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Modeling perspectives on echolocation strategies inspired by bats flying in groups

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HIGHLIGHTS

- We model bats avoiding obstacles by emitting and receiving echolocation pulses.
- We let bats eavesdrop on peers' sensing signals and change pulse emission rate.
- Eavesdropping is beneficial for collision avoidance when measurement noise is low.
- Decreasing emission rate limits sonic interference, but collisions increase.
- Increasing emission rate aids collision avoidance but requires more energy per bat.

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ABSTRACT

Bats navigating with echolocation – which is a type of active sensing achieved by interpreting echoes resulting from self-generated ultrasonic pulses – exhibit unique behaviors during group flight. While bats may benefit from eavesdropping on their peers' echolocation, they also potentially suffer from confusion between their own and peers' pulses, caused by an effect called frequency jamming. This hardship of group flight is supported by experimental observations of bats simplifying their sound-scape by shifting their pulse frequencies or suppressing echolocation altogether. Here, we investigate eavesdropping and varying pulse emission rate from a modeling perspective to understand these behaviors' potential benefits and detriments. We define an agent-based model of echolocating bats avoiding collisions in a three-dimensional tunnel. Through simulation, we show that bats with reasonably accurate eavesdropping can reduce collisions compared to those neglecting information from peers. In large populations, bats minimize frequency jamming by decreasing pulse emission rate, while collision risk increases; conversely, increasing pulse emission rate minimizes collisions by allowing more sensing information generated per bat. These strategies offer benefits for both biological and engineered systems, since frequency jamming is a concern in systems using active sensing.

1. Introduction

Species of bats in the suborder *Microchiroptera* are unique mammals that primarily navigate in their environment using echolocation (Au and Simmons, 2007). They emit directional ultrasounds in pulses (Surlykke et al., 2009), receive reflected echoes to their auditory system through their deformable pinnae (Gao et al., 2011), and constantly interpret the echoes using a powerful neurological signal processing system (Simmons et al., 1979; Horowitz et al., 2004). By analyzing echo harmonic structures, bats are able to differentiate targets from multiple sound reflections (Bates et al., 2011). From a behaviorial perspective, many species of bats are highly social. They live in colonies that range from tens to millions of individuals (Zahn, 1999; Betke et al., 2008). They may exhibit collective behavior (Couzin, 2007) on fast time scales, such as their motion in group flight in the wild (Betke et al., 2008), and slower time scales, such as their roost selection dynamics (Kashima et al., 2013). Within their colonies, bats are able to fly in high densities (Gillam et al., 2010; Betke et al., 2007) at fast speeds (Theriault et al., 2010), while avoiding collisions with peers and obstacles in the environment.

Bat group flight is a unique phenomenon that involves both complex sensing and behaviorial strategies. A major source of the complexity is a bat's use of echolocation as an active sensing mechanism (Kreucher et al., 2005; Musiani et al., 2007) which allows

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interference from peers' sounds. The interference from active sensing can be both constructive and destructive, which is evidenced by bats' so-called eavesdropping and frequency jamming avoidance behaviors, respectively. Eavesdropping behavior is defined as bats listening and reacting to peers' pulses and echoes (Barclay, 1982; Chiu et al., 2008) in situations wherein they do or do not emit pulses. Frequency jamming happens when bats emit pulses of frequencies that overlap the frequency bandwidth of peers' pulses, which may be inevitable for bats flying in large groups in natural settings (Gillam et al., 2010; Betke et al., 2007; Theriault et al., 2010). It has been demonstrated that bats are able to shift the frequencies of their ultrasounds in situations tailored to produce jamming (Gillam et al., 2007; Hiryu et al., 2010; Bates et al., 2008), thus avoiding potentially destructive interference, and recent work has shown incidences of offensive jamming between wild bats during hunting which may necessitate such accommodations (Corcoran and Conner, 2014). Bats are also observed to cease vocalization in the presence of peers in laboratory settings (Chiu et al., 2008; Jarvis et al., 2013), which may allow them to simultaneously eavesdrop on peers' information and avoid jamming. There are currently few studies, however, documenting bats' behavior during flight in the wild and in dense groups.

Mathematically, animal behavior can be modeled as a multi-agent system, where each agent in the group is subject to behavioral rules (Vicsek et al., 1995). Collective behavior at the group level, such as fish schooling (Abaid and Porfiri, 2010; Lopez et al., 2012), bird flocking (Ballerini et al., 2008) and ant lane formation (Couzin and Franks, 2003), may be simulated using these so-called agent-based models when agents are equipped with specific sensing and response schemes (Sumpter, 2006). Rules prescribed to individuals for collective behavior may include repulsion from peers, alignment of velocity directions, and attraction to peers' positions (Aoki, 1982; Couzin et al., 2002). These rules are realized in models by building either discrete decision-making (Vicsek et al., 1995; Aoki, 1982; Couzin et al., 2002) or potential functions (Strefler et al., 2008). Agent-based modeling is also applied to study multi-agent systems in other disciplines, such as population dynamics (Wang et al., 2012; Droz and Pekalski, 2001), predation-prey interactions (Olson et al., 2013; Angelani, 2012; Lin and Abaid, 2013), cell chain migration (Wynn et al., 2012), and disease or parasite transmission (Jiang et al., 2012; Tully et al., 2013).

In this work, we establish an agent-based model to study echolocation strategies which include eavesdropping and changing pulse emission rate inspired by bats emerging from a cave. In the model, bats are designed to fly through a three-dimensional tunnel of rectangular cross-section while avoiding collisions with peers and boundaries, referred to as obstacles. They emit pulses of unique frequencies, and use echoes generated by their own pulses and eavesdropped echoes and pulses from peers to locate obstacles. We note that, although bats echolocate in nature using diverse calls that may be constant frequency or frequency modulated, the acoustic signature of calls are not considered in this model since time is discretized into steps which each can contain a single call. Bats in the model obtain exact obstacle locations with their own pulses, while they estimate obstacle locations using echoes and pulses from their peers perturbed by random noise with a fixed probability distribution; we call this penalty on eavesdropping "measurement noise". In a simulation study, we find that eavesdropping is beneficial in collision avoidance when measurement noise is low. In this case, bat pulse emission rate is balanced between emitting pulses to reliably avoid collisions and varying pulse emission rate to avoid frequency jamming and conserve energy for echolocation, which is quantified using defined cost functions relevant to both biological and engineered systems. This model may help better understand bats' group behavior and inspire control algorithms for robotic teams that use active sensing (Li et al., 2010; Zhuo and Xiao-ning, 2011).

2. Modeling

2.1. Model description

In the following, we describe the model for the acoustic field generation and for bat behavior.

2.1.1. Sensing setup

We consider an agent-based model with the agents, "bats", flying through a three-dimensional tunnel using echolocation and tasked with collision avoidance. The N bats are modeled as self-propelled particles moving with a constant velocity magnitude s in discrete time. The three-dimensional tunnel is a cuboid with side lengths L_x, L_y and L_z, which are the width, length and height of the tunnel, respectively. To model echolocation, we consider that each bat emits a pulse of a unique frequency according to an independent, identically distributed Bernoulli random variable with a constant pulse emission probability p at each time step. The pulse is considered to cover a three-dimensional sensing space, a spherical cone, inspired by a simplified bat sonar beam pattern (Surlykke et al., 2009; Bates et al., 2011; Jakobsen and Surlykke, 2010). The apex of the spherical cone is the bat's position; its side length equals the bat's sensing range r_s; and its opening angle is the bat's angular range of sensing ϕ. The bat's velocity vector originates at the spherical cone's apex and aligns with its central axis. We define a repulsion zone as a sphere of radius r_r centered at the bat's position. Peers and boundaries with positions in this zone are considered to be obstacles and are perceived by the bat as too close, so the bat performs a collision avoidance maneuver. A schematic of the sensing space and the repulsion zone for bat i, $i = 1, 2, \ldots, N$, is shown in Fig. 1.

2.1.2. Echo generation

When a bat emits a pulse at a given time step, echoes are reflected from peers and boundaries that occupy the bat's sensing space simultaneously. These echoes are considered as the bat's "self-echoes" as they result from the bat's pulse. Echoes generated by pulses from peers in the group are called "peers' echoes". Echoes exist for a single time step and they occupy hemispheres of a constant radius r_e, because bats and boundaries are assumed to have surfaces that reflect sound homogeneously. The emitted pulses and reflected echoes are both considered to be incident at the same time step, since we select a discrete time step large enough for sound to propagate through the full echo hemisphere.

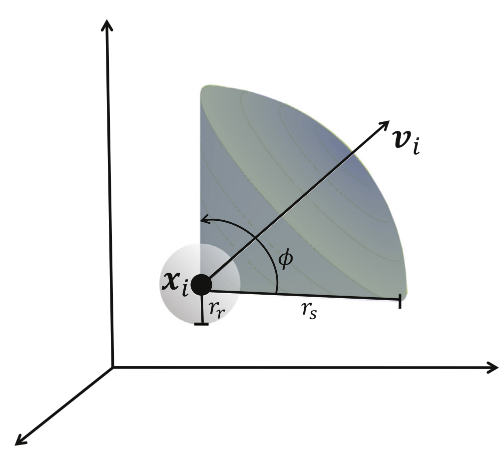

Fig. 1. Schematic of three-dimensional sensing space and repulsion zone for bat i. The bat has position $\mathbf{x}_i$ and velocity $\mathbf{v}_i$. The spherical cone shows the bat's sensing space with sensing range r_s and angular range of sensing ϕ. The gray sphere shows the bat's repulsion zone with radius r_r.