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Collision avoidance during group evasive manoeuvres: a comparison of real versus simulated swarms with manipulated vision and surface wave detectors

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Coordinated group motion has been studied extensively both in real systems (flocks, swarms and schools) and in simulations (self-propelled particle (SPP) models using attraction and repulsion rules). Rarely are attraction and repulsion rules manipulated, and the resulting emergent behaviours of real and simulation systems are compared. We compare swarms of sensory-deprived whirligig beetles with matching simulation models. Whirligigs live at the water's surface and coordinate their grouping using their eyes and antennae. We filmed groups of beetles in which antennae or eyes had been unilaterally obstructed and measured individual and group behaviours. We then developed and compared eight SPP simulation models. Eye-less beetles formed larger diameter resting groups than antenna-less or control groups. Antenna-less groups collided more often with each other during evasive group movements than did eye-less or control groups. Simulations of antenna-less individuals produced no difference from a control (or a slight decrease) in group diameter. Simulations of eye-less individuals produced an increase in group diameter. Our study is important in (i) differentiating between group attraction and repulsion rules, (ii) directly comparing emergent properties of real and simulated groups, and (iii) exploring a new sensory modality (surface wave detection) to coordinate group movement.

1. Introduction

Attraction–repulsion (AR) rules are at the heart of understanding and modelling crowds, flocks, herds and swarms [1–5]. AR rules are commonly used in self-propelled particle (SPP) models of grouping [1,3,4]. These models try to make accurate representations of AR to compare with an empirical system of interest. One way to compare the efficacy of a model is to make a similar manipulation in both empirical and model systems and to test for similar emergent outcomes [5]. However, few of these previous models have tried to address the influence of sensory deprivation on emergent group properties. Also important in these models is how different mixes of individual rules influence emergent properties such as group speed, diameter and nearest neighbour distance (NND) [3]. In order to test how variation in AR rules influences the emergent behaviour of a group, we created an SPP model that mimics empirical manipulations of a swarming insect, the whirligig beetle. This is a useful approach in two ways. First, it is a test of the model to see whether prior assumptions are supported. Second, it helps us understand whether emergent behaviours of a group are simple by-products of the rules that individuals follow, or whether they go beyond the default group behaviours one would expect [5]. For example, previous studies suggest that individuals with a larger-than-average preferred NND would automatically occupy the outside of groups without explicitly knowing where the outside was [6]. We constructed a simulation model to help understand the experimental work in which the AR could be decreased, and these decreases could be implemented bilaterally or unilaterally (on the one side).

Attraction and repulsion in real animals can be studied, in part, by hypothesizing that different senses are predominantly responsible for each and then manipulating those senses experimentally. The influence of sensory deprivation on grouping has been studied only in a few species of fish and insects. Partridge & Pitcher [7] found that blinded saithe (*Pollachius virens*) schooled 'normally', but that repulsion was interfered with when the lateral line receptors were blocked: NND decreased and collision rate increased. Other fish studies in which the lateral line was disabled confirm that eyes are important for initial schooling, but the lateral line is important for close spacing [8]. For insects, detection at close range for repulsion is generally associated with mechanoreceptors such as antennae. In cockroaches, antennae were more important than eyes in avoiding collisions with solid objects [9]. In locusts, leg mechanoreceptors are mostly responsible for stimulating movement [10]. In many of these studies, bilateral deprivation is carried out, but unilateral deprivation would have allowed a finer scale understanding of the individual's movement rules by providing an internal control to see whether surgery influenced the specific direction moved rather than the whole animal movement.

Whirligig beetles (Gyrinidae) are an excellent system for examining sensory systems and movement rules because they are easily marked and filmed as they swim at the surface of the water [11,12]. They form groups of non-related individuals whose primary function is predator avoidance. Many of the emergent properties of the group are also similar to fish, including flash expansion (FE) [13]. FE is a stereotyped rapid outward movement of each group member away from the group centre in response to a predator attack [13]. Whirligigs have a variety of predators, including fish and birds [12]. FE typically lasts a few seconds, and each animal moves 10–15 body lengths before re-aggregating. Despite these similarities with fish, whirligig beetles may use different sensory modalities to coordinate grouping. Whirligigs have two dorsal eyes looking upwards into the air and two ventral eyes looking downwards into the water. Bilaterally blinded whirligigs, and those in the dark, do not group [11]. In addition, the proportion of blinded beetles influences the speed of group escape [14]. Instead of a lateral line system, whirligigs detect close objects (approx. 1 m away; WL Romey 2000, personal observation) by a unique detector of waves on the water's surface. The lower part of the antennae floats on the water surface and when it is deflected, the Johnston's organ generates a nerve impulse [15]. Previous studies have shown that antennae are critical for detecting the vibrations of food or mates [15,16], although no prior studies have assessed the role of antennae in grouping.

We compare the results of an empirical manipulation with a group simulation in which AR mechanisms are manipulated and the individual and emergent properties are measured. For the whirligig experiments, we made unilateral blocks to vision or antennae then measured the resting dimensions of groups and several parameters of their FE. Specifically, we measured collision rates, turn direction, group position, speed of response to predators, NND and group diameter. We predicted that if vision is primarily responsible for within group attraction (and predator avoidance) eye-less beetles (EYE−) would have a greater resting group diameter and NND, no difference in the speed of FE, no difference in collision rate and no unilateral collision avoidance response. We predicted that surface wave detection is primarily responsible

for within group repulsion and that antenna-less beetles (ANT−) would have a smaller resting group diameter and smaller NND, slower FE time, increase in collision rate and unilateral collision avoidance response. This work is important because it: (i) directly compares sensory mechanisms responsible for attraction versus repulsion, (ii) tests eight hypothesized grouping simulation models, (iii) examines whether unilateral sensory manipulations lead to unilateral movement responses and (iv) explores the use of surface waves in coordinating group movement.

2. Methods

We present abbreviated methods here, but for full details of both empirical and simulation methods, see the electronic supplementary material. Whirligig beetles (*Dineutes discolor*) were collected from the Raquette River in Potsdam, NY, USA and maintained and filmed in the laboratory. EYE− beetles had either their left or right eye (dorsal and ventral) painted over with a black oil-based paint pen (Faber Castell). ANT− beetles had either their left or right antenna removed at the base. Three types of groups were assembled for filming: (i) control groups with no sensory deprivation, (ii) ANT− groups with the antenna of half the beetles removed and (iii) EYE− groups with the eyes of half the beetles blocked. Treated beetles were marked on their dorsal elytra as to their treatment whereas the rest of the beetles were left unmarked to have the most natural swarm mates. Replicate groups (72 groups of 24 beetles each) were acclimated in a 1 m diameter experimental tank and filmed before and during an FE elicited by a visual predator model passed quickly over the tank. The digital video was then analysed frame by frame and with IMAGEJ [17] for the following properties: collision rate, turn direction, mean NND, identity of first beetle to startle, position (outside or inside) of first beetle to startle, distance to the centre, group diameter before and after the FE, and duration of FE. General linear-mixed models (GLMMs) and general linear models (GLMs; SPSS v. 20) were used to analyse individuals in groups while controlling for date and order of filming. Time (date and filming order) influenced the overall tightness of grouping, because beetles catch different amounts of food depending on the previous week's weather and the exact amount of time in the laboratory. Individual groups were included as a random effect in the statistical model.

A simulation model, previously developed by several of us [3], was modified (SWARMSIM v. 2) and used to test several hypotheses about how individual movement rules impact group emergent properties such as NND and diameter in the pre-FE part of the whirligig studies. The direction of movement of each particle is influenced by an attraction/repulsion force that depends on the distance between individuals. The model is written in NETLOGO programming language [18], and details on the movement rules are further defined in [3] and the electronic supplementary material. We started with a default set of parameters (control) and from this created four hypotheses (ant-H1–ant-H4) for how removing the antennae would influence simulated repulsion rules and three hypotheses (eye-H1–eye-H3) for how obstructing the eyes would change the attraction rules. For simulation ant-H1, we decreased repulsion while keeping attraction the same. Ant-H2 was composed of an equal mix of ant-H1 and control individuals. In ant-H3, we limited individuals to unilateral perception (180° to the right) as our beetles would have. Ant-H4 was an equal mix of ant-H3 and control individuals. For eye-H1, we reduced the individual's viewing distance from 100 to four units. For eye-H2, we decreased attraction while keeping repulsion the same in all individuals. Lastly, eye-H3 was a mix of eye-H2 and control individuals.
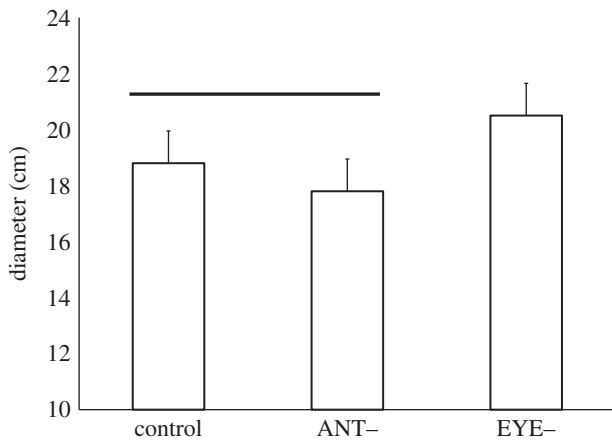
Figure 1. Marginal means and s.e. of the group diameter of whirligig beetles before the flash expansion (i.e. pre-FE). Any two bars not connected by horizontal lines above them are significantly different in the treatment × date interaction.

Figure 2. Marginal mean and s.e. of the flash expansion (FE) time for each of the three types of whirligig groups (30 frames per second). Any two bars not connected by horizontal lines above them are significantly different in the treatment × date interaction.

3. Results

(a) Whirligig: pre- and post-flash expansion

Prior to FE, the mean group diameter of eye-less groups was larger than the control, whereas the mean antenna-less diameter was not different (figure 1). Specifically, there was a significant treatment × day interaction effect in the average group diameters of the three treatment types (GLMM, treatment ($F_{2,57} = 1.55$, $p = 0.220$), date ($F_{4,57} = 2.33$, $p = 0.067$), treatment × date ($F_{8,57} = 2.17$, $p = 0.043$)). Post-FE, there was no significant difference in the diameters of the three types of treatment groups (GLMM, treatment ($F_{2,57} = 2.27$, $p = 0.112$), date ($F_{4,57} = 3.09$, $p = 0.023$), treatment × date ($F_{8,57} = 0.88$, $p = 0.542$). Both ANT− and EYE− individuals were significantly more often on the outside of groups relative to control beetles within the same group (GLMM for distance to the centre of ANT− beetles versus control was $F_{1,262.70} = 6.371$, $p = 0.012$, $n = 15$ groups; GLMM for distance to the centre for EYE− beetles versus control was $F_{1,307.12} = 5.436$, $p = 0.020$, $n = 15$ groups). Pre-FE, there were no significant differences in NND between treatment groups (GLMM for NND: treatment tank ($F_{2,510.40} = 0.239$, $p = 0.787$), date ($F_{4,92.79} = 5.185$, $p = 0.001$), treatment × date ($F_{8,510.45} = 0.475$, $p = 0.874$).

(b) Whirligig: during flash expansion

ANT− groups took longer to expand in response to a predator than the control or EYE− groups, whereas EYE− groups took approximately the same time to expand as the control (figure 2). Specifically, there was a significant treatment × day interaction effect on the mean time it took a group to flash expand (GLM: treatment ($F_{2,57} = 1.75$, $p = 0.182$), date ($F_{4,57} = 4.14$, $p = 0.005$), treatment × date ($F_{8,57} = 2.80$, $p = 0.011$)).

Both ANT− beetles and EYE− beetles collided significantly more often during FE than did control beetles in the same group. When comparing the group types, ANT− beetles collided significantly more often than did EYE− beetles. Specifically, for ANT− groups: mean (and s.e.) collisions per frame (CPF) for control = 0.019 (0.003), mean CPF for ANT− = 0.024 (0.003) (GLMM for CPF: treatment ($F_{1,158.25} = 5.23$, $p = 0.024$), date ($F_{4,14.00} = 2.53$, $p = 0.087$), video ($F_{5,14.00} = 0.64$, $p = 0.675$),
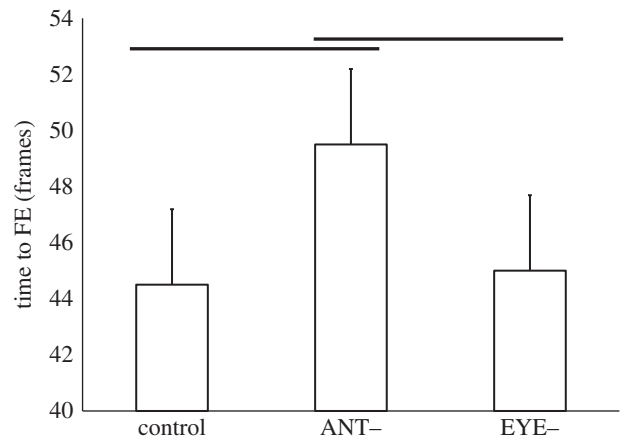
treatment × date ($F_{4,158.36} = 0.46$, $p = 0.763$), treatment × video ($F_{5,158.28} = 1.78$, $p = 0.120$)). For EYE− groups: mean (and s.e.) CPF for control = 0.015 (0.002), mean CPF for EYE− = 0.020 (0.002), (GLMM for CPF: treatment ($F_{1,158} = 5.37$, $p = 0.022$), date ($F_{4,14} = 3.89$, $p = 0.025$), video ($F_{5,14} = 1.96$, $p = 0.147$), treatment × date ($F_{4,158} = 1.46$, $p = 0.217$), treatment × video ($F_{5,158} = 1.41$, $p = 0.225$)). ANT− beetles collided more often than EYE− beetles during FE (GLMM for CPF: treatment ($F_{1,37.21} = 0.82$, $p = 0.372$), date ($F_{4,37.18} = 3.48$, $p = 0.016$), treatment × date ($F_{4,37.18} = 3.26$, $p = 0.022$)).

Unilateral treatments of antenna (but not eyes) led to unilateral turns by the whirligigs. Specifically, ANT− beetles turned significantly more often towards the side of their functioning antenna ($\chi^2 = 23.41$, $p < 0.001$, $n = 74$ beetles; electronic supplementary material, figure S2). For example, beetles with their right antenna removed were four times as likely to turn left than right, and the opposite if their left antenna was removed. By contrast, those with unilateral eye obstructions did not turn significantly in one direction ($\chi^2 = 2.43$, $p = 0.119$, $n = 66$; electronic supplementary material, figure S2).

(c) Simulation

All of the simulations produced coherent groups. For the ANT− simulations, two of the four simulation types produced mean group diameters that were significantly smaller than the control and two that were indistinguishable from the control (figure 3). For the EYE− simulation, two of the three simulation types produced groups with significantly larger diameters than the control (figure 3). The emergent group simulation diameters were qualitatively similar to those seen in the pre-FE whirligig group diameters. Specifically, the proposed movement decision rules for ANT− individuals produced little difference in the group diameter, whereas the proposed movement decision rules for the simulated eye-less groups resulted in a larger group diameter.

The emergent NNDs produced by the simulation was significantly different from the control in a similar direction to the group diameter's would suggest (smaller diameter = smaller NND; electronic supplementary material, figure S3). This differed from that seen in the experimental whirligig
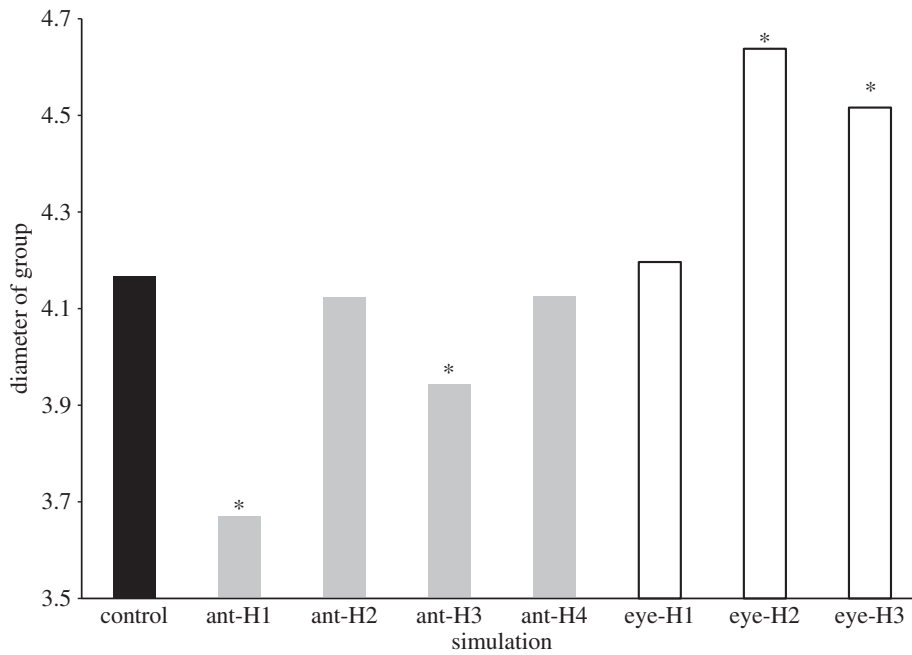
Figure 3. Mean diameter (in body lengths) of eight simulation types ($n = 500$). Standard error bars are minimal (approx. 0.026) and therefore not visible. The solid black bar is the control; grey bars represent simulations of the antenna-less beetles; open bars represent simulations of eye-less beetles. Bars with an asterisk above them are significantly different from the control (t-test, $p < 0.05$).

results in which there was no significant difference in NND between treatments. Movement rules meant to mimic unilateral sensory deprivation (ant-H3) produced a smaller diameter and NND than the control.

4. Discussion

(a) Whirligigs

In our sensory deprivation studies with whirligig beetles, the antennae were clearly shown to be important in grouping and FE. This is one of the first times it has been shown that surface waves help coordinate collective animal motion. We also found that the AR rules are partly mediated by different sensory modalities, with the surface wave-detecting antennae primarily determining repulsion and the eyes primarily determining attraction. For example, in our study, ANT− were more likely to collide with one another during an FE, and it took them longer to achieve a full expansion. Similarly in fish studies, lateral line-deprived individuals collide more frequently [7]. The increased collisions may have caused the observed increase in time that it took the whirligigs to flash expand, though an alternative hypothesis is that they move more slowly. Vision was also found to be important in organizing whirligig grouping and FE.

Unilateral antenna ablation led to specific directions of turns to avoid other beetles, but unilateral blinding did not. This supports the hypothesis that wave detection, not vision, is used for close range repulsion. ANT− beetles turned towards the direction of their good antenna, leaving their 'blind side' towards the obstacle. Eyes seemed to give general information about attraction to other whirligigs but not to coordinate close range manoeuvring and repulsion. One must also account for the fact that individuals within a group also respond to the other group members, so any emergent group responses are influenced and/or diluted by the control beetles and the good eye/antenna.

(b) Simulation model

The four models that simulated antenna removal (ant-H1–ant-H4) produced groups that had significantly smaller diameters and smaller NNDs than the control (figure 3 and the electronic supplementary material, figure S3). However, the experimental whirligig system found no significant change in diameter or NND owing to ablation of an antenna. Therefore, we must reject the four hypothesized simulation rules. Specifically, unilateral antenna ablation does not seem to cause a decrease in repulsion. Empirically, perhaps a beetle with one functioning antenna is still able to accomplish most repulsion functions. Additionally, even though the ANT− beetles collide more often, the overall NND and diameter does not change. Perhaps additional experiments with different numbers and combinations of antenna removal and eye obstruction would reveal more about these attraction/repulsion rules.

For EYE−, there was qualitative match between empirical data (pre-FE) and simulation studies. Two of three EYE− simulations produced significantly larger group diameters than the control (figure 3), which was also true of whirligig beetles (figure 2). This supported the theory that eye ablation might be explained by a reduced level of attraction rather than a reduced viewing distance. Interestingly, even though the NND increased in the simulation owing to the rule changes, the NND in the empirical system did not. This could be explained by the fact that the NND is mostly a result of the antennae, which were fully intact in these EYE− beetles.

Our study is one of the first grouping simulation models in which the influence of lateralized perception on emergent group properties has been examined. One thing not addressed by our simulation and empirical study is that those with reduced vision may form smaller groups. In our empirical work, the experimental tanks were small enough that all of the beetles could detect each other and come together. Similarly, in our simulations, a long enough acclimation period was allowed to achieve one coherent group. Our simulation model suggests

that there is not a synergistic effect on the emergent group dynamics of changing half versus all of the senses of the individuals in a group. Instead, the difference in emergent properties (NND and diameter) between pure and mixed groups, such as when comparing ant-H1 and ant-H2 (or ant-H3–ant-H4) suggests a dilution in response (figure 3). Analysis of simulated FE in future models would be useful in understanding whether the mechanisms could be explained by a simple increase in speed or biased directions away from the centre.

5. Conclusion

Our study is unique in three different ways. First, we isolated and independently manipulated attraction and repulsion in a real system and examined how attraction and repulsion influenced emergent properties of a coordinated group movement. Second, we directly compared real and simulated systems to understand how manipulations of sensors at an individual-level influenced emergent group properties. Finally, our experiment is one of the first to explore a new sensory modality (surface wave detection) to coordinate group movement. Our results have applications to design more realistic grouping simulation models that would apply to a variety of animals and ways in which additional sensors, such as surface wave sensors, could be used for coordinating movements of boats or other automated vehicles [19].

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