Cumulative culture spontaneously emerges in artificial navigators who are social and memory-guided

Edwin S. Dalmaijer

Affiliation
1 School of Psychological Science, University of Bristol, United Kingdom

Contact details
Dr Edwin Dalmaijer, University of Bristol, School of Psychological Science, 12a Priory Road, Bristol, BS8 1TU, United Kingdom. Email: edwin.dalmaijer@bristol.ac.uk

Note before reading
This manuscript was shared to invite (preferably constructive) feedback. I welcome any comments, and in particular those that can improve scholarship. This project was sparked by curiosity, and is not in my main area of research. Hence, I am not as familiar with the literature as you perhaps are, and there is a real chance that I missed important papers in my literature searches. Please do let me know if you feel that I missed important work, by others or by yourself. Your suggestions will be used to revise this manuscript before it is submitted to a journal for (further) peer review.

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Conflicts of interest
The author declares that they have no competing interests (financial or other) that could have influenced or appeared to influence the work reported here.
Abstract
While previously thought to be uniquely human, cumulative cultural evolution continues to be found in non-human animals. It occurs when an adaptive innovation from an individual is repeatedly passed onto consecutive generations through social learning. For example, pigeons who fly alone or in stable pairs show relatively rigid sub-optimal routes, but gradually improve route efficiency over generations of pairs in which experienced members are swapped for naive ones. This raises the question of what the minimally required cognitive architecture is for cumulative cultural evolution to emerge. Here, I aimed to answer this question in artificial agents who employ three main functions: goal-direction, social proximity, and route memory. At the optima for efficiency and generational efficiency improvement, agents replicated cumulative culture observed in pigeons. Naive individuals benefitted from being paired with an experienced navigator, because it allowed them to follow an established route. Experienced navigators also benefitted from being paired with a naive individual due to regression to the goal. Unhindered by route memory, the naive agent’s heading was more likely to err towards the goal. Because of their need for social proximity, experienced agents were biased towards their naive counterparts while following a memorised route. Thus, the presence of goal-erring naive agents improved pair’s route efficiency. The resulting incremental improvements over generations meet all core criteria in current frameworks of cumulative cultural evolution, suggesting that rudimentary cumulative optimisation is an evolutionary mechanism that emerges even in simple systems that prefer social proximity and have a memory capacity.

Keywords
Cumulative cultural evolution; navigation; social proximity; memory; agent-based model; cognitive requirements; pigeon flight
Introduction

Cumulative cultural evolution occurs when individuals share their innovation with the next generation through social means, like teaching or copying. Adaptive innovations that are passed down in this way can be improved upon in the next generation, leading to successive increases in fitness (Boyd & Richerson, 1996; Tomasello, 1999). Incremental socially transmitted improvements that meet core criteria (Mesoudi & Thornton, 2018) for cumulative culture can be found in various species, including song-learning in zebra finches (Fehér et al., 2009) and humpback whales (Allen et al., 2018), tool use in New Caledonian crows (Hunt & Gray, 2003) and chimpanzees (Price et al., 2009; Vale et al., 2017), and task memory in baboons (Claïdière et al., 2014). Innovations that meet extended criteria (Mesoudi & Thornton, 2018) or invoke previously unused natural phenomena (Derex, 2022) are frequently argued to be uniquely human.

One particularly striking example of non-human cumulative cultural evolution is found in homing pigeons (Columba livia), who are suboptimal navigators that develop and remember idiosyncratic routes when flying alone or in pairs (Biro et al., 2004). While paired birds fly more efficient routes than individuals (Pettit et al., 2013), even greater performance is achieved when pairs fly in generations between each of which an experienced pigeon is swapped for a naive one (Sasaki & Biro, 2017). The original authors interpreted this as evidence for pigeons’ capability to pool information between individuals for innovation, to learn and decide through collective intelligence, and to evaluate performance so that worse innovations can be pruned (Sasaki & Biro, 2017). Later analysis of the same data further explored the intra-pair dynamic of information exchange and leadership (Valentini et al., 2021a).

These interpretations assume relatively complex cognition, including the social combination and evaluation of information. While pigeons may be capable of this, the data do not rule out that less sophisticated organisms could show similar results. In other words: it remains unclear what the minimal cognitive requirements are for cumulative culture to emerge.

Here, I propose a minimal cognitive architecture in artificial agents that are bound by only four core rules derived from avian navigation. The first is goal direction, akin to birds’ solar (Kramer, 1952) and magnetic compasses (Keeton, 1974); the second is social proximity, based on the tendency of birds to fly together (Biro et al., 2006); and the third is route memory, which in pigeons depends on visual landmarks (Lau et al., 2006) and improves over consecutive flights (Mann et al., 2011). The fourth is continuity, to avoid implausibly erratic patterns. There is no deliberate social exchange of information, communal decision-making, or evaluation of outcomes.

Existing models of cultural evolution vary from describing social inheritance of single traits through offspring’s imperfect copying of parents and population (Cavalli-Sforza & Feldman, 1973), to describing the inter-relationships of cultural elements (Buskell et al., 2019; Enquist et al., 2011; Gabora & Steel, 2021; Lewis & Laland, 2012). The current approach is different, because it describes individual navigation, and cumulative culture is an accidental outcome.
Figure 1 (previous page) – The top row shows paths from artificial agents (introduced here), and from pigeon data published by others (Valentini et al., 2021b). Each line represents the final flight in a generation. The first generation comprises a single individual; a naive individual was added in the second generation; and in all later generations the most experienced individual was replaced with a naive individual. Solid lines show lone or experienced individuals, dotted lines show naive ones. Agents navigated by sampling from a weighted mixture of Von Mises distributions (bottom row). These were centred on bearings towards the goal (green), other agents (blue), and landmarks along a memorised route (purple); and the previous heading (yellow). The bottom-left panel shows these Von Mises distributions in a radial plot, with arrows indicating each component’s centre and weight. The bottom-right panel shows the distributions in non-radial space, with their weighted sum (black).

The proposed model is a weighted mixture of Von Mises distributions $\Phi$, with weights $w$ (Equation 1, and 2-8 in Materials and Methods). To produce the next heading in journey $i$ at time $t+1$, an agent combines information from time $t$ on bearings towards the goal $b_{\text{goal}}$, the next memorised landmark $b_{\text{landmark}}$, and other agents’ estimated future position $\hat{b}_{\text{other}}$. As in birds, not all bearings are equally precise, which is reflected in components’ spread parameter $\kappa$. For example, there is larger uncertainty about where the (solar/magnetic compass) goal is compared to where the next (visual) landmark along a well-memorised route is. To prevent unnaturally jerky movements, the final component ensures continuity by sampling from a narrow distribution that is centred on the current heading. For a full account of the algorithm, please refer to Materials and Methods.

$$h(i, t+1) = w_{\text{goal}} \Phi(b_{\text{goal}}, \kappa_{\text{goal}})$$
$$+ w_{\text{social}} \Phi(\hat{b}_{\text{other}}, \kappa_{\text{social}})$$
$$+ w_{\text{memory}} \Phi(b_{\text{landmark}}, \kappa_{\text{memory},i})$$
$$+ w_{\text{continuity}} \Phi(h(i, t), \kappa_{\text{continuity}})$$

Agents travelled in three conditions that mapped onto work in pigeons (Sasaki & Biro, 2017): solo, paired, and an experimental condition with generational turnover. In the solo and pair conditions, one or two agents made 60 consecutive journeys. In the experimental condition, a naive replaced an experienced agent every 12 journeys. A total of 10 clean runs were done for each condition, for each set of weight parameters. Spread parameters were fixed at $\kappa_{\text{continuity}}=8.69$ (equivalent SD=0.35), $\kappa_{\text{goal}}=1.54$ (1.0), $\kappa_{\text{social}}=2.18$ (0.80), $\kappa_{\text{memory},1}=0.85$ (2.0) to $\kappa_{\text{memory},5}=6.78$ (0.40), based on model fits for pigeon data.
Results and Discussion

Artificial navigators show generational improvements in route efficiency

Efficiency was computed as the Euclidean distance between start and goal divided by the travelled distance (Sasaki & Biro, 2017), and varied between 0 (never reached the goal) and 1 (straight line from start to goal). Artificial navigators showed a gradual increase in route efficiency, and generational improvements in the experimental condition. Parameters were optimised for final-route efficiency (Figure 2, first row), or generational improvements (Figure 2, second row); with data from pigeons falling halfway in between (Figure 2, third row).

These results indicate that artificial navigators showed cumulative culture in the form of generational efficiency improvements, similar to pigeons.

Figure 2 – Progression of route efficiency as a function of flight number. The top panel shows results for the optimum for final efficiency (w\text{goal}=0.20, w\text{social}=0.175, w\text{memory}=0.300), the middle panel for generational improvement (w\text{goal}=0.025, w\text{social}=0.125, w\text{memory}=0.375), and the bottom panel shows pigeon data published by others (Valentini et al., 2021b). Lines show mean values over 10 independent runs, and shaded area 95% confidence intervals. In the experimental condition, a naive agent replaced an experienced one in each generation; in the solo condition, a single agent made all journeys with no generational turnover; and in the pair condition, two agents journeyed together without turnover.
Naive agents benefit by copying established routes

In the experimental condition, naive individuals could benefit from following an experienced agent that had already established route memory. Compared to the pair condition, naive individuals indeed showed more efficient paths (Figure 3). As $w_{goal}$ increased, this benefit became limited to early journeys. It increased with $w_{social}$, and was highest for intermediate levels of $w_{memory}$.

**Figure 3** – Each panel shows the difference in route efficiency between naive agents in the experimental condition (generational turnover), and the first 12 journeys from agents in the pair control condition (without generational turnover). Positive differences indicate that naive agents had better route efficiency compared to control. Each panel represents a combination of $w_{goal}$ and $w_{social}$ parameters, while darker lines indicate higher levels of $w_{memory}$. Lines represent averages across 10 independent runs, and their shaded areas the 95% confidence interval.
Experienced agents benefit from regression to the goal

While it is perhaps obvious that naive individuals benefitted from following experienced agents’ memorised routes, more surprising is that experienced agents also benefitted from the presence of a naive individual. This occurred to a process of regression to the goal.

Compared to extreme samples, random samples drawn from a Von Mises distribution are more likely to be towards the distribution’s centre. This is referred to as regression to the mean. Similarly, an experienced agent sampled new headings from a mixture of Von Mises distributions that incorporated their memorised (suboptimal) route. A paired naive agent sampled from a mixture of distributions that incorporated the goal, but not a memorised route. Samples from the naive agent were thus more likely to be towards the goal compared to the experienced agent. Because agents seek social proximity, their headings were biased towards each other. The presence of a naive individual should thus have biased experienced individual towards the goal.

This was born out empirically, as the relative bearing towards naive agents was more likely to also be in the direction of the goal (Figure 4). This was primarily true for lower values of $w_{memory}$, and increased with $w_{social}$. Regression to the goal allowed naive agents to memorise slightly more efficient routes than their paired experienced agent. An example of this is illustrated in Figure S3.
**Figure 4** – Each panel shows the distribution of relative bearings towards the naive agent from the perspective of the experienced agent in generations 2-5 of the experimental condition. Positive values on the x-axis indicate bearings towards the goal, and negative values bearings away from the goal. At higher levels of $w_{\text{memory}}$ (lighted colours), peaks at $-\pi$ and $-\pi/2$ indicate that naive agents travelled alongside or behind experienced agents. Distributions are generally right-heavy, indicating a bias of naive individuals to be positioned in the general direction of the goal. This tendency increases as a function of $w_{\text{social}}$, and to a lesser extent as a function of $w_{\text{goal}}$. 
Efficiency increases with repetition and memory
The efficiency of the first journey was lower for single agents compared to pairs, and was generally higher as a function of $w_{\text{goal}}$ (Figures S1-S2, first row). Efficiency for the final generation (best out of 12 journeys in the 5th generation) was again higher for paired compared to single agents, and was better as $w_{\text{memory}}$ increased (Figures S1-S2, second row).

Route efficiency increased between first and last journeys, primarily as a function of $w_{\text{memory}}$, with higher values resulting in larger increases (Figures S1-S2, third row). Decreases in efficiency only occurred under high values (over 0.5) of $w_{\text{social}}$ in the experimental condition.

The ten highest final-generation route efficiencies in the experimental condition averaged 0.945, and parameters $w_{\text{goal}}=0.19$, $w_{\text{social}}=0.18$, and $w_{\text{memory}}=0.31$. For the pair condition, efficiency was 0.941, $w_{\text{goal}}=0.24$, $w_{\text{social}}=0.13$, and $w_{\text{memory}}=0.32$; and for solo 0.931, $w_{\text{goal}}=0.27$, and $w_{\text{memory}}=0.35$.

These results suggest that the proposed model is sufficient for goal-directed and memory-guided navigators to function, with a clear optimum in parameter space.

Efficiency increases over generations
Generational improvement was computed as the average difference in route efficiency between consecutive generations. To reduce the impact of random fluctuations, the most efficient (typically the final) routes were taken as representative within each generation. The first generation in the experimental condition was omitted, to avoid comparisons between single and paired journeys.

The highest average generational efficiency increase was 0.092, and achieved at $w_{\text{goal}}=0.025$, $w_{\text{social}}=0.125$, and $w_{\text{memory}}=0.375$ in the experimental condition. The highest improvements in efficiency were achieved at low $w_{\text{goal}}$ values, likely because this offers the largest space for improvement without individuals completely missing the goal. For parameters closest to the final-route efficiency peak ($w_{\text{goal}}=0.20$, $w_{\text{social}}=0.175$, and $w_{\text{memory}}=0.30$), efficiency increased an average of 0.010 per generation.

These results suggest that the proposed model produces generational improvements in line with cumulative cultural evolution within boundaries in parameter space. Highest improvements were seen for poor goal-direction, but meaningful improvements were still observed at the optimum for route efficiency.

Parameter estimates in pigeons
Equation 1 was fitted to data published by others (Valentini et al., 2021b). For pigeons (N=12) flying in stable pairs, average parameter estimates were $w_{\text{continuity}}=0.58$, $w_{\text{goal}}=0.14$, $w_{\text{social}}=0.16$, and $w_{\text{memory}}=0.12$; with $\kappa_{\text{continuity}}=8.14$ (equivalent SD=0.36), $\kappa_{\text{goal}}=1.54$ (1.0), $\kappa_{\text{social}}=2.10$ (0.82), $\kappa_{\text{memory},1}=0.28$ (1.98) to $\kappa_{\text{memory},5}=6.83$ (0.40).

That these estimates did not align exactly with agents’ efficiency or cumulative culture peaks could suggest that pigeon behaviour was optimised for more than efficiency and its socially
transmitted improvements. It also suggests that the proposed model is insufficient to capture the complexity of pigeon social navigation behaviour, which is in line with interpretations put forward by others (Sasaki & Biro, 2017; Valentini et al., 2021a).

**Cumulative cultural evolution in artificial navigators**

Agents met the core criteria for cumulative cultural evolution in an influential framework (Mesoudi & Thornton, 2018), as their behaviour (1) showed variation introduced by interaction between individuals, (2) was passed on through social interaction, (3) improved performance, and (4) repeated over generations. Notably, agents did not meet any of the extended criteria, such as functional dependence, diversification into lineages, recombination across lineages, exaptation, or niche construction (Mesoudi & Thornton, 2018). Their behaviour could be described as optimisation within a set of phenomena, i.e. “Type I” cumulative cultural evolution (Derex, 2022); but they could not achieve the expansion of such a set (“Type II”), which is core to some human cultural innovations.

**Conclusion**

The minimal cognitive architecture of goal-direction, social proximity, and long-term memory is sufficient for the emergence of “core” or “type I” cumulative cultural evolution. It is driven by regression to the goal over generations: as agents in a pair align their headings towards each other, experienced agents travel along a remembered route, while their naive counterparts introduce a subtle goal-directed bias.
**Materials and Methods**

**Artificial navigators**

Artificial navigators were agents that embarked on journeys from a set starting point to a set goal, although they did not always reach this goal. They were bound by four rules, each implemented as an iterative sampling process from a Von Mises distribution. The centre of each distribution was determined by a bearing, and the spread by certainty of information. At each time point, an agent’s heading was updated by sampling each distribution, and computing a weighted circular mean (Equation 1). Weights were set at agent initialisation, and added up to 1. Spread parameters were based on empirical data (see under “Experimental Design”).

The first rule was **goal direction**. The centre of this distribution was the bearing towards the goal $b_{\text{goal}}$, its spread parameter was $\kappa_{\text{goal}}$, and its weight $w_{\text{goal}}$. The bearing was computed from the coordinates of the goal $(x_{\text{goal}}, y_{\text{goal}})$ and agent at time $t$ $(x_t, y_t)$ (Equation 2). The purpose of this rule was to orient agents towards the goal.

\[
(2) \quad b_{\text{goal}} = \arctan_2(y_{\text{goal}} - y_t, x_{\text{goal}} - x_t)
\]

The second rule was **social proximity**. This distribution’s centre was the bearing towards another agent’s estimated future position $\hat{b}_{\text{other}}$, its spread parameter $\kappa_{\text{social}}$, and weight $w_{\text{social}}$. This bearing was computed from an agent’s position at time $t$, $(x_t, y_t)$, and other agent $j$’s expected position at time $t+1$ (Equation 3). The expected position of agent $j$ at time $t+1$ was estimated on the basis of their velocity $v$ (which was kept constant) and their heading $h_{j,t}$ at time $t$ (Equation 4).

\[
(3) \quad \hat{b}_{\text{other}} = \arctan_2(\hat{y}_{j,t+1} - y_t, \hat{x}_{j,t+1} - x_t)
\]

\[
(4) \quad (\hat{x}_{j,t+1}, \hat{y}_{j,t+1}) = (x_{j,t} + v \cos(h_{j,t}), y_{j,t} + v \sin(h_{j,t}))
\]

The third rule was **route memory**. This was established during an agent’s first journey, in which the positions of 10 landmarks were committed to memory. These landmarks were equally spaced along the travelled route. During consecutive journeys, an agent attempted to fly from one landmark to the next by sampling from a Von Mises distribution with centred on the bearing towards the next landmark $b_{\text{landmark}}$, with spread $\kappa_{\text{memory},i}$ for journey $i$, and weight $w_{\text{memory}}$ (Equation 5). There were no memorised landmarks in the first journey, so the spread for $\kappa_{\text{memory},1}$ was set to 0, resulting in a completely uniform distribution. For all following journeys, $\kappa_{\text{memory},i}$ was set to 0.27,
0.58, 1.11, 2.18, and then plateaued at 6.78. This was analogous to a linear decrease in standard deviation from 2.0 to 0.4, and was based on model fits to pigeon homing data (see under “Parameter estimates in pigeons” in the Results section). Agents proceeded to navigate towards the next landmark \( l+1 \) if they came within a threshold distance of landmark \( l \). This threshold was set as 10 times the distance agents could travel between time \( t \) and time \( t+1 \).

The gradual improvement in memory precision over several journeys, the anchoring to landmarks, and the number of landmarks per journey were based on Gaussian process models of pigeon navigation (Mann et al., 2011). While the current implementation was less elegant than its inspiration, it was computationally inexpensive, and parsimonious with sampling from distributions of other bearings.

\[
(5) \quad b_{\text{memory}} = \tan^{-1}_2(y_{\text{landmark},l} - y_t, x_{\text{landmark},l} - x_t)
\]

The fourth and final rule was continuity. This assured that during journey \( i \), an agent’s next heading at time \( t+1 \) would be similar to their heading at time \( t \). The continuity component was sampled from a Von Mises distribution centred on current heading \( h(t) \), with spread parameter \( k_{\text{continuity}} \) and weight \( w_{\text{continuity}} \).

Finally, agents set their next heading by drawing random samples \( a \) from each of the Von Mises distributions described above, and computing their weighted circular mean (Equation 6-8).

\[
(6) \quad h(t+1) = \arctan_2(\bar{y}, \bar{x})
\]

Where:

\[
(7) \quad \bar{y} = \sin(a_{\text{goal}})w_{\text{goal}} + \sin(a_{\text{other}})w_{\text{social}} + \sin(a_{\text{memory}})w_{\text{memory}} \\
+ \sin(a_{\text{continuity}})w_{\text{continuity}}
\]

\[
(8) \quad \bar{x} = \cos(a_{\text{goal}})w_{\text{goal}} + \cos(a_{\text{other}})w_{\text{social}} + \cos(a_{\text{memory}})w_{\text{memory}} \\
+ \cos(a_{\text{continuity}})w_{\text{continuity}}
\]
Software was implemented in Python (version 3.8.10) (Van Rossum & Python Community, 2021) (for tutorials, see (Dalmaijer, 2017; Oliphant, 2007)), using external libraries Matplotlib (version 3.4.3) (Hunter, 2007), NumPy (version 1.21.3) (Harris et al., 2020), SciPy (version 1.7.1) (Virtanen et al., 2020), and utm (version 0.7.0) (Bieniek, 2020).

**Experimental design**

Agents travelled in three conditions that mapped onto work in pigeons (Sasaki & Biro, 2017): solo, paired, and in an experimental condition with generational turnover. In the solo and pair conditions, one or two agents made 60 consecutive journeys. In the experimental condition, a naive replaced an experienced agent every 12 journeys. A total of 10 clean runs were done for each condition, for each unique combination of parameters, resulting in a total of 32370 simulations.

Agents travelled 70 distance units per 1 time unit. While these values were arbitrarily chosen, they impact sampling frequency, and thus parameter estimates. Agents travelling at lower velocities sample the mixture model with less distance in between samples. This should result in a higher continuity weight, to stabilise the route. In sum, while units of both distance and time are arbitrary, locations of peaks in weight parameter space are specific to the current settings.

Weight parameters were varied in a wide and a narrow space. In the wide range, \( w_{\text{goal}} \) and \( w_{\text{social}} \) varied from 0.1 to 0.7 in steps of 0.05, and \( w_{\text{memory}} \) from 0.05 to 0.7 in steps of 0.05, resulting in 557 unique combinations. The narrow range aimed to zoom in on where route efficiency and generational efficiency increase were best. In this narrow range, \( w_{\text{goal}} \) and \( w_{\text{social}} \) varied from 0.025 to 0.25 in steps of 0.025, and \( w_{\text{memory}} \) from 0.025 to 0.7 in steps of 0.025, resulting in 2680 unique combinations.

Spread parameters were fixed at \( \kappa_{\text{continuity}}=8.69 \) (equivalent SD=0.35) , \( \kappa_{\text{goal}}=1.54 \) (1.0), \( \kappa_{\text{social}}=2.18 \) (0.80), \( \kappa_{\text{memory,1}}=0.85 \) (2.0) to \( \kappa_{\text{memory,5}}=6.78 \) (0.40), based on model fits for stable pigeon pairs (see under “Parameter estimates in pigeons” in the Results section). This data (Valentini et al., 2021b) was published alongside an analysis on leadership in pairs of naive and experienced pigeons (Valentini et al., 2021a), and seems to have been the source data for an earlier publication on generational improvements in efficiency (Sasaki & Biro, 2017).

**Data reduction and statistics**

Individual pigeon GPS data (defined by latitude and longitude) published by others (Valentini et al., 2021b) was converted to Universal Transverse Mercator (UTM) coordinates (grid zone 30U). Samples with velocities under 25 or over 150 km/h were excluded from flights, to filter out breaks and (apparent) GPS glitches. Flights were completely excluded if they contained coordinates further than 17.03 km (twice the start-goal distance) away from the point midway between start and goal. Finally, flight coordinates were reduced by taking every 20\(^{th}\) sample, to fit agent velocity settings (the average inter-sample distance was 3.5 meters, whereas agents’ step size was set to 70). Unlike the original paper, no further exclusions were done, and incomplete flights were not imputed.
Best parameter fits for pigeon flight data were determined through maximum likelihood estimation. This is an established way of deriving parameter estimates for mixture models of Von Mises distributions, for example in research on visual short-term memory (Bays et al., 2009).

Simulation results were averaged between paired agents and over independent runs within the same condition and parameter settings, but inferences on the basis of statistical tests were avoided. Instead, patterns of route efficiency and generational efficiency were presented as a function of weight parameters, alongside route and efficiency examples. Inferences were made on the basis of holistic interpretation; and readers are invited to scrutinise figures, data, and models.

**Open materials**

All code and data has been made publicly available through open repositories on GitHub ([https://github.com/esdalmaijer/artificial_navigators](https://github.com/esdalmaijer/artificial_navigators)) and the Open Science Framework ([https://osf.io/2tf3v](https://osf.io/2tf3v)).
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Version history

v2, 2022-06-29

- **Methodological detail in introduction.** In an attempt to slightly improve the algorithmic detail in the introduction despite a tight word limit, references to the “Materials and Methods” section were included.

- **Reorganisation of results.** Previously, figures 2 and 3 related to the optima in parameter space for route efficiency and generational increase in efficiency, respectively. These were moved to the “Supplementary Information” (now figures S1 and S2), to prioritise results relating to the increase in efficiency within and between generations. The results are still described in words in the main manuscript, but figures had to be moved due to a limit on display elements in the intended journal.

- **Clarification of parameter space visualisations.** Additional detail was included in the captions of figures S1 and S2, to clarify their colour schemes.

- **How naive agents benefit from experienced navigators.** Under the heading “Naive agents benefit by copying established routes” in the “Results and Discussion” section, the relative efficiency benefit (compared to the pair condition) for naive individuals is now visualised in Figures 3.

- **How experienced navigators benefit from naive agents.** A new visualisation (Figure 4) was added under the heading “Experienced agents benefit from regression to the goal”. It shows the distribution of relative bearings towards the naive agent from the perspective of the experienced agent. This illustration of regression to the goal in data further supports the theoretical argument already put forward in the previous version.

- **Route accumulation between generations.** The inter-generational shift in routes is now visualised in S3. It shows how landmarks shift in each of the three conditions, due to naive agents copying experienced agents and regression to the goal.

v1, 2022-06-13

- Original submission to arXiv.
SUPPLEMENTARY INFORMATION

Cumulative culture spontaneously emerges in artificial navigators who are social and memory-guided

Edwin S. Dalmaijer

Affiliation
1 School of Psychological Science, University of Bristol, United Kingdom

Contact details
Dr Edwin Dalmaijer, University of Bristol, School of Psychological Science, 12a Priory Road, Bristol, BS8 1TU, United Kingdom. Email: edwin.dalmaijer@bristol.ac.uk

Keywords
Cumulative cultural evolution; navigation; social proximity; memory; agent-based model; cognitive requirements; pigeon flight

Supplementary Information
This is supplementary information to a preprint (see page top for title, version, and date).
Figure S1 (previous page) – Each panel shows a measure of route efficiency as a function of $w_{\text{goal}}$ (upwards on the y-axis), $w_{\text{social}}$ (rightward on the x-axis), and $w_{\text{memory}}$ (outwards on the disks). The first row shows the efficiency of agents’ first journeys, with lighted colours indicating higher route efficiency. The second row shows the efficiency for agents’ final journey (after 5 generations with 12 journeys each), again with lighted colours indicating better route efficiency. The third row shows the increase (green) or decrease (pink) in efficiency between first and final journey. The fourth row shows the average increase (green) or decrease (pink) between consecutive generations. Efficiency was computed as route length divided by Cartesian distance between start and goal. In the experimental condition, a naive agent replaced an experienced one in each generation; in the solo condition, a single agent made all journeys with no generational turnover; and in the pair condition, two agents journeyed together without turnover.
Figure S2 (previous page) – This figure is similar to Figure S1, but zoomed in on a more narrow parameter space. Each panel shows a measure of route efficiency as a function of $w_{\text{goal}}$ (upwards on the y-axis), $w_{\text{social}}$ (rightward on the x-axis), and $w_{\text{memory}}$ (outwards on the disks). The first row shows the efficiency of agents’ first journeys, with lighted colours indicating higher route efficiency. The second row shows the efficiency for agents’ final journey (after 5 generations with 12 journeys each), again with lighted colours indicating better route efficiency. The third row shows the increase (green) or decrease (pink) in efficiency between first and final journey. The fourth row shows the average increase (green) or decrease (pink) between consecutive generations. Efficiency was computed as route length divided by Cartesian distance between start and goal. In the experimental condition, a naive agent replaced an experienced one in each generation; in the solo condition, a single agent made all journeys with no generational turnover; and in the pair condition, two agents journeyed together without turnover.
Figure S3 (previous page) – This figure shows an example of a single complete run through all conditions and generations. The top row shows the route efficiency for each path. The corresponding paths are drawn rows 2-4 (second: experimental condition, third: solo control condition, third: pair control condition). Columns indicate consecutive generations (with experienced-to-naive turnover in the experimental condition, and no turnover in the control conditions). Lighter lines indicate earlier journeys (1-12 within each generation). Solid lines show the first agent, and dotted lines the second. In generations 2-5 in the experimental condition, the first is the experienced agent, and the second is naive. Black dots indicate route landmarks memorised by the first agent, and white dots for the second agent. Crucially, only in the experimental condition, landmarks slowly converge towards the optimal route from start (top right) to goal (bottom left).
Figure S4 – Histograms of the final-path efficiency (left column) and the mean generational increase in efficiency (right column) for the wide parameter range (top row) and the narrow parameter range (bottom row). In the experimental condition (red), a naive agent replaced an experienced one in each generation; in the solo condition (grey), a single agent made all journeys with no generational turnover; and in the pair condition (blue), two agents journeyed together without turnover. The histograms were computed over all unique combinations of parameters, each represented as the mean over 10 independent runs. For both parameter ranges, the experimental condition shows more combinations of parameters for which final-path efficiency and generational increase in efficiency are relatively high.
Table S1

Parameter estimates from N=12 pigeons that flew in pairs; from data collected by others (Sasaki & Biro, 2017; Valentini et al., 2021b, 2021a). For each κ value, an equivalent standard deviation is reported between round brackets.

| \(w_{\text{continuity}}\) | Average | Min  | Max  |
|-----------------------------|---------|------|------|
|                             | 0.580   | 0.220| 0.828|
| \(w_{\text{goal}}\)       | 0.139   | 0.058| 0.380|
| \(w_{\text{social}}\)     | 0.159   | 0.001| 0.497|
| \(w_{\text{memory}}\)     | 0.122   | 0.002| 0.281|

| \(\kappa_{\text{continuity}}\) | Average | Min   | Max   |
|---------------------------------|---------|-------|-------|
|                                 | 8.14 (0.362) | 3.75 (0.560) | 100 (0.100) |
| \(\kappa_{\text{goal}}\)      | 1.54 (1.000) | 0.490 (1.69) | 4.78 (0.49) |
| \(\kappa_{\text{social}}\)    | 2.10 (0.82)  | 0.301 (1.94) | 100 (0.100) |
| \(\kappa_{\text{memory},1}\)  | 0.283 (1.98) | 6.70e-4 (4.00) | 100 (0.100) |
| \(\kappa_{\text{continuity},5}\) | 6.66 (0.404) | 2.32 (0.768) | 344 (0.0540) |

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