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ORIENTATION CUES USED BY ANTS

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SUMMARY

The cues used for orientation during homing were examined in ants from 3 subfamilies, i.e. *Atta laevigata, Acromyrmex octospinosus, Acromyrmex rugosus, Trachymyrmex urichi; Ectatomma ruidum* and *Pseudomyrmex termitarius,* by means of a Y-maze experiment. The results showed that ants use various cues for orientation through a maze. For each ant species, the cues may be classified in a kind of species-specific hierarchy according to their importance during homing. In addition to visual and chemical orientation, empirical evidence supporting the existence of a topochemical is presented. *P. termitarius* uses a kinesthetic sense for orientation. Learning of the cues in the laboratory is not directly related to the respective hierarchy used for orientation through a maze by each species, but seems to be inversely correlated with the social complexity of the species. The number of cues used for orientation correlates directly with the social complexity of the species. A divergent evolutionary development of orientation strategies, even among closely related species, is proposed.

RESUME

Modalités d'orientation utilisées par les fourmis

Les modalités d'orientation utilisées dans le retour au nid sont étudiées au moyen de labyrinthes en Y dans 3 sous-familles de fourmis : *Atta laevigata, Acromyrmex octospinosus, Acromyrmex rugosus, Trachymyrmex urichi, Ectatomma ruidum* et *Pseudomyrmex termitarius.* Les résultats montrent que les insectes utilisent plusieurs stratégies pour s'orienter dans le labyrinthe. Pour chaque espèce, les différentes modalités sont classées par ordre d'importance dans leur utilisation lors du retour au nid. Outre les repères visuels et chimiques, apparaît l'existence d'une orientation topochimique. *P. termitarius* utilise dans son orientation un sens kinesthétique. L'apprentissage des repères par la fourmi au laboratoire n'est pas en relation directe avec la hiérarchie des modalités d'orientation utilisées par chaque espèce dans le labyrinthe et apparaît en corrélation inverse avec la complexité sociale des espèces ; le nombre de repères utilisés augmente par contre avec le degré évolutif de l'insecte. Une évolution divergente de ces stratégies d'orientation, même dans des espèces proches phylogénétiquement, est proposée.

INTRODUCTION

Orientation in an heterogeneous environment is one of the basic survival problems most animals have to resolve. What were the cues used ? How many cues are used for orientation ? Do different orientation mechanisms exist ? Do optimal orientation systems exist ? Do some features of the orientation systems of animals from different phyla converge in evolution ?

In order to answer some of these questions, the cues used for orientation by foraging ant workers were studied. Ants were chosen as a model, because of their diverse foraging habits, their diverse social systems and their known orientation abilites.

Orientation in ants is thought to be regulated mainly through odor trails and visual cues (VOWLES, 1950 ; CARTHY, 1951 ; JANDER, 1963 ; WILSON, 1971 ; DUMPERT, 1978 ; JAFFE and HOWSE, 1979 ; HÖLLDOBLER, 1980 ; WEHNER, 1982 for example) although naturalists of the last century and beginning of this century hinted to various different orientation mechanisms in ants (BETHE, 1898 ; PIERON, 1904 ; FOREL, 1928). Few experimental works showed the use of cues different from visual signals and trail following. Exemples are known for the use of tactile stimuli during orientation in Ecitoninae (TOPOFF and LAWSON, 1979 ; SCHONE, 1984) and gravity stimuli in different ant species (VOWLES, 1954 ; JAFFE, 1980 ; VILELA *et al.*, 1987). Maze learning has been reported for *Formica pallidefulva* and *Formica rufa* (SCHNEIRLA, 1953 ; BERNSTEIN and BERNSTEIN, 1969), although without any regard to the orientational stimuli involved. Recent work showed that ants use many different cues in a kind of hierarchy for orientation (JAFFE, 1980 ; VILELA *et al.*, 1987).

This work explores some of the cues possibly used for orientation in the Myrmicinae from the tribe Attini *Atta laevigata* (Fr. Smith), *Acromyrmex octospinosus* (Reich), *Acromyrmex rugosus* (Fr. Smith) and *Trachymyrmex urichi* Forel ; in the Ponerinae *Ectatomma ruidum* Roger and in the Pseudomyrmecine *Pseudomyrmex termitarius* (Fr. Smith).

MATERIALS AND METHODS

Insects

Queenright ant colonies were collected in the field and kept in the laboratory at 28 ± 2° C and 70 to 80 % RH. Colonies were illuminated with neon lights for 12 h per day and were kept for at least 5 weeks before using them in experiments

Fifteen *Ectatomma ruidum* and 12 *Pseudomyrmex termitarius* colonies were collected at Sartenejas, Estado Miranda ; 6 colonies of *Acromyrmex* c.f. *rugosus* at La Cortada del Guayabo, Estado Miranda ; 4 of *Acromyrmex octospinosus* at Barlovento, Estado Miranda, 4 *Atta laevigata* colonies at Chaguaramas, Estado Monagas ; and 9 *Trachymyrmex urichi* colonies at Cagua, Estado Aragua, Venezuela.

General observations

All colonies used had mature nests, with sizes on the maximal range found in the field (*table II*) except *Atta laevigata* where we used a two year old colony with approximately 50,000 workers. Colonies in the field were observed during 30 min periods at different hours.

Laboratory experiments were performed once the colonies had been acclimated in the laboratory, the daily foraging activity cycle of the colonies was studied using a video system which helped to count the total number of workers in the foraging arena (F on *fig. 2*) each 30 min during a 24 h period.

The maze

The maze consisted of three transparent plastic tubes (*fig. 1*) connected to a paper pentahedron so as to maintain an angle of 120° between the arms. At the end of each arm a paper beaker was connected and covered with a plastic foil.

Orientation experiments

One end of the maze was connected to the foraging arena of the respective colony (system I, *fig. 2*) until one exploring worker reached one of the beakers (B1 or B2, *fig. 2*) at the two arms of the maze. Then the beaker with the ant was disconnected from the

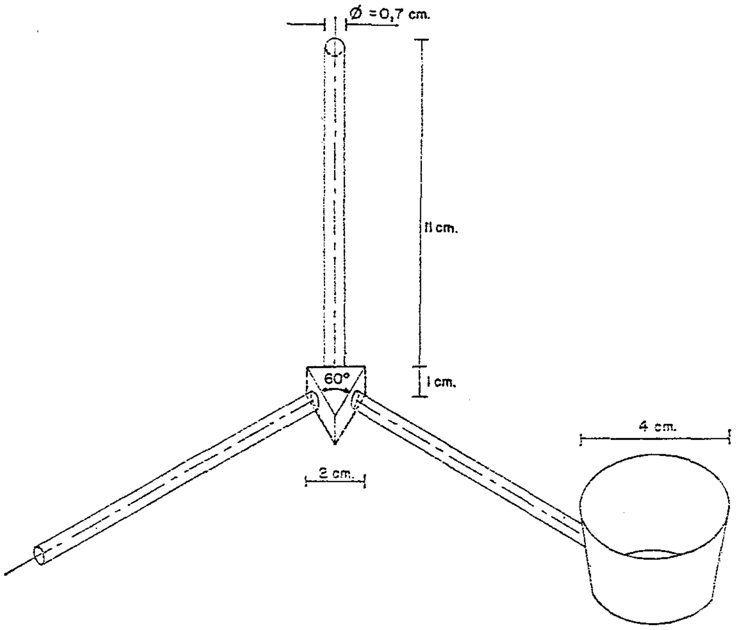

Fig. 1. — Y-shaped maze showing plastic tubes held together by an paper pentahedron. Only one paper beaker at the end of an arm is indicated.

Fig. 1. — Labyrinthe en Y montrant les tubes de plastique maintenus par un pentahèdre de papier. Seul un gobelet de papier est représenté à l'extrémité d'un bras du labyrinthe.

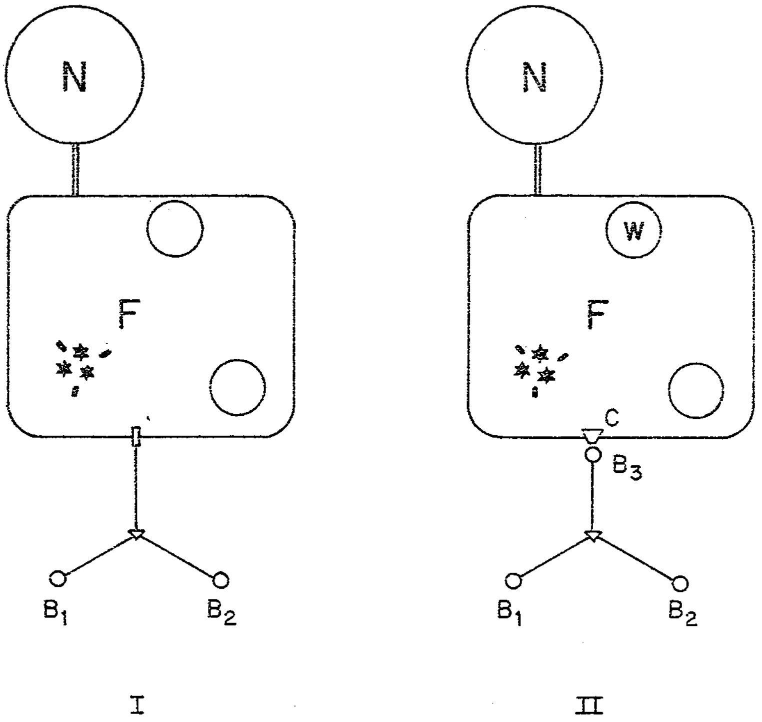

Fig. 2. — Design of the experimental layout, indicating the position of the ant nest (N), the foraging arena (F), water source (W), maze with paper beakers (B1, B2, B3), and cork (C) closing the exit from the foraging arena in sustem II.

Fig. 2. — Dispositif expérimental indiquant les positions respectives du nid (N), de l'aire de fourragement (F), de l'abreuvoir (W), du labyrinthe avec ses gobelets de papier (B1, B2, B3) et du bouchon (C) obturant la sortie de l'aire de fourragement dans le système II.

maze and the maze was disconnected from the foraging arena of the nest (system II, *fig. 2*). The exits from the foraging arena and from the beaker were then sealed with a cork (C). For the test, either the same or a new maze was placed in the corresponding position with beakers connected to its 3 arms. The arm formerly connected to the nest was then placed as close as possible to its former position but leading to an empty beaker (B3). The ant was left in its beaker for 30 min before connecting it to the corresponding arm of the maze. Preliminary experiments with the 6 species had shown that after a minimum of 30 min of isolation, workers walked preferentially toward the nest when released on the foraging arena of its colony.

After the beaker with the ant (either B1 or B2) was reconnected to the corresponding position of the maze, the time taken by the worker, from the moment it exited the beaker and entered the maze to the moment it exited from one of the arms into one of the two remaining beakers, was noted. Each ant was tested only once and thus was sacrificed after the test.

The experimental conditions prevailing during the test were a combination of the situations (on/off/inverted) for three types of orientation cues, as described below :

Visual cues present (V+)

The maximum amount of light was made available, i.e. neon lights illuminated the laboratory and the maze was not covered. These cues refer to any visually perceived signal coming from inside or outside the maze. These may include the use of visually perceived landmarks, orientation using the position of light sources, shadows, polarized light from uncontrolled sunlight or from refectations of plastic or glass objects.

Visual cues absent (Vo)

Illumination was reduced to a minimum by covering the maze with aluminum foil, placing a carton box over it and using red light in the laboratory during the experiment.

Odor cues present (O+)

The maze previously explored by the trapped worker was used for the test. These stimuli refer to all chemical and tactile signals present inside the maze. The odors (tactile inputs or tastes) inside the maze could be due to trails or odor spots deposited by the exploring ant, or to odor, tactile inputs or taste differences due to chemical asymmetries between the arms of the maze caused by minor imperfections in the construction of the labyrinth.

Odor cues absent (Oo)

A new maze, similar to the one previously explored by the captured worker, was used for the test. Here, the ant had no possibility of using any previously memorized chemical marks or specific odor characteristics of the arms of the maze.

Directional cues present (D+)

The spatial layout of the maze was maintained unchanged. The ant was released into the same arm where it was captured. (For example, if the ant was captured in B1, system I, *fig. 2,* it was released in B1 of system II). These cues refer to all types of signals which are affected by a change in the spatial layout of the maze. In addition to chemical, visual and other physical signals, dependent on spatial relations, other mnemotactic mechanisms might function as orientation cues. For example, an internal model of the environment constructed or memorized by the ant so that it can orient its movements with reference to its own body will be misleading if the spatial layout of the maze is changed. These cues refer to a kind of left-right memory by which the ant remembers which direction it has to turn in order to find the nest.

Directional cues inverted (D—)

The spatial layout of the maze-ant system was changed by releasing the ant into the alternative arm. (For example if the ant was captured in B1, system I, *fig. 2,* it was released in B2, system II, by exchanging the beakers).

Results were expressed as the mean with its standard deviation of the time taken to exit the maze ; and as the percentage of ants exiting at the arm of the maze which led into the direction of the nest entering B3 (*fig. 2*), i.e. % of ants homing "correctly".

Learning experiments

The maze was connected to 3 empty beakers (system II, *fig. 2*). A worker from the foraging area of the colony was picked up with plastic forceps, marked with a spot of paint on its gaster or thorax, was isolated for 30 min in a beaker, and was then released into beakers B1 or B2 (system II, *fig. 2*). If the ant exited into B3, it was released into its colony by placing the beaker horizontally on the foraging arena of the colony and the worker was left in its colony for at least 2 hours. If the ant exited the other arm of the maze, it was isolated again in the beaker for 5 min and released into the same arm as the first time by interchanging the beakers. This procedure was repeated until the ant found B3. This constituted a learning trail which was repeated for at least 3 times, always using a new maze. The time taken by the ant to exit the maze and the arm it exited was noted as described before.

Statistics

All tests were performed using the statistical package SPSS-University of Pittsburgh. The foraging rhythm was analyzed with a one way ANOVA and so was the duration of learning trails. The effect of the independent variables V, O and D on the duration of maze-running was analyzed with a three-way ANOVA. Student's t-test showed specific differences among means. Frequencies of correct homing, i.e. percentage of ants homing correctly, were compared with a 50 % random outcome using the binomial test. Data for each species was analyzed separately.

RESULTS

General observations

Our field observations, confirmed by laboratory experiments reported on *table I* showed that the 6 terrestrial species studied had different foraging and exploration habits. The Attini (*T urichi, A. octospinosus, A. rugosus, A. laevigata*) had mainly nocturnal foraging habits although *A. octospinosus* and *A. laevigata* foraged mainly around sunset and sunrise. *E. ruidum* foraged more or less uniformly during the whole 24 h cycle whereas *P. termitarius* foraged mainly at mid-day. During cloudy days, fild colonies of *P. termitarius* reduced their foraging activity during the day, whereas those of *A. laevigata* increased it.

P. termitarius seemed to be the least efficient navigator in the field. We seldom saw a worker walking straight back to the nest entrance after collecting a termite worker placed next to it during its exploratory trip. Instead workers rather approached the nest using an irregular and tortuous path. All Attine workers navigated straight back to the nest after an exploratory trip in the field, even in the absence of trails (see also Jaffe *et al.*, 1979). *E. ruidum* workers seemed to be more unpredictable as both of the above described behaviors were seen in this species. Species of *Atta* and *Acromyrmex* seemed to be strongly dependent on trails in the field as all nests studied showed conspicuous trunk trail systems (see *table II*).

Table II summarizes some features related to nest structure and social complexity of the species studied. The species selected for this study varied enormously in complexity of nest structure and size of mature colonies.

Table I. — Daily foraging activity rhythm of the ant species studied. Percentage of the maximum number of foraging workers observed are given. Mata are means from 6 replicate observations.

Tableau I. — Rythme journalier de l'activité de récolte des espèces étudiées. Pourcentage du nombre maximum d'ouvrières récolteuses observées. Les données résultent de 6 observations.

	Daytime			/	Night				ANOVA
Hour :	6	9	12	15	18	21	24	3	6	P
Species :										
P. termitarius	25	44	100	61	62	42	16	4	25	< 0.01
E. ruidum	80	100	94	76	95	96	87	82	80	> 0.1
T. urichi	19	36	11	44	100	69	80	99	19	< 0.01
A. octospinosus	84	77	15	18	100	65	40	46	84	< 0.05
A. rugosus	100	17	23	9	59	64	62	75	100	< 0.05
A. laevigata	81	68	39	37	100	94	50	42	81	< 0.05

Table II. — General characteristics of adult colonies of the ant species studied (Personal observations over a period of 15 years of field work).

Tableau II. — Caractéristiques générales des colonies adultes des espèces étudiées (observations personnelles sur une période de 15 ans de travail de terrain).

Species	Colony size Nr of individual	Trail system	Nest	
			Nr of entrances	Nr of chambers
P. termitarius	0.5—2×10^2	no trails	1	1
E. ruidum	0.5—2×10^2	no trails	1	1—2
T. urichi	10^2 — 10^3	rudimentary trails	1—2	3—5
A. rugosus	10^4 — 10^5	trunk-trails	> 5	1—5
A. octospinosus	10^4 — 10^5	trunk-trail	> 5	5—20
A. laevigata	10^6 — 10^7	complex trails	> 20	> 100

The general impression of the observers was that the foraging behavior of the ants, acclimated to the laboratory, resembled those observed in the field. No behavior of the ant colonies, if compared to field colonies, indicated that flickering of the neon lights affected their exploration and foraging behavior.

Orientation cues

Table III shows the percentage of ants homing correctly in laboratory experiments for each experimental situation. From these results we may

Table III. — Percentage of workers homing correctly in the maze in the presence (+) or absence (o) of visual (V) and olfactory (O) cues with normal (+) or inverted (—) directional (D) cues.

Tableau III. — Pourcentage d'ouvrières s'orientant correctement pour retourner au nid en présence (+) ou absence (o) de repères visuels (V) et chimiques (O) avec un repérage directionnel (D) normal (+) ou inverse (—).

Experiment	1	2	3	4	5	6	7	8
V	+	o	+	o	+	o	+	o
O	+	+	o	o	+	+	o	o
D	+	+	+	+	—	—	—	—
Atta laevigata	100 **	75 *	63 *	45	65	65	80 **	55
Acromyrmex octospinosus	94 **	64 *	69 *	48	84 **	68 *	62	44
Acromyrmex rugosus	75 *	80 **	80 **	40	65	70 *	60	55
Trachymyrmex urichi	90 **	68 *	60	54	80 **	87 **	/	/
Ectatoma ruidum	85 **	35	72 *	/	80 **	60	80 **	/
Pseudomyrmex termitarius	74 *	75 *	81 **	/	22 **	29 *	22 **	27 *

* and ** indicate $p < 0.05$ and < 0.01 respectively, if the number of ants homing correctly is compared with a random binomial distribution (i.e. 50 % correct homing).
Sample = 20 for each percentage.

deduce the orientation cues used by each species by comparing two experimental situations differing only in the form of presentation of one of the three groups of orientation cues (V, O, D). Thus, we have 4 different comparisons to test each of the orientation cues. One of these comparisons is to the control situation, where all possible orientation cues available in the laboratory are present (column 1 in *table III*). If one of these comparisons showed different percentages of ants homing, we concluded retrospectively, that the factor whose absence affected the orientation ability or the motivation for homing of the respective workers, was at least partially responsible for the orientation abilities evidenced when it was available to the homing worker.

The analysis of the data revealed that all species tested were able to home corectly when light, olfactory and directional cues were present simultaneously (column 1, *table III*). That is, the majority of the workers tested exited the maze, so as to enter the foraging arena of the colony, if the maze had not been disconnected. Light seemed to be of primary importance for *E. ruidum* as they homed randomly in the absence of it (column 2). Homing in a new maze disoriented only *T. urichi* if light cues were available for orientation (column 3), but most species got disoriented in a new maze in the dark (column 4). *E. ruidum* was not tested in the dark with a new maze but was unable to home correctly even in an familiar maze in the dark (column 2).

Directional cues seemed to be of primary importance for *P. termitarius.* In all experimental situations where the directional cues were inverted, irrespective of the presence or absence of other cues (colums 5-8, *table III*), workers homed incorrectly and exited preferentially (statistically significant) the arm of the maze where the nest would have been, if changes in the position of the ant relative to the nest are ignored.

A. laevigata also depended on directional cues, as we could note that workers were unable to home in the inverted original maze (column 6) and could home only in the presence of light in a new maze (column 7). In the absence of light and olfactory cues, workers orientated at random (column 4 and 8). Also *A. rugosus* seemed to be affected by the inversion of the directional cues (column 6 vs 5, 7, 8).

Table IV gives the times taken by worker ants when homing through the maze. These varied between 120 and 1510 s. Except for *A. octospinosus* we observed in all cases a significant switch to exploratory behavior, i.e. a significant increase in the time taken to cross the maze when some of the cues were missing. The results of the 3 way analysis of variance for each species

Table IV. — Time (mean (SD) in s × 10) taken to exit theY maze under the same experimental conditions os in *Table III.* The probability of each of the three independent variables explaining variability, calculated with a 3 way analysis of variance, is given under ANOVA (* indicate $p < 0.05$; $n > 20$).

Tableau IV. — Temps (en s × 10) utilisé par les ouvrières pour sortir du labyrinthe en Y dans les mêmes conditions expérimentales que celles décrites au *tableau III.* La probabilité de produire la variation observée est calculée pour chacune des 3 variables indépendantes avec l'analyse de variance à 3 dimensions et est donnée par ANOVA (* indique $p < 0,05$; $n > 20$).

Experiment		1	2	3	4	5	6	7	8	
Experimental	V	+	o	+	o	+	o	+	o	
condition	O	+	+	o	o	+	+	o	o	ANOVA
	D	+	+	+	+	—	—	—	—	V O D
Atta		18	86	61	122	108	97	55	151	* * *
laevigata		(10)	(69)	(67)	(74)	(70)	(71)	(45)	(61)	
Acromyrmex		60	54	45	64	54	38	44	52	— — —
octospinosus		(10)	(74)	(30)	(69)	(47)	(24)	(38)	(44)	
Acromyrmex		59	89	34	91	12	57	61	117	* * —
rugosus		(71)	(69)	(51)	(93)	(15)	(65)	(51)	(84)	
Trachymyrmex		57	49	87	73	52	86	/	/	— * —
urichi		(63)	(35)	(46)	(52)	(37)	(48)			
Ectatomma		21	27	33	/	19	31	27	/	* * —
ruidum		(22)	(31)	(35)		(23)	(39)	(41)		
Pseudomyrmex		97	91	97	/	109	90	95	95	— — *
termitarius		(28)	(29)	(31)		(51)	(27)	(56)	(55)	

(ANOVA in *table IV*) confirmed that for *A. laevigata* all three type of cues significantly affected homing; for *A. rugosus* and *E. ruidum*, olfactory and visual cues affected homing significantly; olfaction alone seemed to affect homing in *T. urichi*; and for *P. termitarius*, the directional cues were the only ones which affected homing. Results for *A. octospinosus* were not statistically significant.

If data from *table III and IV* are considered together we find that among the group of cues tested, *P. termitarius* uses only directional cues (excluding those based on visual and olfactory stimuli) for orientation; *E. ruidum* uses mainly visual cues, but is also affected, although to a smaller extent, by changes in olfactory cues; *T. urichi* uses mainly olfactory cues for orientation and seems to be affected by visual stimuli only to a small extent. The *Acromyrmex* species use the three type of cues tested for orientation, with olfactory cues as the most important ones followed by the visual cues. *A. laevigata* seems to rely mainly on visual cues, followed by olfactory cues and then by directional ones.

Table V. — Percentage of ants homing correctly (%) and time taken to home (t: mean ± sd in s × 10) for each of three consecutive learning sessions (i.e. learning trails). Experimental conditions were: V+, Oo, D+, with the two exceptions indicated.

Tableau V. — Pourcentage de fourmis retournant correctement au nid (%) et temps utilisé pour chacune des 3 sessions consécutives d'apprentissage (t, s × 10). Les conditions expérimentales sont: V+, Oo, D+, avec les 2 exceptions indiquées.

Trail		1	P 1 vs 2	2	P 2 vs 3	3	P 1 vs 3
Pseudomyrmex	%	40		67		40	
termitarius	t	175 ± 193	—*—	92 ± 8	—*—	156 ± 162	
Ectatomma	%	40		40		75	
rudium	t	24 ± 23		19 ± 15		19 ± 15	—*—
Trachymyrmex	%	37		58		81	
urichi	t	13 ± 11		12 ± 10	—*—	9 ± 5	—*—
Acromyrmex	%	45		70		60	
rugosus	t	88 ± 65	—*—	141 ± 124		144 ± 138	—*—
Acromyrmex	%	55		55		65	
rugosus (Vo)	t	150 ± 122		123 ± 75		143 ± 108	
Acromyrmex	%	43		39		61	
octospinosus	t	3 ± 2		3 ± 3	—*—	2 ± 1	—*—
Atta	%	30		40		80	
laevigata	t	197 ± 149		242 ± 158	—*—	163 ± 61	
Atta (Vo)	%	40		35		60	
laevigata	t	206 ± 184		206 ± 184	—*—	132 ± 43	—*—

—*— indicate significant differences of the means of t between the indicated trails ($p < 0.05$, Students t-test).

The underlined percentages differ statistically from a random binomial distribution ($p < 0.05$, Sample size = 20 replicates for each mean).

The way *Acromyrmex* and *Atta* use olfactory cues is different (columns 6-7, *table III*). For *Atta*, changes in directionality affect homing in old mazes, not so for *Acromyrmex* which find their nest in old mazes even if released from a different arm.

Learning during orientation

Table V summarizes the results of the learning tests. We noted that *P. termitarius* was the only species showing a significant reduction of the homing time at the second learning trail, although at the third trail workers seemed to switch to exploratory behavior as the time spent in the maze increased significantly. Reduction of the homing time at the third learning trail was shown by *E. ruidum, T. urichi, A. octospinosus* and *A. laevigata*, but only *E. ruidum, T. urichi* and *A. laevigata* reached statistically significant correct homing tendencies at the third learning trail. *A. rugosus* did not seem to learn under these conditions but seemed to increase its tendency toward exploratory behavior.

Only in the presence of light did *A. laevigata* reached percentages of ants homing correctly significantly different to chance levels. *A. rugosus* appeared to switch faster to exploratory behavior if maximum illumination was provided, apparently because under these conditions, ants homed faster during the first trail (*table V*).

DISCUSSION

Our behavioral observations only allows to conclude about the physiological capabilities of these insects in using certain cues for orientation. Thus, we do not want to speculate about the possible ecological and biological significance of the results, as they are based on behavior in a possibly "unnatural" situation.

The results however allow to conclude as to the importance of specific cues among the group of cues we tested. The nature of the effect is though unclear. Ants could either become disoriented and thus home incorrectly or they could switch their motivation and for example engage in exploratory behavior instead of homing. Both situations could explain a change in the time ants spent in the labyrinth or a change in the proportion of ants exiting a specific arm of the maze. In spite of this, the experiments performed show clearly that all species are able to home correctly when all our controlled orientation cues are provided, indicating that under the experimental situation designed ants showed orientation abilities and motivation for homing.

The expermental design allows to separate four groups of orientation cues, i.e. visual, olfactory, directional and others. "Other cues" are those which were not specifically tested for in these experiments such as environmental odors outside the maze or the earths magnetic field.

The use of visual cues

Our findings confirm earlier ones (VILELA *et al.*, 1987) with Attine ants which showed that visual cues are used by these ants for orientation. The amazing fact is that *P. termitarius*, the completely diurnal species, is not dependent on visual cues under the circumstances tested.

The use of chemical cues or the possible existence of a topochemical sense

All species tested, except *P. termitarius*, rely on chemical cues for their orientation. The nature of these cues is not clear although it is improbable that exploring workers lay odor trails, as the route taken for homing in a natural situation is generally not the same as that made during exploration. In *Atta* and *Acromyrmex* spp (JAFFE and HOWSE, 1979 ; JAFFE, 1983) for example exploring foragers home using the shortest route, shortcutting the route made during exploration. Thus, the orientation behavior observed for *A. laevigata, A. octospinosus A. rugosus* and *T. urichi* could be explained through the existence of a kind of topochemical sense (in the sense of FOREL, 1928). That is, "ants orientate by memorizing features of the natural odor environment produced by all the animate and inanimate objects present". This sense would allow the ant to detect a three or four dimensional odor environment and thus would suffice for orientating. We have to assume thus that inside the maze the ants are able to detect small heterogeneitys of the plastic tubes, due to slightly different chemical composition or chemicals absorbed onto the surface.

Our results present some empirical evidence as to the existence of a topochemical sense. We showed that workers find their way home through the maze in the absence of visual cues, even when ants were released into a different arm of the maze to that they had explored before (columns 5 vs 7, 5 vs 6 and 6 vs 8 in *table III*). If ants were following a self-laid trail with no specific polarity, we would expect them to exit any of the arms with a trail, i.e., the workers should make incorrect choices in tests from column 5 and 6 (*table III*), although in column 5, an orientation based on visual cues is still possible and ants could rely on them to make their choice. Our results indicate correct homing in those circumstances, except for *P. termitarius.*

Other cues which could explain the behavior discussed above are : A topotactile sense, by which ants use physical characteristics of the surface of objects in the environment to orient (TOPOFF and LAWSON, 1979). This sense would be identical to a topochemical sense except that in the later objects are perceived at a distance, without directly touching them, through the chemicals they emanate. Thus, if we accept the broad meaning of "chemical", i.e. "material substance", both senses may be called topochemical. Another possibility is the use of the earth's magnetic field. Results of earlier work with Attines exclude this last possibility and support the use of a topochemical sense by these ants (JAFFE, 1980 ; VILELA *et al.*, 1987).

Chemical marks, placed at the entrance of the maze by the exploring worker, could also explain the behavior observed. Also, polarized trails, indicating the direction in which they were deposited, could be possible orientational elements which are indistinguishable from a topochemical sense in our experimental situation. The lack of coincidence between the exploratory path and that taken by the same worker when homing in a natural situation (see discussion above), make these explanations unrealistic, although they can not be excluded as our experiments were quite "unnatural". In conclusion, the most satisfactory explanation of the results discussed above is that at least some ant species use a "topochemical sense" for orientation.

The kinesthetic sense

Our results showed that *P. termitarius* used no olfaction or vision during homing. Neither can a possible use of the earth's magnetic field explain the homing pattern observed here, as workers exited the arm of the maze following a reversed turning-path, irrespective of any of the other cues, even against the original position respect to the earth's magnetic field. We think that the case of *P. termitarius* clearly shows that at least some species use a kind of kinesthetic memory.

This kinesthetic sense, was first defined by PIERON (1904) as a memory of the movements (turns in our case) made by the insect. The kinesthetic sense is equivalent to what we today know as inertial navigation in aeronautics, i.e. orientation through memorizing and integrating speeds, directions and turns. This sence has, more recently, been related to "idiothetic" cues (SHONE, 1984). This sense, if dimensioned to our maze-running problem, is equivalent to a left-right-turn memory, which imply that the ant remembers the type of turns it has to make in order to return, or the distance it has to walk before making a turn. The existence of the kinesthetic sense was refuted by most authors as a non real conjecture (see discussion in WILSON, 1971 for exemple), but workers of *P. termitarius* seem to orient memorizing the route made during exploration, probably using its own body as a reference for orientation. The nature of this internal cue is difficult to know, but we might imagine a leftright turn memory, or an inertial positioning memory, etc., which would require either movement propioreceptors or gravity and acceleration sensors, together with mnemonic capabilities. It is curious to note that the species with the most developed eyes (i.e. *P. termitarius*) and thus supposed to be more heavily dependent on visual cues, is the only one which do not rely on them when orientating through a maze.

Social complexity, orientation cues and learning

Our results reveal that the socially more complex species, *Acromyrmex spp* and *Atta* (JAFFE, 1984, 1987) use many different cues for orientation, whereas the socially more primitive ones, *Trachymyrmex, Pseudomyrmex* and *Ectatomma,* seem to rely on a few of them. Each species has its own hierarchy of cues used for homing, or uses a specific kind of orientation cue, different from even a closely related species, as the case of the Attini show. These differences found among the orientation cues used, may reflect different foraging strategies, or different adaptations to the environment.

The ability to learn to run through the maze, using only visual and/or spatial cues for homing, does not seem to be related to the position of these cues in the hierarchy of each species. Thus, *E. ruidum,* mainly dependent on visual cues for orientation, learned to orientate with visual cues at about the same speed as *T. urichi,* which was rather dependent on olfactory cues. The presence or absence of light did not affect the learning ability of *A. rugosus* but did affect that of *A. laevigata.* This may be related to other findings (ROSENGREN, 1977 ; HENQUELL and ABDI, 1981) which showed the existence of social facilitation in which the aquisition of visual memory of the environment is mediated by olfactory trails.

The learning ability appears to be inversely correlated to the social complexity of the respective species. The socially more primitve species, *P. termitarius, E. ruidum* and *T. urichi* (JAFFE, 1984, 1987), clearly learned under the experimental conditions tested whereas among the more socially complex Attini only *Atta* showed clear learning. *Atta* is the species with the most sophisticated social sysem among ants (VILELA *et al.,* 1987). This may be correlated to earlier findings with ants showing an increase in the complexity of the nervous system with increased social organization up to a point where a simplification of the individuals nervous system was apparent (JAFFE and PEREZ, 1989).

General conclusions

The hierarchy of cues used for orientation in a more natural environment may be different to that found here, which could be more similar to orientation mechanisms naturally employed underground by these ants. But the very fact that each species showed a specific hierarchy under our experimental conditions indicates that they differ in their orientation strategy. Therefore, orientation among ants seems to be a very variable phenomena with no apparent optimal solution, indicating a divergent evolutionary development of orientation strategies, even among closely related taxa or among species with the same ecological adaptations.

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