Individual pause-and-go motion is instrumental to the formation and maintenance of swarms of marching locust nymphs

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\textbf{Running header}: Intermittent motion in locust swarming
The principal interactions leading to the emergence of order in swarms of marching locust nymphs was studied both experimentally, using small groups of marching locusts in the lab, and using computer simulations. We utilized a custom tracking algorithm to reveal fundamental animal-animal interactions leading to collective motion. Uncovering this behavior introduced a new agent-based modeling approach in which pause-and-go motion is pivotal. The behavioral and modeling findings are largely based on motion-related visual sensory inputs obtained by the individual locust. Results suggest a generic principle, in which intermittent animal motion can be considered as a sequence of individual decisions as animals repeatedly reassess their situation and decide whether or not to swarm. This interpretation implies, among other things, some generic characteristics regarding the build-up and emergence of collective order in swarms: in particular, that order and disorder are generic meta-stable states of the system, suggesting that the emergence of order is kinetic and does not necessarily require external environmental changes. This work calls for further experimental as well as theoretical investigation of the neural mechanisms underlying locust coordinative behavior.

Key Words: Intermittent animal motion, swarming, locusts, collective motion, biological modeling and simulation
Introduction

From ancient times and still today, the fascinating phenomenon of locust swarms continues to threaten agriculture and challenge science. One of the main difficulties in predicting and controlling locust outbreaks is that of our insufficient understanding of the fundamental principles underlying locust swarming. The challenge lies in connecting or deciphering the dynamic interactions between the behavior of individual animals, the coordinated activity of crowds consisting of millions of animals, and the environment. From a theoretical point of view, locust swarming is a quintessential example of collective motion (Vicsek et al, 1995; Toner and Ramasawamy, 2005; Vicsek and Zafeiris, 2012), bearing resemblance to the formation and dynamics of schools of fish (Tunstrom et al., 2013), flocks of birds (Ballerini et al., 2007; Hemelrijk and Hildenbrandt, 2012), human crowds (Helbing, 2001), cells and bacteria (Ben-Jacob et al., 2012), and even artificial agents (swarming robots; Dorigo and Sahin 2004). Indeed, the emergence of novel group-level behaviors has been described in terms such as "swarm intelligence" (Beni and Wang, 1989; Bonabeau et al., 1999) or the "mind of the swarm" (Klarreic, 2006), referring to the congruence in behavior of swarms composed of very different individuals.

Locusts, nonetheless, retain a special fascination for both scientists and laymen. These short-horned grasshoppers demonstrate density-dependent polyphenism (Pener and Simpson, 2009). At high population density, locusts actively aggregate, forming large hopper bands or adult swarms. In particular, the vast groups of gregarious nymphs that march in unison offer an exceptional model for the study of animal collective behavior.

Recent laboratory and field experiments in the desert locust, *Schistocerca gregaria*, and the Australian plague locust, *Chortoicetes terminifera*, have suggested that collective movement is, as previously reported (Ellis, 1951), highly dependent on the density of animals in the group, and is mediated by combinations of social pair-wise interactions such as avoidance, alignment, and attraction (Buhl et al., 2006, 2011). It was also demonstrated that groups can switch direction without external perturbation. A dominant feature characterizing locust behavior is an intermittent, pause-and-go, walking pattern. This behavior was recently thoroughly studied in single isolated locusts by Bazazi et al. (2012), who found that pause duration is correlated with a high probability of turning. This result suggests that pauses relate to instances in which
individuals make a decision - in this case on direction. The pause-and-go walking pattern was also observed in our own field observations during a recent desert locust outbreak in Israel’s Negev desert in the spring of 2013 (Ayali et al., unpublished).

A putative mechanism for locust swarming and marching behavior was recently, suggested, based on an escape and pursuit strategy, and driven by cannibalism (Bazazi et al., 2008, 2011, 2012; Hansen et al., 2011). The general point of view underlying this somewhat attractive model is that animals chase their peers (conspecifics) in order to eat them, while at the same time, they flee from others to avoid being eaten (but see Buhl et al., 2011). Several additional models have been suggested to describe the emergence of collective behavior in marching locusts, such as Viscek-type models (Yates et al., 2009; Kolpas et al., 2009; Bode et al., 2010), in which individuals align themselves with their neighbors with some error (noise) and continuous intego-differential models (Edelstein-Keshet et al., 1998; Topaz et al., 2012). In the Viscek model and its variations (Vicsek et al, 1995; Vicsek and Zafeiris, 2012) the system can be in one of two phases-disordered or ordered - in which synchronization is either low or high, respectively. The transition between the phases depends on some parameters such as the amount of noise (Vicsek et al, 1995). All previous models successfully predict that while in the ordered phase the swarm can be in one of several metastable states, which can be characterized by an order parameter (see below). However, the switch between order and disorder has been related to some change in external conditions, such as density (Yates et al., 2009) or the animals' diet (Bazazi et al., 2011). Moreover, these modeling attempts are largely heuristic and are somewhat unsuccessful in linking the physiological and sensory conditions of the animal and the social interactions they infer.

The current work was aimed at providing novel insights into the mechanisms responsible for locust coordinated behavior. The principal interactions leading to the emergence of order in swarms of marching locust nymphs was studied both experimentally, using small groups of marching locusts in the lab, and using computer simulations. Specifically, motivated by the experiments of Buhl et al. (2006) and Bazazi et al. (2012), here we focused on the instrumental role of individual pause-and-go motion in the formation and maintenance of the collective motion in swarms of marching locust nymphs. The major sensory triggers and fundamental mechanisms leading to collective behavior within the swarm were inferred from behavior
analysis. Preliminary electrophysiological investigation of the processing of visual inputs, relevant to the dynamic interactions between animals in a marching swarm lend further support to our hypotheses. Assisted by simple models, we show that intermittent motion has a pivotal role in the development and evolution of order and disorder within the swarm, as every time an animal starts moving it makes a small decision on whether or not to join the crowd.

**Materials and Methods**

**Animals**

A colony of the desert locusts, *Schistocerca gregaria* (Forskål) were raised at the Department of Zoology, Tel Aviv University, Israel in a controlled temperature of $30^\circ$C and 35-60% humidity, under 12D:12L cycle. Additional radiant heat was provided by 25W incandescent electric bulbs during daytime to reach a final day temperature of 35-37$^\circ$C. The locusts were fed daily with wheat seedlings and dry oats. Locusts, approaching the gregarious phase, were reared in 60-liter metal cages at a density of 100-160 animals per cage over many generations. All experiments were performed on nymphs of the final (Vth) nymphal-instar (3-4 cm in length and ~0.5 cm in width). For a set of preliminary neurophysiological experiments, we used, in addition to the crowded animals, also nymphs approaching the solitarious phase. For this purpose, hatchlings from eggs laid by crowded locusts were isolated within 4 hours of hatching. Each newly hatched nymph was individually placed in a 1.5 liter metal cage and kept under isolation in conditions similar (all but the density) to the above.

**Behavioral setup**

We conducted a series of experiments in which a group of crowded-reared last larval instar nymphs were freely moving in a homogenous circular arena with a diameter of 50cm (see Figure 1A and Movie S1 for typical experiments). The arena was composed of a flat blue Perspex sheet limited by an outer flexible blue plastic circular wall (50 cm diameter × 55 cm high; Figure S1). The lower 10 cm of the arena's walls were thinly coated with glycerin to prevent nymphs from climbing. The arena was placed in our temperature controlled room ($30^\circ$C) and lit from above.
by a single central 100W incandescent electric bulb. Nymphs were introduced to the arena in three different densities as detailed in Table 1, all high enough to allow the formation of synchronized movement (Ellis, 1951; Buhl et al., 2006; 2001). Nymphs were continuously monitored and recorded using a Sony HDR-XR550E digital camera with a 25 fps rate for later off-line analysis (Table 1 also presents duration of the experiments). Using a novel, custom-designed continuous multiple-target tracking method (see Multi-target tracking in SI, Figure S2), we simultaneously tracked the movement of all individuals with high spatial and temporal resolution (full HD allowed a detailed analysis of the behavior of each individual. Tracking data is available online at http://u.math.biu.ac.il/~arielg/researchPages/PLoS1intermittentMotionData.html

**Analysis of behavior**

Several behavioral events were defined as follows:

**Pause or Go:** To eliminate noise, an animal was considered to be moving if its speed was above a threshold for more than 10 consecutive frames. An animal was considered as pausing (or stopping) if its speed was below the same threshold for more than 20 frames. See figure S3 for the distribution of speeds in experiments.

**Walking initiation:** Walking initiation events were defined as transitions from pausing to movement periods. Such events were divided into those that occurred while the locust was being touched by one or more other nymphs and those that occurred without any tactile stimuli.

Next we averaged the number of walking locusts within a radius of 5 cm of the walking initiating nymph. This averaging was done over 300 consecutive frames (corresponding to 12 seconds), 150 before walking initiation and 150 after. The average change in the number of moving individuals surrounding a locust right before it started moving was the key visual stimulus we identified and utilized.

**Walking direction:** In order to determine the direction in which animals walk, we first observed that nymphs rarely changed their direction while walking - we observed but a few occurrences over several hours of experiments. Thus, we concentrated on the initial walking direction upon walking initiation. We compared three directions: head direction (measured at 5 frames prior to
the event), initial walking direction (measured 10 frames past walking initiation), and the average direction of the active crowd (the order parameter, see below).

**The order parameter**

To quantify order and synchronization in the system, we defined the instantaneous order parameter as the average velocity of walking animals in the angular direction. More precisely,

$$\phi = \frac{1}{Nf} \sum_{k \text{ is walking}} w_k,$$  \hspace{1cm} (1)

where $N$ is the number of animals, $f$ is the fraction of walking animals and $w_k$ is the speed of the $k$th animal in the angular direction: $w_k = v_k \hat{n}_k$, where $v_k$ are animal velocities and $\hat{n}_k$ are normalized vectors pointing in the counter-clock-wise angular direction. When no animals are moving, the system does not have a preferred direction and $\phi = 0$. Thus, $|\phi|$ is a measure of the level of coordination within the swarm. The sign of the order parameter indicates the direction of the swarm: Positive $\phi$ refers to counter-clock-wise (CCW) motion, while negative $\phi$ indicates clock-wise (CW) motion. Note that $\phi$ is different than the order parameter used by many authors since here it depends only on walking animals (See also Kolpas et al., 2009).

**Modeling and Simulation**

In order to test the predictions derived from the behavioral experiments, two types of self-propelled particles models were simulated, a detailed model and a simplified model.

**Detailed Model:** The first model was a detailed approximate version of the actual animal-animal interaction observed experimentally. In this model, $N$ particles representing individual animals are distributed randomly on a circle with radius $\hat{R}$, modeling an annulus in which locusts effectively move. Each particle heads either CW or CCW and can either stand or move at a constant speed. In this respect, the model is similar in spirit to traffic cell models and is also related to the a-synchronous model suggested by Bode et al. (2010). See the SI for a precise mathematical statement of the model.
The dynamics is determined by specifying the probability of a particle to start or stop moving and to change its head direction (turn). To be more specific, the model is defined by the particles' (individuals') probability to pause or start moving, and turn.

Pausing: A moving particle can pause due to two reasons, assumed to be independent: spontaneously, or following collisions with other particles.

Walking initiation: Standing particles can start moving due to three reasons, assumed to be independent: spontaneously, following tactile stimulation (collisions with other particles) or following visual stimulation (the average distance to conspecifics at the front is decreasing or the average distance at the back is increasing).

Turning: A particle that is starting to walk has a given probability of turning, which depends on its orientation relative to the order parameter. As observed in the experiments, the probability of turning depends on whether a particle is oriented with or against the crowd.

Table 2 details all model parameters and their default values. Other similar choices of simulation rules have been considered. For example, the probability of animals to start walking spontaneously may be drawn from the empirical distribution reported for isolated locusts in (Bazazi et al., 2011). Simulations suggest that results are not sensitive to the precise expressions used.

In the detailed model all parameters are drawn from our analysis of the experiments. Given that the size of the experimental arena is comparable to the observed interaction distance between individuals (Figure S4), particles in the detailed model align with a global order parameter that includes all moving particles. As explained in the results section, we find that the probability of turning depends on $\phi$. For simplicity, we assume a linear dependence,

$$p_{\text{turn}}^k = \begin{cases} 
\alpha + \beta_\phi \phi(t) & h_k(t) \phi(t) < 0 \\
\alpha + \beta_\lambda \phi(t) & h_k(t) \phi(t) \geq 0 
\end{cases}$$

(2)

where $p_{\text{turn}}^k$ denotes the probability that particle $k$ makes a U-turn, $h_k(t)$ is the head orientation ($\pm 1$) of particle $k$ and $\alpha$, $\beta_\phi$ and $\beta_\lambda$ are parameters.
Simplified model: The second model was a simplified version that included a few key features of the actual locust dynamics, which we found to be essential for describing the macroscopic properties of the swarm. In addition, the simplified model considers larger swarms. For this reason, all interactions between particles are taken to be local. While the general setup of $N$ particles moving intermittently on a one dimensional circle is the same as in the detailed model, the interaction between particles is modified as follows (See the SI for a precise mathematical statement of the model).

Pausing: Spontaneous only with a fixed probability.

Walking initiation: Either spontaneous or locally triggered. We define an increased probability for starting to walk whenever the number of moving particles is higher than a given threshold.

Turning: the probability of turning depends on a local version of the order parameter $\phi_k(t)$, which is the average head direction of all moving animals that are located up to a fixed threshold distance $r$ from animal $k$. For simplicity, we assume a linear dependence with a minimum,

$$p_{k}^{\text{turn}} = \begin{cases} \max \{\alpha + \beta_w |\phi_k(t)|, \gamma\} & h_k(t)\phi_k(t) < 0 \\ \max \{\alpha + \beta_h |\phi_k(t)|, \gamma\} & h_k(t)\phi_k(t) \geq 0 \end{cases}.$$  

Table 3 details all model parameters and their default values.

Electrophysiology

Details of the dissection, DCMD nerve recording, visual stimulation and data analysis are provided in the Supplementary Material. In short, fifth-instar locust nymphs were anaesthetized and their legs removed ($n=8$; 4, gregarious and 4 solitarious phase). Extracellular recordings of the DCMD spikes were made with silver hook electrodes from the neck connectives (DCMD action potentials can be faithfully identified by their large amplitude and characteristic response to visual stimuli). Computer generated visual stimuli were presented via two computer monitors in the front and back of the animal. Each animal was presented with four different visual stimuli (30 repeats each): single, or multiple simultaneous cues, approaching from the back, or receding in the front. Action potential times (relative to maximal object size), number and frequency were comparatively calculated.

Results

Intermittent motion
Most importantly, we found that desert locust nymphs in a crowd present a walking pattern of intermittently switching between standing and walking (various colored lines and circles in Figure 1A). Figure 1B shows a typical sequence of pause-and-go periods. The distribution of spontaneous pause times (in the absence of stimulus) could not be obtained directly from the experimental data, since pause times were interrupted by the external stimuli. In order to estimate the mean spontaneous pause time, each pause segment was labeled according to the event it ended with – tactile, visual or none. The first two were treated as right-censored events. A right-censored maximum likelihood estimate yielded an average spontaneous pause time of 2.3 seconds. Similarly, walks were terminated either spontaneously or due to tactile stimuli, considered as censoring. Due to the shape of the distribution of walking times we modeled the spontaneous walking time as a sum of two independent exponentially distributed random variables with different averages. A right-censored maximum likelihood estimate yielded 0.16 and 4.06 seconds.

Walk durations were well approximated by independent exponential random variables (Figure 1C). This observation indicates that animals terminate walks at random and the process has no memory (a Markov process). In contrast, pause times (Figure 1D) have a fat-tailed distribution that seems to decay with a power law scaling of approximately 2 (compare with Bazazi et al., 2012, who found for single locusts a scaling factor of 1.67). The power law distribution suggests underlying information processing with memory, supporting our hypothesis that decision-making is involved during pauses. It is important to note that the intermittent walking does not seem to be an artifact of our experiments or the lab conditions, as it was also a dominant feature of individual locust hoppers in the recently observed naturally occurring marching bands observed in Israel’s Negev desert (e.g. Movies S2 and S3).

Next, we looked for the mechanisms involved in the decision of a standing locust to initiate or resume walking (rejoin the marching crowd). We explored various potential triggers by scanning all walking initiation events in our experiments (all in all some 70,000 events). The most consistent factor was found to be an increase in the average number of walking animals in close proximity of the standing individual (compare the purple line in Figure 2A to the green line denoting randomly selected frames). Further investigation revealed that in many cases walking initiation was preceded by the standing individual being touched (or “bumped”) by a walking
animal (Figure 2B). Indeed 54% of walking initiation events could be explained by tactile stimuli. The distribution of touch angles is depicted in Figure S5A. As expected, tactile-stimuli-related walking-initiation events were preceded by an increase in the average number of walking animals in close proximity of the touched locust (blue line in Figure 2A). This phenomenon may well be a result of the physical constraints of the experimental arena, as “bumping” was rarely seen in the wild marching bands (movies S4 and S5).

Interestingly, when focusing on all walking initiation events that did not involve tactile stimuli (46%), and again looking at the average number of walking animals in the vicinity of the standing individual, data was still markedly different from that generated by random (compare the red and green lines in Figure 2A), suggesting an additional mechanism beyond tactile stimuli, that is responsible for walking initiation (or resumption of walking) by a standing locust. This additional mechanism translated to the standing locust seeing a decrease in the number of moving animals in its vicinity. To further investigate the visual stimulus that potentially induces walking initiation we separately examined the optical flow in the front versus the back part of the walking-initiating animal's visual field (Figure 2C, D). We found that, on average, right before an animal (which is not being touched) starts moving it senses a reduction in the number of moving individuals in front of it, or an increase in the number of moving individuals behind it (Figure 2E). Assuming different, 1-13 cm, radius spheres around the standing locust, we tried to determine the effective range of visual interactions between the nymphs. To do so, control curves were calculated for each radius using 10,000 cases of random frames and random animals and were deducted from the walking initiation curves (Figure S4). We then tested whether curves of subsequent radii differ in their distribution, using a set of two-samples Kolmogorov-Smirnov tests. We found that for both the front and back visual fields, beyond a radius of 9 cm, the curves are not statistically different (Table S1).

The described interactions may be reminiscent of the escape-and-pursuit behavior mentioned above. They are consistent with the results of the visual occlusion experiments reported in (Bazazi et al., 2008), as, similarly, we suggest a strong dependence on visual inputs. However, the behavior we identified is not directed at the individual locust. Moreover, locust tend to walk in transitional-parallel paths (Figure 1A, movies S1, S2 and S3). They regularly walk in the direction their body axis is pointing (Figure S5B shows the distribution of angles between the
head direction before walking and the velocity direction after, i.e., the turning angle), and rarely change their direction, nor turn back (make a U-turn) while walking.

**Turning and the build-up of synchronization**

We observed that both the decision to start walking and specifically to walk “with the crowd” are closely correlated with the order in the system (see Materials and Methods for definition of the order parameter).

We tested the evolution of the overall fraction of “walkers” and the order parameter ($\phi$) during the first 15 minutes in our experiments, see movies S4 and S5. The build-up and persistence of order is depicted in Figure S6. The size of $\phi$ and the fraction of walkers were correlated with a correlation coefficient of 0.38, showing that the tendency of animals to join their conspecific increased with the number of walkers. As explained above, we observed that nymphs rarely changed their direction while walking and thus we concentrated on the turning event during movement initiation. We find that turning depends on the level of order in the system. Figure 2F shows the probability of changing orientation (from CW to CCW or the other way around) as a function of the order parameter. The probability of animals to start walking in the same direction as the crowd (blue line in Figure 2F), becomes larger than the probability of walking against it (Red line in Figure 2F) as $|\phi|$ increases. This is a key observation, which is essential to the emergence of order and synchronization within the marching band.

Based on these findings, the mechanism underlying the build-up of synchronization can be described as a positive feed-back on the fraction of walkers: an increase in $f$ increases the frequency of walking stimulus and therefore tends to increase the number of walkers. Since all animals occasionally stop, $f$ fluctuates around a meta-stable equilibrium value. The correlation between $f$ and $|\phi|$ implies that qualitatively the order parameter behaves similarly. The main difference is that, due to symmetry, $\phi$ has two meta-stable equilibrium points related to CW or CCW directions, $\pm \phi_{\text{max}}$.

The positive feed-back mechanism described above can be disrupted due to large fluctuations, which may be considered as rare events. With a large enough number of walkers, the bias in the
direction of movement implies that the sum $\sum_{k \text{ is walking}} w_k$ in Eq. (1) is proportional to the number of walkers $Nf$, and $\phi$ approaches one of its meta-stable values. However, when the number of walking animals is small, fluctuations dominate and $w_k$ are practically random. This implies that $\sum_{k \text{ is walking}} w_k \sim \sqrt{Nf}$ and $|\phi| \sim 1/\sqrt{Nf}$. Therefore, an increase in $f$ results in a decrease in $|\phi|$. We conclude that under the mechanisms described above, the disordered state $\phi = 0$ should also be meta-stable. This is qualitatively different from the prediction of previous locust models in which, while the system is in an active phase (high $f$), disorder is an intermittent, unstable state of the system (Yates et al., 2009; Kolpas et al., 2009; Bode et al., 2010; Buhl et al., 2011). More precisely, we identify meta-stable states, characterized by regions in the $f-\phi$ plane in which the dynamics is confined to for relatively long times. Transitions between such regions should be rare and the time between them distributed exponentially. Four meta-stable states are depicted in Figure 3A: a relatively static state in which most of the animals are standing, and three active states in which most of the animals are moving. The three active states can be classified according to the order parameter and correspond to one disordered and two ordered movement patterns - CW and CCW. Even though the time that the system spends in the static state is short, its impact on the dynamics is pivotal, as a large percentage of transitions are to and from this state (see also Kolpas et al., 2009). Intuitively, it is easier for the system to change its orientation by first reducing the number of walkers, and thus locally increasing the influence of fluctuations.

Order and disorder under pause-and-go movement

To further quantify this behavior, we describe the effective dynamics of $\phi$ as an approximate diffusion process (Buhl et al., 2006; Bode et al., 2010) of the form

$$d\phi = F(\phi)dt + \sqrt{D(\phi)}dW,$$  (2)

where $W$ is the Weiner process (Brownian motion). In (2), $F(\phi)$ is the effective drift function that describes the dynamics of the average $\phi_i$. Indeed, denoting the average order parameter at time $t$ by $m(t) = E[\phi_i]$, the time evolution of $m(t)$ is given by the ordinary differential equation $dm/dt = E[F(\phi_i)]$. The effective diffusion function $D(\phi)$ describes, loosely speaking, the
amount of noise that the system is subject to. The functions $F(\phi)$ and $D(\phi)$ can be approximated from the dynamics as

$$F(\phi) = \frac{1}{\Delta t} \langle \phi_{t+\Delta t} - \phi_t \rangle_{\phi}$$

$$D(\phi) = \frac{1}{\Delta t} \langle (\phi_{t+\Delta t} - \phi_t)^2 \rangle_{\phi}$$

where brackets denote averaging over all frames in which the order parameter is in some range of $\phi$ and $\Delta t$ is the time between frames. Figure 4A depicts $F(\phi)$ and $D(\phi)$ obtained from experiments. As expected, $D(\phi)$ has a maximum at $\phi = 0$. This is a small numbers effect which is a direct consequence of intermittent movement behavior (compare with Huepe and Aldana, 2004; Yates et al., 2009; Bode et al., 2010). The meta-stable states of the system are characterized by stable zeros of the drift function $F(\phi)$. Stable means that the system will return to the zero point following a small perturbation. In other words, close to the stable point, if $\phi$ increases, $F(\phi)$ is negative, which means that, on average, $\phi$ will decrease. On the other hand, if $\phi$ decreases, $F(\phi)$ is positive, and $\phi$ will increase back to the fixed point. Other zeros of $F(\phi)$ are unstable to small perturbations. Unfortunately, the data for $F(\phi)$ are too noisy to conclude the existence of a meta-stable disordered state at $\phi = 0$ (A meta-stable disordered state is weakly discernible in Yates et al., 2009; their figure 2B).

We suggest that the fundamental process, which governs the dynamics of the swarm, is that of visual-flow-based repeated decisions that each individual animal makes regarding when to pause or start walking, and in what direction. Moreover, the individual pause-and-go strategy has profound implications for the macroscopic behavior of the swarm, as it facilitates the emergence of collective order. We sought to test these hypotheses and predictions by a mathematical model.

**Modeling and Simulation**

The dynamics obtained in our experiments were simulated using two types of self-propelled particles models. The first, a detailed model, which includes an approximated version of the actual animal-animal interaction observed experimentally, and the second a simplified model.
The detailed model: This model was used to verify the consistency of our description of the dynamics as deduced from the experiments. In addition, simulations allow an extensive investigation of the contributions of the different model constituents and ample sampling. See Figure 3B and movie S6 for a snapshot from a simulation.

Figure 3C shows the evolution of the fraction of walkers, $f$, and the order parameter, $\phi$, in a typical simulation. The distribution if $\phi$, $f$ and the correlation between them is depicted in figure S7. As described above, we identify four meta-stable states, corresponding to a static state in which most of the animals are standing, and three active states corresponding to one disordered and two ordered movement patterns - CW and CCW. Accordingly, the dynamics of the model can be well approximated by a four-state continuous time Markov chain. The probability of being in each state as well as the transition times is depicted in Figure 3A. Waiting times between transitions are approximately exponential, in agreement with the Markov assumption (Figure S8A). Figure 4B shows the effective drift and diffusion functions as obtained from the detailed model, see also Figure S9. Compared with the experimental result, Figure 4A, the general trend is similar. However, the experimental data is too noisy for a precise comparison. As predicted, we find that in simulations, $F(\phi)$ has five roots, corresponding to the fixed-points of $\phi$. Two of these points are unstable, while three are stable – referring to one disordered and two ordered states. The sensitivity of this prediction to the model parameters is examined in the SI section and summarized in figures S10 and S11.

The shape of the effective diffusion coefficient $D(\phi)$ can be compared with two previous models: Yates et al. (2009) and Bode et al. (2010). Yates et al. (2009) suggest a model in which time is continuous. In simulations, time steps are taken synchronously, i.e., the positions and orientations of all particles are updated together. As a result, the shape of $D(\phi)$ is flat. It does not show a peak around $\phi = 0$ and the authors needed to introduce a non-trivial, ad-hoc $\phi$ dependent, noise term in order to account for this observation. Bode et al. (2010) show that changing simulations to an asynchronous scheme, in which particles are updated at random (Poisson distributed) times, qualitatively reproduces the correct form for $D(\phi)$ without any special assumptions on noise. In our model, random waiting times are analogous to the asynchronous scheme of Bode et al., 2010), which accounts for the observed diffusion. However,
the model of Bode et al. does not show the positive feedback between the order parameter and
the number of walkers and hence does not explain the meta-stable disordered state.

**The simplified local model:** The detailed model described above captures the system dynamics
as observed in experiments quantitatively. However, due to the relatively large number of model
parameters (see Table 2), it is difficult to understand the importance of each parameter and its
effect on the swarm dynamics. Accordingly, in order to identify the key principles leading to the
kinetic order-disorder transition as predicted by our experiments with marching locust bands, the
detailed model described above was simplified, stripping it of many of the experimental details.
As a result, we can no longer expect a quantitative agreement between simulations and
experiments. In the simplified model, we assume that whenever the number of moving particles
around a standing individual is above a given threshold, the standing individual has an increased
probability to start walking. In addition, all interactions between particles are taken to be local.
This implies that the instantaneous description of a particle does not depend on the order
parameter of the entire system, but only on a local version that considers a few close neighbors
(See the Materials and Methods and SI sections for details).

Once again, the dynamics fits the 4-state CTMC picture depicted in figure 3A with slightly
different occupancy frequencies, transition probabilities (Tables S2) and waiting times (Figure
S8B). Interestingly, the time the system spends in the small f regime decreases, but its effect on
the dynamics increases as most of the transitions between meta-stable states happen through it.
Simulations with more particles yield similar results. In fact, the four-state CTMC approximation
becomes more even accurate with larger N.

As explained earlier, the probability of an animal to change direction depends on the local order
around it. In other words, it is the "social" interaction that determines the probability of
individuals to join the crowd or walk against it. Indeed, Figure 4C shows that by changing this
probability, specifically $\beta_A$ and $\beta_W$ in Eq. 3, the available meta-stable states can change. With a
lower probability of turning against the direction of the crowd, only a single disordered state
exists; while with a higher probability, only ordered states exist. However, within the range of
parameters corresponding to the experimental conditions, all three states are accessible. Thus, the
social interaction between individuals determines the available macroscopic states of the system.
and the proportion of time the system "gets-stuck" in each state before transitioning to a different one. The sensitivity of these observations to some of the other model parameters is examined in the SI section and summarized in figure S12.

A related observation was presented by Bhattacharya and Viscek (Bhattacharya and Viscek, 2010) who modeled collective decision in lading bird flocks. In their model, each bird has an internal state that describes a bird's tendency to land, similar to stopping in locusts. This state is influenced by neighboring birds, which results in a sharp transition to a stationary state in which the entire flock lands within a short time. However, in their model, stopping is not reversible and a bird that landed does not take off again.

**Neurophysiological evidences for the role of visual cues in locust collective movement**

We sought to offer preliminary evidence supporting the role of visual cues in the decision of a locust to join the marching crowd, by first demonstrating that visual stimuli, related to locust marching and animal interactions within a marching swarm evoke consistent neuronal responses. We presented gregarious locusts at the Vth nymphal stage with two basic visual stimuli (Figure 5), based on those observed in our experimental arena and supported by the model: either objects approaching in the rear visual field, or receding in the front visual field (Fig 2C, D). Simultaneously, we recorded extracellularly the locusts’ DCMD neurons. As mentioned earlier, these motion-sensitive neurons were very thoroughly studied in adult locusts in relation to looming objects during flight, either fast approaching predators or flying locusts in a collision course (e.g. Judge and Rind, 1997; Gabbiani et al., 1999; Ribak et al., 2012). It is, however, important to note that here we used very different stimulus parameters as we simulate walking nymphs (much slower moving, significantly lower $l/|v|$ ratio; see Materials and Methods).

In the absence of visual stimulation, the DCMD fired at a low spontaneous rate of $0.696\pm0.863$ spikes/sec ($n=4$). All nymphs showed similar responses to an approaching object, which resembled typical DCMD looming responses (Figure 6A). Firing started early during the approach phase and its rate increased gradually as the object grew larger. Peak firing rate
preceded the approaching object's maximal size by approximately 2 sec. The DCMD response to receding objects was also consistent with previous observations (Rind and Simmons, 1992; Simmons et al., 2013), with a peak firing rate aligned with the receding object's maximal size (Figure 6B). The firing rate then gradually decreased as the object grew smaller.

An approaching object generated a significantly higher number of elicited spikes compared to a receding one (37.5±9 spikes and 19.8±7 spikes respectively, repeated measures ANOVA, $F_{1,6}=8.96$, $p=0.024$). We found no effect for the type of stimulus (i.e. approaching vs. receding) on peak firing rate ($F_{1,6}=0.29$, $p=0.61$). Each stimulus was presented 30 times consecutively (see SI), and data revealed a strong effect of trial number on the number of elicited spikes ($F_{29,174}=3.1$, $p<0.001$), i.e. habituation of DCMD response, which will be described in details below.

Based on our behavioral observations and model, we expected multiple simultaneous visual cues to induce a stronger visual response compared to single cues. Each of the nymphs was therefore presented with two additional kinds of visual stimuli: two objects approaching in the back visual field (Figure 5) and two objects receding in the front visual field. The DCMD responses between all four kinds of stimuli (single or multiple stimuli, recession or approaching) were compared, over all 30 trials, including peak firing rate and number of spikes. We found that visual stimulus type affected mean peak firing rate ($F_{3,12}=4.28$, $p=0.028$; single recession 164±40 spikes/sec, single approach 177±30 spikes/sec, multiple recession 224±31 spikes/sec, multiple approach 239±35 spikes/sec), with a significantly higher peak firing rate induced by multiple visual cues compared to single ones ($p=0.0045$). A similar effect was found when analyzing the mean number of spikes ($F_{3,12}=16.5$, $p<0.001$; single recession 19.8±7 spikes, single approach 38±9 spikes, multiple recession 30.5±6.8 spikes, multiple approach 66±14 spikes; $p=0.0015$ for multiple versus single cues). Both mean peak firing rate and mean number of elicited spikes were affected by trial number ($F_{29,348}=1.5$, $p=0.05$ and $F_{29,348}=2.8$, $p<0.001$, respectively). These habituation effects are further discussed below.

Finally, we examined our findings in light of locust phase polyphenism. In accordance with (Matheson et al., 2004), we hypothesized that while habituated, the DCMD of gregarious animals will respond more adaptively to visual stimuli of different intensities, compared to
solitarious animals. More specifically, in response to multiple visual cues, we expected a more pronounced response in gregarious animals compared to solitarious ones.

Solitarious animals were presented with the same four types of visual stimuli, including single and multiple approaching and receding objects, and their DCMD response was recorded and analyzed as above. In the absence of visual stimulation, we observed no phase-dependent differences in the DCMD activity (solitarious: $0.7 \pm 0.86$ spikes/sec; gregarious: $0.9 \pm 1.0$ spikes/sec; Mann-Whitney $U=7$, $p=0.88$, 6 df). Figure 6B presents a typical DCMD response of one gregarious and one solitarious locust to consecutive repetitions of the four types of stimuli used (single or multiple, approaching or receding). While the first visual stimulus induced strong responses in both phases ($47 \pm 23$ spikes for solitarious and $46 \pm 21$ spikes for gregarious locusts), by the last trial, solitarious animals showed a much weaker response than gregarious ones ($25.1 \pm 15.4$ spikes and $37 \pm 23$ spikes respectively; Figure S13). This represents strong habituation, to a level of 53% of the initial response, in solitarious nymphs, compared to weaker habituation in gregarious animals, to a level of 79% of the initial response.

Following (Matheson et al., 2004), datasets of consecutive repeated recordings were fitted with a single exponential of the form $y=y_0+ae^{-bx}$ (see SI and Figure S14). Analysis showed that the two phases differ in their habituation fitted regression lines ($F_{2,22}=8.54$, $p=0.0018$). This effect was due to a difference in the gradient of the habituation curves ($p=0.0025$) and not in their intercept ($p=0.18$), suggesting a different intrinsic habituation rate for each of the two phases, as expected. While, habituation was also expressed in the effect of trial number on the DCMD peak firing rate ($F_{29, 667}=2.319$, $p<0.001$), the change in this parameter did not differ between the phases. Mean instantaneous firing rate across trials is also shown in figure 6B. Most interestingly, and consistent with our expectations, was a phase-related difference in the mean number of spikes induced in response to the movement of single versus multiple objects. Overall the gregarious nymphs showed a higher number of spikes than solitarious animals in response to multiple approaching stimuli as well as to receding ones, both kinds of stimuli relevant to a marching swarm.

Discussion
Locust phase polyphenism and swarming

It is important to address the consistency of our new description of locust behavior with the wealth of previous knowledge. Ever since Uvarov (1921) suggested his theory of locust phases, locust phase polymorphism has been established as one of the most striking examples of environmentally-induced phenotypic plasticity. Ample research has demonstrated that the gregarious-swarming and migrating phase differs from the solitary-sedentary one in a multitude of phenotypic traits, but first and foremost in its behavior (Simpson et al., 1999; Pener and Simpson, 2009; Verlinden et al., 2009). Gregarious *S. gregaria* have been characterized by a strong attraction to conspecifics, which translates to active aggregation behavior (Ellis, 1964; Uvarov, 1966). They were also reported to be generally more active than solitarious locusts. The question remains as to whether these principal behavioral characteristics are sufficient to account for the locusts’ strong propensity to wander in huge bands of marching hoppers (or in flying swarms of adults). Specifically, are these characteristics also responsible for the striking coordinated behavior and synchronization seen in the marching bands?

Previous studies have suggested different models to account for what has seemed to be missing in our knowledge of locust behavior (e.g. a cannibalistic impulsion; Bazazi et al., 2011; Hansen et al., 2011). Here we suggest that the coordinated marching behavior of locust swarms is manifested by repeated decisions taken by individual animals to initiate or resume walking. Yet, it is actually the outcome of the fundamental locomotion-related behavioral characteristics of locusts in the gregarious phase. These recurring decisions can be explained simply by the high propensity for walking, supported by sensory stimuli conveyed by the optical flux in the vicinity of the animal (due to the behavior of others in the crowd).

**Visual stimuli and swarming behavior**

There have been several reports presenting density-dependent differences in the processing of different sensory modalities between the locust phases (e.g. Fuchs et al., 2003; Matheson et al., 2004; the latter referring specifically to visual stimuli). We show for the first time that the DCMD neurons convey information relevant to the locust response to small, slow moving objects (such as other marching locusts). We used the DCMD response as a “proof of concept” and by no mean imply that this is the only or even major motion sensitive sensory pathway employed during marching and swarming. While other motion sensitive neurons have been
described in locusts, a recent study by Simmons et al. (2013) supports our choice to focus on the DCMD. In this study of larvae of the migratory locust, the authors report that from as early as hatching the larval DCMD neurons already respond selectively to objects approaching the locust and that they discriminate between stimulus approach speeds (tested speeds were 0.5 -5 ms⁻¹). Both approaching and receding stimuli were tested, and interestingly it was found that the response change with development: strong response to receding stimuli early in life, changes towards the adult stage into an improved response to objects approaching on a collision course. It should be noted that swarming and marching starts in the desert locust as early as a few days after hatching. Again, in accordance with our focus on the DCMD, Dick and Gray (2014) suggest that this pathway is capable of responding uniquely to complex aspects of object motion, including translation and trajectory changes at different velocities. Matheson et al. (2004), showed phase-related difference in the DCMD response of adults to flight-related looming objects, while in habituated state. It was suggested that tuning the DCMD responses to the speed and size of approaching objects may infer gregarious animal with specific responses to approaching locusts or approaching predators. Similarly, we suggest that during the larval stages gregarious locusts are almost constantly surrounded by moving nymphs. So while the swarm is on the move, their DCMD is in a continuously habituated state, yet still well-tuned to small, slow approaching or receding objects. This flow on the animals’ visual field is instrumental in the repeated decision taken to join the crowd, facilitating and coordinating the marching behavior of the swarm.

The difference in neural processing of visual stimuli between the solitarious and gregarious nymphs offers a simple and sufficient mechanism for the spontaneous emergence of large locust swarms in the latter. In solitarious nymphs visual stimuli are quickly habituated, and thus they are less inclined to walk (smaller \( f \)), which corresponds to low order (smaller \( \phi \)). As a result, fluctuations are large and the system is in a disordered meta-stable state. On the other hand, gregarious nymphs have an increased probability to start walking (higher \( f \)), which is sufficient to push the swarm into a highly ordered state. Of course, this is just one aspect of the complex phenomena of locust swarming.
**Metastability and intermittent motion**

Pause-and-go or, in general, intermittent motion, occurs in a wide variety of organisms (O'Brien et al., 1990; Kramer and McLaughlin, 2001). For example, it is well known that many types of fish swim in a burst-and-coast motion, possibly to optimize energy usage (Fish, 2010). These discrete bursts of movement associated with rapid changes in speed and orientation parallel the repeated decisions sequence described here for locusts. Indeed, it has been recently shown that the dynamics of fish schools can be depicted using a diagram similar to Figure 3A consisting of stationary (low activity), ordered (polarized or milling), and disordered meta-stable states (Tunstrøm et al., 2013).

The similarities between fish and locusts suggest that the pause-and-go strategy may lead to a generally applicable dynamic pattern in which both disordered and ordered states are meta-stable. Transitions between ordered and disordered states are not necessarily caused by external or internal changes but are, rather, dynamic states of the system. In particular, there is no phase transition between order and disorder in the sense of statistical physics (Vicsek et al., 1995; Vicsek and Zafeiris, 2012). The effect of the environment and other parameters, such as the animals’ concentration (Buhl et al., 2006), diet (Bazazi et al., 2011) or behavioral phase (Topaz et al., 2012), lies in changing the probability of the system to be in either one of the meta-stable states, and in changing the transition rates between the two states while in equilibrium. In the future, it would be interesting to compare the behavior of locusts with that of other organisms showing intermittent motion and look for a more general theoretical explanation.
Figure legends

**Figure 1**

The motion of a single animal is characterized by an intermittent pause-and-go motion. Upon every walking initiation an animal makes a decision of whether or not to swarm based on tactile and visual stimuli. (A) A snapshot from an experiment showing the path of individual animals over 3 seconds. Filled circles show the location of pauses. (B) A typical sequence of pause-and-go transitions in a single animal. (C) The distribution of pause times shows a power-law decay. (D) The distribution of walk times is well approximated by an exponential distribution.

**Figure 2**

Experimental results: (A) The average number of animals walking within 5cm of to an individual that is starting to walk. The vertical line shows the time of walking initiation. Green line: random frames and animals. Purple line: all walking initiation events. Blue line: tactile stimuli-related events. Red line: non-tactile events. (B-D) Zoom-in showing the interaction between conspecifics. (B) Tactile interaction (C) Visual stimulus from the front and (D) Visual stimulus from the rear. (E) The average number of walking animals before and after walking initiation (time=0). Colors indicate front (red), back (blue) and both (green). (F) The probability of changing orientation (U-turn) when resuming movement is a function of the order parameter. As \( \phi \) increases, the probability of turning in the direction the crowd moves (blue) becomes larger than the probability of turning against it (red). As expected, fluctuation at small \( |\phi| \) are large since the system spends a relatively short amount of time in this state. The line shows a linear least squares fit as a guide to the eye.

**Figure 3**

Detailed model results. (A) The dynamics of the system can be approximated by a coarse-grained continuous-time Markov chains with four states: A relatively static state in which most of the animals are standing, and three active states in which most of the animals are walking. The
three active states can be classified according to the order parameter and correspond to one disordered and two ordered movement patterns. Numbers show the relative time the system spends in each state and the transition rates as obtained in simulations of the detailed model. (B) A snapshot from simulation showing standing (black) and moving (CW-blue, CCW-red) agents. (C) The time evolution of the fraction of walkers (red) and order parameter (blue) in a typical simulation.

Figure 4

Effective dynamics of the order parameter in experiments. (A) Experiments. 1. The effective drift. The zeros of $F(\phi)$, corresponding to fixed points, cannot be observed due to a large statistical error. 2. The effective diffusion shows a clear peak at small values of $|\phi|$. Compare with Yates et al. (2009). The blue dotted line indicates the statistical error. (B) Detailed model. 1. The effective drift shows three meta-stable states. 2. The effective diffusion. (C) Simplified model – the predicted behavior of large swarms. The figure shows the effective drift function as obtained in a simplified model with several hundred particles. By changing the probability of turning, the admissible meta-stable states of the system are either 1. Only disordered, 2. Only ordered 3. Both ordered and disordered. Hence, social interactions determine the macroscopic dynamics of the system. Statistical errors in (B) and (C) are of the order of the size of the symbols.

Figure 5

Experimental setup and visual stimuli used for DCMD recording. Locust was mounted in between two computer monitors (1366 x 768 pixels; A, side view; B, top view showing only front monitor). Details of the relative position of the animal in relation to the screens' surface are shown, as well as an example of one stimulus type (two objects approaching in the back visual field) as seen on the back monitor (C, looking at the animal from the front).
Typical response of the DCMD to approaching (A) and receding (B) stimuli. DCMD spike occurrence times (blue) were extracted from the extracellular recordings (black). Individual raster trials were then smoothed with a 20 ms Gaussian window and an evaluation of the instantaneous firing rate (red) was calculated by normalizing the resulting waveform so that its integral equals the number of spikes in the trial. (C) Firing patterns of DCMD in a solitarious and a gregarious animal, in response to the four types of visual stimuli. Each raster plot includes the response of DCMD to 30 sequential stimulations of the same kind, with the first at the bottom of the stack. Mean instantaneous firing rate across trials is shown in the histogram below each raster plot. While the response of DCMD to a single approach and recession bear similarity between the two phases, gregarious nymphs show higher numbers of spikes in response to multiple approach and recession than solitarious animals.

<table>
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<tr>
<th>Trial number</th>
<th>Number of nymphs</th>
<th>Density (locusts/m²)</th>
<th>Duration of recording (min)</th>
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<tr>
<td>1</td>
<td>34</td>
<td>173</td>
<td>60</td>
</tr>
<tr>
<td>2</td>
<td>38</td>
<td>193</td>
<td>180</td>
</tr>
<tr>
<td>3</td>
<td>54</td>
<td>275</td>
<td>130</td>
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Locust density and duration of the experimental trials.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Default value</th>
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<tr>
<td>$N$</td>
<td>Number of particles</td>
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</tr>
<tr>
<td>$R$</td>
<td>Arena radius</td>
<td>25</td>
</tr>
<tr>
<td>$\Delta x$</td>
<td>Grid spacing. Determines average velocity.</td>
<td>0.15</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Probability to turn at $\phi = 0$</td>
<td>0.062</td>
</tr>
<tr>
<td>$\beta_w$</td>
<td>Slope of probability to turn with the direction of the crowd as a function of $\phi$</td>
<td>-0.021</td>
</tr>
<tr>
<td>$\beta_A$</td>
<td>Slope of probability to turn against the direction of the crowd as a function of $\phi$</td>
<td>-0.055</td>
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<td>$p_{\text{stop}}^S$</td>
<td>The probability (per time step) to stop spontaneously</td>
<td>0.0082</td>
</tr>
<tr>
<td>$p_{\text{stop}}^T$</td>
<td>The probability (per time step) to stop when in the same location as another particle.</td>
<td>0.51</td>
</tr>
<tr>
<td>$p_{\text{move}}^S$</td>
<td>The probability (per time step) to start moving spontaneously</td>
<td>0.015</td>
</tr>
<tr>
<td>$p_{\text{move}}^T$</td>
<td>The probability (per time step) to start moving when in the same location as another particle</td>
<td>0.36</td>
</tr>
<tr>
<td>$p_{\text{move}}^V$</td>
<td>The probability (per time step) to start moving when the visual stimulus is on</td>
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</tr>
<tr>
<td>$d_B$</td>
<td>Threshold for the visual stimulus at the back of the animal</td>
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</tr>
<tr>
<td>$d_F$</td>
<td>Threshold for the visual stimulus at the front of the animal</td>
<td>2</td>
</tr>
<tr>
<td>$r$</td>
<td>Interaction distance</td>
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</tr>
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Parameters in the detailed model
Table 3

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<th>Description</th>
<th>Default value</th>
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<td>$\beta_A$</td>
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<td>$p_{\text{stop}}$</td>
<td>The probability (per time step) to stop (only spontaneously)</td>
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<tr>
<td>$\gamma$</td>
<td>Minimal turning probability</td>
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<tr>
<td>$p^S_{\text{move}}$</td>
<td>The probability (per time step) to start moving spontaneously</td>
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<tr>
<td>$p^r_{\text{move}}$</td>
<td>The probability (per time step) to start moving due to stimulus</td>
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<td>Threshold for the stimulus</td>
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<tr>
<td>$r$</td>
<td>Interaction distance</td>
<td>5</td>
</tr>
</tbody>
</table>

Parameters in the simplified model
References:


Fish FE (2010) Swimming strategies for energy economy. Fish swimming: an etho-ecological perspective 90-122


Figure 1
Figure 2
Figure 5
Figure 6
Supplementary Information

Multi-target tracking

The video processing algorithm is divided into three stages: pre-processing, object identification and post-processing. The algorithm was implemented in Matlab.

1. Pre-processing: Movies are converted into a sequence of jpeg images using the software VirtualDub.
2. Object identification: Each frame in the movie is analyzed to find the number of animals and their instantaneous positions and orientations. See below for details.
3. Post-processing: This stage consists of four parts.
   i. Identifying which individual in one frame corresponds to which in subsequent frames.
   ii. Identifying periods of motion and rest using a repeated moving median method.
   iii. Smoothing trajectories and head orientations using a LOWESS method (Hen et al., 2004).
   iv. Calculating velocities.

Object identification: Video and image analysis of the sequence of images making up a movie is performed in three layers related to pixels, objects and post-processing.

Pixel analysis: Every pixel in every frame has an RGB color content which consists of three numbers from 0 to 255, showing the intensity of Red, Green and Blue in the pixel. Since gregarious locusts are typically yellow, grey and black, while the background of the arena was blue, the color content of each pixel can be used to classify pixels into “animal” or “background”. To this end, a single frame is taken and analyzed by hand. Specifically, a few animals are painted red while some area of the background is painted blue. Figure S2A shows one such painted frame and Figure S2B for the RGB content of the pixels, before it was painted. One can see that the RGB content of the pixels consists of two clusters, as depicted in figure S2B. The classification problem is solved using a Support Vector Machine with a quadratic kernel applying the training and classification functions in Matlab's bioinformatics toolbox. Using this technique, each frame can be represented as a binary matrix showing which pixels are suspected to be a part of an animal and which are background. See figure S2C for an example.

Objects analysis: The result of the previous layer is a binary matrix for each frame. This matrix is noisy and the classification of pixels is often incorrect. To this end animal pixels are united into connected regions using the regionprops function in Matlab's image processing toolbox. Each region is smoothed and analyzed according to size and area. Objects with shapes that are uncharacteristic of locusts are discarded. Figure S2D shows a labeled image and the remaining objects.

Post-processing: Objects are identified and numbered relative to locations on the previous frame (figure S2E). Then, we form a list of points in the arena, in which three points are placed along the principle axis of each animal. Figure S2F shows the Voronoi graph of such points where all edges passing inside animals are omitted. The resulting graph is a good characterization of the space each animal occupies. The edges of the graph represent a boundary between animals and
are used to separate animals in the subsequent frame. This is a new feature that increases the success of the tracking algorithm to continuously follow individuals even at very small separations.

**Detailed model and simulations**

Previous experiments show that bands of marching locusts can spontaneously switch between states of coherent motion (Buhl et al., 2006). This occurs even without any apparent reason, implying it is an intrinsic property of the dynamics. Similar dynamical transitions can be observed in other organisms (Tunstrom et al., 2013) and artificial models (Bode et al., 2010; Topaz et al., 2012). Thus, understanding the reasons for these sudden transitions in coherent motion is crucial for understanding the dynamics and the emergence of order and disorder in general, and in locust movement in particular. We propose a one dimensional model which captures the essential dynamics and interactions obtained by our detailed analysis of experiments. This detailed model successfully reproduces movement patterns that quantitatively agree with experimental ones. The model offers increased flexibility in analyzing different situations and dynamical regimes, which are inaccessible by experiments, in particular due to limited sampling.

The model consists of \(N\) particles representing individual locusts that move in a one dimension circular domain with radius \(R\), modeling an annulus in which the locusts effectively move. Both the time and position of particles are discretized, where each time step corresponds to a single frame in the recorded experiments (\(\Delta t = 1/25\text{sec}\)) and the circular domain is discretized uniformly with grid points \(G = \{i\Delta x|i = 1 \ldots L\}\) such that the grid spacing \(\Delta x = 2\pi R/L\) is the average walking distance between frames. See Figure S3 for the distribution of walking speeds. The state of the system is defined by the positions, \(x_k(t) \in G\), head orientations \(h_k(t) \in \{-1,1\}\) corresponding to clockwise (CW) or counter clockwise (CCW) direction, and a Boolean variable indicating whether particles are moving or not, \(w_k(t) \in \{T,F\}\), respectively. Hence, in our model all particles either stand or move at a constant speed—at each time step moving particles shift one grid point either CW or CCW depending on the head orientation. In this respect, the model is similar in spirit to traffic cell models. The model is also related to the a-synchronous model suggested by Bode et al. (2010). The dynamics is determined by specifying the probability of a particle to start or stop moving and to change its head direction (turn). Figure 3B shows a snapshot from simulation.

**Initial conditions:** Each simulation was initialized with a uniform distribution on the entire states space.

**Stopping:** Following experimental observations, a moving particle can stop due to two reasons: spontaneously, with probability \(p_{\text{stop}}^s\), or by colliding with a different particle, i.e. tactile stimulus, with probability \(p_{\text{stop}}^T\). Assuming independence, the overall probability for particle \(k\) to stop is

\[
p_{\text{stop}} = 1 - (1 - p_{\text{stop}}^s)(1 - p_{\text{stop}}^T 1_{\min|x_j-x_k|<\sigma}) ,
\]

where \(1_A\) denotes the characteristic function of an event \(A\), i.e.,
Walking initiation: Following experimental observations, standing particles can start moving due to three reasons:

- Tactile stimulation: After being touched by other moving particles. Movement will occur with a probability $p_{\text{move}}^T$.
- Visual stimulation: when particles in front of the locust move away or when particles behind it move closer. Movement will occur with a probability $p_{\text{move}}^V$.
- Spontaneously: without any apparent stimulation, with probability $p_{\text{move}}^S$.

Assuming independence, the overall probability for particle $k$ to stop is

$$p_{\text{move}} = 1 - (1 - p_{\text{move}}^S)(1 - p_{\text{move}}^T)_{\min_{x_i} | x_j - x_i | = 0}(1 - p_{\text{move}}^V)_{S_B > d_B \land S_F > d_F}.$$ 

Here, $S_B$ is the sum of speeds of particles behind the animal (relative to its orientation) up to an interaction distance $R$, $S_F$ is the sum of speeds of particles in front of the animal up to an interaction distance $R$, $d_B$ and $d_F$ are threshold constants. More precisely,

$$S_B = \sum_{j \neq k} h_j,$$

$$S_F = \sum_{j \neq k} h_j,$$

$$A^B_k = \left\{ j : w_j \land (x_k - x_j)h_k \geq 0 \land 0 < |x_k - x_j| \leq R \right\},$$

$$A^F_k = \left\{ j : w_j \land (x_k - x_j)h_k \leq 0 \land 0 < |x_k - x_j| \leq R \right\}$$

$$A_k = A^B_k \cup A^F_k.$$

The dependence on $t$ and $k$ is suppressed for short hand. In words, $A_k$ is the set of particles moving within a distance $R$ from particle $k$, $A^B_k$ and $A^F_k$ are partitions to the back and front of particle $k$, respectively.

Turning: As observed in experiments, particles can change their direction only by stopping and then turning. This gives a more detailed representation of locust movement than other models that assume continuous movement and turning. A particle which is starting to walk has a given probability of turning. This probability depends on its orientation relative to the order parameter. We recall that the order parameter is defined as

$$\phi_k(t) = \begin{cases} \frac{1}{|A(t)|} \sum_{j \in A(t)} h_j(t) & |A(t)| > 0 \\ 0 & |A(t)| = 0 \end{cases}$$

where $A(t)$ is the set of moving particles at time $t$,

$$A(t) = \left\{ j : w_j \right\},$$

and $|X|$ denotes the number of elements in a set $X$, i.e., $|A(t)|$ is the number of moving particles at time $t$. Note that the fraction of walking animals is given by

$$f(t) = \frac{|A(t)|}{N}.$$
As observed in the experiments, the probability of turning depends on whether a particle is oriented with or against the crowd. For simplicity, we assume a linear dependence on $\phi$:

$$P_{\text{turn}} = \begin{cases} 
\alpha + \beta_W |\phi(t)| & h(t)\phi(t) < 0 \\
\alpha + \beta_A |\phi(t)|(t) & h(t)\phi(t) \geq 0 
\end{cases}$$

Note that as $\phi \to 0$ there is no preferred direction and the probability is $\alpha$ regardless of orientation.

**Simulation results:**

Simulation parameters were scaled to fit experimental values and *All* parameters values were fitted according to statistics obtained from the experimental data: $N = 34, R = 0.25\text{m}, \alpha = 0.062, \beta_W = -0.021, \beta_A = -0.055, p^{\text{move}}_T = 0.36, p^{\text{move}}_V = 0.04, p^{\text{Stop}}_T = 0.51, r = 5\text{ cm}, \bar{v}_1 = \bar{v}_2 = 0.5 \text{ cm/sec}$. Figure 3C shows the time evolution of the fraction of walkers and the order parameter in one typical simulation.

Simulations and comparison with experiments enables seeing whether the model provides a good description of the actual behavior. All averages are calculated from 1,500 simulations, each simulation corresponds to an experiment of about 30 minutes long.

**Order parameter:** In its active state (high $f$) the system has three meta-stable states; two ordered states in which $|\phi|$ is close to 1 and a disordered state around $\phi = 0$. The average order parameter (in absolute value) is 0.62 with a standard deviation of 0.05, which is consistent with the experimental value of 0.56 (See figure S10A).

**Number of walkers:** The average fraction of moving particles is 0.62 with a standard deviation of 0.01, which is consistent with the experimental value of 0.62 (figure S10B).

**Correlation between the order parameter and the fraction of walkers:** As in the experiment, the order parameter is positively correlated with the fraction of moving particles; the average correlation is 0.13 with a standard deviation of 0.06. The experimental value (0.38) is slightly higher (figure S10C).

**Coarse-graining**

As discussed in the main text, one of the fundamental observations in this paper is that the dynamics can be divided into four meta-stable states, depicted in Figure 3A: A relatively static state, in which most of the animals are standing, and three active states, in which most of the animals are walking. The three active states can be classified according to the order parameter and correspond to one disordered and two ordered movement patterns - CW and CCW. In order to verify this assumption we divide the states space into four well-separated regions according to $f$, the fraction of walking particles, and $\phi$, the order parameter:

1. Low movement: $f < 0.5$.
2. High movement, ordered CCW rotation: $f > 0.6$ and $\phi < -0.5$.
3. High movement, disordered state: $f > 0.6$ and $|\phi| < 0.4$.
4. High movement, ordered CW rotation: $f > 0.6$ and $\phi > 0.5$. 

4
The fraction of time that the system spends in each of the states along with the transition probabilities are given in Figure 3A.

One of the tests for verifying our assumption that the complex dynamics of the system can indeed be approximated by a continuous-time Markov chain (CTMC) is that waiting times between transitions should be independent and exponentially distributed. Figure S8A shows the density function of waiting times along with the maximum likelihood fit to an exponential variable.

**A continuous approximation for $\phi$**

In order to further verify which meta-stable states the system has, the effective dynamics of $\phi(t)$ is approximated by a diffusion process of the form

$$d\phi = F(\phi)dt + \sqrt{D(\phi)}dW_t,$$

Where $W_t$ is a Weiner process and $F(\phi)$ and $D(\phi)$ are the drift and diffusion, respectively. Following Yates et al. (2009), $F$ and $D$ can be approximated from the dynamics as

$$F(\phi) = \frac{1}{\Delta t} \langle \phi(t + \Delta t) - \phi(t) \rangle_{\phi},$$

$$D(\phi) = \frac{1}{2\Delta t} \left\{ \langle (\phi(t + \Delta t) - \phi(t))^2 \rangle_{\phi} \right\},$$

Where $\langle \cdot \rangle_{\phi}$ denotes averaging over all frames in which the order parameter is in some neighborhood of $\phi$.

The invariant density of the process can be written as (Gardiner, 2004)

$$f(\phi) \sim e^{-U(\phi)},$$

where the potential, $U(\phi)$ is given by

$$U(\phi) = -\int_{-\infty}^{\phi} \frac{F(s)}{D(s)} ds + \log(D(\phi))$$

Figures 4B and S11 show the parameters of the effective diffusion as obtained from simulations. Compare also with the experimental result, Figure 4A. The potential $U$ has three local minima, two at high values of $|\phi|$ ($|\phi| \approx 0.8$), corresponding to the ordered states, and a shallower one at $\phi = 0$. This implies that on average, ordered states persist for long periods. This can also be observed from the shape of $f(\phi)$ depicted in figure S11D. The fourth meta-stable state, relating to low values of $f$, cannot be observed since this method averages over all values of $f$. This implies that the effective diffusion equation for $\phi$ does not reveal the full coarse-grained behavior of the system.

**Different parameter values**

In order to test the model's sensitivity to parameters as well as study swarming in conditions other than those in our experiments, we vary some of the model parameters. In particular, we are interested in understanding which parameters may "ruin" one of the metastable states—either the ordered or disordered ones. We find that all states are robust and do not depend on fine tuning of parameters. However, the probability to find the system in a disordered or ordered state as well as the transition rates between them may vary.
A few interesting observations are worth noting.

- If the system is too dilute, the disordered state may not be stable (top row of Figure S12). This can be explained by noting the particularly high diffusivity at small values of $\phi$ in this case.

- If the probability to start moving following one of the stimuli is high than disordered state may not be stable (middle and bottom rows of Figure S12). This may be due to the fact that any small fluctuation immediately brings almost full synchronization.

- If the system is too large the ordered state may not be stable (middle row of Figure S13). This unintuitive result can be explained by the fact that with a large system, it is difficult to achieve full synchronization with a local interaction. As a result, the probability to turn towards or against the swarm remains fairly similar. This behavior is an artifact of the global definition of $\phi$ used in the detailed model and does not exist in the simplified, local model presented below.

**Simplified, macroscopic model and simulations**

In order to identify the key principles leading to the kinetic order-disorder transition as predicted by our experiments with marching locust bands, the detailed model described above was simplified, stripping it from many of the experimental details. In addition, all interactions between particles were taken to be local. This implies that a particle does not depend on the order parameter of the entire system, but only on a local version that considers a few close neighbors. Similar to the previous section, the model consists of $N$ particles representing individual locusts that move in a one dimension circular domain. However, since we are more interested in the characteristics of the dynamics at a large number of particles, the domain of simulation is taken to be the segment $[0,2\pi]$ with periodic boundary conditions. Except for this difference, the state of the system is defined by $x_k(t)$, $w_k(t)$ and $h_k(t)$, $k = 1 \ldots N$ and $t = 0 \ldots T$, as described in the previous section. We recall that, $A_k(t)$ denotes the set of moving particles within the interaction distance $r$,

$$A_k(t) = \{j : w_j \land |x_k - x_j| \leq r\}.$$  

Similarly, $|A_k(t)|$ denotes the number of neighbors of $k$, i.e., the number of elements in $A_k(t)$. The dynamics of the system is again specified by the probabilities of particles to start walking, stop or turn.

- **Stopping**: Spontaneous only with probability $p_{\text{stop}}$.

- **Starting**: Either spontaneous or locally triggered. The key characteristic of both the tactile and visual walking stimulus described in the experiments and the detailed model is that the frequency an animal is exposed to the stimulus increases with the number of animals walking in its vicinity. Thus, we define an increased probability for starting to walk whenever the number of moving particles is higher than a given threshold. Assuming independence, the overall probability a standing particle will start moving is

$$p_{\text{move}} = 1 - (1 - p_{\text{move}}^S)(1 - p_{\text{move}}^T |A_k(t)|_{\geq n}) .$$
• **Turning**: Particles turn only when switching from a standing \((w_{k}(t) = F)\) to a moving state \((w_{k}(t) = T)\). The probability of turning depends linearly on the local order parameter (with a minimum \(\gamma\))

\[
P_{\text{turn}} = \begin{cases} 
\max \{\alpha + \beta_{w} |\phi_{k}(t)|, \gamma\} & h_{k}(t)\phi_{k}(t) < 0 \\
\max \{\alpha + \beta_{w} |\phi_{k}(t)|, \gamma\} & h_{k}(t)\phi_{k}(t) \geq 0
\end{cases},
\]

where

\[
\phi_{k}(t) = \begin{cases} 
\frac{1}{|A_{k}(t)|} \sum_{j:A_{k}(t)} h_{j}(t) & |A_{k}(t)| > 0 \\
0 & |A_{k}(t)| = 0
\end{cases}.
\]

**Simulation and results**

We report results of simulations performed with \(N = 100\) particles and an interaction radius \(r = \pi / 10\). Since the length of the arena is set to \(2\pi\), the interaction length, which is 10 times smaller, has on average 5 particles. We stress the fact that in this simulation, all interactions and events are local. In other words each particle senses only a range \([x_{k} - r, x_{k} + r]\). Other parameters are \(p_{\text{stop}} = 0.03\), \(p_{\text{move}} = 0.004\), \(p_{\text{move}}^{T} = 0.05\), \(n_{s} = 2\), \(\alpha = 0.06\) and \(\gamma = 0.003\).

It is well known that locusts, which were reared at different conditions, respond differently to their conspecifics. In order to test the impact of different animal-animal interactions on the dynamics of the marching band, we vary the slopes of the turning probabilities \(\beta_{w}\) and \(\beta_{w}^{T}\). In particular, we demonstrate that three dynamical regimes are possible for \(\phi\) : a single disordered state, two ordered states, or all three (1 disordered + 2 ordered). In addition, the low mobility (small \(f\)) is always meta stable. Figure 4C depicts the effective drift in these three regimes. The effective diffusion is similar to results obtained with the detailed model (see Figure 4B). Parameters are \(\beta_{w}^{T} = -0.08\) and

1. Single disordered state: \(\beta_{w} = 0\).
2. One disordered and two ordered states: \(\beta_{w} = 0.05\).
3. Two ordered states: \(\beta_{w} = 0.5\).

Focusing on the latter case, in which both ordered and disordered states coexist, we demonstrate again that the dynamics can be approximated by continuous-time Markov chains with four states:

1. Low movement: \(f < 0.57\).
2. High movement, ordered CCW rotation: \(f > 0.6\) and \(\phi < -0.55\).
3. High movement, disordered state: \(f > 0.6\) and \(|\phi| < 0.5\).
4. High movement, ordered CW rotation: \(f > 0.6\) and \(\phi > 0.55\).

Tables S2 shows occupancy frequencies and transition probabilities. Values are rounded to the nearest 5%. Figure S7B shows waiting times between transitions and a maximum likelihood fit to exponential random variables. We find that the fit to a CTMC is improved. Interestingly, the time the system spends in the small \(f\) regime decreases, but its effect on the dynamics increases
as most of the transitions between meta-stable states happen through it. Simulations with larger $N$ yield similar results. In fact, the four-state CTMC approximation becomes more accurate.

**Different parameter values**

Finally, in order to test the model's sensitivity to parameters, we test the effective slow dynamics as a function of the number of particles, $N$, the density, $\rho$, and the interaction radius, $R$. Figure S14 shows that as the system becomes denser or larger, the dis-ordered state becomes more pronounced. However, the dependence of the interaction distance $R$ is small as long as it is above some critical value.

**Electrophysiology**

**Dissection and recording:** Experiments were performed on 8 fifth-instar locust nymphs (S. gregaria), four approaching the solitarious phase, and four approaching the gregarious phase. Within each phase-group, half the animals were males and half females. Locusts were anaesthetized in CO$_2$ and all six legs were amputated. Each locust was then placed upside down over plasticine shaped to suit its body size, and was secured using pins located along the sides of the body. The head was gently pulled forwards and stabilized using pins. The soft cuticle of the neck connectives was dissected away to reveal the underlying cervical connectives, each of which include a DCMD axon. Fat tissue and tracheas were cleared and locust saline was added as necessary to keep the tissue submerged. The locusts were turned upside up following electrode placement and was left for 5 min before any records of responses to visual stimuli were made.

Extracellular recordings of the DCMD spikes were made with silver hook electrodes (50 mm diameter, A-M systems, Carlsborg, Washington, USA) placed under the left connective and insulated using Parafilm (Pechiney Plastic Packaging Company, Chicago, Illinois, USA) and petroleum jelly. The spikes have the largest amplitude in the connective and have a characteristic response to visual stimuli. Experiments were carried out at 24–28°C. Signals were recorded at a sampling rate of 20 kHz using a differential amplifier (Model 1700, A-M Systems) and were stored on the computer using an A-D board (Digidata 1200, Axon Instruments, Inverurie, Scotland) and Axoscope software (Axon Instruments). The recorded data were analyzed using DataView (W. J. Heitler, University of St. Andrew, http://www.st-andrews.ac.uk/~wjh/dataview/).

**Visual stimulation:** Animals were mounted in between two 18.5” LED monitors (Samsung SyncMaster S19B300, Seoul, South Korea) with a display area of 230 mm (vertical) x 410 mm (horizontal), which were positioned perpendicularly to the locust's long axis. The right eye was aligned with the center of both screens in azimuth, positioned 100 mm away from both screens and 10 mm above the bottom of the screens' surface, subtending 128×71 deg (Figure S8A). Each monitor had a resolution of 1366 x 768 pixels, a spatial resolution of 0.3 mm and a refresh rate of 75 Hz. The luminance of the monitors was 250 cd/m$^2$.

Both monitors were controlled by a single personal computer. Stimulation programs were written in MatLab. Stimuli were based on visual interactions observed in the behavioral experiments and
were composed of dark squares moving against a bright background with constant velocity of either 2 or 8.4 cm/sec (representing two extremes of the speed range of marching nymphs in our arena), either receding or approaching the experimental animal. The dimensions of the images ranged from a minimum of 8 (width) x 4 (height) mm to 85 x 15 mm. These proportions correspond to visual angles of 4.58° to 47.7° in width and 2.29° to 8.58° in height.

Based on Gabbiani et al (1999), the rate of expansion of the object on the eye is determined by the ratio between the half size of the object \( l \) and the approach velocity \( v \), i.e., \( l/v \). For a constant approach velocity, the angular extent increases slowly at first and then more rapidly as the object nears the eye. We simulated objects with a transversal value of \( l/v = 506 \) or 2125 msec and a height value of \( l/v = 89 \) or 375 msec, for the fast and slow objects respectively. These values, describing very small and slow objects, are significantly higher than those usually used for looming objects.

Four different visual stimuli were presented to each nymph. Each animal was exposed to 30 repeats of each visual stimulus, giving 120 stimuli in total. One recording of a solitarious nymph's DCMD response to a single receding object was omitted due to low signal to noise ratio. A square started its simulated movement in a 10 seconds long stationary position. It then approached or receded for 6 seconds and stopped again, remaining stationary for 10 seconds. Five seconds separated one stimulus from the next. All objects reached both the minimal and maximal size described above.

**Data analysis:** Spike times were obtained by applying a threshold to the recorded potential traces to detect the largest spike, which was always that of DCMD. Spike times are defined and expressed here as "time relative to maximal object size", which is defined as time 0. These data were used to calculate the number of spikes and peak firing rate elicited by each visual stimulus and to construct raster plots and peristimulus time histograms. To examine the time course of the response in DCMD, the spike times were transformed to instantaneous spike frequencies by applying a 20 ms Gaussian smoothing filter (see Gabbiani et al., 1999), with the integral of the smoothed waveform scaled to equal the number of spikes in the trial.

Data were plotted using Matlab and statistical tests were performed using STATISTICA (StatSoft, Tulsa, Oklahoma, USA). When analyzing spike number and peak firing rate samples we applied square root transformation over data and performed a Repeated measures ANOVA, which included planned comparisons. Gradient and intercept analysis of habituation regression curves was performed by a Factorial ANOVA. Both ANOVAs were followed by Tukey's Honestly Significantly Different (HSD) post-hoc test. \( P \)-values of 0.05 were deemed statistically significant. Results are described as means ± standard deviations while standard errors (S.E.) were used for plotting.
SI references


### Table S1

<table>
<thead>
<tr>
<th>Tested radii (cm)</th>
<th>Front visual field</th>
<th>Back visual field</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>D</td>
<td>p-value</td>
</tr>
<tr>
<td>1//2</td>
<td>1.00</td>
<td>1.79E-133</td>
</tr>
<tr>
<td>2//3</td>
<td>0.99</td>
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<td>3//4</td>
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<td>2.59E-18</td>
</tr>
<tr>
<td>4//5</td>
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<td>4.17E-11</td>
</tr>
<tr>
<td>5//6</td>
<td>0.28</td>
<td>1.31E-10</td>
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<tr>
<td>6//7</td>
<td>0.20</td>
<td>9.53E-06</td>
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<td>7//8</td>
<td>0.16</td>
<td>5.64E-04</td>
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<tr>
<td>8//9</td>
<td>0.13</td>
<td>0.0113</td>
</tr>
<tr>
<td>9//10</td>
<td>0.09</td>
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<tr>
<td>10//11</td>
<td>0.05</td>
<td>0.7762</td>
</tr>
<tr>
<td>11//12</td>
<td>0.07</td>
<td>0.3823</td>
</tr>
<tr>
<td>12//13</td>
<td>0.05</td>
<td>0.7762</td>
</tr>
</tbody>
</table>

Saturation of the visual signal in the front and the back visual field. A set of two-samples Kolmogorov-Smirnov tests between sequential radii revealed that the curves in Figure S4 significantly differ from one another between radii of 1-9 cm. Beyond the radius of 9 cm no significant difference was found.
Table S2

(A)

<table>
<thead>
<tr>
<th>State</th>
<th>Frequency</th>
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</thead>
<tbody>
<tr>
<td>1 – low movement</td>
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</tr>
<tr>
<td>2 – ordered CCW</td>
<td>32%</td>
</tr>
<tr>
<td>3 – unordered</td>
<td>10%</td>
</tr>
<tr>
<td>4 – ordered CW</td>
<td>32%</td>
</tr>
<tr>
<td>5 – transitional (not assigned)</td>
<td>19%</td>
</tr>
</tbody>
</table>

(B)

<table>
<thead>
<tr>
<th>State</th>
<th>To 1</th>
<th>To 2</th>
<th>To 3</th>
<th>To 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>From 1</td>
<td></td>
<td>40%</td>
<td>20%</td>
<td>40%</td>
</tr>
<tr>
<td>From 2</td>
<td>95%</td>
<td></td>
<td>5%</td>
<td></td>
</tr>
<tr>
<td>From 3</td>
<td>80%</td>
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<td></td>
<td>10%</td>
</tr>
<tr>
<td>From 4</td>
<td>95%</td>
<td></td>
<td>5%</td>
<td></td>
</tr>
</tbody>
</table>

Approximating the simplified model as a four-state CTMC. (A) The relative time the system spends in each of the four states. Transitional frames are intermittent transitions while between states. (B) Matrix showing the probability of transition from state to state.
**Supplementary material figures**

**Figure S1**

The experimental setup: Several dozen locusts are placed in a plastic circular arena with a diameter of approximately 50cm.

**Figure S2**

Video analysis algorithm. (A) A hand-labeled frame in which animal were painted red and some of the background was painted blue. (B) the RGB content of labeled pixels. The two clusters are separated using a support vector machine. (C) All pixels in each frame are classified as either animal (red) or background (blue). (D) Labeled regions that fit certain size properties. (E) Numbered objects. (F) Voronoi cells associated with individual animals.

**Figure S3**

Experimental results: The distribution of walking speeds.

**Figure S4**

Experimental results. The optical flow in the front (A) and in the back (B) halves of the walking initiating animal's visual field. Each curve shows the average number of walkers at time $t$ from a walking initiation event within a given distance from the animal that is starting to walk. For example, to generate the purple curve we listed all walking initiation events. Suppose that during event 1, animal $k$ start walking at time $t_0$. We counted the number of animals walking within a distance of 5 cm from animal $k$ at time $t_0 - t$ and then averaged over all walking initiation events. Other distances we calculated in a similar manner. While in the front, a walking initiation is preceded by a reduction in the number of moving nymphs, an increase in the same parameter is seen in the back. In both halves of the visual field the signal saturates at around 9 cm, suggesting that above this radius no further visual information regarding the animal's surrounding is obtained.
Figure S5

Experimental results: Angles. (A) A histogram showing the distribution of angles in which animals that started walking due to a tactile stimulus were touched. (B) The angle between the head direction 10 frames before walking and the velocity vector five frames after walking started.

Figure S6

Experimental results. The time-evolution of the order parameter (blue) and fraction of walking animals (red) in the three experiments described in Table 1. The two variables are correlated with an average correlation coefficient of 0.38.

Figure S7

Detailed model results: The distribution of the average order parameter (A), average fraction of moving particles (B), and the correlation between the two (C) in 1500 simulations with length corresponding to 30 minutes of experiment time.

Figure S8

The distribution of waiting times between transitions in the 4-states CTMC approximation. (A) The detailed model. (B) The simplified model. x: state 1, o: states 2 and 4, +: state 3. Solid, dashed and dotted curves are a maximal likelihood fit to an exponentially distributed random variable from states 1, 2+4 and 3, respectively.

Figure S9

Detailed model results: Parameters for the diffusion equation describing the effective dynamics of the order parameter $\phi$, showing three meta-stable states. (A) The drift $F(\phi)$ with three stable roots. (B) The diffusion coefficient $D(\phi)$ has a maximum around zero. (C) The potential $U(\phi)$, and (D) The probability density function $f(\phi)$.

Figure S10

Variation of parameters in the detailed model. Top row: number of particles $N = 10$ (blue), 15 (red), 34 (green-experimental value), 100 (black). Middle row: Probability to start moving following touch $p_{move}^V = 0.1$ (blue), 0.2 (red), 0.3674 (green-experimental value), 0.4 (black), 0.5 (purple). Bottom row: Probability to start moving following the visual stimulus $p_{move}^T = 0.02$ (blue), 0.03 (red), 0.039 (green-experimental value), 0.05 (black), 0.06 (purple).
Figure S11

Variation of parameters in the detailed model. Top row: Probability to stop moving following touch \( p_{\text{stop}}^T = 0.3 \) (blue), 0.4 (red), 0.5083 (green-experimental value), 0.6 (black), 0.7 (purple). Middle row: \( N/L = \text{const} \). \( N = 10 \) (blue), 15 (red), 34 (green-experimental value), 50 (black), 70 (purple). Bottom row: Interaction radius \( r = 3 \) (blue), 4 (red), 5 (green-experimental value), 6 (black), 7 (purple). As \( r \) changes the average number of interacting neighbors, this is also equivalent to changing the interaction thresholds \( d_B \) and \( d_F \).

Figure S12

Variation of parameters in the simplified model. Left column: effective drift, middle column: effective diffusion and right columns: effective potential. Top row: dependence on \( N \), Middle row: dependence on \( \rho \) and bottom row: dependence on \( R \).

Figure S13

Phase related differences in DCMD response. (A) The habituation observed in the elicited number of spikes was more substantial in solitarious nymphs than in gregarious ones (blue and red respectively). (B) Average number of spikes elicited by single and multiple stimuli for each phase. Gregarious (red): single object 28.64±4.31, multiple objects 48.32±7.61. Solitarious (blue): single object 27.87±5.28, multiple objects 30.31±5.19. *** Planned comparisons revealed a significant difference between the phases in the number of spikes elicited in response to movement of multiple objects and a difference in the response to single versus multiple approaches within the gregarious group (\( p<0.001 \)).

Figure S14

A triple interaction between phase, stimulus type and habituation was not found. Habituation is presented separately for gregarious (dark line) and solitarious (bright line) animals and for each of the different visual stimuli, using regression lines fitted for the log-transformed number of spikes. Under all four visual conditions, the solitarious nymphs' regression lines were sharper in negative gradient.
**Movie captions**

**Movie S1.** A short clip showing a 2 minutes example of an experiment in real time.

**Movie S2.** Stop and go motion in the field. Southern Israel, 2013.

**Movie S3.** Stop and go motion in the field. Southern Israel, 2013.

**Movie S4.** A short clip of an experiment with tracking results showing the build-up of motion. x5 speed-up.

**Movie S5.** A short clip of an experiment with tracking results showing synchronization as a preference to the clock-wise direction. x5 speed-up.

**Movie S6.** A short clip showing the switching between synchronized states in the detailed model.
Figure S4
Figure S7
Figure S8
Figure S9
Figure S11
Figure S13
Figure S14