A STUDY OF ANTS' NUMERICAL COMPETENCE

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The main point of proposed approach to study ants' cognitive abilities is that our experiments provide a situation in which insects have to transmit information quantitatively known to the experimentalist, in order to obtain food. One may measure the complexity of tasks they solved in order to pass definite pieces of information from scout ants to foragers. Our previous experiments, basing on ideas of Information Theory, had shown that aphid – farming ants (Formica polyctena, F. sanguinea, Camponotus saxatilis) are able to memorise and transmit messages concerning sequence of turns towards a hidden trough of syrup and to use the simplest regularities to compress the information. In the experiments placed here counting and number related skills are described. We selected the most high social red - wood ants Formica polyctena to transmit information (1) on the ordinal number of a given side-branch in a linear maze and (2) on the numerical co-ordinates in a grid – type maze of a node at which syrup has been hidden. One of the experimental set-ups consisted of a "tree-trunk" with branches that ended in empty troughs, except for one which was filled with syrup. Another set-up consisted of a lattice of grid, in which location of a goal-node relative to a start-node can be specified as a pair of Cartesian coordinates. The foragers of F. polyctena were separated into teams of 5-8 individuals, each with one scout. All laboratory ants were marked with coloured labels. To start the experiment, an ant scout was placed at a randomly numbered trough containing food and then allowed to return to the nest on its own. The duration of the ensuing contact between foragers and the scout was measured. Then we removed the scout and the foragers had to search for the food by themselves. The experiments were so devised as to eliminate all possible ways that may help to find food, except for distant homing. The consistently high success of the foragers in finding the food suggests that scouts are able to count within a range of several tens, and to transmit this information to their foragers. Analysis of time duration of ants' contacts enables us to hypothesise how they use numbers and numerical co-ordinates in their communication.

I. Introduction

The communication systems of animals have been a matter of special research interest to ethologists. Studying communicative means of different species is a good tool to judge about their cognitive abilities. Direct dialog with apes and grey parrots based on adopted human languages has revealed astonishing mental skills such as ability to abstract, to extrapolate, to count, to plan behaviour, and to use the experience gained in new situations (Gardner, Gardner, 1969; Pepperberg, 1987; Savage-Rumbaugh and Lewin, 1994 and others). At the same time, surprisingly few are known yet about natural communication systems in animals. Although it is intuitively clear that many high social species have to possess complex language, only two types of natural communications have been decoded up to the present. First, one of the most complicated of the known natural "languages" in animals is the symbolic honey bee "Dance language". Based on a distant homing system, discovered by K. Von Frisch (1923, 1950) it was later intensively studied using different methods including robotics (Michelsen, 1993). The second communicative system being deciphered concerned acoustic signals of danger which

were deciphered for vervet monkeys (Struhsaker, 1967; Seyfarht et al., 1980) and later for several other species (Pereira, Macedonia, 1991; Slobodchikoff et al., 1991 and others).

The main difficulties in the analysis of animal "languages" appear to be methodological. Many workers have tried to directly decipher animal language by looking for "letters" and "words" and by compiling "dictionaries". The fact that investigators have managed to compile such "dictionaries" for a few species only, appears to indicate not that other animals lack "languages", but that adequate methods are lacking.

We have suggested a new approach to study quantitative characteristics of communicative systems and important properties of animal intelligence. The main point of this approach is not to decipher signals but to investigate just the process of information transmission by measuring time duration which the animals spend on transmitting messages of definite lengths and complexities. This allows us to estimate intellectual potentials by observing the communicative process. Our previous experiments, based on ideas of Information Theory, have shown that ants probably have an even more intricate form of communication than the honeybee. As reported here, we also succeeded in studying numerical properties of insect cognitive capacities, namely their ability to perform limited counting and to memorise simple regularities, thus compressing the information available (Reznikova, Ryabko, 1993, 1994, 2000; Ryabko, Reznikova, 1996). In this paper we describe the experiments which demonstrate red - wood ants as being able to count within several tens, and transmit this information to their nestmates. Analysis of time duration of ants' contacts enables us to hypothesise how they use numbers and numerical coordinates in their communication. We suppose that only a few highly social ant species use such a complex communication system based on cognitive processes.

II. Design of the experiments

The experiments were performed on *Formica polyctena* as a group retrieving species with a high level of social organisation. In various years 5 colonies of this species were used. Ants lived in a laboratory arena (200 x 200 cm), in a transparent nest (10 x 20 cm). The arena was divided into two sections: a smaller one, containing a laboratory nest, and a bigger one with an experimental system (see details in: Reznikova, Ryabko, 1994). Both sections were connected by a plastic bridge, which was from time to time removed to modify the set-up or to isolate the ants. Each of the colonies consisted of about 2000 ants. All experimental ants were marked with coloured labels and fed by sugar syrup only in the experimental set-up once every 2–3 days.

All series of laboratory experiments were performed by a common schedule: we provided a situation in which insects had to transmit information, quantitatively known to the experimentalist, in order to obtain food. Therein the time spent by the scouting ant on contact with foragers was measured.

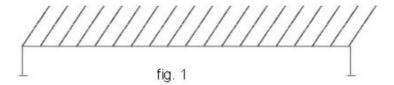
As this had shown before (Reznikova, Ryabko, 1994, 1996), the foragers of this species separated into "teams" of 5-8 specimens, each with one scout. As soon as the scout found food, it informed the members of its foraging team. In each series of experiments we placed scouts on the place with the trough containing food, using tweezers. The scout returned to the nest on its own. Sometimes the scout contacted its team at once, and the group began moving towards the set-up. In this case, after the scout 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 trough alone. Sometimes it made errors and only found the food-containing trough after visiting some empty ones. Then it returned to the nest again, contacted only one team, and either remained with the team or left it. In the first case the scout was isolated and we watched its foraging team. In the latter case we let the scout to repeat its trips, sometimes up to four times, before it was able to mobilise the foragers.

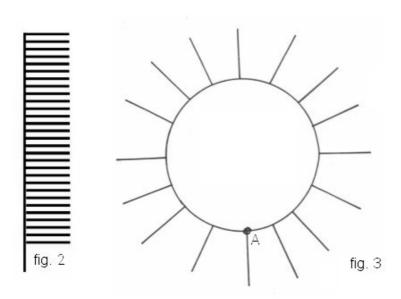
In all the cases of mobilisation, we measured the duration (in seconds) of the contact between the scout and the foragers together in the transparent laboratory nest. We considered the beginning of contact to occur when the scout touched the first forager ant, while we took the end of contact to be the moment when the nest was abandoned by the first two foragers. Contacts were followed by numerous antennal movements. Scouts touched one to four foragers in turn, sometimes two simultaneously. When the scout repeatedly returned to the trough alone, we measured the duration of each of its contacts with foragers. Only the duration of the last contact, followed by the foragers' abandonment of the nest, was taken into account. As a rule, all of the previous contacts were brief (1-5 sec.) and resulted in food exchanges.

Each series of experiments was preceded by "training" stages as long as 4 weeks, during which the ants explored set-ups and got accustomed to the work regime. At that time, we picked out actively working ants and marked them. Then, "incapable" scouts which either could not memorize well the way to the trough or could not mobilise their groups were revealed and discarded from further experiments. The experiments were so devised as to eliminate all possible ways helpful to finding the food, except distant homing, i.e. information contact with a scout. During contact between a scout and foragers in their nest, the experimental apparatus was replaced by a similar one with all troughs empty to avoid the use both of an odour track and the food odour. So, following their contact with the scout, the foragers visited troughs that were fully empty. When a compact "team" reached a goal, they were given a trough with syrup immediately, i.e. the trough at the goal was filled. The search was considered a success when the team came to the correct place leaving behind not more than 1 ant. An unsuccessful search, when the team failed to come or came in a small number (more than 1 forager behind) was called a failure.

The first series of 51 experiments conducted on a "comb-like" setup consisted of a long horizontal plastic "trunk" with 25 equally spaced plain plastic branches, of 6 cm length, also horizontal (fig. 1). Each branch ended in an empty trough, except for one filled with syrup. Ants came to the initial point of the trunk over an additional small bridge (the set-up was mounted on glass props covered with slippery oil to prevent the ants from moving in a straight line).

Fig. 1–3: the "comb"-like set-ups: a horizontal trunk (1), a vertical trunk (2) and a circle (3).

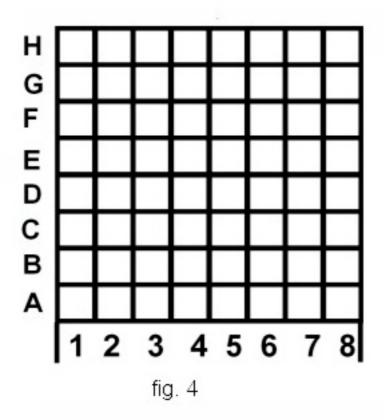




The second series of 31 experiments were carried out on a set-up with vertically situated branches (fig. 2). In order to test whether the time of transmission of information about the number of the "branch" depends on its length, as well as on the distance between the "branches", another set of 16 experiments was carried out on a similar "vertical trunk" in which the distance between the "branches" was twice as great, and the "branches" themselves were three times and five times longer (for different series). The series of 38 experiments was conducted on a "circle-like" set-up (fig. 3).

The preliminary investigation of the capacity of the ants for the transmission of information about co-ordinates of an object was carried out by means of a "Cartesian co-ordinate" set-up, a flat grid of thin metal rods (8 by 8, 6 by 6, 5 by 5 lines, fig. 4). Every set-up was fixed so that the ants could only reach the starting point of the maze across a small bridge (point A in fig. 3). The further movements were possible only along the lattice rods. During the experiments the trough containing food was placed at various nodes of the lattice, while on the other nodes the empty troughs were placed.

Fig. 4: the Cartesian - co-ordinates set-ups: "lattice" (4)



III. Results

The ants ability for information transmission on the number of objects

In total, 32 scout-foragers groups ("teams") worked in three kinds of set-ups. The teams abandoned the nests after they were contacted with scouts and moved towards the trough lacking their guides 152 times (note that we specially removed the scouts). In 117 cases the team immediately found the correct path to the trough, without making the wrong trips to empty troughs. In the remaining cases, ants came to the empty troughs, and began looking for food by checking neighbouring branches. In all experiments (31 in total), foragers failed to find the food containing trough when "incapable" scouts were working. Such scouts were removed from the working part of the arena.

Since all set-ups had no less than 25 branches, the probability to find the correct trough randomly is less than 1/25. Thus, the ratio we obtained experimentally can with high probability be accounted by information transmission from scouts. We note that the probability of finding the food-containing trough randomly in 117 cases out of 152 is less than 10 ⁻¹⁰. In addition, ants, including scouts, placed in the set-up, without having information on which trough contained food, usually failed to find the food, even though they actively searched for it.

Table 1. The results of experiments in the "vertical trunk 1".

Exp. Number	Number of food-	Duration of scout-	Working team
	containing branch	forager contact	number
1	10	42	I
2	10	40	II
3	10	45	III
4	40	300	II
5	40	280	IX
6	13	90	II
7	13	98	I
8	28	110	III
9	28	120	X
10	20	120	X
11	20	110	III
12	35	260	III
13	35	250	X
14	30	160	I
15	30	170	III

Table 2. Values of correlation coefficient (r) and regression (a, b) coefficients.

Type of setup	Sample size	Number of branches	r	$a \pm \Delta a$	$_{ m B}\pm\Delta_{ m b}$
Vertical trunk 1	15	40	0.93	7.3 ± 4.1	-28.8 ± 0.51
Vertical trunk 2	16	60	0.99	5.88 ± 0.44	-17.11 ± 0.65
Horizontal trunk 1	30	25	0.91	8.54 ± 1.1	-22.2 ± 0.62
Horizontal trunk 2	21	25	0.88	4.92 ± 1.27	-18.94 ± 4.75
Horizontal trunk 2	38	25	0.98	8.62 ± 0.52	-24.4 ± 0.61

Data obtained on the set-up "vertical trunk" are shown in Table 1 and on the graphic. In all setups the relation between the number of the branch i and the duration of the contact between the scout and the foragers t was linear, and may be described by the equality t = ai + b. The coefficient of correlation between t and i was high for different setups (Table 2).

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 when the counter-clockwise path was much shorter; we do not know the reasons for this. It is also interesting to note that on the "vertical trunk" after contact with the scout foragers climbed quickly to the upper end of the trunk, and then slowly returned to the food-containing branch; thus we numbered the branches starting from the upper end of the trunk.

The ants ability for information transmission on the co-ordinates of objects

In total, 5 scout-foragers groups worked in 2 set- ups. The teams abandoned the nests after they were contacted with scouts and moved towards the trough 40 times (note that we specially removed the scouts). In 31 cases the team found the correct path to the trough in less than 5 min. It is interesting to note that, contrary to situation when the ants had to choose the "right" branch, in a lattice the foragers moved from the initial point quickly, but not in a compact group, and reached the "node" with the trough each by its own pathway. Data on the time spent by the scouts on contact with their groups are presented in Table 3.

Table 3. Results on experiments on "Cartesian Co-ordinates" set-ups.

(Co-ordinates of		of foragers	Time spent by the
Experimen	Experime	trough containing	reaching (+) and not		scout for contact
tal set-up	nt number	food) the trough	with foragers (sec.)
1			"+"	´,,	
8x8	1	G_7	4	2	60
"lattice"	2	B_{6}	5	2 2	70
	3	B_{6}	3	1	80
	4	B_{6}	5	0	65
	5	D_4	4	2	90
	6	D_4	4	2	100
	7	D_4	7	1	95
	8	H_4	6	2	90
	9	H_4	5	0	105
	10	G_2	5	1	110
	11	G_2	5	0	105
6x6	12	C_2	6	0	60
	13	C_2	7	0	55
	14	C_4	5	0	70
	15	E_2	6	0	44
	16	E_2	5	1	52
	17	E_2	6	1	48
5x5	18	C_6	4	0	40
	19	C_6	4	0	45
	20	C_6	5	1	40
	21	C_2	6	2	50
	22	B_1	4	0	56
"globe"	23	B_4	3	0	80
	24	B_4	4	1	72
	25	B_4	4	0	65
	26	D_4	4	0	50
	27	D_4	4	0	58
	28	D_2	6	1	45
	29	D_2	5	2	52
	30	D_2	3	0	50
	31	D_2	3	0	50

Table 4. Results on control experiments on "Cartesian Co-ordinates" set-ups.

Tuble II Tiesu	Experiment	Co-ordinates of trough	Number of ants	Results of 15-
Experiment	number	containing food	visiting the maze	min.search
al set-up				
8x8	1	G_7	12	+
"lattice"	2	B_{6}	7	-
	2 3	B_{6}	10	-
	4	B_{6}	6	-
	5	D_4	12	-
	6	D_4	4	-
	7	D_4	1	-
	8	H_4	9	-
	9	H_4	5	+
	10	G_2	8	-
6x6	11	C_2	8	-
	12	C_2	8	-
	13	C_4	6	-
	14	E_2	4	-
	15	E_2	9	+
	16	E_2	2	-
5x5	17	C_6	4	-
	18	C_6	5	+
	19	C_6	6	-
	20	C_2	6	-
	21	B_1	3	-
"globe"	22	B_4	3	-
	23	B_4	9	+
	24	B_4	10	-
	25	D_4	11	-
	26	D_4	10	-
	27	D_2	6	+
	28	$\overline{\mathrm{D_2}}$	7	-
	29	$\overline{\mathrm{D}_{2}}$	12	_
	30	$\overline{\mathrm{D_2}}$	3	-

In order to test whether the foragers actually are guided by the information obtained from the scouts, a series of control experiments was carried out in which all of the ants were given the opportunity of access to an 8 by 8 "lattice", on one of the "nodes" of which the trough with syrup was found, and were able to walk about it for 15 min (let us recall that in the experiments the scout was purposely placed on the trough). The results are presented in Table 4. A result in which during the allotted time (15 min.) at least one ant found the food, was considered positive. No one forager found food in 24 cases out of 30.

Let us introduce two statistical hypothesis. H_0 : the probability of finding the food in which the foragers obtained the information from the scouts is the same as in the experiments with free search for the food; the alternative hypothesis H_1 : the probability of finding food by "directed" foragers is greater than in cases of free search for the needed point. In order to test H_0 against H_1 we use the chi-squire test. Computations show that hypothesis H_0 is rejected in favour of H_1 at a significance level of 0.001. Thus, it follows from the data presented that ants are capable of transmitting the information about the co-ordinates of objects.

IV. Discussion

The most parsimonious explanation of results concerning ants ability to search the "right" branch in the "comb"-like and "circle"-like set-ups is that they can estimate the number of objects and transmit this information to each other. Presumably they may pass messages not about the number of the branch but about a distance to it or about the number of steps and so on. Even if it is so, this shows ants as being able to use quantitative values and pass the information about them. But it is worthy of noting that the relation between the number of the branch and the duration of the contact between the scout and the foragers is well described by the equality t = ai + b for different set-ups which are characterised by different shapes, distances between the branches and lengths of the branches. The values of parameters a and b are close and do not depend either on the lengths of the branches nor on other parameters. All this enables us to suggest that ants transmit the information just about the number of the branch.

The results of the experiments with lattice set-up, showed that the ants are able to memorise and transmit information regarding the location of a trough containing food in a plane. At this stage we do not consider hypothesis about mechanisms of coding or representation of such information in ants' communication.

Summarising, our data support the hypothesis that communicative means of red - wood ants allow them to code and pass the information about numerical characteristics and co-ordinates of objects. This adjusts with recent data on co-ordination of working processes and division of labour within small working "teams" in this species in natural condition. It has revealed that, in order to obtain honeydew, a foraging group of 5 - 10 specimens has to search for a certain leaf with an aphid colony within such a huge 3- dimension space as a tree is for an ant. Successfulness of activity of these groups depends on activity of the scouts which attract "shepherds", "watch ants" and "transporting ants" to a new aphid colony (Novgorodova, Reznikova, 1996; Reznikova, Novgorodova, 1998).

There are many situations in a history of studying of cognition in animals when applying an adequate method, animal behaviour students essentially changed imaginations about limits of intellectual possibilities of their subjects, particularly, of their numerical competence. Thus, close treatment and examination of a chimpanzee (*Pan troglodytes*) applying a method of sample-choice, revealed its ability to count within limits of two objects only (Kohts, 1923). The use of sequential responding task, allowed to show a subject of the same species as being able to respond to Arabic numerals between 1 and 9 and to suggest that an ape might form the integrated 9 - item linear representation (Matsuzawa, 1985; Tomonaga, Matsuzawa, 2000).

The numerical capacities of several avian and mammalian species have been examined since the beginning of the last century using a wide variety of numerical tasks. It has been shown that rats and birds, in particular, pigeons, crowns and parrots, are capable of executing a particular numbers of discrete responses, quite precisely when the required number of responses is low but not so precisely when the response requirement is high (see Butterworth, 1999). Recently the use of symbolic numeral stimuli allowed to demonstrate in pigeons a flexible constructive- counting-like behaviour that involved the production of up to six responses conditional upon the separate pre-presentation of up to six numeral symbols (Xia et. al, 2000). Crows turned out to be able to choose the greater array from pairs of numerousness not only in the range of 1-12 but also 10 - 20 (Zorina, 1997) although earlier they have been believed to discriminate objects within limits of 7 only (Koeler, 1956). The use of animal's natural "languages" for studying their intellectual capacities, particularly, numerical skills, amazingly has never been applied, although very impressed results have been achieved in this area by means of intermediate languages (Boysen, 1992; Pepperberg, 1994).

Studying processes of information transmission within ant's colony may serve as a good background for starting with applying natural communicative means of animals to estimate limits of their cognitive abilities. As far as cognitive processes in social insects are concerned, excellent learning capacities have been demonstrated in ants and bees. Some experiments have shown

these insects as being capable of abstraction, extrapolation and of solving rather complicated tasks in order to get bearings (Reznikova, 1982; Collet et al., 1993; Lehrer, 1996). Recent studies have revealed a great deal of flexibility of foraging strategies in ants (Mercier, Lenoir, 1999). At the same time, the bounds of insects' numerical competence are still remain unclear. Only few findings concern this theme. Thus, at least, protocounting abilities of the honeybees have been demonstrated basing on experiments in which insects had to use number of landmarks as the criteria to find the feeder (Chittka et al., 1995; Menzel et al., 1996). It is also known that ants of several species are able to estimate quite precisely numbers of encounters with members of other colonies on their feeding territories (Reznikova, 1980, 1994, 1999; Gordon, 1994; Brown, Gordon, 2000).

It is important to note that information transmission from the scouts to the foragers is possible only for a few high social ant species which possess structured co-operation and division of labour between leaders and followers. In spite of wide spread of solitary foraging in different ant species, collective behaviour and decision-making in the majority of species are based on numerous interactions among individuals which use local information and follow rather simple algorithms (Detrain et al., 1999). Isolated instances have been described up to now concerning teams in the army ants *Eciton burchelli* (Franks, 1996) and *Dorylus wilverthi* (Franks et al., 1999) as well as teams in group retrieving *Formica* species including a key individual and followers (Robson and Traniello, 1999). According to Anderson and Franks (2001), "teams" revealed by ours (Reznikova, Ryabko, 1990, 1994, 1996), as well as "dance groups" in honey bees (Waddington, 1989) should more properly be called "cliques", *sensu* Holldobler and Wilson (1990:343) who defined a clique as a "group of workers whose members recognise one another as individuals to accomplish some task".

For ants, the bounds of applying of our approach are limited by set of species with social style of life basing on division of labour within "cliques".

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