Entropy of city street networks linked to future spatial navigation ability

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The cultural and geographical properties of the environment have been shown to deeply influence cognition and mental health[1–6]. Living near green spaces has been found to be strongly beneficial[7–11], and urban residence has been associated with a higher risk of some psychiatric disorders[12–14]—although some studies suggest that dense socioeconomic networks found in larger cities provide a buffer against depression[15]. However, how the environment in which one grew up affects later cognitive abilities remains poorly understood. Here we used a cognitive task embedded in a video game[16] to measure non-verbal spatial navigation ability in 397,162 people from 38 countries across the world. Overall, we found that people who grew up outside cities were better at navigation. More specifically, people were better at navigating in environments that were topologically similar to where they grew up. Growing up in cities with a low street network entropy (for example, Chicago) led to better results at video game levels with a regular layout, whereas growing up outside cities or in cities with a higher street network entropy (for example, Prague) led to better results at more entropic video game levels. This provides evidence of the effect of the environment on human cognition on a global scale, and highlights the importance of urban design in human cognition and brain function.

Cognitive abilities, including spatial navigation, have been shown to correlate with specific genotypes[17]. However, research on brain plasticity supports the notion that experience shapes brain structure as well as function[2,3]. In particular, cultural and geographical properties of the environment have been shown to deeply influence cognition and mental health[4,6]. In rodents, exploring complex environments has a positive effect on hippocampal neurogenesis and cognition[1,5]. In humans, spatial navigation activates the hippocampus[18], and continuous navigation of a large complex city environment increases posterior hippocampal volume[19]. However, how the environment in which one grew up affects later cognitive abilities remains poorly understood for two reasons. First, human environments are manifold and much harder to characterize than a rodent's cage. Second, collecting cognitive data of large samples from populations living in different environments is very costly[20]. To overcome these limitations, we measured non-verbal spatial navigation ability in 3.9 million people across all countries and examined a subset of this data (397,162 people, in 38 countries). We used a cognitive task embedded in a video game that is predictive of real-world navigation skill[16,21,22]. Although the task has been described previously[16], we now report data that have not been previously published. We focused on spatial navigation because of its universal requirement across cultures, and parallels to rodent studies[23,24]. We quantified the complexity of participants' environments with OSMnx, a tool that gives access to the street network topology of cities anywhere in the world[25]. We found that, on average, people who reported having grown up in cities had worse navigation skills than those who reported growing up outside cities, even when controlling for age, gender and level of education. This difference between people from cities and those from non-city areas varied across countries, being—for example—more than six times larger in the USA than in Romania. To investigate these variations we computed the average street network entropy (SNE) of the biggest cities of 38 countries; grid-like cities (for example, Chicago) have a small SNE, whereas more organic cities (for example, Prague) have a higher one. We found that growing up in cities with a low SNE led to better performance at video game levels with a regular layout, whereas growing up outside cities or in cities with higher SNE led to better performance at more entropic video game levels. .

We used the Sea Hero Quest database, which contains the spatial navigation behaviour of 3.9 million participants measured with a mobile video game, 'Sea Hero Quest' (SHQ)[16,22]. SHQ involves navigating a boat in search of sea creatures (Fig. 1a–f). Performance in SHQ has been shown to be predictive of real-world navigation ability[21]. It has also allowed participants who are at high risk of Alzheimer's disease in the preclinical stages to be differentiated from participants who are at low risk[26]. Here we focused on the wayfinding task[16], in which players are initially presented with a map indicating the start location and the location of several checkpoints to find in a set order. To provide a reliable estimate of spatial navigation ability, we only examined data from

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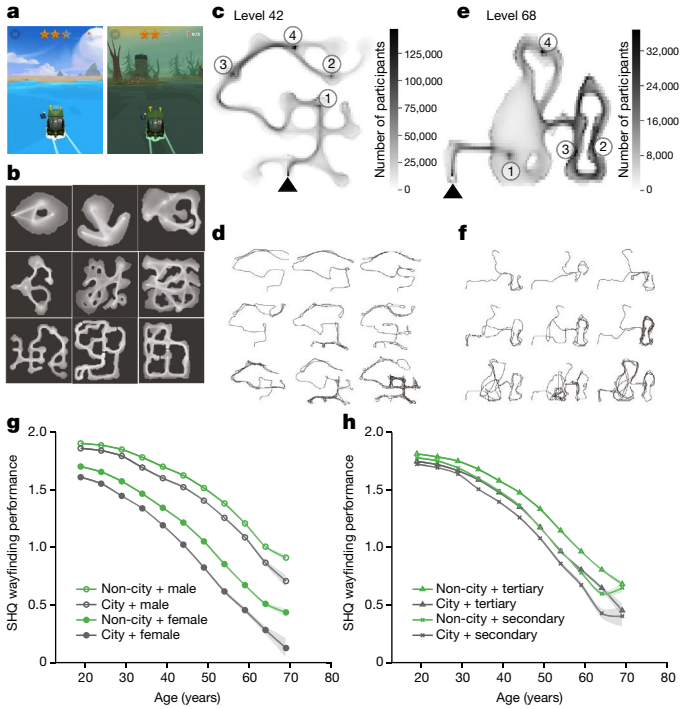


Fig. 1 | Wayfinding task. a, Screenshots from the game Sea Hero Quest (SHQ). See also Supplementary Video 1. **b**, Nine examples of trajectory heat maps out of the 75 SHQ levels. **c**, **e**, Heat maps of the trajectories of all participants in level 42 (**c**; n = 171,887 participants) and level 68 (**e**; n = 40,251 participants) of SHQ. The black triangle represents the starting position, and the circled numbers represent the ordered checkpoints that the participants must reach. **d**, **f**, Examples of trajectories in level 42 (**d**) and level 68 (**f**) of SHQ. **g**, **h**, Association between environment and SHQ wayfinding performance stratified by age, gender and education (**g**, gender and age; **h**, education and age). The SHQ wayfinding performance is computed from the trajectory length and has been averaged within five-year windows. See Extended Data Fig. 7 for a breakdown of the environment classes. Error bars, standard error; centre values, mean.

participants who had completed a minimum of 11 levels of the game, and who entered all their demographics (Methods). This resulted in a total of 397,162 participants from 38 countries being included in our analysis (Supplementary Table 1, Extended Data Fig. 1). Among them, 212,143 individuals were male (mean age: 37.81 ± 13.59 years old) and 185,173 were female (mean age: 38.67 ± 14.92 years old).

Spatial ability across demographics

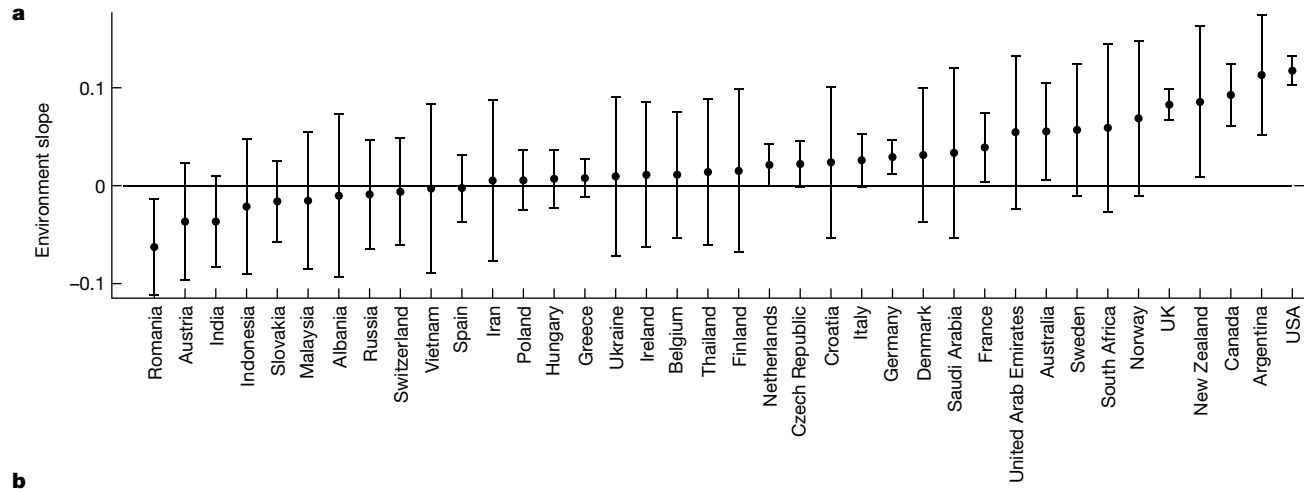
To quantify spatial ability, we defined the 'wayfinding performance' metric (WF), which captures how efficient participants were in completing the wayfinding levels, while correcting for video-gaming skills (Methods). We performed the same analysis for path integration levels and obtained similar results (Supplementary Methods, Extended Data Fig. 2). A multivariate linear regression was calculated to predict wayfinding performance on the basis of age, gender, education and environment. Age had the strongest effect ($F_{1,397157}$ = 61,389, P < 0.001, η^2 = 0.127, Hedge's g = 0.98, 95% confidence interval (CI) = [0.97, 0.99]), followed by gender ($F_{1,397157}$ = 20,665, P < 0.001, η^2 = 0.043, Hedge's g = 0.44, 95% CI = [0.43, 0.45]), education ($F_{1,397157}$ = 1,476.9, P < 0.001, η^2 = 0.003, Hedge's g = 0.13, 95% CI = [0.13, 0.14]) and environment ($F_{1,397157}$ = 1,628.8, P < 0.001, η^2 = 0.003, Hedge's g = 0.09, 95% CI = [0.09, 0.10]). The Hedge's g of age is computed between participants younger than 25 years old (n = 88,101) and participants older than 55 years old (n = 59,982). Figure 1g, h represents the effect of the environment on WF stratified by age, gender and education. We replicate previous studies showing that wayfinding performance decreases with age[27,28], male individuals perform better than female individuals[29] and performance increases with the level of education[30,31]. We also now report that participants who were raised outside cities are more accurate navigators than city-dwellers. Having a tertiary level of education while having grown up in a city is roughly equivalent to having a secondary level of education while having grown up outside cities in terms of wayfinding performance. The sample sizes for each demographic and country are available in Supplementary Table 1. Given the magnitude of the dataset, most effects are likely to always be significant below the 0.001 threshold. In the following text we will focus on effect sizes as they are independent of sample size. We computed Hedge's g values between the city and not-city groups. To marginalize the effect of age, we computed Hedge's g values within five-year windows. Averaged over all age groups, g = 0.13, 95% CI = [0.12, 0.14], with positive values corresponding to an advantage for participants who grew up outside cities. As shown in Extended Data Fig. 3, Hedge's g remained stable across different age groups, which is notable as it might be hypothesized that the influence of the environment in which one grew up would fade with age. This stability is consistent with the literature on the timing of exposure to an enriched environment in mice, showing that an early exposure to an enriched environment could provide a 'reserve'-like advantage that supports an enduring preservation of spatial capabilities in later life[32].

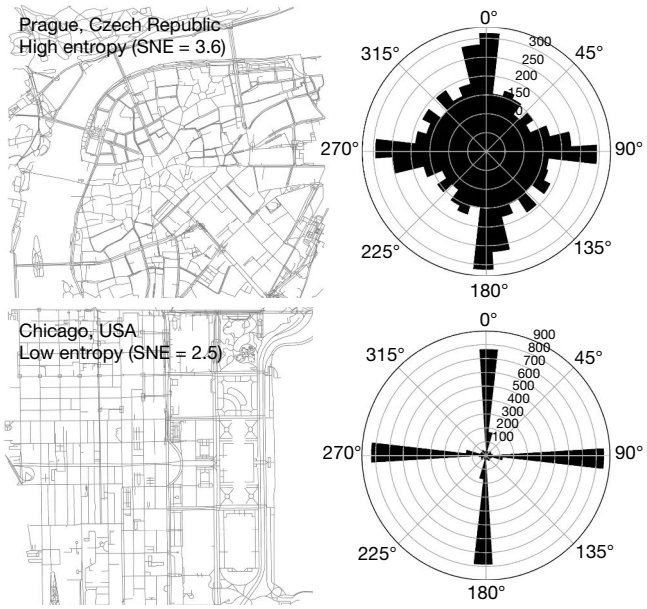
Spatial ability across countries

To quantify how spatial ability and environment are associated across countries, we fitted a linear mixed model (LMM) for wayfinding performance, which included fixed effects for age, gender and education and a random effect for country, with random slopes for environment clustered by country: WF_{perf} ~ age + gender + education + (1 + environment/country). Figure 2a represents the environment slopes for each country; positive values indicate an advantage for participants who were raised outside cities (see Extended Data Fig. 1c for a world map). In terms of Hedge's g, this spectrum ranges from Romania (g = −0.03, 95% CI = [−0.10, 0.04]) to the USA (g = 0.19, 95% CI = [0.17, 0.21]). Extended Data Figure 4 illustrates this difference in effect size across age groups in different countries. For instance, although the effect size is close to being null in Germany, growing up in cities in the USA costs the equivalent of ageing five years in terms of spatial ability.

Association with SNE

To explain the variations in the association between environment and spatial ability across countries, we hypothesized that countries with lower effect sizes contain cities with more complex layouts; this places greater demands on navigation, and thus hones the navigational skills of individuals who grow up in them. The effect of city topology on human spatial ability has previously been theorized in the urban design literature[33,34], but empirical studies on street networks are limited in their scope, mostly owing to constraints in data availability, gathering and processing[35,36] (although see ref. [37], in which GPS trajectories produced by 14,380 pedestrians in Boston and San Francisco were analysed). To overcome these limitations, we coupled our global dataset with the OSMnx toolbox, which provides the street network layout for anywhere in the world through OpenStreetMap (OSM)[25,38]. Street network complexity is a manifold concept, and many metrics have been proposed to quantify it. Shannon's information entropy[39] is arguably the simplest and the most general measure of network complexity, from neural to spatial networks[40–43]. The entropy of a variable can be interpreted as the average level of uncertainty inherent in its possible outcomes. Here, we computed the Shannon entropy of the city's distribution of street orientations. The smaller the entropy, the less complex—that is, the more ordered—the city street network (see examples in Fig. 2b, Extended Data





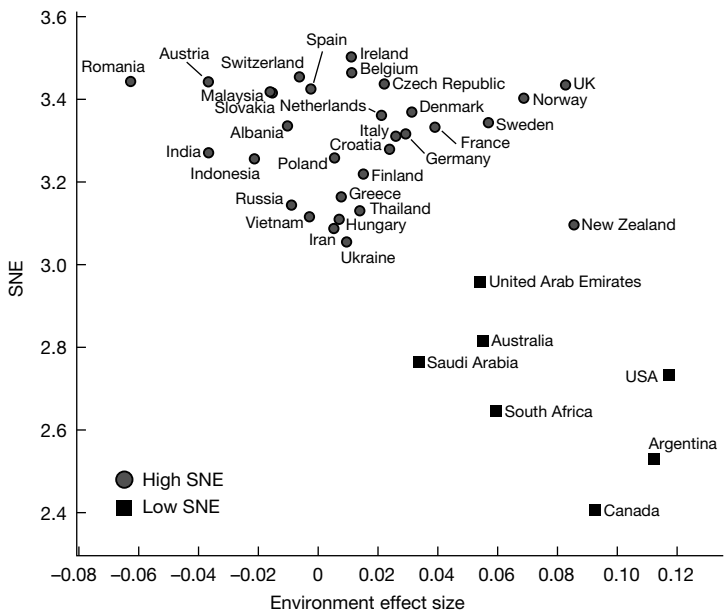


Fig. 2 | SNE and environment effect in 38 countries. a, Differences across countries. We fitted a LMM for wayfinding performance, with fixed effects for age, gender and education, and random environment slopes clustered by country (n = 397,162 participants). We plotted the environment effect sizes (country slopes) for each country, with positive values indicating an advantage for participants who were raised outside cities. See Extended Data Fig. 1c for a world map. Error bars, standard error. **b**, Left, two example cities with low (Chicago, USA) and high (Prague, Czech Republic) SNE. See also Extended Data Fig. 5). As SHQ participants only reported their home country, and not finer-grained regional information, we computed the SNE, defined as the average of the entropy of the 10 biggest cities of each country in terms of population, weighted by the city population (Supplementary Table 2). Thus, we had one SNE value per country. Figure 2b represents the SNE of countries as a function of their environment slope from the above mixed model. Most of the countries have a similar SNE, which corresponds to the typical organic street pattern of old city centres (for example, France, Romania and Spain, but also Thailand or India). However, some other countries have distinctly smaller SNE, which corresponds to the orthogonal grid—a very common planned street pattern (for example, the USA and Argentina). The bivariate correlation between a country's SNE and its environment slope is significant (Pearson's $r(36) = -0.60$, $P < 0.001$, 95% CI = [−0.78, −0.30]). This validates our hypothesis: the lower the SNE (that is, the simpler the street network), the worse the spatial ability of the people who grew up in cities compared to their compatriots who were raised outside cities. This effect remained when we controlled for gross domestic product (GDP) per capita (linear regression predicting environment slopes, GDP per capita $t(35) = 4.02$, $P < 0.001$, SNE $t(35) = -5.86$, $P < 0.001$; see Methods). We did not find a correlation between GDP per capita and SNE ($r(36) = 0.14$, $P = 0.40$; Extended Data Fig. 6a).

Fig. 5. Middle, distribution of the street bearings across 36 bins of 10°. Right, Average SNE as a function of the environment effect size (random environment slope) in each country. Positive values indicate an advantage of participants raised outside cities compared to their urban compatriots. The average SNE is the weighted average over the 10 most populated cities of the country, weighted by their population. Squares and circles correspond to the low-SNE and high-SNE country groups, determined with k-means.

Other street network complexity metrics

Although SNE captures the spatial organization of a city, metrics based on the graph theoretic network measure topological properties of the cities, which could also have a role in shaping navigation skill. Across our 380 cities we measured the betweenness, closeness and degree centrality, average circuity, average neighbourhood degree, clustering coefficient and average street length[43,44] (Methods). After applying the Bonferroni correction for multiple comparisons, we found that

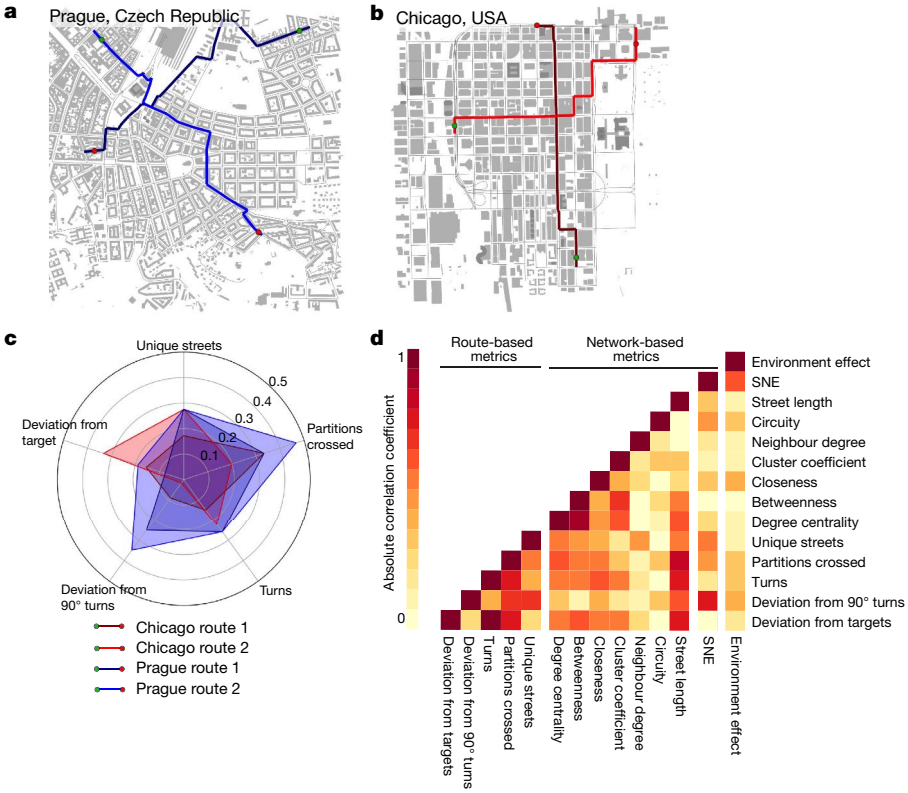


Fig. 3 | Comparison of SNE with other measures of city complexity. a, **b**, We simulated 1,000 routes in each of the 380 included cities. Four example representative routes in two contrasting cites with high (**a**; Prague, Czech Republic) and low (**b**; Chicago, USA) SNE are shown. **c**, We derived five key variables from each route: number of turns of greater than 50°; number of unique streets; deviation from regular 90° turns at each turn; overall deviation from the target; and number of transitions in the partitions in street network structure. The spider plot shows the route variables for these four routes. For a full visualization of the average of the 1,000 routes in the 380 included cities, see Extended Data Fig. 8. We also explored a range of other graph-theoretic measures that are commonly considered for spatial analysis of cities. **d**, Absolute correlation coefficient between all the metrics and the environment effect size. SNE is by far the metric most correlated to the environment effect size.

only circuity (network distance/Euclidean distance) was significantly correlated with SNE ($r(36) = 0.47$, $P = 0.02$), which is consistent with a previous study[43]. This indicates that less-regular city layouts are associated with paths across them that require more deviation around obstacles (Fig. 3).

We next sought to identify the mechanisms by which exposure to a high SNE would lead to a better navigation ability. We surmised that navigating cities with irregular street layouts would require increased demands on: (1) keeping track of the goal direction, owing to greater varying street angles; (2) spatial or prospective memory for street names and upcoming turns, owing to the human tendency to minimize the streets and turns in an irregularly laid-out city[45,46]; and (3) more hierarchical planning across neighbourhoods, owing to the larger number of neighbourhoods that might occur in irregular cities. Such demands would be likely to enhance the capacity of neural systems that underlie orientation, prospective memory and planning abilities[19,47]. To empirically determine whether the specific variables we propose are linked to SNE, we used agent-based modelling to simulate 1,000 routes through each of the 380 cities to quantify the number of turns, number of streets, deviation from a 90° turn, overall deviation from the target and number of crossed partitions in street network (Methods, Fig. 3). After applying the Bonferroni correction for multiple comparisons, we found that turns and the deviation from the goal were not significantly higher in high-SNE cities, indicating that these may not be key factors in enhancing navigation skill. Rather we found that SNE was significantly correlated with deviation from 90° turns ($r(36) = 0.77$, $P < 0.001$), number of streets ($r(36) = 0.57$, $P < 0.001$) and number of partitions crossed ($r(36) = 0.48$, $P = 0.007$). Thus, it appears that having to accommodate turns that deviate from 90° and having to navigate more streets and neighbourhoods are key to enhancing navigation skill. We incorporated all network and route measures into a linear model to predict the environment effect size, and did not find a significant equation ($F(10,25) = 1.44$, $P = 0.21$). On the other hand, when using SNE only as a predictor, a significant equation was found ($F(1,36) = 20.1$, $P < 0.001$; see Methods). This implies that it is the combination of navigational challenges that high-SNE cities provide that is important for enhancing the navigational skill of the inhabitants.

Association with game level topology

We next tested the symmetrical effect; that is, whether different SHQ level topologies interact with the effect of the participant's home environment. Here our hypothesis was that people growing up in environments with more complex topologies might perform better at more elaborate, entropic SHQ levels. Conversely, people growing up in regular cities might perform better at regular SHQ levels. We used *k*-means to split the countries into two SNE groups, revealing a low-SNE group and a high-SNE group (Fig. 2b). We defined the SHQ level entropy as we did for the cities, with the' distribution of orientations computed from the level's simplified Voronoi map (see Fig. 4a, Methods for details). To include in our analysis as many level topologies as possible, we ran the following analysis on a subset of included participants who completed all SHQ levels (75 levels, 9,439 participants). We fit two LMMs for wayfinding performance: one with the participants from low-SNE countries ($n = 2{,}021$) and the other with the participants from high-SNE countries ($n = 7{,}418$). Both models had fixed effects for age, gender and education, and a

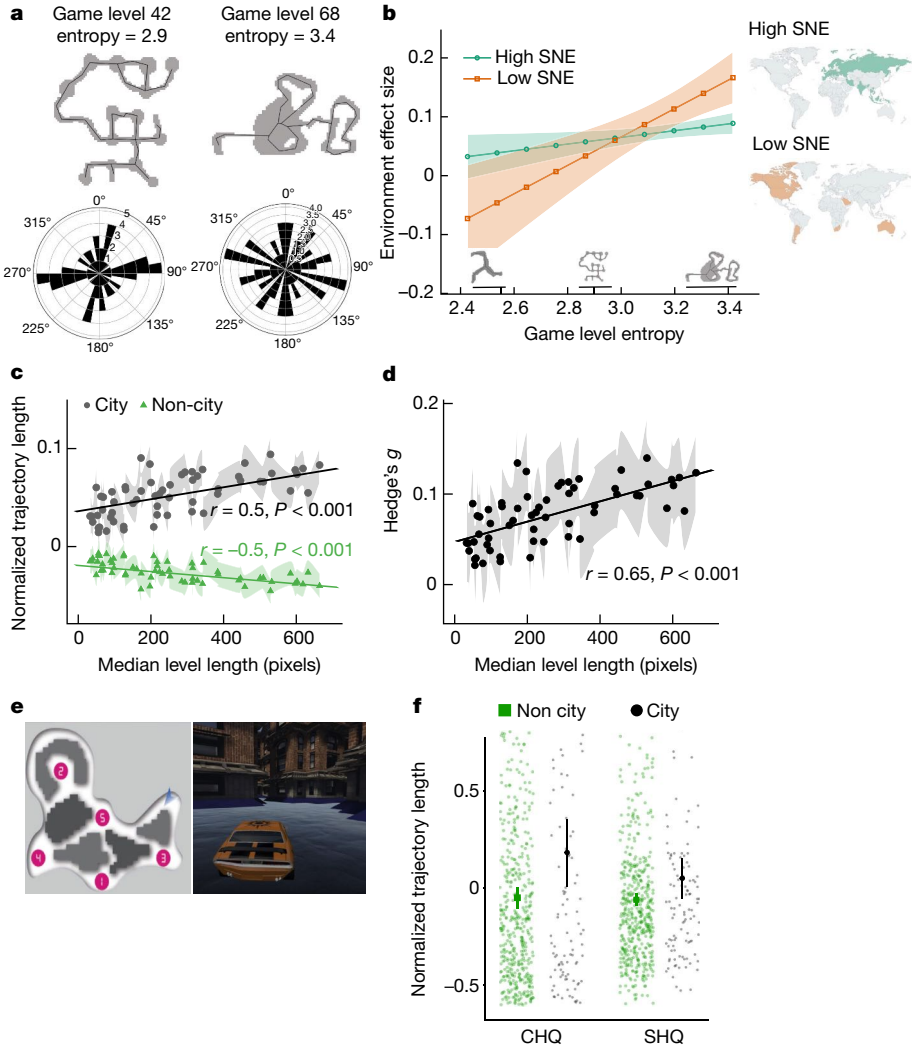


Fig. 4 | Participants are accurate at navigating more entropic game levels when they grew up in more entropic environments. a, The entropy of the SHQ levels is computed from the bearing distribution (rose plot), shown for two example levels. **b**, Least square regression lines of the environment effect size on game level entropy for the high-SNE and low-SNE country groups (see mini-maps and Fig. 2b). We included the players who played all of the SHQ wayfinding levels (n = 10,626 participants). Positive values indicate an advantage of participants raised outside cities. Low-SNE environment slopes are negative for low-entropy SHQ levels, suggesting that in less entropic SHQ levels, people who grew up in less entropic cities perform better than their compatriots who grew up outside cities. **c**, Normalized trajectory length as a function of the level length. Trajectory lengths have been z-scored for each level. The level length is estimated by the median length over all the players. **d**, For each level, the effect size of the environment on the normalized trajectory length as a function of the level length median. Positive Hedge's g values correspond to longer trajectories (that is, worse wayfinding performance) for city participants. **e**, Screenshots from CHQ, a city-themed version of SHQ. The map and image show one of the five levels tested. **f**, Association between environment and trajectory lengths in SHQ and CHQ (n = 599 participants). Centre values, mean. Error bars, 95% CI (all panels).

random effect for level, with random slopes for environment clustered by level: $WF_{perf} \approx$ age + gender + education + (1 + environment/level). We included all the wayfinding levels (n = 42). Figure 4b represents for each level its entropy as a function of the environment slope s_{low} computed from participants in the low-SNE countries, and s_{high} computed from the high-SNE countries. Positive values correspond to an advantage of participants growing up outside cities. We observed that the only negative environment slopes correspond to low-SNE participants in less entropic levels, suggesting that people used to less entropic environments perform better in less entropic SHQ levels. The correlation coefficient was higher between the entropy of the levels and the low-SNE environment slopes (Pearson's correlation $r_{low} = 0.57$, $P < 0.001$) than between the entropy of the levels and the high-SNE environment slopes (Pearson's correlation $r_{high} = 0.44$, $P = 0.003$). This correlation slope difference did not reach statistical significance (Fisher's $z = 0.77$, $P = 0.22$, 95% CI for $r_{high} - r_{low} = [-0.46, 0.20]$).

People living in city centres typically travel shorter distances than people living in suburbs or in more rural environments, as a result of the denser arrangement of local activity locations[48,49]. Thus, we hypothesized that participants from cities would have a better wayfinding performance at SHQ levels that require shorter trajectories. To test this hypothesis, we normalized the participants' trajectory lengths at each level (M = 0, s.d. = 1) and plotted them against the corresponding median game level length, taken over all the participants. The performance (inversely related to the normalized trajectory lengths) of city participants decreased with the median game level length, whereas it increased for non-city participants (Fig. 4c). There was a positive correlation between the effect size (Hedge's g) of the environment on normalized trajectory length and the median level length (Pearson's $r = 0.50$, $p < 0.001$; Fig. 4d). We computed a multiple linear regression with the environment effect size as the response variable and the level entropy and median trajectory length as the predictors. We found that

both entropy ($F_{1,39} = 5.20$, $P = 0.02$, $\eta^2 = 0.12$) and median trajectory length ($F_{1,39} = 13.71$, $P < 0.001$, $\eta^2 = 0.26$) were significant predictors of the environment effect size.

Replication with City Hero Quest

Although our virtual levels varied entropy from open waters to narrow inlets (Supplementary Video 1), the SHQ navigation task was simulated in rural settings (rivers and ocean terrain) and may potentially favour participants who reported growing up outside cities. To test this hypothesis and directly replicate the environment effect with an independent sample, we designed a city-themed version of SHQ called City Hero Quest (CHQ) and tested participants with it alongside SHQ. In CHQ, the players performed the same task as in SHQ, but driving a car in city streets (Fig. 4e, Supplementary Video 2. We collected data from new participants on five SHQ levels and five CHQ levels matched for entropy and difficulty to test whether our SHQ results transfer to a city context (Extended Data Fig. 6b–d). A total of 599 participants were recruited in the USA through the crowdsourcing platform Prolific. We chose to collect data from the USA as it was the most represented country in the Prolific participant pool, and a country with a high environment effect size in the initial SHQ dataset. Sample size justification and a full description of this new task are available in the Supplementary Methods. The same data analysis pipeline was applied to the SHQ and the CHQ data. As shown in Fig. 4f, the effect size of the environment on the normalized trajectory length is similar with SHQ data (Hedge's $g = 0.27$, 95% CI = [0.06, 0.47]) and CHQ data (Hedge's $g = 0.34$, 95% CI = [0.14, 0.54]), with positive values indicating an advantage (that is, shorter trajectories) for participants who grew up in non-city environments. The difference between the CHQ and the SHQ environment effect was not significant (Supplementary Information). This is also consistent with the effect size we found in the initial SHQ dataset when considering participants in the USA on the same levels (Hedge's $g = 0.30$, 95% CI = [0.18, 0.42]). Because participants also provided their current environment (city or non-city), we were able to show that the effect of the current environment on CHQ or SHQ performance did not reach significance (Supplementary Information). This suggests that the childhood period is key to predicting future spatial ability.

Conclusions

By investigating population-level cognitive performance in 38 countries, we show that people are better at navigating in environments that are topologically similar to where they grew up. We show that this association is independent of age, gender, video games skill and education. Participants who grew up in less entropic cities show better performance at less entropic game levels, whereas participants who grew up in more entropic cities are better at navigating more complex game levels. Similarly, participants who grew up in cities generally perform better in game levels in smaller spaces than they do in game levels in larger spaces, whereas participants who grew up outside cities are better in larger game levels than in game levels in smaller spaces. These results support the idea that humans develop navigation strategies that are aligned with the type of environment they are exposed to, which become suboptimal in other environments (Supplementary Discussion). Our findings indicate that the environment in which one grew up is associated with cognitive ability, and that this association is stable across the lifespan. Future research will need to consider how these differences emerge during childhood and adolescence, during which time abrupt changes in ability can occur[50].

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-022-04486-7.

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Methods

Informed consent and ethics approval

This study has been approved by the UCL Ethics Research Committee. The ethics project ID number is CPB/2013/015.

Participants were made aware of the purpose of the game within the opening screen. Demographics were provided by consenting participants in two steps. First, their age, gender and home country were asked. Then, after having played a few levels, participants were invited to provide further information such as their level of education and the type of environment in which they grew up. They were asked whether they were willing to share their data with us and were guided as to where they could opt out. The opt-out was always available in the settings.

Data

The design and the data collection process for SHQ have been thoroughly described previously[16].

Video game. In this study we focused on the wayfinding task. At the beginning of each wayfinding level, participants were shown locations (checkpoints) to visit on a map. The map disappeared, and they had to navigate a boat through a virtual environment to find the different checkpoints. Checkpoints were generally not encountered in the order of passage, but rather had to be navigated to by returning from one checkpoint to another (Fig. 1). Participants were encouraged to collect as many 'stars' as possible across the levels: the faster the more stars were obtained. The first two levels were tutorial levels to familiarize the participant with the game commands.

Participants. A total of 3,881,449 participants played at least one level of the game; 60.8% of the participants provided basic demographics (age, gender, home country) and 27.6% provided more detailed demographics (home environment, level of education). To provide a reliable estimate of spatial navigation ability, we examined data only from participants who had completed a minimum of 11 levels of the game (including the first 4 wayfinding levels: levels 6, 7, 8 and 11) and who entered all their demographics. We removed participants of over 70 years old because we previously showed a strong selection bias in this group that caused their performance to be substantially higher than would be expected in unselected participants of the same age[16]. We also removed participants from countries with fewer than 500 players, or with education or environment levels more than 10-fold imbalanced. This resulted in 397,162 participants from 38 countries being included in our analysis (Supplementary Table 1, Extended Data Fig. 1).

Demographic information. Among the included participants there were 212,143 male individuals (mean age: 37.81 ± 13.59 years old) and 185,173 female individuals (mean age: 38.67 ± 14.92 years old). The levels (n = sample size) of education were: university (n = 166,714), college (n = 111,463), high school (n = 107,849) and no formal (n = 11,290). We merged the university with the college levels owing to their ambiguous meaning in some countries, and the high school with the no formal level owing to the relatively low sample size of the latter. Hence, in our analysis the education variable had two levels: secondary and lower (n = 119,139) and tertiary (n = 278,177). The levels of home environment were: city (n = 109,111), suburbs (n = 131,738), mixed (n = 80,266) and rural (n = 76,047). We merged the mixed, suburb and rural levels together to facilitate the interpretation of the effect of growing-up in city (n = 109,111) and non-city (n = 288,051) environments. City environments are distinguished from other settings owing to the higher propensity for active, self-propelled travel (for example, walking, cycling) relative to passive, car - or public-transport-based travel[51], which results from the denser arrangement of local activity locations. We furthermore anticipate that where participants have stated growing up in a city environment there is a definitive and salient personal association with a city underlying this selection, whereas in other cases (for example, suburban, mixed) this association is less clear, and better described as non-city. Both factors are common across international settings. Indeed, the observed clear difference between the city group and the other three groups, but little dissociation between the other three groups supports this approach (Extended Data Fig. 7). To further validate this city–non-city dichotomy, we asked the participants in the CHQ follow-up experiment the street they lived on in their home environment, and computed the entropy of the street network (SNE) in a spatial window around it (see Supplementary Methods). We then compared the SNE of people who reported having grown up in a city (n = 114), suburb (n = 326), rural (n = 84) or mixed (n = 75) environment. As shown in Extended Data Fig. 9, the SNE in cities was significantly lower than the SNE in the other environments. We ran a one-way ANOVA with the reported home environment as independent variable and the SNE as dependent variable and found a significant effect of home environment ($F(1,3) = 25.72$, $P < 0.001$). Post-hoc pairwise t-test Bonferroni-corrected for multiple comparisons showed that the SNE of a city environment was significantly lower than the SNE of all the other environments (all $P < 0.001$). We found no significant difference in the SNE of mixed versus rural ($P = 1$), suburbs versus mixed ($P = 0.20$), and a small difference in the SNE of suburbs versus rural ($P = 0.02$).

For the analysis on the game level entropy, we included the participants that played all the SHQ wayfinding levels (n = 10,626). There were 5,219 male individuals (age: 41.89 ± 15.95 years old), 5,407 female individuals (age: 41.98 ± 16.32 years old), 7,429 with tertiary education, and 3,604 grew up in cities.

Behavioural data. We collected the trajectory of each participant across each level. The coordinates of participants' trajectories were sampled at Fs = 2 Hz. The geospatial analysis was performed with Python (versions 2 and 3), and the other analyses were done with MATLAB (R2018a).

Metrics

Geospatial analysis. We focused on the quantification of the structural complexity of larger cities instead of the complexity of areas outside cities. This is because city streets can be more strictly compared with one another. On the other hand, areas outside cities can be heterogeneous both within and between countries, which makes the country-level averaging of their parameters problematic.

SNE. We used the OSMnx Python toolbox (v.1.1.2) to download the street network topology of cities from OSM[25]. For each included city we created a street network graph from OSM data within a 1,000 ×v1,000-m^2 box around the city geographical centre. The use of a bounding box in the city centre is reflective of the wider city structure, and avoids issues related to classifications of regions, and administrative boundaries. This definition also has stronger persistence over time (considering city growth during the theoretical period of our analysis)[52]. To define the city geographical centres, we used the (latitude, longitude) coordinates provided by OSM. Then, we computed a 36-bin edge bearings distribution (1 bin every 10°), taking 1 value per street segment. We initially took twice as many bins as desired, then merged them in pairs to prevent bin-edge effects around common values like 0° and 90°. We also moved the last bin to the front, so, for example, 0.01° and 359.99° were binned together. We calculated the Shannon entropy of the city's distribution of orientations:

$$H = -\sum_{i=1}^{36} P(o_i)\log(P(o_i)), \quad (1)$$

where i indexes the bins, and $P(o_i)$ represents the proportion of orientations that fall in the ith bin[43]. For each of the 38 countries included in our analysis, we defined the average SNE as

$$\mathrm{SNE} = \frac{1}{\sum_i \alpha_i} \sum_{i=1}^{10} \alpha_i H_i, \quad (2)$$

where $(H_i)_{i\in[1.10]}$ are the Shannon entropies of the 10 biggest cities in terms of population, and α_i is the population of the ith city (see Supplementary Table 1).

As OSM mapping relies on contributions from volunteers, we considered that this could introduce a bias, with some countries being more densely mapped than others. So we compared these SNE values to the ones based on the city centre (latitude, longitude) coordinates provided by Google Maps. We computed SNE values both from the network of drivable public streets ('drive') and from the network of all non-private streets and paths ('all'). The 'drive' network is a more reliable and consistent source of long-term street network data, given that it represents the major established roads in each city. The 'all' network, by in addition covering pathways and pedestrian zones, is more susceptible to between-country variation in volunteer mapping practices and recent planning initiatives. We found little variation (Extended Data Fig. 10c). We also varied the size of the street network box around the city centres. If the bounding box were too big it could go beyond the city boundaries (especially for smaller cities), but if too small it might not be representative of the whole city. We computed SNE values for boxes of 500 × 500, 1,000 × 1,000, 2,000 × 2,000 and 5,000 × 5,000 m^2. Again, our results remained stable across the different sizes (Extended Data Fig. 10c).

Graph-theoretic metrics. Graph-based measures are calculated on the 'primal' representation of the road network for each study area, in which junctions are represented by nodes and roads as edges. This representation is typical in the calculation of road-network-based graph metrics. The metrics selected were chosen on the basis of their widespread use in describing street networks, and full description of their implementation can be found in a previous report[25].

Circuity. This measures the of the sum length of all edges divided by the sum of Euclidean distances between nodes. Thus, it captures the extent of deviation that is required from the most direct route when moving between two points on a network[53].

Mean cluster coefficient. This measure records the ratio of number of connections with neighbours over the total of number of possible connections, taken as a mean for all nodes. As such, it captures the degree close to which there is high interconnectivity between nodes in a network[54].

Mean closeness centrality. Closeness represents how close a node is to all other nodes within a network. It has been demonstrated to align closely with locations of activities[55] and correlated with activity in the anterior hippocampus when navigating[56]. The mean value for all nodes is taken.

Mean betweenness centrality. Betweenness centrality measures the extent to which a node features on shortest paths between all node pairs. Again, we use the mean value for the network, which indicates the extent to which flows of people may be spread or concentrated across the network[40].

Mean degree centrality. This measure records the fraction of nodes that each node is connected to, taken as a mean for all nodes in the network. It reflects the extent of connectivity between nodes on a network[57], is suitable for analysis interconnectivity in small areas and is correlated with posterior hippocampal activity during navigation[56].

Mean neighbour degree. This measures for each node the mean degree of all neighbouring nodes, and reflects the degree of local node connectivity.

Mean street length. This measures the mean length of street segments, and thus is an indicator of block length. This provides a measure of the density of the street network.

Route-based metrics from agent-based simulations. All routes were calculated based on a 'dual' representation of the road network, whereby road segments are modelled as vertices and costs between vertices (for example, distance, angular change) are modelled as network edges. The Djikstra algorithm was used for identifying the optimal paths, with road length used as the optimization measure. For each city, 1,000 routes were generated for 2 randomly selected origin and destination nodes (road segment centre points). For each path, the following measures were extracted.

Unique streets. Sum of the unique street names provided by OSM that are encountered along the route.

Partitions crossed. Sum of unique partitions encountered during the route. The road network was partitioned using the Louvain community detection algorithm on the dual graph, setting edge cost as angular change. These partitions have been used a proxy for deriving perceived neighbourhood boundaries[58], and have demonstrated consistency with well-known regions, such as Soho and Mayfair in London (Extended Data Fig. 5).

Snapped angular change. Angular deviations are calculated as the angle of incidence between two adjacent road segments, on the basis of the connecting straight-line segments on each road polyline. The sum of absolute angular change between two consecutive road segments along a route from 0° or 90° (whichever is closer). We examined this measure because past work has shown that spatial memory for target locations is better after 90° or 180° rotations than other angular changes[59]. Memory for the angle of turns is biased towards right angles[60]. This suggests that it is easier to develop precise memories for low-SNE cities than for high-SNE cities. High-SNE cities would then require more training and learning, thus training navigation abilities.

Turns. Sum of turns between two consecutive segments surpassing 50° in either direction, with more turns being indicative of higher perceived cognitive distance[61]. We computed the same metric with 60°, and the results remained stable.

Angular deviation from target. The sum of the angular deviation from the destination, recorded at each road segment. Specifically, this is recorded as the sum of differences between the angular change between two consecutive segments and the angular direction of the target from the first segment. During navigation angular deviation from the target positively correlates with activity in the posterior parietal lobe[62–64]. The posterior parietal lobe is a core part of the brain regions needed for effective navigation of familiar places[47].

Video game analysis. Wayfinding performance. As in a previous study[16], we computed the trajectory length in pixels, defined as the sum of the Euclidean distance between the points of the trajectory. To control for familiarity with technology, we normalized the trajectory lengths by dividing them by the sum of their values at the first two levels. The first two levels only reflected video gaming skill (motor dexterity with the game controls) as no sense of direction was required to complete them. We defined an overall wayfinding performance metric corrected for video gaming skill (WF) as the first component of a principal component analysis across the normalized trajectory lengths of the first four wayfinding levels (levels 6, 7, 8 and 11; 60.5% of variance explained). As this metric is based on the trajectory length, it varies as the opposite of the performance: the longer the trajectory length, the worse the performance. We took the additive inverse of the metric and added an offset, so that WF = 0 corresponds to the worst performances. The Pearson's correlation coefficient between WF and the sum of the trajectory lengths of the first two levels (video gaming skills) is weak: $r = 0.10$, $P < 0.001$, bootstrapped 95% CI = [0.09, 0.10]. The implementation of WF is available in the code presented in the 'Code availability' section.

Game level entropy. We calculated the Shannon entropy of the SHQ level's distribution of orientations in a similar manner to that used for the cities. To create the equivalent of 'streets' in the levels of the

game, we computed the Voronoi regions from the layout of the game level, and took their edges. The boundaries of the Voronoi regions are considered equivalent to road centre lines in the city context. We then used the Douglas–Peucker algorithm to simplify the line made of the connected segments[65] (Fig. 4a). For all game levels, we used a maximum offset tolerance between the original and the simplified line of three pixels. The entropy of the orientation distribution of the game level's segments was then computed with equation (1).

Statistical analysis

Further details are available in the Supplementary Information.

LMM computation. The parameters of the linear mixed models were estimated with the maximum likelihood method, and the covariance matrix of the random effects were estimated with the Cholesky parameterization.

Low-SNE and high-SNE country clustering. We partitioned the 38 countries into two clusters on the basis of their SNE with the *k*-means algorithm. We used the squared Euclidean distance metric. We ran the algorithm 1,000 times and the arrangement never changed. The first group (low SNE) comprised Australia, Canada, South Africa, Saudi Arabia, the United Arab Emirates, the USA and Argentina, with mean SNE = 2.69, s.d. = 0.18. The second group (high SNE) comprised all the other countries, with mean SNE = 3.30, s.d. = 0.13.

Hedge's *g*. Hedge's *g* between group 1 and group 2 is defined as

$$g = \frac{(m_1 - m_2)}{s^*_{\text{pooled}}},$$

where m_i is the mean of group i, and s^*_{pooled} is the pooled and weighted standard deviation:

$$s^*_{\text{pooled}} = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2)}{n_1 + n_2 - 2}}$$

with n_i the sample size of group i, and s_i the standard deviation of group i.

The 95% confidence intervals displayed in this manuscript are exact analytical confidence intervals based on iterative determination of noncentrality parameters of noncentral t or F distributions[66].

Confidence intervals for Pearson's correlation coefficient. To estimate the uncertainty around Pearson's correlation coefficient, we computed its percentile bootstrapped 95% CI. At each iteration, we resampled pairs of observations with replacement and computed their correlation values. We iterated this process 1,000 times. We then sorted the correlation values and took the 2.5 and 97.5 percentiles obtained to yield a 95% CI. We illustrate this process for the correlation between SNE and environment effect size in Extended Data Fig. 10.

Linear regression predicting environment effect sizes (country slopes) based on SNE and GDP per capita. A multiple regression was calculated to predict the environment slopes based on SNE and GDP per capita. A significant equation was found ($F(2,35) = 22.40$, $P < 0.001$) with $R^2 = 0.56$: environment slopes = $0.28 + 8.5 \times 10^{-7}$(GDP) − 0.09(SNE). Both SNE ($t(35) = -5.86$, $P < 0.001$) and GDP per capita ($t(35) = 4.01$, $P < 0.001$) were significant predictors of environment slopes.

Modelling the environment effect with SNE versus all the other metrics. Two linear regressions were calculated to predict the environment slopes based on the following.

(1) SNE only (model 'SNE only'): environment slope ≈ SNE. We found a significant equation ($F(1, 36) = 20.1$, $P < 0.001$), adjusted $R^2 = 0.341$, Bayesian information criterion (BIC) = −142.11.

(2) All of the other metrics (model 'other metrics'): environment slope ≈ unique streets + turns + partitions crossed + deviation from 90° turns + deviation from targets + street length + neighbour degree + circuity + clustering coefficient + closeness centrality + betweenness centrality + degree centrality. We did not find a significant equation ($F(10, 25) = 1.44$, $P = 0.21$), adjusted $R^2 = 0.125$, BIC = −105.18.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

A dataset with the preprocessed trajectory lengths and demographic information is available at https://osf.io/7nqw6/?view_only=6af022f2a7064d4d8a7e586913a1f157. Owing to its considerable size (around 1 terabyte), the dataset with the full trajectories is available on a dedicated server: https://shqdata.z6.web.core.windows.net/. We also set up a portal where researchers can invite a targeted group of participants to play SHQ and generate data about their spatial navigation capabilities. Those invited to play the game will be sent a unique participant key, generated by the SHQ system according to the criteria and requirements of a specific project. https://seaheroquest.alzheimersresearchuk.org/ Access to the portal will be granted for non-commercial purposes. Future publications based on this dataset should add 'Sea Hero Quest Project' as a co-author.

Code availability

The Python and MATLAB (R2018a) code that allows the presented analyses to be reproduced is available along the preprocessed trajectory lengths and demographic information at https://osf.io/7nqw6/?view_only=6af022f2a7064d4d8a7e586913a1f157.

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Author contributions H.J.S., M.H. and A.C. supervised the project. H.J.S., M.H., A.C., S.G., C.G., R.C.D., J.M.W. and C.H. designed the research. A.C., E.M., G.F. and D.Y. analysed data. A.C., E.M. and H.J.S. wrote the paper.

Competing interests The authors declare no competing interests.

Additional information

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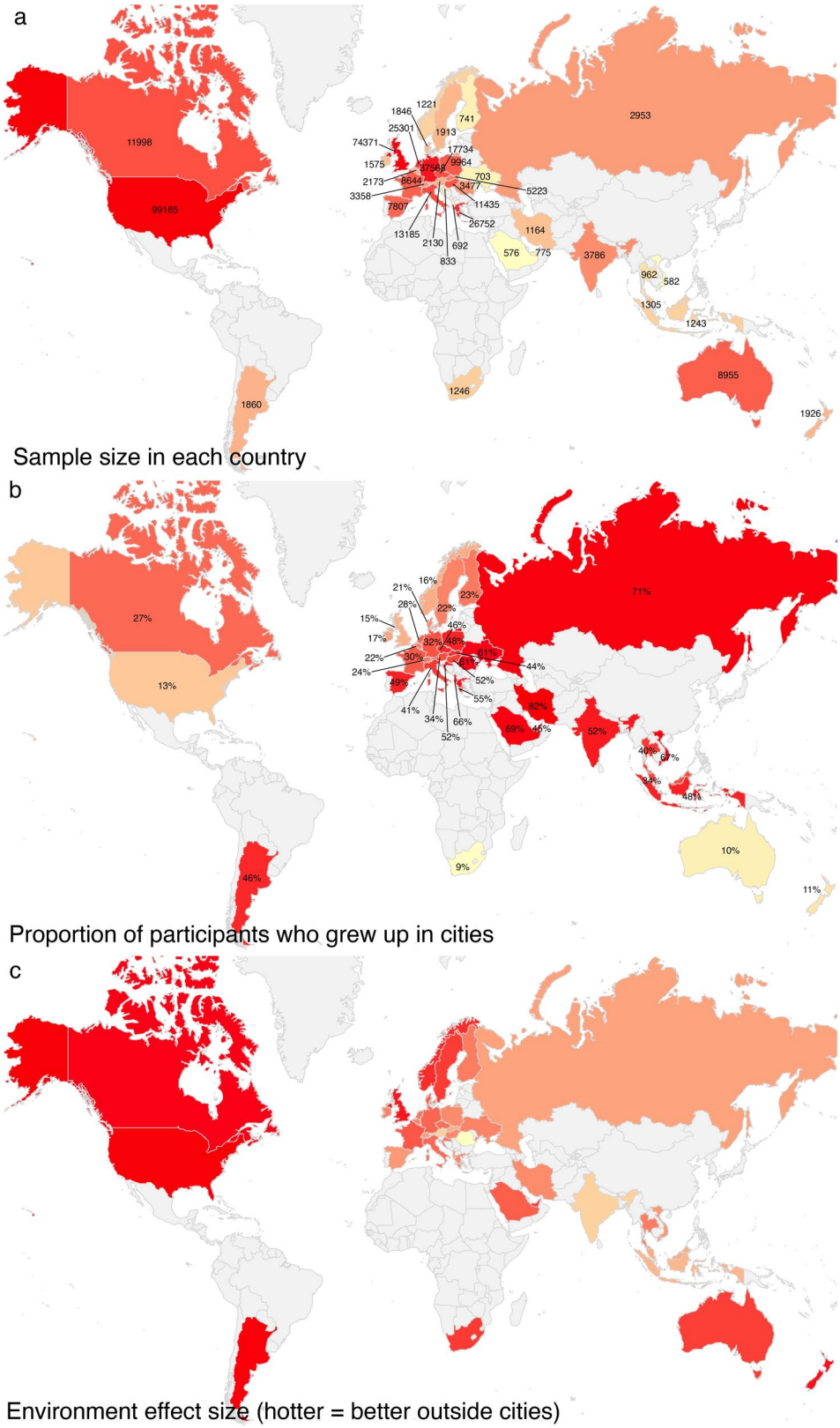
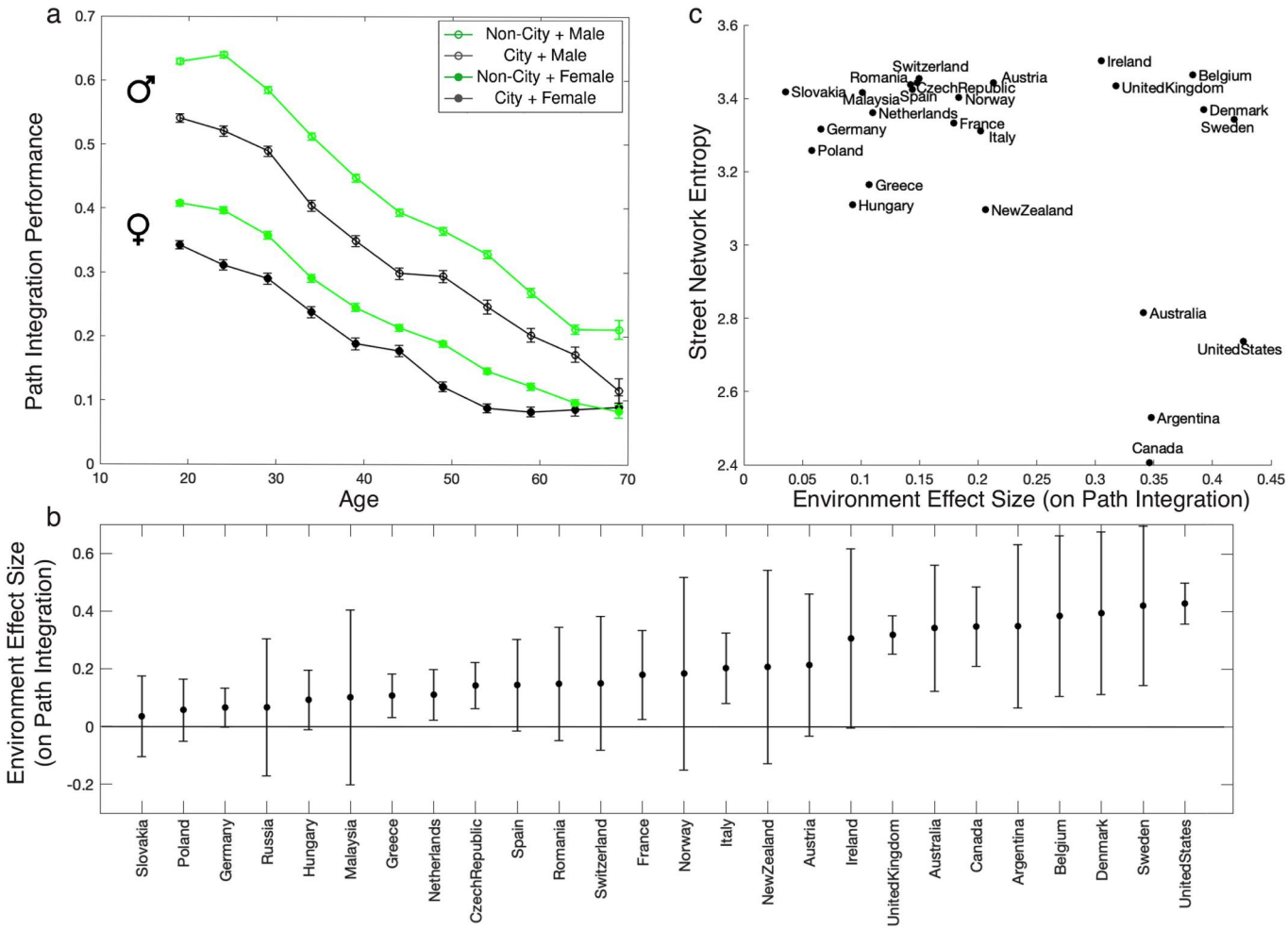
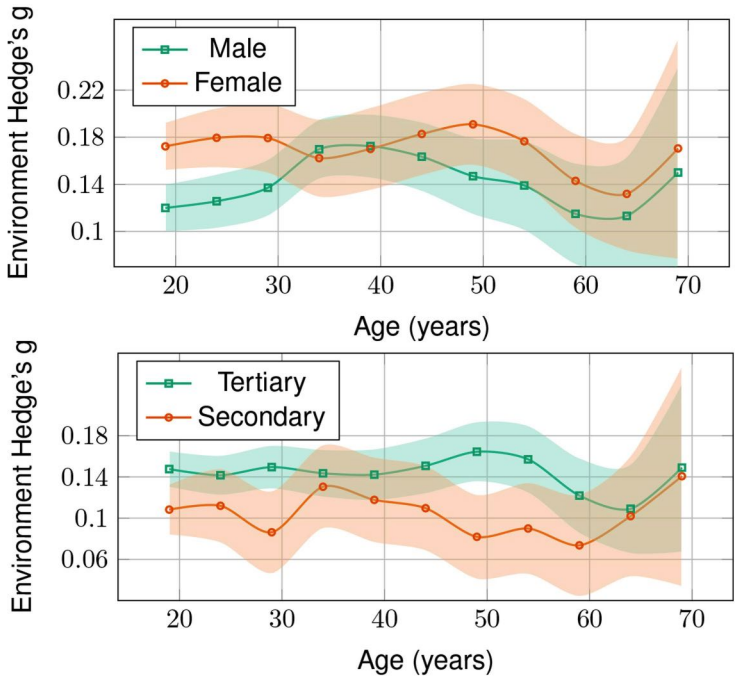


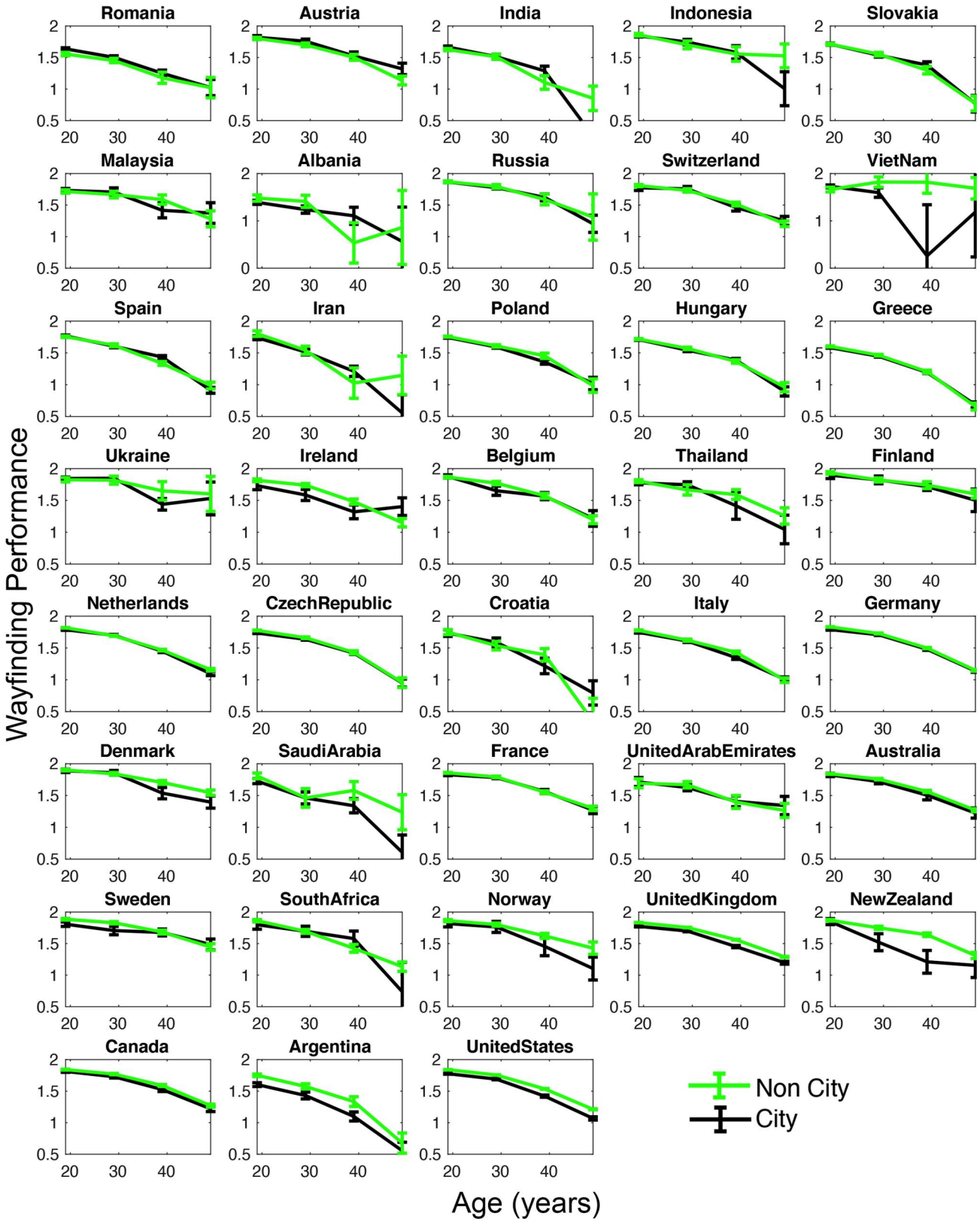
Extended Data Fig. 1 | Colour-coded world maps. a, Sample size. **b**, Proportion of city participants. **c**, Environment effect size computed from a LMM predicting wayfinding performance, with fixed effects for age, gender and education, and random environment slopes clustered by country. The environment effect sizes are the environment slopes clustered by country, identical to the values in Fig. 2a.



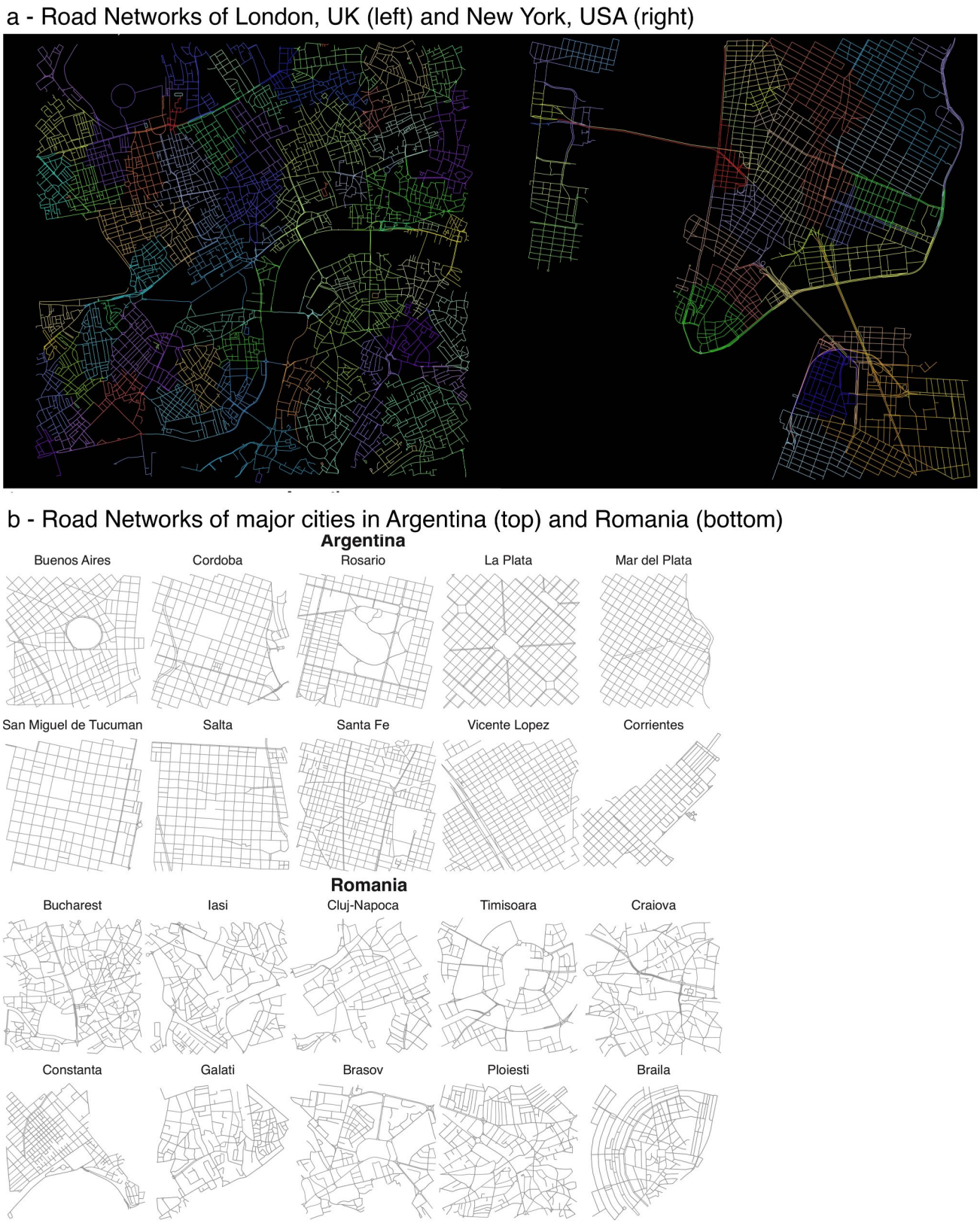
Extended Data Fig. 2 | Association between age, home environment, country and path integration performance. a, Path integration performance as a function of age for male and female participants who grew up in city and non-city environments. Path integration performance is averaged within 5-year windows, centre values correspond to the means. **b**, Difference of the effect of growing up outside cities on path integration performance across countries. We fit a logistic mixed model for path integration performance, with fixed effects for age, gender and education, and random environment slopes clustered by country, see Supplementary Methods. Positive values indicate an advantage for participants raised outside cities. **c**, SNE as a function of the environment effect size (random environment slope) in each country, as in Fig. 2b, see Supplementary Methods. All error bars correspond to standard errors, $n = 182{,}122$ participants.



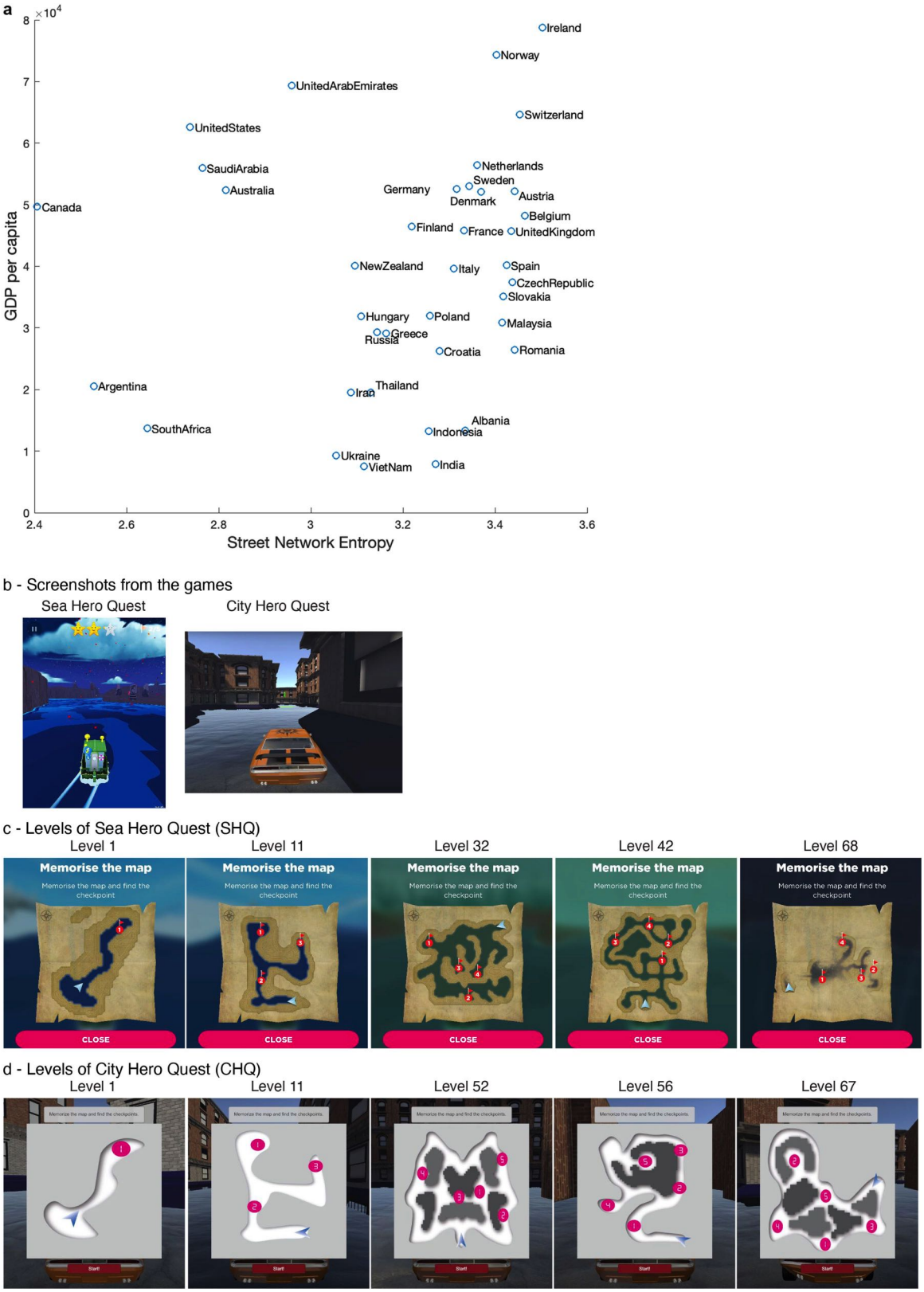
Extended Data Fig. 3 | Environment effect size across age, gender and level of education. Effect size is quantified with Hedge's *g*, within five-year windows. Positive values correspond to an advantage for participants who grew-up outside cities. Error bars correspond to 95% CI and the centre values correspond to the means.



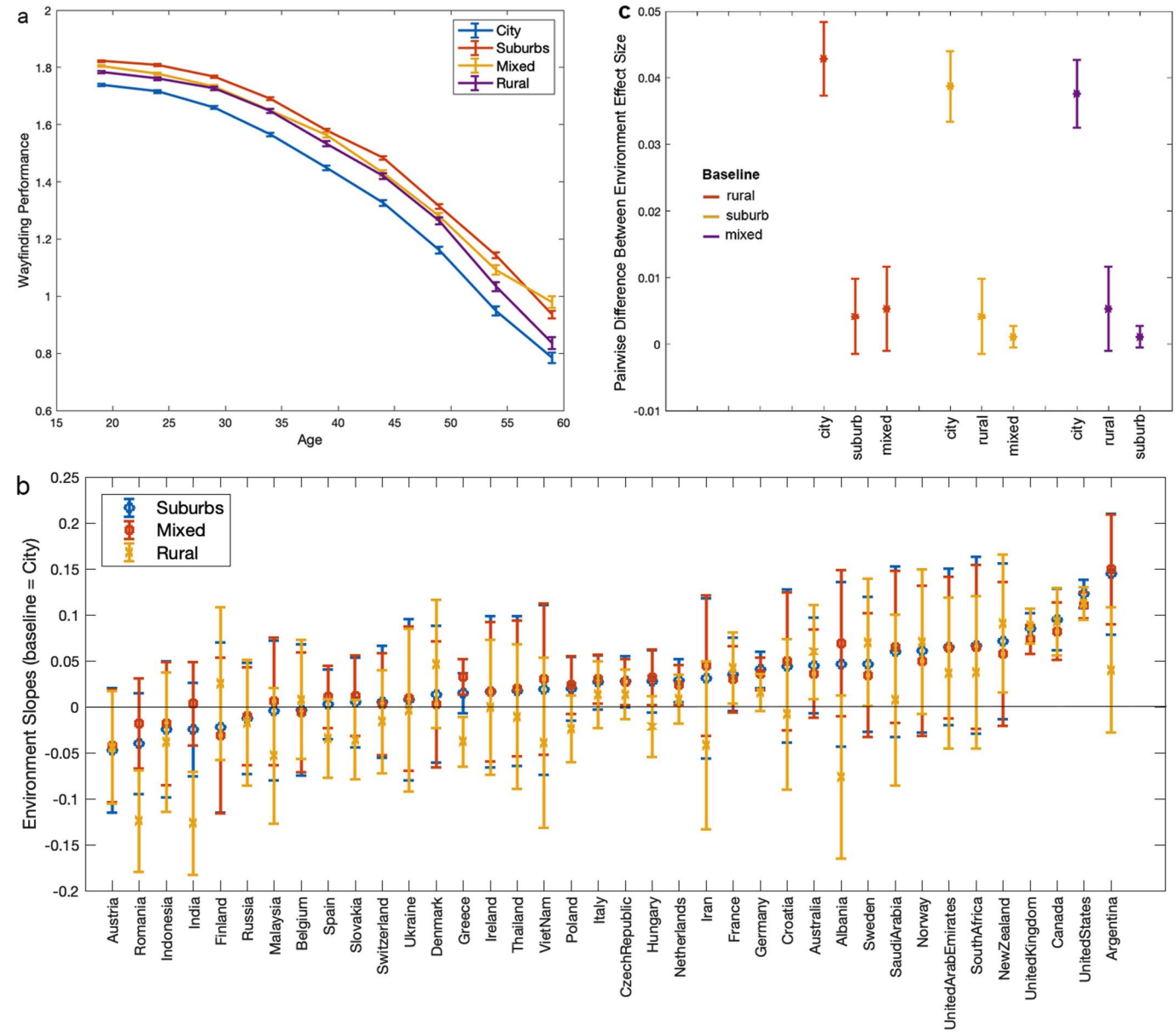
Extended Data Fig. 4 | Wayfinding performance in city and non-city environments across age, in each country. Wayfinding performance is averaged within 10-year windows. Error bars correspond to standard errors and centre values correspond to the means. Note that these values correspond to raw wayfinding performance; that is, they have not been corrected for age, gender or education. Note: Vietnam and Albania *y* axis lower bound is 0 to allow display of data points, instead of 0.5 for the rest of the countries. Altogether, we included $n = 397{,}162$ participants.



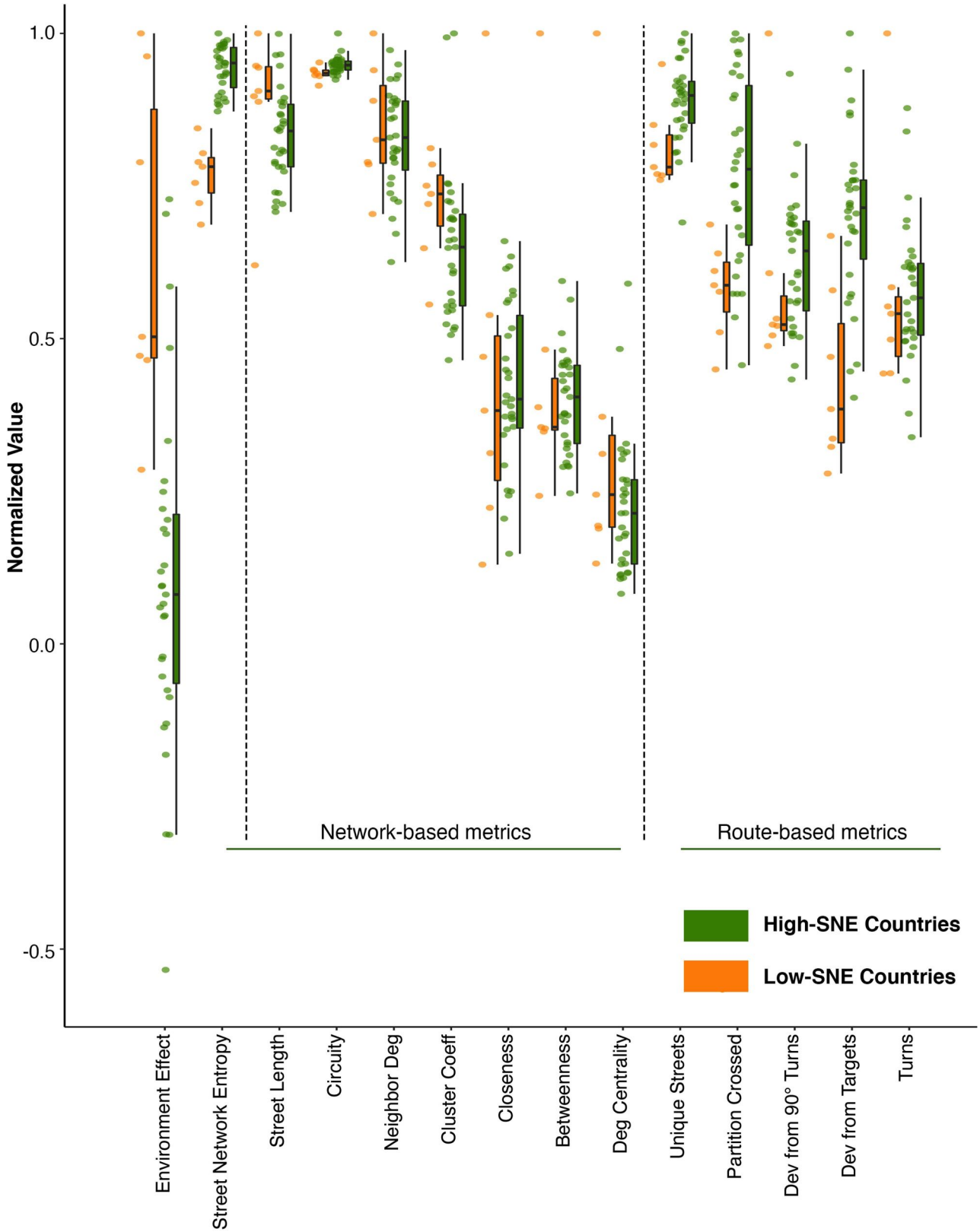
Extended Data Fig. 5 | Examples of city street networks. a, The road networks of New York City (USA, right) and London (UK, left) have been partitioned using the Louvain community detection algorithm on the dual graph, setting edge cost as angular change. The road networks within a 3×3 km^2 box around the city centres are represented. **b**, Street network of the 10 biggest cities in terms of population in Argentina and in Romania. We used OSMnx to gather the "drive" OSM network within $1{,}000 \times 1{,}000$-m^2 boxes around each city centre. The reasons behind these differences are mostly historical. In South America, grid city design is characteristic of Hispanic American colonization, while disorganized street networks correspond to the typical organic street pattern of old European city cores.



Extended Data Fig. 6 | Association between GDP per capita and SNE in City Hero Quest, a city-themed version of Sea Hero Quest. a, GDP per capita as a function of SNE. **b**, Screenshot from SHQ (left) and CHQ (right). **c**, Subset of SHQ levels used in the second experiment run on Prolific. **d**, CHQ levels used in the second experiment.

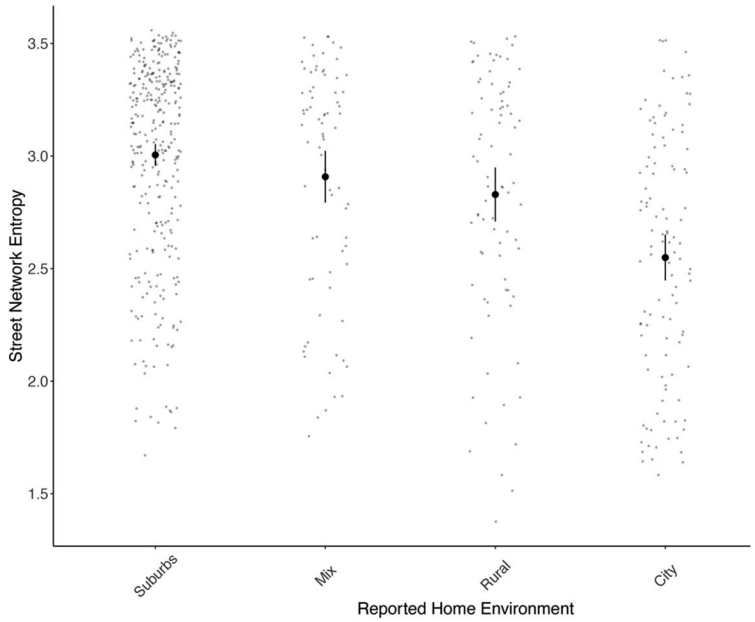


Extended Data Fig. 7 | Association between age, home environment, country and wayfinding performance. a, Wayfinding performance as a function of age for participants who grew up in city, suburb, mixed and rural environments. Data points correspond to the wayfinding performance averaged within 5-year windows. **b**, Difference in the effect of growing up outside cities on wayfinding performance across countries. We fit a linear mixed model for wayfinding performance, with fixed effects for age, gender and education, and random environment slopes clustered by country, as in Fig. 2a. Suburbs, mixed and rural environment slopes are represented, with City environment as baseline. Positive values correspond to an advantage compared to growing up in cities. Countries are ranked according to their suburb slope. The slopes of the different non-city environments are highly correlated: Pearson's r(suburb, mixed) = 0.97, $p < 0.001$, r(suburb, rural) = 0.72, $p < 0.001$, r(mixed, rural) = 0.53, $p < 0.001$. The country ranking is very similar to the one with only 2 classes (city / non-city): Spearman's r(non-city, suburb) = 0.85, $p < 0.001$, r(non-city, mixed) = 0.73, $p < 0.001$, r(non-city, rural) = 0.94, $p < 0.001$. *P* values are from a t-test testing the hypothesis of no correlation against the alternative hypothesis of a nonzero correlation. **c**, Pairwise differences between random environment slopes shown in panel b, averaged over countries. We show that the average difference in effect size between the city environment and the other 3 environments (city-rural, city-mixed, city-suburb) are around 10 times larger than the difference between the 'non-city' environments (rural-mixed, mixed-suburb, rural-suburb). This supports the approach to cluster together rural, mixed and suburb environments. All error bars correspond to standard errors, $n = 397{,}162$ participants.

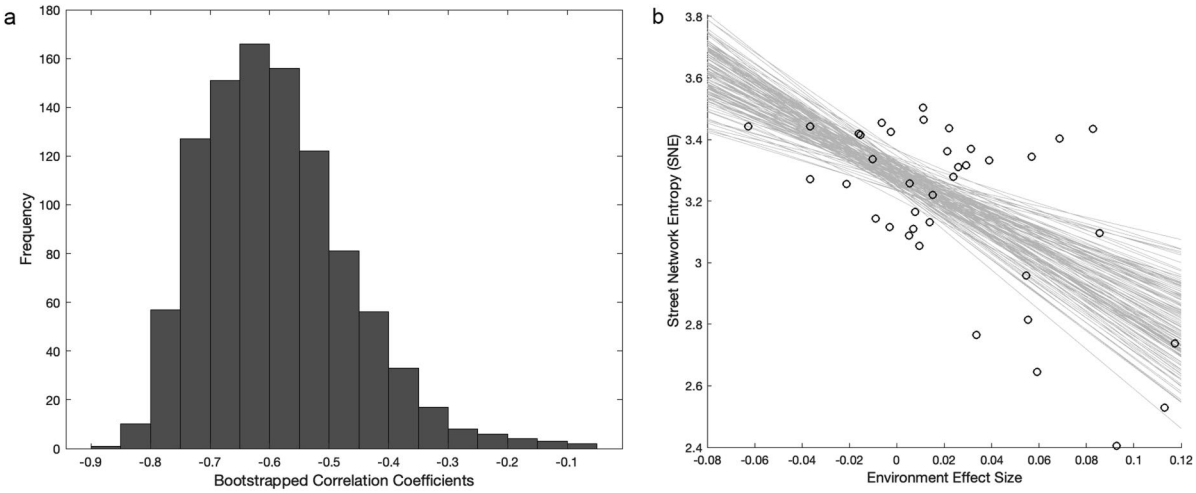


Extended Data Fig. 8 | See next page for caption.

Extended Data Fig. 8 | Environment effect size and city complexity measures in high-SNE and low-SNE countries. In each of the 380 included cities we computed a range of metrics to quantify different aspects of its complexity. We then took an average of these metrics weighted by the city population to have one value per country. We normalized these values by dividing them by their maximum. Network-based metrics - On top of the SNE used in this study, we computed other graph-theoretic measures commonly considered for spatial analysis of cities: average street length, circuity, neighbourhood degree, clustering coefficient, closeness centrality, betweenness centrality, and degree centrality. Route-based metrics - we simulated 1,000 routes in each city, and quantified five key variables derived from each route: number of unique streets, number of transitions in the partitions in street network structure, deviation from regular 90° turns at each turn, overall deviation from the target and number of turns above 50°. Individual data points correspond to countries ($n = 38$). In the box plots, the horizontal bar represents the sample median, the hinges represent the first and third quartiles, and the whiskers extend from the hinges to the largest/lowest value no further than ±1.5 × IQR from the hinge (where IQR is the inter-quartile range).



Extended Data Fig. 9 | SNE across reported home environments. SNE computed at the home addresses of the 599 participants to the follow-up experiment CHQ as a function of the reported type of home environment. The size of the square boxes used to compute the SNE were adjusted for the average street density within each reported environment (see Supplementary Methods). Error bars correspond to standard errors and centre values correspond to the means.



c

	City centre	Bounding box size (m)	Type of street network	correlation
SNE1	GM	500	drive	r=-0.60, $p < 0.001$
SNE2	GM	500	all	r=-0.52, $p = 0.001$
SNE3	**OSM**	**1000**	**drive**	r=-0.60, $p = 0.001$
SNE4	OSM	1000	all	r=-0.57, $p = 0.001$
SNE5	GM	1000	drive	r=-0.64, $p = 0.001$
SNE6	GM	1000	all	r=-0.58, $p = 0.001$
SNE7	GM	2000	drive	r=-0.58, $p = 0.001$
SNE8	GM	2000	all	r=-0.53, $p = 0.001$
SNE9	GM	5000	drive	r=-0.54, $p < 0.001$
SNE10	GM	5000	all	r=-0.50, $p = 0.001$

Extended Data Fig. 10 | Estimation of the robustness of the Pearson's correlation between SNE and environment effect size. Bootstrapped correlation coefficients computed from 1,000 resampling with replacement. **a**, Histogram of the computed correlation coefficients. We obtained $r = -0.60$, 95% CI = [−0.78 −0.30]. **b**, Regression lines for each sample. **c**, Pearson's correlation between environment effect size and different SNE calculations. The SNE set in bold is the one used in this manuscript. OSM = OpenStreetMaps, GM = Google Maps. *P* values are from a t-test testing the hypothesis of no correlation against the alternative hypothesis of a nonzero correlation.

nature research

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Reporting Summary

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Sea Hero Quest - The data was collected via Sea Hero Quest, a video game using Unity 3D (Unity Technologies, Copenhagen Denmark) for smart phones and tablets (apple and android devices). 'Sea Hero Quest' (SHQ) was released on 4 May 2016 on the App Store for iOS and on Google Play for Androids. If the participant agreed, their data were anonymously stored in a secure T-Systems server in Germany. The application was managed by T-Systems' scalable Docker offering called 'AppAgile' which is operated out of T-Systems' datacenter to ensure data integrity and data privacy according to German data security law. City Hero Quest - City Hero Quest is a desktop virtual reality game designed to parallel Sea Hero Quest within an urban setting. The game was built in Unity 3D physics games engine (https://unity.com/) with all virtual structures modeled in Blender 3D modeling software (www.blender.org). To control the back end and log experimental variables, we used Unity Experimental Framework (UXF), an open source set of packages for Unity 3D designed for human behavioral research. Participants were recruited in the United States via the crowdsourcing platform Prolific. After providing their informed consent and an initial screening, participants were redirected to a Gorilla webpage. Gorilla is a cloud based research platform supporting behavioral experiments online. Participants completed a demographic questionnaire, and were given instructions to first install Sea Hero Quest on their mobile, and then install City Hero Quest on their personal computer. After completing both tasks, participants emailed us their data along with their unique identifying number.
Data analysis	Data was analyzed with Matlab (R2018a) and Python (2 and 3) scripts. Street networks have been gathered with the OSMnx (1.1.2) Python toolbox. The code allowing to reproduce the presented analyses is available at https://osf.io/7nqw6/?view_only=6af022f2a7064d4d8a7e586913a1f157.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

A dataset with the preprocessed trajectory lengths and demographic information is available at https://osf.io/7nqw6/?view_only=6af022f2a7064d4d8a7e586913a1f157
Due to its considerable size (~ 1 To), the dataset with the full trajectories is available on a dedicated server: https://shqdata.z6.web.core.windows.net/.
We also set up a portal where researchers can invite a targeted group of participants to play Sea Hero Quest and generate data about their spatial navigation capabilities. Those invited to play the game will be sent a unique participant key, generated by the Sea Hero Quest system according to the criteria and requirements of a specific project. https://seaheroquest.alzheimersresearchuk.org/
Access to the portal will be granted for non commercial purposes.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☒ Behavioural & social sciences ☐ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description

This is a quantitative study about how people navigate. Participants were asked to play Sea Hero Quest, a spatial navigation video game, and to enter some demographic information about themselves. We also ran a follow-up study with a smaller number of participants playing City Hero Quest, a city-themed version of Sea Hero Quest.

Research sample

Sea Hero Quest - We aimed at collecting as many participants as possible with diverse profiles. A total of 3,881,449 participants played at least one level of the Sea Hero Quest. 397,162 participants from 38 countries were included in our analysis (see Data exclusions section) Among the included participants there were 212,143 males (mean age: 37.81 ± 13.59 years old) and 185,173 females (mean age: 38.67 ± 14.92 years old). The levels (N = sample size) of education were: secondary and lower (N=119,139) and tertiary (N=278,177). The levels of home environment were: city (N=109,111) and non-city (N=288,051). This sample is one of the largest in human behavior quantitative research, other sample sizes in the literature being typically 100 times smaller.

City Hero Quest - Participants were recruited in the United States via the crowdsourcing platform Prolific. We chose to collect data from the US as it was the most represented country in the Prolific participant pool, and was one of the countries with the highest environment effect size in our initial SHQ dataset. We collected complete data from 599 participants with a city/non-city ratio of 0.19 (114 city dwellers). There were 299 males and 300 females, the mean age was 27.0 years (SD=8.1 years). City dwellers grew up in 65 different cities across the US.

Sampling strategy

Sea Hero Quest - The aim of this study was to collect a global dataset of how people navigate. Thus, we collected as many participants as possible with demographic profiles as diverse as possible.

City Hero Quest - To determine the sample size, we computed a power analysis based on the effect size of the home environment obtained in the initial SHQ dataset. Since we planned to test participants in the US, we used an effect size Hedge's g = 0.20 (in the initial dataset, g = 0.19, 95%CI=[0.17, 0.21]). We also took into account the imbalance between city and non-city participants. In the initial dataset in the US we had 12,931 city and 86,254 non-city participants, so a ratio of 0.13. Here we decided to use a ratio of 0.20 to increase the statistical power. The required sample size to detect an effect size of g = 0.20 with 2 imbalanced groups (20% - 80%) with 80% statistical power is N1=200, N2=800 (pwr R package, based on (Cohen 1988) Because testing 1000 participants on Prolific is time consuming due to the screening and technical assistance required, we performed a sequential analysis while the data collection was in progress. Sequential analyses make it possible to perform high-powered informative experiments while sparing human and economic resources. They are widely used in large-scale medical trials. At an interim analysis, data collection can be stopped whenever the results are convincing enough to conclude that an effect is present, while controlling the Type 1 error rate, see (Lakens 2014) We used Pocock boundary (Pocock 1977), which lowers the alpha level to the same value for each interim analysis such that the overall alpha level remains .05. Here, we planned to perform 5 interim analyses, so 1 every 200 participants. This means that for the association between the home environment and spatial ability to be considered significant and to decide to stop the data collection, the alpha needs to be <0.1 for the first interim analysis, <0.2 for the second, <0.3 for the third, <0.4 for the fourth, or <0.5 for the complete dataset. A significant alpha threshold was met at the third interim analysis, both for CHQ ($p < 0.001$) and SHQ ($p = 0.016$). At this point, we collected complete data from 599 participants with a city/non-city ratio of 0.19 (114 city dwellers). There were 299 males and 300 females, the mean age was 27.0 years (SD=8.1 years).

Data collection

Sea Hero Quest - The app was produced using Unity 3D (Unity Technologies, Copenhagen Denmark) for smart phones and tablets (apple and android devices). It was released on 4 May 2016 on the App Store for iOS and on Google Play for Androids. It was available in 17 languages: English, French, German, Spanish, Macedonian, Greek, Croatian, Dutch, Albanian, Hungarian, Roma- nian, Slovak,

Czech, Polish, Portuguese, Italian, and Serbian. Within the opening screen and the Journal menu, participants were made aware of the purpose of the game. They were asked whether they were willing to share their data with us and were guided to where they can opt out. The opt out was always available in the settings. The website for the game (http://www.seaheroquest.com) was linked to from the About menu and provided full information about the study and what the data was going to be used for. If the participant agreed, their data (boat trajectory, flare accuracy and demographics) were anonymously stored in a secure T-Systems server in Germany. The application is managed by T-Systems' scalable Docker offering called 'AppAgile' which is operated out of T-Systems' datacenter to ensure data integrity and data privacy according to German data security law. The data are owned by Deutsche Telekom and then licensed to University College London for analysis. Each participant was identified by a universally unique identifier (user-uuid), a 128-bit number commonly used to identify information in computer systems. Participant's sessions were identified by another universally unique identifier (instance-uuid). Only completed levels were stored and analyzed.

City Hero Quest - City Hero Quest is a desktop virtual reality game designed to parallel Sea Hero Quest within an urban setting. The game was built in Unity 3D physics games engine (https://unity.com/) with all virtual structures modeled in Blender 3D modeling software (www.blender.org). To control the back end and log experimental variables, we used Unity Experimental Framework (UXF), an open source set of packages for Unity 3D designed for human behavioral research. Participants were recruited in the United States via the crowdsourcing platform Prolific. After providing their informed consent and an initial screening, participants were redirected to a Gorilla webpage. Gorilla is a cloud based research platform supporting behavioral experiments online. Participants completed a demographic questionnaire, and were given instructions to first install Sea Hero Quest on their mobile, and then install City Hero Quest on their personal computer. After completing both tasks, participants emailed us their data along with their unique identifying number.

Timing

The Sea Hero Quest data was collected between June 2016 and March 2019. The Sea Hero Quest data was collected over August and September of 2021.

Data exclusions

Sea Hero Quest - 60.8% of the participants provided basic demographics (age, gender, home country) and 27.6% provided more detailed demographics (home environment, level of education, see Methods). To provide a reliable estimate of spatial navigation ability, we examined the data only from participants who had completed a minimum of eleven levels of the game (including the first 4 wayfinding levels: levels 6, 7, 8 and 11) and who entered all their demographics. We removed participants above 70 years old because we previously showed a strong selection bias in this group causing their performance to be substantially higher than would be expected in unselected participants of the same age (Coutrot 2018). We also removed participants from countries with fewer than 500 players, or with education or environment levels more than 10-fold imbalanced. This resulted in 397,162 participants from 38 countries included in our analysis, (see Table S1).

City Hero Quest - The data collection was split into eight batches. Each batch was prescreened using the same set of restrictions: United States as `current country of residence', United States as `Nationality', ethnicity provided by the user (not screened for any specified ethnicities), Prolific approval rate of greater than or equal to 90%, and Mac OS / Ubuntu / or Windows as `Computer Operating System'. Finally, participants from previous batches were excluded from all subsequent batches. Prolific approval was determined by player upload of both sets of data – Sea Hero Quest and City Hero Quest – to an anonymous OneDrive server. Partial datasets were approved but excluded from analysis.

Non-participation

Sea Hero Quest - A total of 3,881,449 participants played at least one level of the game. 38.2% of the participants did not provide basic demographics (age, gender, home country) and 72.4% did not provide more detailed demographics.

City Hero Quest - No pre-screened participant dropped out from the experiment.

Randomization

Participants were not allocated into experimental groups.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☐	☒ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Human research participants

Policy information about studies involving human research participants

Population characteristics

397,162 participants from 38 countries were included in our analysis (see Data exclusions section) Among the included participants there were 212,143 males (mean age: 37.81 ± 13.59 years old) and 185,173 females (mean age: 38.67 ± 14.92

years old). The levels (N = sample size) of education were: secondary and lower (N=119,139) and tertiary (N=278,177). The levels of home environment were: city (N=109,111) and non-city (N=288,051).

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Several strategies were taken to advertise for participants. The creative agency Saatchi and Saatchi developed and created several adverts about the study with high end production values and an emotive story to motivate players to join. The game play was linked to helping a person collect the pages of his fathers travel journal that had been lost and needed to be found. The game itself allowed players to share progress and the upgrading of their boat via Facebook and Twitter. T-mobile specifically advertised the game to its million of customers. Alzheimer's research UK promoted it to its supporters. Finally, the world's most watched youtuber, Pewdiepie, was recruited to publish a promotional video1, resulting in over 2 million views in 5 days. This advertising led to Sea Hero Quest becoming for a day the downloaded app on the Apple App store and creating a 'moment' on Twitter. This snowball effect we attributed to why we were able to recruit 3.9 Million participants drawn from every country in the world.

City Hero Quest - City Hero Quest is a desktop virtual reality game designed to parallel Sea Hero Quest within an urban setting. The game was built in Unity 3D physics games engine (https://unity.com/) with all virtual structures modeled in Blender 3D modeling software (www.blender.org). To control the back end and log experimental variables, we used Unity Experimental Framework (UXF), an open source set of packages for Unity 3D designed for human behavioral research. Participants were recruited in the United States via the crowdsourcing platform Prolific. After providing their informed consent and an initial screening, participants were redirected to a Gorilla webpage. Gorilla is a cloud based research platform supporting behavioral experiments online. Participants completed a demographic questionnaire, and were given instructions to first install Sea Hero Quest on their mobile, and then install City Hero Quest on their personal computer. After completing both tasks, participants emailed us their data along with their unique identifying number.

Ethics oversight

This study has been approved by UCL Ethics Research Committee. The ethics project ID number is CPB/2013/015

Note that full information on the approval of the study protocol must also be provided in the manuscript.