POLISH ACADEMY OF SCIENCES • MUSEUM AND INSTITUTE OF ZOOLOGY
MEMORABILIA ZOOLOGICA

MEMORABILIA ZOOL.	48	219–236	1994

Zhanna REZNIKOVA, Boris RYABKO

Experimental study of the ants' communication system, with the application of the Information Theory approach

Abstract. In the laboratory experiments devised on the basis of the Information Theory, ants (*Formica polyctena* FOERST., *F. sanguinea* LATR., *Camponotus saxatilis* RUZS.) had to transmit a definite amount of information to each other in order to obtain food. The ants were able to memorize and pass up to 6 bits of information, and the time of communication was proportional to the amount of information. The results evidenced the existence of a developed "language behaviour" in species with a high level of social organization and have showed them as being able to use "text" regularities for information coding. A special series of experiments demonstrated the ants' ability to count and to transmit numbers.

INTRODUCTION

Due to their social mode of life, ants can occupy the key position in most ecosystems and they really have no equal rivals within the complex of predators. The success of ecologically dominant ant species must be due, at least in part, to their complex spatial-temporal organization. A lot of paper have been published on the spatial pattern and different ways of territory utilization (DLUSSKY 1965, 1967, ROSENGREN 1971, 1977, HÖLLDOBLER, WILSON 1977, 1978, 1990, ZAKHAROV 1991, and others). The works of PISARSKI (1972, 1973, 1982) made a valuable contribution to the development of our knowledge in the field of ants' complex territorial behaviour. He formulated a classification of ant societies in the light of the Evolution Theory (PISARSKI 1978).

Obviously, ecologically dominant ant species are especially dependent on recruitment systems to control their environment (HÖLLDOBLER 1983). The ants' communication system is one of the most controversial issues in ethology. These insects are known to use different communicative ways for recruitment: chemical trails, sound signals, kinopsis (reaction to the excited scout behaviour), tandems etc. (WILSON

1971, HÖLLDOBLER 1971, 1976, 1982, ZAKHAROV 1972, DLUSSKY 1981, REZNIKOVA 1982, 1983). But it is not known yet, whether ants can inform their nestmates of the distance and direction of food sources as is the case in the honeybee, whose "Dance Language" was discovered by VON FRISCH (1923, 1965), and nowadays it is being intensively investigated (LINDAUER 1961, LOPATINA 1971, LEVCHENKO 1976, KIRCHNER et al. 1988, MICHELSEN et al. 1990). Honeybee dances are the most complex of the known communication forms in insects. According to MANNING (1979), "the world should admit that information as a symbolic form is available not only to man, but to such a modest creature as the honeybee".

WASMANN (1899) suggested the existence of a tactile, or antennal, code in ants. Attempts were made to decipher ants' phrases, e.g. "I need food". Recently developed experimental methods and filming provided fundamental works devoted to analysing the antennal code. The sequence of antennal movements was studied in different aspects: when ants share food, during recruitment to food, during social relations (HÖLLDOBLER 1976, 1985, ETTERSCHANK, ETTERSCHANK 1982, BONAVITA-COUGOURDAN 1983). It was revealed, that the development and sequence of such signals occurred during a complicated ontogenetic process, followed by contacts with adults (BONAVITA-COUGOURDAN, MOREL 1984, MOREL 1986). On the grounds of the studies of trophallactic interrelations of *Myrmica* LATR. and *Lasius* FABR. it was concluded that antennual movements had no structural unity of signals and replies (LENOIR 1973a,b, LENOIR, JAISSON 1974, 1982). Thus, the question of the existence of a developed tactile "language" in ants is still open.

We suggest another approach to studying communication systems: to investigate the very process of information transmission. Thereat, by the term "information" we mean the concrete quantitative value introduced by SHANNON (1948). It is a natural idea to apply the Information Theory for investigations of the communication system, because the object of this science presents general principles and reliable communication systems. WILSON (1971) used the Information Theory approach to estimate the quantitative volume of the ability of the honeybees and the ant *Solenopsis saevissima* F. SMITH to memorize the location of a food source. But there have been no experiments on animal communication systems with the application of the Information Theory approach.

The main point of our approach is that a given experiment provides a situation, in which ants, to obtain food, should transmit information quantitatively known to the experimentalist. In the first series of experiments this information concerns the sequence of turns towards the food (REZNIKOVA, RYABKO 1984, 1986, 1990, 1991). In the second series the ants should transmit information on the number of objects, within some tens (REZNIKOVA, RYABKO 1988). The theoretic-informative approach allowed to evidence the presence of potentially unlimited number of communications in the ants' "language" and estimate the rate of the information transmission. We also succeeded in studying some properties of the insects' intellect: their ability to count and memorize the simplest regularities providing the compression of the information.

MATERIALS AND METHODS

The maze "binary tree"

To investigate the processes of information trasmission we used a new laboratory system, called a "binary tree", where each "leaf" of the "tree" ended with an empty trough, except one with syrup. The simplest design was a "tree" with two "leaves" and two troughs, with syrup in one of them (Fig. 1a). In such a situation an ant scout should transmit one bit of information to its nestmates: go to the right or to the left. In other experiments the number of forks on one branch was increased up to 6 (Fig. 1b shows a labyrinth with 4 forks). The sequence of turns was randomly taken by tossing a coin.

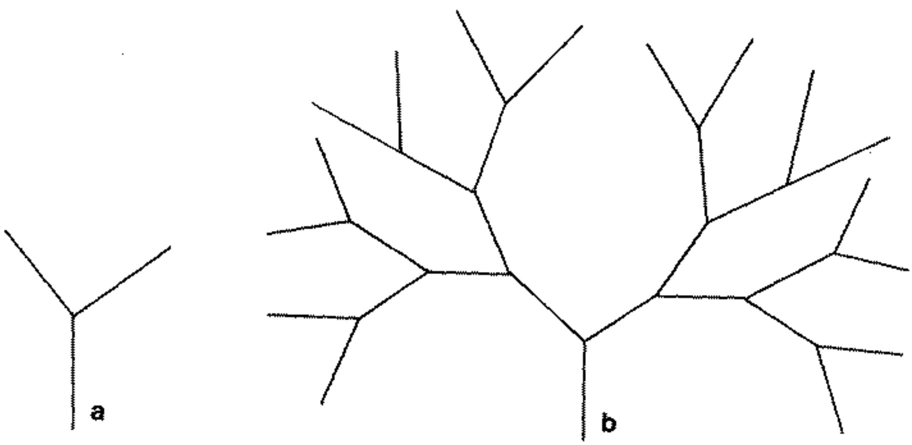

Fig. 1. The maze "binary tree" with one fork (a) and four forks (b).

The quantity of information to be transmitted by a scout to foragers equals the number of forks on one branch. The labyrinth was made of plastic sticks (50 mm) and balls (10 mm) (Fig. 2). To prevent access to food in a straight line, the labyrinth was placed in a bath (600 × 600 mm) with water. The ants reached the initial points of the labyrinth going over a bridge (Fig. 3).

The trunks

To investigate the ants' ability to count and to transmit information on the number of objects we used an experimental set, consisting of a long vertical "trunk" with evenly distributed branches of equal length, made of matches or thin planks (Fig. 4a). Each branch ended in an empty trough, except for one filled with syrup. To study whether the duration of information transmission of the branch number depended on length of the branches as well as on the distance between the branches we carried out a similar series of experiments (16 altogether) on a "vertical trunk 2" with branches five times longer and twice as far apart than in the previous version (i.e.

Fig. 2. A *F. polyctena* team on the "binary tree". (Photo Zh. REZNIKOVA).

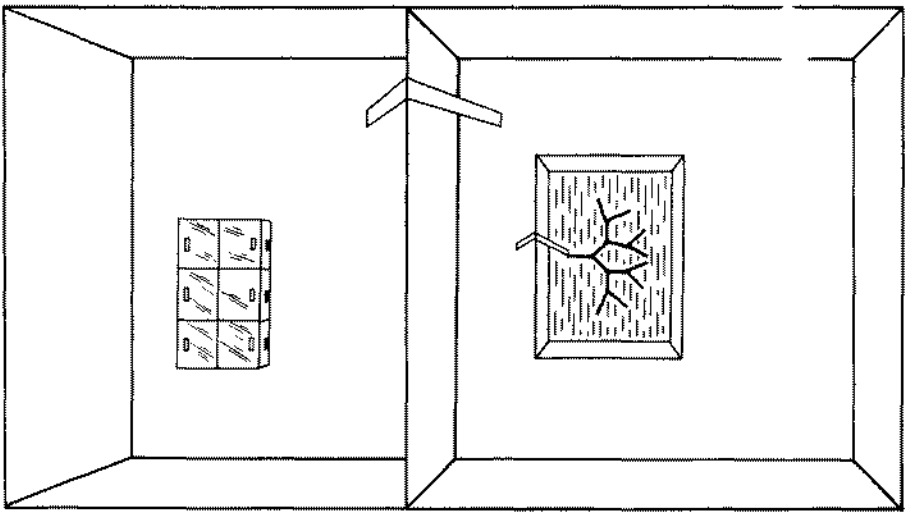

Fig. 3. The laboratory arena with the maze "binary tree".

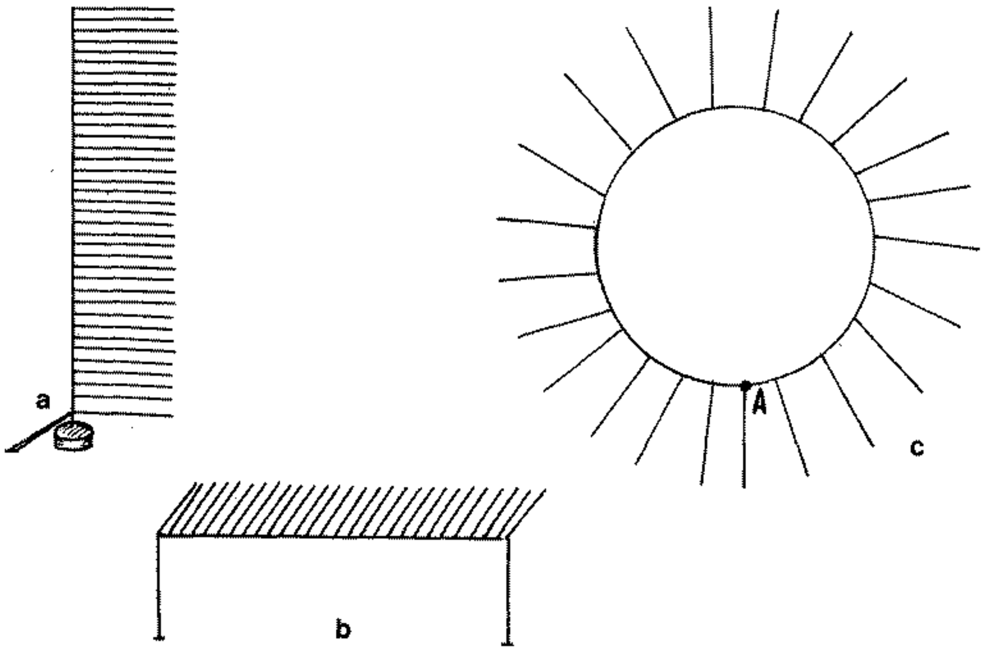

Fig. 4. The laboratory set-ups: "vertical trunk (a), "horizontal trunk" (b) and "circle" (c).

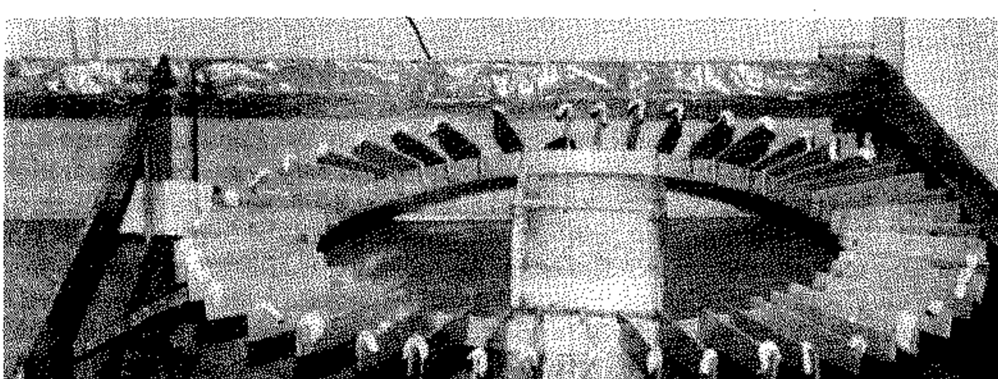

Fig. 5. The laboratory set-up "circle". (Photo Zh. REZNIKOVA).

"vertical trunk 1"). To eliminate the dependence of the duration of information transmission on a set-up form or on the spatial orientation etc., 30 experiments were performed on the horizontal set-up ("horizontal trunk"; Fig. 4b) and 38 – on a circular set-up (Fig. 4c, 5). Ants came to Point A of the "circle" and to the initial point of the "horizontal trunk" over a bridge (the set-up was mounted in a bath with water to prevent the ants from moving in a straight line).

During the experiment the troughs were placed on randomly numbered branches: for example, in the first series the food was on Branch No 10, in the second – on Branch No 40, etc., so that up to 4 teams, active on that particular day, were working on Branch number *i*. Foragers of the other teams were not permitted to visit the experimental set-up during this series.

The maintenance of the laboratory groups

Colony fragments, consisting of workers with the queen and brood were housed in plexiglass nests (10 × 15 × 12 cm), which made the observations of their contacts possible. It should be noted that not all natural ant colonies were useful for the experimental study of their communication system. Thus, of 10 *Formica polyctena* FOERST. colonies, studied for 6 years, only 4 were useful. The natural colony from which laboratory groups were taken, consisted of about 10^5 workers and these were not very agressive.

The laboratory groups (6 of *Formica polyctena*, 2 of *F. sanguinea* LATR., 1 of *Camponotus saxatilis* RUZS., 2 of *Formica cunicularia* LATR., and 1 of *Myrmica rubra* L.) were kept separately on arenas (150 × 50 cm) divided into 2 sections: a smaller one, containing a nest, and a bigger one with the experimental system (Fig. 3). Both sections were connected by a plastic bridge, which was occasionally removed to change the maze or to isolate the ants.

The ants were fed once in two or three days, only in the maze and that stimulated their search for food. All the ants were labelled with an individual colour mark.

Recognition of the "working teams" among the ants

In all series of the experiments with the "binary tree" the ants fed for 10–12 days in a maze with one fork. In these cases the foragers left their nest and arena as a result of collective excitement and imitation. Up to 200 workers visited the trough with syrup. The ants' behaviour was sharply changed with following a complication of the task: when the trough with syrup was placed on one of four "leaves" of the second turn of the "binary tree". The laboratory colony included "teams" which had 1 scout and 5–8 recruits: the scout attracted to food only its team. *F. polyctena* and *F. sanguinea* had 8–9 working teams and *C. saxatilis* – only one per day. The teams were revealed in special preliminary experiments. Not all of the scouts managed to memorize the way towards the maze; moreover, the number of such scouts was dropped with the complication of the task, e.g. in the case of two forks all active groups were working, while in the case of six – only 1 or 2.

Description of the experiments

During the main experiment we placed a scout on a trough containing food, then the scout returned to the nest by itself. Sometimes the scout contacted its team at once, and the group began moving towards the set-up. In this case after the scout had contacted the foragers we removed the scout and the foragers had to search for the food by themselves. But more often the scout returned to the nest, then left it and went back to the trough alone. Sometimes it made mistakes and only found the trough with food after visiting some empty ones. Then it returned to the nest again, contacted the team and either remained with the team or left it. In the former case the scout was isolated, while in the latter case the experiment was repeated. Sometimes the scout had to make up to four trips before it was able to mobilize the foragers. In all the cases of mobilization we measured (in sec.) the duration of the contact between the scout and the foragers in the transparent nest. Its touching the first ant was considered to be the beginning of the contact, while nest leaving by the first two foragers was considered to be the end. Those contacts were followed by fairly numerous antennal movements. The scouts touched from one to four foragers in turn, sometimes two simultaneously. When a scout repeatedly returned to the trough alone, we measured the length of each of its contacts with foragers. Only the duration of the last contact, followed by the foragers' leaving the nest was taken into account.

Precautions

The experiments were so devised as to eliminate all possible ways helpful to finding food, except distant homing, i.e. information contact with a scout. During contact of a scout and foragers in their nest, the experimental set-up was replaced by a similar one to avoid the use of the odour track. A statistical analysis considered only the first trip of the group after its contact with the scout, because the maze presumably lacked any chemical odour trail.

To avoid both the trail and the food odour a special series of experiments was carried out. While the scout was inside the nest, we replaced the whole maze by a new one with all troughs empty. So, following their contact with the scout, the foragers visited troughs empty on purpose. Such experiments were called "examinations". Ants were fed during the intervals between those "examinations", but they had no food during any particular "examination".

It is worth noting, that in all those experiments the ants had no possibility to make use of their earlier experience. For example, Table 1 shows the seasonal "history" of every foraging group of *F. sanguinea* during the experiment with the "binary tree". Group I "mastered" the sequence of the turns "LL", "LR", "LL" and "RR", "RL" and "LL", "LLL" and "LLR", "LRLL", "RRR", "LLLLL" on 14, 16, 18, 20, 22 and 25 June, and 2 and 5 July 1984, respectively. Group VIII – "RLLLR", "LLL" and "RRR", "LRLL", "RRLRL" and "RRRRR", "LLLLL", "RRRRR" on 22, 25 and 29 June, and 2, 5 and 9 July 1984, respectively.

Note, that not all groups worked throughout the whole season, and sometimes new groups were observed to be active. To find and watch such groups 3 or 4 special tests with a simplified maze were carried out. Such data were obtained on 27 June, 13 and 23 July 1984 for the *F. sanguinea* laboratory colony.

Table 1 shows, that each group had to use different roads towards the troughs; so, the ants could not use earlier experience.

Table 1. Visiting the maze by *F. sanguinea* (June–August 1984)

Date[1]	Sequence of the turns	Teams visiting the maze successively[2]
1	2	3
14 June	LL	I,II,V,VI
16 June	LR	I,II,III,IV,V,VI
18 June	LL	I,II,III,V
18 June	LR	II
18 June	RR	I,II,III,V,VI
20 June	RL	I,II,IV,V
20 June	LR	II
20 June	LL	I,II,III
20 June	LLR	II,V,VI
22 June	LLL	I,III,IV,V,VII
22 June	LRLL	II,III,IV
22 June	LLR	I,II,III,IV,V
22 June	RLLL	III,IV,VI,VIII
25 June	LLL	IV,V,VII,VIII,IX
25 June	RRR	III,VI,VII,VIII
25 June	LRLL	I,II,III,IV
25 June	RRLRL	II,IV,VI
29 June	LLL	II,III,VI
29 June	LLR	III,IV,VI,VII
29 June	LRLL	II,III,VIII
29 June	RLLLR	II,VII
2 July	LLL	III,IV,IX,X
2 July	RRR	I,II,IV,IX,X
2 July	RRLRL	VIII,IX,X
2 July	RRRRRR	IV,VIII,IX
5 July	RRRRRR	XI,XII
5 July	LLL	XI,XII
5 July	RRLRL	VII,XII
5 July	LLLLLL	I,VII,VIII,XI
7 July	LLLLLL	II,VII,IX,X
9 July	RRRRR	III,V,VII,VIII,X
9 July	RLRLRL	IV,V,IX,XI
11 July	RLRRRL	V,VI,IX,XI
11 July	RRLRRR	XII,XIII
16 July	RRR	II,IV,VI,XI,XII
16 July	RRRRRR	III,V,X,XI,XII
16 July	RLRRRL	X,XIII
18 July	LRLRLR	II,VII,IX,X

Table 1 (contd).

1	2	3
18 July	RRR	VI
21 July	RRLRRR	IV,V,VII,IX
21 July	LRLLRL	X,XII
21 July	RLRLRL	V,IX,XI
25 July	RLRLRL	IV
25 July	RRLRRR	XIII,XIV
25 July	LRLLRL	X,XII
27 July	RRLRRR	XIV
27 July	LRLLRL	X
27 July	LLLLL	IV,V,VII
30 July	LLLLL	IX,X,XII
2 August	LLLLL	XIII,XIV,XV

[1]The experiments of 24 and 27 June, and 14, 20, 24 and 29 July were failed because there was no mobilization.

[2]Symbols of teams correspond to symbols of scouts.

RESULTS

Evidence of information transmission

As already mentioned, capable scouts not only quickly memorized the rational way in the "binary tree", but easily learned it again, when the sequence of the turns was changed during a given experiment. All groups, contacting such scouts chose the correct way, without investigating other "leaves". Some ants, after making false turns, reached the leading foragers quite easily (see: the data in Table 3 for details).

Table 2 presents those cases, in which ants were specially introduced into the maze, without contacts with a scout. They were permitted to search for food for 30 minutes. If the maze had more than 3 turns, they usually failed to find the food during this period. Such ants, checking the way towards their nest, often returned to the bridge and began searching again. Note, that during all the experiments scouts were specially introduced into the maze because their "leaf" checking to find the food was usually unsuccessful.

Now, we shall present a thorough analysis of the experiments made in 1985 and 1986 on *F. sanguinea*. Table 3 gives the results of the "examinations", when ants visited the maze, after empty troughs had been placed there. We shall first prove the existence of information transmission in ants. We compare Zero Hypothesis H_0 (foragers occasionally find a trough) with Hypothesis H_1 (they find food thanks to the received information). The probability of a chance finding of the correct way towards the trough in the maze with 3 forks is $(1/2)^3$. Table 3 shows that in three cases (lines 2, 3, 4) the groups of foragers failed to find the food; in 5 cases (lines 8, 9, 10, 12, 19) 1–3 ants were left behind the group and in 12 cases all foragers correctly reached those "leaves", where their scout had found food. In these experiments a correct search can be considered a "success", while an unsuccessful search, when the team

Table 2. Searching for the trough by ants without preliminary contacts with the scout

Species	Sequence of the turns	Number of ants finding (A) and not finding (B) the trough within 30 mins[1]	
		A	B
F. sanguinea	LLRL	*	5 **
	RRLLR	–	6
	RRLRL	–	4
	RRRRR	–	3 *
	RLRRRL	–	2 ***
F. polyctena	LRRL	*	8
	RRLR	1	6 *
	RLLLR	–	7
	LRRRL	–	2 **

[1]Numerals mean the number of foragers and asterisks – the number of scouts.

Table 3. Results of the *F. sanguinea* "exams"

No.	Date	Scout	Sequence of the turns	Foragers (symbols)		
				achieving the aim in a compact group	achieving the aim after some mistakes	unsuccessful foragers
1	20 Dec '85	I	RRR	3,4,5,6,7,8,9	–	–
2	20 Dec '85	II	LRR	–	–	2,13
3	20 Dec '85	II	LRR	–	–	11,12,14
4	5 Jan '86	III	RRR	–	–	4,13,15,16,17
5	5 Jan '86	III	RLR	2,13,18,19,20,21	–	–
6	5 Jan '86	III	RRL	2,4,13,18,19,20	–	–
7	5 Jan '86	III	RLL	2,4,18,19,20,24	–	–
8	10 Jan '86	IV	LRL	25,26,28	29,30,31	–
9	10 Jan '86	IV	RLL	11,13,25,27	31,32	–
10	10 Jan '86	V	RLL	13,25,26,27	31,32	–
11	13 Jan '86	VI	LRL	36,37,38	–	–
12	13 Jan '86	VI	LRL	36,37,38,39,40	41,42	–
13	13 Jan '86	VI	LLR	38,39,40,41,42	–	–
14	17 Jan '86	VII	LRR	37,43,44,45,46	–	–
15	17 Jan '86	VII	LLL	37,44,45,46	–	–
16	17 Jan '86	VII	RLL	37,44,45	–	–
17	20 Jan '86	VIII	LLL	47,48,49	–	–
18	20 Jan '86	VIII	LRL	47,48,49,50	–	–
19	23 Jan '86	IX	LLR	4,12,51,52	53,54	–
20	23 Jan '86	IX	RLL	4,52,53,54	–	–

Table 4. Visiting the maze by ants of different species [a – numbers of foragers' groups that achieved the aim following their contact with scouts; b – the same with 1–3 being back; c – number of foragers' groups that failed to achieve the aim; *P* – probability of the given distribution with realization of H_0 hypothesis, i.e. lack of information transmission (– – no data)]

Sequence of the turns	*F. sanguinea*				*F. polyctena*				*C. saxatilis*			
	A	B	C	*P*	A	B	C	*P*	A	B	C	*P*
LL	8	2	1		12	3	2		5	2	1	
LR	6	1	0		9	1	0		4	1	0	
RR	5	0	0		6	1	1		6	0	0	
RL	6	0	0		8	0	0		7	0	0	
In general	25	3	1	<0.001	35	5	3	<0.001	22	3	1	
RLR	–	–	–		10	3	3		5	1	0	
LLL	8	3	1		–	–	–		–	–	–	
RLL	–	–	–		8	2	0		–	–	–	
RRR	8	2	1		6	0	0		5	0	1	
LRL	6	1	1		–	–	–		–	–	–	
In general	22	6	3	<0.001	24	5	3	<0.001	10	1	1	<0.001
LRLL	4	0	1		–	–	–		–	–	–	
LRRL	–	–	–		7	0	2		3	0	0	
RRLR	–	–	–		6	1	1		–	–	–	
LLLL	4	1	1		–	–	–		3	0	1	
In general	8	1	2	<0.001	13	1	3	0.001	6	0	1	
RRRRR	5	0	2		5	0	0		3	0	0	
RLLLR	7	0	0		8	0	1		5	1	0	
RRLRL	6	2	0		6	1	2		3	0	1	
RLLRR	–	–	–		4	0	0		–	–	–	
LRRRL	–	–	–		4	0	1		4	1	1	
In general	18	2	2	<0.001	27	1	4	<0.001	15	2	2	<0.001
RRRRRR	3	0	2		3	2	1		2	0	1	
LLLLLL	4	1	2		5	1	1		3	1	0	
LRLRLR	3	0	2		3	2	1		2	0	1	
RLRLRL	3	0	1		2	2	0		–	–	–	
RLRRRL	4	1	3		4	1	3		2	1	0	
RRLRRR	3	0	3		4	0	0		2	0	0	
LRLLRL	2	0	0		3	1	0		2	0	1	
In general	22	2	13	<0.001	24	9	16	<0.001	13	2	3	<0.001

failed to come or came in a small number was called a "failure". Thus, we have results of 20 independent Bernoulli tests, where the probability of "success" (P) in the case of the realization of H_0 is $(1/2)^3$, against H_1, where $P > 1/8$. There were 12 "successes" and 8 "failures". To verify H_0 against H_1, we used the binomial criterion (the tables in: HOLLANDER, WOLF 1973). In our case H_0 was rejected in favour of H_1, $P < 0.001$. Thus, the obtained data showed, that the ants had not used any trail or food odour (note that we had changed the maze and the troughs were empty). In addition, this table shows the scouts' ability to transmit information on absolutely different routes towards the bait during one experiment (e.g. lines 9–10, 11–13, 14–16, etc.). So, the ants could not use the earlier experience.

Now we shall analyse the experiments made from 1982 to 1984, where different cases involved different numbers of forks (1–6) (Table 4). It should be emphasized that during one day the scouts worked in the "binary tree" with different sequences of the turns and even different numbers of the forks. In this situation we again compare Hypothesis H_0 (they find food randomly) with Hypothesis H_1 (they find food thanks to the obtained information). The probability of a chance finding of the correct way with i number of forks is $(^1/_2)^i$. In all cases H_0 is rejected in favour of H_1, $P < 0.001$. Thus, the obtained data confirm information transmission in three species with group foraging and exclude any orientation mechanisms, except the use of information transmitted by the scouts. No "language" behaviour was observed in singly foraging *F. cunicularia*. The foragers learned the way towards the maze, while making up to 30 trips per day, but they did not try to recruit other members of their colony. Not more than 5 ants were active in the maze per day.

M. rubra workers utilize multiple recruitment systems (DLUSSKY et al. 1978). In our experiment they used olfactory cues, but when we changed the maze, they had to do without odour trails. In these cases they resorted to only solitary foraging, just as *F. cunicularia*.

Evaluation of information transmission rate

In our experiments the quantity of information (in bits), necessary for choosing the correct way towards the maze, equals i, the number of the forks. We assumed that the duration of the contacts between the scouts and foragers (t) was $\alpha i + \beta$, where i was the number of the forks, α – coefficient of proportionality, equal the rate of the information transmission (bit/min), and β was the introduced constant, since ants can transmit information not related directly to the task, i.e. to the signal "food".

From the obtained data we evaluated the parameters of linear regression and the sample correlation coefficient (r) (Table 5).

In all cases the correlation between the duration of the contacts and the amount of information (the numbers of the forks i) turned out to be close to linear, probably due to the high value of the sample correlation coefficient (Table 5). This confirms our hypothesis (all values of correlation coefficient significantly differ from 0 at $P =$ 0.01).

In *F. sanguinea*, *F. polyctena* and *C. saxatilis* the rate of the information transmission (α), derived from equation $t = \alpha i + \beta$ is 0.738, 1.094 and 1.189 bit/min, respectively.

We do not consider these values as specific constants, as they may vary. Note, these data are considerably less, that of human communication (YAGLOM, YAGLOM 1973).

Table 5. The parameters of linear regression ($t = \alpha i + \beta$) and sample correlation coefficient (r) (explanations of the symbols in the text)

Species	$\alpha \pm \Delta\alpha$	$\beta \pm \Delta\beta$	r
F. sanguinea	0.738 ± 0.053	–0.768 ± 0.094	0.962
F. polyctena	1.094 ± 0.050	0.619 ± 0.460	0.791
C. saxatilis	1.189 ± 0.018	0.334 ± 0.032	0.967

Theoretic-informative tests of ants' "intellect"

The ability to grasp regularities quickly and use them for coding and "compression" of information should be considered as being one of the most important properties of language and its carrier's intellect. Thus, the length of a given text should be proportional to the complication of the information, e.g. it is easier for man to remember and transmit the sequence of the forks "LR LR LR LR LR", than the shorter but random one "RL LL RR LR".

We tried to analyse the question whether ants, with their "language" (and "intellect") can apply simple "text" regularities for compression (here the "text" means the sequence of the turns towards the maze) (Table 6).

Table 6. Duration of transmitting information on the way to the trough by *F. sanguinea* scouts to foragers (no. 1–8 – regular turn pattern; no. 9–15 – random turn pattern)

No.	Sequence of the turns	Mean duration (sec)	SD	Numbers of experiments
1	LLL	72	8	18
2	RRR	75	5	15
3	LLLLL	84	6	9
4	RRRRR	78	8	10
5	LLLLLL	90	9	8
6	RRRRRR	88	9	5
7	LRLRLR	130	11	4
8	RLRLRL	135	9	8
9	LLR	69	4	12
10	LRLL	100	11	10
11	RLLLR	120	9	6
12	RRLRL	150	16	8
13	RLRRRL	180	22	6
14	RRLRRR	220	15	7
15	LRLLRL	200	18	5

As there is no algorithmically evaluated quantitative measure of text complication so, strictly speaking, we can only verify whether ants and humans have the same notion of simple and complex texts. Evidently, most people perceive the sequence of the forks of the 5th and 6th lines (Table 6) as simpler than of the 7th and 8th lines which, in turn, are simpler than the random ones of the same length (lines 13–15). The time of the information transmission on the sequence of the forks in ants appeared increased with the complication of the task (lines 5–8 and 13–15).

This could be proved statistically. We compared the main Hypothesis H_0: the time of the information transmission does not depend on text complexity, with Hypothesis H_1: this time actually depends on it. This experiment consisted of 7 series with the sequence of the turns of equal length (Table 6: lines 5–8, 13–15). The total number of the turn sequence orders, according to the duration of the transmission is 7! of which 2!2!3! are in line with H_1. The probability of obtaining such an order according to H_0 is very small: $^{2!2!3!}/_{7!} = {}^{1}/_{210}$. Thus, we conclude that Hypothesis H_1 has been realized: the simpler the text the less time for information transmission.

It is interesting, that the ants began using regularites to compress only quite large texts: to transmit information of regular sequences of the length "3" of the first and second rows (Table 6) they spent even a little more time than on the random sequence of the same length of the 9th row.

The ants' aptitude for information transmission on the number of objects

These experiments were carried out with *F. polyctena*. As in the experiments with the "binary tree", a number of scouts turned out to be unable to transmit the correct information on the number of a food-containing branch. Groups which successfully found the way to the trough did not show any significant differences in the duration of information transmission of the number of a given branch, and, therefore, the data for all teams were combined. Note, that of the 26 teams which participated in the experiments scouts of 19 teams successfully transmitted the information on the branch number and 7 teams failed to do this. Generally the teams left their nest after they had been contacted and went towards the trough 130 times. In 99 cases the teams immediately found the correct path to the trough, without making any trips to empty troughs. 15 series of experiments with five scouts and their teams were performed in the set-up with vertically distributed branches (Table 7).

Table 7. The course of the "vertical trunk 1" set-up experiments with *F. polyctena*

No.	Date	No. of the food-having branch	Duration of a scout-forager contact (sec)	Working team
1	10 July '84	10	42	I
2	10 July '84	10	40	II
3	10 July '84	10	45	III
4	14 July '84	40	300	II
5	14 July '84	40	280	IV
6	17 July '84	13	90	II
7	17 July '84	13	98	I
8	17 July '84	28	110	III
9	17 July '84	28	120	V
10	19 July '84	20	120	V
11	19 July '84	20	110	III
12	19 July '84	35	260	III
13	19 July '84	35	250	V
14	23 July '84	30	160	I
15	23 July '84	30	170	III

Since all set-ups had no less than 25 branches the probability of finding the correct trough at random was less than $^1/_{25}$. Thus, the ratio we experimentally obtained can be accounted only for information transmission from the scouts: in 90 cases out of 130 the probability of randomly finding the food-containing trough was less than 10^{-10}

Moreover, ants, including scouts, placed in the set-up and given no information as to which trough contained food usually failed to find the food, even though they actively searched for it.

The data obtained on the set-up "vertical trunk 1" are shown in Fig. 6. The relation between the number of the branch i and the duration of the contact between the scout

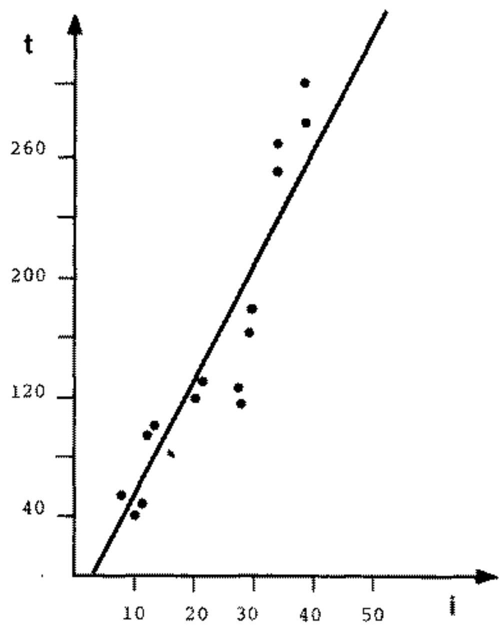

Fig. 6. The relations between the number of the branch (i) and the duration of the contact between a scout and foragers (t) in *F. sanguinea* (the set-up "vertical trunk 1").

and foragers t was linear, and described by the equality $t = \alpha i + \beta$. The coefficient of correlation between t and i was high (1st line in Table 8 with the values of α and β). These parameters were also measured for other set-ups (Table 8).

Table 8. Coefficients of correlation linear regression equation in the experiments with *F. sanguinea* with different set-ups applied (explanation of the symbols in the text)

Set type	Sample size	Maximum i	r	$\alpha \pm \Delta\alpha$	$\beta \pm \Delta\beta$
Vertical trunk 1	15	40	0.93	7.30 ± 4.10	−28.80 ± 0.51
Vertical trunk 2	16	60	0.99	5.88 ± 0.44	−17.11 ± 0.65
Horizontal trunk	30	25	0.91	8.54 ± 1.10	−22.20 ± 0.62
Circle	30	25	0.98	8.62 ± 0.52	−24.40 ± 0.61

On the "circle" the food-containing branch was numbered from the point A counting clockwise because in all cases the foragers moved only in this direction, even though the clockwise way was much shorter (the reasons are unknown). It is interesting, that on the "vertical trunk" foragers, after contacting the scout, first quickly climbed the upper margin of the trunk, then slowly returned to the food-containing branch, and therefore we also numbered the branch from the upper end of the trunk. It is interesting, that quantitative characteristics of the ants' "number system" are close to some archaic human language: the length of the code of a given number is proportional to its value (IVANOV 1967). For example, the word "finger" corresponds to "1", "finger, finger" to number "2" and so on. In modern human languages the length of the codeword of a number i is approximately proportional to $\log i$ (for large i).

CONCLUSIONS

These results suggest the following picture of the ants' communication system and their intellectual capacities:

1. Ants are able to memorize and transmit 1–6 bits of information;
2. There is unlimited quantity of potentially possible messages in the ants' "language";
3. The duration of information transmission is proportional to the quantity of information;
4. Ants spend considerably less time on transmission of information on regular sequences of turns than on random ones of the same length. In other words, they use short "phrases" for simple messages;
5. Ants are capable of counting up to several dozens and their communication system allows them to transmit numbers.

We suppose that only a few species with a high level of social organization use such a complex communication system as distant homing which is suitable for complicated situations.

Acknowledgements. These investigations were partly supported by the Russian Foundation of Fundamental Investigations (grant nos. 93-04-7733 to Zh. Reznikova).

REFERENCES

BONAVITA-COUGOURDAN A. 1983. Activité antennaire et flux trophallactique chez la Fourmi *Camponotus vagus* SCOP. Insectes soc., Paris, **30**: 428–442.

BONAVITA-COUGOURDAN A., MOREL L. 1984. Les activites antennaires au cours des contacts trophallactiques chez la Fourmi *Camponotus vagus* SCOP. ont-elles valeur de signal. Insectes soc., Paris, **31**: 113–131.

DLUSSKY G. M. 1965. Okhranyaemaya territoriya y murav'ev. Zh. obshch. Biol., Moskva, **26**: 479–489.

DLUSSKY G. M. 1967. Murav'i roda Formika. Nauka, Moskva, 236 pp.

DLUSSKY G. M. 1981. Principi kommunikacii u murav'ev. Chtenia pamyati N. A. HOLODKOVSKOGO. Nauka, Leningrad, pp. 3–33.

DLUSSKY G. M., VOLCIT O. V., SULKHANOV A. V. 1978. Organizaciya gruppovoj furazhirovki u murav'ev roda *Myrmica*. Zool. Zh., Moskva, **57**: 65–77.

ETTERSHANK G., ETTERSHANK A. 1982. Ritualized fighting in the meat ant *Iridomyrmex purpureus* (SMITH) (*Hymenoptera, Formicidae*). J. Aust. entomol. Soc., Indooroopilly, **27**: 97–102.

FRISCH VON K. 1923. Über die Sprache der Bienen. Zool. Jb., Jena, **40**: 1–119.

FRISCH VON K. 1965. Tranzsprache und Orientierung der Bienen. Springer-Verlag, Berlin, 540 pp.

HOLLANDER N., WOLF D. 1973. Nonparametric statistical methods. New York, 518 pp.

HÖLLDOBLER B. 1971. Recruitment behaviour in *Camponotus socius*. Z. vgl. Physiol., Heidelberg, **75**: 123–142.

HÖLLDOBLER B. 1976. Recruitment behaviour, home range orientation and territoriality in harvester ants *Pogonomyrmex*. Behav. Ecol. Sociobiol., Berlin, **1**: 3–44.

HÖLLDOBLER B. 1982. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* WHEELER (*Hymenoptera, Formicidae*). Behav. Ecol. Sociobiol., Berlin, **9**: 301–314.

HÖLLDOBLER B. 1983. Territorial behaviour in the green tree ant (*Oecophylla smaragdina*). Biotropica, Lawrence, Kans., **15**: 241–250.

HÖLLDOBLER B., WILSON E. O. 1977. Weaver ants: social establishment and maintenance of territory. Science, New York, N.Y., **195**: 900–902.

HÖLLDOBLER B., WILSON E. O. 1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (LATREILLE) (*Hymenoptera, Formicidae*). Behav. Ecol. Sociobiol., Berlin, **3**: 19–60.

HÖLLDOBLER B, WILSON E. O. 1990. The Ants. Springer-Verlag, Berlin, 12 + 732 pp.

IVANOV V. 1967. Yazyk v sopostavlenii s drugimi sredstvami peredachi i khraneniya informacii. In: Dokl. Konf. po Pererabotke Informacii. Vip., Moskva, **7**: 44–50.

KIRCHNER W. H., LANDAUER M., MICHELSEN A. 1988. Honeybee dance communication: acoustical indication of direction in round dances. Naturwissenschaften, Berlin, **75**: 629–630.

LENOIR A. 1973a. Les communications antennaires durant la trophallaxie entre ouvriéres du genre *Myrmica*. In: Proc. Cong. IUSSI, London, pp. 226–233.

LENOIR A. 1973b. Influence de sections de tarses antérieurs sur le comportment de trophallaxie de deux espéces de fourmis: *Myrmica scabrinodis* NYL. et *Lasius emarginatus* OL. C.R. 96 Cong. nat. Soc. savantes. Toulouse, Sciences, **3**: 531–540.

LENOIR A., JAISSON P. 1974. Les communications tactiles interindividuelles au cours des relations trophiques dans les sociétés de Fourmis. Bull. Audiophonal., **4**: 107–120.

LENOIR A., JAISSON P. 1982. Evolution et rôle des communications antennaires chez les Insectes Sociaux. In: Social Insects in the Tropics (ed. by P. JAISSON). Univ. Paris-Nord, **1**: 157–180.

LEVCHENKO I. A. 1976. Peredacha informacii o koordinatakh istochnika korma u pchely medonosnoj. Naukova Dumka, Kiev, 250 pp.

LINDAUER M. 1961. Communication among social bees. Harvard Univ., Cambridge, Mass., 350 pp.

LOPATINA N. G. 1971. Signal'naya deyatel'nost' v cem'e medonosnoj pchely (*Apis mellifera*). Nauka, Leningrad, 154 pp.

MANNING A. 1979. An introduction to behaviour. E. Arnold Ltd., 360 pp.

MICHELSEN A., ANDERSEN B. B., KIRCHNER W., LINDAUER M. 1990. Transfer of information during honeybee dances, studied by means of a mechanical model. In: Sensory Systems and Communication in Arthropods. Advances in Life Sciences. Birkhauser Verlag, Basel, pp. 284–300.

MOREL L. 1986. Ontogenesis of the antennal activity associated with food transfer in the callow worker ant. Dev. Psychobiol., New York, N.Y., **19**: 413–426.

PISARSKI B. 1972. La structure des colonies polycaliques de *Formica* (*Coptoformica*) *exsecta* NYL. Ekol. pol., Warszawa, **20**: 111–116.

PISARSKI B. 1973. Struktura społeczna *Formica* (*C.*) *exsecta* NYL. (*Hymenoptera; Formicidae*) i jej wpływ na morfologię, ekologię i etologię gatunku. IZ PAN, Warszawa, 134 pp.

PISARSKI B. 1978. Evolution of competitive behaviour in social insects. Proc. 8th Symp. Social Insect Section PES, Puławy, pp. 17–21.

PISARSKI B. 1982. Territoires et territorialisme de *Formica* (*Coptoformica*) *exsecta* NYL. Memorabilia zool., Wrocław, **38**: 163–203.

REZNIKOVA J. I. 1982. Interspecific communication between ants. Behaviour, Leiden, **80**: 84–85.

REZNIKOVA Zh. I. 1983. Mezhvidovye otnosheniya myrav'ev. Nauka, Novosibirsk, 205 pp.

REZNIKOVA Zh. I., RYABKO B. Ya. 1984. Teoretico-informacionnyj analiz yazyka murav'ev. VI Mezhdunar. Simp. Teor. Inform., Moskva, pp. 147–151.

REZNIKOVA Zh. I., RYABKO B. Ya. 1986. Issledovaniya yazyka murav'ev metodami teorii informacii. Probl. Peredachi Inform. Moskva, **3**: 103–108.

REZNIKOVA Zh. I., RYABKO B. Ya. 1990. Information Theory approach to communication in ants. In: Sensory Systems and Communication in Arthropods. Advances in Life Sciences. Birkhauser Verlag, Basel, pp. 305–308.

REZNIKOVA Zh. I., RYABKO B. Ya. 1991. Experimental investigation of ants language communicative means. In: 22nd Intern. Ethol. Conf. Abstracts. Otani Univ., Kyoto, p. 63.

ROSENGREN R. 1971. Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (*Hymenoptera, Formicidae*). Acta zool. fenn., Helsinki, **133**: 1–105.

ROSENGREN R. 1977. Foraging strategy of wood ants (*Formica rufa* group). I. Age polyethism and topographic traditions. Acta zool. fenn., Helsinki, **149**: 1–30.

SHANNON C. 1948. A mathematical theory of communication. Bell System Techn. J., **27**: 623–656.

WASMANN E. 1899. Die Psychischen Fähigkeiten der Ameisen. Zoologica, Stuttgart, **26**: 1–133.

WILSON E. O. 1971. The Insect Societies. The Belknap Press Harvard Univer. Press. Cambridge, Mass., 548 pp.

YAGLOM A. M., YAGLOM I. M. 1973. Veroyatnost' i informaciya. Moskva, 510 pp.

ZAKHAROV A. A. 1972. Vnutrividovye otnosheniya u murav'ev. Nauka, Moskva, 216 pp.

ZAKHAROV A. A. 1991. Organizaciya soobshchestv y murav'ev. Nauka, Moskva, 277 pp.

Zh. REZNIKOVA
Biological Institute
Laboratory of Insect Ecology
Frunze St. 11, Novosibirsk
630 091, Russia

B. Ya. RYABKO
Novosibirsk Telecommunication Institute
Dept. Appl. Mathematics and Cybernetics
Kirov St. 86, Novosibirsk
630 102, Russia

STRESZCZENIE

Badania eksperymentalne nad systemem porozumiewania się mrówek z zastosowaniem teorii informacji

W warunkach laboratoryjnych badano zdolność mrówek *Formica polyctena* FOERST., *F. sanguinea* LATR. i *Camponotus saxatilis* RUZS. do przekazywania informacji o drodze do źródła pokarmu. Wykazano, że: 1) mrówka jest w stanie zapamiętać i przekazać do 6 bitów informacji; 2) system porozumiewania się mrówek pozwala im na przekazanie potencjalnie nieograniczonej liczby wiadomości; 3) czas przekazywania informacji jest proporcjonalny do jej ilości; 4) przekazywanie informacji o regularnych zmianach kierunku marszruty trwa znacznie krócej, niż gdy zmiany kierunku są przypadkowe (przy tej samej długości drogi); 5) mrówki potrafią "liczyć" do kilkudziesięciu i przekazywać taką wiadomość. Przypuszczalnie tak złożonym systemem komunikowania się dysponują tylko gatunki o odpowiednio wysokim poziomie organizacji społecznej.
