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Insect navigation and path finding

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Abstract. Insects have a brain weighing about a tenth of a milligram. Nevertheless some insect species exhibit amazing performance in finding their daily paths when looking for food or shelter. Some species have even found their ecological niche in being excellent navigators and hence can survive in extreme habitats. One remarkable and well studied model is the Saharan desert ant *Cataglyphis fortis* that outruns its competitors by performing egocentric navigation. By using skylight cues as a compass and counting steps it is able to find its way without using external visual cues. In comparison, the Australian desert ant *Melophorus bagoti* employs route learning strategies, where it visually learns and in tests recalls every point of their route. In studying the insects' strategies we can learn a great deal on how little information can be used to perform a navigational task. Also the way of how information is processed within such a tiny brain is intriguing. The conclusions drawn from this research are nowadays not only used to understand human behavior but find their way into technical design.

1 Introduction

Evolutionarily challenged organisms optimize among others in terms of energy expenditure (e.g. avoiding detours), information processing (e.g. energy, reliability), safety (e.g. risk avoidance), failure avoidance (e.g. simplicity, redundancy, failure tolerance). While the qualitative performance is similar - field of neuroethology (behavior associated with sensory information), to outline the lessons learnt on insect navigation so far and finally present some rough ideas for space related technical application.

Figure 1. *Desert ant* Cataglyphis fortis *initiating a foraging run.*

1.1 Insect cognition

Animal orientation can be differentiated into two big fields: While migration is dealing with the relocation of an animal - sometimes over many generations - from

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one place to another, (ii) navigation denotes the systematic return to a previously left point of reference. Both types are found in different taxa, ranging from bacteria to whales. In the following I will focus on the central place navigation techniques as found in insects for a couple of reasons. The insect model is a very variable one and many different ”technical solutions” are realized by them. The system architecture of insects is a rather simple one compared to vertebrate models and in consequence easier to understand: First of all the hardware (i.e. brain) is very small and hence simple. Secondly, the behavioral patterns are reduced to the elementary motivations: defense (fight), maintenance (food intake), and reproduction. Since we deal with social insects, where the queen suppresses the workers' reproductive behavior the discrimination of the two remaining motivations is much simpler than when studying a vertebrate model with its huge variety of motivations and behaviors. In many cases, the food items found during a foraging trip cannot be eaten by the insect itself. In consequence the mission goal becomes a rather abstract one, where the agent-ant has to decide if the item found fulfills the profile set by the super-organism. On top of that, it is technically easy to work with insects and so insect models have become very popular among behavioral scientists. Central place foraging on the other hand is the type of behavior that involves highly elaborated signal processing, both in terms of precision and time, and hence appears to be the technically more interesting system. While a migratory animal will interrupt its behavior once a suited living ground is found, a navigating forager is forced to locate the exact point of reference - usually the nest - in order to fulfill its mission.

1.2 Insects qualify in several aspects as models

When reviewing the panel of this workshop you will find two two other contributions on insects as model animals for technically oriented studies and application. In a way, this stresses the fact of the amazing success of the insect Bauplan both for the variability of the exoskeleton and the performance neuronal system. While mechanical aspects will be dealt by Stanislav Gorb, Nicolas Franceschini will introduce the insects' visual autopilot. Using both mechanical and neuronal tools, the insects become able to perform high level tasks - also called insect intelligence or insect cognition - such as navigation. In combining the results of these complementary approaches, we will not only learn more about the biological model, but also may be able to transfer this knowledge to technical design.

2 Mastering egocentric navigation: the Saharan ant *Cataglyphis*

One of the best studied models for insect navigation is the Saharan desert ant *Cataglyphis*. Several *Cataglyphis* species have found their ecological niche in areas that seem devoid of live: Desert areas containing almost no vegetation and even less animal live seem not to provide acceptable living conditions. Nevertheless, once spending some time, the observer will discover numerous rather large (approx 1 cm body length) ants with quite a distinct body shape and a rather fascinating behavior: In this featureless habitat, they run at rather high speeds (up to 1 m/s) in a seemingly determined manner toward an invisible goal at the end of their trajectory. Indeed, the ant will eventually disappear in a small inconspicuous hole in the ground - the entrance to the colony's nest, hosting up to a few thousand individuals. A deeper study will reveal, that emerging from this nest, a cohort of ants will go foraging for food throughout the day, performing one of the most fascinating behaviors in animal kingdom. Every little ant will leave the nest for a distance of up to twenty thousand times their own body length, and search for a single food item - a dead insect for example that succumbed to the atrocious climatic conditions. Once successful, the ant will turn around and in a determined manner steer back home to the nest in a direct line without getting lost. Even in the absence of any visual cue, i.e. landmarks, the ants will successfully locate their nest and immediately initiate another foraging run. This behavior is somewhat different to the commonly known routes that can be observed in the majority on the European ant-species. Wood ants for example establish a route to a feeding site, i.e. a dead mouse, by placing olfactory marks along the way. Other ants will follow this route and easily find the food source. Each of the ants will add its olfactory share to the route and in consequence, the route will be reinforced and even attract more ants, until the source is getting exploited. Now this approach does not work with desert ants for several reasons. Firstly, the light sand in the desert has little cohesion and hence the route marked onto it will be carried away easily by wind. If not the wind, the dry and hot climate will - secondly - evaporate the pheromones too fast in order to allow for a stable marking. And - thirdly - there are almost not abundant food sources available that would require

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or justify establishing a route. Food items are sparsely distributed and hence can usually be carried away by a single ant. Passing on the knowledge of a feeding site to a nest mate would not contribute to the colony's success. On the other hand, each ant that can be found outside the nest follows the very same programme of searching for food and then safely and quickly navigating home. Hence desert ants are an ideal study model for (biological) autonomous agents.

2.1 The compass

Cataglyphis ants navigate egocentrically, i.e. without using external visual cues. This implies that they constantly monitor their own movements and update the knowledge of their position in respect to the nest, the home vector. Path integration - as the basis of vector navigation - requires knowledge of the direction, distance and inclination of the current segment of the path in order to calculate the home-vector. The by far best studied element of desert ant navigation is the compass mechanism with which the ants determine rotation around the vertical axis. The work on the skylight compass of insects started with von Frisch's [3] Nobel-awarded discovery that bees use polarized light to determine flight directions. In short, many insects, including *Cataglyphis* have a part of their compound eye specifically adapted for compass tasks. The dorsal rim region, i.e. a small part on the very top of the head, has eyes that are sensitive to polarized UV-light of a preferred angle arranged in a fan shape configuration [12, 2, 10]. Theoretical considerations propose the existence of three integrator neurons that are tuned to different directions and subsequently pass on the information of direction to so called (and proposed) compass neurons. However, there are some apparent constraints when exploiting the polarization of the sky for directional purposes. (i) Light, has to be present. This means only during day and nights with full moon, the quality of the signal is good enough for the ants. (ii) Visibility to the sky has to be granted to a degree of about 20% that is free of clouds. (iii) During the day the sun turns at changing speed. The compensation of the rotation of the sky-pattern has to be performed accordingly. (iv) During the year, the so called ephemeris function changes its position, and hence, the pre-programmed compass has to be adaptive to that as well. (v) Finally, the ephemeris on the south hemisphere is flipped. Even more so if the colony is located between the two tropics and hence the December worker has to cope with a flipped version of the curve, the July worker is confronted with - both potentially being clones. The relationship between genetically inherited and deductively learnt information on the current shape of the ever changing ephemeris function is addressed in currently ongoing studies.

2.2 The odometer

In contrary to the compass mechanism, it has long been an open question on how desert ants measure distances run. Several hypotheses had been posted, i.e. monitoring the energy spent, or the time spent to cover a certain distance. Both were discarded for various reasons and hence only exploiting visual cues and proprioceptive ones (i.e. own movement) remained. While flying insects such as bees use optic flow for optometry, this factor plays only a minor role in running animals (16%, [8, 7]). A series of studies finally demonstrated, that distance estimation is performed by a pedometer, i.e. a step integrator. In order to proof this hypothesis, [13] trained ants to forage to a feeder. Once arrived at the feeder, the ants' leg lengths were manipulated by microsurgery operations, leading to longer (stilts) and shorter leg lengths (stumps). Once released in a test array, the ants on stilts overestimated the way home and performed their search pattern behind the position of the virtual nest, while the stumps-ants under estimated the distance and looked for the nest entrance at an earlier point of their search. However, as step length changes with speed of locomotion, the ants do not only sum up the number of steps, but also incorporate the step length. Studies on the kinematics of running ants have not revealed the sensory mechanism responsible, but point towards force sensors in the animals' leg, i.e. muscular tension receptors or strain sensing campaniform sensilla in the exoskeleton.

2.3 Integrating inclined paths

The initiator for Wittlinger's studies was an experiment performed some years earlier and that revealed and interesting feat: When outbound ants, i.e. on the way from the nest to the feeder, were running on a corrugated path, i.e. crossing a series of several artificial hills, they performed much longer path than the actual beeline between nest and feeder measures. Once equipped with a food item and placed into a flat channel, the ants performed the typical nest search after they had covered the shorter of the two distances [14, 15]. Obviously, they integrated the inclination of the paths run and calculated the ground projection, which was the basis for the home vector. This performance can be explained only by means of proprioceptive monitoring of the inclined surface during walking. All other hypotheses such as visual integration of inclination, or energy and time measures fall to fundamental flaws. However, the exact mechanisms of monitoring inclination for means of path integration has not been found so far. Again, force feedback during walking currently seems the most favored explanation.

2.4 Coping with errors

A typical foraging run of a desert ant can involve about 20 thousand single steps which are integrated to continuously update the information on the shortest way back to the nest - home vector. It is evident, that even slightest errors may severely deviate the animal from its track and induce fatal consequences. In the following I want to outline some of the techniques used by the ants' navigational toolkit in order to maintain a satisfactory success rate.

Systematic search

Once the ant has performed its run back home and the home vector reaches a state close to zero, it will switch from the linear path to a series of loops with increasing diameter with the cross point centered on the position of the expected nest entrance. With this systematic loops, the ant will search for the nest entrance in the vicinity with an intensity following a statistic distribution.

Linear and angular undershooting

In linear test set-up, the estimated nest entrance moves toward the feeder with increasing homing distance. In angular outbound paths, the return angle is systematically pointing not toward the virtual nest but toward an estimated nest entrance moved along the outbound path. An ant that has performed several foraging runs, will know the visual features of along the usually taken path better than those ”behind” the nest (ants show high sector fidelity). Once a known structure is identified, the previously lost nest entrance is easier to be located.

Resetting the vector

During each foraging run, the ant will incrementally accumulate errors on the position of the nest. The reference point with the highest significance to the animal is the nest. Hence, only in the nest eventual (or induced) errors on the vector will be deleted. Every ant leaving the nest for a foraging run will be in an initial zero-vector state.

Exploiting external cues

Even in the most homogeneous environment once in a while, unique structures appear and hence can be exploited by the ant for navigational purposes. May this be visual landmarks such as tussocks or stones, tactile landmarks [9] such as the roughness of the ground or even olfactory landmarks not connected with food or nest scent. These landmarks may temporarily override the path integrator, but not reset it.

3 Coping with the labyrinth: the *Melophorus*-approach

Cataglyphis is not the only genus of ants that occupy the niche of hot and dry habitats. In the south of Africa we find *Ocymyrmex velox* and in the Australian outback *Melophorus* bagoti. The later one exhibits a quite fascinating approach to cope with the peculiarities of its habitat: Numerous and densely placed tussocks form rather a huge labyrinth than a free and uniform are such as we can find it in the Sahara [6]. In consequence, finding its way home in a time efficient manner is not only a matter of getting direction and distance right, but also avoiding dead ends. In addition to that, potential predators can hide much easier and hence a safe route is worthwhile to have. In consequence, *Melophorus* ants establish routes to an installed feeder and maintain these routes rather conservatively. On top of that, the outbound route and the inbound route do not have to be identical. On the other side a displaced ant will initiate search loops and once it found its previously learnt route immediately recognize it - if it is the right one - and continue to follow the route without hesitation. The exception to be made is, that an ant on outbound motivation will not recognize its inbound route and vice versa. Now the most intriguing question is, on how an ant with a brain of approximately 0.1 mg will be able to remember every section of a sequence of several thousands of ”snapshots” and quickly retrieve the right match in the instant of being confronted with it. Obviously, it cannot be a simple hard-drive with a series of bitmaps that are constantly screened. Even more so in the sight of recent results that showed that ants can learn and retrieve up to three separate routes. Theoretical studies on feature extraction and localization try to shed light onto this so far not understood mechanism.

4 Insect intelligence in the space context

The the selection pressure acting upon the forgaging abilities of the species introduced in the present account has led to an optimisation of the ants' major survival feature: The navigational toolkit. Several different systems act in parallel in order to allow for the ant to perform successfull navigation. Although it is impossible to determine what "Evolution had in mind" we can indentify a number of basic demands that appear to be set during the evolutionary development. An ant brain is rather small and computing power as well as data storage is highly restricted for several reasons. Both energy constraints [5, 1] as well the general Bauplan do not allow for indefinite expansion of brain tissue. Hence incoming data has to be highly reduced to the relevant and only the relevant bits. Extracting behaviorally interesting features from the incoming data has to be performed in a real time manner since predators are not known to wait. Additionally, the calculations performed have to be done so in a reliable way, since errors cannot be monitored or corrected during a foraging run. Also rebcalibration is only known for subsystems such as the compass. The vector is only reset in the colony. On top of all that the ant has to deal with insufficient sensory data. Its knowledge of the world is highly limited and it can be assumed also noisy. The study of these highly evolved and carefully tuned system allows us to draw some conclusions that can not only entertain biologists, but also lead to a systematic application in technological development.

- Each *Cataglyphis*-ant is able to perform foraging runs with 20.000 translational steps including rotations and inclines, integrating iteratively every single vector at a precision sufficient enough to relocate the nest while running on a sometimes slippery ground in a rather shakey manner. Neuronal mechanisms of data fusion, error elimination, and the lot may provide new tools for various applications.

- The architecture of the e-vector analyzers including the subsequent hard-wired data processing leads to a fully functional skylight compass. It is robust enough to work under suboptimal conditions such as almost obscured sky or even during full moon nights. Still, it is a simple electronic system that has already found its way into a technological demonstrator [4, 11]

- Only little exposition to the sunlight is necessary to determine the current shape of the ephemeris function. Understanding the balance between preprogrammed and acquired knowledge including the minimum input necessary to perform this task may lead to a deeper understanding for adaptive mechanisms in autonomous systems.

- Not all available data is used by the sensory system. Which features of a visual scenery is finally memorized (snapshot) and subsequently compared to the actual scenery? The algorithms that are used by the technological competetor to locate the nest with visual cues could be usefull for ones own projects.

- On top of that, the Australian ant, *Melophorus bagoti*: How does such a small and rather unintelligent being memorize and retrieve every single point of its route(s)? Again feature extraction, data compression and comparison algorithms could be an interesting starting point in machine vision projects.

- One of the big questions in animal navigation in general is the dispute between map-like representation or procedural knowledge of the habitat. The current state indicates that the use of maps seems to be rather unprobable since simpler models allow to explain all current data. Might autonomous exploration vehicle be better off to use this form of "mapping" their environment?

- One of the most amazing observations is that foraging ants usually fall to predators but only rarely get lost or miscalculate their energy budget. The ant-controlled part of a foraging excursion appears to be rather robust and "mission proof". Examples are the self elimination of inevitable errors or the temporary dominance of the visual navigation system over the egocentric one during nest search. The basis on which information is evaluated and trusted can inspire the development of autonomous, redundant systems in space applications

The lessons that can be learnt from systematic analysis of biological systems is not only a time worthy activity but may also lead to new insights for technical applications. Biological systems are subobtimal in the respect that they have to follow the genetic history of the Bauplan and cannot design freely in space and material. However, the solutions achived are sometimes unique and justify a deeper look. On the other side, technological research has the big advantage that the competetor may be analyzed at any time and subsequently imitated if the solution appears to be better. The competetors emanating from nature should not be underestimated.

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