35$) for most trials, suggesting that the allocentric condition was more difficult. There was a significant trial x condition interaction as well, $F(8.17, 343.08) = 3.54$, $p = .001$, $\eta_p^2 = .08$, GG, indicating that the time needed to find the platform decreased more over trials for the allocentric condition compared to the egocentric condition. There was no significant main effect of group or a significant group x condition interaction, meaning that sequence-space synesthetes and controls showed similar performance in both conditions. Figures 5C and D show performance over trials for both groups for the Allocentric 2 and the Egocentric 2 conditions, respectively. Similar results were found for performance measured by Path Length, except for a significant main effect of condition (Table S2 and Fig. S2 in the Supplementary Materials).

Control measures

There were no significant differences between groups for any of the control measures, meaning that any variations in the ability to correctly perform the task did not affect the results. The descriptive and inferential statistics are presented in the Supplementary Materials (Table S6).

Effects of synesthetic features on performance

Individual differences in the manifestation of SSS were taken into account in further analyses to see if some specific synesthetic features contributed to the enhanced performance of synesthetes in the Allocentric 1 and Egocentric 1 conditions. First, the specific hypothesis of enhanced performance in the Allocentric 1 condition of synesthetes among the ability to rotate their spatial forms was tested with a repeated measures ANOVA with the between-subjects factor group (rotation yes/no) and the within-subjects factor trial (16 trials). As shown in Figure 6, it seemed that synesthetes with the mental rotation ability learned faster in the Allocentric 1 condition compared to synesthetes who could not do this. This effect was however not significant (first eight trials ($F(1, 21) = 2.72$, $p = .11$, $\eta_p^2 = .12$)). The groups consisted of 15 synesthetes with the rotation ability and eight synesthetes who could not do this. A synesthete was classified as having the rotation ability if he or she had this for at least one of the sequences.

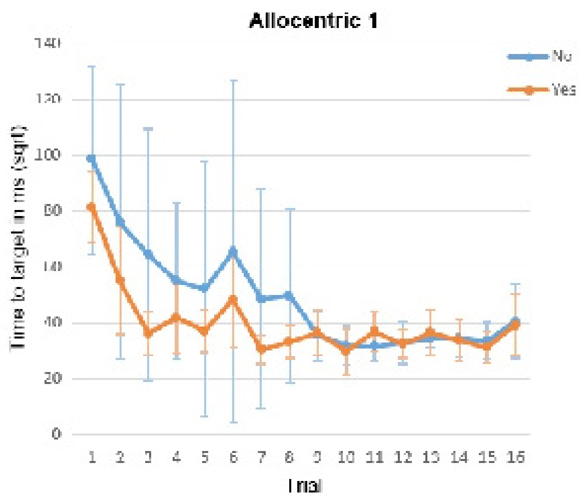

Fig. 6. Graph showing the performance over trials measured by the time needed to find the platform in the Allocentric 1 condition. The orange line shows the performance of synesthetes who were able to mentally rotate their spatial forms and the blue line the performance of synesthetes who could not do this. Error bars reflect the 95% confidence interval. Synesthetes with the mental rotation ability seemed to perform better during the learning phase.

Six other synesthetic features with different manifestations among sequence-space synesthetes were taken into further exploratory analyses to see if some of these features contributed to the better performance of synesthetes. The features taken into account were: association vs. projection, perceiving the spatial form in a two-dimensional vs. three-dimensional space, the ability to mentally move over the form (yes/no), the ability to zoom in and out (yes/no), whether the form itself moves with time (yes/no) and the presence of additional visual features like colour (yes/no). A synesthete was classified as having the ability if he or she demonstrated or reported this ability for at least one of the sequences. These features were taken as between-subject factors in separate repeated measures ANOVAs with only the synesthete group. No further effects of synesthetic features on performance were found for the Allocentric 1 and Egocentric 1 conditions. However, analyses amongst the Allocentric 2 and Egocentric 2 conditions revealed a few effects concerning synesthetic features that represent an allocentric (form itself moves) and egocentric (move over form) perspective on the spatial form. These results are presented in the Supplementary Materials (Fig. S5-S7). It is important to note that due to the many exploratory analyses that were performed (six synesthetic features x four conditions), some of these observed effects could have been significant by chance (i.e., at least one significant effect was expected for 24 analyses with a significance level set at $\alpha = .05$).

Next to these exploratory analyses with synesthetic features, it was examined whether the performance of synesthetes was modulated by the complexity of their synesthetic experience. A complexity score – based on synesthetic features and synesthetes' drawings – was taken as a covariate in a repeated measures ANCOVA with the within-subjects factor trial (16 trials). This complexity score did not significantly modulate the performance of synesthetes for any condition (all $F(1, 21) < 2.74$, n.s.).

Furthermore, participants were asked about their daily navigation strategies, but due to insufficient difference in used strategies among participants, this factor could not be taken into analysis. Most participants reported to use allocentric navigation strategies or a combination of both allocentric and egocentric strategies, whereas almost no one reported to favour egocentric navigation strategies.

Discussion

The aim of this study was to investigate whether SSS is beneficial for spatial navigation. To test this, sequence-space synesthetes and control participants performed a virtual Morris Water Maze task involving two allocentric and two egocentric navigation conditions in which they had to find a hidden platform. Known cognitive benefits of SSS, in particular, the ability of synesthetes to mentally rotate their spatial forms, were expected to be reflected in enhanced performance on this navigation task. Indeed, sequence-space synesthetes showed better performance in one of the allocentric conditions and one of the egocentric conditions (i.e., Allocentric 1 and Egocentric 1, the two original test conditions developed by Feigenbaum and Morris, 2004). Specifically, synesthetes with the ability to mentally rotate their spatial forms seemed to learn faster during the first trials of the allocentric task. As Ring et al. (2018) suggested, especially for this task, mental rotation is important for successful performance. Participants had to change position while the platform and the objects remained fixed. Participants thus saw the display from a different perspective on every trial and had to mentally rotate it back to its original perspective (Ring et al., 2018). For the egocentric condition, in which sequence-space synesthetes showed enhanced performance as well, none of the synesthetic features that we took into account were found to specifically contribute to their better performance. In this task, the platform and the participant kept the same positions, while the objects rotated. The current results add to the existing literature concerning the cognitive benefits of SSS and are consistent with the previously found mental rotation advantage.

It may seem surprising that sequence-space synesthetes did not perform significantly better than controls in the other allocentric and egocentric tasks (i.e., Allocentric 2 and Egocentric 2, the two conditions added by Ring et al., 2018). However, in this allocentric task, the platform moved along with the objects while the participant kept the same position and in this egocentric task, the platform moved along with the participant while the objects remained fixed. This movement of the platform with either the objects or the participant does never happen in everyday environments (Ring et al., 2018). Normally, when we navigate to certain destinations (e.g., buildings), these buildings do not change in space. They remain at fixed locations, like the platform did in the Allocentric 1 and Egocentric 1 tasks. Therefore, the first allocentric and egocentric tasks seemed to better reflect spatial navigation in daily life. An analysis with all four conditions in one repeated measures ANOVA confirmed that the Allocentric 2 and Egocentric 2 conditions were significantly more difficult than the Allocentric 1 and Egocentric 1 conditions ($F(1, 42) = 4.35$, $p = .043$, $\eta_p^2 = .09$). Averaged over trials, it took more time to find the platform in the second conditions ($M = 48.97$, $SD = 15.88$) compared to the first conditions ($M = 44.59$, $SD = 12.83$). Figure 5 clearly demonstrates this as well by less smooth learning curves for these conditions compared to the Allocentric 1 and Egocentric 1 conditions.

The enhanced performance of synesthetes compared to controls in the two original task conditions cannot be explained by any differences between synesthetes and control participants in the ability to follow the task instructions, since there were no differences between groups in any of the control measures (i.e., the number of times they left the pool area, the number of times they lifted the pen from the screen and the number of times they could not find the platform within 60 seconds). Also the experienced time interval between tasks, indicated by the time they needed to complete the distractor task, was not different between groups. An alternative explanation for the observed group difference in task performance is that sequence-space synesthetes might have been more interested in participating, causing them to be more motivated to perform well. However, this alternative explanation cannot fully account for the observed results, because there was no performance difference between synesthetes and controls in either the place learning condition (i.e., the control task), the control measures, the learning curve over trials or in the Allocentric 2 and Egocentric 2 conditions. The existence of a motivational difference between groups would have been evident in differences in performance here.

Ring et al. (2018) only found differences between groups on the original task conditions as well. Interestingly, they found that individuals with ASD performed significantly worse than control participants in the Allocentric 1 task, while the current study demonstrated that individuals with SSS performed significantly better than controls in this exact same task. This implies that the previously found link between ASD and synesthesia, i.e., synesthesia is more common among individuals with ASD, with a prevalence of 20% Baron-Cohen et al., 2013; Neufeld et al., 2013), is not reflected in performance on this virtual MWM navigation task. Since spatial navigation is a complex mental task involving many sub-processes, it is very well possible that the two groups do not converge to similar performance on the MWM task. Recent studies indicate that the shared cognitive characteristics between SSS and ASD seem to mainly involve elevated attention to detail (Mealor et al., 2016; Ward et al., 2017).

An interesting question is whether SSS is an adaptive, rather than an epiphenomenal, cognitive function. Perhaps the synesthetic visuospatial experiences remain to exist throughout generations because they are beneficial for a broad range of cognitive functions. The possibility of synesthetes to mentally manipulate the spatial forms (e.g., rotating the forms in order to see them from multiple perspectives) is beneficial for spatial thinking and, as the current study suggests, for spatial navigation. The ability to easily keep an overview of things that need to be done (without a planner) is clearly a memory related advantage and remembering important events and dates, like birthdays, is socially relevant as well. When sequence-space synesthetes are asked whether they experience any benefits of their visuospatial forms, most of them indeed report to experience a memory advantage and state that they cannot imagine living without the visuospatial forms. SSS thus clearly has personal importance. The current data adds to the debate whether SSS could indeed be an adaptive cognitive function.

Concerning the methodological aspects of the current study, there is one important difference compared to the study performed by Ring et al. (2018). We focused in our analyses on the time that was needed to find the target and the length of the path that was taken to find the target, while they focused on the percentage of time that was spent in the target quadrant. The latter measure, however, did not seem to be the most suitable, in contrast to what Ring et al. (2018) suggested. The first reason to doubt this measure is that during one of the conditions (Allocentric 2) the platform was always at the border of two quadrants (i.e., in between the ball and chair and moved along with these objects). Therefore, it was not possible to correctly define the target quadrant for trials in this condition. The second reason was the absence of a correct reflection of a learning effect over trials (Fig. S1 and S3 in the Supplementary Materials). We assumed that the time spent in the target quadrant should increase over trials, when participants started spending more time searching in the correct quadrant containing the platform. In practice, we observed that after learning, participants moved in one straight line from the starting point to the platform. In this way, they spent almost no time searching in the quadrant containing the platform. Ring et al. (2018) chose this measure because of its frequent use in the literature and its reduced vulnerability to variation among participants since it is expressed as a percentage of the total search time. Ring et al. (2018) suggested that a high variation among participants might have added noise to the data of Time to Target and Path Length and possibly obscured any differences between groups. However, based on our measurements and observations, the reasons they put forward do not seem to outweigh the two major problems that come along with this measure.

A caveat of the current study is that we did not include an additional mental rotation task in order to confirm whether mental rotation performance was indeed correlated with performance in the Allocentric 1 condition. The enhanced performance of synesthetes with the ability to mentally rotate their spatial forms, observed during the learning phase of this allocentric task, was not significant. A positive correlation between a mental rotation task and the Allocentric 1 condition therefore would have added to the evidence in favour of the contribution of synesthetes' mental rotation ability to the enhanced performance in this condition. Future studies should aim to replicate this observed mental rotation advantage of synesthetes for allocentric navigation with a larger sample size, because the current study only included 15 synesthetes with the mental rotation ability and eight synesthetes without this ability.

One might argue that the Allocentric 1 condition could still be egocentric due to continuous updating of participants' own spatial position relative to the platform during their movement in between trials to any of the four sides of the screen. So instead of finding the platform by using the object cues, participants might represent and update the relation between the platform and their own position (Simons & Wang, 1998). This so-called viewer-centered representation may trigger an egocentric strategy. In order to ensure that the Allocentric 1 condition can only be solved by using allocentric navigation strategies, in future studies, participants could be moved in a different way disrupting visual, vestibular and proprioceptive information. This prevents the updating mechanism to adjust for changes in participants' position (e.g., participants could be moved in a spinning wheelchair while covering their eyes, like in Simons and Wang, 1998).

Another suggestion for future studies with the aim to further investigate spatial navigation skills of sequence-space synesthetes is to conduct a navigation experiment in a virtual reality set-up. Such a set-up would more realistically reflect navigation in daily environments compared to the current approach. Therefore, it would convey different and perhaps converging information in order to answer the question whether sequence-space synesthetes have enhanced spatial navigation skills. A virtual reality experiment could thus expand on the current findings. These future studies could explore as well which specific synesthetic features contribute to the enhanced egocentric navigation of sequence-space synesthetes, since the features that we took into account could not explain this enhanced performance.

		Consistency test	
		SSS	**Con**
Report + drawing	**SSS**	20	3
	Con	13	8

Fig. 7. Scheme representing the suggested classification of participants based on the consistency test (Rothen et al., 2016) and the actual classification based on self-report and drawings. Three sequence-space synesthetes and thirteen control participants would have been misclassified when using a consistency cut-off score.

In addition to the results of the MWM task, this study gave more insights into reliable classification of sequence-space synesthetes and control participants. The consistency test (Rothen et al., 2016) was a valuable addition to check whether synesthetes consistently chose the same locations for items of sequences, but using only a consistency cut-off score would have led to an incorrect classification of participants. For the average area-based consistency score, Rothen et al. (2016) suggested to use a cut-off score of 0.2029% of the total monitor area, resulting in a cut-off score of 4207 for our study. Using this score would have led to the classification presented in Figure 7, which is highly deviant from the classification based on self-report and drawings. Rothen et al. (2016), however, increased the fit of their classification by excluding participants who had used certain strategies (e.g., placing items of a sequence on a horizontal straight line). We did not exclude these control participants which could explain this classification difference.

Instead of only using the results of the consistency test, drawings and participants' descriptions of their synesthetic experiences gave more confidence in correctly distinguishing sequence-space synesthetes from controls. Most studies investigating synesthesia have distinguished synesthetes from controls by using both subjective reports and consistency tests (Brang, Teuscher, Ramachandran, & Coulson, 2010). The current study demonstrated that drawings of spatial forms can serve as an important classification tool as well. Drawings of synesthetes were generally more complex and characterized by certain shapes (e.g., closed forms), while controls commonly arranged items of a sequence in rows or columns. This is consistent with previous reports of synesthetes experiencing months mostly in circular arrangements, while controls use rows or single straight lines as default (e.g., Brang et al., 2010; Eagleman, 2009). Importantly, synesthetes showed a tendency to connect items of a sequence within a form by blocks or lines. None of the control participants did this. This fits with synesthetes' reports that an item of a sequence – in particular, months and days – often "encompasses a region of space rather than a single location" (Brang et al., 2010, p. 316). Next to shape and complexity, this tendency of connection is therefore an important feature that characterizes synesthetes' drawings and may contribute to classification.

Conclusion

Sequence-space synesthetes have enhanced spatial navigation skills in a virtual navigation task. This study provides the first evidence for a spatial navigation benefit in SSS and the next question is whether these results translate to spatial navigation in daily environments. The findings of the current study add to the existing literature showing cognitive benefits of SSS and are consistent with the previously found mental rotation advantage. This study therefore contributes to a better understanding of SSS at a cognitive level and – the finding that mental rotation seems to be important for allocentric navigation – extends our knowledge about the cognitive processes involved in allocentric spatial navigation strategies.

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