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Explaining World-Wide Variation in Navigation Ability from Millions of People: Citizen Science Project Sea Hero Quest

H. J. Spiers,^a A. Coutrot,^{b,c} M. Hornberger^d

^a*Department of Experimental Psychology, Division of Psychology and Language Sciences, Institute of Behavioural Neuroscience, University College London*

^b*Laboratoire des Sciences du Numérique de Nantes, CNRS*

^c*Laboratoire d'Informatique en Image et Systèmes d'information, CNRS*

^d*Norwich Medical School, University of East Anglia*

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Abstract

Navigation ability varies widely across humans. Prior studies have reported that being younger and a male has an advantage for navigation ability. However, these studies have generally involved small numbers of participants from a handful of western countries. Here, we review findings from our project Sea Hero Quest, which used a video game for mobile and tablet devices to test 3.9 million people on their navigation ability, sampling across every nation-state and from 18 to 99 years of age. Results revealed that the task has good ecological validity and across all countries sufficiently sampled ($N = 57$), age is linked to a near-linear decline in navigation ability from the early 20s. All countries showed

Results from project Sea Hero Quest are reviewed, in which 3.9 million people across 63 countries took part in an online app-based virtual assessment of navigation skill. Key findings to date are: a) navigation skill declines linearly across the adult life span, b) a male advantage partially predicted by metrics of gender inequality across countries, c) navigation skill is geographically clustered across our planet, with Nordic people, north Americans and antipodeans performing best across countries sampled and d) growing up in cities with grid-like layout has an overall negative impact on navigation skill.

Correspondence should be sent to H. J. Spiers, Department of Experimental Psychology, Division of Psychology and Language Sciences, Institute of Behavioural Neuroscience, University College London, London, UK. E-mail: h.spiers@ucl.ac.uk

2 a male advantage, but this varied considerably and could be partly predicted by gender inequality.
3 We found that those reported growing up in a city were on average worse at navigating than those
4 who grew up outside cities and that navigation performance helped identify those at greater genetic
5 risk of Alzheimer's disease. We discuss the advantages and challenges of using a mobile app to study
6 cognition and the future avenues for understanding individual differences in navigation ability arising
7 from this research.

8 *Keywords:* Dementia; Wayfinding; Culture; Spatial cognition; Gender; Aging; Games
9

1. Introduction

14 Some humans are able to rapidly learn the layout of a new place, and others can become
15 lost easily (Burles & Iaria, 2020; Ekstrom, Spiers, Bohbot, & Rosenbaum, 2018; Weisberg
16 & Newcombe 2016; Wolbers & Hegarty, 2010). Understanding this variation in behavior is
17 important, not only for providing insights into cognition and brain function, but for the capac-
18 ity to detect and monitor the progression of Alzheimer's disease (AD), where deficits in spatial
19 memory appear early in the disease (Coughlan, Laczo, Hort, Minihane, & Hornberger, 2018).
20 AD affects over 50 million people worldwide, and its prevalence is increasing in countries
21 with an aging population: This number will be more than triple by 2050 (Alzheimer's Disease
22 International, 2018). Thus having the capacity to detect and monitor the disease is important,
23 particularly if there is the future possibility of treatment requiring early interventions. More-
24 over, given the challenges of creating a test that is widely available and not culturally affected,
25 such as those that use verbal material, this format is particularly attractive.

26 While developing a test of spatial navigation has been of interest, there have been sur-
27 prisingly few advances. Spatial navigation is not an ability that can easily be tested in stan-
28 dard testing rooms used for clinical assessment, as these cannot be controlled or manipulated
29 sufficiently for standardized assessment. Thus, virtual reality (VR) is a core tool that has
30 been turned to solve this problem (Coughlan, Laczo, et al., 2018). Given that AD prevalence
31 increases with age, the use of VR raises challenges because the older aged population tends to
32 have less familiarity with VR and may struggle with operating controls. This has been a sig-
33 nificant challenge in the past with desk-top VR controlled by a joystick or mouse. The recent
34 advent of widespread touch screen technology on tablet and mobile devices has changed that.
35 Such devices provide a much more intuitive appeal to older populations. An additional chal-
36 lenge faced when developing a test of spatial navigation is collecting a sufficient sample, large
37 enough to account for the wide variation in human ability. Testing thousands of people on a
38 VR task is time-consuming and costly.

39 Here, we review recent research by our team that surmounted the challenge of mass testing
40 by developing a flat-screen VR navigation task in a video game app—Sea Hero Quest—on
41 tablet and mobile devices that collected data in every country worldwide, assessing the perfor-
42 mance of 3.9 million people (Coutrot et al., 2018, 2020). We discuss how this was achieved,
43 what the results have revealed about human spatial navigation, and also future directions.
44

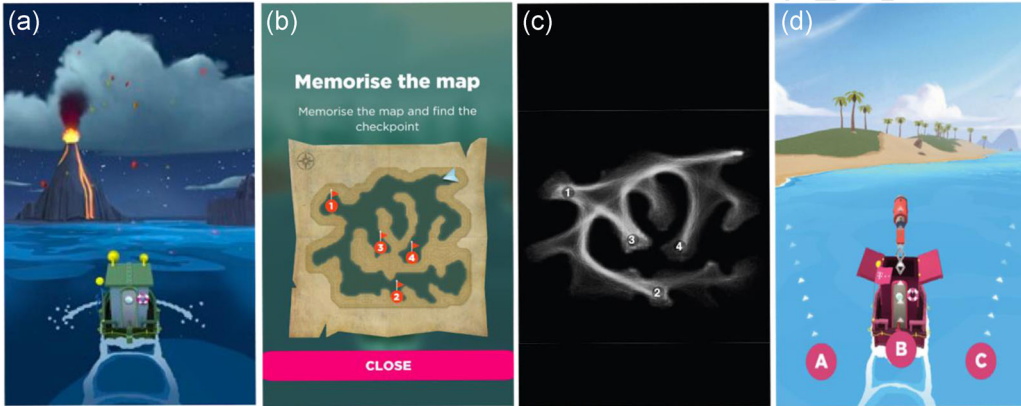


Fig 1. Task design (a-b) Wayfinding task: A map of the level featuring the ordered set of checkpoints to reach is presented and disappears when the game starts. (c) Superposition of 1000 individual trajectories randomly sampled from Level 32. (d) Path-integration task: After navigating the level, participants must shoot a flare back to the starting point. Reproduced from Coutrot et al. (2018).

2. Development of a worldwide virtual assessment of navigation ability: Citizen science on a global scale

The project arose from the intention of Deutsche Telekom (T-mobile) to engage people with a campaign using mobile phones to achieve a positive change in the world. The idea proposed by one of us (MH) of creating a navigation task in an engaging video game that could provide the benchmark assessment of navigation ability was chosen as the project they would support, with HS brought in as co-lead for the scientific development. This led to the engagement of creative agency Saachi and Saachi and the video games company Glitchers Ltd., who created the navigation test embedded in the video game, Sea Hero Quest (see Morgan, 2016). Alongside the commercial side of the project, careful guidance and grant support was given throughout the full length of the project by the charity Alzheimer's Research UK and led one of us (AC) to join the team to analyze the data. Two key design issues needed addressing: (a) What tests would work in a successful video game? (b). How can data be collected remotely from participants playing the video game on their phones?

The idea of testing navigation by steering a boat through oceans and marshes in search of sea creatures came from the game developers, the Glitchers Ltd.: Max Scott-Slade, Hugo Scott-Slade, and Matt Hyde. We found this approach beneficial for two reasons: (a) for many learning to steer a boat in the real world is difficult, and this makes the challenge of learning the game controls appear more consistent with the real world, (b) with water, it is clear where you can go and where you cannot go. Through discussions with the Glitchers and collaborators, three spatial tasks were selected for ease in a touch screen video game (Fig. 1a). While a logical choice would have been to test memory using a variant of the famous Morris Water Maze, in which the participant must locate a hidden location somewhere in a large circular pool or arena (Moffat, Zonderman, & Resnick, 2001; Morris, Garrud, Rawlins, &

2 O’Keefe, 1982), we opted not to use this because it requires regular circling behavior in VR.
3 This could potentially cause nausea, and the repetitive experience would be less engaging for
4 participants. Instead, we opted to examine wayfinding, path integration, and spatial working
5 memory (Fig. 1).

6 Wayfinding refers to the demand to travel through an environment to a remembered or
7 indicated goal location (Wiener, Büchner, & Hölscher, 2009). Wayfinding was chosen as it
8 forms a common part of the everyday navigation experience. Remembering the way to the
9 shops, traveling to a gallery to meet friends, and navigating an unknown city in search of a
10 restaurant are all examples of wayfinding (Ekstrom et al., 2018). Wayfinding is also a task in
11 which numerous studies have examined gender differences and the neural correlates (Ekstrom
12 et al., 2018). To keep the task short for maximum engagement with a large sample, we tested
13 wayfinding by providing participants with a map that displayed check-points to reach in a
14 numbered order that had to be memorized (Fig. 1b). The participant had unlimited time to
15 view the map before they began navigation to the checkpoints. Participants were rewarded
16 three stars if they reached the checkpoints quickly, two if slower, and if they took too long,
17 an arrow indicating the direction to the checkpoints appeared and they received one star. The
18 45 check-point levels created varied in a range of parameters: the number of checkpoints, the
19 complexity of the environment, the size of the environment, the presence of local and global
20 landmarks, fog, surprise forced detours and, in the later levels, waves. These were included to
21 allow the analysis of the impact of environmental features on navigation but also to vary the
22 game experience.

23 Path integration is the ability to use self-motion information to determine the distance and
24 direction traveled from a point of origin and calculate a homing vector to the origin (Wiener
25 et al., 2009). A path integration task was chosen due to prior work suggesting it may help
26 discriminate AD from other dementias (Tu, Spiers, Hodges, Piguet, & Hornberger, 2017).
27 Our path integration task (flare levels) required following a path to collect a flare gun and
28 shooting it back to the start of the level, choosing the correct direction (Fig. 1d). There were
29 15 of these levels included in the game. Spatial working memory in our case was a memory for
30 a set of locations recently visited in a virtual radial maze (Bohbot, Lerch, Thorndycraft, Iaria,
31 & Zijdenbos, 2007). The virtual radial maze helped provide a separate measure of spatial
32 memory but also a measure of strategy use. Five radial mazes were included in the game as
33 bonus levels. In these, participants had to collect hidden stars from the end of three of the
34 six arms in the radial maze, with three arms blocked. After collecting all three stars, all arms
35 were unblocked and the participants had to collect the stars from the arms that had previously
36 been blocked. After solving the task, participants were also asked whether they navigated by
37 counting the arms or used a landmark or a combination.

38 In addition to the three spatial tasks, every fifth level of the 75 levels in the game included
39 a task in which participants were required to chase and photograph a sea monster. Each of
40 these 15 levels required tapping left or right to move the boat only left or right to avoid
41 oncoming rocks and waves. If successful, after a short period, the view switched to a view
42 through a camera, and the participant was required to capture a photograph for their log in
43
44

2 the game menu. This was included to vary the gameplay and create photographs that could
3 allow users to share progress, helping to disseminate the game via social media. The data
4 from these levels were not recorded to minimize the data being transferred and stored with
5 the app. Because a measure of visuomotor video games skill was measured in the time taken
6 to complete tutorial Levels 1 and 2, it was decided the extra data from these monster chase
7 levels was not essential.

8 To collect data from millions of participants worldwide, it was necessary to optimally col-
9 lect the data and advertise the game. Data was recorded locally to the participant’s device and
10 sent encrypted to a secure server, in this case, run by T-mobile. Consent for this was provided
11 by the UCL ethics board, and informed consent was provided with the game. Several strate-
12 gies were taken to advertise for participants. Saatchi and Saatchi Ltd. played a key role in
13 the development of the project in this direction, creating several film and animation adverts
14 about the study with high-end production values and a developing emotive story linked to
15 dementia to motivate players to join. The gameplay was linked to helping a person collect the
16 pages of his father’s travel journal that had been lost and needed to be found. The game itself
17 allowed players to share progress and the upgrading of their boats via Facebook and Twitter.
18 T-mobile specifically advertised the game to its millions of customers. Alzheimer’s Research
19 UK promoted it to its supporters. Finally, the world’s most-watched YouTuber, Pewdiepie,
20 was recruited to publish a promotional video, resulting in over 2 million views in 5 days.
21 This advertising led to Sea Hero Quest becoming the most downloaded app on the Apple
22 App store for a day and creating a “moment” on Twitter. This snowball effect is what we
23 attributed to being able to recruit 3.9 million participants drawn from every country in the
24 world.

25 26 27 *2.1. Worldwide participants*

28
29 Since this dataset was recorded in a less controlled way than in a classic lab-based exper-
30 iment, the first challenge was to filter out less dedicated players, for instance, the ones who
31 played a couple of levels with their friends around a beer and quit the game early. To ensure
32 a good tradeoff between sample size and amount of data per player, we included in the anal-
33 ysis participants who played at least the first six wayfinding levels (Level numbers 1, 2, 3, 6,
34 7, and 8) from a total of 45 levels and the first two path integration levels (Levels 4 and 9).
35 We only included participants who entered their demographics (57% of the total). Looking
36 at the participant age distribution, we noticed two big spikes, at 18 and 99 years old. These
37 were likely due to participants younger than 18 (whose data we could not collect for ethical
38 reasons) or participants who did not bother honestly entering their age, and instead chose one
39 of the extrema of the spectrum. We discarded these participants. To further reduce selection
40 bias and ensure stable cross-country comparisons, we only included participants from coun-
41 tries with at least 500 valid participants. For our first publication (Coutrot et al., 2018; we
42 kept collecting data for another year), this left us with 558,143 participants from 57 countries,
43 312,886 males (age: 34.97 ± 14.39 years old) and 245,257 females (age: 35.98 ± 15.50 years
44 old).

2.2. Quantifying spatial ability (SA)

Optimal navigation will travel the shortest distance to the goal (shortest length of the trajectory), whereas inaccurate navigation will create long paths to the goal (long trajectories). Thus, akin to many other studies (e.g., Spiers, Burgess, Hartley, Vargha-Khadem, & O’Keefe, 2001) we used the length of the trajectory as the simple metric to quantify SA. We considered that video game experience might bias performance, with players familiar with gaming on smartphones and tablets having an advantage in keeping the boat on the path chosen rather than colliding with obstacles. Therefore, we normalized durations and trajectory lengths by dividing them by the sum of their values at the first two levels, where there are no choices and no need for spatial navigation. For more details on controlling familiarity with technology, see Coutrot et al. (2018).

2.3. Effect of age, gender, and nationality on SA

The angles to start digging into this massive dataset—one of the biggest behavioral datasets recorded for scientific purposes—were almost endless. We decided to start with the most obvious ones, that is, to check whether we could replicate some well-known results from the literature. We first verified whether SA declined with age (Anguera et al., 2013; Ghisletta, Rabbitt, Lunn, & Lindenberger, 2012; Lindenberger, 2014) and whether males performed better than females (Linn & Petersen, 1985; Nazareth, Huang, Voyer, & Newcombe, 2019; Reilly & Neumann, 2013). We fit a mixed model for SA, with fixed effects for age and varying slope for gender, nested within nationality: $SA \sim \text{age} + (\text{gender} | \text{country})$.

For age, across all included countries, we observed a similar pattern of a linear decline in SA with age between 19 and 70 years old. However, after 70 years of age, performance counterintuitively started to rise again. This was probably due to a strong selection bias in older participants: people above 70 years old playing video games for scientific research on their smartphones or tablets are likely in the upper band of their age group, cognitively speaking. This should be considered as a warning when generalizing effects measured in older participants to the general older population. This holds true in classic lab-based studies, which could lead to an even stronger selection bias, as physically going to a research facility to be tested can arguably constitute a stronger filter than simply playing games on a mobile device.

For gender, we observed an overall advantage of males over females (Cohen’s $d = 0.29$, 95% CI = [0.27, 0.31]), consistent with the literature (Nazareth et al., 2019). However, this gender effect greatly varied across countries, from $d = 0.09$ in Norway to $d = 0.48$ in Argentina. These variations in effect size across countries can be associated with gender inequalities in society, assessed by the World Economic Forum’s Gender Gap Index (GGI), which reflects economic and political opportunities, education, and well-being for women. We reported a positive correlation between GGI and the country-level gender effect size ($r = .62$, $p < .001$). This association remained significant after controlling for countries’ GDP per capita, suggesting that the gender effect is not simply related to countries’ wealth but also to the improvement of the role of women in society. While biological differences between sexes

2 may underly some of the gender differences in navigation performance, the weak effects sizes
3 we found in several countries (e.g., Norway) suggest that societal factors such as access to
4 education have a significant impact on gender differences in spatial navigation. More research
5 to explore the impact of education on navigation ability and how this may be related to gender
6 differences across nations is particularly warranted.

To assess the impact of nationality on spatial navigation, we fit a mixed model for *Spatial Ability*, with fixed effects for age and gender and random effect for nationality: $SA \sim \text{age} + \text{gender} + (1 | \text{country})$. The variance partition coefficient indicates that 1.7% of the variance in *Spatial Ability* can be attributed to differences between nationalities, after correcting for age and gender. We found that the country-level SA is not geographically random but strongly correlated with GDP per capita ($r = .69, p < .001$). This is likely due to numerous variables correlated with GDP per capita and associated with better spatial abilities, such as level of education (Skirbekk & Loichinger, 2012)—particularly in science (Gunderson, Ramirez, Beilock, & Levine, 2012; Uttal, Meadow, Hand, Warren, & Newcombe, 2013) - or ability to travel (Poumanyong, Kaneko, & Dhakal, 2012). However, country-level attributes other than GDP per capita and GGI can explain the observed distribution of SA. For instance, the car culture in North America and Australia can explain why these countries are more successful than GDP-equivalent European countries that rely more on public transport (Maguire, Woollett, & Spiers, 2006; Sandamas & Foreman, 2015). However, this hypothesis fails to explain why the Nordic countries are at the top of the nation ranking. One possibility might be that the Nordic countries share a culture of participating in a sport-related to navigation: orienteering. They have a tradition of teaching orienteering in schools (Annerstedt, 2008) and winning medals in the Orienteering World Championship. Across the 19 nations represented in the top 100 rankings, performance in orienteering is significantly correlated with countries' *Conditional Modes* (corrected country performance from our model) in SHQ (Pearson's correlation $r = .55, p = .01$), even after correcting for GDP per capita. This is a post hoc hypothesis and should be considered with care, but we believe that this observation illustrates the potential for future targeted research to evaluate the impact of cultural activities on cognitive performance.

2.4. Does growing up in a city or outside cities impact navigation ability?

In addition to age, gender, and nationality, we have explored the impact of other demographics. One such demographic is whether participants reported growing up in a city or outside a city. We found that on average, a rural or mixed city/rural upbringing leads to better navigation ability than city upbringing, see Fig. 3a (Coutrot et al., 2020). Notably, this result held when controlling for educational attainment. However, the negative effect of growing up in cities was mitigated by the topology of their street network (Fig. 3b). The largest effect was observed in cities with a low street network entropy (SNE; i.e., a regular layout, like Chicago, USA, see Boeing, 2019). In cities with high SNE (i.e., more organic, like most old European city centers), this effect was much reduced. Moreover, we observed that participants who grew up in cities with low SNE performed better at less entropic SHQ levels. Altogether, these results suggest that people are better at navigating in environments topologically similar to where they grew up, which highlights the importance of urban design on human cognition.

2.5. *Real-world validity*

Despite the effort we invested into designing a user-friendly game and analytically separating video gaming skills (speed of tutorial completion) from SA, we considered that it was plausible that Sea Hero Quest does not accurately reflect real-world navigation skills. To navigate in Sea Hero Quest, one needs to update one's perspective in the game coordinates rather than with whole-body rotations in the real world. Notably, previous studies found that navigation performance in the real world correlates with navigation performance in virtual environments (Conroy, 2001; Cushman, Stein, & Duffy, 2008; Moffat et al., 2001), and they mainly used desktop or immersive displays, while our dataset has been collected via a mobile video game. To directly assess the generalizability of our data to the real world, we tested participants with Sea Hero Quest and with a similar real-world navigation task in the streets of London (the United Kingdom) and Paris (France; Coutrot et al., 2019). We found a significant correlation between real-world navigation performance and performance on SHQ levels that specifically test navigation (in London, $r = .46$, $p = .01$; in Paris, $r = .57$, $p = .001$). No such correlation was found when comparing performance on the tutorial (where SA was not required) levels with real-world navigation performance ($r = .06$). Thus, at least in these urban settings, Sea Hero Quest seems to capture real-world navigation performance.

2.6. *Understanding how the environment impacts navigation performance*

The environment can have a dramatic impact on how difficult it is to navigate. Walking to the next room is easier than a trek across the Sahara desert. A core research question is what features of the environment are particularly important in determining difficulty. Key factors appear to be: the size of the environment, the number of decision points, the number of regions of space, the presence of distinct fixed landmarks, and the organization/disorganization of the space (Arthur & Passini, 1992; Conroy, Hoelscher & Spiers 2015; Ekstrom et al., 2018; Raubal & Egenhofer, 1998).

The majority of Sea Hero Quest wayfinding levels were designed by Ruth Dalton and Christoph Hoelscher to vary in these properties, allowing analysis of how wayfinding behavior is related to such factors (Coutrot et al., 2018). Our preliminary analysis indicates that indeed the number of decision points and topological structure of the environment has an impact on wayfinding difficulty (Yesiltepe, Dalton, Ozbil Torun, Dalton, Noble, Hornberger, & Spiers, 2019). Global landmarks have less of an impact on navigation than we had predicted (Yesiltepe, Dalton, Ozbil Torun, Dalton, Noble, Hornberger, Coutrot, & Spiers, 2019). Exploring this further, it was possible to quantify the distinction between local and global landmarks by the extent to which they were in view during the navigation task (Yesiltepe, Dalton, Ozbil Torun, Noble, et al., 2020). Furthermore, we found that seemingly insignificant features (such as a cluster of reeds) could be considered important landmarks and that current models of extracting saliency in images were unable to predict what would be considered a useful landmark (Yesiltepe, Ozbil Torun, et al., 2020; Yesiltepe, Dalton, Ozbil Torun, Coutrot, et al., 2020; Yesiltepe, Dalton, Ozbil Torun, Hornberger, & Spiers, 2020). This highlights the importance of the location (e.g., at waypoints) of landmarks for navigation (Caduff & Timpf,

2 2008). Future research in this direction will explore how individual differences interact with
3 the environment features to explain navigational choices and trajectory patterns.

4 5 2.7. *Is Sea Hero Quest reliable for test-retest?*

6
7 A key aspect in the development of new cognitive tests is their reliability not only to detect
8 the effects of interest but also whether those effects can be elicited repeatedly across test
9 sessions. Such test-retest reliability is commonly established for clinical tests that require
10 longitudinal follow-up of patients, however, it is rarely conducted for experimental cognitive
11 tests. Since SHQ has the potential to track people's navigation performance over time and to
12 potentially use this as a clinical marker for incipient AD, the establishment of test-retest reli-
13 ability was a key element for our SHQ research, especially to determine the degree to which
14 baseline and follow-up assessments produce consistent results. For example, participants may
15 learn to apply strategies at retest that improve their navigation accuracy or efficiency, reducing
16 its test-retest reliability.

17 We, therefore, conducted a test-retest study with middle-aged people, who underwent SHQ
18 testing at baseline and an average follow-up at 18 months (Coughlan, Puthusseryppady, et al.,
19 2020). The retest delay was chosen to reflect appropriate time windows to follow up people
20 for long-term longitudinal studies. The results revealed that some measures of SHQ showed
21 moderate test-retest reliability, such as distance traveled, whereas others showed only low test-
22 retest reliability, such as SHQ duration. Interestingly, this reliability could also be confirmed
23 for "at-genetic-risk" of AD participants, who showed similar results.

24 Overall, SHQ shows good test-retest reliability, similar to existing spatial navigation tests
25 such as the 4 Mountains Test (Chan et al., 2016). However, the choice of outcome variable
26 impacts the reliability measurements, with distance traveled emerging as the most reliable
27 measure to track navigation changes in SHQ over time.

28 29 2.8. *Can SHQ be helpful to monitor variation in skill for those at-genetic-risk of AD?*

30
31 The test-re-test findings also highlight that at-genetic-risk of AD participants can be suc-
32 cessfully tracked over time, which has clear implications for incipient disease monitoring.
33 To investigate the at-genetic-risk angle further, we conducted a study in a large cohort of
34 participants, either at-genetic-risk or not (Coughlan et al., 2019).

35 The genetic risk factor we selected as the most critical was apolipoprotein E (APOE).
36 APOE is the most common genetic risk factor for AD, with epidemiological studies show-
37 ing that carrying the heterozygous form (e3:e4) increases people's risk four-fold for AD and
38 the homozygous form (e4:e4) increases the risk 12-fold, compared to the wild type (e3:e3)
39 APOE alleles (Corder et al., 1993). The exact reasons why APOE increases the risk for AD are
40 still being investigated, but it has been implicated with potential changes to blood-brain bar-
41 rier integrity and reduced microglia activity, thus slowing down the removal of beta-amyloid
42 fibrils—a key culprit in the onset of AD.

43 There has been an increasing interest in the APOE cohort as a disease model for incipi-
44 ent cognitive changes for AD. Previous studies have shown that APOE carriers at increased

2 genetic risk show changed navigation behavior with overshooting of navigation targets and
3 preference for border areas (Coughlan, Zhukovsky, et al., 2020). It has been speculated that
4 APOE induced grid cell changes in the entorhinal cortex and are responsible for these spe-
5 cific navigation changes, as distance traveled and landmark spatial resetting are critical factors
6 mediated by the entorhinal cortex (Kunz et al., 2015).

7 We replicated the previous finding with SHQ, by showing that at-genetic-risk (e3:e4 &
8 e4:e4) participants traveled longer distances within the game than APOE wildtype (e3:e3)
9 participants (Coughlan et al., 2019). Further, we replicated the finding that at-genetic-risk
10 participants traveled closer to the borders within SHQ, potentially to compensate for incip-
11 ient grid cell linked changes in the entorhinal cortex. A critical advantage that SHQ has to
12 previous studies is that the same APOE navigation effect can be detected with virtually no
13 training and much quicker. Previous experimental designs relied on participants learning spa-
14 tial environments over repeated trials, with some learning paradigms taking as long as 1 h.
15 By contrast, SHQ requires no learning of environments, but still results in the same effects,
16 allowing inclusion with other cognitive tests for dementia assessment (Coughlan, Flanagan,
17 et al., 2018). This is also consistent with the premise that the cognitive problems linked to the
18 APOE gene variants are related to spatial disorientation rather than learning per se.

19 The other final advantage which SHQ has is that it allows for a more personalized detec-
20 tion of navigation changes. Not only can we detect group differences between genetic-risk
21 groups, but we can also compare each at-genetic-risk participant to their age, gender, and
22 country-matched peers, via the large normative SHQ dataset. Even for a single age, gender,
23 and country, the large data of SHQ allow to compare some at risk of AD against at least 700
24 healthy peers. What additional information does this individual comparison provide? The key
25 additional information is that it allows to benchmark at risk of AD people against their peers,
26 thus showing whether they perform within the benchmark navigation performance or further
27 off it. The rationale is that the further off people at-risk of AD perform, the more likely their
28 navigation-specific brain regions are affected by incipient AD pathophysiology. The distance
29 from the mean performance allows, therefore, to potentially determine how close people are
30 to being at risk of developing AD, which has clear diagnostic, prevention, and treatment
31 implications.

32 33 *2.9. Using machine learning to learn efficient representations of the trajectories*

34
35 So far, we quantified the SA measured in Sea Hero Quest with very simple metrics, mainly
36 based on the length of the trajectories followed by the participants to complete the levels.
37 The longer the trajectory, the more participants got lost, the worse the performance. Although
38 very intuitive, this metric fails at capturing many aspects of SA. For instance, two participants
39 could follow two very different trajectories with exactly the same length. Our metric would
40 not be able to separate these participants, even though they used completely different naviga-
41 tion strategies. To overcome this issue, we need to develop more sophisticated approaches to
42 represent and quantify the strategies developed by the players. Spatial trajectories are spatial
43 patterns that contain a wealth of information arising from the complex interaction between the
44 environment and the navigator's decisions. Several trajectory-mining approaches have been

2 proposed in many fields such as traffic forecasting, object motion prediction, ecology, behav-
3 ioral, and clinical neuroscience (Damascène Mazimpaka & Timpf, 2016). The most popular
4 approach is trajectory clustering, which aims at discovering groups of similar trajectories in
5 terms of intuitive features such as their coordinates, angle, speed, or curvature (Bian et al.,
6 2018). Another approach is to learn efficient representations of the trajectories directly from
7 the raw data, using artificial neural networks (ANNs; Wang et al., 2019). ANNs can learn
8 more efficient representations than hand-crafted features, but they are often black-boxes, and
9 it is hard to interpret the concepts learned by the models. We recently proposed an ANN-based
10 model learning trajectory representations and connecting them to participants' demographics
11 in an interpretable way (Dubois et al., 2021). It relies on three parallel modules capturing
12 different aspects of the signal (spatial, temporal, and spectral), allowing the user to under-
13 stand which parts of the trajectories most contribute to the output. Future studies will use
14 these approaches to further understand the origins of the differences in performance across
15 the demographics.

17 *2.10. Addressing the limitations and challenges of using mobile apps for research*

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19 Using a mobile app to examine navigation ability has provided an unprecedented capac-
20 ity to understand human behavior on a mass scale. However, there are several limitations
21 and challenges with this approach. Some of the key challenges are the real-world validity of
22 a mobile phone test, bias in the sample of participants, the limited demographic questions
23 posed, and the trade-off between a highly engaging video game and rigorous cognitive test-
24 ing. We have discussed previously our exploration of the real-world validity of our test, and
25 below, we consider the other issues.

26 All human psychology studies have a bias in who volunteers to take part (Henrich, Heine,
27 & Norenzayan, 2010). Mobile apps combined with a citizen science provide the capacity
28 to reach out beyond university students, broader age ranges, people with less education, and
29 across different countries. However, people in older age groups will be less likely to engage in
30 downloading video games to phones and tablet devices, thus skewing the sample to a younger
31 age. Fortunately for Sea Hero Quest, the mass popularity meant that even with this skew,
32 we were able to sample 100,000s of people over 50 years and 1000s over 80 years across
33 many countries and from people with lower educational backgrounds (Coutrot et al., 2018).
34 However, as discussed previously, we observed a significant selection bias after the age of
35 around 70 years (Fig. 2e). After the age of 70 years, performance steadily increases with
36 age. Given the wealth of evidence for a negative impact of aging on cognition (Lindenberger,
37 2014), this result is not plausible as a direct measure of the general populace. Rather it seems
38 more likely that post 70, participants who are willing to engage in a research-based app game
39 will increasingly be healthy agers who are motivated to participate in studies. See Coutrot
40 et al.'s (2018) supplemental information for details on our analysis of selection bias in the
41 data. Documenting this bias is important as we believe that if it is present in our data, it is
42 also likely to present in conventional lab-based experiments. Indeed, the filter represented by
43 playing a game on a smartphone might not be stronger than the one represented by asking
44 participants to physically come to a research facility.

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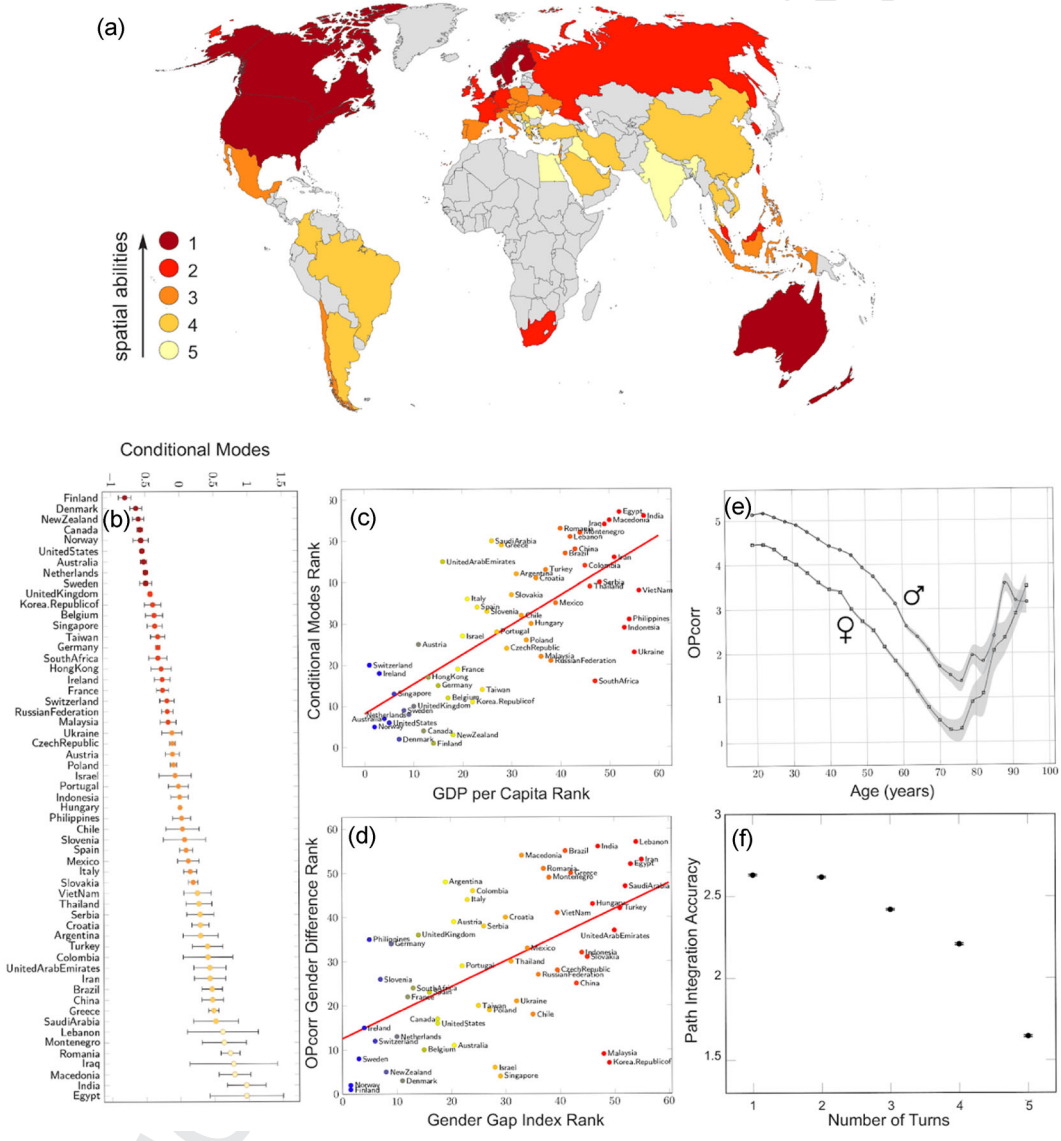


Fig 2. Spatial ability (SA) distribution across age, gender, and nations. (a-b) Five world clusters of people with similar SA corrected for video gaming skill. We used a multilevel model to predict SA with a fixed effect for age and gender and random effect for nationality. Conditional modes represent the country-level performance (the lower the better). (c) Correlation between country performance (CM) and GDP per capita ($r = .69, p < .001$). (d) Correlation between gender estimates and Gender Gap Index ($r = .62, p < .001$). (e) Evolution of SA across age and gender. Data points correspond to the average Overall Performance, corrected by video games skill within 3-year windows. Error bars correspond to SEs. (f) Path-integration accuracy (number of stars) versus path complexity (number of turns). This plot includes participants that completed all five levels ($N = 19,038$). Error bars correspond to SEs. Reproduced from Coutrot et al. (2018).

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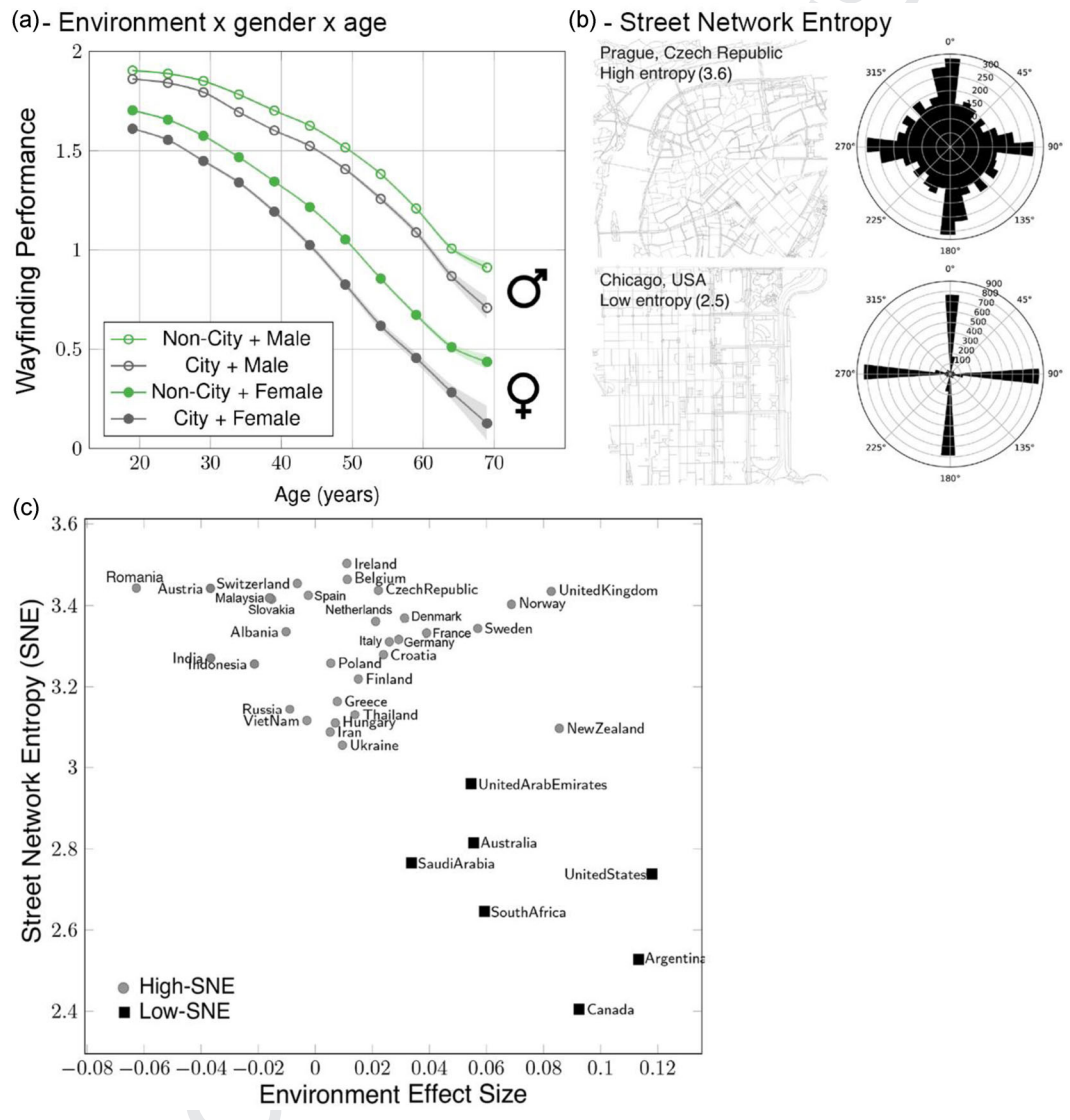


Fig 3. Effect of the upbringing environment on SA. (a) Association between *Environment* and *Wayfinding Performance* stratified by age, gender, and education. The *Wayfinding Performance* is computed from the trajectory length and has been averaged within 5-years windows. Error bars represent standard error. (b) Two examples are cities with low (Chicago USA) and high (Prague, Czech Republic) street network entropy (SNE; Boeing, 2019). (c) Average SNE as a function of the environment effect size (random environment slope) in 38 countries. Positive values indicate an advantage of participants raised outside cities, compared to their urban compatriots. Average SNE is the weighted average over the 10 most populated cities of the country, weighted by their population. Adapted from Coutrot et al. (2020).

2 Unlike some other apps aimed at research, such as *The Great Brain Experiment*
3 (Smittenaar et al., 2015), Sea Hero Quest was designed to be an engaging video game that
4 people would play purely for fun while also generating data. This was done in order to maxi-
5 mize the sample size from the data collected. As a part of this design, rather than halt game-
6 play with many demographics questions, we focused on key demographics, and the players
7 were awarded “virtual badges” for answering the questions. The questions were also framed
8 with images to make them more comprehensible and to engage participants with the ques-
9 tions. We ideally would have invited participants to provide answers to more questions via an
10 online survey. However, because Sea Hero Quest was designed to securely store anonymized
11 data directly from the app, we were not able at the time of launching the app to find a way to
12 link participants to a web-based survey of further demographics. Future research will be able
13 to address this.

14 An important limitation from this research is to consider that Sea Hero Quest examines a
15 particular set of spatial skills, such as interpreting a map and memorizing it to navigate to
16 a set of goals in the right order. People in traditional communities can navigate with excep-
17 tional skill in highly complex environments such as oceans, deserts, and tundra (Ekstrom
18 et al., 2018; Levinson, 2003). Such environments are learned from early life and are encoun-
19 tered over many years of experience. Individual variation in such skill is not something an
20 app on a mobile device can easily aid our understanding of. It will be important in future
21 work to explore the links between the skill of highly expert navigators such as London taxi
22 drivers (Griesbauer, Manley, Wiener, & Spiers, 2021; Maguire et al., 2006; Spiers & Maguire
23 2008). Moreover, it would be beneficial to understand how navigation performance in Sea
24 Hero Quest relates to other spatial and nonspatial performance, given evidence that spatial
25 navigation may be distinct from performance on more object-based spatial tasks (Malanchini
26 et al., 2020), nonspatial association memory (Ngo, Weisberg, Newcombe, & Olson, 2016),
27 or autobiographical memory (Fan, Abdi, & Levine, 2021). Our large online sample from Sea
28 Hero Quest can separate spatial navigation ability from video games skill (tutorial levels), but
29 we cannot dissociate it from general cognitive ability, “g,” as it was not possible to incorpo-
30 rate other general IQ tasks with our funded time-lines for the research. However, past research
31 suggests a large portion of the variance in spatial navigation is separable from measures of
32 general cognitive ability (Malanchini et al., 2020). Thus, we would expect our measure of
33 spatial navigation ability to be separable to a significant extent from a general cognitive
34 ability.

36 **3. Future Directions**

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38 There are a range of different future advances that may come from this approach to under-
39 standing navigation. It will be important to understand how the other demographics we col-
40 lected impact navigation skills. These include the impact of education, handedness, sleep, and
41 self-rated navigation ability. Future research exploring machine learning and approaches to
42 trajectory prediction holds much promise for examining the large trajectory data created by
43 Sea Hero Quest. This research might for example identify that participants become less pre-
44 dictable with age. It could be that men are more predictable in Sea Hero Quest environments

lacking landmarks (Reilly & Neumann 2013). Data collected from an immersive VR version of Sea Hero Quest for the Samsung Gear VR device has yet to be examined in detail and may shed more light on the disorientation in relation to various individual differences.

Combining Sea Hero Quest with neuroimaging or neural recording methods will be useful for exploring whether brain structure or function can predict performance metrics from Sea Hero Quest. Current research is divided on whether variation in hippocampal structural measures can be linked to performance; with some studies reporting a correlation (Bohbot et al., 2007; Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013; Hartley & Harlow, 2014; Brunec et al., 2019; Hodgetts et al., 2020) and others reporting no correlation (Clark et al., 2020; Maguire et al., 2003; Weisberg, Newcombe, & Chatterjee, 2019). Sea Hero Quest would be beneficial in that the participants can be selected to cover a useful range in the distribution of individual differences. Past studies may have studied too few individuals with poor navigation skills or high navigation skills making it difficult to explore the full range. Functional imaging studies have shown important individual differences in activity patterns (Ekstrom et al., 2018; Hartley, Maguire, Spiers, & Burgess, 2003; Patai et al., 2019; Wolbers & Hegarty, 2010). Sea Hero Quest would allow quantification of a range of variables linked both to the variation in environments used in the game (Yesiltepe, Dalton, Ozbil Torun, N. Dalton, Noble, Hornberger, & Spiers, 2019) as well as other graph-theoretic metrics found to be related to hippocampal activity, such as degree centrality (Javadi et al., 2017). Combining neuroimaging data with the mass trajectory data may allow exploration of whether patterns of activity in key brain regions enhance forecasting of future trajectories, potentially predicting when individuals will backtrack (Javadi et al., 2019). Similarly, recording the gaze behavior of participants playing Sea Hero Quest would be particularly interesting since spatial information acquisition happens in large part through the visual sense.

One missing line of research so far in spatial cognition has been the use of longitudinal cohort studies. Testing thousands of such individuals would provide links to much broader and detailed assessments of performance over a lifetime and allow for analysis of changes in performance as these cohorts are followed up. So far, Sea Hero Quest has explored spatial navigation over the age of 18 and we have found a general decline in performance. This raises the question: At what age does navigation ability peak? Hopefully, future studies with those under 18 will help address this key question. At the other end of life, we hope that Sea Hero Quest will be a useful tool for monitoring cognitive function in AD (Coughlan, Zhukovsky, et al., 2020).

4. Conclusion

The global reach of mobile phone-based game applications has enabled the mass testing of millions of people in a manner not feasible a decade ago (Gillan & Rutledge, 2021). Our project Sea Hero Quest has shown that it is possible to assess the impact of individual differences in spatial navigation ability across 3.9 million people, sampling population data in 57 countries (Coutrot et al., 2018; Coutrot et al., 2020). Our results replicated prior small sample studies: Age had a strong negative impact on performance, and there was an advantage

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2 for males and those with greater education (Coutrot et al., 2018, 2020). Extending beyond
3 prior studies with population data, we were able to show that such patterns also exist in non-
4 Western countries and that the economic wealth of a country (GDP) predicts its population's
5 average navigation performance (Coutrot et al., 2018). We were also able to reveal a relation-
6 ship between gender inequality of a country and how large the gender disparity was in the
7 spatial navigation skill (Coutrot et al., 2018), indicating that cultural differences in how men
8 and women are treated impact spatial navigation ability. Most recently, we have revealed that
9 growing up in the city of countries with griddy cities (e.g., Chicago) has an overall negative
10 impact on navigation skill in the game (Coutrot et al., 2020). We have also briefly discussed
11 how Sea Hero Quest has been useful for monitoring changes in skill for those at risk of AD
12 (Coughlan et al., 2019; Coughlan, Zhukovsky, et al., 2020) and exploring broader metrics
13 of spatial performance with artificial neural networks (Dubois et al., 2021). Future research
14 with Sea Hero Quest will allow a variety of studies to be done remotely with healthy and
15 clinical populations. Analysis of this rich data has still much to reveal in helping address the
16 individual differences in spatial navigation ability.

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20
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