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Wehner, R

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R. Wehner

Zoologisches Institut,
Universität Zürich

Panting desert ants – and how they navigate¹

Imagine going out to the desert and shifting your gaze from the vaulting sky downwards to the surface of the earth. Then you might encounter one of the most fascinating creatures inhabiting these vast expanses of desert floor. *Cataglyphis* by name, these small navigators steer their courses for hundreds of metres across sand-dunes, gravel-plain or salt-pan terrain and having found food return directly to the starting point of their foraging journey – with seemingly unerring precision (fig. 1, 2). The way these animals navigate has been the focus of a multidisciplinary research project including studies in neurophysiology, neuroanatomy, behavioural biology, informatics and robotics. However, before I start to illustrate and discuss these endeavours let me draw your attention to a question that is more in line with the topic of this conference: how is it that *Cataglyphis* can survive under the extremely harsh conditions of the desert environment in which it is active during the hottest times of day and year?

The ecological niche which *Cataglyphis* occupies within the desert ecosystem is that of a thermophilic scavenger. In winter the ants hibernate underground, but in summer, when all other insects and spiders are active only during the night-time hours, *Cataglyphis* is the only diurnal forager. It collects the corpses of those nocturnal arthropod companions that have not escaped the burning sun on time and have consequently succumbed to the heat and desiccation stress of their deadly surroundings. This is the time when *Cataglyphis* ants equipped with high titres of heat-shock proteins start their

foraging activities. Their critical thermal maxima and upper lethal temperatures are higher than in any terrestrial organism studied so far (*Cataglyphis bombycina*: $53.6 \pm 0.8^\circ\text{C}$ and $55.3 \pm 1.1^\circ\text{C}$, respectively). However, there is yet another problem that desert animals, especially small ones, have to cope with, namely desiccation stress. Even though the *Cataglyphis* cuticle is nearly water-tight, the ants cannot avoid losing water during their exhalation phases and it is at this juncture that the pneumologist might get startled.

Respiration and ventilation of *Cataglyphis* are not only different from the general mammalian pattern, but are subject to an extremely strong selection pressure: to compromise between efficient gas exchange and effective minimisation of respiratory water loss during CO_2 output (fig. 3). This is especially so because of the very high water vapour saturation deficit that occurs at the high temperatures prevailing during the ant's foraging times.

The ant's solution to this trade-off between high rates of gas exchange and low rates of water loss is an extremely discontinuous ventilation pattern. Large amounts of CO_2 can be stored in the liquid phase – in the haemolymph, the insect's blood. Consequently, a negative pressure (up to -50 Pa) develops in the endotracheal system, so that air (and with it O_2) is sucked in continuously through the partially opened spiracles without any active ventilation. In contrast, CO_2 (and with it H_2O) is expelled discontinuously during short respiratory bouts, once the CO_2 storage capacity of the haemolymph has been reached. It is only then,

¹ President lecture at the Annual meeting of the Swiss Society of Pneumology (Morschach, June 24–25, 1999)

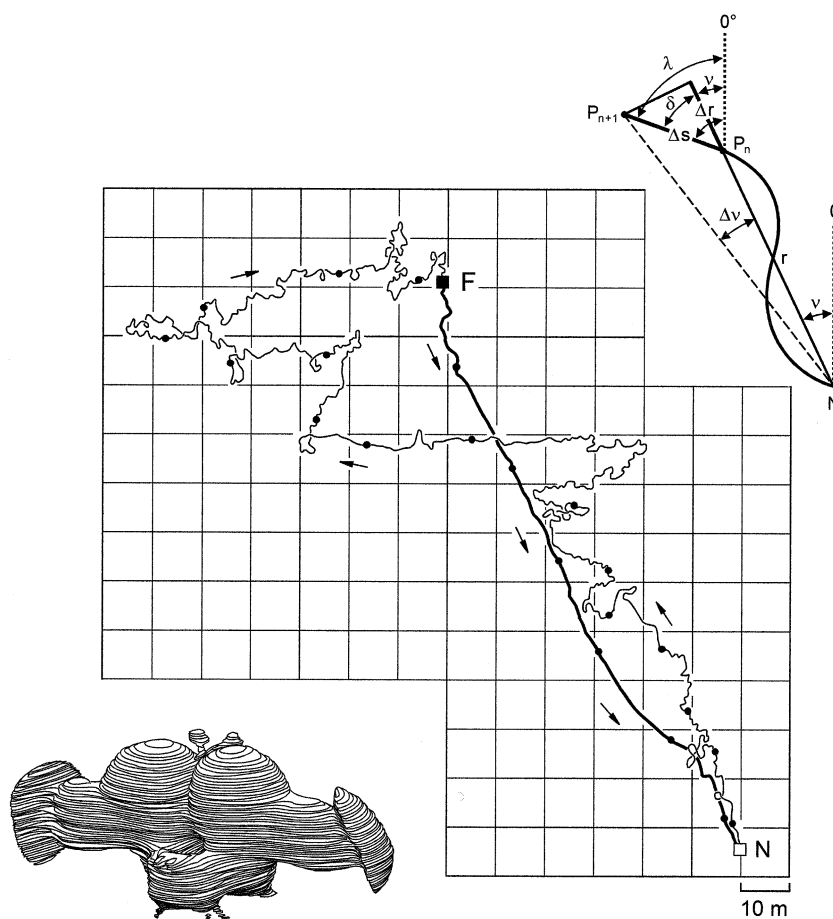
Correspondence:
Prof. Dr. Rüdiger Wehner
Winterthurerstrasse 190
CH-8057 Zürich

Figure 1

Cataglyphis bicolor leaving the entrance of its subterranean colony and setting out for a large-scale foraging journey. Photograph by the author.

**Figure 2**

Foraging path (thin line) and return path (thick line) of *Cataglyphis fortis*. Time marks (black dots) are given every 60 s. N = nesting site; F = feeding site. Inset at upper right: geometrical structure of the path-integration algorithm. Inset at lower left: anatomical reconstruction of the ant's cockpit, a 0.1-mg brain.



when the spiracles open fully for short periods of time, that water loss can occur. Direct observations of spiracular activity and recordings of endotracheal pressure as well as simultaneous gas exchange measurements clearly show that gas flow is tidal rather than bi- or unidirectional (fig. 4). The two pairs of thoracic spi-

racles act as high-capacity gateways to the tracheal system and are responsible for nearly 90% of overall gas exchange. To sum up: with their extreme requirement for water conservation *Cataglyphis* ants employ a pronounced discontinuous ventilation pattern. They do not rely on diffuse ventilation, which otherwise

Figure 3

Meso- und metathoracic spiracles (at lower left and right, respectively) and their positions on the alitrunk of *Cataglyphis bicolor* (see arrows in upper figure). Scale bars: 1 mm (upper figure) and 50 μm (lower figures). Preparation and photographs of SEM figures by E. Meyer, Zoology (Neurobiology) Zurich.

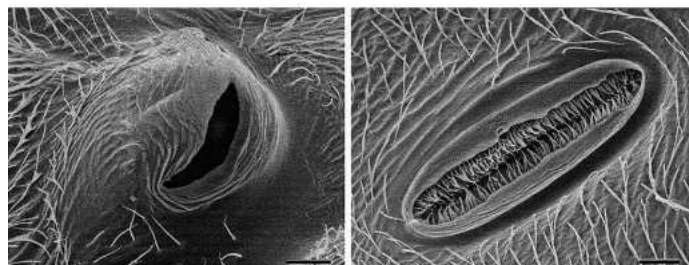
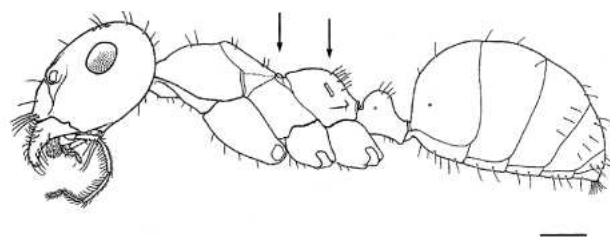
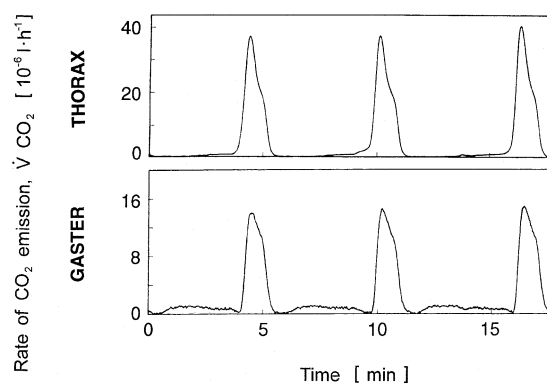


Figure 4

Rate of CO₂ emission during discontinuous ventilation in a 35-mg *Cataglyphis bicolor*. Note that the recordings from the thoracic (upper graph) and abdominal spiracles (gaster: lower graph) are on different scales.



navigational tasks the *Cataglyphis* brain has to accomplish. While integrating its path a *Cataglyphis* forager must measure all angles steered, gauge all distances covered, and integrate these data into a mean home vector (fig. 2). Hence, the ant's cockpit must be equipped with a compass (for determining directions), an odometer (for gauging distances), and an integrator (for combining these angular and linear components of movement). The ant's navigational toolkit contains a number of different modules, or subroutines, to accomplish these various tasks.

would be sufficient to supply the insect's gas exchange needs. But the desert environment calls for special mechanisms not only of gas exchange but also of water retention. Let me now return from this digression into respiratory physiology and focus again on the

In the present account it might be especially intriguing to elaborate a bit on the compass system because the compass used by *Cataglyphis* is based on a skylight pattern (the pattern of linearly polarised light or e-vector pattern) that we humans are unable to see (fig. 5). This pat-

Figure 5

Polarisation (e-vector) pattern of skylight. The picture at the upper left was taken through a 180° fish-eye lens vaulted by a Perspex hemisphere. The latter was equipped with a set of axis-finder polarisers (see lower figure). The sun is at the horizon. The figure in the upper right depicts a schematic representation of the e-vector pattern (sun elevation 60°). Photographs by the author.

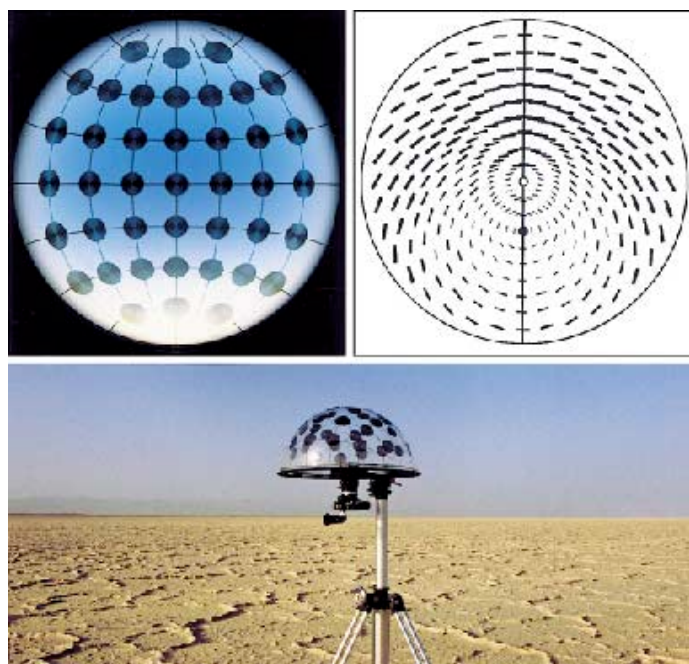
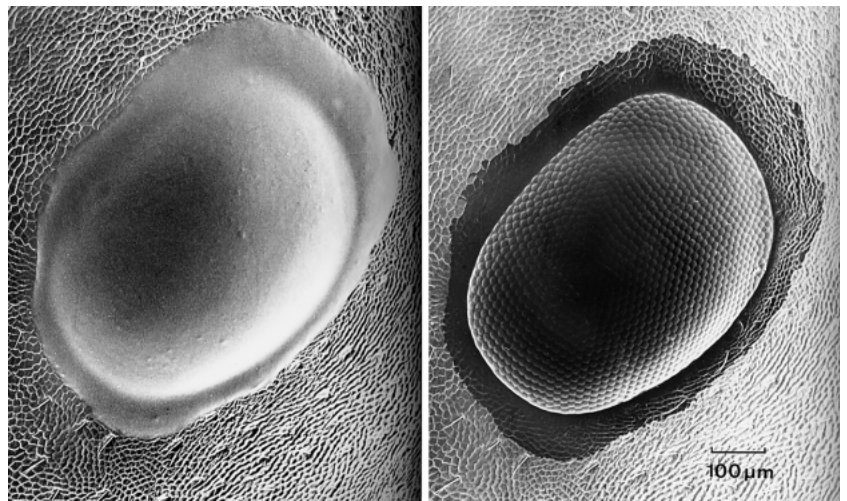
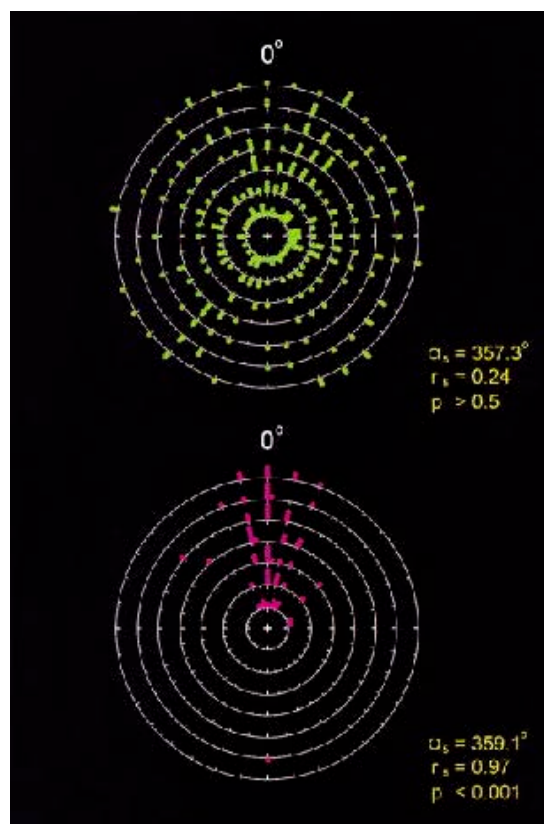


Figure 6

Contact lens covering a compound eye of *Cataglyphis fortis* (left figure). In the right figure the contact lens has been removed. The transmission properties of the contact lens restrict the ant's skylight vision to a particular band of spectral wavelengths. Preparation and photographs by P. Antonsen, Zoology (Neurobiology) Zurich.

**Figure 7**

Compass orientation of *Cataglyphis bicolor*, in which either – and exclusively – the green (long-wavelength) receptors or the ultraviolet (short-wavelength) receptors are stimulated (see upper and lower figure, respectively). The home direction is indicated by 0°. In the first case the ants move in random directions (upper graph). In the second case they are oriented as perfectly as the untreated controls (lower graph).



tern of the electric (e-) vectors of light is caused by the scattering of sunlight at the air molecules within the earth's atmosphere. A set of specialised photoreceptors located at the uppermost dorsal rim of the ant's compound eye is sensitive to particular aspects of scattered skylight: the ultraviolet range of the spectrum and the orientation of the e-vector of light. The extraordinary polarisation sensitivity of the "skylight sensors" results from molecular and cellular specialisations. Within a given photoreceptor cell the absorption axes of the rhodopsin molecules are all aligned in one particular direction. As intracellular electrophysiological recordings from individual photo-

receptors show, it is this e-vector direction to which the cell is tuned. If, in particular behavioural experiments, the ants are equipped with contact lenses that stimulate only the green – rather than the UV-type of receptor, or if the dorsal rim area is blocked out, the ants behave as though lost (fig. 6 and 7).

Populations of many retinal e-vector sensors converge onto a small number of (most probably three) binocular "compass neurons". These compass neurons have e-vector tuning axes that are the mean of the tuning axes of the peripheral input sensors. Due to the different populations of sensors contributing to each compass neuron, the tuning axes of the three compass neurons vary by about 60°. Consequently, each point of the compass, i.e. each direction, in which the ant might be facing, is characterised by a particular response ratio of these three compass neurons. As simple as this might sound, there is at least one further complication. As the e-vector pattern in the sky is generated by the scattering of sunlight, its spatial layout varies with the elevation of the sun and the response ratios of the compass neurons that define the points of the ant's compass vary accordingly. *Cataglyphis* solves this problem by recalibrating its compass every time it sets out for a new foraging journey. It does so by performing small rotatory movements whenever it leaves its subterranean colony. Most probably it is during these "graceful little minuets" that *Cataglyphis* generates its celestial look-up table.

Having dwelt at some length on the ant's compass system let me skip the odometer and the integrator and proceed to another aspect of navigation. Path integration, as any egocentric system of navigation, is prone to the accumulation of random errors. Hence, the tip of the

global vector is blurred rather than pointed. Supplementary systems are needed for finally pin-pointing the goal and it is here that landmark guidance comes to the fore.

Cataglyphis locates its pin-hole sized nest opening with fair precision by referring to the landmark panorama along the horizon skyline. Recent experiments using arrays of artificial landmarks have shown that the ant while approaching its goal continually compares its current retinal image of the landmarks with the stored (“snapshot”) image that it has previously taken at the goal and moves so as to reduce the discrepancy between the two. As the snapshot is a two-dimensional image of the three-dimensional landmark array, this matching-to-memory strategy confounds distances and sizes. But this is not too much of a limitation, because under natural condition it is always to the same configuration of landmarks that *Cataglyphis* will return. Furthermore, ants equipped with particular contact lenses clearly demonstrate that the snapshot is retinotopically fixed. Apparently, the ants learn a view from the goal while pointing in a particular direction. Interocular transfer does not occur. For example, when trained with the left eye (and with the right eye occluded) and later tested with the right eye (and with the left eye occluded) *Cataglyphis* is unable to recognise the very same landmarks to which it has successfully responded just a few minutes ago. What could be a more vivid demonstration of the retinotopical organisation of snapshot memories than the result of this intriguing experiment?

As mentioned above, the inherently noisy path-integration system must be supplemented by additional navigational subroutines. Piloting by means of familiar landmarks is the most powerful of these supplementary systems. But

if landmarks are absent, for instance in flat and featureless salt-pan terrains, *Cataglyphis* resorts to a final emergency plan: a systematic search strategy. This search plan consists of a number of loops pointing in all directions and continually increasing in size, but always centred about the point where the goal is most likely to be. In other words, the search density function is adapted to the target probability function. As we have later been told, this system is nearly identical to the one used by the US Navy when searching for missiles lost by the US Air Force. We have computer-simulated this search strategy as well as the matching-to-memory and skylight-compass algorithms, and have implemented the latter two schemes into robotics simulations.

In conclusion, the strategies used by *Cataglyphis* in compass steering, path integration, landmark guidance, and other modes of navigation are not what a human mathematician would call all-inclusive solutions to the underlying abstract problems. The ant uses simple tricks adapted to its particular needs. These tricks work perfectly well within the animal’s behavioural framework and ecological setting. For example, *Cataglyphis* cannot take an aerial view of its foraging terrain and hence cannot accomplish and use a topographic map of sorts. For the ant there has been neither the opportunity nor the need to indulge such desires. On the other hand, the way in which *Cataglyphis* employs a number of navigational modules used in parallel or in sequence is as sufficient as it is elegant.

What are the more general messages to be gleaned from the ant’s performances? As a general result the insect’s “intelligence” lies in the specific interlocking of a great number of special-purpose subroutines. These subroutines are intricate adaptations tailored to particular environmental conditions. In the *Cataglyphis* “cockpit” – a 0.1-mg brain – different neural pathways are employed to mediate different control systems, and it is the collective interaction of various modules that sets the stage for intelligent behaviour to arise. Hence, the smart insect navigator picks up useful information through various sensory channels, that is, relies on massively parallel processing regimes. In this context, the performance of these small desert navigators may provide an object lesson for studies in artificial intelligence and robotics. Technologically speaking we may move from living eyes to seeing machines. Already now, there are not only cataglyphid ants but also cataglyphoid robots that roam the desert floor (fig. 8). The design of these robots has

Figure 8

The mobile robot Sahabot 2 equipped with a panoramic visual system. The system consists of a digital CCD camera and a conically shaped mirror (on the left side of the figure). The visual system is able to take and store landmark pictures of the robot’s 360° skyline and to compare the current image with the stored one. This is analogous to what the ant’s brain accomplishes. The robotics work is done in cooperation with the Institute of Informatics, University of Zurich (R. Pfeifer). Photograph by the author.



been inspired by the ant's sensory and neural performances. It might promote future attempts to achieve complex behaviour by the interactions of rather simple subroutines.

Human problem solving relies on first principles, that is, on reasoning based on mathematics and logic. These general-purpose solutions tend to be computationally complex and sensitive to noise. In contrast, animal systems which

have not been designed on the drawing board but have evolved through natural selection are remarkably reliable and robust. Hence, recent approaches in artificial intelligence take advantage of the effective and computationally efficient "short-cut" solutions at which biological systems – such as those of *Cataglyphis* – have arrived.

Suggested reading

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