

Social networks improve leaderless group navigation by facilitating long-distance communication

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Abstract Group navigation is of great importance for many animals, such as migrating flocks of birds or shoals of fish. One theory states that group membership can improve navigational accuracy compared to limited or less accurate individual navigational ability in groups without leaders (“Many-wrongs principle”). Here, we simulate leaderless group navigation that includes social connections as preferential interactions between individuals. Our results suggest that underlying social networks can reduce navigational errors of groups and increase group cohesion. We use network summary statistics, in particular network motifs, to study which characteristics of networks lead to these improvements. It is networks in which preferences between individuals are not clustered, but spread evenly across the group that are advantageous in group navigation by effectively enhancing long-distance information exchange within groups. We suggest that our work predicts a base-line for the type of social structure we might expect to find in group-living animals that navigate without leaders [*Current Zoology* 58 (2): 329–341, 2012].

Keywords Collective motion, Social networks, Group navigation, Network motifs, Many-wrongs principle, Individual-based model

Many animals navigate in groups (Krause and Ruxton, 2002; Simons, 2004, and references therein). Accurate and cohesive navigation is important for group-living animals when searching for food, when migrating, and for them to gain the benefits of group membership, such as reduced predation (Krause and Ruxton, 2002). Group navigation directly affects the dispersal patterns of animals and therefore possibly population and evolutionary dynamics (Simons, 2004). In theory we can distinguish between two mechanisms for group navigation. The first mechanism, known as the “Many-wrongs principle”, assumes that all individuals possess a similar amount of information and that the pooling of this information in groups results in more accurate navigation, as individual navigation errors are suppressed by group cohesion (Bergman and Donner, 1964; Simons, 2004). The second mechanism suggests that few informed individuals lead or guide the rest of the group (e.g. Couzin et al., 2005). In reality it is likely that a combination of these two mechanisms occurs, but here we focus on the first concept and therefore leaderless group navigation.

Empirical work on different species of birds has

found that flocks navigate more accurately than singletons (Bergman and Donner, 1964; Biro et al., 2006). Other research suggested that this was not the case (Benvenuti and Baldaccini, 1985). To date, the strongest support for the Many-wrongs principle is provided by experiments with humans (Faria et al., 2009). It has been suggested that many confounding factors covarying with group size, such as varying individual navigational ability or navigation strategy, could dilute the observable effects (Faria et al., 2009; Biro et al., 2006). This highlights the importance of theoretical approaches that allow the systematic investigation of the possible mechanisms of group navigation.

Theoretical investigations of collective motion often rely on individual-based models which have been essential in demonstrating how group movement and navigation could emerge from simple rules and entirely local interactions between individuals (Reynolds, 1987; Couzin et al., 2005; Codling et al., 2007). Using such models, the Many-wrongs principle has been simulated for groups moving towards a fixed target position (Codling et al., 2007) or in a fixed target direction (Grün-

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baum, 1998) where the latter is equivalent to moving towards a target position at infinity. Grünbaum suggests improved navigation for larger groups. Interestingly, Codling and co-workers suggest that at low levels of environmental turbulence or noise, individuals derive a navigational benefit from group membership, while this is not the case for high levels of environmental turbulence.

Previous theoretical work has greatly improved our understanding of the possible mechanisms for group navigation in animals but has not considered social connections between individuals. Many group-living animals show social preferences for particular individuals (Croft et al., 2008, Whitehead, 2008). These inter-individual preferences affect the movement of animals within groups and the movement of groups as a whole. For example, guppies *Poecilia reticulata* prefer to shoal with familiar conspecifics (Griffiths and Magurran, 1999) and the majority of pedestrians walk in small social groups (Moussaïd et al., 2010).

We explicitly distinguish between the underlying social preferences and the interactions between individuals. Often, the social preferences of animals, possibly a result of familiarity or kinship, change slowly over time. In contrast, the interactions between individuals, such as collision avoidance, change more frequently and are often determined by spatial proximity. By representing individuals as “nodes” and interactions or social preferences as connections or “edges” between nodes, we can use network theory to express both social preferences and interactions between individuals (Bode et al., 2011b). In our research, we assume that the “social network” of underlying preferences remains unchanged over time, whereas interactions between individuals change quickly and are based on spatial proximity. In our framework social preferences of different strength impact on interaction preferences between individuals to a varying extent.

This outlines the general approach of our ongoing work to investigate the impact of social networks on group movement dynamics. We focus on continuous group movements and have argued that social networks could play an important role in the movements of animals at the group and population levels (Bode et al., 2011b). Extending a previously developed and biologically relevant framework for modelling collective motion (Bode et al., 2011a), we have demonstrated how social networks could affect the formation of groups at the population level, the positioning of individuals within groups and detailed leader-follower dynamics in

non-navigating groups (Bode et al., 2011c). Elsewhere, we explore the role of social networks in group navigation with leaders (Bode et al., 2012). In this paper, we hypothesise that underlying social networks can impact on leaderless group navigation (Many-wrongs principle). We address the question of which, if any, social network is the most beneficial to leaderless group navigation by simulating navigating groups with specifically generated underlying social preference structures.

1 Materials and Methods

1.1 Model

We simulate groups of N individuals, represented by position vectors x_i and instantaneous velocity vectors v_i ($i=1, 2, \dots, N$), navigating through continuous two-dimensional space towards a fixed (unit length) target direction vector, t_{true} . Each individual balances two behavioural states. The first state implements individual navigation. In the second state individuals follow the commonly adapted “Avoidance-Alignment-Attraction” approach (e.g. Reynolds, 1987; Couzin et al., 2005) and interact with other group members within their sensory zone (a circle of radius r_A , with an omitted blind angle α , centred on the individual). The sensory zone of individuals is divided into hierarchical interaction zones of radius r_R , r_O and r_A which dictate the interaction between individuals, as described below ($r_R < r_O < r_A$). We assume that all individuals react to their environment with an identical stochastic rate and implement individual updates according to the following pseudo-code:

(1) PICK individual i at random ($i=1, \dots, N$; equal probabilities, with replacement).

(2) IF $r < p_{target,i}$, $r \sim U(0,1)$, r a random number THEN obtain preferred movement direction w_i by aligning with t_{true} (navigation error, see below).

(3) ELSE

PICK individual j at distance $d_j = |x_i - x_j|$ from i ($d_j < r_A$) with probability p_j (see below).

IF $d_j < r_R$ THEN w_i is directly away from j (repulsion).

IF $r_R < d_j < r_O$ THEN $w_i = v_j$ (alignment).

IF $r_O < d_j < r_A$ THEN w_i is directly towards j (attraction).

(4) turn v_i by at most β degrees per second towards w_i .

IF i navigates, repulses or aligns THEN move i at speed v_O along v_i .

IF i attracts THEN move i at speed $2v_O$ along v_i .

Based on comparisons to empirical results (Bode et al., 2010), individuals move at different instantaneous

speeds according to their behaviour. One algorithmic update step of our model has length Δt seconds and consists of N realisations of steps (1)–(4). In simulations, we record the positions of individuals every $T=\lambda\Delta t$ seconds, where $\lambda \geq 1$. Therefore, the movement of individuals between two consecutive model outputs is the sum over a number of updates. We fix $\Delta t=0.05$, but refer the reader to previous work on the effect of this parameter (Bode et al., 2010).

Throughout, without loss of generality, we set t_{true} to be the x-axis. We implement imperfect individual navigation in two ways. First, the size of the probability $p_{target,i}$ denotes a trade-off between social interactions and navigation for individuals (see steps (2) and (3) above). The larger $p_{target,i}$, the more i focuses on navigating, whilst ignoring conspecifics and vice versa. Second, at the start of simulations, the target direction perceived by individuals is perturbed once, rotating t_{true} by an angle drawn from a uniform distribution over the interval $[-\mu, \mu]$ degrees.

This implementation of navigation ability contrasts with previous work in which the navigation ability of individuals is represented by an error that is added to the target direction at each update (e.g. Codling et al., 2007, Guttal and Couzin, 2010). We come back to this point in the discussion. Our approach could be interpreted as individuals having randomly biased information about a target direction which they follow with more or less certainty.

Two factors determine the probability p_j for choosing individual j in step (3) above: the distances between individuals and the social preference individuals have for each other. Suppose individual i has neighbours $k=1, \dots, k_i$ (defined by not being in the blind spot of i at distances $d_k=|x_i-x_k|$ from i , where $d_k < r_A$). Furthermore, denote the preferences of individual i for its neighbours by $e_{ik} \geq 0$. Then individual j is chosen with probability,

$$p_j = (e_{ij} / d_j) / (\sum_k (e_{ik} / d_k)).$$

with a cut-off for values of d_k close to zero, but in practice this is almost never activated (extending previous work that only considered weighting of p_j according to the value of d_j ; Bode et al. 2011a).

We can vary the preferences e_{ab} individuals a and b have for each other across the group. This means that an updating individual is more likely to react to the position and movement of one or a number of specific individuals as opposed to the rest of the group for a given fixed distance between individuals (“preferential updating”). Therefore, the values of e_{ab} denote weighted edges (preferences) between nodes (individuals) a and b

in a network of N nodes in total. In this way we can impose a weighted social network of preferences on the interactions in our modelling framework. We consider undirected networks, where $e_{ab}=e_{ba}$, assuming that preferences between individuals are reciprocated.

Simulations of our model are performed in unbounded space and are started from random initial positions and orientations within a box of side-length r_O , to ensure that individuals are aggregated initially. To avoid recording transitional data after starting simulations, we run simulations for 500 seconds and only record data from the last 10 seconds of our simulations, as suggested previously (Couzin et al., 2005). Parameter values were chosen to ensure that in the control case (all e_{ab} have the same value) stable and coherent groups formed. Since this work is intended as an illustration of principle, we confined the parameter space: $N=100$, $T=1s$, $r_A=150m$, $r_O=20m$, $r_R=3m$, $v_O=3m/s$, $\alpha=270^\circ$, $\beta=100^\circ/s$.

For further details, examples for the biological relevance of our approach and a biological interpretation of our algorithm we refer the reader to the supplementary discussion and previous work (Bode et al., 2010; 2011a; 2011c).

1.2 Generation of underlying networks

To simplify our analysis we restrict the weights of edges in underlying social preference networks to “strong” and “weak” connections. If they are not linked by strong preferences, individuals in the social networks we consider are connected by weak connections. This takes into account that individuals can react to conspecifics even if they do not have strong preferences for them. Typically we set the connection weights to $e_{ab} = 1$ for weak connections and $e_{ab} = s = 100$ for strong connections (the relative difference between these measures is the only thing that matters). We use two methods to distribute strong preferences across groups:

Erdős-Rényi method: Strong connections are added independently from the set of all possible connections with probability p_{erdos} (Erdős and Rényi, 1960).

“Preferential attachment” method: To include strong connections, we start with a small number of nodes m_{sf} , then add nodes and m_{sf} strong connections connected to them, attaching the new node to other nodes with strong connections by preferential attachment (Barabási and Albert, 1999).

This allows us to construct social networks in which few individuals have high numbers of strong connections (“Preferential attachment” method) or randomly generated networks which cover many possible scenarios for large enough ensembles (Erdős-Rényi method).

These networks of preferences contrast with the control case in which all individuals have equal preference for each other. Unless otherwise stated, we generate new networks for each simulation.

1.3 Data analysis

From simulations, we record summary statistics quantifying cohesion, deviation from t_{true} of groups and the displacement of groups along t_{true} .

We define cohesive groups based on the perception range of individuals. Individuals are considered to be connected if they are within a distance of r_A from each other. A group is defined as a set of individuals that are connected to each other, either directly or via other individuals. Therefore, individuals in separate groups are further than r_A from each other. Since we are interested in group navigation, we focus on cases when only one cohesive group is present, but record the proportion of simulations that resulted in more than one group (probability of fragmentation, $P(Fragmentation)$). To find the direction of motion of a group, we measured, d_{group} , the normalised vector between the centre of mass, CoM , of the group ($CoM = \sum_i x_i/N$) ten seconds before and at the end of our simulations, as suggested previously (Couzin et al., 2005).

The navigation accuracy of groups is measured by the “deviation from the target direction”, φ . We define this as $\varphi = \arccos(d_{group} \cdot t_{true})/180^\circ$, where $a \cdot b$ denotes the scalar product of the vectors a and b . Values of φ close to zero correspond to high navigation accuracy, whereas higher values ($0 < \varphi < 1$), correspond to lower navigation accuracy. If we simulated single individuals with maximal navigation error $\mu = 180^\circ$, as described above, we would find on average $\varphi = 0.5$.

To investigate the extent to which groups travel in the target direction in the course of a simulation, we measure the displacement of groups in the target direction. Since t_{true} is the x-axis, we record the size of the x-component of the centre of mass of the group at the end of the simulation.

1.4 Relating network structure to navigation performance

We collect network summary statistics for the suite of generated social networks to assess what type of networks result in more accurate group navigation. All network statistics are calculated in R (R Development Core Team, 2009) using the “igraph” package (Csardi and Nepusz, 2006). We analyse the network structures as binary networks by thresholding the networks so that we examine the structure of the strong connections only. Therefore, the degree of a node is the number of strong

connections the node or individual has in the network. The average degree, coefficient of variation and skewness are found from the distribution of degrees for networks. The average path length counts the average number of steps along (strong) connections to get from any node to any other node in the network. These network summary statistics indicate how the strong connections are distributed across the group.

To measure the clustering of connections in our networks, we count the number of times particular sub-structures, or motifs, appear in the networks. Network motifs have been used widely to distinguish between networks or to characterise networks (Milo et al., 2002; Shen-Orr et al., 2002). Fig. 1 illustrates the motifs we consider and explains why we choose these motifs. The “clustering coefficient” is often used to quantify the clustering of connections in networks (e.g. Newman, 2010). It measures the probability for two nodes that have a connection to the same node to be connected themselves. This measurement is captured in the count for motif 7. High counts of this motif correspond to a high clustering coefficient.

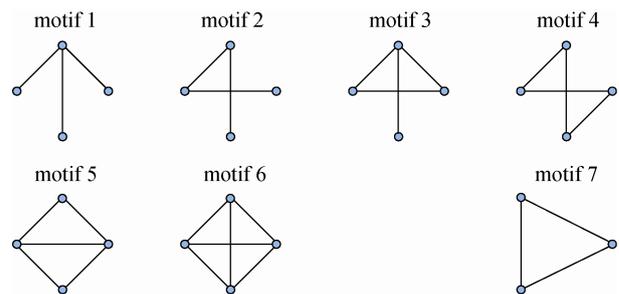


Fig. 1 Illustration of network motifs used to characterise underlying social networks

We count the number of times these different sub-structures or connectivity patterns occur within the social networks we generate. Differences in occurrence of network motifs indicate differences in the structure between networks. In line with other work on network motifs, we only consider connected motifs in which all nodes in the motifs can be reached from all other nodes via one or multiple connections. We do so because in this analysis we are interested in patterns of strong social connections and not their absence. The presence or absence of strong social connections and their distribution across individuals is captured in other network summary statistics introduced in the main text. We consider all possible connected sub-structures between four individuals as this provides a manageable number of substantially differing connectivity patterns. Motif 7 is included because of its connection to the clustering coefficient (see main text).

To assess the impact of network properties on navigation accuracy we use linear regression separately for each network statistic. We cannot fit a general linear model including more than one network statistic to the data, as any two of the network statistics may depend on

each other in a non-trivial way. We control for false discoveries in our multiple comparisons by using adjusted significance thresholds (Bonferroni correction).

2 Results

We assume that on average all individuals have the same knowledge and certainty of the true target direction (i.e. all individuals have the same value of μ and $p_{target,i}$). We consider different underlying social networks and investigate how varying μ , the size of the error in individual navigation, and $p_{target,i}$, individuals' probability to align with the target direction, affects the deviation from the target direction, ϕ , of simulated groups. On a coarse level, the simulations produce roughly similar results for different underlying social networks (Supplementary figure 1). For $p_{target,i}=0$, individuals do not navigate and ϕ takes high values. Generally, for increasing μ , the quantity ϕ increases and for increasing $p_{target,i}$ it decreases. However, large values of $p_{target,i}$ in combination with large values for μ lead to frequent fragmentation of groups. This is due to the trade-off between navigation and reacting to conspecifics inherent in $p_{target,i}$. For large values of $p_{target,i}$

individuals mostly ignore their conspecifics and groups fragment if μ is large enough to ensure that individuals disperse in different directions.

Fig. 2 shows ϕ and the proportion of fragmenting groups, $P(\text{Fragmentation})$, for varying μ and $p_{target,i}=0.05$ and $p_{target,i}=0.3$. Fig.2a shows that groups with underlying social networks consistently deviate less from the target than the control case. The differences in ϕ are small (about 3°), but over long times this results in large errors. We use Wilcoxon signed rank tests on the mean values to assess the significance of these differences: Control vs Random (C-R): $W=66$, $P=0.000977$; Control vs Preferential attachment (C-PA): $W=66$, $P=0.000977$; Preferential attachment vs Random (PA-R): $W=17$, $P=0.175$. While the differences between the control case and the two types of underlying social networks are statistically significant, the differences between the two types of underlying social networks are not (using a significance threshold of $0.05/3=0.017$, adjusted for three comparisons.). For $p_{target,i}=0.3$ (Fig.2c), this improvement in navigation accuracy for groups with underlying social networks disappears; although in part this is only due to the adjusted significance thresh-

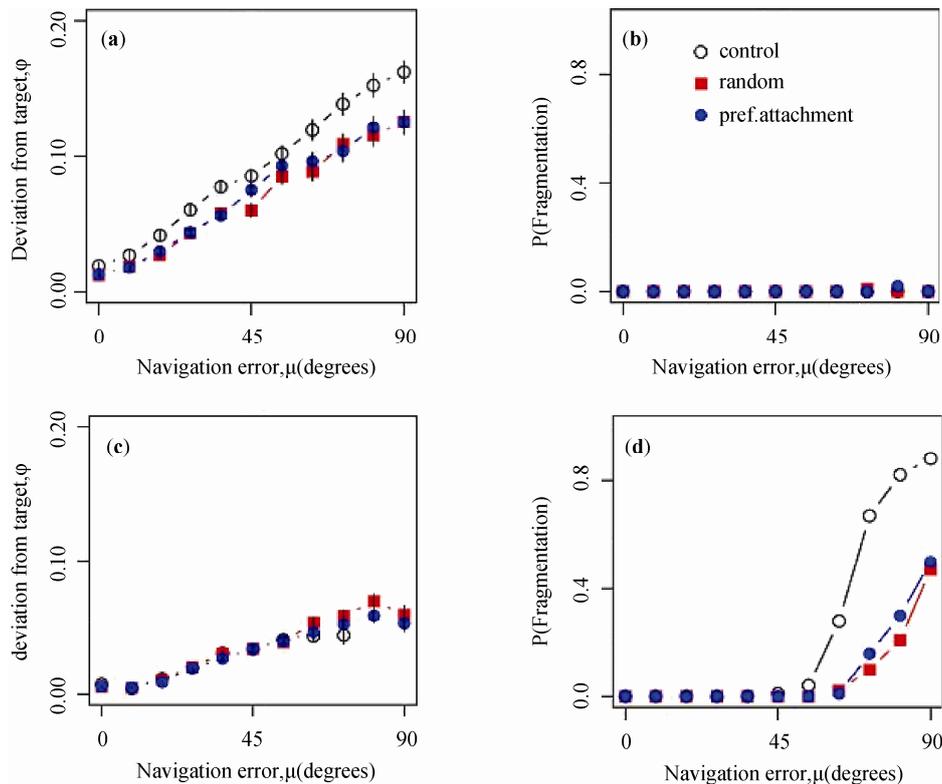


Fig. 2 Deviation from the target direction, ϕ , and proportion of fragmented groups

$P(\text{Fragmentation})$, for varying navigation error, μ , and fixed probability to align with the target direction, $p_{target,i}$. (a,b) $p_{target,i}=0.05$, (c,d) $p_{target,i}=0.3$, networks: $p_{endos}=0.21$ for random networks and $m_{sf}=11$ for preferential attachment networks. Error bars show standard errors. Results are averaged over 100 replicates. Underlying social networks lead to reduced ϕ for low $p_{target,i}$ (a) and in reduced $P(\text{Fragmentation})$ for high $p_{target,i}$ (d), compared to the control case.

old (*C-R*: $W=19$, $P=0.734$; *C-PA*: $W=25$, $P=0.820$; *PA-R*: $W=57$, $P=0.0322$). For $p_{target,i}=0.05$ most groups are coherent, while for $p_{target,i}=0.3$ groups fragment for $\mu > 45^\circ$ (see Fig.2b and d, respectively). In the case of fragmenting groups, we find that underlying social networks improve the coherence of groups.

Our simulations suggest that for low values of $p_{target,i}$, underlying social networks result in reduced deviation from the target direction and for high values of $p_{target,i}$, underlying social networks improve cohesion of navigating groups.

To establish that the findings in Fig.2 are a result of underlying social networks and to test their robustness, we gradually increase the strength of the strong connections, s , in the underlying social networks, keeping the strength of weak connections constant. Fig.3 shows that increasing s from $s=1$ (control case, all connections have equal strength) results in a decrease of ϕ (Fig.3a). The probability for groups to fragment is not affected by this (Fig.3b). The displacement of groups in the target direction also increases with increasing s (Fig.3c). We find this effect, at least qualitatively, for different group sizes and underlying networks of different densities (see Supplementary figures 2, 3, and 4). The supplementary figures show that the trends in the summary statistics for increasing s can be rather noisy. In addition, for our parameters and number of replicates, we could not find the same trends in small groups of ten individuals, for example (data not shown). This may be due to the variation in initial conditions and other stochastic effects in our model (see also below). However, the qualitative trends are robust over a range of parameter values.

Having established that social networks can have an

effect on group navigation, we proceed to investigate which network characteristics lead to the best group performance. We generate large numbers of random underlying social networks, typically twenty-thousand, keeping all other model parameters fixed to values for which underlying social networks result in improved group navigation for non-fragmenting groups, as established above (see Table 1 and for an illustration Fig.4). Throughout this analysis we threshold networks to only consider the structure of the strong connections.

As a first step, we generate random underlying social networks with varying numbers of strong connections. We find that the number of strong connections present, captured by the average degree of the underlying social networks, has a statistically significant effect on ϕ (Table 1, first column and Fig.4). Higher average values of ϕ correspond to higher average degrees than lower average values of ϕ (Fig.4c). We find that on average the lowest values of ϕ correspond to network structures with slightly less than half of all possible connections (Fig.4c). Since the number of connections present in networks strongly influences network motif counts and therefore makes it difficult to distinguish between the effect of the particular structure of motifs, we will refrain from discussing the results for this case and only list them in Table 1.

To control for these effects, we fix the number of strong connections we include into the underlying social networks (Table 1, second column). Again, we find statistically significant effects of certain network characteristics on the navigation performance of groups. Most prominent is the increase in ϕ with increasing coefficient of variation of the degree distributions (Supplementary figure 5). The coefficient of variation measures

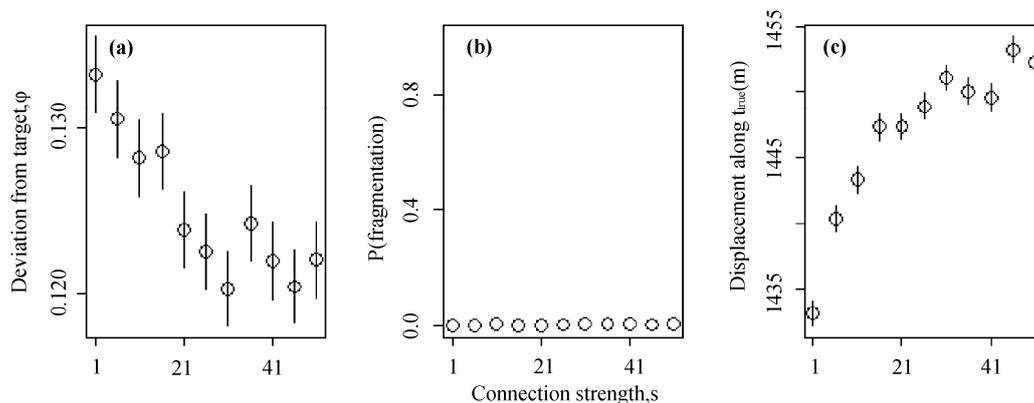


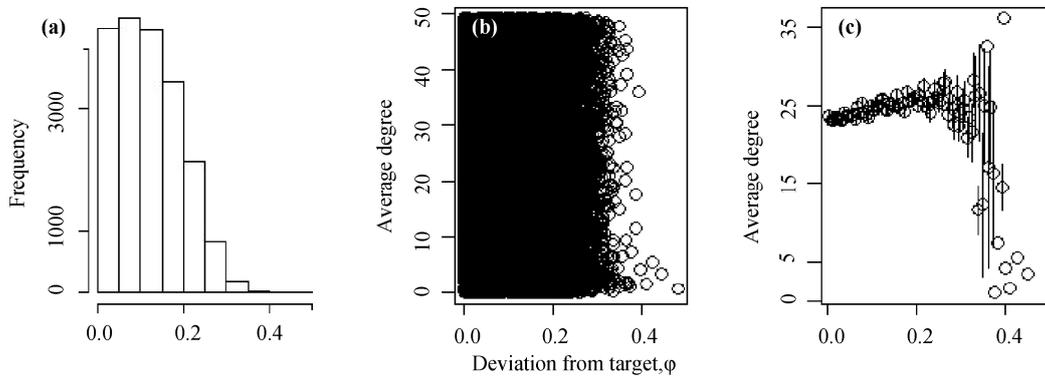
Fig. 3 The effect of increasing s , the strength of the strong connections, s , in randomly generated underlying social networks

We show the deviation from the target direction, ϕ (a), the proportion of fragmented groups (b), and the average displacement of groups in the target direction (c). Error bars show standard errors. We use 1000 replicates per parameter combination. Network parameters as in Fig.2, and $p_{target,i}=0.1$, $\mu=90^\circ$. The decrease in ϕ and the increased displacement in the target direction with increasing s indicate a clear impact of underlying networks on navigating groups

Table 1 Linear regression with deviation from the target direction, φ , as response variable and network summary statistic as explanatory variable

Network statistic	Random networks	Random with fixed number of edges	20 replicates of top 1000 networks
av. path length	$F_{1,19804} = 8.87, P = 0.003^{**}$	$F_{1,19966} = 0.369, P = 0.544$	$F_{1,19972} = 0.703, P = 0.402$
av. degree	$F_{1,19804} = 49.1, P = 2.55 \times 10^{-12}^{**}$	fixed	fixed
CV of degree distrib	$F_{1,19773} = 0.018, P = 0.894$	$F_{1,19966} = 9.93, P = 0.002^{**}$	$F_{1,19972} = 0.056, P = 0.813$
Skewness of degree distrib.	$F_{1,19773} = 4.91, P = 0.027$	$F_{1,19966} = 0.197, P = 0.657$	$F_{1,19972} = 1.46, P = 0.227$
Motif 1 count	$F_{1,19806} = 23.9, P = 1.03 \times 10^{-6}^{**}$	$F_{1,19966} = 1.84, P = 0.175$	$F_{1,19972} = 0.004, P = 0.952$
Motif 2 count	$F_{1,19806} = 23.1, P = 1.58 \times 10^{-6}^{**}$	$F_{1,19966} = 7.15, P = 0.008^*$	$F_{1,19972} = 0.282, P = 0.595$
Motif 3 count	$F_{1,19806} = 4.16, P = 0.041$	$F_{1,19966} = 4.59, P = 0.032$	$F_{1,19972} = 0.650, P = 0.420$
Motif 4 count	$F_{1,19806} = 3.93, P = 0.048$	$F_{1,19966} = 0.056, P = 0.814$	$F_{1,19972} = 0.0003, P = 0.987$
Motif 5 count	$F_{1,19806} = 56.3, P = 6.42 \times 10^{-14}^{**}$	$F_{1,19966} = 7.21, P = 0.007^*$	$F_{1,19972} = 0.436, P = 0.509$
Motif 6 count	$F_{1,19806} = 55.1, P = 1.19 \times 10^{-13}^{**}$	$F_{1,19966} = 3.022, P = 0.0822$	$F_{1,19972} = 0.0248, P = 0.875$
Motif 7 count	$F_{1,19806} = 2.22, P = 0.136$	$F_{1,19966} = 0.005, P = 0.943$	$F_{1,19972} = 0.068, P = 0.795$

To avoid false discoveries due to multiple comparisons we use the adjusted significance thresholds (Bonferroni correction) $0.05/11=0.0045$ (**) and $0.1/11=0.0091$ (*). Parameters for groups: $N=50, p_{target,i}=0.1, \mu=72^\circ, s=100$; and networks: p_{erdos} uniformly distributed between 0 and 1 for the first column, number of edges fixed to the average equivalent of $p_{erdos}=0.47$ for the second and third column (intercept for linear model fit in first column). The networks in the third column are 20 replicates of each of the 1000 networks which led to the lowest φ out of the networks created for the second column. Results are shown for 20000 independently generated networks (one simulation per network) in columns one and two. Differences in the degrees of freedom for the linear model fits are a result of fragmented groups and networks with $p_{erdos}=0$.

**Fig. 4** Deviation from the target direction, φ , for one simulation for each of 20000 independently generated random underlying social networks with probability for a connection to be strong, p_{erdos} uniformly distributed between 0 and 1

(a) Histogram for the distribution of the values for φ . (b) φ plotted against the average degree of the underlying social networks. (c) Mean over average degrees across 100 bins of φ of equal size. Error bars show standard errors. A clear trend becomes visible in the data for $\varphi < 0.3$. For larger values of φ there is insufficient data. Linear regression on the raw data in (b) confirms the statistical significance of the trend observed in (c) (see Table 1).

the dispersion of distributions and this finding therefore suggests that it is beneficial for group navigation if the strong connections are distributed more evenly across individuals. Furthermore, we find a significant increase in φ with decreasing counts of motif 2 and a decrease in φ with decreasing counts of motif 5. Both motifs are substructures with four nodes. Motif 2 includes three edges, whereas motif 5 has five edges (Fig. 1). From this we tentatively conclude that clustering of connec-

tions on small subsets of nodes (motif 5) is on average detrimental to navigational accuracy. Interestingly, changes in the counts of motif 7 did on average not have a significant effect on φ . This suggests that only considering the clustering coefficient and no network motifs would have provided less insight into the system. The fact that it is beneficial to have a lack of motif 5 but not motif 7 suggests that clustering of nodes only decreases navigation accuracy if the networks are characterised by

closely clustered regions of four or more nodes. A detailed explanation as to why this finding is not reflected in counts of motif 6 and 1 is beyond the scope of this work. One possibility is that as a result of our network construction technique and the number of strong connections included, there may be insufficient numbers of motifs 6 and 1 for significant differences between networks.

So far our results suggest that including slightly fewer than half of all possible strong social connections (average degree) that are equally distributed across all individuals (low coefficient of variation of degree distribution) into underlying social networks results on average in better group navigation than for other networks.

Finally, to test the impact of initial conditions and to attempt to characterise beneficial underlying social networks further, we use replicates of networks that result in the lowest values of φ in the previous set of networks. We find that initial conditions have a strong effect on group navigation accuracy in our simulations. While the deviation from the target direction, φ , of the chosen networks in the previous simulations was below 0.05 (see Supplementary figure 5a), the new simulations result in values of φ larger than 0.4 (see Supplementary Fig.6). Furthermore, we find no significant effect of any network summary statistic on the group navigation performance (Table 1, third column). In conclusion, the random initial conditions in our simulations cause a lot of variation between simulations and while we can detect differences between networks on a coarse scale, it is not feasible to find one “optimal” network that results in the smallest possible deviation from the target direction for the set of parameters investigated.

3 Discussion

Our results suggest that under some circumstances even randomly generated underlying social networks can improve the navigation accuracy of leaderless groups or reduce their risk to lose cohesion. The social networks we impose differ from the control case in which all individual have equal interaction preferences for each other. Our findings only hold on average over large ensembles of networks and simulations and there is considerable variation across simulations with identical underlying social networks. This has to be taken into account when interpreting our results.

On an evolutionary scale for species occurring in large numbers in many large groups, it appears that if better navigation on average is required, then any distribution of social preferences (random) might be bene-

ficial. This could apply to small fish that move in shoals and show social preferences to particular conspecifics (e.g. guppies, Griffiths and Magurran, 1999 or sticklebacks, Ward et al. 2002).

Small groups of less than fifty individuals may navigate more accurately if they have specifically “optimised” social networks. However, our research does not focus on such small groups and without a specific context it is difficult to pinpoint the exact structure of “optimal networks”. For example, the initial conditions we have used may be far more general than what occurs in animal groups. We might expect that positioning within groups may be intricately linked to positions in underlying social networks (Hemelrijk, 2000, Bode et al., 2011c) and knowledge or motivation of individuals (Krause and Ruxton, 2002). Furthermore, the navigational accuracy of individuals may be linked to their social position in a group.

Our search for an “optimal network” suggests a possible mechanism for our finding that underlying social networks can improve the navigation accuracy of groups. Recall that networks with slightly fewer than half of all possible strong connections and with a low coefficient of variation of the degree distribution result, on average, in a smaller deviation from the target direction. Network motif counts indicate that a particular type of clustering of network connections is detrimental to navigation performance. We suggest that these network characteristics result in a situation in which individuals do not only react to small subgroups of nearby and preferred conspecifics, but have preferred individuals nearby and at larger distances from them in the group. In such cases our preferential updating scheme results in more efficient long-range communication when compared to purely distance-dependent interactions in the absence of social preferences. Long-range communication enhances group coherence and information pooling.

The simulation model we use differs in several aspects from other individual-based models for group navigation. For a discussion and justification of our algorithm with asynchronous updates, the model output and update rate parameters, T and Δt , differing behaviour-dependent speeds and distance-dependent interaction probabilities p_j , we refer the reader to previous work on our theoretical framework (Bode et al., 2010; 2011a;c). As mentioned in the methods section, our implementation of the navigation error differs from other models in the literature. To test the effect of this we have repeated the simulations for Fig.2, implementing a dynamic navigation error similar to Codling et al (2007).

Supplementary figure 7 shows that we recover the results from Fig.2a,b, but not for Fig.2c,d. This is because the alternative implementation of the navigation error results in fewer group fragmentations for our choice of parameters. Since we predominantly investigate improved navigation in cohesive groups we have not performed extensive parameter scans in an attempt to reproduce Fig. 2c,d.

Earlier studies on the Many-wrongs principle have highlighted the importance of group sizes in this context (Codling et al., 2007; Faria et al., 2009). While we consider different group sizes (Supplementary figures 2, 3, and 4), a systematic investigation of group size effects on our results is beyond the scope of this paper.

In conclusion, our results serve as an illustration of principle that social networks can affect leaderless group navigation and we suggest one possible mechanism. Our work suggests interesting avenues for future research. For example, considering the potential benefits of any social preferences, should all migrating animals display social preferences? If they do not, what is different about them? Are better informed individuals usually better socially connected in collectively moving groups?

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Supplementary Discussion

Model implementation

The exact algorithmic update of each individual over one update step, Δt , has no direct physical meaning. We observe the sum of a number of updates. The output of our model is obtained by recording the positions of individuals every $T = \lambda \Delta t$ seconds, where $\lambda \gg 1$. Therefore, the movement of individuals between two separate model outputs consists of an average over the sum of a number of updates (averaging over changes in instantaneous velocity) and the overall effect is for each individual to compose a kinetic average of its surroundings. Increasing Δt for fixed T results in the model output being composed of the average of an increasing number of shorter “steps” while the average speed of individuals is constant. For example, low values of Δt result in more synchronized and cohesive groups than higher values of Δt (Bode et al., 2010). For more details on the effect of the parameter Δt we refer the reader to an earlier publications relating to this model (Bode et al., 2010; 2010b).

Our assumption of higher attraction speeds is based on the hypothesis that individuals need to move faster when they are interacting with individuals further away (e.g. to catch up with them), but is also necessary for the recovery of realistic distributions of individual speeds (Bode et al. 2010a).

In our model individuals update asynchronously, sample information from their sensory zone and decide probabilistically between navigating and interacting with other group members. Other models implement synchronous updates, explicitly include averaging over behaviours and use relative weightings to balance navigation and interactions between group members (e.g. Couzin et al., 2005; Codling et al. 2007). We argue that the difference between our model and the ones mentioned above lies predominantly in the algorithmic implementation. While this does affect the dynamics, the basic ideas underlying our model and other models are similar in that individuals react to multiple other group members, averaging over pairwise interactions, and balance navigation against these interactions with other group members. Previous work demonstrates that our approach produces dynamics qualitatively comparable to the dynamics produced by other models and that our approach provides a good qualitative fit to key features of empirical systems in one, two and three spatial dimensions (Bode et al. 2010; 2010b; 2011a). These pub-

lications also provide more detailed comparisons of our approach to other modelling approaches.

Long-range information transfer versus social networks

Considering interactions/information transfer between individuals, we can choose interaction ranges between the limits of two extreme cases: all-to-all communication and very localised interactions (extreme case could even be physical interactions, such as collisions). We could ask whether including social connections leads to significantly different results compared to a model moving closer to all-to-all interactions/communication than our model.

We have not tested this and can therefore not give a definite answer. What our work demonstrates is that given a certain framework of distance-dependent interactions, the inclusion of interaction biases can lead to effective long-range information transfer. Essentially this is a demonstration of principle, suggesting a possible mechanism for long-range interactions in animal groups whereby local interactions can still result in effective long-range interaction transfer if they are occasionally supplemented by socially motivated long-range interactions. This is interesting, especially in the light of recent findings suggesting that interactions between schooling fish are predominantly short-range (Katz et al., 2011; Herbert-Read et al., 2011).

“Optimal” networks: random versus preferential attachment

In our search for optimal networks we have only considered social networks generated randomly. Over large ensembles these randomly generated networks should cover a wide range of possible scenarios, including networks similar to the ones generated by preferential attachment. Our findings seem to indicate that network generated by preferential attachment with few highly connected individuals may result in reduced group navigation accuracy. However, in figure 2 we did not find evidence for this. Networks constructed by preferential attachment could provide an alternative mechanism for improved long-range communication via highly connected individuals. It may be that over the 20000 random networks we generated there were not sufficient numbers of networks similar to the ones generated by preferential attachment to allow for a conclusive comparison.

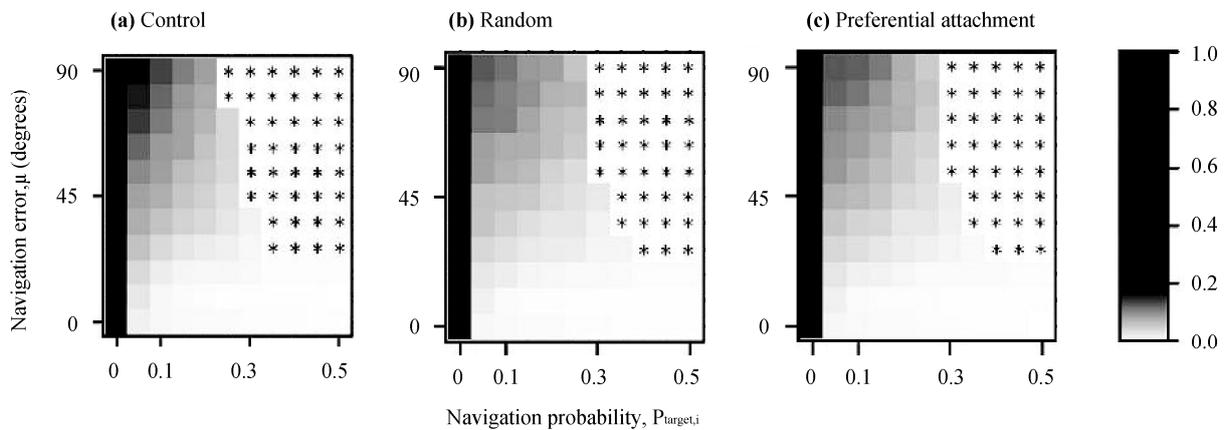
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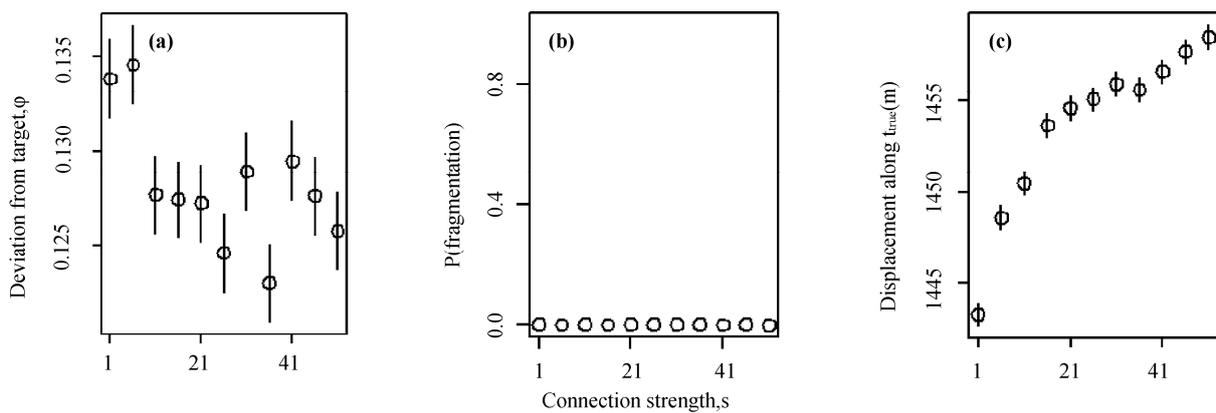
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Katz Y, Tunström K, Ioannou CC, Huepe C, Couzin ID, 2011. Inferring the structure and dynamics of interactions in schooling fish. *Proc.Natl. Acad. Sci. USA*, 108: 18720–18725.



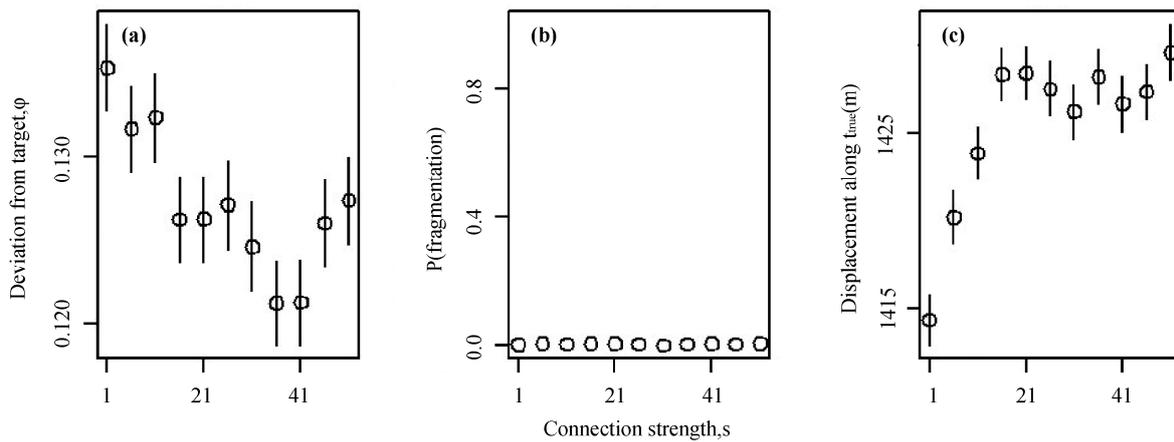
Supplementary Fig. 1 Deviation from the target direction, ϕ , for different values of the navigation error, μ , and probability to align with the target direction, $p_{target,i}$

The colour code indicates values for ϕ . The average values of ϕ of non-fragmented groups were considered in the analysis and only parameter combinations for which at least 75 percent of groups (out of 100 simulations) remained coherent are shown. Areas marked by asterisks in the upper right hand side of the plots are missing data due to group fragmentation. Parameter as given in the methods section of the main text. Note how ϕ increases for increasing μ and decreases for increasing $p_{target,i}$.



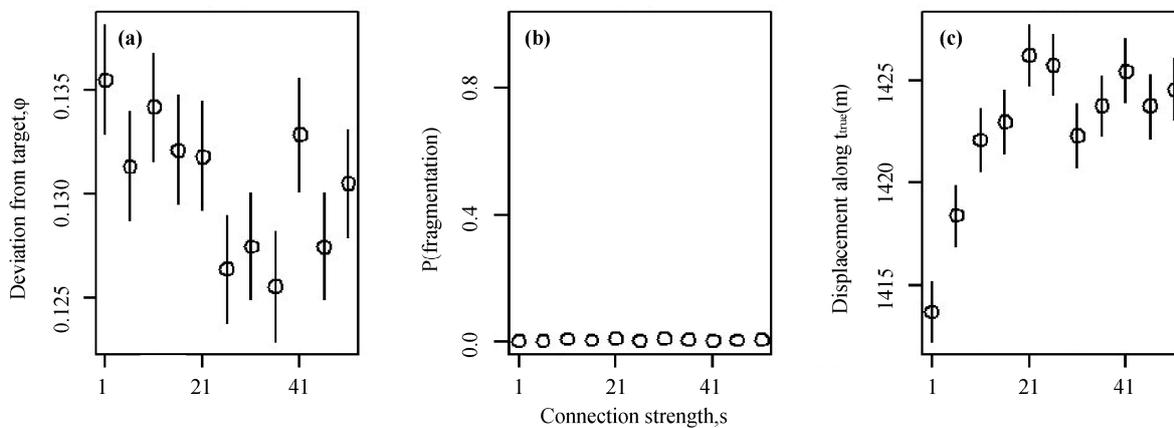
Supplementary Fig. 2 The effect of increasing s , the strength of the strong connections in underlying social networks

We show the deviation from the target direction, ϕ (a), the proportion of fragmented groups (b), and the average displacement of groups in the target direction (c). Error bars show standard errors. We used 1000 replicates per parameter combination. Only random underlying social networks are used. Parameters as in figure 2, but $N = 200$, $p_{target,i} = 0.1$, $\mu = 90^\circ$. Compare this to figure 3 in the main text. Although stochastic effects obscure the trends somewhat, the decrease in ϕ and the increased displacement in the target direction with increasing s indicate a clear impact of underlying networks on navigating groups.



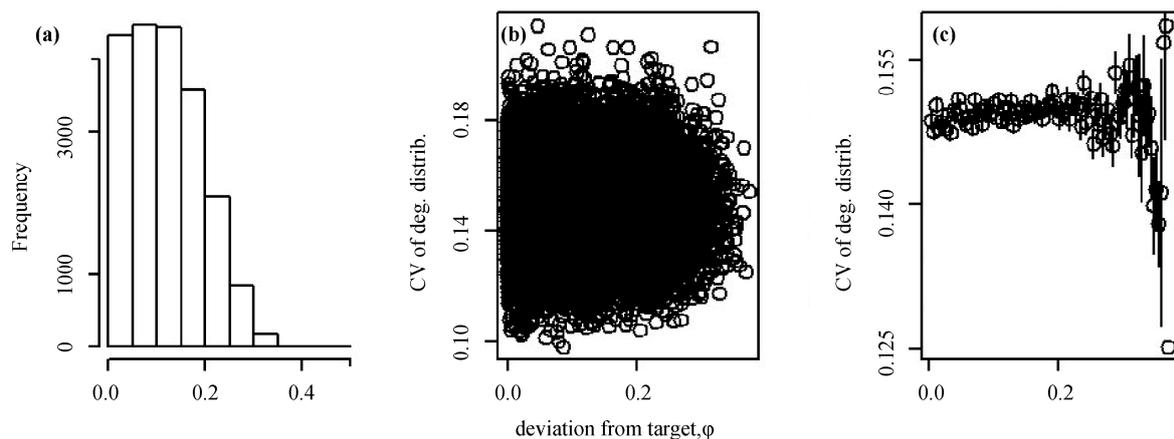
Supplementary Fig. 3 As supplementary figure 2, but $N = 50$, $p_{target,i} = 0.1$, $\mu = 90^\circ$

Compare this to figure 3 in the main text. Although stochastic effects obscure the trends somewhat, the decrease in ϕ and the increased displacement in the target direction with increasing s indicate a clear impact of underlying networks on navigating groups.



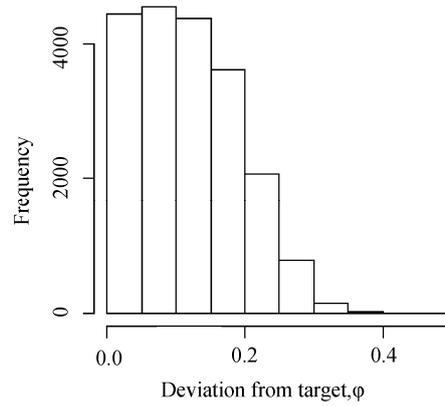
Supplementary Fig. 4 As supplementary figure 2, but $N = 50$, $p_{target,i} = 0.1$, $\mu = 90^\circ$, and $p_{erdos} = 0.4$

Compare this to figure 3 in the main text. Although stochastic effects obscure the trends somewhat, the decrease in ϕ and the increased displacement in the target direction with increasing s indicate a clear impact of underlying networks on navigating groups.



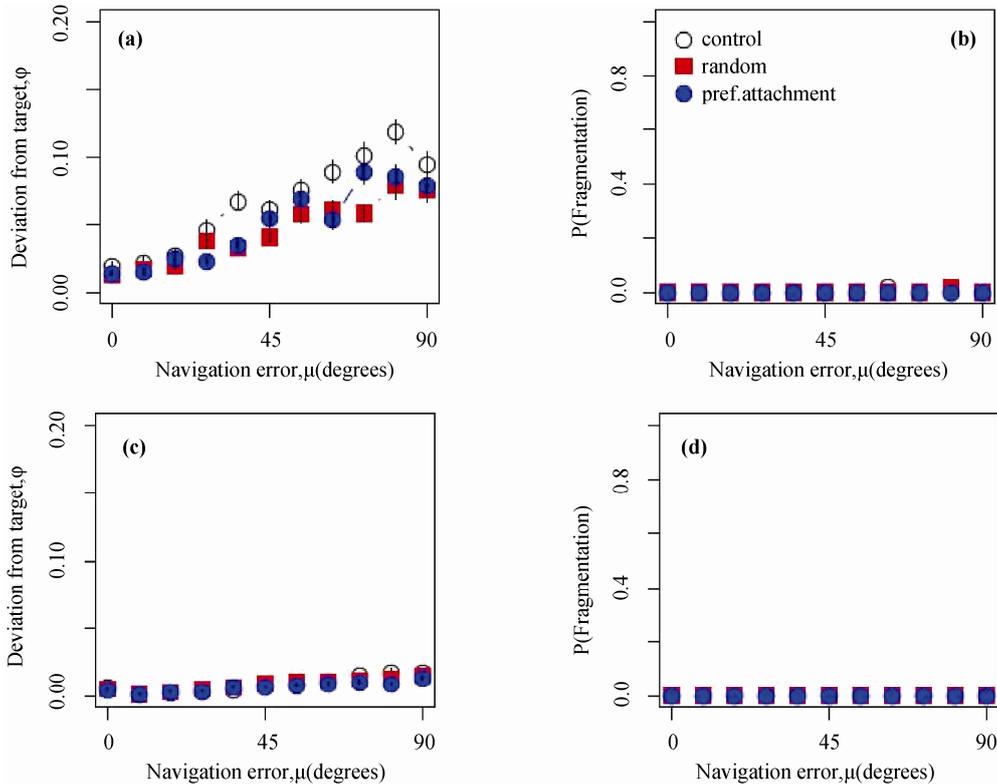
Supplementary Fig. 5 Deviation from the target direction, ϕ , for one simulation for each of 20000 independently generated random underlying social networks with fixed number of edges equivalent to $p_{erdos} = 0.47$

(a) Histogram for the distribution of the values for ϕ . (b) ϕ plotted against the coefficient of variation of the degree distribution of the underlying social networks. (c) Mean over coefficients of variation across 100 bins of ϕ of equal size. Error bars show standard errors. A trend becomes visible in the data for $\phi < 0.3$. For larger values of ϕ there is insufficient data (compare to (a)). Linear regression on the raw data in (b) confirms the statistical significance of the trend observed in (c) (see table 2 in the main text). Parameters as in table 2 in the main text.



Supplementary Fig. 6 Histogram for the values of the deviation from the target direction, ϕ for 20 simulations for each of 1000 independently generated random underlying social networks that resulted in low ϕ in one previous simulation

See main text and caption of table 2 for more detail. Parameters are given in table 2 in the main text. Compare this to the distribution of ϕ in supplementary figure 4. Despite the networks being selected for low ϕ , initial conditions result in a wide spread of ϕ .



Supplementary Fig. 7 Implementing a dynamic navigation error

Instead of rotating the true target direction individuals follow only once before the start of simulations, we rotate the perceived target direction each time individuals follow the navigation behaviour in the same way as for the non-dynamic navigation error. Compare this figure to figure 2 in the main text. We show the deviation from the target direction, ϕ , and the proportion of fragmented groups, $P(\text{Fragmentation})$, for varying navigation error, μ , and fixed probability to align with the target direction, $p_{\text{target},i}$. (a,b) $p_{\text{target},i} = 0.05$, (c,d) $p_{\text{target},i} = 0.3$, networks: $p_{\text{endos}} = 0.21$ for random networks and $m_{\text{sf}} = 11$ for preferential attachment networks. Error bars show standard errors. Results are averaged over 50 replicates. (a) Underlying social networks lead to reduced ϕ for low $p_{\text{target},i}$ compared to the control case. This implementation of the navigation error results in fewer group fragmentations and without extensive parameter scans we cannot reproduce the finding of figure 2 (d) in the main text that social networks lead to reduce group fragmentation for higher values of $p_{\text{target},i}$.