Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae)[1]

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Summary. For navigation, desert ants apply piloting and dead-reckoning strategies based on terrestrial and celestial visual cues, respectively. Visual spatial memories, rather than general concepts derived from landmark constellations, are most probably used to define points on earth by nearby landmarks. The visual field of a specialized dorsal part of the ant's retina is mapped on to the celestial sphere to consider the possibility that similar mechanisms are used to define directions on earth by exploiting skylight patterns present at infinity.

According to some recent reports[2], insects are able to store retinal images and later to compare these stored images with current ones by applying some type of matching procedure. This capacity of the visual spatial memory most remarkably reveals itself in the numerous accounts of insect homing, when insects repeatedly return to the same point on earth, be this 'home' a nesting site, a foraging station, or just a place to meet a mate. However, what cannot be disentangled from most of the numerous accounts mentioned in the literature[3] is whether homing is really governed by a system relying on landmark memories or by some type of dead-reckoning strategy. The experiments described here allow us to isolate both types of navigation and thus to study the problem of visual spatial memory in more detail.

Individual specimens of *Cataglyphis bicolor* are trained to an artificial landmark panorama consisting of 2 small black cylinders, 10.8° high, 6.6° wide and positioned at an angular distance of 180°. In order to prevent natural landmarks interfering with the experimental markers, an ant colony is transferred to a completely new area in the middle of a hard desert plain. At this new site the nest opens by an inconspicuous small entrance hole on the surface of the plain. This procedure of 'nest transplantation' also allows us to control and quantify the learning process. After training, individual ants are taken directly from the nest entrance and are then transferred to a new (testing) area where either the same landmark constellation (controls) or a modified one (tests) has been installed. Due to this experimental procedure, no type of dead-reckoning system can be involved in homing. Recording of the ants' searching (homing) paths is facilitated by means of an orthogonal grid painted on the hard desert plain (mesh width 0.5 m) and an electronic timer, by which the positions of the ants are plotted at preset time intervals[4].

In this short communication only 2 questions shall be raised: a) Is it a specific memory picture that the ants use in homing, or do they apply a more general rule in defining home in terms of the overall distribution of landmarks? In the latter case[5], for instance, the ant's strategy could be to search for home 'just in the middle between 2 identical landmarks'. b) How does the accuracy of homing depend on the distance of the markers?

Figure 1 deals with the first question. In the control experiments the ants' searching paths are clearly concentrated about the zero-point[6] (figure 1,a). However, if the markers are positioned at double the distance apart, but not

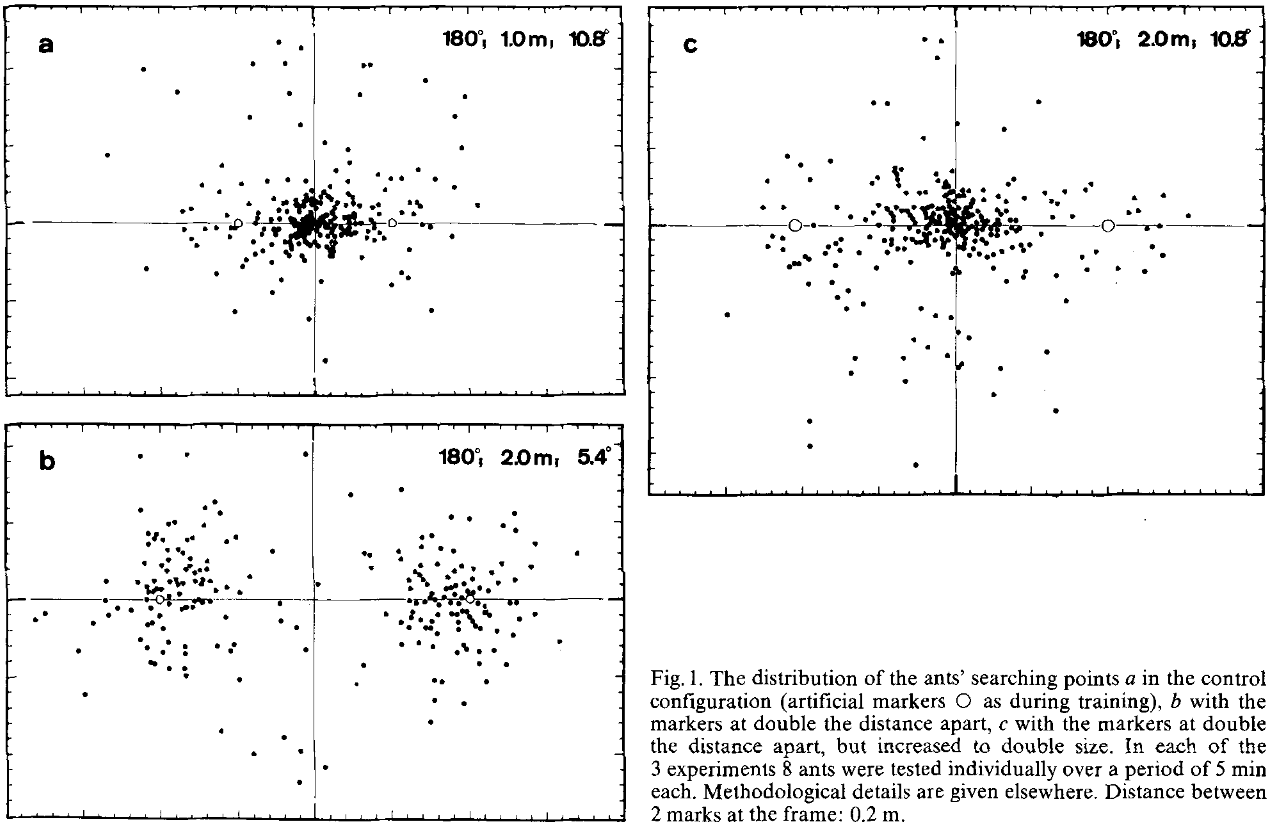

Fig. 1. The distribution of the ants' searching points *a* in the control configuration (artificial markers O as during training), *b* with the markers at double the distance apart, *c* with the markers at double the distance apart, but increased to double size. In each of the 3 experiments 8 ants were tested individually over a period of 5 min each. Methodological details are given elsewhere. Distance between 2 marks at the frame: 0.2 m.

increased in absolute size, so that their angular extent is decreased by half, the ants do not search at all at he zero-point, but close to the 2 individual markers (figure 1,b)[7]. Doubling the size of the markers at double the distance apart just re-establishes the searching pattern of figure 1,a (figure 1,c). The most likely interpretation of this finding is that the insect tries to match a stored image with the current one and that it thus seems to rely on retinal images rather than to apply a general rule. This conclusion is supported by further experiments including sets of 3, 4, or 6 markers[8]. By an elegant set of experiments performed in bees Anderson[5] has recently favoured the view that the homing insect uses a more general concept. According to his 'distribution' model it is the overall configuration of landmark constellations rather than the properties of the individual markers (size, angular separation, etc.) that governs the insect's strategy. Due to this idea the homing strategy should be relatively invariant against the size of the markers. However, in ants it is certainly not. If supplementary parameters are then incorporated into the distribution model (as has deliberately been done by the author), the principal difference between the distribution model and a model relying on memory pictures is weakened.

As to the 2nd question, homing accuracy significantly decreases with increasing separation distance of the markers, even provided that the distant markers are of the same angular extent as the close markers when viewed form the zero-point. For example, 15 per cent of all searching points are confined to an area of 0.16 m^2 centered around the zero-point, if the markers are 1 m apart from the zero-point. For a distance of 3 m the corresponding number is only 6 per cent. This result is to be expected, just for geometrical reasons. Motion parallax becomes less reliable in defining home, the farther away the markers are from home.

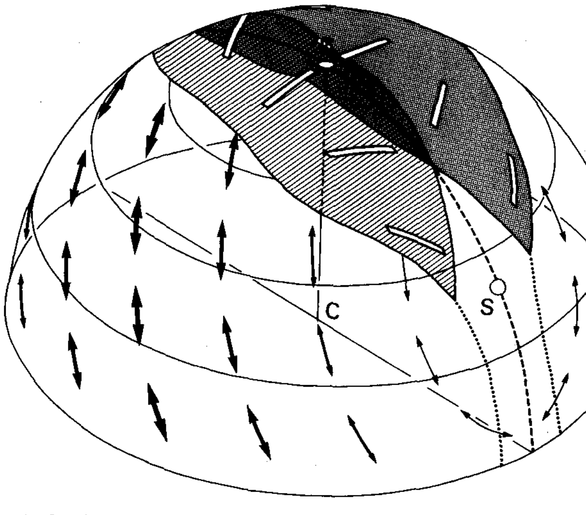

Fig. 2. The pattern of skylight polarization and how the visual fields of certain parts of the ant's retina are mapped on to it. Direction and degree of polarization are indicated by the direction and thickness of the double arrows, respectively. In the simplified representation given here, based on primary scattering of the direct light of the sun, the e-vectors of linearly polarized light form tangents on concentric circles around the sun. The whole skylight pattern, including spectral cues not shown here, is symmetrical about the solar vertical (dashed line). If the ant is heading for the sun's azimuth, the shaded parts of the sky are viewed by specialized areas of the ant's left and right retinae (hatched area, seen by the left eye, stippled area seen by the right eye). The white bars mark the directions of the transverse axes of the rhabdoms, i.e. the directions of one set of retinal analyzers. The shaded areas as well as the narrow zone between the 2 dotted lines constitute the ant's range of binocular overlap. Parallels of latitude are given for 20°, 40°, and 60°. C, centre of the celestial hemisphere (positio â of the ant); S, sun; Z, zenith.

Let us elaborate a bit on the latter argument: with increasing distance of the markers from home the spatial position of home is determined less precisely. If the markers are at infinity, home - being a specific *point* on earth - is not defined at all. What is then defined instead, is a *direction* on earth. The most important patterns that desert ants encounter at infinity are skylight patterns caused by the scattering of light within the earth's atmosphere. These patterns are due to spatial variations of the degree and direction of polarization as well as of the spectral composition of skylight. As insect eyes are sensitive to both polarized and UV light, conspicuous skylight patterns should be available to insects.

In the ant's dead-reckoning system, skylight patterns are used as directional cues[9]. (For the moment these patterns shall be regarded as stationary. This seems justified at least as far as the duration of the ants' foraging trips is concerned[10].) From behavioural experiments[11] it is known that a certain well-defined part of the ant's retina plays an important role in skylight navigation. In that part of the eye, in which the rhabdoms strike by considerable size and a specific arrangement of the rhabdomeres[12], the principal axes of the retinal analysers are mapped uniformly on to the celestial sphere (figure 2)[13]. This result has been obtained by 3 types of measurement: by 1, mapping the transverse axes of the rhabdoms and 2, determining the viewing directions of these rhabdoms (both relative to the co-ordinate system of the eye), and 3. by filming head (and eye) positions in freely running ants. Thus the directions of view as well as the directions of the polarizational analysers of single ommatidia can be translated from eye co-ordinates to celestial co-ordinates. This translation allows for mapping the skylight pattern on to the ant's retina. As during foraging and homing an ant does not perform pitching and rolling movements of its head about its transverse and longitudinal body axes, respectively, all variations within the retinal image are due to rotations of the ant about its vertical body axis. In figure 2, in which an ant is supposed to face the sun's azimuth, the specialized dorsal parts of the ant's left and right retinae - looking contralaterally - are mapped on to the celestial hemisphere. The regular pattern, by which the retinal analyzers view the sky, encourages one to determine the variations in the retinal excitation pattern that arises when the ant rotates about its vertical axis underneath the sky (paper in preparation). Furthermore, when the ant adjusts the dorsoventral axis of its head by 45° to the horizontal, as it usually does[11], the line of the horizon corresponds with another remarkable structural feature within the ant's retina. This could provide the ant with some type of horizon detector used for the visual stabilization of its head position.

It might well be that the orientation by visual spatial memories is a much more general strategy in the visually guided behaviour of insects than hitherto expected. Visual spatial memories might not only be used in defining *points* on earth by landmark patterns available at *finite* distances, but also in defining *directions* on earth by skylight patterns present at *infinity*[14].

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[1] Supported by the Hescheler Foundation (Zurich) and the Swiss National Science Foundation grants Nos 3.529-0.75 and 3.313-0.78.

[2] R. Wehner, J. comp. Physiol. *77*, 256 (1972); T.S. Collett and M.F. Land, J. comp. Physiol. *100*, 59 (1975).

3 The literature on homing by use of landmark memories is summarized in R. Wehner, Handbook of Sensory Physiology, vol. VII/6B, Vision in Invertebrates. Springer, Berlin, Heidelberg, New York, in press.

4 The experiments described here were performed near Maharès, Tunisia (34.58° N, 10.50° E) during summer 1976. They are only part of a larger project on ant homing by the use of landmark cues ('piloting') (R. Wehner et al., in preparation).

5 G. van Beusekom, Behaviour *1*, 195 (1948); A.M. Anderson, J. comp. Physiol. *114*, 335 (1977).

6 The zero-point is defined as that point within the testing area that marks the position of the nest in the training area.

7 As an additional control experiment has assured, the ants can well be trained to the zero-point of the landmark configuration shown in figure 1, b.

8 The retention of landmark memories has been tested by keeping individual ants isolated in the dark for up to 10 days. They still exhibited homing capacities similar to those shown in figure 1, a.

9 R. Wehner and P. Duelli, Experientia *27*, 1364 (1971); P. Duelli and R. Wehner, J. comp. Physiol. *86*, 37 (1973). Of course, in order to define 'home', a dead-reckoning (vector navigation) system has also to rely on some means of measuring distances.

10 R. Harkness and R. Wehner, Endeavour, N.S. *1*, 115 (1977).

11 R. Weiler and M. Huber, in: Information Processing in the Visual Systems of Arthropods, p. 287. Springer, Berlin, Heidelberg, New York 1972; P. Duelli, J. comp. Physiol. *102*, 43 (1975); R. Wehner, Fortschr. Zool. *23* (1), 148 (1975); and unpublished data.

12 P.L. Herring, Cell Tissue Res. *169*, 247 (1976).

13 F. Räber, Thesis, submitted to the University of Zurich. For a corresponding analysis in bees see E. Sommer, Thesis, submitted to the University of Zurich.

14 For some general rules about how insects could determine compass directions by skylight cues at any time of the day see K. Kirschfeld, M. Lindauer and H. Martin, Z. Naturforsch. *30c*, 88 (1975), and S. Rossel, R. Wehner and M. Lindauer, J. comp. Physiol. *125*, 1 (1978). What the concept of visual spatial memory would imply in that respect is that the ant would have to be able to rotate a stored image in its head (by 15°/h about the north-south axis of the celestial sphere; the latter is not shown in figure 2).

Regeneration induced in the forelimbs by treatment with vitamin A in the froglets of *Rana breviceps*[1]

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Summary. Young froglets of *Rana breviceps* do not possess the power to regenerate forelimbs after amputation through metacarpals. However, 5 min immersion of limb stumps in an oily solution of 150,000 IU vitamin A palmitate immediately after amputation, and once on each of the 3 subsequent days, induced definite though hypomorphic regeneration in 100% cases.

With few exceptions the anuran amphibians lose the power to regenerate limbs by the end of their larval life. However, several workers have succeeded in inducing at least some regeneration in the amputated limbs of adult frogs by various experimental procedures[2-6]. Polezhayev has suggested that one of the requirements for inducing regeneration in the otherwise non-regenerating limbs is intensification of dedifferentiation of cells of stump tissues[4]. Recent studies have shown that treatment with excess of vitamin A palmitate promotes early post-amputational regenerative changes in limb stumps of toad tadpoles by intensifying dedifferentiation resulting in the formation of good blastemas. While continued exposure to vitamin A excess inhibits post-blastemal developments[7], good and even hyper-regeneration occurs if the vitamin treatment is discontinued after blastema is established. The present experiments were made to investigate whether vitamin A treatment could be a means to induce limb regeneration in young post-metamorphic frogs which otherwise do not possess this capacity.

Materials and methods. In young, 15-20-day-old froglets of *Rana breviceps* (Schneider), the left forelimb was amputated through the middle of metacarpal region. The vitamin preparation employed was Arovit (Roche, India) which is an oily solution of vitamin A palmitate. Administration of the vitamin by injection (75 IU and 300 IU per injection) or keeping the operated froglets partly immersed in 100 IU/ml solution of the vitamin resulted in heavy mortality within 2 days. However, the following technique proved successful: The operated limbs of experimental group of froglets were dipped in the oily solution containing 150,000 IU vitamin for 5 min immediately after amputation and then for the same duration once on each of the following 3 days with no further treatment on the remaining 12 days of the experiment. The froglets of both treated and untreated (control) groups were maintained in aquaria resembling small ponds at room temperature (30-32 °C) with a light source to attract small insects to provide food at night.

Results. By the end of 15 days following amputation, forelimb stumps of all the 14 froglets of the untreated group had healed up indicating complete absence of regenerative power. 1 representative case if this group is shown in figure 1. There was, however, very definite though hypomorphic regeneration in all the 11 vitamin-treated forelimb stumps of the experimental group of froglets. The regenerates showed positive attempts at morphogenesis of distinct digit-like structures in all cases. In 4 cases there had developed 4 and in the remaining 7 cases 3 such digital structures per regenerate. 4 representative cases of this group are shown in figures 2-5.

Discussion. The results provide very definite evidence that even very brief local treatment of amputated forelimbs of

Fig. 1. A case of nonregenerating untreated stump of a forelimb amputated through metacarpal region in a froglet of *Rana breviceps.*