Report

Current Biology

Synergistic Benefits of Group Search in Rats

Highlights

- Search strategies of rats in a maze revealed by using automated video tracking
- A decision-making hierarchy allows rats to surpass random search behavior
- Social interactions improve the efficiency in finding the target
- Agent-based simulations confirm emergent collective benefits of simple decision rules

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In Brief

Nagy et al. advance a classical problem-solving task to uncover the underlying characteristics of collective search in groups of rats. Behavioral experiments and a bioinspired computational model reveal that optimal search performance emerges when individuals rely on a combination of independent exploration and following social cues.

Nagy et al., 2020, Current Biology *30*, 4733–4738
December 7, 2020
https://doi.org/10.1016/j.cub.2020.08.079

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Report

Synergistic Benefits of Group Search in Rats

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https://doi.org/10.1016/j.cub.2020.08.079

SUMMARY

Locating unpredictable but essential resources is a task that all mobile animals have to perform in order to survive and reproduce. Research on search strategies has focused largely on independent individuals [1–3], but many organisms display collective behaviors, including during group search and foraging [4–6]. One classical experimental search task, informing studies of navigation, memory, and learning, is the location of a reward in a confined, complex maze setting [7, 8]. Rats (*Rattus norvegicus*) have been paradigmatic in psychological and biological studies [9, 10], but despite rats being highly social [11, 12], their group search behavior has not been investigated. Here, we explore the decision making of rats searching individually, or in groups, for a reward in a complex maze environment. Using automated video tracking, we find that rats exhibit—even when alone—a partially systematic search, leading to a continuous increase in their chance of finding the reward because of increased attraction to unexplored regions. When searching together, however, synergistic group advantages arise through integration of individual exploratory and social behavior. The superior search performances result from a strategy that represents a hierarchy of influential preferences in response to social and asocial cues. Furthermore, we present a computational model to compare the essential factors that influence how collective search operates and to validate that the collective search strategy increases the search efficiency of individuals in groups. This strategy can serve as direct inspiration for designing computational search algorithms and systems, such as autonomous robot groups, to explore areas inaccessible to humans.

RESULTS AND DISCUSSION

Experimental and theoretical work has identified mechanisms by which individuals might be able to enhance their navigational or search performances by being in groups [13], such as the statistical aggregation of multiple opinions [14] or the emergent capability of groups to climb environmental gradients [15]. It is often difficult to distinguish between these different "collective" mechanisms (and many studies have not done so), yet understanding these processes in detail is important and will also facilitate the development of technologies that can benefit society by exploiting the evolved strategies employed by real organisms [16–18].

Here, we investigate the potential collective maze-solving capabilities in rats (*Rattus norvegicus*) by employing automated tracking to investigate the underlying characteristics of group search behavior. To do so, we design an experimental arena consisting of repeated Y-maze structures (each structure is a symmetrical connection of three tunnels). Our search arena is equivalent to a hierarchical binary tree with 16 endpoints (trivalent or 3-Cayley-tree) (Figures 1 and S1) and corresponds to the simplest multiple-choice decision-making system. Each endpoint is equipped with a water dispenser, but only one (selected randomly) of the 16 possible targets provides a reward (i.e., water) during a search trial. In each trial of the search task, water-deprived rats (16 of each sex) have the opportunity to locate water at one of the maze endpoints either individually (henceforth: single trials) or in same-sex groups of 8 (henceforth: group trials). Each trial lasts 10 + 5 min, i.e., if rats fail to find water within 10 min, we add 5 additional min. For each trial, the rats are placed in the "start chamber" (Figure 1C); after entering the maze, we track the rats and reconstruct their individual trajectories by using a custom-written automated software.

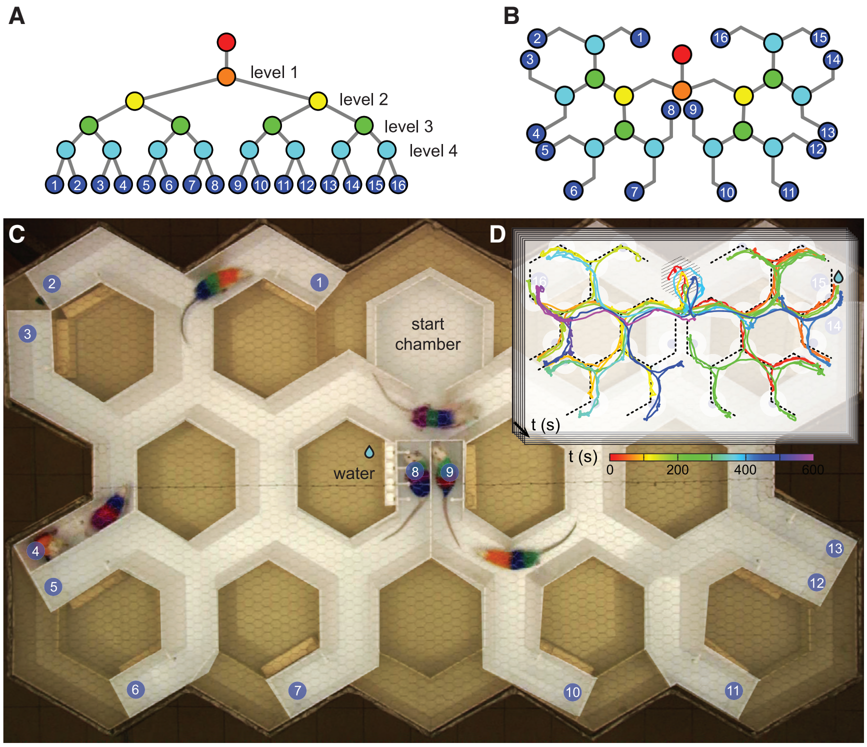

Figure 1. Experimental Setup Consisting of Repeated Y-Maze Tunnels Organized as a Hierarchical Binary Tree Network with Symmetrical 120° Junctions

(A) Hierarchical binary tree with 4 decision points and 16 endpoints. Endpoints (blue dots; labeled from 1 to 16) correspond to possible reward locations (water dispenser). Each node represents a junction.

(B) Experimental layout of the same network.

(C) Example frame of the video recording showing color-coded rats in the experimental setup during a group trial. Image brightness and contrast were inhomogeneously adjusted to mask areas inaccessible to the rats. Rats start the trial in the "start chamber" (top middle), and rewarded endpoint is marked by a water symbol (here in the middle). Walls were tilted at 75° to allow full coverage of the area with a single camera from above. Rats were automatically identified and tracked on the basis of their unique 3-color barcodes (see also Figure S1 and Video S1).

(D) Example trajectory of a rat during a single search. Time is indicated by track color (to allow visualization of repeated visits). Dashed lines correspond to tunnel midlines; the hatched area is the start chamber.

First, each rat completes a single search training period ("single 1–7") (Figures S2A–S2D; STAR Methods) and then all rats perform the search task alternately alone or in groups (trials "single 8–13" and "group 1–12"; see Video S1). To address the differences in problem-solving capabilities of individuals when isolated and when they are in groups, we only use the individual performance data of trials single 8–13, because these trials are conducted during the same time period as the group trials (alternating between conditions) after the rats are habituated with the experimental setup and the task. Individuals typically take, on average, 35 s more to find the water than when searching in groups (32% relative increase; Figure 2A) (Welch test; $n = 32$; $p = 0.008$; see also Figure S2E). This difference in performance is not caused by individuals moving faster in the social context; individual speeds are similar between single (0.30 ± 0.07 m/s; mean ± SD) and group conditions (0.32 ± 0.03 m/s; paired t test; $n = 32$; $p = 0.21$). Also, individuals' variation in speed remains stable across trials (Figure S2F) and the different conditions (Pearson's $r = 0.861$; $n = 32$; $p < 0.001$) (Figure S2G), suggesting that the decreased group search time does not simply result from social excitement.

To explore the mechanisms underpinning the enhanced group performance, we first examine the efficiency of the entire group. Note that, even without social interactions, pseudo-collective effects can potentially arise, e.g., the time to target of the first individual is expected to decrease with increasing sample size, because the larger the group the more likely it is that it contains an "expert" [19]. Also, if individuals of a group respond similarly to the same environment, their behavior might appear as if they interacted with each other. Thus, to compare search times between single and group searches, we pool individual trials of 8 rats to analyze them as a virtual group. To do so, we first rank

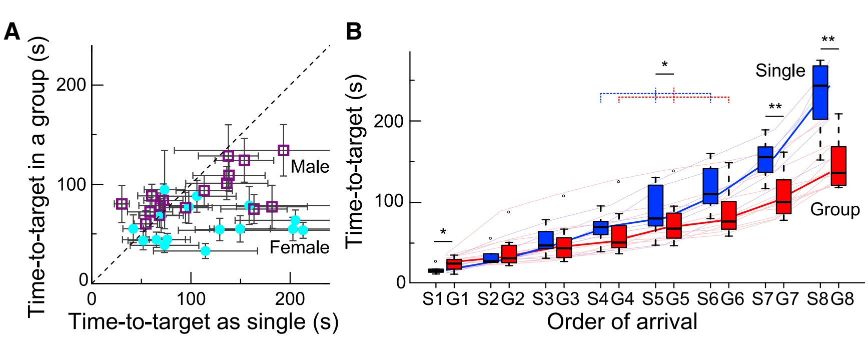

Figure 2. Individual Time to Target for Group and Single Conditions

(A) Markers (cyan circles, females; purple squares, males) depict mean individual time to target of single (x axis; single 8–13) against group trials (y axis; group 1–12). Error bars show SE. See also Figure S2.

(B) Time to target in the order of arrival (ranks). Boxplots show distributions across different trials of single (blue) and group (red) trials. Boxes represent the first and third quartiles, the line within the box indicates the median, whiskers show the minimum and maximum values, and dots are outliers. Thin curves correspond to separate trials; thick curves are the median for each condition. Boxplots are shifted sideways (compared to curves) for better visibility. Group and single conditions differed for ranks 7 and 8 (**$p < 0.01$; two-tailed t test). Also, the combined data of ranks 4–6 differed between single and group trials (*$p < 0.05$; see details in STAR Methods).

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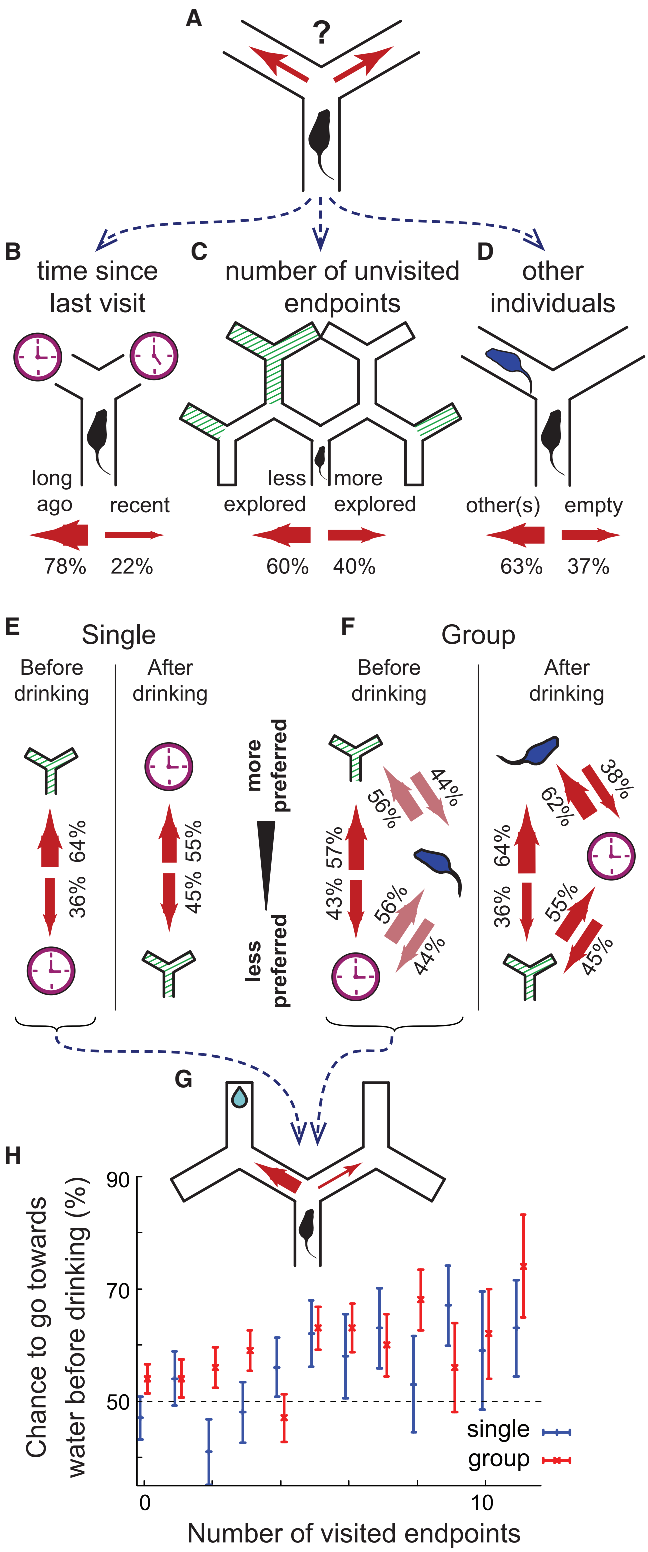

Figure 3. Decision Making Factors and Their Hierarchy

(A) Junction decision: rats have to choose one of two tunnels.

(B–D) Decision factors leading to unequal choices. Preferred tunnels were those that (B) were visited longer ago (if visited before), (C) led to more unexplored endpoints, and (D) contained other individual(s). Thickness of arrows corresponds to probabilities of moving toward the different tunnels during group trials before drinking.

(E and F) When two factors (depicted as symbols from B–D) were in conflict, choices indicated a hierarchy of influencing factors. Arrow pairs show the relative preference of going toward either factor for single/group trials and before/after drinking separately. Dark red arrows indicate significantly different choices compared with the random expectation of 50% ($p < 0.05$); light red arrows highlight not significantly different choices (Figure S2; Tables S1 and S2). On the basis of the preferred choices, factors were ranked into a hierarchy of priorities with the most important factors on the top.

(G and H) Probability of finding water as a function of the progress of the exploration (measured by the number of visited endpoints) and calculated for symmetric decision points where both options led to the same number of endpoints. Error bars represent SD.

time to target for every single rat from lowest to highest to compare them then to the equivalent rank of the group trials (i.e., time to target for 1st,..., 8th rat). This allows us to identify pseudo-collective effects and to contrast them to real synergistic, collective effects.

Rats in groups find targets significantly more quickly than single trials (Figure 2B). To test this, we first compare each ranking in the two conditions ($n_{single} = 6$; $n_{group} = 12$). For the 7th and 8th individuals, time to target was significantly lower in the group condition (Welch test; $p = 0.007$ and 0.005, respectively), although it was significantly higher for the 1st rat (Welch test; $p = 0.048$). None of the other rankings showed a significant deviation. When combining data of the 4th, 5th, and 6th rankings into a single trial (after subtracting the group condition's median of the relevant ranking), we also observed significant differences between the search conditions (Welch test; $n_{single} = 18$; $n_{group} = 36$; $p = 0.028$). Thus, only the first rat tends to be faster when searching alone, but this performance difference between singles and groups reverses, and increases in strength, as more group members find the target (Figure 2B). Note that groups perform better despite the fact that individuals of a group can block each other's paths through the maze and also engage in not-search-related social interactions (e.g., play-fighting and grooming) (Video S1).

To understand individual decision making during the collective search process and to explore the origin of the increased performance when in groups, we focus our analyses on the directional decision made by rats at each junction (i.e., passing through junction center from one tunnel to another) (Figure 3). Due to the symmetrical layout of each junction, we pool the data of all junction decisions ($n_{single} = 55{,}077$ and $n_{group} = 79{,}986$). We examine junction decisions in relation to the focal individual's search motivation (i.e., before or after it drank water) and search history (i.e., which of the two "forward" tunnels was visited last or led toward more/less visited areas of the maze). For the group trials, we also explore (1) the influence of group mates by considering the presence of visible conspecifics nearby, (2) whether a tunnel was visited previously by others (potentially providing olfactory cues), or (3) whether the focal rat has met with individuals who had already found the water. First, we determine the influence of each factor separately by testing whether the ratio of individual choices (in relation to the examined factor) differs from the expected 50% at each junction (Figure 3; details in STAR Methods), assuming that all other factors would impact both choices equally. We find that, during group trials, before a rat

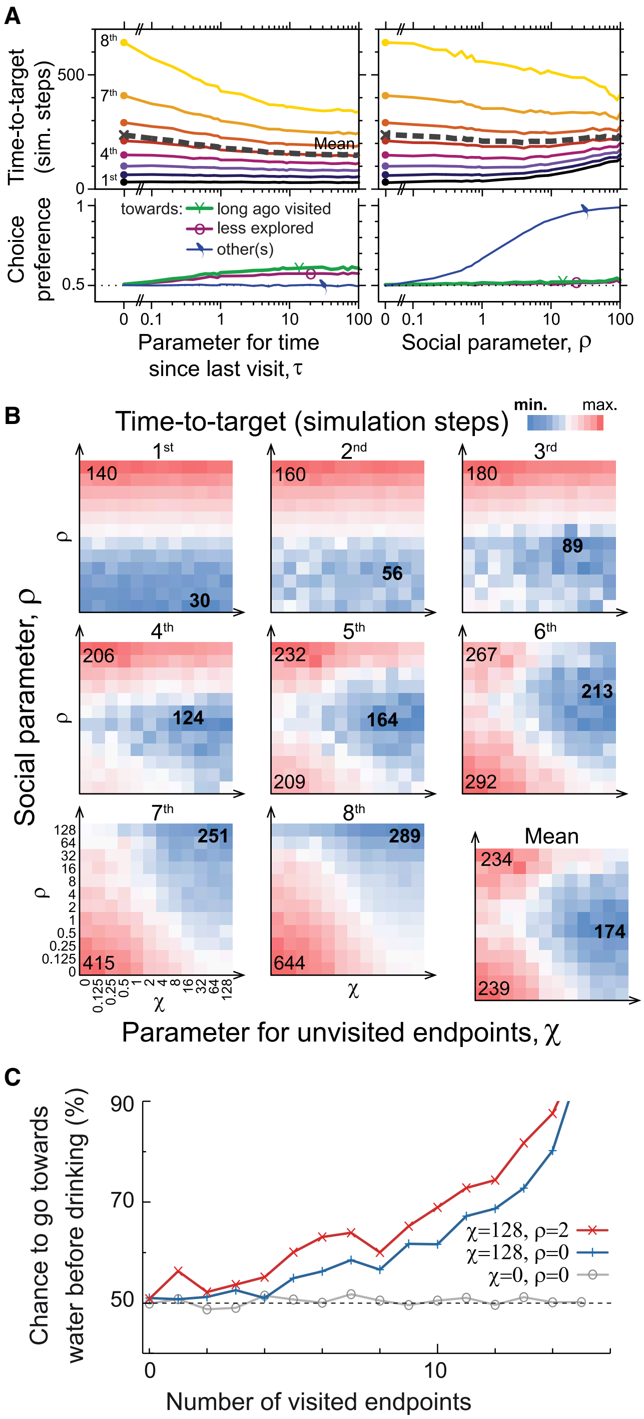

Figure 4. Effects of Different Parameters on Search Efficiency and Choice Preference in Agent-Based Simulations

(A) Time to target (top) and choice preferences at junctions (bottom) depending on time since last visit (τ; left) and social cues (ρ; right); all other parameters are 0. Curves represent time to target in agents' arrival order (1^{st}–8^{th}) and mean (dashed curve), which characterizes the overall performance of each rat (as the order of arrival is random in each round).

(B) Time to target (color coded) as a function of the number of unvisited endpoints χ (x axis) and ρ (y axis); τ = 0. Subplots represent arrival order (1^{st}–8^{th}) and mean (bottom right). Location and value of local maxima and minima (bold) are shown on each subplot. Varying τ and ρ gave qualitatively similar results (see Figure S3D). See also Figure S4 and Video S2.

(C) Probability of finding the target in the computational model as a function of the progress of the exploration (calculated as in the experiment; Figure 3H). 3 sets of parameters are shown (in all sets τ = 0): χ = 0, ρ = 0 (gray), no individual preferences (exploration related or social); χ = 128, ρ = 0 (blue), representing single search; and χ = 128; ρ = 2 (red), representing group search.

has found the water, three factors influence junction decisions most strongly: a rat moves with higher probability (1) toward a tunnel that was visited longer ago (78% versus 22%), (2) into the direction that leads to more unvisited endpoints (60% versus 40%), and (3) toward visible conspecifics (63% versus 37%) (Figures 3B–3D and S2H; Table S1). Yet, individuals who found the water are not followed more frequently (Fisher's exact test; p = 0.806), and regions that have been explored by others are not visited more frequently compared with random choices (binomial test for p = 0.5; $n_{\text{visited by conspecific(s)}}$ = 24; $n_{\text{not visited by conspecifics}}$ = 14; Z = 1.45; p = 0.072) (see STAR Methods). After the individual locates the water (after drinking), the number of unvisited endpoints becomes less important (Table S1). The influential factors are similar for rats searching singly (Table S1). Note that, the change in the probabilities is rather an effect of time and does not directly depend on the drinking state of the rat (Figure S2I). We do not find any sex-related differences when examining the choice probabilities of junction decisions (Table S1), so we conclude that the collective search characteristics are similar between the two sexes, although we cannot completely rule out other possible differences between the sexes.

Next, we examine the relative importance of these effects by looking at junction decisions where two factors are in conflict. Using pairwise comparisons, we establish a hierarchy of the different factors that influence directional choice (Figures 3E and 3F). Before finding the water, rats are most likely to turn into the tunnel that results in visiting more unvisited endpoints in both group and single conditions (Figures 3E and 3F). In group trials, the second and third most influential factors are the presence of conspecifics and the timing of the last visit. Thus, when still searching for water, the exploration of new areas tends to be more important than following group mates (in the group trial) and also more influential than the timing of previous visits (in single and group trials). Once a rat has drunk water, the weighting of these factors (i.e., the hierarchical order of preferences) changes in that visiting unexplored areas becomes the least important factor in both single and group trials (Figures 3E and 3F). Individuals (groups and singles) continue to explore the maze but return to the water source several times, i.e., more frequently than they visit other endpoints without water. We examine this by exploring how many other endpoints were visited between the first and second visit of a given endpoint (target versus non-rewarded endpoint). We choose one specific endpoint at the opposite location as the non-rewarded endpoint (mirrored along the axis of symmetry in the experimental setup). Between the first and second visit, individuals visited on average 7.2 endpoints. This was significantly different from the non-rewarded endpoint (second visit after 11.1 endpoints; t test; n_{first} = 164; n_{second} = 109; p < 0.001). Rewarded endpoints had higher revisiting probabilities throughout search trials (Figure S2J). This behavior might also contribute to the enhanced search performance of the groups, as rats visiting repeatedly the drinking site might attract others to the water.

To examine whether the preferences we observe in our experiments increase maze-solving ability, generally, we employ individual-based simulations of group search in a maze-structure identical to our setup (see STAR Methods). At each decision point (equivalent to junction decisions), the probability of choosing a direction depends on three weighting parameters (mimicking the most influential factors identified during the experiment): social cues (ρ) and individuals' search history (time since last visit [τ]; number of unvisited endpoints [χ]). When examined separately, each parameter improves overall group performance when compared with random searches of individuals in groups (Figures 4A and S3). Increasing the anisotropy of the decision controlled by the two parameters related to search history (τ and χ) results in both cases to less self-overlapping trajectories, thereby improving search efficiency continuously, which would also be the case during single searches. The social factor (ρ) is found to provide additional benefits in a complex, non-monotonous way: increasing ρ results in a longer time to target for the first rat but reduces search time after 3–4 individuals have already located the target (Figure 4); both are in agreement with the experimental findings. This finding is even enhanced when we include additional parameters in the simulation to represent the rats' searches more precisely (see STAR Methods). Further, when examining performance while varying two parameters (χ and ρ), minimum search time corresponds with choice preference probabilities that are qualitatively similar to the experimental data (Figures 4B and S3D–S3I; Video S2).

We have revealed here a decision making hierarchy employed by rats that generates a systematic search pattern, resulting in a strong increase in the probability to locate a target in a maze as more and more unrewarded endpoints are visited (Figures 3G, 3H, and 4C). This hierarchy, which weighs the reliance on previous experience (i.e., exploring unvisited parts of the maze) and social information (i.e., moving toward group members), makes the group more efficient than with the same number of individuals in isolation. The performance of individuals in groups increases, even though the interactions between individuals is relatively local (because the design of the maze, following natural tunnel systems, does not allow the transmission of long-range visual cues). A "follow others" mechanism in combination with the avoidance of previously visited tunnels provides synergistic advantages to the group. However, as our simulations confirm, highly efficient searches emerge only when individuals exhibit a combination of individual exploratory and social behavior, as each behavior alone results in a sub-optimal performance (Figure 4B). Our integrated experimental and theoretical approaches offer new insights into how synergistic effects that arise from individuals' spatial knowledge types and social information enhance the performance of members of a collective. Understanding these types of evolved, natural collective phenomena can have potential applications in various fields, including the study of human mobility (e.g., traffic control, crowd management, or disease propagation) [20–22]. Also, our observations might be useful for designing groups of autonomous robots equipped with specific sensors and local communication capabilities to explore an unknown area in a distributed fashion [18, 23, 24].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2020.08.079.

A video abstract is available at https://doi.org/10.1016/j.cub.2020.08.079#mmc5.

ACKNOWLEDGMENTS

We thank all the people who helped during the experimental work, especially Niké Nagy, Valéria Németh, Gergő Somorjai, Otília Stark, Eszter Papp, Dániel Ábel, and Katalin Schlett. We acknowledge funding from the Max Planck Institute of Animal Behavior. This research was partially supported by a grant to T.V. establishing the HAS-ELTE Statistical and Biological Research Group, the DFG Centre of Excellence 2117 "Centre for the Advanced Study of Collective Behaviour" (ID: 422037984), and the Hungarian Academy of Sciences (a grant to the MTA-ELTE 'Lendület' Collective Behaviour Research Group, grant number 95152). A.H. was supported by the ÚNKP-16-1 New National Excellence Program of the Ministry of Human Capacities and E.K. from the ERC starting grant 680040. I.D.C. acknowledges support from the NSF (IOS-1355061), the Office of Naval Research (ONR) (N00014-19-1-2556), the Struktur- und Innovationsfunds für die Forschung of the State of Baden-Württemberg, the Deutsche Forschungsgemeinschaft (DFG) (German Research Foundation) under Germany's Excellence Strategy, EXC 2117-422037984, and the Max Planck Society. A.F. was supported by the CNV-Foundation, the Hans und Helga Maus-Stiftung, and the James Heineman research award of the Minerva Stiftung.

AUTHOR CONTRIBUTIONS

M.N. and T.V. conceived the idea and designed the project; A.H., E.K., and M.N. performed the experiment and collected the data; G.V. designed the computer-vision software framework for tracking; M.N. designed the maze, the data analysis, and the visualizations; A.H. and M.N. analyzed the data and coded the simulation; and M.N. and A.F. wrote the paper with contributions from E.K., I.D.C., and T.V. All authors revised the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: April 22, 2020
Revised: July 21, 2020
Accepted: August 24, 2020
Published: September 24, 2020

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Rattus norvegicus (Rat): 16 adult males, 16 adult females, Wistar	Toxi-Coop Zrt, Hungary	fHsdBrlHan:WIST
Software and Algorithms		
Custom-written video analysis software	[26]	https://github.com/vasarhelyi
Trajectory data analysis and computer simulations	Python (v2.7.12)	https://github.com/nagymate80/CollectiveMaze
Deposited Data		
Trajectory data of all trials	This paper	https://doi.org/10.17632/8g9rgh4ssk.1

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Mate Nagy (nagymate@hal.elte.hu).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

Trajectory data are available at https://doi.org/10.17632/8g9rgh4ssk.1. Recorded video sequences were analyzed offline with a custom-written software to obtain individual positions and orientations (for details see SI Methods of [26] or download the latest source code from https://github.com/vasarhelyi). Trajectory data analyses and computer simulations were conducted using custom-written dedicated scripts in Python (v2.7.12). The scripts to run analyses included in this paper have been deposited in the public depository Git Hub, and are available at: https://github.com/nagymate80/CollectiveMaze

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subjects

We used 32 Wistar rats (16 females and 16 males; fHsdBrlHan:WIST; ordered from Toxi-Coop Zrt, Hungary) in this study. The rats arrived on 01/08/2015 with an age of ~70 days. Rats were separated into 4 same-sex groups each containing 8 rats that were housed and tested together. Animals were housed in polypropylene cages (sized 63 × 53 × 15 cm^3) under controlled temperature (21 ± 2°C) and light conditions (12-h light/dark cycle; dark from 8am to 8pm) with *ad libitum* access to food and a shelter. Typically 3-7 h before the experiment, rats were deprived of water. Outside of that period they had *ad libitum* access to water. Housing cages were cleaned once a week. We measured the weight of each individual twice a week to check for potential weight loss. None of the rats lost weight in-between two consecutive measurements.

Ethical guidelines

The procedures comply with national and EU legislation and institutional guidelines. The experiments were performed in the animal facilities of the Eotvos University, Hungary, and according to Hungarian legislation and the corresponding definition by law (‘1998. évi XXVIII. Törvény’ 3. §/9. — the Animal Protection Act), non-invasive studies on animals bred for research are currently allowed to be performed without the requirement of any special permission (PE/EA/1360-5/2018).

METHOD DETAILS

The repeated Y-maze

We set up an experimental arena consisting of repeated Y-maze structures. Each Y-maze structure is a symmetrical connection of three tunnels (at an angle of 120°). The design of our search arena is equivalent to a hierarchical 4-level binary tree with 16 endpoints (trivalent, or 3-Cayley; Figures 1 and S1). The walls of the maze were made of white opaque plexiglass (5 mm thick); 15 cm high, and tilted at 75°. The tilting assured an unobstructed field of view for the single camera mounted on the ceiling. Each tunnel was 30 cm long (at the midline), 10cm wide at the bottom, and 17.5 cm at the top. The maze was covered by a wire mesh with hexagonal holes (3.75 cm in the diagonal) to avoid rats climbing out, but also ensuring visibility for the camera, and access to fresh air for the rats. The size of the maze was a compromise between providing enough space to ensure free movements and exploration options for multiple rats, and accessibility from all sides for the experimenter. The lengths of the tunnels ensured that a rat could only see its local neighborhood, and not other parts of the maze, when approaching a junction. Because of camera restrictions regarding the field of view, we had to ensure that all tunnels fitted on a 2D plane (size: 2.7 m x 1.6 m). To summarize, we aimed for a design in which: *i*) the maze has 4 levels of binary choices resulting in 16 endpoints; *ii*) it has a 2D layout; *iii*) all junctions are symmetrical (with a 120 degree turn); *iv*) all junctions are identical to each other, *v*) all corridors have the same length and identical to each other, and *vi*) the full layout of the maze is globally symmetrical. But it is not possible to fulfill all these desired criteria at the same time. Therefore, we needed to make compromises to relax some of these requirements. We decided to give priority to criteria *i*, *ii*, *iii* and *iv*, and keep them fully fulfilled. As for criteria *v* and *vi*, we aimed to find a solution that differs from the ideal case as little as possible. In practice, we adjusted the lengths of some tunnels while keeping the angle of the 120° symmetrical junctions identical. We shortened six tunnels by ~7% (those leading toward the endpoints 4, 5, 8, 9, 12, 13 - we define them as "Type-4" endpoints); we doubled the length of the two tunnels that connected the root of the network; and the path leading to endpoints 2, 3, 14, 15 (Type-2) are unvaried, but these endpoints are close to one another in the physical space. The unchanged endpoints are 1, 6, 7, 10, 11, 16 (Type-1). Each endpoint contained a water dispenser, identical to those of the rats' home cage. During the trials, the water dispenser of one randomly selected endpoint contained water. In order to secure that this layout did not affect the results, we compared the time-to-target for the different endpoint types, and found no significant differences between the endpoint types (*Welch*-test, $n_{\text{Type-1}} = 62$, $n_{\text{Type-2}} = 49$, $n_{\text{Type-4}} = 75$, Type-1 versus Type-2 p = 0.229, Type-1 versus Type-4 p = 0.793, Type-2 versus Type-4 p = 0.431). During the group trials, the rewarded endpoint contained three additional water dispensers so that multiple rats could drink simultaneously. From the viewpoint of the last junction, rewarded and unrewarded endpoints looked identical.

Experiments

The experimental maze was in the same room as the housing cages. Experiments were conducted during the dark (active) period. All experiments were performed between 03-08-2015 and 13-09-2015. Each rat was marked with a unique 3-color barcode on its back using nontoxic "Special Effects" hair dye in 5 distinctive colors (Red: Nuclear Red, Orange: Napalm, Green: Sonic Green, Blue: Londa color 0/88, Purple: 4 units Atomic Pink and 1 unit Wild Flower). These codes were applied/renewed twice (on 03-08-2015 and 31-08-2015). We video recorded all trials using a low light sensitive camera fixed to the ceiling (Sony HDR-AX2000, 2.9 × 1.8 m^2 field of view, 1920 × 1080 resolution, 25 fps de-interlaced).

To familiarize the rats with the environment, each individual was placed for 30 min into the hexagonal compartments of the maze. During the first four days, this habituation period was done individually once a day; afterward, for the next six days, it was performed in groups of four twice a day. Next, the rats experienced an experimental period for 26 days during which they were filmed while performing a search-task either individually or in groups. Each of the 32 rats were trained seven times individually ('*single 1-7*') to get familiar with the arena and search task. Individual searches were conducted every other day during the first 14 experimental days. During the next 12 days, rats were tested by alternating between single and group conditions (trials: '*single 8-13'* and '*group 1-12*'). During the first trials, we observed a learning, habituation, or familiarisation period in which rats become familiar with the setup and search task. During this period, the search patterns were affected by the rats' unfamiliarity with the setup. This can be seen for example when looking at the speed of the individuals on Figure S2F. Group trials started once the rats were familiar with the experimental setup, so that their behavior was less affected by this initial transient phenomenon. The experienced trial conditions were determined by sex. On odd days, females performed the search once individually (the timing of the trial was determined randomly), and males were tested twice in groups (in the morning and in the evening). On even days, this pattern was reversed (i.e., females twice in groups, males once individually). When analyzing the morning (group trial 1, 3, 5, 7, 9, 11) and the evening trials (group trial 2, 4, 6, 8, 10, 12) separately or only the first 6 of the group trial (to eliminate any effect of increased statistics or learning), we observe the same significant differences in the time-to-target between the reduced group trials and single searches (*Welch*-tests, n = 32, $\text{group}_{1,2,3,4,5,6}$: p < 0.001; $\text{group}_{1,3,5,7,9,11}$: p < 0.001; $\text{group}_{2,4,6,8,10,12}$: p = 0.007; see also Figure S2E). We also explored whether the time of the day at which the experiment was carried out impacted the rats' speed or time-to-target during single searches, but did not find any evidence (speed: Pearson's $r = 0.077$, n = 187, p = 0.298; time-to-target: Pearson's $r = -0.0078$, n = 187, p = 0.915, Figure S2D). Finally, in order to explore whether the experimental protocol impacted the level of thirst of singly searching rats (which would not be true for group trials), we separate the data of the single trials into two sets depending on the order of arrival at the target (ranks 1^{st} to 6^{th}, and 7^{th} to 8^{th}). The water deprivation times of ranks 1-6 and ranks 7-8 did not significantly differ (t test, $n_{1\text{-}6} = 144$, $n_{7\text{-}8} = 45$, $t = 0.0024$, p = 0.998).

At the beginning of the experiment, rats were placed and detained in the 'start chamber for 2 min. Next, the experimenter removed the door to the maze, left the room, and observed the experiment through a screen from the outside. Each trial lasted 10 min (or until the rat finished drinking, if it was drinking at that 10 min mark). If rats failed to find water during the test period, as a first step we added additional 5 min, and as a second step guided them to the filled water dispenser to let them drink. In the single trials this occurred to 9, 2, 2, 1, 1, 1 individuals in the first 6 trials respectively, and to one individual during trial 13. After removing the rat(s), we moved the water dispenser to a new location, and thoroughly cleaned, disinfected, and dried the entire maze to avoid the use and transmission of olfactory cues between and within trials.

Training period

We observed that *time-to-target* (time passed until an individual located the water) decreased drastically during the first three single trials, and remained stable during single trial 4-7 (Figure S2A). This was also the case for individual speed of motion which stabilized after single trial 3 (Figure S2F). To check whether the length of the water deprivation period (varying between 3 to 10 h but typically between 3 to 7 h; Figures S2B and S2C) affected individual motion speed and time-to-target, we pooled data from all single trials after the third trial (to exclude the initial familiarization). We excluded data when rats did not find water during the 10-minute experiment, because the familiarization with the task was not complete. Length of water deprivation period did not correlate with motion speed (Pearson's $r = -0.067$, n = 317, p = 0.23) or time-to-target (Pearson's $r = -0.032$, n = 317, p = 0.56). n corresponds to the number of individual trials. Although different trials of the same rats are not statistically independent as motion speed and time-to-target were correlated between trials, this could serve as a conservative upper estimation and the lack of significance suggests that there was no effect. Thus, the asymptotic increases of time-to-target and motion speed indicate that the rats became familiar with the experimental procedure. Thus, we could compare directly the performances during the following single trials ('*single 8-13*') with that of the group trials ('*group 1-12*').

Females moved faster than males both in single and group conditions (*Welch*-test, $n_{male} = n_{female} = 16$, p = 0.005 and 0.002, respectively). In the single condition, females and males did not differ in mean time-to-target. But in the group condition, females were significantly faster in reaching the water (*Welch-test*, $n_{male} = n_{female} = 16$, p = 0.74 and < 0.001, respectively). Although we observed that an individual's speed was consistent between single and group conditions (see above), we detected a secondary effect when examining the speeds of males and females separately. Slower individuals during single searches moved slightly faster when in groups, but still slower compared to the other individuals. This, however, was only apparent in males. We discovered this by analyzing the difference between average time-to-target during the single and the group searches as a function of the difference between average speed during the single and group trials (all: Pearson's $r = -0.095$, n = 32, p = 0.603; males: $r = -0.761$, n = 16, p = 0.0006; females: $r = 0.266$, n = 16, p = 0.320).

As a consequence of the observed consistent individual differences in speed (see also Figure S2G), faster individuals have a higher likelihood to arrive earlier at the target compared to others. Nevertheless, as the target is always at a new location, these individuals may visit several unrewarded end points, causing them to arrive later. Along those lines, by chance it is possible that individuals that are usually slow may also arrive first at the target. To investigate this phenomena, we analyzed the order of arrivals in the group conditions for the 12 group trials. We found that each individual arrived at the target in a relatively random pattern. In the group of 8 rats, each individual arrived in some trials in the first half (as rank 1 to 4) and also in the second half (as rank 5 to 8) of the group. To explore whether the order at which individuals arrived was random, we correlated arrival orders between different trials. We used the most conservative approach by treating each measurement as an independent data point (which would be the case if the arrival order was completely random and independent in all trials). Using this approach, we detected a weak positive correlation between arrival orders of successive trials. This effect originated mainly from females (all: Pearson's $r = 0.193$, n = 186, p = 0.008; males: $r = 0.090$, n = 96, p = 0.385; females: $r = 0.321$; n = 90; p = 0.002). We investigated this further by exploring the persistencies of the correlations in arrival order. We analyzed the correlation between individual arrival orders in trials that were 1, 2 or 6 trials apart from each other. (For trials 1 apart - all: Pearson's $r = 0.116$, n = 186, p = 0.116; males: $r = 0.092$, n = 96, p = 0.370; females: $r = 0.138$; n = 90; p = 0.196; for trials 2 apart - all: Pearson's $r = 0.046$, n = 186, p = 0.534; males: $r = -0.077$, n = 96, p = 0.459; females: $r = 0.185$; n = 90; p = 0.081; and for trials 6 apart - all: Pearson's $r = -0.058$, n = 186, p = 0.430; males: $r = -0.012$, n = 96, p = 0.905; females: $r = -0.090$; n = 90; p = 0.398). As we detected no significant correlations, we are confident that our statement that individuals arrive in any order at the target is valid.

Motion analysis

We simplified the two-dimensional trajectories of each individual by projecting their positions to the midline of the tunnels. This midline is a graph/network representation of the structure of the maze. This results in a quasi-one-dimensional motion along the edges. To do so, we converted the x-y coordinates of the individuals' positions into positions on this graph representation of the maze (Figure S1B).

Computer simulation of group search

We employed an agent-based simulation with a design that corresponded to the experimental maze setup. Agents (n = 8) moved on a binary tree with $m = 4$ decision points and $2^m = 16$ possible endpoints to locate a randomly chosen target. At the beginning of each simulation trial, all agents were placed at the root of the hierarchical tree (equivalent to the start chamber). To transit an edge (equivalent to the experimental tunnel), an agent needed 3 time steps. Asynchronous random-order updates were used; during each time step all agent either moved one step along an edge or chose a new edge to enter (if located at a node of the network, equivalent to a junction). The probability of choosing an edge was proportional to $p = (1+\rho \cdot n_{partners}) \cdot (1+\tau \cdot t_{last\_visit}) \cdot (1+\chi \cdot r_{unvisited})$, where ρ is the parameter for social cues, $n_{partners}$ is the number of agents on that edge, τ is the parameter for the visiting history of edges, t_{last_visit} is the number of time steps since the edge was last visited (or, if not yet visited, since the beginning of the simulation), χ is the parameter for the visiting history of the endpoints, $r_{unvisited}$ is the ratio of unvisited endpoints (i.e., the number of unvisited endpoints reachable through that edge divided by the total number of endpoint reachable from this junction without turning back). $r_{unvisited}$ was set to 0, if the agent was coming from a direction where the two choices would lead to an unequal number of endpoints. Note that the strengths of the three parameters were different, because of the different ranges of the influencing variables: $n_{partners} \in [0,7]$, $t_{last\_visit} \in [0, \infty]$ (but typically [0,1000]), $r_{unvisited} \in [0,1]$. Agents turned back only at endpoints and agents stopped when reaching the target (in the main model). Yet, we also explored different extended models to study how the simulation results change when individuals could turn back at any location, or when they could continue their exploration after the target was located. To capture this in the simulation, we included that individuals had a fixed (10%) chance to turn backward and reverse their direction of motion at a junction. In a different model, we varied the time that successful agents remained at the target (between 10 to 200 simulation steps) before they continued their exploration, but with a fixed probability to turn toward the water at every junction (*CTTW*, chance of turning toward water). We present the results of these extended models as well as the effect of group size in Figure S4. The findings are in agreement with the original model. For each parameter setting, we performed 1000 simulation runs to obtain mean time-to-target and choice preference probabilities (Figures 4, S3, and S4). Individuals in the model have equal chances to arrive at the target in every order, because individual abilities are identical, and because the target is at random locations. Thus, who will be first or last will be determined stochastically. This means that over the 1000 runs, individuals will exhibit an average time-to-target that is equal to the group's average. Also, when observing an increased average group performance, it means that each individual experienced this average benefit after multiple trials as the stochastic processes are averaging out. The code of the simulation was written in Python using the *igraph* package [27].

Our agent-based simulations of the group searches revealed that both parameters characterizing individual search history (τ, χ) were inherently connected with each other. This means τ also influenced how often edges leading to more/fewer visited endpoints were chosen, and χ affected whether recently more/less visited areas were explored. Thus, while changing only one search history related parameter (τ or χ; Figures S3A–S3C), we found anisotropy in both metrics measuring junction decisions (proportion of going toward edges visited long ago and more unvisited endpoints). Similarly, because there is a funneling effect when individuals move to less explored areas, the probability of going toward neighbors was also influenced by the probability to move toward unvisited parts of the maze (and vice versa).

QUANTIFICATION AND STATISTICAL ANALYSIS

Analyses of the decision-making process

To examine the junction decisions, we pooled data from all junctions not taking the travel direction of the focal individual into account, when we examined factors that did not depend on the direction of travel (time since last visit, or presence of conspecifics). When we examined factors that depended on the maze subsection that the rat moved to (e.g., amount of unexplored areas, or water location), we only pooled those events during which the focal individual came from the direction of the start chamber (the root of the hierarchical tree network) to ensure that the topology of the possible choices were symmetrical.

To analyze the decision-making process at the junctions in relation to different individual and group factors, we carefully examined each decision event defined as a rat moving into a different tunnel after passing through the junction area (i.e., 10 cm around the junction center). Because the two tunnels ahead could differ when considering individual experiences (e.g., time since the last visit, areas with more/less unvisited end points, attraction to conspecifics), we were able to define conditional probabilities for these different factors based on the occurrences of the different choices. For each factor, we tested whether individual choices were different from the null hypothesis that the two choices have the same ratio ($p^* = 50\%$ and $q^* = 50\%$), while assuming all other factors would impact both choices equally. We calculated a z value as $(p-p^*)/\sigma$ where $\sigma = \sqrt{p^*q^*/n}$ is the expected standard deviation, and searched for the corresponding p values (Figure 3; Table S1).

In our study, we performed several statistical tests. To account for multiple comparisons we present a correction for the significance in Table S2 [25].

Factors influencing junction decisions

We tested whether the choice of the focal rat was influenced by the search success of the encountered conspecifics, because rats that already found the water could exhibit a noticeable change in behavior or smell differently. To test this, we compared the chance of going toward a conspecific (when the direction concurred with the water location, and the focal individual did not yet find water) in cases when the other individual found (64%, n = 299) or did not find the water yet (61%, n = 868).

In addition, we tested whether individuals can use olfactory cues from other individuals by going toward or avoiding areas that have been explored by others. We only examined events fulfilling the following criteria: *i*) the focal individual did not drink yet (to be in the state of motivated search); *ii*) arrived to the junction for the first time (to eliminate bias coming from personal search history); *iii*) came from the direction of the start chamber (to ensure symmetricity of the choices); *iv*) the junction belonged to level 2 or 3 (to exclude level 1 which is located at the start chamber, and level 4 where the tail of drinking individuals could still be visible; see notation of the levels on Figure 1A); *v*) only one of the junction's forward options has been visited by other individual(s), and *vi)* no other rats were visible in the tunnels (as that would clearly bias the choice). We calculated the number of choices for both forward options (the tunnel visited by conspecific(s) versus the one unvisited by others) to test if individuals moved with higher (or lower) probability than expected from unbiased choices to the tunnel that could potentially still contain olfactory cues.