Diffusion, anti-diffusion, and the stability of animal groups

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Abstract

Group living animals form aggregations and flocks that remain cohesive in spite of internal movements of individuals. This is possible because individual group members repeatedly adjust their position and direction of movement in response to the position and motion of other group members. Recent literature has focused on investigating the 'interaction responses' that mediate group coordination empirically from tracking data of real animal groups of various species. Here, we develop a complementary theoretical approach in which we consider how the spatial organisation of a group would change in the complete absence of interactions. In this condition, the group would disperse in a way that can be characterised in terms of Fick’s diffusion equations. We can hence address the inverse theoretical problem of finding the individual level interaction responses that are precisely required to counterbalance diffusion and preserve group stability. We show that an individual-level response to neighbour densities in the form of a Weber’s law (a well-known law describing the functioning of sensory systems, which essentially corresponds to a response to gradients normalised over local densities) results in an ‘anti-diffusion’ term at the group level. On short time scales, this anti-diffusion restores the initial group configuration in a way which is reminiscent of methods for image deblurring in image processing. We further show that any non-homogeneous, spatial density distribution can be preserved over time if individual movement patterns have the form of a Weber’s law response. Our study identifies a general form underlying all collective animal interaction responses and points to a link between collective behaviour and the fundamental functioning of perceptual systems.

Author summary

Many group-living animals form aggregations and flocks that remain stable over relatively long time scales in spite of the fact that individual members of the group continuously exchange their positions, some individuals leave the group and other individuals join. Clearly, group stability is only possible because each individual member of the group implements appropriate ‘rules of interaction’ with conspecifics whose overall effect is to maintain group cohesion. Are these interaction rules different from species to species, or do they also possess universal characteristics, shared across all species? In our article we show that if group stability and the spatial distribution of densities are preserved over time, individual-level interactions are also constrained to take a precise form. More precisely, individuals must move up a gradient of neighbour densities, but do so in inverse proportion to the local density. Interestingly, this particular type of response corresponds precisely to how animals of different
species process sensory stimuli and estimate intensities and quantities (known as Weber’s law, or the fundamental law of psychophysics). In this respect, our study points to a general link between collective behaviour and the fundamental functioning of perceptual systems.

Introduction

Gregarious and social animals are capable of forming aggregations and flocks that maintain a relatively stable global configuration in spite of individual animals joining or leaving the group and continuously changing their position relative to each other. Examples of such aggregations span the whole animal kingdom from molluscs (e.g. [1]), to insects (e.g. [2]) and crustacea (e.g. [3]) to vertebrates (reviewed in [4]). If these groups can remain cohesive and maintain a stable, coherent organisation over time, this is possible because each member of the group continuously tracks the position or density of its surrounding neighbours and implements appropriate movement responses that effectively preserve group stability.

A large number of recent empirical studies has aimed at identifying the individual-level interaction responses that mediate group formation and stability empirically from tracking data of different animal species (e.g. [5–10]). Together, these studies have supported the idea that group formation requires at least some form of inter-individual attraction. However, different studies have pointed to different attraction rules in different species, such as for instance attraction directed to one single individual at a time or simultaneously to multiple neighbours, relevant neighbours selected based on metric or topological distance, etc.

The problem is compounded by the fact that the interaction responses of animals of different species ultimately depend on the sensory modalities mediating the interaction (vocal calls, vision, pheromones), and on the underlying neural circuits involved, which are inevitably different from one species to another. In fact, there is a large variability across the sensory systems of different animals, with only very few ‘perceptual laws’ that are shared both across taxa and across sensory modalities. One such ‘universal’ perceptual law is the Weber-Fechner law [11], which states that the ability of a sensory system to discriminate between two physical quantities decreases in inverse proportion to the magnitude of the quantities being compared. To make an example, we can easily tell the difference between a cluster of five objects and a cluster of eight, but we cannot as easily identify the difference between -say- a cluster of 55 and one of 58 [12]. Weber’s law has been established for humans as well as for a wide range of animals ranging from ants [13], to fish [14], to corvids [15], and to primates [16] and occurs in different sensory modalities. Because Weber’s law controls the ability of animals to ‘count’ the number of neighbours in different directions, it could likely play a role also in collective aggregation phenomena.

Here, we adopt an inverse theoretical approach (inspired by [17] and [18]) towards understanding the rules of interaction that mediate the stability of animal groups: instead of trying to observe and quantify interactions for a given animal species, we consider the theoretical problem of an animal group whose member individuals do not interact. In the absence of interactions, the dynamics of the group is dominated by diffusion processes which can be accurately characterised in terms of Fick’s diffusion equations [19] under simple assumptions of random motion and absence of interactions. We can hence address the inverse theoretical problem of finding which individual-level interaction rules are required to precisely counter-balance the effects of diffusion and preserve group stability.
Evolution of densities in the absence of interactions

In the absence of interactions, the movement in a random direction of individuals results in a change of densities over time that is well described by the diffusion equation [19]. Here we recall it briefly for the one dimensional case (the problem is analogous in a higher dimensional space).

For convenience, we imagine the space to be subdivided in cells of equal width $\Delta x$ and we indicate with $C(x, t)$ the density of individuals (e.g. number of individuals over volume of the cell) at the position $x$ and time $t$ (fig. 1). We focus on density, not on the absolute number of individuals, so that our quantities do not scale with the size of the cells. Within a certain time interval $\Delta t$ a fraction $2D$ of individuals present in each cell move to one randomly chosen adjacent cell. This determines the following equation for the evolution of $C$:

$$C(x, t + \Delta t) = C(x, t) + D[-2C(x, t) + C(x + \Delta x, t) + C(x - \Delta x, t)]$$

(1)

where the density at some position $x$ depends on the previous density at the same position, minus the fraction of individuals that moved to the neighbour cells, plus the individuals that moved into the cell from the neighbouring ones. In the limit for $\Delta t$ and $\Delta x$ small, equation (1) becomes

$$\frac{\partial C}{\partial t} = D\frac{\partial^2 C}{\partial x^2}$$

(2)

where $D' = D\frac{(\Delta x)^2}{\Delta t}$ (see the appendix for a derivation).

The solution of the diffusion equation is

$$C(x, t) = C(x, 0) * G(0, \sqrt{t})$$

(3)
whereby the initial distribution \( C(x, 0) \) is convolved with a Gaussian \( G(0, \sqrt{t}) \) that becomes larger and larger in time. In practice, it is as if the initial distribution was replaced by an increasingly ‘blurred’ version of itself.

**Individual-level responses based on Weber’s law produce collective-level anti-diffusion**

Weber’s law states that the perceptual ability of an animal to discriminate between sensory stimuli of different intensity is directly proportional to the difference of intensity and inversely proportional to the local value of intensity. If the ability of an individual animal to discriminate densities of neighbours in different directions follows Weber’s law, we can investigate how this type of response would affect the evolution of local densities in the same one-dimensional discretised example of figure [1](see also the appendix for another intuitive justification for the choice of focusing on Weber’s law in the case of normally distributed densities). In order to contrast diffusion, each individual in \( x \) must have a tendency to move to an adjacent cell at \( x + \Delta x \) if the concentration at the destination cell is higher than the concentration at \( x \). Assuming that the ability to discriminate different concentrations follows Weber’s law, the probability for an individual to move between \( x \) and \( x + \Delta x \) is given by

\[
p(x \to x + \Delta x) = \begin{cases} 
\gamma \frac{C(x+\Delta x) - C(x)}{C(x)}, & \text{if } C(x + \Delta x) > C(x) \\
0, & \text{otherwise}
\end{cases}
\]  

(4)

where \( \gamma \) is a proportionality constant. Considering that there are \( C(x) \) individuals that apply this rule, this will result in a net flow from \( x \) to \( x + \Delta x \) equivalent to \( \gamma (C(x + \Delta x) - C(x)) \) if \( x + \Delta x \) is the cell with higher concentration. If instead the cell with higher concentration is the one at \( x \), particles will flow in the opposite direction, but their flow will turn out to be also proportional to \( \gamma (C(x + \Delta x) - C(x)) \).

As a result the net change of density at \( x \) will be:

\[
C(x, t + \Delta t) = C(x, t) - \gamma \left[-2C(x, t) + C(x + \Delta x, t) + C(x - \Delta x, t)\right]
\]  

(5)

whose continuous version is:

\[
\frac{\partial C}{\partial t} = -\gamma' \frac{\partial^2 C}{\partial x^2}
\]  

(6)

where \( \gamma' = \gamma (\Delta x)^2 \). Equations [5] and [6] are identical to the diffusion equations [1] and [2] except for the sign of the diffusion coefficients \( D \) and \( \gamma \). Importantly, however, their biological justification is completely different: the diffusion equation results from the total absence of interactions, while a response based on Weber’s law implies an active decision process (see also [20] where a similar ‘anti-diffusion’ term was obtained, although in a slightly different context).

Care should be taken however that the derivation of the anti-diffusion equation [5] from individual-level Weber’s law responses (eq. [4]) involves some simplifications. First, equation [5] is a mean field approximation of equation [4]. Second, if the number of particles or individuals in a cell is close to zero, the probability for these particles to move to an adjacent higher density cell will increase (the denominator of equation [4] is small), but the flow can never exceed the number of available particles. There is no control for this in equation [5] which means that simply applying this equation can potentially lead to some cells taking negative values.

**Restoring arbitrary distributions**
Because a response to concentration gradients based on Weber’s law results in a change in concentrations that is analogous to an anti-diffusion, if such a response is implemented by all individuals in a group, it will have the net effect of partially restoring the distribution that was originally altered by diffusion. To visualise this, consider the example in the top row of figure 2. The example depicts the hypothetical case of animals aggregated at two high density spots, with densities close to zero elsewhere (fig. 2-A). Coloured dots mark the positions of randomly selected particles. In the absence of interactions, diffusion operates on densities, which for the purpose of figure 2 we implemented by iterating 300 times a 2D version of equation 1 with parameter $D = 0.01$. The superposed particles also move to a random cell adjacent to their current position with probability $D$. Figure 2-B shows the resulting density distribution and the trajectories of the selected particles. Applying 300 iterations of anti-diffusion response (a 2D version of equation 5) results in a new spatial distribution (fig. 2-C) where densities are very similar to those in the original distribution.

An analogy with the problem of deblurring in image processing

Our problem of animals recovering a group configuration that was previously altered by diffusion is closely related to the problem of deblurring in image processing. In fact, a grayscale image can be seen as a density distribution (for instance by assimilating bright colours to high density regions and dark colours to low density regions). Random movements starting from that distribution correspond to blurring the image, and the task of image deblurring algorithms is that of recovering an image similar to the original one. It is well known in the human and computer vision literature that blurred images can be partially restored by subtracting their convolution with a Laplacian operator, in a similar way to what equation 5 does. In fact, the diffusion equation 2 indicates that the local change in luminance $\partial C$ when we blur the image by a small amount $\partial t$ is proportional to the Laplacian of the original image:

$$\frac{\partial C}{\partial t} = D \left[ \frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2} \right]$$

(7)

A simple approach for restoring the quality of the initial image is that of playing the diffusion process for negative time scales [21] in a way which is analogous to what is done by equation 5.

Figure 2 D-E illustrates the diffusion and Weber’s law based anti-diffusion applied to a greyscale image. The original image (fig. 2-D) is initially blurred when each of the intensity levels of a pixel randomly diffuses to the neighbouring pixels (fig. 2-E). Implementing a Weber’s law based gradient-climbing response such as the one described in equation 4 restores much of the details that were present in the original image. The only difference between this gradient-climbing approach and classical image deblurring by substraction of a laplacian convolution is that our approach is based on equation 4 while the convolution with a laplacian implements directly equation 5 which can be derived from it. Unlike gradient climbing, subtracting the laplacian convolution can produce images with negative values; in the context of image processing this is usually resolved by rescaling the image histogram to the allowed range of pixel intensities (e.g. 0-255 for 8-bit images).

Animal movements within stable density landscapes

The previous examples focused on a somewhat artificial situation whereby particles initially diffuse without interacting and then converge again by implementing a Weber’s law based gradient climbing response. More realistic is the situation in which a group or a population of animals occupy the environment according to a non-homogeneous density distribution which remains
Fig 2. Weber’s law based anti-diffusion restores spatial distributions after diffusion. A Hypothetical two-dimensional density distribution representing two ‘animal groups’ with a circular profile and homogeneous internal density. Brighter regions indicate higher density. The coloured dots indicate the position of randomly selected individuals. After a given number of iterations of random diffusion-like movements (300 in this example), individuals have moved with random trajectories producing a smoothed density distribution (B). In C a density distribution similar to the original (A) distribution is restored by each individual climbing the density gradient with a Weber’s law response rule (parameter $\gamma = D$ and same number of iterations: 300). Figures D, E and F illustrate an identical process to that in A, B and C, but here the starting density distribution (D) is a greyscale image. Random diffusion of the individuals that form the distribution in D has the effect of blurring the image (producing the image in E) and anti-diffusion restores a similar image to the original (in F). In both examples the luminance map is updated based on a mean-field approach (that is, densities are updated in proportion to the calculated probability instead of by actually drawing movement decisions from the probability distribution).
stable over time in spite of individual animals moving across the landscape. Here, we are not making any claims about the actual mechanisms that allow maintaining stable group configurations: these could involve inter-atraction among individuals (gregarious behaviour), but could also more simply result from attraction to environmental resources that are localised in space (e.g. animals remaining in the proximity of a water source).

We model this situation by assuming that animals occupy the environment according to a non-homogeneous density landscape, that for simplicity we map to a discrete lattice. Animals are simulated in the model as particles that can move from one cell of the lattice to the adjacent cells, but we impose that the density landscape remains unchanged.

Suppose that the number of individuals at two adjacent cells \( i \) and \( j \) is respectively \( N_i \) and \( N_j \) (fig. 3). If the density landscape remains stable, \( N_i \) and \( N_j \) must remain constant over time (and this for all cells, not just for \( i \) and \( j \)). The easiest way in which this can be achieved is if at any given time the flow \( \phi(i,j) \) from \( i \) to \( j \) is equal to the flow \( \phi(j,i) \) in the opposite direction.

Assuming that \( j \) is the cell with higher density \( N_j > N_i \), we can say that the individuals that move from \( j \) to \( i \) do so because of diffusion alone, while the individuals that move from \( i \) to \( j \) can do it because of diffusion or because of some form of gradient climbing described by an \textit{a priori} unknown function of local densities \( f(N_i, N_j) \).

We then have

\[
\phi(i,j) = N_i D + N_i f(N_i, N_j) = N_j D = \phi(j,i)
\]

which gives

\[
f(N_i, N_j) = \frac{D(N_j - N_i)}{N_i}
\]

Weber’s law is hence a solution.

We tested in simulation if particles moving within an overall stable density landscape appear as if they were following Weber’s law response to densities. First, we created a number of 2-dimensional random density landscapes (obtained as low-pass filtered noise). Then, we generated random particle trajectories with the double constraint that (i) the total amount of time spent by a trajectory at a particular location is proportional to the density at that location, and that (ii) at each time step the net flow of particles between two locations is equal to the flow in the opposite direction (see Methods for details; an example of one such density landscape and of some of the corresponding trajectories is illustrated in figure 3(b)). The probability for particles to move between two adjacent locations calculated over all the trajectories and binned as a function of the local densities at the source \( N_i \) and at the target location \( N_j \) is illustrated in figure 3(c). While the flow of particles is identical in both directions, individual particles necessarily have a higher probability of moving from low to high density regions. Intuitively, this is easily understood as a consequence of the fact that fewer particles are available in lower density cells, and as a consequence they are required to move more often to counterbalance the flow from higher density cells. More precisely, the simulated particles responded to local densities with an apparent Weber’s law response, whereby the slope of the probability of moving from \( i \) to \( j \) is inversely proportional to \( N_i \) (fig. 3(d)). These simulations show that as long as the overall spatial density distribution is maintained, individual group members will appear to respond to their neighbours with a Weber’s law type response.
Fig 3. Flow of individuals across a network of ‘sites’. (a) The simplest way in which a non flat density landscape can remain stable over time is if the flows of individuals moving across each edge in one direction is balanced by the flow moving in the opposite direction. We built a series of density landscapes such as in (b) whereby each pixel represents a network node and it is directly connected by an edge to its four adjacent pixels. Particles move randomly across the landscape with the constraints that the density distribution is preserved at all times. (c) The probability for a particle to move from node $i$ to node $j$ increases linearly with the difference of density between the target $N_j$ and the source node $N_i$. The slope of this relation, obtained from a linear fit along the dotted lines depicted in (c) is inversely proportional to the local density $N_i$ (panel (d)).

**Long term dynamics of iterated diffusion and anti-diffusion**

While Weber’s law based responses to densities can counteract diffusive forces and are likely to be consistently observed in stable groups with an internal dynamics, can density responses based on Weber’s law alone support group stability? Because of the linearity of the diffusion and anti-diffusion equations (eq. [2] and [6]), a combination of diffusion and anti-diffusion has only one stationary state with homogeneous density. The homogeneous density state is stable -and the group disperses across the environment- when diffusion is stronger than anti-diffusion (when $D > \gamma$). When instead the anti-diffusion prevails ($\gamma > D$), the homogeneous state becomes unstable and the model predicts the formation of explosively larger groups. In particular, the dynamics of the aggregation is such that the higher spatial frequencies (small spatial scales / small group sizes) are amplified or attenuated faster than lower frequencies (see appendix). An important consequence of this is that as soon as the regulation mechanism is noisy, the high frequency noise is quickly amplified.

It is important to remember that in making the considerations above we were relying on two assumptions. The first assumption is that diffusion and anti-diffusion take place simultaneously and the gradient climbing response is perfectly accurate. In reality, if the anti-diffusion response is not implemented immediately the anti-diffusion
Fig 4. Pattern formation from iterated diffusion and anti-diffusion. (a) and (c) Spatial patterns produced on a 128x128 lattice after 15000 iterations of the model described in methods; the starting distribution is random white noise. In both figures $\gamma = 0.9$. In (a) $D = 0.13$, while in (b) $D = 0.17$. After multiple iterations of the simulation steps, a pattern emerges at a single spatial scale. This is clearly visible in figures (b) and (d), which plot the amplitude spectrum of the Fourier transform of the patterns in (a) and (c), respectively.

will take place on a distribution that has already been altered by some uncompensated diffusion. Similarly, if the gradient climbing response is noisy, i.e. it also diffuses a bit, this will also result in some uncompensated diffusion. The second assumption is that local densities can grow with no upper limit. In real world aggregation phenomena, however, densities will reach a saturation at some point. Here, we incorporate these additional elements in a discrete model of diffusion and anti-diffusion. The model uncouples in time diffusion and anti-diffusion, and implements a saturating anti-diffusion response to prevent densities from increasing above a saturation point (see methods for details).

Under these conditions, we do observe the appearance of spatial patterns of a characteristic scale, at least for some parameters (see fig. 1). While our particular implementation of this long-term model may lack biological realism, for instance in relation to the temporal separation between diffusion and anti-diffusion periods, alternative models that also incorporate a reaction time in the response of individuals are likely to predict the formation of patterns with a characteristic scale: it is implicit in the nature of the diffusion equation that the introduction of events with a characteristic temporal scale -for instance a fixed reaction time in the response to neighbours, also leads to the appearance of spatial patterns with a characteristic spatial scale.

Discussion

Gregarious animals can form non-homogeneous density distributions and aggregations that persist over time scales typically much longer than the speed of dispersion and movement of individual animals. In our study we show that group stability constrains the individual-level interaction rules that mediate group cohesion, which are required to follow Weber’s law.

Weber’s law describes a general functioning principle of sensory systems. Traditionally, Weber’s law based sensory perception has been discussed in relation to the mechanisms and to the constraints of information processing in the brain [22, 23]. Here, we have shown that Weber’s law is also an essential property of collective interactions in stable animal groups.

Sensory perception plays a fundamental role in guiding the interactions of an animal with its environment [24], so it can reasonably be expected that the fundamental properties of sensory systems also play a role in shaping inter-individual interactions and collective behaviour. Previous studies have already established the relevance of decision-making mechanisms based on Weber’s law for explaining collective decision-making in ants, bees and fish [13, 25, 27]. Theoretical studies also
indicate that Weber’s law response results from optimal pooling of group-level information for collective decision-making [27].

In the present study, we do not make any assumptions about the mechanisms or about the optimality of the decision-making rules in individual animals. Our only assumption is that animal groups remain stable over long time scales, compared to the time scale of individual animal movements. We further assumed that in the absence of interactions group dynamics would be described by diffusion. Because of the generality of these assumptions, we can conclude that Weber’s law response to animal densities is a general property of all stable groups.

We should however be careful not to conclude that all animal aggregation phenomena depend on Weber’s law based responses to neighbour densities. Many animal aggregations can be produced also in the complete absence of social interactions and of gregarious behaviour. This is the case for instance when animals are attracted to an environmental feature such as a source of water or a particular type of vegetation. In this case, group stability would be predominantly mediated by the external attractor. Yet, our analysis shows that if we erroneously consider that the attraction responses are directed to other group members and not to the environmental feature, also in this case we would observe a response in the form of a Weber’s law to neighbour densities. In some animal species, group members might implement different response rules, involving both inter-individual attraction and repulsion. As long as the overall effect of these interactions is that of keeping the group stable, we would observe a Weber’s law type of response to neighbour densities, without it necessarily being the underlying mechanism.

Our model is not a morphogenetic model: the type of response to neighbour densities based on Weber’s law that we describe here cannot be used to predict the size or the shape of the groups formed by animals of a particular species. We argue that this is an inevitable consequence of the ‘universality’ of Weber’s law: animal groups present a huge variation of size and shape across species which is unlikely to be accounted for by a single shared perceptual rule. In addition, the size of animal groups is typically widely distributed also within one single species, suggesting that its regulation depends on other factors, such as merge and split phenomena, rather than being determined by sensory responses alone [28–30].

While we do actually show that an aggregation model based on Weber’s law can lead to the formation of patterns at a fixed scale, this scale is mainly determined by the delay that we introduced between diffusion and anti-diffusion. We could try to find a resemblance between the patterns produced in our long-term iteration model and the spatial distribution of individuals in certain animal groups, such as for instance mussel beds [1]. However, we think that it is safer to argue that these pattern formation phenomena leading to a small characteristic spatial scale have little biological relevance in general, for instance because at such small spatial scales the positioning of individuals is more affected by direct individual to individual interactions than by the generic Weber’s law response that we consider here.

Paradoxically, while we predict that individual-level interaction responses based on Weber’s law should be observed in stable animal groups, Weber’s law alone cannot explain the formation of groups of a particular form or size and is not sufficient by itself to explain the stability of pre-existing groups (because of reaction times and amplification of noise). We can conclude that Weber’s law based interactions are a necessary but not entirely sufficient feature of stable group.

Our study points to a general relation between Weber’s law and collective behaviour. While Weber’s law can explain several perceptual phenomena, there are many instances in which sensory perception deviate from Weber’s law behaviour. Future studies should try to relate also deviations from Weber’s law, as well as other
perceptual phenomena, to collective behaviour. For example, many sensory stimuli remain undetected when their intensity falls below a perception threshold. In the context of social interactions, perceptual thresholds for responding to conspecifics can directly affect the way how animals rely on private vs. social information for taking decisions.

Our approach for deriving interaction responses in animal groups is complementary to other studies based on direct observations of interacting individuals. While direct observations of behaviour inform us about how animals of a particular species interact, our approach informs us about which individual-level interactions are ‘unavoidable’ given a particular collective phenomenon. In this particular case, individual-level responses in the form of Weber’s law are unavoidable in stable density groups. We are confident that in future our approach can be extended to the study of also other more complex forms of group coordination.

Methods

 Movements within stable density landscapes In order to explore the interaction responses compatible with maintaining a stable density landscape we first created random density landscapes and then we simulated movements of particles over each landscape while imposing that the flows of particles in alternate directions over each edge is balanced for each time step.

 The random density landscapes were obtained as low-pass filtered two-dimensional noise: we first created a 2D array of random values uniformly distributed within a given range and then we removed high spatial frequencies by convolving with a two-dimensional Gaussian distribution). We tested multiple landscapes with different values of average density, amplitude of modulation and spectral composition.

 The probability for an individual particle to move from a cell \( i \) to an adjacent cell \( j \) was calculated as follows: first we calculated the flows of particles that would move from \( i \) to \( j \) through diffusion alone, \( F_{ij}^{\text{fwd}} = DN_i \). Then we immediately compensated these flows by moving an identical number of particles in the opposite direction. These particles are selected randomly among those available in \( j \) and could be the same that had just moved from \( i \) to \( j \) with probability \( F_{ij}^{\text{fwd}} / (F_{ij}^{\text{fwd}} + N_j) \). As a result, the net flow of particles that moved from \( i \) to \( j \) because of diffusion and were not put back during the compensatory step is \( F_{ij}^{\text{D}} = F_{ij}^{\text{fwd}} - (F_{ij}^{\text{fwd}})^2 / (F_{ij}^{\text{fwd}} + N_j) \), and it is associated with a net compensatory flow from \( j \) to \( i \), \( F_{ji}^{\text{C}} = F_{ij}^{\text{D}} \). By imagining that the same process also takes place in the opposite direction, with diffusion from \( j \) to \( i \), and a compensatory movement from \( i \) to \( j \), the total flow between \( i \) and \( j \) is \( F_{ij}^{\text{D}} + F_{ij}^{\text{C}} \).

 Long-term dynamics of iterated diffusion and anti-diffusion

 We implemented a simulation in which an initial density distribution is altered by alternating steps of diffusion and anti-diffusion in discretised time steps. The first step is a simple diffusion step:

\[
C(x, y, t + 1) = C(x, y, t) + D \triangle (C(x, y, t))
\]

where

\[
\triangle (C(x, y, t)) = -4C(x, t) + C(x + 1, y, t) + C(x - 1, y, t) + C(x, y + 1, t) + C(x, y - 1, t)
\]

The anti-diffusion step is similar to all previous examples, but we also include an additional term to prevent densities from becoming negative, or from exceeding a
maximum positive value.

\[ C(x, y, t + 2) = C(x, y, t + 1) - \gamma \Delta (C(x, y, t + 1)) C(x, y, t + 1) [1 - C(x, y, t + 1)] \]  

(12)

In the examples shown in figure 4, the initial condition is a uniform random distribution. And the distribution shown corresponds to 15000 simulation steps.

Supporting information

S1 File. Computer scripts used in the analyses. The compressed folder contains the Matlab scripts used for the simulations and for the analyses.

S1 Appendix. Derivation of the continuous diffusion equation. The continuous diffusion equation can be derived from the discrete equation by considering the Taylor series approximation of \( C(x, t + \Delta t) \) around \( C(x, t) \):

\[ C(x, t + \Delta t) = C(x, t) + \Delta t \frac{\partial C}{\partial t} + \ldots \]

and the Taylor series approximation of \( C(x + \Delta x, t) \) around \( C(x, t) \):

\[ C(x + \Delta x, t) = C(x, t) + \Delta x \frac{\partial C}{\partial x} + \frac{(\Delta x)^2}{2} \frac{\partial^2 C}{\partial x^2} + \ldots \]

When these are plugged into equation 1, the first spatial derivatives cancel each other out and the remaining equation is \( \Delta t \frac{\partial C}{\partial t} = D \frac{(\Delta x)^2}{2} \frac{\partial^2 C}{\partial x^2} \). We then collect the parameters \( \Delta t, D \) and \( (\Delta x)^2 \) into a new constant \( D' \).

A training problem: recovering Gaussian distributions.

Imagine to release a certain number of animals at a single location \( (C(x, 0) \) is a delta function). Equation 3 tells us that, in the absence of any interactions, after some time \( t \) the individuals will be distributed according to a Gaussian distribution \( G \) centered around the release point and whose variance is proportional to \( t \).

One first question that we can ask is, what kind of movement response would allow the group to temporarily contrast the spreading process and revert from the spatial distribution that was produced at time \( t \) to the distribution that existed before, at time \( t - \Delta t \) (fig. 5).

In this simple case comes to our help the fact that we just want to convert a Gaussian distribution (the distribution at time \( t \); dotted distribution in figure 5) into another Gaussian distribution (that existed at some previous time \( t - \Delta t \) (shaded distribution in figure 5). The simplest way in which this can be achieved is if each individual moves towards the direction of higher local density by an amount \( \Delta x \) proportional to its own current distance \( x \) from the centre of the distribution.

In practice, however, we should assume that individuals do not have a global perception, that is, they do not know directly their own position relative to the centre of the distribution. They can, however, estimate the number of neighbours locally around their own position and its local variation in different directions. In the case of Gaussian distributions, it is easy to verify that there is one function of these local quantities that is proportional to the distance from the centre of the distribution: this is the gradient normalized over the local density \( x = -\nabla G \sigma^2 \), where \( \nabla G = \frac{\delta G}{\delta x} \) indicates the gradient of the Gaussian distribution (because \( \frac{\delta G}{\delta x} = -\frac{\partial}{\partial x} G \)). Expressions of the form \( \nabla f \) are well known in psychophysics and correspond to Weber’s law.

Internal movements within a Gaussian probability landscape that remains stable over time.

Here we consider a Gaussian distribution stable over time, but assuming that individuals move freely within this distribution, that is, the global distribution does not change, but there are internal movements inside this distribution.
Fig 5. Individual movements to contrast gaussian diffusion. We consider the simple example of individuals distributed across space according to a Gaussian density distribution. If each individual aims at recovering

Fig 6. Apparent Weber’s law response of randomly moving particles in a Gaussian density distribution. (a) Simulated x position of a particle that moves randomly across a Gaussian probability landscape depicted in (b). (c) Average movement (± standard deviation) of the particle as a function of its current position. Individual particles are observed to move towards the centre of the distribution with a step

For each individual we simulate Normally distributed x positions with time correlation.

Notice that the slope of the regression line is not 1 but 2/π. This results from attenuation and the value of the slope is related to the average absolute deviation of the Normal distribution, which is $\sqrt{2/\pi}$.

Amplification and attenuation of different spatial harmonics around the homogeneous state.

We consider the evolution of $C$ around an homogeneous steady state where a small perturbation $\delta$ is applied: $C(x, t) = C_s + \delta(x, t)$. We choose a form for $\delta = e^{\omega t} e^{ikx}$ which allows us monitoring the temporal and spatial evolution of the perturbation.

If diffusion and anti-diffusion act simultaneously, we have:

$$\frac{\partial C}{\partial t} = +D \frac{\partial^2 C}{\partial x^2} - \gamma \frac{\partial^2 C}{\partial x^2} \quad (13)$$

The equation implies an immediate response of individuals to the diffusion event, so that in practice it is equivalent to a slower diffusion (if $D > \gamma$) or slow anti-diffusion
(if $\gamma > D$).

The time derivative in equation (13) can be rewritten around the homogeneous state as

$$\frac{\partial C}{\partial t} = \left( \frac{\partial C}{\partial t} + \frac{\partial \delta(x,t)}{\partial t} \right),$$

and similarly for the space derivative

$$\frac{\partial^2 C}{\partial x^2} = \left( \frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 \delta(x,t)}{\partial x^2} \right).$$

As the derivative of the constant parts are equal to zero, equation (13) around the homogeneous state becomes

$$\frac{\partial \delta}{\partial t} = (D - \gamma) \frac{\partial^2 \delta}{\partial x^2},$$

from which we have $\omega \delta = (D - \gamma) - k^2 \delta$ which indicates that the speed $\omega$ at which harmonics of a given frequency $k$ are amplified or attenuated (depending on the sign of $D - \gamma$) is proportional to the square of the frequency: high frequency harmonics are both amplified faster when anti-diffusion prevails and attenuated faster when diffusion prevails.

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