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Insect Navigation and Communication in Flight and Migration: A Potential Model for Joining and Collision Avoidance in MAVs and Mobile Robots Fleet Control



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Insect Navigation and Communication in Flight and Migration: A Potential Model for Joining and Collision Avoidance in MAVs and Mobile Robots Fleet Control

Zhanshan (Sam) Ma
Computational Biology & Bioinformatics Lab, KIZ
Chinese Academy of Sciences, PRC &
Computer Science Dept. & iBEST, University of Idaho, USA

Axel W. Krings
Computer Science Department
University of Idaho
Moscow, ID 83843, USA

Richard Millar
Department of Systems Engineering
Naval Postgraduate School
Patuxent River NAS, MD, USA

Feng Wang
Computer Science Department
Kunming Univ. of Science and Technology
Kunming, 650223, P. R. China

Jun Chao
Kunming Institute of Zoology (KIZ)
Chinese Academy of Sciences,
Kunming, 650223, P. R. China

Abstract—The human being should be awarded the championship of navigation on the planet, on the virtues that they not only have invented and manufactured the compass, GPS, aircraft, vessel, spacecraft, but also have demonstrated exceptional *non-instrumental navigation skills*.¹² The Austronesian expansion from the Asian mainland into the Pacific performed by the Pacific navigators, who eventually populated the most remote islands of the Pacific about 4000 years ago, is a vivid example (Wehner 1998). However, animals, especially flying birds and insects are strong contenders. Monarch butterflies can migrate up to 2000 miles from their reproductive sites in the eastern US and Canada to their over-wintering sites in the forests of Mexico, and it is postulated that they may possess a biological equivalent of a low-resolution GPS system that is based on the magnetic field of the earth. In fact, even the long-legged ants (*Cataglyphis fortis*) in the Saharan desert use the dead-reckoning navigation strategy, which is attributed to the Polynesians, but the ants apparently have acquired the capability much earlier, given the relative short evolutionary history of humans. In this article, we briefly review the state-of-the-art research on insect navigation and communication used in flight and communication, with the objective to inspire cross-disciplinary studies in aerospace engineering, biology and computer science. After a brief review, we overview and identify seven cross-disciplinary research topics that may draw on inspirations from insect navigation and communication in flight and migration. These topics include: *ants colony inspired swarm intelligence, honeybee inspired group decision-making, insect sociobiology, MAV/mobile robot flight control and remote control of insect flights, optimal migration strategy, Quorum sensing, and joining and collision avoidance for MAV fleet control*. An interesting question one may pose is:

given the rich and advanced navigation and communication technologies humans have already invented, such as satellite-based GPS, the Internet, and cellular wireless communication, why do we still expect to possibly learn from insects? A simple answer is that the *distributed* and *self-organized* nature of insect navigation and communication systems makes it simple but very robust due to their highly adaptive nature. For example, without satellites, the GPS system will break down, but the *biological GPS* of monarch butterfly can operate in natural conditions without even using a battery.

Keywords: Insect navigation, insect flight and migration, insect communication, micro-aerial vehicle (MAV), joining and collision avoidance, quorum sensing.

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1. INTRODUCTION

Studies of insect and bird flights have generated significant insights and applications in aerospace engineering and mobile robotics. However, there have been few studies on the potential application of the communication “protocols” and mechanisms utilized by insects in long-distance flight and migration to engineering problems. In biology, the

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problem of insect communication in flight and migration is often approached from the individual perspective, rather than from a group or population perspective. For example, the recent study on monarch butterflies, which can migrate up to 2000 miles seasonally and is one of a handful of the most extensively studied migrant insects, reveals that this butterfly possesses the molecular capability to sense the magnetic field of earth and therefore can use geomagnetic fields during their spectacular long-distance migration. However, little is known about possible communication or interactions between the butterflies during their migration. Can we assume that the swarm of the butterflies is self-organized during the migration? Are there any additional communication protocols and mechanisms among the individuals to coordinate the migration process?

Bee dancing as a communication language is another extensively studied field and has inspired several important computing algorithms for *group formation* and *task allocation* in *scheduling theory* and *computational intelligence*, but has not been applied to flight control communications in engineering. Besides the two previous examples of Monarch butterfly and bees, a third extensively studied insect is migrant locusts, whose switch or phase transition from solitary lifestyle to massive swarm has been explained with *percolation theory*.

The study of animal navigation has been justifiably dominated by the study of birds. The combination of innate and learned behaviors makes the navigation of birds extremely flexible (Wiltschko & Wiltschko 2009). Birds can utilize a wide array of cues from the environment and, in the meantime, their learned mechanisms are also perfectly adapted to the *local situation*. The study of insect navigation has benefited hugely from comparative studies with its counterpart in ornithology, but the long-standing doubts to the learning capacity of insects have hindered more serious studies on the role of insect learning in their navigation and communication. Although research on insect learning *per se* has made enormous advances in the last few decades (e.g., Dukas 2008), the study of insect navigation with a learning dimension is largely limited to the honeybee *dance language*, and a coherent theory on insect navigation, communication, and learning is still missing.

Some of the navigation principles and mechanisms used by insects (especially the dragonfly and locust) have already been applied to mobile robots control. In this paper, we suggest that the somewhat fragmented studies on insect navigation and communication in flight and migration, represented by the studies of three model insects: monarch butterflies, bees, and migrant locusts, may offer useful inspirations for developing navigation and communication protocols useful for MAV fleet control. It seems that the recent advances in monarch butterfly research have been centered on the *individual* flight navigation by exploiting geomagnetic sensing. Instead, the study of bee dancing is focused on the communication interactions *among*

individuals. Interestingly, the study of locusts demonstrates the potential application of *complexity science* theory such as *percolation modeling*.

We postulate that insect migration could be controlled by some kind of distributed, self-organizing, and adaptive mechanisms, regardless of the different mechanism at the individual level, because their limited cognitive capability and lack of communication language do not allow them to develop complex, centralized control systems such as we humans adopt in *aerial traffic control*. Yet, monarch butterflies apparently demonstrate extraordinary feat in conducting themselves to undergo the long-distance migration process. If such protocols and mechanisms can be formally defined with mathematical models, they can be applied to coordinate the fleet of MAVs with missions that are too dangerous for manned flight vehicles to perform. One potential application is *joining* and *collision avoidance* control for unmanned aerial vehicles (UAV and MAV) and mobile robots fleets.

The remainder of this article is organized as follows: Sections 2-4 presents an overview of the studies on insect navigation and communication during flight and migration, including the study on joining and collision avoidance behaviors conducted in entomological research. Section 5 reviews existing applications of the inspirations from insect navigation and communication to aerospace engineering and mobile robotics. This section also presents a perspective on performing cross-disciplinary research that is tailored to generate inspirations for the applications to MAV and mobile robotics controls.

2. AN OVERVIEW OF INSECT NAVIGATION

2.1. Overview of insect navigation

Although the study of insect navigation can be traced back as early as 1900s, a first comprehensive entomological review of this field appears to have been done by Mittelstaedt (1962), who focused on the key capabilities of insect orientation from a modern control theory perspective. Mittelstaedt (1962) believed that there is a control system in the body of insects that controls the spatial relations of insects—orientation, which is not limited to the flight orientation. That review was more like a perspective on the control of insect orientation from an engineering viewpoint than on then existing biological studies, perhaps because there were relatively few biological studies. Mittelstaedt's (1962) work belongs to the type of studies, which Wehner (1998) referred to as the theoretician's *grand theory on navigation*, which has been in active debates for more than a century (Viguier 1882, Matthews 1953, Gould 1985, 1986). Most of those grand theories have been built upon animal's utilization of information from sky and its celestial bodies for astronavigation. For example, the sun-arc hypothesis suggested that birds could estimate their position relative to home by comparing the actual movement of the sun along its arc with the remembered one at home. This implied that

animals must possess sufficient memory, good eyesight (however, most insects cannot even see the stars), and accurate sense of time, and more demanding, the sufficient astronomical knowledge. As summarized by Wehner (1998), regarding astronavigation, little experimental evidence demonstrates that insects may have adopted a heliocentric or a general geocentric view of the sky light world surrounding them. Animals do not have any idea in their mind that the earth is a globe and nor do they perform complex spherical geometric computing of their positions. Instead, birds and insects should perform their navigation tasks in more immediate and approximate ways, perhaps also simpler than what theoreticians have proposed for them. This nevertheless may present opportunities for engineers to get design inspiration from the relatively simple principles and mechanisms employed by insects. It is obvious that those simpler navigation skills have survived millions of year's natural selection and work perfectly well for insects. In fact, there have been many successful studies that demonstrate the inspirational value of insect navigation and communication for solving engineering and computing problems.

The first truly comprehensive review on insect astronavigation with a focus on then existing biological studies appears to have been published by Wehner (1984). In contrast, by the time of Wehner's review in 1984, many ideas on insect navigation seemed to have become well-accepted. Wehner cited a few examples that had appeared in textbooks: "(a) *the insect is informed exactly about the azimuthal position of the sun at any time of the day; (b) it is able to infer correct position of the sun from any particular point of the pattern of polarized light in the sky; (c) it performs true vector navigation (by using a skylight compass and a means of measuring distance).*" A contribution Wehner (1984) made in the review is to point out that some then accepted statements are not exactly true, and he suggested that insects seem always to approach the underlying navigation problems approximately, rather than exactly.

Most studies on insect navigation have been performed with social insects, especially with central place foragers such as ants and bees. Three navigation strategies have been identified with social insects: *path integration*, *goal localization* and *systematic search*; the first two are more prevalent than the systematic search, which insects seem to use as the last resort (Wehner and Menzel 1990). *Path integration* (see the Glossary Box), also known as *dead reckoning* (a strategy used by humans) uses a self-centered coordinate system, and animals must always maintain a vector that store their relative positions to their starting points (home). With the *goal localization* strategy, animals store some kind of two-dimensional snapshots of the landmarks from the start points (goal) and, upon return, they continuously compare the remembered snapshots with the current retinal images. Finally the so-termed *systematic search* is essentially a *local search* from a computational perspective.

From a computation system perspective, to compute such complex navigation strategies, insects must possess sufficient *sensory* (input) and *cognitive* (computing) capacities. For example, a question that has generated heated debates is: does the insect actually have complex *cognitive maps* to perform their potentially map-based behaviors? One would expect that, given the simplicity of their brains, insects may just use simpler computational intelligence approaches for navigation, rather than building complex cognitive maps. Another perplexing question is: how those nocturnally active insects navigate when the intensity of light can be 11 magnitudes lower compared with the bright sunlit world? Even in the sunlit setting, the task to insect compound eyes appears extremely demanding given the simplicity of their visual systems. We will discuss these two important aspects of navigation, i.e., sensory and cognitive capability of insects in the next two subsections (Sections 2.3 and 2.4), with focus exclusively on the visual navigation and cognition systems. But before discussing them, to show the general flavor of insect navigation, we first briefly describe two examples of navigation mechanisms adopted by many *hymenopteran* (ants and bees) and *lepidopteran* (butterflies and moths) insects. These two *orders* of insects should be the most extensively studied insect groups regarding insect navigation; perhaps the only exceptions are the studies on dragonflies and locusts (Ma & Krings 2008, Ma et al. 2009a, 2009b). Our introduction here on the two examples is based on Wehner (1998), and readers should refer to the original paper for details.

The first example is the utilization of the so-termed *E-vectors* (see the glossary box) as compass by the long-legged desert ants (*Cataglyphis fortis*) who roam about the vast area of Saharan desert, separately travel for several hundreds of meters to capture their preys and then return to their central place—a tiny hole leading to their underground colonies. Somewhat amazingly, their return path is close to a straight line to their colonies.

First, it should be pointed out that during the course of the day, the E-vector pattern is variable with the elevation of the sun with non-uniform speed, depending on both time of year and geographical latitude. This implies that, if the ants are presented with individual E-vectors, or combinations of E-vectors, rather than with the entire skylight pattern (which may be impossible for insects to get). Furthermore, if ants use the compass only episodically during outbound foraging or their returns to the colonies, then the ants should deviate by consistent error angles from their homeward paths. These error angles and the underlying systematics can be used to reconstruct a *stereotype template*—the ant's internal representation of the daylight sky. This template is a map of the sky used by the ants *invariably* under all possible skylight conditions. With this *template metaphor*, the key to understand the E-vector supported navigation is to understand how the ants could navigate correctly by using a map that is not a correct copy of the outside world. In other words, the ants only know some general characteristics

rather than the detailed spatial structure of the daylight patterns. It turns out that this basic information is sufficient for the navigation purpose of desert ants because their foraging trip is short (tens of minutes, rather than hours).

The *E-vector compass* is only part of the complex navigation system the desert ants use, i.e., the *path-integration* or *dead reckoning* strategy (algorithm) mentioned previously (also see the Glossary box) by which the ants maintain the information about the distance vector (not E-vector) pointing from their current position toward the central place by integrating the angles steered and the distances covered. In addition, path-integration is error-prone to cumulative errors, and the ants possess backup strategies to prevent interference from random noises. One important backup system that ants adopt is the use of landmark information. The desert ants can remember the snapshots of the landmarks of their home, and later try to match them with the current retinal image. This, however, does not mean that the ants assemble some type of mental topographic maps of their homes—the *cognitive map*, which still has little supportive experimental evidence. The landmark information may also be used along the routes frequently traveled. For example, during foraging, ants might learn a series of snapshots and later try to match their current retinal images with the sequentially-retrieved snapshots. If the path-integration and landmark cues still fail to give the ants right information, they may resort to *systematic search*.

The second example we briefly introduce is the navigation strategy employed by the monarch butterfly (*Danaus plexippus*). Each winter, millions of these butterflies migrate from their breeding sites in Canada and Eastern US to their over-wintering sites in the forests of Mexico. The migration distance is up to two thousands miles. The returning migration in the spring is less spectacular, because most of them stop after reaching the coast states Texas and Louisiana and lay their eggs on the milkweed plants and then die. After two or more short-lived breeding generations, the offspring slowly spreads back northwards and eastwards (Wehner 1998).

It has been conjectured that monarch butterflies use geomagnetic information of the earth for the navigation in their long distance migration (Lohmann 2010). Recent molecular studies have revealed that two forms of the butterfly *Cryptochrome* possess the molecular capability to sense magnetic fields (Gegear 2010). The related study also shows that the circadian clock for time correction with the Sun compass exists in the antenna of the monarch butterflies, rather than in the brain (Merlin et al. 2009). However, the exact navigation mechanism used by monarch butterflies is still little known. Actually, the magnetic field perception by animals was once dismissed as a physical impossibility, but later studies confirm its existence in animals such as sea turtles, lobsters, and more recently monarch butterflies. From a cognitive map perspective, these animals, in effect, possess a low-resolution biological

equivalent of the GPS (Global Positioning System), which is based on Earth's magnetic field instead of satellite signals (Lohmann 2010).

In summary, as pointed out by Wehner (1998), it is unlikely that there is a unitary navigation mechanism that governs insect navigations. The problem with the grand theories in animal navigation is the implicit assumption that animals understand first principles such as spherical geometry and triangular geometry, which insects may not need nor could have acquired during their evolutionary and individual histories. Birds, the best candidate for true astronavigators, still largely depend on a great number of special purpose subroutines suitable to the particular environment that the bird may encounter *en route*. Animal navigation must be studied in the context of evolutionary history (Wehner 1998), and the environment and ecology of the animals cannot be ignored neither.

2.2. Visual navigation by nocturnal insects

Warrant & Dacke (2011) presented a state-of-the-art review on the visual navigation performed by *nocturnal* insects, apparently the most challenging navigation tasks for insects. Insect vision undoubtedly plays the most important role in navigation, especially for flying insects. Especially, nocturnal insects possess superb night vision and color-recognition capability; they can fly through complicated forests at night. The compound eyes of nocturnal insects are well adapted to the dim nightlight that can be eleven orders of magnitude lower than the daylight. Interestingly, the navigation mechanisms nocturnal insects adopt are very similar to those of their diurnal relatives, and the differences are that they use the moon and its polarized light, rather than the sun and its polarized light. Polarized lights are circular patterns of light surrounding sun or moon, and they move along with the sun or moon. The polarized light associated with the moon is a million times dimmer than its counterpart with the sun, but nocturnal insects can still detect the moon's light pattern and use it as their navigation compass. Nocturnal insects can also use terrestrial cues for navigation at night but the performance depends heavily on the contrast of the landmarks with their background (Warrant & Dacke 2010).

However, nocturnal insects have solved some extremely challenging optical problems, but much of the exact mechanism is still little known. These problems are demonstrated by the apparent gap between some theoretical predictions (impossibility) and actual behavior performed by the nocturnal insects. One of the anomalies is demonstrated by the nocturnal hawk moth that may distinguish a blue disk from different grey disks in starlight. Nevertheless, the photoreceptors of this insect can only absorb up to 16 photons during each visual integration time, which is theoretically insufficient to reliably distinguish color. The photoreceptor of some nocturnal bees can only absorb a single photon every six visual integration times, but they can still safely land on their nests (Warrant &

Dacke 2010). The only hypothesis that has been proposed to reconcile this apparent discrepancy is that when light becomes dim, insects integrate signals over longer periods of time to improve visual reliability. The slower photoreceptors actually make this extended signal integration (summation) possible. Of course, this slow temporal is not suitable for detecting fast-moving objects, and the strategy is therefore adopted by slowly flying animals. An alternative strategy is to sum more photons in space—the transition dim light may activate specialized neurons, which may connect the outputs of ommatidia together into groups. Each group may collect many more photons over a much wider visual angle. A tradeoff with this strategy is unavoidable loss of spatial resolution.

2.3. Visual cognition of insects supporting navigation

As mentioned previously, there have been heated debates on whether or not insects possess cognitive maps for navigation ever since the idea was proposed in the study of birds. However, recent advances in the study of visual cognition by social insects have reinvigorated this field and the evidence seems to suggest that social insects such as ants and bees can perform extremely sophisticated visual cognition that is previously considered only doable by vertebrates. Readers are referred to Weber et al's (2011) excellent review of this topic for further information. The following summary is drawn from this article.

Due to the conventional reluctance to view insects as capable to perform non-elemental and high-order learning, the interest in insect cognition only began to pick up in the 1990s (Weber et al 2011). The dominant models for studying insect learning have been bees, ants, flies, and wasps. Advances in the new century suggest that bees are not simple reflex machines and they may possess exceptional non-elemental learning that were not suspected in invertebrates. One remarkable example is the individuals' capability to recognize their distinctive identity. For example, *Pachycondyla villosa* ant queens may recognize each other by olfactory, cuticular cues. Another example is that the individuals of paper wasp, *Polistes fuscatus*, recognize each other through learning the yellow-black patterns of the wasp faces and/or abdomens. An even more surprising discovery is that bumble bees may imitate (copy) other bees' learned foraging preferences by observing their choices of visual, rewarded targets (Weber et al. 2011).

Therefore, recent studies seem to suggest that social insects such as honeybees, ants and bumble bees may be able to perform sophisticated non-elemental learning. There is neural evidence to show the attention and experience dependent changes in visual discrimination. Honeybees seem to be capable of responding to new things that they have never encountered before in an adaptive manner, although the response depends on their previous experience.

3. INSECT COMMUNICATION IN FLIGHT AND MIGRATION

Karl von Frisch, who shared the 1973 Nobel Prize of Physiology and Medicine with Konrad Lorenz and Nikolaas Tinbergen, pioneered the study of the honeybee (*Apis*) dancing language and proposed the astounding theory that honeybees can advertise the information on the location of food and other resources through body movements which he called dances (von Frisch 1967). These dances, done by foragers on their return to the nest to recruit other foragers, may be distinguished as two types: round dance and waggle dance. He hypothesized that round dance conveys information that desirable food source is close to the hive but does not convey information on its location. The waggle dance is used when the food source is more than 100 meter from the hive. The latter type of dance provides information on the distance and direction of the food source. In a recent study, Gardner et al. (2008) suggested that the two types of dances are a continuum and there is no obvious switch between the two. Honeybees are able to convey information on the direction, distance and relative profitability of flower patches to hive mates using waggle dance, and the experienced honeybees can also steer naïve recruits from dangerous flowers containing cues of predators (Abbott & Dukas 2009). In a series of debates, Gruter & Farina (2009a, b) Brockmann & Sarma (2009) discussed the importance of the different decision-making strategies (that are adopted by the dance followers) in understanding the role of dance language in modulating the foraging of the bee colony. They also debated the relative importance of social information (communicated via dance language) and private information (some foragers follow their own exploration of food sources) for colony foraging. Although we are not in a position to judge which group of the authors are closer to the truth, we believe that the issues in the debate are indeed important. Perhaps a more holistic research strategy is needed to study the colony foraging strategy. Specifically the group selection and superorganism paradigms developed in the study of ants colonies, together with evolutionary game theory modeling may offer an effective research approach to resolve the issues debated, because it appears that the core issue in debate is what the optimal strategy for the colony as a whole is.

Obviously, navigation and communication are closely related. The former is mainly individual behavior, and the latter can have much broader scope but is poorly studied in literature. There are even fewer studies that were designed to address both navigation and communication in the same framework, but the study of honeybees, and perhaps ants foraging, are exceptions. In the case of honeybees, the function of dancing is to communicate the navigation routes to the food source they discovered to their recruits in the colony. Similar scenarios exist in the case of ants colony. Therefore, at this stage, the studies on honeybee hives and ants colonies should have accumulated the most insightful information to draw inspiration for engineering applications. Besides the classic work by von Frisch (1967), Dyer (2002) presented a comprehensive review on honeybee dance from a biological perspective, and more recent advances can be

found in (Abbott & Dukas 2009, Gruter & Farina 2009a, b Brockmann & Sarma 2009).

Two aspects discussed in Dyer’s (2002) review, which we summarize as follows (Figure 1 & 2), should be particularly interesting to engineers.

The *first* aspect is the communication of spatial information from dancer to follower. Indeed, the sensory and integrative mechanisms that mediate the flow of spatial information through the dance communication system have been a critical topic in the study of dance language. Figure 1, redrawn from Dyer (2002) shows the key steps of the information processing and communication involved.

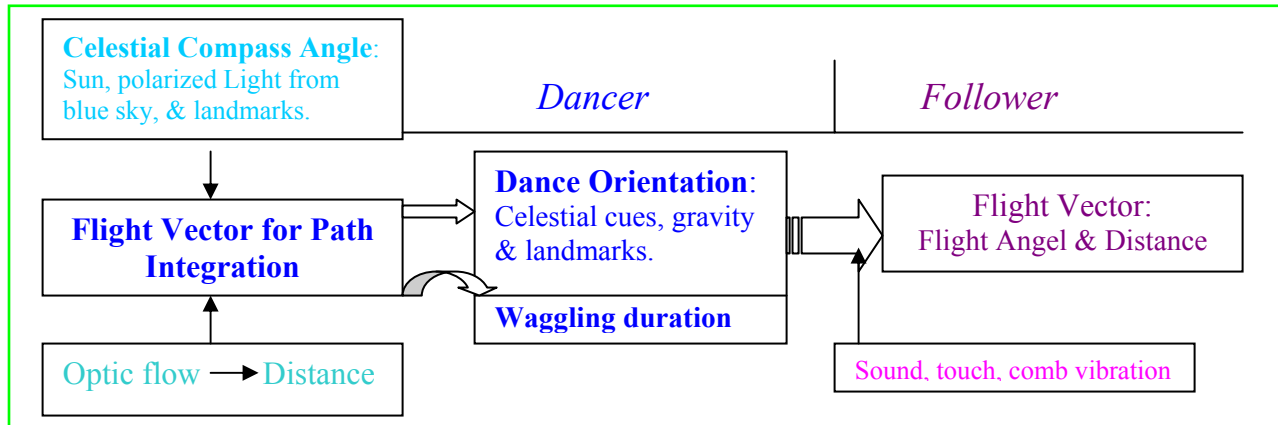


Figure 1. Communication of spatial information from dancer to follower in honeybee dance language (Redrawn based on Dyer 2002).

In Figure 1, the left and middle boxes depict the process that dancer gets the navigation information on the food source. This side is more about navigation problem, and dancers use compensated celestial cues to compute the flight vector that contains the information of the food source in the form of the distance and direction relative to the sun. This vector is the output of path integration algorithm and is stored in memory. The information will be used for navigation on subsequent trips to the food source. The information is also encoded in the waggle dance to its followers. Landmark information might also be used to help the navigation and communication, especially in cloudy days when sunlight is not sufficient, but experimental evidence is not sufficient to support the claim. Instead, it is suggested that gravity information may play a more important role than landmarks when celestial cues are not sufficient. To encode the vector information in dance language, bees must measure her body orientation relative to environmental features available in the nest, which is usually different from those she originally learned during the foraging trip. She also needs to translate the distance she flew into the duration of waggle dance. The information encoded in dance must be communicated to her followers—the other bees who will be observing her dance. The right side of Figure 1 shows the process of the followers to obtain the information from dancer. It has been found that three types of signals are communicated: airborne sound produced by the dancer’s wings and perceived by the follower’s antenna, comb vibration induced by the dancer and detected by the follower via the subgenual organs, and tactile cues detected by the follower’s antenna (Dyer 2002).

communication system. Natural selection should have optimized the dance communication system. It is likely that evolution would need to resolve some potential conflicts in foraging strategies from the perspectives of both individual and the colony as a whole. Figure 2 is redrawn from Dyer’s (2002) review, and the graph shows how dance communication is modulated in terms of both the innate quality of food resource and the need of the colony.

There is a significant difference between the above-mentioned two aspects. The first aspect emphasizes the processing and communication of spatial information, and the second aspect emphasizes the decision-making process in assessing the resource (nectar, water, pollen, new site) quality and the colony’s need. A critical parameter that determines the level of recruitment for a specific resource is the number of dance runs (circuits) performed by bees who discovered the resource. As it will be discussed in Section 5, the parameters like the number of dance circuits (runs) is tuned in the bee colony inspired swarm intelligence algorithms in computer science.

The *second* aspect that is of particular importance for engineering applications is the modulation of the dance

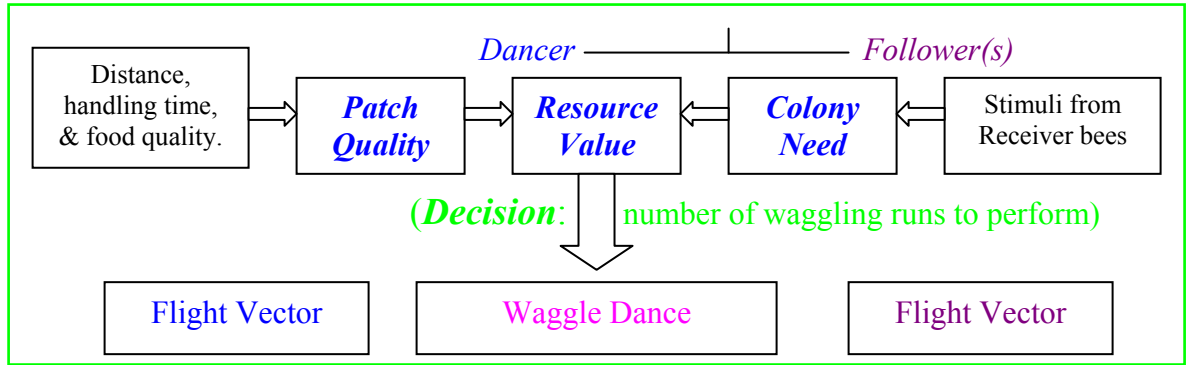


Figure 2. Modulation of dance communication system of honeybees, redrawn based on Dyer (2002).

4. INSECT JOINING AND AVOIDANCE BEHAVIOR

Social insects such as bees, ants, and termites seem to stay together in most of their lifetimes, which seems to be one primary reason why we classify them as social insects. However, the boundary between social and non-social insects is not that clear. If the criterion for being social is to stay together, then many insects, at least in some stage of their lives qualify for being social. Readers are referred to the excellent monograph by Costa (2008) for the sociality in insects.

The study of interactions (including communication) in social insects (colonies) is obviously important. Honeybee dances and the operation of ants colony have been extensive studies in biology. We briefly introduced bee dance in the previous section. The study of ants colony is equally impressive and many excellent monographs have been written [e.g., Holldobler & Wilson (2009), Gadau & Fewell (2009)]. We refer readers to those excellent literature sources. In this section, we instead briefly review the interaction (specifically joining and avoidance behavior) in non-social insects. There are two reasons for our bias for non-social insects in this article: one is that there are few reviews on this topic, especially we are not aware of any in the context of engineering applications, and another reason is that the model of interactions among non-social insects may actually be closer to the configurations of the MAV or mobile robot fleets.

Prokopy & Roitberg (2001) presented an excellent review on joining and avoidance behaviors from the perspective of behavior biology, but they also discussed significant amount of modeling and analysis of the behavior. The following introduction is based on Prokopy & Roitberg (2001). An advantage with behavior-biology-based models is that many of them are formulated as evolutionary game theory models, which are optimization models and may be easily transformed into models for describing engineering problems.

In biology, the problem of *joining and avoidance*, which Prokopy & Roitberg (2001) reviewed, has strict behavior and biological classification and context. The context of research on the joining and avoidance behavior is often limited to conspecific and consensual to avoid confusion with anti-predatory (inter-specific behavior) and courtship (between two sexes). Obviously, these behaviors may have very different biological mechanisms and the underlying selection forces in the evolutionary history can be very different. Similarly, the underlying mechanism and evolutionary history that shape the similar joining and avoidance behavior in social insects can be very different from that of the non-social insects. While these distinctions must be recognized in biological studies, we are less concerned with them in this article. What may be particularly useful for searching biological inspiration from the joining and avoidance behavior can be the following inequality model (see Prokopy & Roitberg 2001 for details):

$$f(VR, c, n) > P_f \sum_{i=1}^T \sum_{j=1}^N P_{VR_i} f(VR_i, c, n_j) \quad (1)$$

This inequality captures the essential aspects of the game strategies individuals may adopt in their determination of behavior. The left side of the inequality indicates that the focal individual that chooses to join will receive some payoff as a function of sharing or taking the resource, VR , with n local conspecifics, and experiencing some competition process c . On the right side, the payoff for a solitary model is described, which depends on the likelihood of finding a resource (P_f) or resource-holding sites with the size from 1 to T , as well as the probable distribution of conspecifics across those resources. The goal of the model analysis is usually to derive the evolutionary stable strategies (ESS) of response to conspecifics. When inclusive fitness (the benefits to relatives) is considered, the analysis can be much more complex.

The above described joining/avoidance behavior biology problem can be treated as a prototype for MAV or mobile robots fleet control. The communication and grouping (cluster formation) in MAV fleet is usually ad-hoc and

dynamics. The joining and leaving (avoidance) of MAVs should be optimized with the control goal of the fleet.

Back to the behavior biology perspective reviewed by Prokopy & Roitberg (2001), it has been found that when the individuals behave independently, the distribution of individuals adopting joining or avoidance strategies can be solved analytically as the evolutionary stable strategy (ESS). Existing experimental studies have been conducted primarily for group-foraging birds such as pigeons.

The above model can also consider the actions of individuals after joining a group. For example, when new individuals join in, the resource consumption may be up and individuals may be more diligent in finding new resources. Similarly, in MAV or robots applications, individuals should be adaptive to suit the needs of the cluster. Beyond join/avoidance decision, the model can also consider the decision on whether or not to invite new individuals. It has been found that some beetles only invite others when there is a benefit for the sender (Prokopy & Roitberg 2001).

The model [Eq. (1)] can also assume that each individual has two states (status): one is the physiological state and another is the information state (Prokopy & Roitberg 2001). The information state can deal with learned behavior such as experiences from encounters. It is assumed that insects are non-omniscient Bayesian foragers who update their information state with each encounter.

The model can also be extended to study population level problem. The benefit for joining/avoidance at population level can be very different from that for an individual. For example, with the classic logistic model,

$$dN/dt = rN(1 - N/K) \quad (2)$$

where N is group size, K is environment capacity, and r is the per capita intrinsic rate of increase. The r is often treated as a measurement of fitness. If the per capita r is plotted against N , then the relationship is usually linear (negatively). But if the plot is made for per group fitness, the relationship may be parabolic. In other words, the optimum density from an individual or population perspective can be very different. In behavioral biology, the focus is on individual fitness since it is believed that natural selection is primarily operated at the individual level. In the case of MAV or robot fleet control, the focus is most likely on the group level.

One may expect that *partition of time* can be an important mechanism for insects to avoid collision, but there are few studies from the perspective of collision avoidance. Most of the studies on time-partition have been performed in the context of ecological niche (e.g., Kronfeld-Schor & Dayan, 2003).

5. EXISTING AND PERSPECTIVE APPLICATIONS

There have been extensive interdisciplinary studies with the objective to draw inspiration on insect flight, navigation,

and communication. Numerous monographs and review papers have been published on this field, and we do not attempt to perform any comprehensive survey in this paper. In the following, we only mention a list of the applications that have been attempted in computer science and engineering. We mentioned some review papers, in our opinion, that may have not received sufficient cross-disciplinary attention they deserve. Finally, we also present a list of topics that we believe should generate significant cross-disciplinary advances if due research diligence is spent on, but our suggestions can be conjectural at this stage.

5.1. Ants colony inspired swarm intelligence.

Ants colony optimization (ACO), also known as ants colony based swarm intelligence, is now a near mature computational intelligence approach (e.g., Bonabeau et al. 1999, Dorigo & Stützle 2004). One important feature of ACO, which we do not discuss in this paper, is the chemical nature of the ants communication that depends on pheromone. Although we emphasize visual communication in this article, which may be particularly important for navigation, insect sensory and communication systems are multimodal. The chemical communication system (especially olfactory system) of insects is perhaps only matched by vertebrates. In fact, chemical ecology, a discipline emerged in the 1980s with one of its focuses on the study of infochemicals (also known as semiochemicals), was started and is still dominated with the study of insect pheromone. It is now known that pheromone may have also been used by plants and humans. Starting literature for chemical communication can be found in references such as (Wyatt 2003, Carde and Millar 2004, Dicke & Takken 2006, Ma et al. 2008, Ma & Krings 2009, Dressler & Akan 2010).

5.2. Honeybee inspired group decision-making.

This is a field that has a similar long history with the study of ants colony inspired computing, and the results are equally rich and inspiring (e.g., Detrain et al. 1999, Detrain and Deneubourg 2006). Artificial bee colony (ABC) algorithm is one of the recent bee-colony inspired optimization approaches (Karaboga & Basturk 2008, Quijano & Passino 2010, Zhang et al. 2010).

It is obvious that the selection of *nest site* should be one of the most critical decisions social insects must make in groups. Entomological research has revealed that the selections of nest site in the so-termed swarm-founding social insects (at least for the ants and bees studied) are remarkably similar—a distributed, non-hierarchical group-decision making process (Visscher 2007). Visscher's (2007) excellent review presented a comprehensive survey of the field from the biological perspective. According to Visscher (2007), individual scouts are responsible for discovering potential nest sites and they integrate multiple properties into measurements of their qualities. The candidate sites then compete for a limited number of nest-site scouts. When

a sufficient number of scouts are attracted to one of the candidate sites, a *quorum sensing* mechanism will trigger the mass movement of the colony. The previously discussed bee dancing is used by bees for nest selection, but the nest selection is more demanding with the so-termed requirement of *unanimity*—a colony can only relocate to just one new site. The mechanisms for coordinating the actual movement to a new nest can be different in different insects.

5.3. Insect sociobiology—sources for rich inspirations.

The underlying biological mechanisms for ant and bee colony inspired swarm intelligence, discussed in the previous two topics, have been systematically explored in insect sociobiology for more than half a century (Wilson 1971). The comparative study of social insects with human societies has a long history and was somewhat controversial initially. The exploration of the field can be traced back to the early 1900s, but it was E. O. Wilson's (1971) "*Insect Societies*" that formally established *sociobiology*, which has become a well-respected field of science today. Recently resurgent interests in biomimicry or biomimetics also seem to have focused on the self-organization mediated by stigmergy (Holbrook et al 2010). Scientists and engineers have been trying to apply those organization algorithms discovered in social insects for organizing the activities in human societies.

Even a brief introduction on insect sociobiology is beyond reach of this article. Beside Wilson's (1971) classic volume, which is certain still worthy of reading, three more recent volumes also stand out: Holldobler & Wilson (2009), Gadau & Fewell (2009), and Tautz (2008). In insect sociobiology, recent advances seem to have been centered around: *transitions in sociality evolution, communication, neurogenetic basis of social behavior, and theoretical exploration on social organization from a complexity science perspective* (Gadau & Fewell 2009).

5.4 MAV & robot flight control & Remote control of insect flights

Using insects as design model for MAV and mobile robots has been reviewed by several authors (Mueller & DeLaurier. 2003, Wang 2005, Ma et al. 2009a, 2009b, and Wu 2010). Insects are the best flapping flight 'vehicle' at intermediate range of *Reynolds number* in nature and offers an ideal model for designing small MAVs. There are many monographs on insect wings and flights (e.g., Brodsky 1994, Grodnitsky 1999, Dudley 2000, Tennekes 2009). According to Pornsinsirak et al. (2001), the aerodynamics of flapping flight, in particularly for MAV size (with wingspan of less than 15 cm), is still not fully explored and there have been few design rules for flapping-wing aerodynamics, which makes learning from insect potentially more profitable. At least five university laboratories started insect-inspired robots research in approximately the same period about a decade ago, which also set a foundation for

many of the MAV research projects in recent years (see Ma et al. 2008, Ma & Krings 2008 for a brief review).

The current focus of using insects as a model for MAV or robot design is usually on the unsteady aerodynamics of insect flapping flights, and less on navigation and communication. Although we skip insect-inspired MAV design in this paper, their importance is obvious because without good MAV design, the problem to form a fleet of MAVs is out of the question. In the use of insects as models for MAV or mobile robot design, the most widely studied insects are not ants and bees, (with some exceptions, e.g., Srinivasan et al. 2001). Instead, dragonflies (e.g., Berry et al. 2006, Corbet 1999) and locusts are frequently used. This is largely because it is relatively easy to study their flight behavior and/or sensory-nerve system control of their flight. For example, a VLSI chip based on locust compound eyes, known as Lobula Giant Movement Detector (LGMD) for collision detection and motion detection has been built a decade ago (Blanchard et al. 2000, Rind 2005). Some aspects of dragonfly inspired studies were reviewed in Ma et al. (2009a, b).

There is a suggestion to use insects themselves as *biological MAV* or NAV (Nano Aerial Vehicle) (Sato et al. 2009), which may ultimately falls into the category of *biological weapon* but its acceptance should certainly be carefully scrutinized for obvious reasons. Technologically, it is possible to control insect flight remotely with an implantable radio-equipped miniature that stimulates neural system of an insect (Sato et al. 2009). In biology, the technology can be helpful for studying the flight behavior of insects. In engineering, even if insects are not allowed to be used as biological MAV/NAV, the technology of remote control should still be useful for studying insect-inspired MAV or robots.

5.5. Optimal migration strategy

A rigorous definition for migration in biology is not an easy task and we leave it to expert opinions in the field (e.g., Dingle & Drake 2007, Akesson & Hedenstrom 2007). An important point we should be aware of is that migration involves two levels: *individual* and *population* level. At the individual level, the focus is *behavior*, and at the population level, it is ecological and evolutionary implications. Translate the problem into the counterpart of MAV or mobile robots fleet control. At the individual level, we are interested in drawing inspiration from individual behavior of migratory insect such as their flight and navigation controls. At the population level, we hope to draw on *communication* and *coordination* mechanisms used by insect populations in their migration for engineering design. Currently, much of our understanding of insect migration is still limited to the individual level and this is reflected in previous sections on insect navigation mechanisms. An understanding at the population level should be equally important for engineering and computing applications. The various topics listed in this section from swarm intelligence, quorum sensing, to joining

and collision avoidance all are primarily concerned with population level studies.

One additional point to mention is that insect migration appears to be very “*passive*” in the sense that environmental factors such as wind exert critical influence (Gatehouse 1997, Reynolds et al. 2010). It is postulated that migrants are able to align themselves with the direction of the flow using a turbulence cue, and therefore add their air speed to the wind speed, which may significantly increase their migration distance (Reynolds 2010). In some occasions, it is difficult to distinguish between insect drift and migration. For example, the insect drift cases documented by Lazzari et al (2008) are equally impressive, although one probably would not call them migration. Perhaps it makes little difference for insects regardless what we call its movement either drift or migration, both are struggling for survival. This may explain the extreme challenge to develop a rigorous mathematical model for insect migration, and the attempt to reveal optimal migration strategies turns out to be even more difficult. Still, excellent studies have been conducted to explore the optimal strategies of insect migration (e.g., Srygley et al. 2008).

5.6. Quorum sensing for group decision-making and collision detection.

Quorum sensing (see the Glossary Box) is a group decision-making behavior exhibited by many bacteria and social insects. One essential feature with quorum sensing is that the decision is made in a distributed or decentralized manner in the lack of centralized guidance. Another essential property is that an individual’s decision relies on the decisions of others, usually the local better-informed neighbors, which operate like a self-reinforcing positive feedback loop. These two properties are typical in self-organized systems, and accordingly, self-organization has been suggested as the mechanism that controls quorum sensing. At least three advantages have been suggested for quorum sensing. First, the interdependency of individuals may help to keep group coherent; the other two benefits are the speed and accuracy in reaching consensus (Sumpter & Pratt 2009). Sumpter & Pratt (2009) developed a simple mathematical model that shows that an animal’s probability of exhibiting a behavior is a sharply nonlinear function of the number of other individuals already performing this behavior. They argued that systems relying on such quorum sensing can reach cohesive consensus of the best option but still allow adaptive tuning of the trade-off between decision speed and accuracy. Quorum sensing is also a primary mechanism used by social insects in their nest selection (Visscher 2007).

5.7. Joining and collision avoidance.

Compared with the six topics we briefly reviewed previously, the problems of *joining and collision avoidance* have received relatively little attention from the cross-disciplinary researchers of insect-inspired computing and

communication. This by no means implies that the problem is less important. It should be obvious that joining and collision avoidance are the most fundamental processes that influence nearly every aspect of a fleet of MAVs or robots: from topology, communication, to task performance. The reason why it appears to be an ignored field may have to do with the inherent difficulty of studying the problem at the population (in biology) or cluster (group of MAVs or robots) level. Among the significant complexities arising at the ‘population’ of MAVs or robots, perhaps the first one that must be addressed is to make sure that the nodes can get along with each other well—the problem of cluster formation and collision avoidance. Only when there is a functional cluster, one can look into the problem of optimizing the performance for fulfilling specific tasks.

We argue that all six previously discussed topics can be relevant for devising a comprehensive approach to the problem of joining and collision avoidance. Indeed, we wrote the entire article with a central objective to search for inspiration for addressing the problem. The first two topics: ants-colony based swarm intelligence and honeybee inspired group decision making can serve as general optimization algorithms for devising optimal cluster formation. The third and fourth topics, MAV and mobile robot flight control, and remote control of insect flight offer insights for studying MAVs and mobile robots at individual node level. The fifth topic on optimal migration strategies is important because migration in biology is more than flight with a *destination*. The navigation and communication (coordination) involved in migration is far more complex than those in short-distance dispersal flight. Even if we assume that the *navigation* of insects is essentially the same at both individual and population level (*i.e.*, navigation is not influenced by one’s neighbors), the communication occurs at the population level. Unfortunately but justified, past and current entomological research on the control of insect migration has focused on the endocrine (hormone) control and metabolic physiology of fly fuels (fat body). Other than the studies on honeybee dancing, ant pheromone communication, and the phase transition between solitary and migratory dimorphism of locusts, there are few studies on the communication or coordination mechanism during migration. Nevertheless, we argue that the study of communication mechanisms in insect migration is a field that may generate important inspiration for dealing with the problem of *dynamic* joining and collision avoidance in MAV or robots fleet control.

Finally, we argue that quorum sensing mechanisms and protocols discovered in social insects may also be applied to control node clustering for MAV and robots fleet control. Node (e.g., sensor nodes that control MAV or robot communication) clustering or joining may be controlled by self-organized positive feedback, and quorum sensing may offer an effective strategy for cluster formation. Collision detection is a problem that may be better addressed with negative feedback mechanism, but quorum sensing can be

utilized to detect the level of crowding and can therefore help to detect the collision.

6. GLOSSARY BOX (in alpha-beta order)

Cognitive map: Tolman (1948) invented the term cognitive map, which is the mental analogue of a topographic map—an internal representation of the geometric relationships among noticeable points in the animal’s habitat (Wehner & Menzel 1990). Whether or not insects possess cognitive maps is still in debate.

E-vector: E-vector is a pattern of polarized light in the daytime sky. The pattern is not visible to humans, but some insects such as desert ants can use it for navigation. The pattern provides insects a wide-field skylight compass that is coupled to the sun movement [see Wehner 1994 for details of the pattern].

Navigation: Most insects and vertebrates possess the navigation capability to depart from and return to fixed points in their habitats, such as nutrient sources, mating spots, and nests or resting places. It is believed that they can determine and maintain a course or trajectory by using cognitive maps or some simpler computational algorithms (Gallistel 1989). Navigation is often interchangeably used with *orientation* or occasionally *homing*. The term astronavigation refers to the navigation that uses information from the sky and its celestial bodies.

Path-integration (Dead-reckoning): Path integration is the method of navigation that was employed by sailors without the need for landmarks, requiring only a compass and odometer to monitor the path the sailor travels, and it is also called dead reckoning. The dead reckoning strategy is known to be employed by many animals, including ants. The continuously updating PI information forms a home vector(HV), which represents the distances to a fixed location, e.g., the nest of ants.

Polarized light pattern of the sun: The light pattern is produced when the sun’s light is scattered in the atmosphere, provide a directional reference that is essentially equivalent to that provided by the sun. Many insects can obtain compass information from the polarization patterns of light coming from blue sky.

Polarized light pattern of the moon: This is the counterpart of polarized light of the sun but is million times dimmer. It is a circular pattern that is centered around the moon. The polarized light arises because of the atmospheric scattering of moonlight as it travels toward earth (Warrant and Dacke 2011).

Quorum sensing:

Quorum sensing is a communication and decision-making mechanism, by which a group (colony) of sensors (bacterial cells or social insects) sense, assess, and communicate signals from each other. In general, this is a distributed and self-organized communication system, and is usually self-regulated by the density of sensors. In bacteriology, it refers to the regulation of gene expression in response to fluctuations in cell-population density; quorum sensing bacteria can produce and release chemical signal molecules termed autoinducers and its concentration is dependent on the cell density (Miller & Bassler 2001).

The usage of quorum sensing in entomology is a relatively recent phenomenon. It is often termed quorum responses, and emphasizes a mechanism for group decision-making or consensus-building. Quorum response can be described with a mathematical model, which correlates the probability for an individual to choose an option with the number of other individuals in the colony who have already committed to the same choice. This function is usually non-linear (Sumpter & Pratt. 2008). Quorum response sometimes is referred to as “wisdom of crowds.” Obviously, quorum sensing or response, when described with a mathematical model, should be very useful for studying group behavior such as cooperation and communication.

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BIOGRAPHY

Zhanshan (Sam) Ma obtained his Ph.D in Computer Science and Entomology in 2008 and 1997, respectively, both from the University of Idaho. He was a senior network/software engineer from 1998 to 2006 in the IT industry. He is a Computational Biologist at the University of Idaho, working on the NIH (National Institute of Health) Human Microbiome Project (HMP). His research interests include reliability, survivability, and security of distributed networks and aerospace systems, theoretical and computational biology, bioinformatics, bio-inspired computing and communication, evolutionary game theory, and strategic information warfare. He has been keeping dual track publishing in both Computer Science and Biology with approximately 50 peer-refereed journal and 20 peer-refereed conference papers. He is also a Professor and the Director of the Laboratory for Computational Biology and Bioinformatics at Kunming Institute of Zoology, the Chinese Academy of Sciences.

Axel W. Krings is a Professor of Computer Science at the University of Idaho. He received his Ph.D. (1993) and M.S. (1991) degrees in Computer Science from the University of

Nebraska - Lincoln, and his M.S. (1982) in Electrical Engineering from the FH-Aachen, Germany. Dr. Krings has published extensively in the area of Computer & Network Survivability, Security, Fault-Tolerance, and Real-time Scheduling. In 2004/2005 he was a visiting professor at the Institut d'Informatique et Mathématiques Appliquées de Grenoble, at the Institut National Polytechnique de Grenoble, France. His work has been funded by DoE/INL, DoT/NIATT, DoD/OST and NIST.



Richard Millar is an Associate Professor with the Naval Postgraduate School Department of Systems Engineering, based at the Patuxent River Naval Air Station. He has 35+ years experience in the design and development of gas turbine engines and their integration with aircraft propulsion & power systems. He has worked in this field at General Electric, United Technologies, Rolls-Royce, Boeing, Lockheed Martin and BAE Systems prior to joining NAVAIR in 2003.

Dr. Millar acquired a B.Eng and M.Eng. (Carleton) and an MSc in Management (as an MIT Sloan Fellow sponsored by United Technologies) prior to working for the US Navy. In 2007 he received a D.Sc. in Systems Engineering from The George Washington University with the financial support of NAVAIR. Dr. Millar has an active research program currently focused on the systems engineering and development of integrated instrumentation / sensor systems for use in the test & evaluation, CBM & PHM and control of aerospace equipment.

Feng Wang obtained his Ph.D in Information System in 2011 from the Kochi University of Technology. He is a professor of Kunming University of Science and Technology, and a director of key lab of computer application technology in Yunnan province. He has been keeping track publishing in Computer Science with approximately 20 peer-refereed journal and 10 peer-refereed conference papers including ACM CHI and UIST.

Jun Cao received his PhDs in Neurobiology in 2002 from Kunming Institute of Zoology (KIZ), Chinese Academy of Science. He is currently a Professor at KIZ, and has published more than 20 papers in peer-refereed journals such as *Journal of Neuroscience*, *Hippocampus*. His research has been focused on the functionality of *synaptic plasticity*.