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Spatial memories and cognition in insects

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ABSTRACT. *Spatial memories and cognition in insects*.- We first propose a classification of the different types of spatial memories observed during spatial orientation in insects: (1) The Read-Only-Memory is stored within the "hardware" of the animal; (2) The Volatile-Memory operates only during the current orientation process and is then reset to zero at the end of each excursion; (3) The Constant-Memory is stored by each individual according to its own experience. Two types of Constant-Memory orientation can be distinguished according to the way they are stored and used: as a file where discrete spatial information can be used in a standard succession and an unvariable sequence (Sequential-Access orientation memory) or as a file in wich the accesss to spatial information can be achieved from any known location (Random-Access orientation memory). At last, we discuss how these mnesic and cognitive processes could be involved during spatial orientation of insects in the complexity of their natural habitat.

KEY WORDS. Spatial memories, Spatial cognition, Insects, Homing, Field orientation

Introduction

Classification of phenomena and observable processes constitutes an essential stage of the inductive approach. Such a formalization wich was first attempted by Aristote, has been shown to be fruitful by stressing common points and differences among living beings and thus allowing for instance the merging and the theorization of the concept of Evolution. A classificatory approach is therefore an useful step to organize the knowledge and to understand the phenomena.

The earliest classifications in the field of spatial orientation appeared at the end of the last century, they were based upon observable processes. They were first proposed by botanists describing plant orientation so as to distinguish it from animal orientation. These classifications actually make a clear dichotomy between fixed living beings from mobile living beings. The table I shows two types of classification according to Fraenkel & Gunn (1940).

The earliest one classifies according to the type of stimulation involved and is not completely systematized as it still mixes vegetal and animal kingdoms; it has been progressively applied to animals at the turn of the century with the behaviorists' early works. The second one, from Kühn (1919, 1929), is based upon the structure of the motor response; it was reviewed by Fraenkel & Gunn (1940) and recently used again by Schöne (1984).

However, during the last decades in the study of behavior, students of spatial orientation have singularly gone beyond the level of the observable to look for the possible intermediate variables and inferred processes. These are deduced by logical inferences from an observation where "it is occurring as if..." shifts soon to "it is occurring like that".

Obviously, such a description of the orientation processes leads to the use of numerous metaphors. The animal often becomes a mathematician or a computer, it measures, it compares, it integrates, it averages, etc...

In order to illustrate this conception of spatial

TABLE I. Types of clasification in the field of spatial orientation.
[Tipos de clasificaci6n de la orientaci6n espacial en la naturaleza.]

Form of the motor response		Type of stimulus	
		Phototaxis	1878
Kinesis			
	Ortho-kinesis	Thermotropism	1883
	Klino-kinesis		
		Rheotropism	1883
Taxes			
	Klino-taxis	Hydrotropism	1884
	Tropo-taxis		
	Telo-taxis	Geotaxis	1888
Transverse orientations		Chimiotaxis	1888
	Light compass reaction		
	Dorsal (or ventral) light reaction	Thigmotropism	1889
	Ventral earth (transverse gravity) reaction		
		Galvanotropism	1889

orientation behavior, a few examples from the literature dealing with homing in insects will be taken. Descriptive terms are, most of the times, used as metaphors, sometimes in an anthropomorphical way, like "navigation, pilotage, dead reckoning". As a matter of fact it is in such a way that a definition of homing was initially proposed by Griffin (in Able, 1980):

-*"direct" piloting*: orientation towards or relative to a target which is directly detectable by the sense organs of the animal.

-*compass orientation*: when orientation is guided by cues showing the direction of a non directly detectable goal.

-*"true" navigation*: which implies the use of both a map and a compass, allowing to find the way to a goal from everywhere within the map range.

The terms route-based or location-based information are also frequently used (e.g. Baker, 1984).

One must not neglect the role played by such metaphorical stages on the way to a true explanation; nevertheless, even when one cannot go beyond such a step, it has to be kept in mind that reality cannot be directly inferred from it.

We have not found an easy way to overpass these steps of classification and/or metaphor elaboration within their intricated context of mathematical and physical models. Although in many respects they tell us a rather simplified reality, it seems that their attractivity is hiding the actual processes, particularly when we try to understand the relationships between an individual and its own world. Such a survey of homing strategies in animals and, more particularly, of field orientation in insects will lead us, instead of being exhaustive, to focus successively on three particular aspects: 1. Spatial memories; 2. Space cognition; 3. Complexity of the natural situtions.

Spatial memories

1. Read-Only-Memory orientation

This type of memory is stored within the "hardware" of the animal as a "Read-Only-Memory". It concerns the inherited basis of orientation (Scapini, 1988) which is not modifiable during the whole life of the individual, even if it is able to inhibit or modulate the expression of this memory by learning new directions.

The Read-Only-Memory orientation of young birds appears during their first migration when they fly towards the wintering area (see Able & Bingman, 1987; Schmidt-Koening, 1975) guided by a locomotor program adapted to the direction and distance to be covered (Berthold & Querner, 1981). Shifts in the directions of migration are even under strong genetic control (Berthold, 1984; Terril & Berthold, 1989).

Although we have well known examples of this kind in Arthropods, particularly within the Italian literature, see e.g. the northward component in the riverine wolf spider *Arctosa varianna* (Papi & Tongiorgi, 1963) or the inherited astronomical direction in the amphipod *Talitrus* (Pardi & Scapini, 1983; Scapini et al., 1985; Ugolini & Scapini, 1988), little is known in insects in this respect (Birukow, 1960).

We can refer to pioneer experiments of Dobzhanski & Spassly (1967) in *Drosophila*, performed in laboratory conditions. They consisted in a selection based upon the sign of the phototactic tendency, separating in a few generations a positive and a negative strain (see also Michutta et al., 1982). In the same way, geographical variations in responses to light in *Drosophila melanogaster* can be correlated to the influence of the X chromosome (in Krause & Kölher, 1984). Inherited factors are also probably responsible for the widespread scototactic tendency observed in many insect species (Michieli, 1963), and particularly in the cricket *Nemobius sylvestris* (Campan & Médioni, 1963). These tendencies are often used in the field by the individuals to orient spontaneously towards the outlines of the low reflecting parts of the landscape, for example a river bank in riverine carabidae (Papi, 1955) or in riverine crickets (Beugnon, 1985, 1986a) or a forest border in *Nemobius* (Campan & Gautier, 1975; Beugnon, 1980). One of the best example in this respect is described by Couturier & Robert (1958) for the may-bug *Melolontha.* In this species adults of both sexes fly, in search for food, towards the highest tree border of the forest outlined above the horizon: this behavior has been called hypsotaxis. The orientation is then performed in the opposite direction by the females coming back in the field for egg laying. The same term is used to describe the spatial orientation of lady-birds flying toward the highest point of a hill or mountain range (Iperti in Campan, 1978) and for winged ants flying towards a summit swarming site (Chapman, 1963).

The Read-Only-Memory orientation could also be put forward to describe astromenotactic orientation behavior showing a constant angle relative to a distant light source, even if there is time compensation, as described by Costa et al. (1986) in the nocturnal orientation relative to the moon in the ground beetle *Scarites laevigatus*. It could also be the same for the internal compass representing a simplified model of the polarized pattern of the skylight (Wehner & Rossel, 1985) or for the species-specific directions exhibited by wide range migrating insects (Baker, 1978).

2. Volatile-Memory orientation

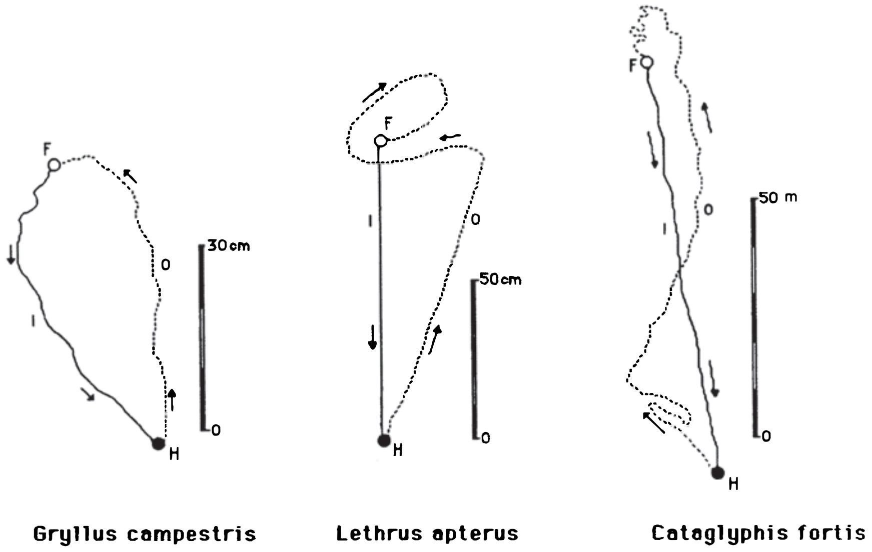
During homing, an animal can retrace its outbound path step by step, and the metaphor usually employed to describe such a return is "route reversal" (Wilstchko, 1983), or "course reversal" (Papi, 1988). The animal can also record spatial information "en route" from the starting point and all along the outward trip and then return directly to home. This type of orientation memory is described as "volatile" because it is systematically reset to zero at the end of each excursion. The Volatile-Memory orientation consists in an integration of internal (idiothetic cues) and/or external information (allothetic cues as terrestrial, celestial and magnetic compasses, etc...) for each segment of the trail, and it corresponds to what has been classically described as a path integration or dead reckoning (Etienne et al., 1986, 1988; Etienne, 1987). Discussion is opened (Wehner & Wehner, 1986) to explain whether during path integration insects refer either to vector integration, where rotations and translations would be integrated simultaneously according to the vector sum hypothesis, or to a distance-weighted mean-direction hypothesis.

Many examples of astrotaxic orientation are quite classical i.e. Wehner & Srinivasan (1981) in the ant *Cataglyphis.* The Volatile-Memory orientation could also explain homing in the beetle *Lethrus* (Frantsevitch et al., 1977) which makes very complex outward journeys followed by straight returns back to its hole. In all these examples (fig. 1), the stored information indicates the astronomical direction which is parallel to the one followed before capture, and then it starts circling in a systematic search behavior.

A good and particularly informative demonstration of the use of "en route" gathered information in homing behavior is given by Ugolini (1981, 1986, 1987) in *Polistes.* The wasps are able to take a correct initial orientation and to home accurately, even if they are released at 2 km from their nest after a passive displacement. The important point is that they must be transported within a transparent tube allowing them to see the environment and to gather external information en route; otherwise homing performances remain very poor. Artificial stimulation during the outward journey with a moving striped panorama shows that they are able to perform a correct initial orientation using simply the movement direction of the visual flux associated with an astronomical guiding; they do not use spontaneously familiar terrestrial landmarks. Furthermore, they are spontaneously able to choose a correct initial orientation by referring only to solar cues as it has been demonstrated by releasing wasps prevented to see the terrestrial environment. When the wasps are released close to their nest, they use familiar landmarks for direct piloting.

Generally speaking, individual homing success of *Polistes* depends on a set of factors: familiarity with the site, which can be acquired with fast and reduced training; distance, as far as the more the distance is important, the poorer the homing score will be; this could also be explained in metaphoric terms as a limit of memory capacity; worker's motivation; number of adults within the nest; hierarchical rank of the individual; type of experimental displacement, such as preventing or not to see the environment during the passive displacement.

Another example of path integration can be drawn from Beugnon & Campan (1989) on homing in the field cricket *Gryllus campestris.* When the insects move actively at a distance of 10 to 80 cm from the hole under clear sky conditions, they home straightward in a proportion of 94%, whatever the rectitude of the outward trip. Under a cloudy cover, homing performances drop dramatically for outward



Gryllus campestris **Lethrus apterus** **Cataglyphis fortis**

FIGURE 1. Examples of Volatile-Memory orientation: *Gryllus campestris* (Beugnon & Campan, 1989); *Lethrus apterus* (Frantsevitch et al., 1977); *Cataglyphis fortis* (Wehner & Wehner, 1986). H=Home; F=Food site; Dotted line=Outward trip; Black line=Inward trip.

[Ejemplos de orientación "Volatile-Memory". H=nido, F=zona de alimentación, ...=recorrido de ida, ___=recorrido de regreso.]

distances ranging between 20 and 40 cm. When passively displaced, most of the crickets get lost and do not home when they are released at a distance from the hole over 20 cm. If we add experimentally a polarizing filter above the walking area during the active outward trip and turn it by 90° at the beginning of the inward journey, the initial orientation is accordingly deviated from about the same angle value. The field cricket starts circling after travelling for a distance approximately equal to its distance from its burrow.

Riverine crickets of the *Pteronemobius* species can also display celestial orientation when they perform evasive swimming. The crickets are able to associate their direction of escape towards some conspicuous landmarks with the astronomical direction leading to the shoreline. A new time-compensated astronomical direction may be learnt when the insect is passively displaced towards a new shore facing a different astronomical direction (Beugnon, 1985, 1987). So it could be said that such Y-axis orientation is of the Volatile-Memory type and it is reset to zero at the beginning of each new evasive behavior. However as the swimming crickets are able to memorize such a theoretical escape direction for several days in captivity (Beugnon, 1986a), the process of memorization of this Y-axis spatial information rather belongs to the following type.

3. Constant-memory orientation

This type of memory is stored in a permanent way but remains open to changes any time during the life of the animal, particularly during earlier stages of its ontogeny. All stored information concerning the familiar cues (terrestrial or celestial) within the home range are grouped within this category.

Many examples could be given to illustrate this type of orientation in insects; nevertheless we have to set apart two different categories according to the nature of the stored information hypothetized.

Either a sequence of images of the panorama at various points of the familiar routes is stored, or the animal builds up a map which it is able to use for navigating from any known point. We will call the first type "Sequential-Access Files" orientation, and the second type "Random-Access Files" orientation.

3.1 *Sequential-Access Files orientation*

Cartwright & Collett (1982) and Wehner (1983) have proposed that pictures of the familiar world and usual routes could be stored in the form of snapshots which would be sequentially organized to lead an insect from one point to another. This model is derived from the earliest works of Forel (1908) (in Schneirla, 1972) who assumed that many species run according to a succession of images and from Ferton's work (1923) (in Wehner, 1981) on the solitary bee *Osmia rufohirta* from which it may be deduced that the insect uses several sequences of visual spatial memories.

This model is a very didactic theoretical view which could be applied for instance to honey bees (Lindauer, 1969; Lauer & Lindauer, 1972), ants (Jander, 1957; Wehner & Menzel, 1969; Wehner, 1983; Hölldobler, 1971, 1974; Rosengren & Fortelius, 1986; Fourcassié, 1985, 1986) and to some other species; it could be theoretically applied to wasps, but Ugolini (1987) has demonstrated that it was not the case.

To support the existence of such snapshots, various arguments are drawn from plenty of works. Wehner & Flatt (1972) showed that workers ants of the genus *Cataglyphis* do not use the same pattern of cues in the outward and the inward journey. Haas (1967) describes (fig. 2) that a male bumble-bee achieves circular trips visiting repeatedly the same flowers in the same spatial sequence. Nevertheless, true and convincing demonstrations are scarce, especially because they concern inferred processes.

Hölldobler (1980) describes the use of the canopy pattern overhanging the trail of an african *Ponerine* ant. In laboratory conditions, one can present a photo of this canopy to the foraging workers and observe a quite well directed orientation behavior; if the picture is turned by 180°, the direction assumed by the ants is completely reversed. Another example is provided by Wehner (1983) in *Cataglyphis* ants trained to forage at equal distance from two vertical cylinders distant of 3 m each other. If the two cylinders are experimentally moved closer by keeping constant their angular size, the training scores remain the same; but if they are

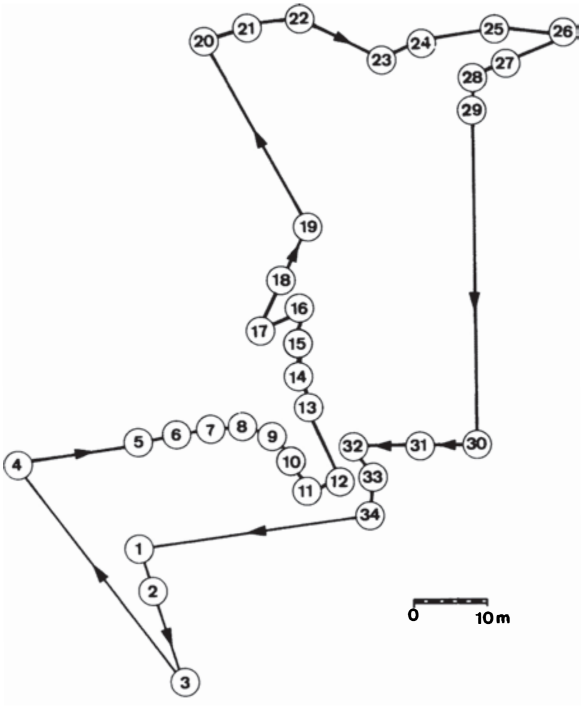


FIGURE 2. A male bumble-bee is patrolling by visiting repeatedly the same flowers and following accurately the same spatial sequence (from Haas, 1967).

[Un abejorro macho patrulla con visitas reiteradas las mismas flores y siguiendo con precisión la misma secuencia espacial (de Haas, 1967).]

moved nearer by keeping constant the real size of the cues, the foragers are disturbed and come at the right distance of only one of both cylinders according to its known angular size. From these experiments, Wehner (1983) came to the conclusion that bees and ants confound size and distance. However experiments in *Nemobius sylvestris* have already demonstrated that insects are able to estimate relative distances by motion parallax. The wood crickets preferentially orientate towards closer landmarks rather than more distant ones having the same apparent size. This preference is only achieved when the crickets perform visual scanning of the two cues within the binocular field (Goulet et al. 1981). Cheng et al. (1987) have come recently to the same conclusion in bees: "Near landmarks are still weighted preferentially even if they have the same apparent size as more distant ones".

Among the most famous examples known up to now, we have to cite the pioneer experiments concerning homing in digger wasps (fig. 3). They demonstrate that the insect localizes its nest according to a pattern of distant as well as proximate cues.

3.2. *Random-Access Files orientation*

First experiments describing the possible use of a map by honey bees were conducted by Gould (1986). Two samples of workers of honeybees are trained to forage either at A (160 m from the hive) or at B (at the same distance) on the experimental site. Foragers trained to visit site A are captured when they leave the hive and transported in the dark at site B. If they were disoriented they should fly randomly. If they do not know the site where they are released they should fly eastward in the compass direction parallel to the one leading from the hive to A. If they are only able to use familiar images they should fly back to the hive and from there, on to A. Actually, they fly directly from B to A, following a new unusual route. From these results (fig. 4) the author concludes that bees have a "locale cognitive" map limited to the home range of the colony.

Control experiments shown that bees trained to forage at site B and then passively displaced to site A directly fly from A to B. It is impossible that a cognitive map includes site A which is not directly visible from B or from the hive, if site A is totally unfamiliar to the bees. Thus to explain these results we have to assume that bees are familiarized with site A, even if they have not foraged in this clearing. According to a model by Cartwright & Collet (1987), bees could associate the direction and distance from the places where snapshots were taken (e.g. from site B and from site A) to the hive and then add the two home vectors (B ⇒ hive + A ⇒ hive) to deduce the direct vector linking B ⇒ A.

Their model of spatial knowledge provides the animal with information concerning its position and its home direction only from known familiar places

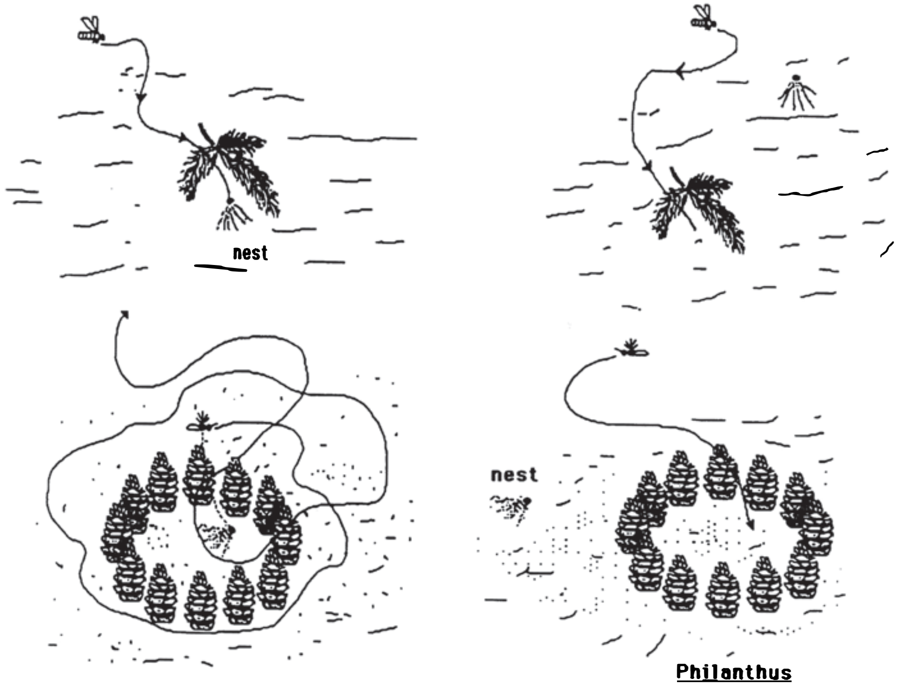


FIGURE 3. Homing of digger-wasps when the proximate cues around the nests are displaced. Above: experiment from Chmurzynski (1964) with *Bembex*. Below: experiment from Tinbergen (1932) with *Philanthus*.

[Retorno al nido de las avispas zapadoras después de que hayan sido retirados los puntos de referencia cercanos.]

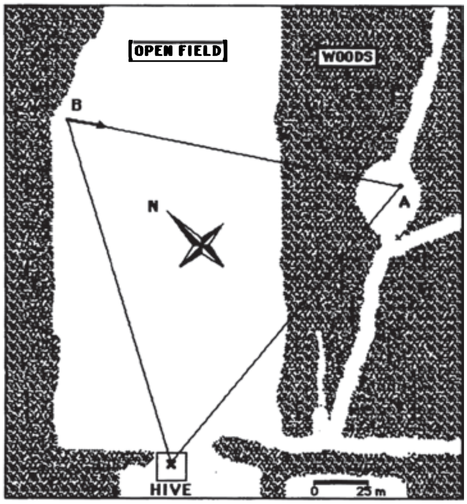


FIGURE 4. Experiment by Gould (1986) suggesting the use of a cognitive map in honeybee. Foragers trained to visit site A are captured when they leave the hive and transported in the dark at site B. Bees fly directly from B to A, following a new unusual route. As some kind of direct piloting from B to A is impossible because of the height of the forest border, all is occurring as if they were using a cognitive map.

[Experimento de Gould (1986) que sugiere la utilización de un mapa cognitivo por la abeja doméstica. Las obreras adiestradas a acudir al punto A son capturadas cuando salen de la colmena y transportadas en la oscuridad al punto B. Las abejas vuelan directamente de B a A siguiendo una ruta nueva e inusual. Al quedar descartado cualquier traslado directo de B a A debido a la altura de la linde del bosque, todo tiene lugar como si utilizaran un mapa cognitivo.]

within its home range. This is why we propose to call it a Random-Access File orientation system where spatial information can be retrieved independently of the linear order of storage as it is in the sequential-access file system.

3.3. *True navigation*

The Random-Access File orientation system allows the animal to identify its current position relative to home or to a foraging site when released within the limits of its home range. Some animals as homing pigeons are still able to compute the direction they should take to home even outside these limits (Wallraff, 1974). In this case, the map used by the birds is at least inferred from olfactory information carried by winds to the home area (see rewiews by Wallraff, 1984 and Papi, 1986). Such a true navigation ability based on the "map and compass" model has not yet been reported in insects.

4. Real-Time orientation

The category called Real-Time orientation describes, at first, all cases of random and systematic searches when there is no use of external spatial information (see a review of homing by random search by Jamon, 1987). Open-loops reactions like prey capture (Schöne, 1984) are also typical of Real-Time orientation because they occur during very short time of integration of spatial cues, with not enough time to allow sensory feedback. Real-Time orientation can be extended to situations when there is a direct and quasi permanent sensory contact with the target, as during positional or stabilizing behaviors (course control) or direct piloting. In this meaning, Real-Time orientation is depending on direct sensory contact and thus may be related to the concept of "sensory information" proposed by Passini (1984a). Such an inmediate orientation can also be applied to trail following, either the trail is provided by the environment (guide line) or by the animal itself (chemical trail of ants, film of mucus in polyplacophores and gasteropodes) as far as the trail leads directly to the goal. Thus, homing occurs in closed-loop conditions with a continuous but rather short feed-back control also described as an osmotropotaxis (Lindauer, 1956). This type of Real-Time orientation describes all the taxic and signal-stimulus responses; it represents a good model for neuroethologists because it is constituted by decision mechanisms detectable and observable in neuronal terms, at the sensory, central and motor levels. A rather complete example is given by the work of Huber and his team about the phonotactic behavior in the field cricket; neuronal mechanisms of detection, information processing, commands and motor events are known with their many possible feed-back loops (Huber & Thorson, 1985).

In this Real-Time orientation process, time constant and event duration are rather short compared to the other orientation processes already described in this paper as far as there is no need for pattern recognition and/or recall of memorized sources of spatial information at each stage of the displacement. However, despite its short time of integration, Real-Time orientation can be preceded by stored information processing. This concerns at least the various stages of signal treatment, such as localization and identification of the spatial information and those of the motor response. This memory is not only a spatial one, it integrates the structure of the signal and the form of the motor response and can be stored as a Read-Only Memory (Innate Releasing Patterns of the objectivist theory) or as a Constant-Memory (for the constructivist theory). Finally, Real-Time orientation is directly linked to the other categories of memories insofar it is involved in the last step of every type of spatial memory orientation afore described: While the planning of spatial behavior is based on memory and inferred information (Passini, 1984b), its execution always occurs during Real-Time orientation.

5. Synthetic classification

We thus propose to associate the origin of the spatial information used during the oriented movement with the metaphor usually used to describe it. Because orientation phenomena have spatio-temporal properties, therefore this classification derived from Beugnon (1986b) and Papi (1988) takes also into account the type of spatial memory which is implied for each category of orientation.

Of course an animal often refers to several kinds of category and as a consequence, the aim of the following table is not to explain the integrated behavior of an individual but merely to give simultaneously a classification of all the well known homing strategies (see table II).

Cognitive aspects of insect field orientation

The first encounter between Psychology and what was the prefiguration of Ethology is due to Darwin (1872) and Romanes (1882) who founded Comparative Psychology. Later on, following the positivism at the beginning of the century, the success of the behaviorism, rejecting the study of all

TABLE II. Synthetic classification of homing strategies.
[Clasificación sintética de las estrategias de retorno al nido.]

Spatial memory	Information	Metaphors
1 Read-Only-Memory	Mainly genetically based	Y-axis orientation Vector Navigation True Navigation
2 Volatile-Memory	Route-based without integration (retrace the outbound path)	Route reversal, Course reversal
3 Volatile-Memory	Route-based with integration (return directly)	Dead reckoning Path integration Vector integration Y-axis orientation Inertial navigation
4 Constant-Memory Sequential Files	Route-based without a map	Piloting, Terrestrial navigation
5 Constant-Memory Random-Access Files	Location-based with a map that is directly adquired	Piloting, Terrestrial navigation Mosaic map
6 Constant-Memory Random-Access Files	Location-based with a map inferred from a bicoordinate grid	True navigation Gradient map
7 Real-Time orientation	Without directional information coming from the goal	Random search Systematic search
8 Real-Time orientation	With directional information coming directly from the goal	Direct piloting
9 Real-Time orientation	Trail based orientation leading to the goal	Trail following Guide and crest line orientation

intermediate variables and logical inferences for explaining the black box, has inhibited for several decades the development of Cognitive Psychology. One has to wait until Tolman (1948) to blow up the vice of behaviorism and to introduce again the cognitive and mental representation in animal psychology. The new encounter between Psychology and Ethology during the sixties (Hinde, 1966) opened again the way to possible reciprocal influences. Thus it is not surprising that since some years, the cognitive vision is settling within the field of ethology, widely using logical inference reasoning. By taking into account the cognitive intermediate variables, one follows a fundamental principle in epistemology, namely the economy in the explanation (Vauclair, 1987a). Either unfortunately or fortunately we take it easy by shifting very often and fast from the "it occurs as if..." to the "it occurs in that way...".

Of course, the field of spatial orientation in animal did not keep away from these cognitivist influences. In most of the cases, inferences are restricted to vertebrates species (see for example a critical review about "cognitive maps" by Thinus-Blanc, 1984, 1987), mammals in particular (Chapuis, 1987). Nevertheless, there can hardly be any doubt about the involment of cognitive processes in learning by insects (Medioni, 1985): "The navigation and communication of honeybees requires them to have some sophisticated cognitive processes" (Roitblat, 1987). With these considerations in mind, the main data presented so far and concerning spatial memories may be read again from a cognitive viewpoint, at least by using some concepts from cognitive psychology. We will discuss here the following three aspects: mental representation, expectancy and intentionality.

1. Mental representation

Mental imagery was already assessed in most of the above described examples of spatial orientation. It is already the case for the Read-Only Memory orientation. For instance, Wehner (1984) supposes "that bees and ants come provided with some kind of celestial map" also called "hard-wired celestial almanac" (Hardie, 1986) as a simplified internal image of the e-vectors pattern of the polarized skylight. According to Rossel & Wehner (1986) the bee scans the sky by rotating its body until it detects when the array of retinal analysers, which provides the structural support of the bee's map, is maximally active that it to say when it matches the distribution of e-vectors which are actually present in the sky.

All is occurring as if, when a digger wasp is leaving its nest, it keeps in mind an image of its local environment (fig. 3). Pioneer experiments by Tinbergen (1932) in *Philanthus* and Baerends (1941) in *Ammophila* are very informative in this respect, as well as latter ones by van Iersel & van den Assem (1965). An interesting work by Chmurzynsky (1964, 1967) demonstrates that the stored image is probably a representation of the whole panorama around the nest of *Bembex*, with a rather accurate knowledge of the spatial relationships between its figural elements. Cartwright & Collet (1982) proposed a model showing how a honeybee could cope its actual retinal image of the landmarks with its internal template of the environment. Let us assume that the chronologically ordered snapshots are also linked in space. The animal could know that one peculiar image is located beside another one at a certain direction and distance. The insect could then have stored a kind of cartography, a "checkboard" of its home range made of juxtaposed images, more comparable to a "mosaic" cognitive map.

To this suggestive speculation may be added the model proposed by Cartwright & Collet (1987) for workers honeybees and concerning the construction of an album of snapshots, taken at different location within their habitat (fig. 5). The model is divided in two different stages: the first one corresponds to the Constant-Memory process "storing and recalling spatial memories" of visited locations and the second stage is linked to the path integration process when bees could associate, to each snapshot, a vector encoding the distance and the direction leading to the hive, as this happens during Volatile-Memory orientation. Bees would be then able to deduce a novel route linking two known sites where snapshots had been taken. According to this model, insects should rely on a Random-Access File orientation system rather than on a Sequential-Access File system.

Whether the orientation phenomena are explained by the use of Sequential-Access or Random-Access

Files, in both cases, mental imagery is inferred. The differences between both these hypotheses are based on the form in which the information is stored, on the nature of the reference system (self-centred or specific locations-centred) and on their operational properties.

a) Insects which use a different Sequential File for each familiar route is directly able to estimate their location in a linear process: "Snapshot of Site 1, snapshot of site 2,........., snapshot of site n-1, snapshot of the Goal (n)".

The Sequential-Access File system is based upon "en route" collected spatial information that is remembered to link one point in space to another one, in a sequentially ordered way. For instance, veteran ants marked in autumn were shown to travel on the same route in the following spring after the hibernation period (Rosengren, 1977). This means that some individuals store sequential topographic visual information of a given route system through the winter up to seven months (Rosengren & Fortelius, 1986).

A particular attention has to be focussed at the last image of the sequence of files (n), insofar as close to the goal, a direct piloting process is sufficient to describe orientation. The use of Sequential Files by insects means that their representation of spatial layout is self-centred: "the system of coordinates moves along with the navigator" (Wehner, 1983).

b) Insects which use Random-Acces Files can plan novel routes by a deductive method (model by Cartwright & Collet, 1987). Granted that two previously visited sites (Site 1 and Site 2) are independent, i.e. without possibility of direct perception from one site to the other, planning of spatial behavior may occur in such a way:

"Snapshot of Site 1 and ⇒ Home (the arrow ⇒ corresponds to the vector indicating the direction and distance to Home) and snapshot of Site 2 and ⇒ Home, from which the bees devise the new route leading Site 1 to Site 2 by vector summation (Site 1 ⇒ Site 2)".

But if the Random-Access System enables bees to plan novel route (field data by Gould, 1986), however it as to be noted that deductive rules used by honey bees could only be applied from known locations. This means that their hive-centred map (Cartwright & Collet, 1987) is a representation of a concrete space based on the association between some definite landmarks, memorized as snapshots, and the spatial information on direction and distance linking these locations to only one definite place: the hive. For these reasons, the random- access file system is not really a true cognitive map universally centred as defined below.

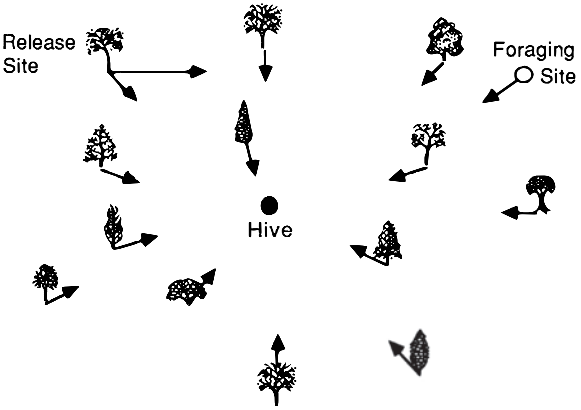


FIGURE 5. Model of spatial representation in bees by Cartwright & Collet (1987). The insect could asssociate a vector indicating the direction and distance linking the memorized image of each familiar landmark and of the food site to the hive (Tree ⇒ Hive and Food site ⇒ Hive). Performing vectorial summation Tree ⇒ Hive + Food site ⇒ Hive allows the bee to deduce the direction and distance leading from any familiar landmark to the food site (Tree Food site).

[Modelo de representación espacial de las abejas elaborado por Cartwright & Collett (1987). El insecto podría asociar un vector indicativo de la dirección y distancia que enlazara la imagen memorizada de cada señal familiar y del punto de alimentación con la colmena (Arbol ⇒ Colmena y Punto de alimentación ⇒ Colmena). La suma vectorial Arbol ⇒ Colmena + Punto de alimentación ⇒ Colmena permite a la abeja deducir la dirección y distancia desde cualquier señal conocida al punto de alimentación (Arbol ⇒ Punto de alimentación).]

c) Another spatial representation, which is not based on the reading of cartographic maps, refers to what could be an extension of the Random-Access System. This spatial representation is close to the concept of "cognitive mapping" and has not yet been demonstrated in insects. The reference is no more limited to the subject or to specific locations but from everywhere. In this case, the rules could be applied wherever the point of entry is located in the space even if not visited before (Sites x or y). However, these novels sites must be perceived from sites already visited on the area (e.g. Site x visible from Site 1 and Site y visible from Site 2). Then the subject could be able to infer new relationships and thus to plan new routes even between:

-Two independent but previously visited sites: Site 1 ⇒ Site 2 (*as with the Random-Access System*).

-A previously visited site and an independent novel site: Site 1 ⇒ Site y and Site 2 ⇒ Site x.

-Two independent novel sites: Site x ⇒ Site y.

We can compare these different types of spatial representations to some of those developed by human beings. Among them, cognitive maps, considered as pictures, could include all relations among objects within a space. Either spatial information is directly acquired by moving through the environment, very often in a sequential form and then represented in a simultaneous way, or spatial information is secondarily acquired, for instance from a cartographic map. Besides this "picture in the head" which is positioned in a specific orientation i.e. north at the top, cognitive map could also correspond to idiosyncratic "orienting schemata" that are directly acquired either by moving through the environment or by viewing it. These orienting schemata are the own persons'perspectives of the environment and their general orientation is not fixed (see Scholl, 1987 for a discussion and experiments testing these theories). The dynamic properties of orienting schemata, the fact that they are based on the direct perception of local landmarks through active locomotion and their self-centred properties intercede for more comparative studies between invertebrates and vertebrates species in this respect. As stated by Honig (1987), work on spatial orientation in bees, "indicates a general strategy which should be adapted for the study of localization in vertebrates". If an animal is captured when leaving home (H) and released after passive transport in total darkness at an unknow place (site R1 and R2) or a familiar one (R3=9) within its home range, different possibilities arise according to the type of spatial representation used (fig. 6). If orientation is only based on Volatile-Memory, either the animal gets lost and moves randomly or it starts a systematic search whatever the point of release. A Constant-Memory orientation with Sequential Access will allow the animal to find the food site by successive steps. The animal just have to recognize some familiar cues (1 to 5) as viewed from the same locations (open circles). From location 5, a directing piloting process is sufficient to guide the animal up to the food site. The return trip could be the route reversal of the outward path (6 to 8) or a new path (8 to 12) leading to home (H) as viewed from familiar locations (black circles). Consequently, the animal will move randomly if released at R1 or R2, and will reach location 10 if released at R3 (=9). A Constant- Memory orientation with Random-Access will allow the animal released at location R3 to move directly toward the food site (northwestward arrow) but not to orientate correctly from R1 or R2. An orientation based on a cognitive map as an "orientating schemata" will allow the animal to orientate correctly from R1 which can be perceived from point 2 for instance, but not from R2 which is located beyond sensory information. At last, an orientation based on a cognitive representation acquired from a cartographic map will allow an human being to move correctly from R2, only if he or she identifies some peculiar cues which existence will be known prior to the releasing (or of course if some guideposts are indicating the path leading from R2 to Home or to the Food site).

The representation should be slightly different for insects that live on a smaller home range and which must know their familiar panorama, even into details. As a matter of fact, the use of Sequential- Access Files, along some familiar routes, becomes completely unuseful in this situation. In the same way, flying insects which use a Random-Access File do not need necessarily a big "album" of snapshots because of storage capacities.

A better hypothesis would be to imagine a circular snapshot sequence, covering the whole panorama (360°), and telling the insect where it is, whatever direction it is facing. In the same way it could be a handicap for an insect to known a linear sequence of images when it has to travel in quite covered area without any view of the sky; it is certainly easier in that

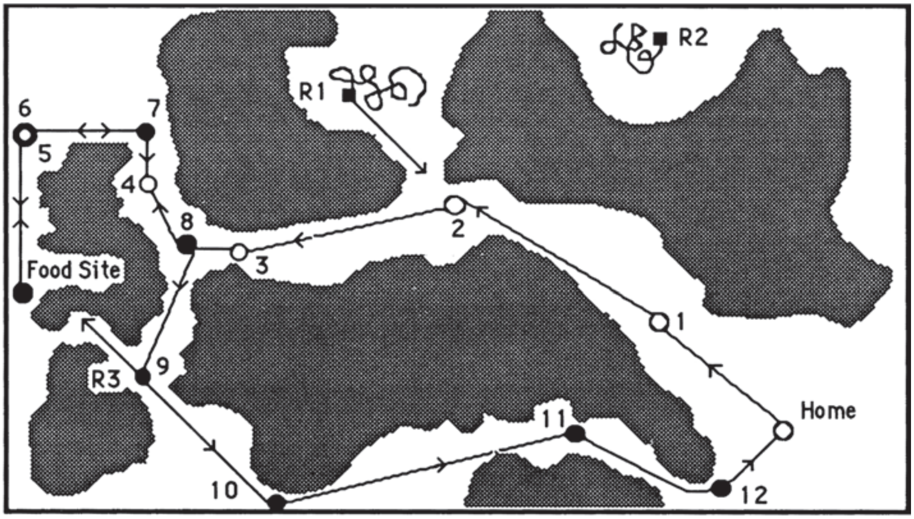


FIGURE 6. Examples of paths displayed by an animal according to its spatial representation system. The outward and inward trips link Home to the Food site. Shadowed areas indicate impassable obstacles masking all the sensory information behind them. See text for other explanations.
[Ejemplos de rutas seguidas por un animal según su sistema de representación espacial. Las excursiones de salida y entrada enlazan el Nido con el Punto de alimentación. Las zonas sombreadas representan obstáculos insalvables que enmascaran toda información sensorial tras ellos. Ver texto para mayor detalle.]

case to refer to an overall image of the canopy (Hölldobler, 1980) or to juxtaposed images allowing an accurate orientation from any point in the space. In this respect, when returning to their nest, stingless bees were shown using a "cascade of snapshots" (Zeil & Wittmann, 1986) in the following sequence: nest environment, nest box, nest entrance. In that case, the visual panorama is memorized as a Sequential File of the same fixed shot but as if it viewed as successive images of a zoom.

As far as unmoving insects are unable to detect unmoving objects (Goulet et al., 1981), one could suggest that their form of imagery does not correspond metaphorically to separated snapshots, but more to a short film. This should allow them to store both spatial and temporal information about the familiar space. As in human beings, the route-based representation of insects could be linearly and temporally organized. This means that during decision execution, the subject expects to find a definite cue at the appropriate time (Passini, 1984b). Furthermore, temporal properties of the imagery could be useful for the processes of distance estimation where treatment of the visual flowfield information is certainly necessary.

Using the concept of representation simplifies also drastically many processes of Real-Time orientation. This does not concern directly the spatial knowledge involved during Real-Time orientation, granted that "In general, one would not assert that a cognitive function is involved when the stimuli controlling the behavior are present at the time of response expression" (Ellen, 1987). Nevertheless, such a concept of representation concerns more the knowledge of the structure of the signals that are remembered prior to the display of Real-Time orientation. Whether it is an image stored within the Read-Only-Memory (Innate Releasing Patterns of the objectivist theory) or whether it is a constructed and learned image of a Constant-Memory type, in both cases, the insect use an image of the signal. Then it has to compare the actual image, perceived in Real-Time, with an internal one. The old principle of reafference provides also a cybernetical model in which such a comparison is performed by insects. This concerns the visual afferences and reafferences of *Eristalis* (von Holst & Mittelstaedt, 1950), which is not very far from the model proposed by Cartwright & Collet (1982).

2. Expectancy

The manifestation of a cognitive expectancy within the field of spatial orientation outdoors is obvious in several experiments with insects where the perceived image is not exactly what it should be. An animal experimentally exposed to such a situation exhibits a behavior which leads us to say "it occurs as if..." the animal was expecting something which does not happen. The best examples in this respect are given when the insect has been passively or actively displaced as in ants (Wehner & Wehner, 1986), in carabids (Frantsevitch et al., 1977) or in crickets (Beugnon & Campan, 1989). When the insects have travelled approximately the expected distance to the nest or the hole and find a mismatch between the perceived setting and their expectancy, they develop a new orientation strategy. Namely the insects stop running straight forward and start circling in a systematic search behavior around the place where the goal is expected to be found.

3. Intentionality

Exhibition of intention movements that are quite obvious in many vertebrates, mammals particularly, has never been extensively described in insect and should be in any case a rather difficult task; we must add to this operational difficulty the resistance of many researchers to attribute such capacities to insects. Inferring cognitive processes in general wins over as many followers as long as they concern either animals phylogenetically close to human beings, for example primates, or domestic animals and pets, unfortunately insects have none of these characteristics. However, it would be very economical to include intention and intentionally in the explanation of homing along a straight route, or in the exploratory behavior of insects looking for a prey or a food source, mainly when its localization and its nature are already known by the animal. For instance, temporal learning in bees and ants is associated with location learning. Not only bees are able to learn up to nine different locations and time per day (Koltermann, 1974 in Harrison & Breed, 1987) but they were also shown to display reactional anticipation (Beling, 1929 in Medioni, 1985). It is in the same way that after several months of hibernation, ants re-establish the previous route system leading to the same aphid colony at the same given location, as already stated, but the point is that this happens before the beginning of aphid activity in spring (Rosengren, 1977).

Complexity of the natural situations

Actually all the reported data about insect orientation in the field show that animals, when not travelling at random, use a great number of spatial information to find a nest or a hole, a shelter place, a food source, a familiar place, etc... Most of the works investigate the type of cues which are used. Such an aim leads obviously to experimental studies in which orientation behavior is modified as the result of the successive manipulation of each element of the environment, by removing or transforming it. Then, one is able to roughly predict, that changing such or such environmental variable has a given probability to induce a particular effect, i.e. the animal is able to use this particular cue. These studies have often been completed by laboratory experiments where a particular sensory modality is involved in quite similar although very much simplified situations.

In natural situations a large number of ecological or physiological variables are involved. These variables are combined with the peculiarities of the individual itself which behaves according to its own history. Then, of course, if we want to understand the activity of an animal in its own world, the proposed models lose much of their predictive value because of their relative simplicity compared to natural situations.

1. Orientation of the red wood-ant

We already know, from the pioneer work of Brun (1914), that workers of the red wood-ants of the *Formica rufa* group are guided in the field by several sensory modalities which are separately or simultaneously used. It is classically admitted that they use terrestrial and celestial cues such as the sun, the moon, or the polarized light pattern of the sky (Jander, 1957; Rosengren, 1971), that they follow chemical trails (Horstmann, 1976), that they take into account gravity and field slope information (Markl, 1964), as well as idiothetic or proprioceptive information (Cosens & Toussaint, 1985). Nevertheless, very few is known in the literature about the way in which this insect is combining all these information to assume an orientation decision, characterized by its initial orientation and the distance it has to travel.

Experiments performed in the laboratory by Fourcassié & Beugnon (1988) attempt to find out how gravity, kinesthetic, chemical and visual information are combined by the workers of a red wood ants, when exploiting a sugar food source in a three dimensional space.

The experimental device is represented in figure 7. The results show that, on the vertical axis, ants take into account simultaneously gravity, chemical and visual information. Orientation on the horizontal four-arm radial maze is mainly guided by external cues with a preference for chemical cues over visual cues in case of conflicting information between both of them.

The same device has been also used in natural conditions (Beugnon & Fourcassié, 1988). In that case, celestial cues do not play any role for guiding the insects. Orientation appears to result mainly from information given by chemical and terrestrial visual cues on the vertical pole, when gravity plays a role, as well as on the horizontal plane. When these two types of spatial information are contradictory, landmarks cues are predominant. Furthermore, idiothetic cues are only used as an additive information to make a choice at the cross-road. On the contrary, chemical trails are essential at night. The authors conclude that their results do support the idea that several categories of directional information are simultaneously used and thus reject the possibility of an absolute hierarchy of cues.

The phenomena are even more intricated for ground orientation in the field (fig. 8). The colonies belong to a polycalic society located in the middle of a spruce forest, at an elevation of 1600 m in a Pyrénées mountain range. As can be seen on the map presented on the figure, the site is cut into a west bank and an east bank by the meanders of a river; both banks are linked by a tree across the river. The main nest is located on the west side, near a group of spruce-trees. The foraging area is located on the west bank and is surrounded, in the south-west, by a mountain range which includes the highest silhouette above the horizon.

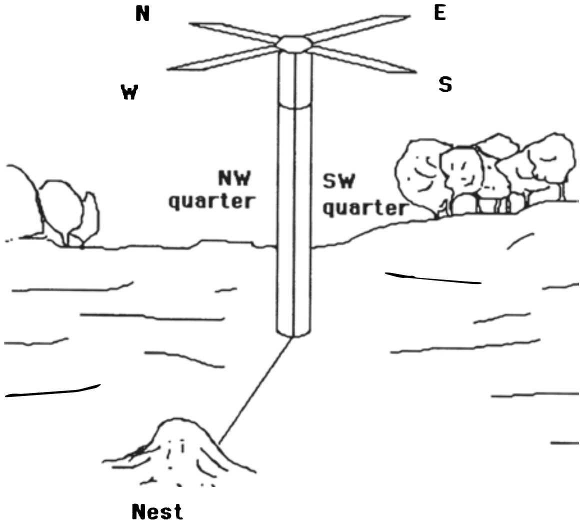


FIGURE 7. Experimental device used by Fourcassié & Beugnon (1988) and by Beugnon & Fourcassié (1988) for studying the orientation of worker ants foraging in a three-dimensional space.

[Dispositivo experimental utilizado por Fourcassié & Beugnon (1988) y por Beugnon & Fourcassié (1988) para estudiar la orientación de hormigas obreras alimentándose en un espacio tridimensional.]

Fourcassié first studied the orientation of workers captured on the cupol of the main nest and released individually on an experimental horizontal platform when all landmarks were kept visible. "Control" workers captured in an alien nest situated westward of the site, were tested in the same conditions. The result show that these workers have a clear and significant tendency to flee southwestward. It is also the case for a sample of ants captured on the main nest but released more than 20 m eastward from the nest. On the contrary if the workers are released at any place within a 20 m radius around the main nest, they flee significantly almost in every case toward the nest. Experiments hiding all or parts of the environment showed that the most effective cues seems to be the group of spruce trees located near the nest; astronomical cues were shown to play a weak role at the level of the population but some individual seem however able to use them. These results have to be compared with the data of Wehner & Menzel (1969) on *Cataglyphis* which show that workers prefer to be guided by terrestrial cues as long as possible and use astronomical information only when the terrestrial cues are missing or when they indicate a wrong direction.

Workers collected on the trails, whichever the direction they were following, home significantly to the main nest when they have been captured on a trail directly issued from it. On the contrary, initial directions are different when they are colected travelling on secondary trails linking secondary nests usually seasonally occupied. The social function of the nest within the polycalic colony from which they are coming is likely to be associated with the prevalence of the orientating cues.

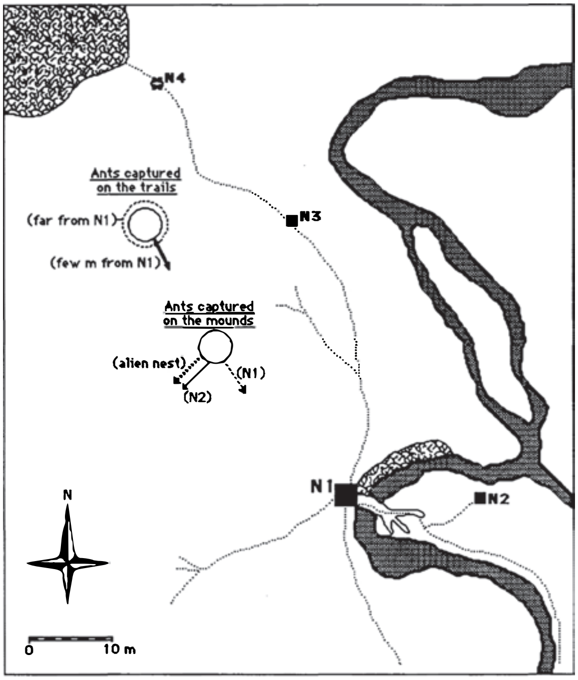


FIGURE 8. Map of the *Formica* colony studied by Fourcassié (1985-1986). Main results of experiments in which animals are captured either at the nest or on the trail and released on an orientation platform, with all the cues kept visible.

[Mapa de la colonia de *Formica* estudiado por Fourcassié (1985-1986). Resultados más importantes de los experimentos en los que los animales son capturados en el nido o en ruta y liberados en una plataforma de orientación, con todas las señales a la vista.]

Rosengren & Fortelius (1986), reporting experiments performed during several years, also report the complexity of the phenomena in the field and stress the difficulty to disentangle them. These authors have studied route fidelity and site allegiance in red-wood ants. They demonstrated that, after seven months of hibernation under the snow, foragers still exhibited a route fidelity and an allegiance to the site they exploited during the previous autumn. This work also demonstrates that kinesthetic information that the insects may gather while living in a particular portion of the cupol of the nest are not involved in the process of route fidelity after wintering. In order to guide their movements on the trail, ants mainly rely on their Constant-Memory of the terrestrial cues given by the canopy above the nest. Disturbances of the magnetic field do not impair their orientation and their route fidelity. Astronomical orientation, when playing a role, is poorly effective and the visual terrestrial cues remain predominant because they provide more faithfull and less variable information.

The results of Fourcassié (1985-1986) as well as those provided by Rosengren & Fortelius (1986) show that if the orientation is rather clear cut, obvious and significant, at the population level or at least at the sample level, the individual variability between the samples as well as between the individuals is very large. "It occurs as if..." each worker, by taking into account many particular variables such diverse as the familiarity with the site or the social function of the nest they are coming from, the instant, the faithfullness and the constancy of the cues, etc... weights the various information that it is able to use before assuming a given orientation direction. No predictive models proposed in the literature allow us to know how such a weighting is achieved, even if each particular experiment can be associated with one type of the spatial memory proposed above with all their inferred cognitive variables.

2. The wood - cricket orientation (*Nemobius sylvestris*)

A second example illustrating the complexity of the natural world deals with the field orientation in the wood-cricket. We will not report here the whole corpus of data collected since 25 years about this cricket species which is widespread in the forests of the temperature world. All these data are reported in Campan et al. (1987); thus we will only comment the synthetic and theoretical last picture of this paper (fig. 9). It shows how each "individual - own world" system builds its own orientation system. Of course the limiting frame of the physiological conditions particular to the species, the ecological conditions particular to the site where each cricket is dwelling and its hereditary characteristics are so many constraints assigned to each individual and to which it is forced to cope. At the end of its embryogeny, when hatching, the young cricket has at its disposal a set of simple taxic tendencies, which are fixing some rules for the exploration of the world and the learning of its spatial and temporal organization: scototaxis, phototaxis, geotaxis, and probably some others we have not yet investigated. Through its progressive familiarization with its world, each individual will transpose these tendencies to the main characteristics of its actual world, such as the visual panorama (pattern of the canopy, distribution of the tree trunks, forest borders and clearings, astronomical cues, sun azimuth, slope, main winds directions, odors distribution, etc...). It builds up its own complex image of the site which has of course common also contains particular information associated with its own individual experience.

Conclusion

If we put aside the three parts of this paper, we are able to associate the various steps of the insect ontogeny to the various kind of spatial memories that we have described.

The Read-Only-Memory orientation corresponds mostly to the information included within the genotype which generates, at hatching, the various basic components regulating insect orientation that will occur in the field.

As early as it is able to build up its own individual experience, each individual, as shown in the wood-cricket species, stores the knowledge it acquires about its home range in a Constant-Memory form. This is progressively realized through processes of associative learning. When insects are subject to predation while they are performing spatial orientation, learning processes have a high survival value, their duration of acquisition is generally short as it is riverine crickets which can learn a new direction in a single trial. By contrast, in the course of their spontaneous daily to and fro migrations, some crickets may associate the direction of a familiar forest border with its astronomical direction by use of visual and/or gravity information, this learning process may last several weeks before being truly effective.

One can safely consider that in every oriented behavioral event, as during search for food located in an unpredictable location, i.e. for living preys, a Volatile-Memory is certainly operating, sometimes as a subtle preparation to an information of the Constant-Memory type. This has been already suggested for *Pteronemobius* species and hypothetized from the work by Cartwright & Collet (1987) in their model of landmark maps for

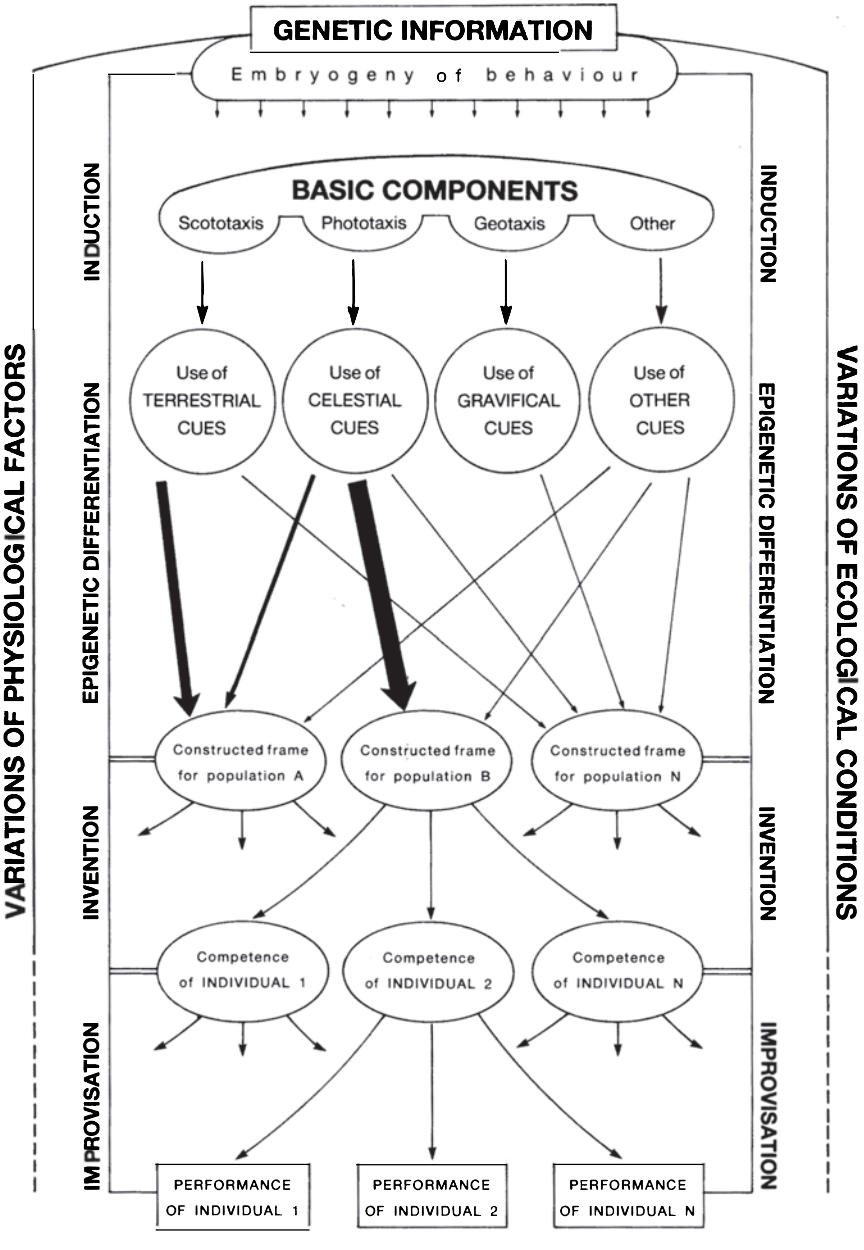


FIGURE 9. Schematic drawing showing the ontogenetic development of spatial orientation in *Nemobius sylvestris* as an example of the construction of an autonomous system constituted by each developping "individual insect - own world" (from Campan et al., 1987).

[Dibujo esquemático que muestra el desarrollo ontogenético de la orientación espacial de *Nemobius sylvestris* a modo de ejemplo de construcción de un sistema autónomo constituido desarrollando cada "individuo insecto - mundo propio" (de Campan et al., 1987).]

honeybees. Such flying insects are able to use the Random-Access File orientation system allowing them to plan novel routes in their familiar area as vertebrate are able to do with the help of a cognitive map (Gould, 1986). Finally, Real-Time orientation is involved in the execution of every movement within the natural environment.

When we take into account the whole complexity of the natural environment, "All occurs as if" the ontogenetical dynamic of each individual, was punctuated by mnesic and cognitive operations complementing each other. Environmental and genetic constraints (Read-Only Memory) as well as cognitive processes (Volatile and Constant-memory systems) thus appear as major mechanisms in the auto-organization of the biological system constituted by each developping individual insect and its own world. Such a model fits in with the general characteristics of the autonomous self-organizing systems. Although it has not a true predictive value, except at the level of the population or at the level of a sample of this population, it presents a true heuristic value because it is able to explain the diversity between individuals as well as between populations, which is always quite obvious in field insect orientation.

Resumen

Recuerdos espaciales y percepción en los insectos.

En principio, proponemos clasificar los distintos tipos de memoria espacial susceptibles de intervenir en los fenómenos de orientación espacial de los insectos:

1) La "Read-Only Memory" es una memoria dependiente de un control genético fuerte.

2) La "Volatile-Memory" permite la adquisición, el almacenamiento y la utilización de la información espacial, en términos de direcciones y distancias. Es sólamente funcional durante la realización del desplazamiento y "reinicializada" al final de este trayecto (fig. 1).

3) La "Constant-Memory" es una memoria espacial almacenada de manera duradera para cada individuo; puede ser modificada, completada o transformada a lo largo de la vida. Pueden distinguirse dos tipos de "Constant-Memory" considerando sus modos de adquisición y utilización. Se puede considerar como fichero secuencial de memorias visuales (Sequential-Access Orientation Memory) permitiendo desplazamientos lineales secuenciales, o como ficheros de acceso directo (Random-Access Orientation Memory) que permiten el establecimiento de nuevos caminos entre puntos conocidos del espacio.

A partir de esta clasificación podemos inferir capacidades cognitivas en los insectos, particularmente en lo que concierne a las posibilidades de representaciones mentales autocentradas y allocentradas.

Por último, discutimos la implicación de estos procesos mnésicos y cognitivos en la orientación espacial de los insectos tal como pueden aparecer en la complejidad del medio natural (fig. 7).

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