Velocity correlations in collectively moving living systems

Ph.D. Thesis

Zsuzsa Ákos
Department of Biological Physics,
Eötvös Loránd University

Advisor:
Prof. Tamás Vicsek,
regular member of HAS

Graduate School of Physics
Doctoral Program for Statistical Physics, Biological Physics and
Quantum Systems

Head of School: Prof. Palla László, D.Sc.
Head of Program: Prof. Kürti Jenő, D.Sc.

Budapest
2013

Introduction

Collective motion emerges in varying sizes and complexities in very diverse systems like macromolecules, living cells, flocks of birds, schools of fish or groups of people. The common denominatior of all these collectively moving systems is the observed collective motion exhibited by the local interactions of the group members. The behaviour of the system, therefore, is substantially different from the behaviour of the individual members of the group.

Simple models based only on local interactions between group members are able to reproduce the ordering and the main features of collectively moving systems; however, many questions remain unanswered. A significant part of the collective motion research focuses on the information transfer the decision making process inside the group, and the underlying factors. This research can help to reveal the working mechanism of particular biological systems and to find solutions to problems where coordinated joint action of the group members, or the prevention of movement coherence is required (e.g., the flight-formation control of air vehicles, or of the prevention of collective cell migration).

The purpose of this thesis is to clarify the working mechanisms and decision making processes of different, collectively moving living systems. The first part of this thesis investigates how a pigeon flock makes its decisions. Specifically, we investigated the leader-follower relationships among flock members during their flight, and whether the more experienced birds took the leading role during homing flights. The second part investigates the interactions of a group of dogs and their owner during their regular, daily walks. We are particularly interested in determining whether there are correlations between leading roles, dominance rank and personality traits measured by ethological questionnaires. The goal of the third part is to characterize collective cell migration during gastrulation using the prechordal plate of the developing zebrafish embryo as a model system, and to investigate the effect of reducing the number of cells on the movement characteristics of the prechordal plate group. Finally, we extend the movement analysis of the prechordal plate cells to the neighbouring epiblast cells in order to determine to what extent these two cell layers influence each others movement.

Methods

Collective motion research typically requires automatised experimental setups and data analysis tools to follow and analyze the movement of the group members simultaneously. According to the diverse nature of the groups that exhibit collective motion, the method cannot be generalised, and often particular experiments require unique solutions.

During the experiments we intended to separate the individual paths of the group members. We used these individual movement trajectories for the analysis. In the case of animal groups (pigeons and dogs), we used GPS devices that we developed to collect individual path data. During the in vivo cell movement analysis, we labelled the nuclei of the cells with fluorescence proteins, and followed these relatively small fluorescence areas (i.e., small compared to cell size) under a multiphoton microscope. Finally, individual three dimensional trajectories were extracted from these images by using a commercially available software (IMARIS).

For data analysis we used tools inspired by approaches common in statistical physics. In order to extract leader-follower relations among group members, we used different time-delayed, directional-correlation functions.

The flock of homing pigeons we used to investigate leader-follower relationships was comprised of ten birds, and three groups of ten pigeons each were used in order to investigate whether the more experienced birds took the leading role during homing flights. This experiment had three different phases. In the first phase, the birds were flying in flocks to maintain a stable leading hierarchy. In the second phase, three randomly chosen birds from each group received extra training in order to gain additional navigational performance. Finally, in the last phase, the birds were released, in the same flock compositions as in first phase, and changes in flight hieracrhy, if present, were recorded.

In order to investigate the interactions of a group of dogs (five hungarian vizsla and a mixed-breed dog) and their owner, we collected movement data from their usual, daily walks. Personality and dominance rank of the dogs were measured by questionnaires that were filled out by the owner.

Collective *in vivo* cell movement data were collected from developing transgenic *gsc*:GFP zebrafish (*danio rerio*) embryos. We analyzed the movement of the prechordal plate (PP) cells to investigate the effect of reduced cell number on the characteristics of the collective migration. We reduced the PP cell number in two different ways: by interfering with PP cell development (injecting *cyclops* morpholino RNA in one cell stage of the embryo), and by inhibiting cell division. To investigate the interaction between PP and epiblast cell layers we worked with mutants in which PP cell groups do not form, and ingression does not occur (Mzoep mutant). With the help of this mutant we were able to examine the movement of epiblast and transplanted PP cells without the effect of ingression.

Results

1. Our research on homing pigeons revealed leader-follower relationships inside the flock and investigated how changes in navigational efficiency affect the overall hierarchy of the flock [1, 2]. Our results demonstrated that:

   a) Homing pigeons established transitive, hierarchical, leader-follower relationships during flight. Certain individuals consistently contributed with relatively more weight to movement decisions than others.

   b) Leading hierarchy was irrespective of flight type (free or homing flight).

   c) Birds in leadership roles occupied positions near the front of the flock.

   d) Changes in flock members navigational efficiency did not affect the overall hierarchy of the flock. Flock members that gained additional navigational knowledge during the experiment (flown home on a shorter and faster route) did not improve their hierarchical position.

2. By investigating the interactions of a group of dogs and their owner we revealed leader-follower relationships between dogs and compared how leading roles are correlated to the dominance rank and personality traits determined by ethological questionnaires [3, 5]. Our results revealed that:

   a) Leading roles among group members were frequently interchanged during walks.

   b) Leading tendency differences between dog pair members were constant in time. Leader-follower networks in the group based on the leading tendency differences were hierarchical.

   c) Leading roles correlated with dominance rank. Dogs that took the leading role during walks were more dominant in everyday agonistic situations.

   d) Leading roles correlated with personality traits. Dogs that took the leading role during walks were more aggressive and more trainable, and more controllable by the owner.

3. To characterise *in vivo* collective cell movements during gastrulation, we analyzed the movement of the prechordal plate of the developing zebrafish embryo as a model system. We examined the effect of reduced cell number on the migration of the PP cell group, and investigated the movement of the prechordal plate cells together with the movement of the epiblast cells, as the two neighbouring cell layers presumably interact with each other [4]. Our results indicated that:

    a) In zebrafish embryos, the prechordal plate cell group with reduced cell number showed less coherent movement compared to normal embryos. Cells were less ordered, and directional correlation between cells was lowered and decreased faster with cell to cell distance.

    b) A zone of epiblast cells placed along the embryonic axis, anterior from shield, moved anterior during the early gastrulation period for a short time period, and then changed their movement direction to the posterior, dominated by the epiboly movement later on in the process.

    c) Epiblast movement during the early gastrulation period was connected to the ingression movement of prechordal plate cells. In the absence of ingression, it cannot be detected. .

Conclusion

Our research on the decision making mechanism of homing pigeons during their flight showed that pigeons established transitive, hierarchical, leader-follower relationships that were resistant to small changes in navigational efficiency. Leadership ranks within flocks did not directly relate to individual navigational experience.

The fact that hierarchies seemed resistant to small changes once they were established indicated that their advantages do not lay in the navigational experience of the leaders. Earlier studies have found that an underlying interaction network in the group can facilitate information transfer and increase navigational accuracy. The transition between two stable hierarchical states is presumably less effective; therefore, stable leader-follower relations are favoured. Consequently, the advantage of hierarchical organization in a group might lay in their stability.

Our results based on research investigating the interactions of a group of dogs and their owner showed that leading roles between dogs changed dynamically during walks. Dogs differed in leading tendency and these differences stayed stable over time. Interaction networks based on leading tendencies show hierarchical organisation. By comparing leading role to dominance rank we found that leadership during walks was related to the dominance rank assessed in everyday agonistic situations, similar to wolf packs, other primates and beef cows. Leadership was also correlated with personality traits: dogs that took the leading role during walks were more aggressive and more trainable, and more controllable by the owner. The results of this research demonstrated the possibility of determining dominance rank and personality traits of an individual based on their logged movement data only

Finally, while the migration of the PP cell group is not yet understood, several factors have been identified that have an affect on their movement characteristics (e.g. E-cadherin). Our experiment showed that cell number is an important factor to maintaining the coherent movement of the group. The observed short-term, anterior movement in epiblast cell layers refined our current knowledge that epiblast movement is solely posterior and dominated by epiboly. Our results based on experiments with Mzoep mutant embryos, as well as transplanted PP cells to Mzoep embryos, demonstrated that the short-term, anterior movement in the epiblast cell layer was connected to the ingression movement of PP cells as it cannot be detected in the absence of ingression.

Related publications

Articles

1. Flack A, **Ákos Z**, Nagy M, Vicsek T, Biro D. (2013). Robustness of flight leadership relations in pigeons. *Animal Behaviour 86*, 732–732

2. Nagy M, **Akos Z**, Biro D, Vicsek T. (2010). Hierarchical group dynamics in pigeon flocks. *Nature 464*, 890–893

Posters

3. **Ákos Zs**, Beck R, Nagy M, Kubinyi E, Vicsek T. (2011) Dog owner interactions: Walking paths of a pack, *DYNACT*, Dresden,Germany.

4. Smutny M, **Ákos Zs**, Heisenberg CP, Vicsek T. (2012) Collective Migration of Prechordal Plate Progenitor Cells during Zebrafish Development. *ZiF Workshop*, Bielefeld, Germany.

Related submitted articles

5. **Ákos Z**, Beck R, Nagy M, Kubinyi E, Vicsek T. Leadership and path characteristics during walks are linked to dominance order and individual traits in dogs, *PLOS Computational Biology*

Not closely related articles

6. **Ákos Zs**, Nagy M, Vicsek T. (2008) Comparing bird and human soaring strategies ("Kinek jobb a siklórepülési stratégiája, a madaraknak vagy nekünk?") Fizikai Szemle *58*, 396–400 - Marx György Nivo Prize

7. **Ákos Zs**, Nagy M, Vicsek T. (2008) Comparing bird and human soaring strategies, *Proc. Natl. Acad.Sci. USA*, *105*(11), 4139-43

8. **Ákos Zs**, Nagy M, Leven S, Vicsek T. (2010) Thermal soaring flight of birds and UAVs, *Bioinspir.Biomim. 5* (4)