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Abstract. Swarms of social insects construct trails and networks of regular traffic via a process of pheromone laying and following. These patterns constitute what is known in brain science as a cognitive map. The main difference lies in the fact that the insects write their spatial memories in the environment, while the mammalian cognitive map lies inside the brain. This analogy can be more than a poetic image, and can be further justified by a direct comparison with the neural processes associated with the construction of cognitive maps in the hippocampus. We investigate via analysis and numerical simulation the formation of trails and networks in a collection of insect-like agents. The agents interact in simple ways which are determined by experiments with real ants.

1 Introduction

The self-organization of neurons into a brain-like structure, and the self-organization of ants into a swarm are similar in many respects. The former, for obvious reasons, has received more attention recently. However, the basic ideas of connectionism and mass action can be traced to the earlier work of Wilson on social insects.[3] Wilson defines communication as “action on the part of an organism that alters the probability pattern of behavior in another organism in a fashion adaptive to either one of both of the participants.”[1, 2] Collective communication, such as that found in social insects, occurs when this communication leads to an emergent behavioral structure (mass action) which is adaptive. This organization, which has been called “mass communication”, [3] occurs in spite of the fact that the individual organisms neither possess, nor are able to communicate, the complex global types of information these structures are able to transmit. Thus, in a certain sense, while the ants are able to construct a cognitive map for their behavior, a good part of this map lies outside of the individual ants.

Unlike simple direct action, which can often be studied by observation of the actual organisms, and broken down into its component parts, collective behavior involves statistical effects of a large number of individual agents. The behavioral coding is expressed in collective rather than in individual

terms, and it is sometimes difficult in the most complex cases to determine which behavioral signals in combination are responsible for a particular collective behavior, and which are sufficient. How then are we to dissect the swarm and determine how individual behavioral components interact, and how they function in the whole? What we would like to do here it to show that it is possible to do theoretical and numerical analysis of this situation. In addition, we point out the similarities between the underlying dynamics, and the emergent properties of the swarm to the organization of cognitive maps in the hippocampus.

In *The Insect Societies* Wilson forecasted the eventual appearance of what he called “a stochastic theory of mass behavior” and asserted that “the reconstruction of mass behaviors from the behaviors of single colony members is the central problem of insect sociobiology.” He forecasted that our understanding of individual insect behavior together with the sophistication with which we would be able to analyze their collective interaction would advance to the point where we would one day possess a detailed, even quantitative, understanding of how individual “probability matrices” would lead to mass action on the level of the colony. By replacing *colony members* with *neurons*, *mass behaviors* or *colony* by *brain behavior*, and *insect sociobiology* with *brain science* the above paragraph could describe the paradigm shifts in the last twenty years of progress in the brain sciences.[4]

In an attempt to realize some of Wilson’s vision we focus here on what we will call “proto-swarms”. A proto-swarm is a minimal combination of behavioral signals, observed and isolated *in vivo*, which are sufficient to form some rudimentary cooperative structure observed in nature. We hope that in this way it might be possible to isolate and study one or more of the underlying mechanisms that allow real organisms to act collectively. We believe that a fuller understanding of the the amount of physiological evolution required to produce a behavioral change can be achieved in this way since it often possible to scan the physiological space of possibilities in rather comprehensive way.

2 The Stochastic Transition Probabilities

Here we will be concerned with the basic behavioral components of the pheromone trail laying and following behavior of individual organisms, and the resulting self-organization of regular patterns of flow, such as trails and networks of regular traffic. Clearly such behavior has proved adaptive, and is widespread amongst the social insects today.

The systematic analysis of the chemical signals of social insects in terms of it component chemicals, their effects on the individuals, and their glandular sources began with the program of Wilson. It has been shown that ants make use of (at least) two different types of sense-data processing, *osmotropotaxis*, a kind of instantaneous pheromonal gradient following, and *klinotaxis*, a se-

quential method.[6] Here we will be interested only in the former of these methods.

The basic osmotropotactic sense datum is a measurement of the difference in pheromone concentration between the antennae. This sense datum is translated onto a response of the organism. Phenomenological forms for this response in various controlled settings have been determined recently.[7, 8, 9] It has been shown that, at least on the phenomenological level, there is a significant amount of noise in the response function. Subsequently, the description we use must be stochastic. This noisiness, as we shall see, is fundamental to the behavior of the swarm as a whole. Whether or not it is fundamental on the level of the sensory processing system is not known, though this is a likely possibility. Already there is some evidence that noise on the intrinsic level plays an important role in information processing in sensory neurons. The relationship is not entirely frivolous, and pheromonal communication has been called the “giant synapse”. In addition, there are a number of fairly obvious physiological and perhaps even evolutionary parallels between pheromones and neurotransmitters. Real ants are able to emit a number of types of chemical signals, and might be understood as “a walking secretory gland”. In the same sense it is now understood that neurons are able to release a number of types of neuro-transmitters.

The state of an individual ant can be described by a “phase variable” containing its position \mathbf{r} , and orientation θ . Noisy pheromone gradient following is formally equivalent to noisy potential gradient following in statistical physics, an analogy which has already been justified in some detail elsewhere.[13, 14, 15] Since the response at a give time is assumed to be independent of the previous history of the individual, it is sufficient to specify a transition probability from one place and orientation (\mathbf{r}, θ) to the next place and orientation (\mathbf{r}', θ') an instant later. At this level of description, the motion of an individual organism is rigorously equivalent to a continuous Markov process whose probabilities are determined at every moment in time by the instantaneous distribution of pheromone $\sigma(\mathbf{x}, t)$.

In [13, 14], the behavior of all possible proto-swarms of this type of swarm was classified and generalized as far as possible via theoretical considerations. In that previous work transition rules were derived and generalized from the noisy response function of Refs. [10, 11, 12], which in turn were found to reproduce a number of experimental results with real ants.[7, 8, 9] The response function can effectively be translated into a two-parameter transition rule between the cells by use of a pheromone weighting function

$$W(\sigma) = \left(1 + \frac{\sigma}{1 + \delta\sigma}\right)^\beta. \quad (1)$$

This function measures the relative probabilities of moving to a cite \mathbf{r} with pheromone density $\sigma(\mathbf{r})$ as discussed in [13, 14]. In order to illustrate this, we consider the following situation pictured in Fig. 1. For simplicity the ant

is constrained to walk along a path until it comes to a fork in the road. At this point the ant chooses according to the weights given in Eq. 1. We fix the pheromone on segment two, $\sigma_2 = 1$, and measure the probability for the ant to choose segment one, W_1 . We can illustrate the degree of response of the ant to differences in scent by varying σ_1 as illustrated in Fig. 2.

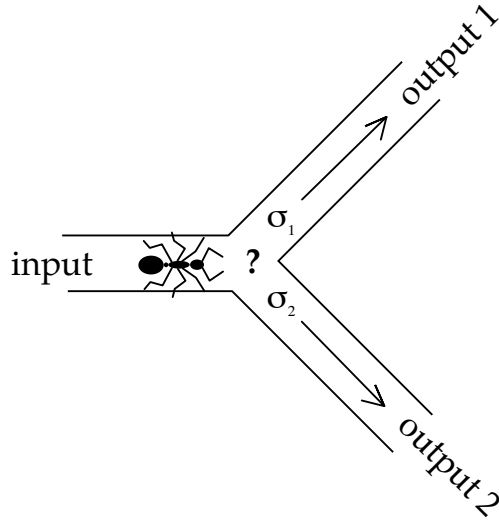


Fig. 1.

The parameter β is associated with the osmotropotaxic sensitivity. Also it can be seen as a physiological inverse-noise parameter or gain. This parameter controls the degree of randomness with which the ant follows the gradient of the pheromone. For low values of β the pheromone concentration does not greatly affect its choice, while high values cause it to follow pheromone gradient with more certainty. Here we call $1/\delta$ the sensory capacity. This parameter describes the fact that the ant's ability to sense pheromone decreases somewhat at high concentrations. This gives rise to a peaked function for the average time an ant will stay on a trail as the concentration of pheromone is varied—a fact which has been observed repeatedly experimentally[16, 17, 18]. This is perhaps significant in light of one of the results presented here: trails and networks form more easily in the presence of this saturation effect. This saturation also can be found in first order sensory neurons in which there is a limited “dynamic range” in which sensory inputs are encoded.

In addition to $W(\sigma)$ there is a weighting factor $w(\Delta\theta)$, where $\Delta\theta$ the change in direction at each step. More work need to be done to determine the precise form of this factor, which takes into account the sensory anisotropy the organisms due to the orientation and motion of the insects. Everything else being equal, very sharp turns are much less likely than turns through smaller angles, thus $w(\Delta\theta)$ is a decreasing (and symmetric) function of the magnitude of $\Delta\theta$. Stated in another way, they have a probabilistic bias in the forward direction. The actual transition probability rate can be calculated after setting the step size, and normalizing.

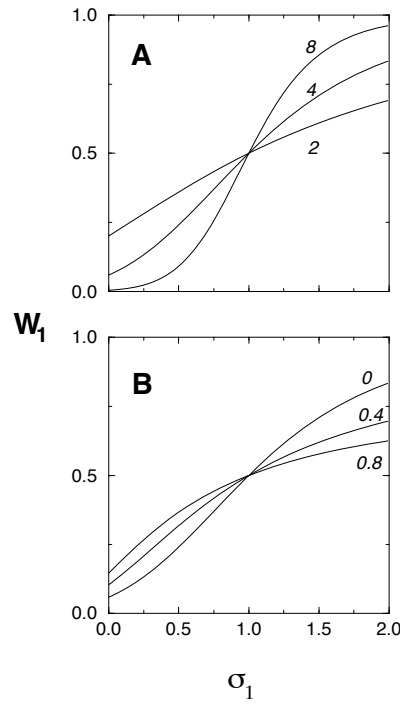


Fig. 2. Response function for (A) $\delta = .2$ and values of β indicated in the figure and (B) $\beta = 4$ and values of δ indicated in the figure.

3 Learning

For the picture of the swarm to be complete it must be supplemented by a description of how pheromone evolves. We assume that each organism emits

pheromone at a given rate η , and that this pheromone remains fixed at the point of emission (no spatial diffusion). As the pheromone evaporates at rate κ from the surface it creates a pheromone vapor, in proportion to its quantity, above the surface which the insects sense. If not constantly replenished the pheromone field and the vapor slowly disappear due to evaporation.

Note that there is no direct communication between the organisms but a type of indirect communication through the pheromonal field. The ants are not allowed to have any memory and the individual's spatial knowledge is restricted to local information about the pheromone density. The pheromonal field contains information about past movements of the organisms, but not arbitrarily far in the past, since the field "forgets" its distant history due to evaporation in a time $\tau \approx 1/\kappa$. Therefore the distribution of pheromone represents the memory of the recent history of the swarm, and in a sense it contains information which the individual ants are unable to hold or transmit. In a gross analogy, memories are believed to be written as a stronger coupling among individual, or groups of neurons. These couplings are strengthened by neural co-activity[19, 20] much in the same way that the pheromonal field is preserved or strengthened by coherent frequent ant traffic.

4 Mathematical Analysis

Since a detailed mathematical analysis of this type of system has already been made[13, 14], we will confine ourselves here to a brief statement of the pertinent results. In addition to the two parameters discussed above another important parameter is the number of ants present, or alternatively, the mean density of ants ρ_0 . The scent decay rate κ and the emission rate η and ρ_0 can effectively be combined into a single stress parameter, the average pheromonal field $\sigma_0 = \rho_0 \eta / \kappa$. The most important theoretical result is the location of the second order phase transition, that is the location of the boundary separating totally random behavior from ordered behavior of various types in the physiological phase space. As shown in [13, 14] ordered behavior sets in when the inequality $\sigma_0 f'(\sigma_0) / f(\sigma_0) - 1/\beta > 0$ holds, where $f(\sigma) = (1 + \sigma / (1 + \delta \sigma))$. This criterion is true for any behavioral function $f(\sigma)$, and allows us to calculate the physiological phase boundaries in $(\sigma_0, \beta, \delta)$ space. For the particular behavioral function used here the transition lies along the curve

$$\beta_c(\delta, \sigma_0) = 1 + 1/\sigma_0 + 2\delta + \delta\sigma_0 + \delta^2\sigma_0. \quad (2)$$

The symmetry which allows for a mean-field type solution for the location of the transition line case is maintained up to the point of the transition and is effectively spontaneously broken at that point. This means the points of transition from disorder to order can be determined theoretically, even in the more general case, but not the resulting patterns, which must be determined via simulations.

In addition to being the major landmark in the physiological parameter space, we believe both on general grounds, and because of the results presented in the next section that the location of this line has significant behavioral implications. Clearly the behavior of groups of real ants is ordered, and this order plays an important role in the functioning of the swarm. Just as importantly, the behavior should not be too rigid and ordered since fluctuation and instabilities might increase the flexibility of response of the mass action. Thus, if there are significant fluctuations in the patterns of mass action this might aid the swarms in responding to a changing environment. We might conclude that the ordered region is a “good” place to be, but near to the transition line in such a way as to optimize the conflicting tendencies of controlled ordered behavior versus flexible random behavior. We will also see in the next section that large fluctuation actually serve to stabilize some of the important pattern of collective behavior of the system.

5 In Numero Swarm Behavior

For the purposes of simulation it is necessary to introduce some discretization of space and time, and to translate the noisy behavioral function observed experimentally into transition rules on this discrete space[13]. The ants will be allowed to move from cell to cell on a square lattice. These discrete rules are merely tools for the approximation of a continuous model, and other discretizations are possible. We allow each ant to take one step on the lattice of points (cells) at each time step. As a result of discretizing the space an individual ant at each time step finds itself in one of these cells, and its sensory input is influenced by the concentration of pheromone in its own cell and each of the eight neighboring cells. In addition, each ant leaves a constant amount of pheromone at the node in which it is located at every time step. This pheromone decays at each time step at a rate κ . Toroidal boundary conditions are imposed on the lattice to remove, as far as is possible, any boundary effects. The normalized transition probabilities on the lattice to go from cell k to cell i are then given by

$$P_{ik} = \frac{W(\sigma_i)w(\Delta_i)}{\sum_{j/k} W(\sigma_j)w(\Delta_j)}, \quad (3)$$

where the notation j/k indicates the sum over all the cells j which are in the local neighborhood of k . Δ_i measures the magnitude of the difference in orientation (direction) for the previous direction the last time the ant moved. Since we are using a neighborhood composed of the cell and its eight neighbors on a square lattice, Δ_i can take only the discrete values 0 – 4, and it is sufficient to assign a number w_i for each of these changes of direction. Here we used weights of (same direction) $W_0 = 1$, and $w_1 = 1/2$, $w_2 = 1/4$, $w_3 = 1/12$ and $w_4 = 1/20$ (u-turn). Once the parameters β , δ and w_i are set, a large number of ants (here we used 307) can be placed on the lattice

at random positions. The random movement of each ant is determined by the probabilities P_{ik} . We usually take the initial condition of the pheromone to be zero at every point on the lattice. Every time step each ant leaves a quantity η (here $\eta = 0.07$) of pheromone in each cell, and the total amount of pheromone σ_i in each cell is decrease at a rate κ (here $\kappa = 0.015$) at the end of each time step.

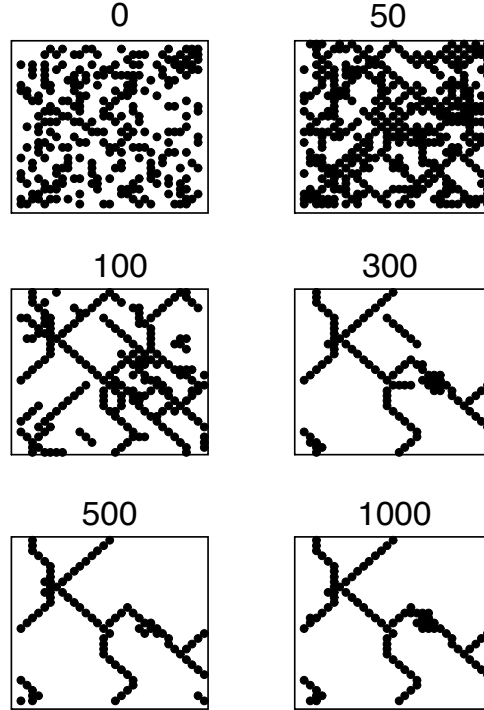


Fig. 3. Snapshots of the evolution of the distribution of ants for the times indicated ($\beta = 3.5$ $\delta = .2$).

In Fig. 3 we show the evolution of the distribution of the ants on a 32X32 lattice as time progresses. As early as a hundred time step a spatial structure begins to emerge consisting of a network of trails. Later on some of the trails are consolidated, and some are lost. This dynamics can also be visualized in Fig. 4 where in the bottom panel the occupancy of a vertical cross-section of the middle of the lattice is plotted. The degree of order can be quantified in many ways. In the top panel of Fig. 4 the dashed line is the coefficient of variation (standard deviation over the mean) of the direction of crossing a

given cell averaged over the whole lattice. The continuous line is the ratio of number of cells which have greater concentration than the equilibrium mean σ_0 over the number of cells with pheromone less than σ_0 .

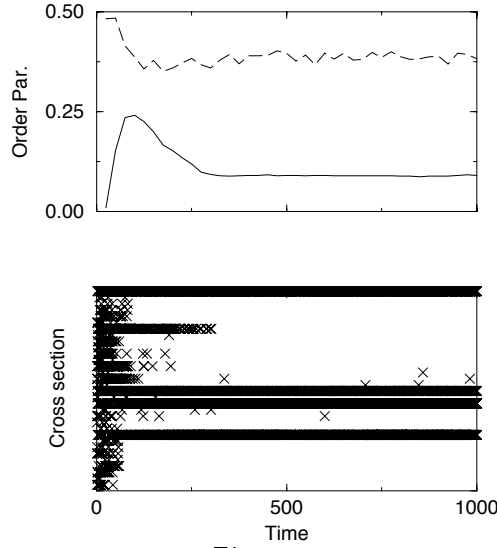


Fig. 4.

Fig. 5 shows the behavior of the system in $\beta - \delta$ parameter space. There are three types of behavior: disorder, patches and trails. Within the latter two regions there are a range of patch sizes, and a range of typical line shapes depending on the precise position within each of the respective regions. Well defined trails form in the region above the phase transition line (ordered phase), but near the transition from disorder. Further away from the order-disorder line the clumping tendency overcome the directional bias, and no lines form. Near the border between lines and patches we observed some hysteresis effects, and preformed lines persist into the region of patches. In the trail forming region of the parameter space shown in the phase diagram in Fig. 5, the ants form well-defined trails.

This is the simplest (local, memoryless, homogeneous and isotropic) model which leads to trail forming that we know of, and the formation of trails and networks of ant traffic is not imposed by any special boundary conditions, lattice topology, or additional behavioral rules. The required behavioral elements are stochastic, nonlinear response of an ant to the scent, and a directional bias. Furthermore the parameters of the system need to be tuned somewhat to the appropriate region, and not any nonlinear rule of the above type will do. If the nonlinear response or the directional bias are removed no lines form, and lines that are already formed do not persist. Notice that the role of the decreasing sensory capacity in this region of the physiological

parameter space it to broaden the range of gain at which ants will be able to form trails. We suspect that the ability of neurons in the hippocampus to form plastic networks will be affected in a similar way.

6 Some Conclusions

The main conclusion to be drawn here is that osmotropotaxic scent following of the very simple kind described above is *sufficient to produce evolution of complex pattern of organized flow of social insect traffic all by itself*, and not just sufficient to allow for trail *following* behavior. We believe this observation may be of some help both in classifying different types of recruitment behaviors, in understanding how this type of behaviors evolved, and its relation to other factors such as tandem running which exist in various mixtures of importance with the types of behavior discussed above.

Since the self-organizing properties of the swarm are instability driven, the structures that form have some very interesting properties with respect to large perturbations. We performed the following experiment: the system was tuned to a region of the phase plane where lines form, and a network of traffic was allowed to form. Then β was decreased so that system is tuned below the transition line ($\beta < \beta_c$). One observes that the ants fall away from their orderly patterns and immediately start executing random walks on the lattice. As a result the pheromone distribution starts to fluctuate more and more randomly. If β is then tuned back to its original value at some time later the line will eventually reform with little or no change. This occurs even if the randomization is allowed to proceed to the point that the pheromonal field is almost totally randomized. For times up to about the decay time $\tau = 1/\kappa$ even small, virtually undetectable memory effects of the field can be amplified causing the patterns to reform without significant changes. We can not resist comparison of this amplification phenomenon with recent results of Wilson and McNaughton[20] in which rat memories seem to be consolidated during sleep states in which the noise is substantially larger than in the walking state.

There are two, seemingly conflicting functional abilities this amplification phenomenon allows the swarm to have. Firstly, organized patterns of behavior are really quite stable with respect to large perturbations which might have an obvious usefulness to operation in a changing and unpredictable environment. Secondly, because the patterns are due to the formation of an initially weak cooperative structure of the right kind, the swarm can act as an information amplifier, and even a weak external perturbation (such as the presence of a food source) might lead to a significant response. Thus the swarm possesses both a long memory, and the ability to learn.

As shown in Fig. 5, lines form a little above the second order phase transition line. In this region there is a cooperative effect between the fluctuations and the ordering effects. Below the transition line, or just above it, the fluc-

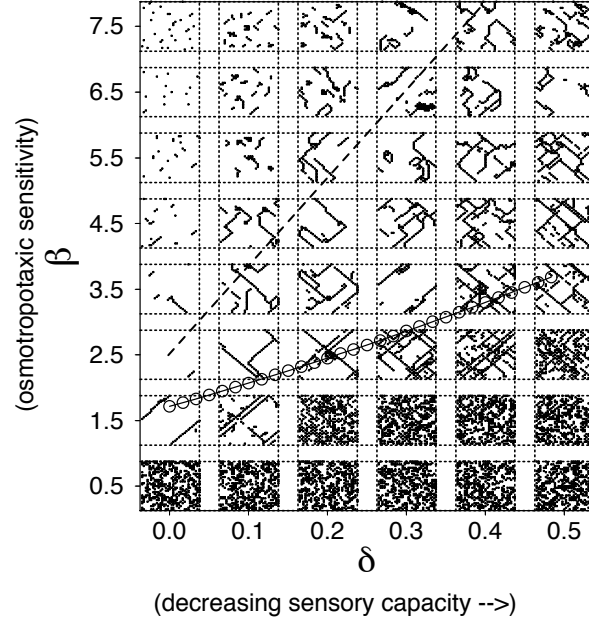


Fig. 5. Physiological Phase Plot: A snapshot of the last two iteration after 1000 time steps starting from a random initial distribution of ants for each δ and β value indicated on the axis. The circles joined by a line is the mean field prediction of a second order phase transition given by Eq. 2. The dashed line is the approximate location of the transition between trails and patches.

tuations are too great, and no cooperative structures form. However, too far above the transition line the fluctuations are suppressed, and the order dominates overwhelmingly. This means that the ants are basically induced to “turn around” with sufficient probability that only patches form. The role of such “U-turns”, has been investigated experimentally and theoretically in [21], where it was also suggested that these u-turns might play an important role in the self-organization of ant traffic.

The region in which the lines form shown in Fig. 5 represents a cooperative effect between the fluctuations and the ordering behavior. The formation of lines can also be understood in terms of the theory in [13, 14]. In the region where lines form the clumping effect is both unstable in the longitudinal direction and stable in the transverse direction of the ant motion, and it is this fact which give rise to the formation of stable line of traffic. The result is a fairly robust region of line formation.

Since information (in the form of the orderly movement of ants from one place to another) can be said to flow only in the region of stable line formation, which lies above the disordered region and below the very ordered region, these results might be thought similar to the hypotheses of “complexity at

the edge of chaos” which asserts that complex behavior emerges in the vicinity of a marginally stable state.[22, 23] However we point out that the system, as far as we know, does not “self-organize” to this region unless it may be said that on the evolutionary time scale the organisms found such behavior adaptive. In addition there is not an “edge” but rather a large robust region where the most complex structures form, and this region is *above*, not *at* marginally stable state. Lastly we do not believe that the reason for this type of behavior has anything to do with the very speculative ones which are sometimes suggested by some researchers.[24, 25]

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