

Dialog with black box: using Information Theory to study animal language behaviour

Zhanna Reznikova

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Abstract In this review, three main experimental approaches for studying animal language behaviour are compared: (1) direct decoding of animals' communication, (2) the use of intermediary languages to communicate with animals and (3) application of ideas and methods of the Information Theory for studying quantitative characteristics of animal communication. Each of the three methodological approaches has its specific power and specific limitations. Deciphering animals' signals reveals a complex picture of natural communication in its evolutionary perspective but only fragmentary because of many methodological barriers, among which low repeatability of standard living situations seems to be a bottleneck. Language-training experiments are of great help for discovering potentials of animal language behaviour but leaves characteristics of their natural communications unclear. The use of the methods of Information Theory is based on measuring the time duration that animals spend on transmitting messages of definite information content and complexity. This approach, although does not reveal the nature of animals' signals, provides a new dimension for studying important characteristics of natural communication systems, which have not been available before. First of all, this approach enables explorers of animals' language behaviour to obtain knowledge just about the ability of subjects for transferring meaningful messages. Besides, the important properties of animal communication and intelligence can be evaluated such

as the rate of information transmission, the complexity of transferred information and potential flexibility of communication systems.

Keywords Animal communication · Experimental approach · Information Theory · Deciphering signals · Intermediary languages

Introduction

In this review, the idea is to compare three main experimental paradigms in studying animal language behaviour and to highlight the new dimension in this field, which is provided by ideas and methods of the Information Theory (Shannon 1948).

The communication systems of animals are a matter of special research interest to ethologists. Attempts to elucidate a question whether animals can exchange meaningful messages are based on a natural idea that the complexity of communication should be connected with high levels of sociality and cooperation in animals' societies (Garner 1892; Lorenz 1952).

In the 1960s and 1970s, elegant but ambiguous experiments were conducted with highly social intelligent animals, which were asked to pass some pieces of information to each other. In Menzel's (1973a,b) classic experiments, a group of chimpanzees living in an enclosure searched for hidden food. Menzel suggested that chimpanzees possess means for transferring information about both location and properties of objects, but it remained unclear how they did this. Evans and Bastian (1969) and later Markov and Ostrovskaya (1990) and Zanin et al. (1990) experimentally investigated the cooperative behaviour of dolphins, which could involve intelligent communication.

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Z. Reznikova (✉)
Institute for Animal Systematics and Ecology,
Novosibirsk State University,
Frunze 11,
Novosibirsk 630091, Russia
e-mail: zhanna@reznikova.net

To get a fish, pairs of dolphins, separated by an opaque barrier, had to press the paddles in the correct order. The obtained results enabled researchers to suggest that dolphins can co-ordinate the behaviour of each other, probably, by means of acoustic signals.

Despite these supportive experiments, the question of existence of developed “languages” in non-humans remained so far obscure. What can be called “language behaviour” in animals and how it differs from communication and speech? How to treat language behaviour in non-humans is heavily influenced by our choice of which definition of language to adopt. Even following broad definitions of language, animal experts are oscillating between questions “Why animals do not have language?” (Cheney and Seyfarth 1997) and “What is so special about speech?” (Hauser 2001).

The term “communication” enjoys a wide variety of meanings, which is of no wonder because communication is a diverse and widespread phenomenon that serves as a substance of any social behaviour. For instance, Vauclair (1996) defines communication as the following: “Communication consists of exchanges of information between a sender and a receiver using a code of specific signals that usually serve to meet common challenges (reproduction, feeding, protection) and, in group-living species, to promote cohesiveness of the group.”

It is often difficult to decide whether animals intend to share information with conspecifics, or they use inadvertent signalling. It is likely that to identify complex forms of animal communication that may be attributed to language behaviour, deliberation can be considered a necessary condition. While a concept of communication is too broad, a concept of “speech” is too narrow for considering the form of information transferring in animals. In the great majority of scientific literature, speech is defined as a form of communication specific to humans (for a review, see Hauser et al. 2002). The concept of “language” should be more useful for reasoning about complex forms of animal communication. It is now agreed that language cannot be described or defined by one single feature, but it is rather a polymorphous concept. Hockett (1963) identified a range of characteristics that described essential features of language. Some of Hockett’s design characteristics can serve as useful criteria to assess claims about animal language. Among them, the following features are listed in ethological literature: interchangeability, specialisation, discreteness, arbitrariness of units, displacement, semanticity, productivity, traditional (cultural) transmission (Hockett 1963; Gardner and Gardner 1980; Fouts et al. 1982). The main difficulties in the analysis of animal “languages” seem to be methodological. At least three main approaches to a problem of animal language behaviour have been applied recently.

The first approach is aimed at direct decoding of animal signals. Although it is intuitively clear that many high social species have to possess complex communications, only two types of natural messages have been decoded up to the present. The matter concerns the symbolic honeybee “dance language” (von Frisch 1947, 1967; Seeley 1995; Dornhaus and Chittka 1999) and acoustic signals of danger, which were decoded for vervet monkeys (Seyfarth et al. 1980) and, later, for several other species (Evans and Marler 1991; Slobodchikoff et al. 1991; Slobodchikoff and Placer 2006; Manser 2001).

The second approach is based on the use of intermediary artificial languages. Being applied to apes, dolphins and one grey parrot, this method has revealed astonishing mental skills in the subjects (Gardner and Gardner 1969, 1998; Premack 1971; Pepperberg 1981, 1999; Herman et al. 1999; Rumbaugh and Savage-Rumbaugh 1994). It is important to note that this way to communicate with animals is based on adopted human languages. Yet surprisingly, few are known about natural communication systems of those species that were involved in language-training experiments.

The third approach to study animal communication has been suggested basing on ideas of Information Theory (Reznikova and Ryabko 1986, 1990, 1994; Ryabko and Reznikova 1996). The main point is not to decipher signals but to investigate just the process of information transmission by measuring the time duration that animals spend on transmitting messages of definite information content and complexity. The experimental paradigm is relatively simple. All we need is to “ask” subjects to transfer the intended quantity of information to each other. This approach enables explorers of animal language behaviour to get the answer for their key question concerning the ability of subjects for transferring meaningful messages. In fact, the idea of the experiments may be reminiscent of the experiments of Menzel (1973a,b) with chimpanzees who had to pass each other the information about the hidden food. However, the main idea of the cited experiments with ants is that now, experimentalists know exactly the quantity of information to be transferred. To organise the process of information transmission between animals, a special maze is used, called by Reznikova and Ryabko (1986) the “binary tree”, where the number and sequence of turns towards the feeder corresponds to the amount and complexity of the information being transferred by animals to each other. Adhering to the main stream of Information Theory, we can consider this method a dialog with a “black box”, that is, studying effects made by signals on the input and output of an agent rather than investigating the nature of the signals. This experimental paradigm provides the new dimension for studying important characteristics of natural communication systems which have not been

available before, and among them are the rate of information transmission, the complexity of transferred information and potential flexibility of communication systems. Application of ideas and methods of Information Theory has already allowed researchers to demonstrate that a few highly social ant species possess possibly one of the most intricate forms of known animal communication (Reznikova and Ryabko 2003).

Decoding and appreciation of animals' signals

Can animals exchange meaningful messages? Understanding natural “languages” of animals seems to be an attractive and hardly achievable skill for humans with which many legends are associated. The title of the book of Lorenz (1952), *King Solomon's Ring*, refers to a legend about King Solomon who possessed a magical ring that gave him the power of speaking with animals. As early as in 1661 Samuel Pepys wrote in his diary about what he called a “baboon”: “I do believe it already understands much English; and I am of the mind it might be taught to speak or make signs” (as cited in Wallmann 1992). More than 200 years later, Garner (1892) experimentally tried to learn the “monkey tongue”. With the help of the phonograph, Garner conducted first playback experiments on several species of apes and monkeys. He artificially changed the elements of the animals' signals and then compared how the subjects reacted to variants of reproduced “words”. In particular, Garner claimed to distinguish a word that meant “food” in the capuchin's “language” from the others, which meant “bread” and “vegetables/fruits”. Garner anticipated some findings of present days. For instance, applying a similar experimental paradigm, Hauser and Marler (1992) found that rhesus macaques produce five acoustically distinctive vocalisations when they find food. Three vocalisations are restricted to the discovery of high quality, rare food items, whereas the other two are given while waiting for lower quality, common food items. It has been proven experimentally that the type of vocalisation produced is influenced by the type of food discovered and not by the discoverer's hunger level (Hauser 2000).

The problems underlying the construction of species' “dictionaries” and to identify categories in their communications have been discussed during the last decades. Many researchers have tried to decode animal languages by looking for “letters”, “words” and “phrases” (Ryabko 1993). With such an approach, it often remains unclear which sounds and gestures have something to do with the language and which do not, and there are also some technical difficulties connected with the high mobility of animals and often with their inaccessibility for recording signals.

Theberge and Pimlott (1969) noted that when studying wolves' ability to produce and distinguish subtle details of acoustic signals, they were challenged by the problem of understanding a foreign culture's sounds lacking a relevant dictionary and any ideas about this culture. Theberge and Pimlott (1969) suggested that wolves were able to transfer the information by changing certain units of their acoustic communication, but the only “word” they managed to decipher was a “sound of loneliness” that wolves produce being placed in isolation, anxious to join others.

Since that, many distinct acoustic signals have been revealed in wolves, African wild dogs (Robbins 2000), bottlenosed dolphins (Janik 2000), primates (see Snowdon et al. 1982) and other highly social and intelligent animals. Acoustic vocalisation in some species of birds and mammals often has a hierarchical structure, with notes grouped into syllables, syllables grouped into phrases and phrases grouped into a song with linear array of phrases (Slater 2003). These data enable researchers to undertake efforts to understand the meaning of animal signals and to test whether species' communications exhibit a language format.

It is likely that a bottleneck for decoding animals' signals is low repeatability of standard living situations, which could give keys for cracking animals' species-specific codes. In fact, animals sometimes behave similarly in repeatable situations, and if these repeatable behaviours are elicited by the distinctive repeatable signals, these behaviours can serve as keys for cracking animals' species-specific codes. Decoding the function and meaning of wild communications is a notoriously difficult problem. Up to now, there are two types of natural communication systems that have been partly deciphered: the fragments of honeybees' “dance language” and acoustic signalisation in several species. In both types of communications, expressive and distinctive signals correspond to repeatable and frequently occurring situations in the context of animals' life.

The dance language of honeybees This is the most complex animal natural “language” that has been decoded, at least partly. Successful forager honeybees (*Apis mellifera*) are able to recruit other bees to a distant food source (or water, or resin) by specific “dance” movements together with other components of communications such as odours and sounds. von Frisch (1923, 1947, 1967) suggested that in the bees' dance language, an abstract, or symbolic, code is used to transmit the information about the direction and distance to a desired object. Years after von Frisch interpreted the symbolism of the dances other components of the bees' communication system have been appreciated (see Gould and Gould 1988; Seeley 1995; Tautz et al. 2001). It is worth to note that honeybees can communicate not only about food by means of dance figures but also about the location

of a new nest site (Lindauer 1961; Camazine et al. 1999; Lewis and Schneider 2000), and that intellectual navigation requests cognitive resources (Menzel et al. 2005). Recently, Land and Seeley (2004) discovered a special “grooming invitation dance” by which bees “ask” their nestmates for helping them to clean those parts of the body that they cannot reach by themselves. Discoveries of new messages in bees’ “language” are based on insightful findings of new repeatable situations in their routine life.

The suggestion that bees have a symbolic language aroused the scepticism of many scientists, who continue to this day to favour the idea that scent alone guides bees to a distant food source (Gould 1976). Nevertheless, the experiments, using an artificial model of a bee, confirmed that the dances do indeed represent a sophisticated form of communication (see Kirchner and Towne 1994). Michelsen and colleagues built a robot bee controlled by a computer that could reproduce intended components of a bee’s dances (Michelsen 1993, 1999; Michelsen et al. 1990). Foraging bees then found new targets, correctly following messages from the robot bee that never left the hive itself.

Although the honeybees’ dance language still remains an outstanding example of successful deciphering of animals’ “language” and it is still considered a single natural non-human communication system that meets the main Hockett’s criteria, many important characteristics of this type of communication have not been revealed yet. In particular, it is still an open question to what extent can bees display creativity and flexibility of communication (Weidenmüller and Seeley 1999; Tanner and Visscher 2005). Some experimental results enable us to suggest that honeybees may appreciate the meaning of messages they receive. Lindauer recalled their joint experiment with von Frisch in 1948 when they moved an observation hive from its normal vertical position to a horizontal position and were surprised to see that bees dancing on a horizontal comb could indicate a direction to a food source (see Seeley et al. 2002). In the experiments of Dyer (1991), bees left the hive when the returning scout indicated that the food was beside a lake. However, they did not leave the hive when they were informed that food was near the middle of the lake. Thus, honey bees appear to interpret the meaning of the dance—possibly by identifying the potential location of food, and then decide whether it is worth making the journey.

Semantic vocalisations in animals: words without a language? The main experimental method for studying acoustic language behaviour in animals is based on quantitative comparative analysis of signals and on playback experiments; researchers record vocalisations that animals emit in distinct living situations, then digitise tapes by computer programmes and break them down into

frequency and timing. Changes in frequency and time are measured, and these data are re-entered into the computer and analysed to see if there are differences between signals. During playback experiments, tapes are played for animals either in their natural form, or artificially changed, for example, slowed or containing added elements. Primates are good candidates to have dictionaries being compiled for them by human researchers. After Garner (1892) who tried to decipher acoustic signals of several primate species with the use a phonograph, many primatologists had been working in this field. During the second part of the twentieth century, lists of possibly meaningful signals have been compiled for several primate species such as signals of greetings, invitations for playing, sex, sharing food, predator alarm, intergroup treat, affiliation, infant distress, discontent, quarrel, nocturnal roll call, cooing with infants and so on (Lawick-Goodall 1968; Green 1975; Marler and Tenaza 1977; Snowdon 1986). A representative “Vervet–English” dictionary has been firstly compiled by Struhsaker (1967). He found that the vervet monkeys in the wild emitted 25 discrete calls referring to different objects and situations. Nevertheless, the majority of signals were not enough distinct and frequently used. Only three “words” seemed to be understandable not only by monkeys but also by human observers. Three different sounds emitted by vervets for three different predators (leopards, eagles and snakes) resulted in three different reactions or escape responses. The calls appeared to function as representational, or semantic, signals. Seyfarth et al. (1980) and Seyfarth and Cheney (1990) applied playback experiments to reveal characteristics of vervets’ communication. In particular, they addressed the question about whether animals can refer to meanings of “words” rather than to their acoustic properties. These findings have dramatically changed common thoughts about acoustic communications in animals, which were believed to be only an expression of their current emotional status. However, Seyfarth and Cheney (2003) accentuate limits of animal acoustic communication and its great difference with the sophisticated language of humans. In particular, to be considered “language-like”, the wild acoustic communication does not meet several important criteria such as displacement and productivity.

Since vervet studies, human comprehension of animal “dictionaries” has been expanded to several other species. For example, West African Diana monkeys, *Cercopithecus diana*, produce acoustically distinct alarm calls in reaction to leopards and crowned-hawk eagles, their main predators. Playback experiments have shown that monkeys treat these vocalisations as semantic signals, in the sense that they compare signals according to their meanings (Zuberbühler 2000). Comparative studies demonstrated several non-primate species as being capable of conveying complex

information through vocal signals. Slobodchikoff et al. (1991) identified prairie dog calls for four predators—human, hawk, coyote and domestic dog. Prairie dogs even can speed up or slow down their signals depending on whether the predator is running or walking through their colony. Meerkats (*Suricata suricatta*) give one alarm call type to mammalian predators, primary jackals and African wild cats, a second alarm call type to avian predators, primary the martial eagle, and a third alarm call type to snakes and to faecal, urine or hair samples of predators (Manser 2001). Development studies suggest that pups possess inherited vocalisations but they definitely need to learn how to respond appropriately to the different alarm call types (Hollén et al. 2006). Not only alarm calls but also food calls may be functionally referential in a sense that they encode information about the kind, quantity and availability of food. The evidence that food calls provide sufficient information to evoke anticipatory feeding behaviour from conspecifics has been obtained from playback experiments with domestic chickens (Evans and Marler 1991). Ravens, *Corvus corax*, emit structurally discrete yells when they approach rich but defended food sources and thus attract conspecifics (Heinrich 1999). Bugnyar et al. (2001) experimentally exposed a group of free-ranging ravens to six feeding situations. Researchers thus modelled distinct repeatable situations and examined what calls emitted by ravens correspond to which kind of food, of which quantity and availability. The different use of long and short yells relative to food availability suggests that short “who” calls provide information about the caller, whereas long “haa” calls may also provide information about the food itself.

Of course, data referred in this section do not pretend for completeness. Nevertheless, one can see that many interesting results have already been obtained by those researchers who were trying to decipher animals’ signals. However, even if we crack fragments of animals’ codes, our knowledge about degrees of divergence between potential and discovered power of species’ “languages” is largely constrained by the current methodology (Ryabko 1993). Only limited data have been obtained yet in evaluation of potential complexity of the information being transferred.

Dialog with animals by means of language-training experiments

The use of intermediary languages for studying “linguistic” and intellectual potential of animals has changed the general concept of animal communication and intelligence. Only 30 years ago, it could be difficult to imagine that animals can learn to associate arbitrary signs with meanings,

to generate new symbols with new meanings, and to use these signs to communicate simple statements, requests and questions; to refer to objects and events displaced in time and space; to classify novel objects into appropriate semantic categories; and to transmit their knowledge to peers and offspring.

There are many excellent books and reviews written by researchers who carried out projects on teaching sign languages to apes (Savage-Rumbaugh and Lewin 1994; Fouts 1997; Patterson and Linden 1981), dolphins (Herman et al. 1984), and an African grey parrot (Pepperberg 1999). In this paper, I briefly describe how this method has influenced the development of studying animal language behaviour.

As early as in 1925, Yerkes suggested the idea to teach chimps sign language used by deaf people to make a dialog between humans and non-humans possible. Ulanova (1950) possibly was the first who taught a primate to use gesture signs to denote desired things. She taught a rhesus macaque to make finger gestures to obtain rewards of different kinds. Different gestures corresponded to different food items (nuts, pieces of apples, bread, strawberry and garden radish) and drinks (coffee, tea and milk). Several projects trying to teach apes developed human language started in 1966, from the project of Gardner and Gardner (1969) who began teaching a chimpanzee the use of American Sign Language (ASL). Similar studies using ASL were carried out using other chimpanzees (Terrace 1979; Fouts 1997), gorillas (Patterson 1978) and an orangutan (Miles 1993). Alternative approaches to teaching apes, a language has been elaborated basing on special devices and thus allowed to compare language abilities of animals more objectively. Premack (1971) elaborated an artificial language in which the words were plastic figures, which varied in shape, size, texture and colour. Plastic words were arbitrary. Sarah, Premack’s brightest chimpanzee, was taught nouns, verbs, adjectives, pronouns and quantifiers; she was also taught same–difference, negation and compound sentences. Premack’s technique has been developed further to a project supervised by Rumbaugh (1977), in which the symbols serving as words—or “lexigrams” as they were called—were displayed on a keyboard connected to a computer. One of the most interesting studies of language learning in primates is that of a bonobo Kanzi (and later of several other pigmy chimpanzees) with the use of lexigram keyboard (Rumbaugh and Savage-Rumbaugh 1994). Series of tests showed that bonobo could both understand and produce sentences. The researchers claim that Kanzi’s communications, made with lexigrams and gestures, were structured according to rules, so he used a simple version of grammar (Savage-Rumbaugh et al. 1998).

The African Grey parrot (*Psittacus erithacus*) Alex has been taught by Pepperberg (1981, 1983, 1999) to use English as an intermediary language. Alex was trained first

to speak with the names of objects (e.g. “key”, “grain”, “paper” and so on). Whenever Alex named an object correctly, he was praised and then allowed to eat it or to play with it. Being trained in this manner during many years, Alex currently uses more than 100 English words correctly to refer to all objects in his laboratory environment that play a role in his life. He answers correctly an astonishing number of questions regarding these objects, such as “What object is blue?”, “What shape is wood?”, “How many are wool?”.

Herman and colleagues study dolphins’ linguistic skills focusing on their language comprehension rather than on language production (Herman 1980, 1990; Herman et al. 1999). The researchers concentrate on dolphins’ receptive competencies, mainly on their capabilities of processing both semantic and syntactic information. The primary syntactic device used in the studies was word order. Dolphins were shown to be capable of understanding that word order changes meaning. Dolphins’ ability to understand whether things are present or missing gave a possibility to test whether they are capable of symbolic reference. Herman and Forestell (1985) constructed a new syntactic frame consisting of an object name followed by a gestural sign called “Question”. For example, the two-item gestural sequence called as “basket question” asks whether a basket is present in the dolphin’s habitat. The dolphin could respond “yes” by pressing a paddle to her right or “no” by pressing a paddle to her left. Over a series of such questions, with the particular objects present being changed over blocks of trials, the dolphin was as accurate at reporting that a named object was absent as she was at reporting that it was present. These results gave an indication that the gestures assigned to objects were understood referentially by the dolphin, i.e. that the gestures acted as symbolic references to those objects. The result from similar studies on sea lions, which revealed much the same findings as with dolphins, can be found in Schusterman and co-authors’ publications (Schusterman and Krieger 1986; Schusterman et al. 2002).

In general, dialogs with several highly social and intelligent species by means of intermediary languages have revealed astonishing “linguistic potential” in them, which includes such important properties of the developed language as propensity for categorisation, creativity and displacement. However, this method does not allow us to judge about the complexity of animals’ natural communications.

What Information Theory furnishes for explorers of language behaviour

It is a natural idea to use the Information Theory approach in investigating animal language behaviour because this

theory presents general principles and methods for studying and development of effective and reliable communication systems. Shannon (1948) developed the basis of Information Theory. The fundamental role of this theory was appreciated immediately, not only in the technology of information transmission, but also in the study of natural communication systems. In particular, in the 1950s and 1960s, the entropies (degree of uncertainty and diversity) of most European languages were estimated. It was revealed that in all human languages, the length of a message correlates with the quantity of information that is contained in this message. It means that one can lodge on two pages twice as much information as on one page. Later information theoretical ideas entered the fields of robotics, linguistics, psychology, physiology, etc. For example, human reaction time under experimental conditions turned out to be proportional to the uncertainty present in the experiment (Yaglom and Yaglom 1976).

Surprisingly, biological applications of Information Theory have been incorporated only in a few studies. Haldane and Spurway (1954) made an attempt to estimate bees’ message comprehension, and they counted 12 bits of information in bees’ standard dances of mobilisation. Wilson (1971) used the Information Theory approach to estimate the quantitative volume of the ability of the honeybees and the ants *Solenopsis saevissima* to memorise the location of a food source. However, there was no experimental paradigm elaborated for direct examination of the properties of animals’ communication.

Ants possess complex forms of communications, and they are known as being able to use a large variety of communication means for attracting their nestmates to a food source (for a review, see Hölldobler and Wilson 1990; Thorne and Traniello 2003). It has remained unclear for a long time whether ants can use distant homing as part of communication system. In this aspect, the so-called tactile (or antennal) “code” has been discussed since Wasmann (1899) first hypothesised such an information transmission system in ants. However, the numerous attempts to decipher ants’ “tactile language” have not given the desired results. It was concluded that antennal movements have no structural unity of signals and replies (Lenoir and Jaisson 1982; Bonavita-Cougourdan and Morel 1984; Hölldobler 1985). At the same time, it is clear that highly social species possess the necessary prerequisites for complex communication. Experimental studies revealed sophisticated forms of social learning in ants (Reznikova 1982, 2001, 2005), in particular in scout-foragers exchange format (Franks and Richardson 2006). Investigations of connections between the behaviour of scouting ants and the characteristics of the food they have found (such as the type, quality and quantity of food) enabled researchers to appreciate a semantic value of ants’ signals (for reviews, see Le Breton and Fourcassié

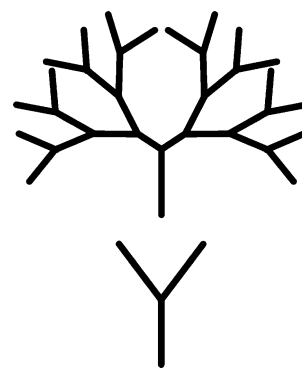
2004; Devigne and Detrain 2006). However, methodological limitations have hampered the progress of studying “linguistic potential” of ants’ communication.

Reznikova and Ryabko (1986, 1990, 2003) applied ideas and methods of Information Theory for studying ants’ communication system. The main point of this approach is not to decipher signals but to concentrate just on the process of transmission of a measured amount of information and thus to evaluate potential power of ants’ “language”. Basing on a dialog with ants’ family as a “black box” and asking them to transfer a definite amount of information, these authors estimated the rate of information transmission in ants, which turned out to be not high (approximately one bit per minute). They also succeeded in studying some properties of ant intelligence, namely, their ability to memorise and use simple regularities, thus compressing the information available.

The experiments provide a situation in which ants have to transmit information quantitatively known to the researcher to obtain food (Reznikova and Ryabko 1994; Ryabko and Reznikova 1996). This information concerns the sequence of turns towards a trough of syrup. The laboratory maze “binary tree” is used where each “leaf” of the tree ends with an empty trough with the exception of one filled with syrup. The simplest design is the tree with two leaves. It represents one binary choice that corresponds to one unite of information introduced by Shannon, the bit. In this situation, a scouting animal should transmit one bit of information to other specimens: to go to the right (R) or to the left (L)—see Fig. 1. In other experiments, the number of forks in one branch increased to six. Hence, the number of bits necessary to choose the correct way is equal to the number of bifurcations, four in this case (Fig. 1).

The experiments (Reznikova and Ryabko 1994, 2003) with binary tree were conducted with ten laboratory colonies of six ant species. Ants were housed in plastic transparent nests that made it possible to observe their contacts. All the ants were labelled with an individual colour mark. The composition of ants’ groups was revealed during preliminary stages of the experiments. In *Formica* ants small cliques within the colonies were discovered which were composed of a “scout” and 5–8 “recruits” (foragers). The total of 335 scouts were used in the main trials. A scout was placed on a trough containing food, and then it returned to the nest by itself. The scout had to make up to four trips before it was able to mobilize the group of foragers. In all the cases of mobilisation, we measured (in seconds) the duration of the contact between the scout and the foragers. When the group began moving to the maze the scout was isolated by tweezers and the foragers had to search for the food by themselves. To prevent access to the food by a straight path, the set-up was placed in a water bath, and the ants reached the initial point of the binary tree

Fig. 1 The maze “binary tree” with one fork and four forks



by going over a bridge (Fig. 2). The experiments were devised so as to eliminate all possible ways helpful to finding food, except information contact with the scout. To avoid the use of an odour track, the experimental set-up was replaced by an identical one when the scout was in the nest contacting its group. The fresh maze contained all troughs filled with water to avoid the possible impact of the smell of syrup. If the group reached the correct leaf of the binary tree, they were immediately presented with the food (video records of the experiments are available at: <http://www.reznikova.net/pictures.html>).

The long-term experiments revealed information transmission based on distant homing within small constant cliques consisting of a scout and foragers in *Formica* s.str. Not all of the scouts managed to memorise the way to the correct leaf on the maze. The number of such scouts decreases with the complication of the task. In the case of two forks, all active scouts and their groups (up to 15 per colony) were working, whereas in the case of six forks, only one or two coped with the task. Evidence of information transmission from the scouts to the foragers came from two sets of data: first, from the statistical analysis of the number of faultless findings of the goal by a group, and second, from special series of control experiments with “uninformed” (“naive”) and “informed” foragers.

The statistical analysis of the number of faultless findings of the goal was carried out by comparing hypothesis H_0 (ants find the “right” leaf randomly) with hypothesis H_1 (they find the goal thanks to obtained

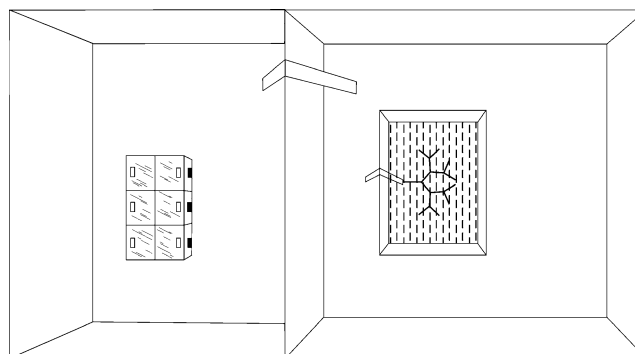


Fig. 2 The laboratory arena with the maze “binary tree”

information), proceeding from that the probability of a chance finding of the correct way with i number of forks is $(1/2)^i$. Experimenters analysed different series of experiment (338 trials in sum), separately for 2, 3, 4, 5 and 6 number of forks. In all cases H_0 was rejected in favour of H_1 , $P < 0.001$ (see Ryabko and Reznikova 1996), thus unambiguously demonstrating information transmission from scouts to foragers.

The special experiments were performed in which naive ants were tested in the maze. Researchers compared searching results in the ants that had and had no previous possibility to contact the scout (the “informed” and “naive” ants, correspondingly). The naive and “informed” ants were allowed to search for the food during 30 min. In more agile *F. pratensis*, the time spent on searching the trough by “informed” and “uninformed” specimens were compared (Reznikova and Ryabko 2003; Novgorodova 2006). For example, in *F. pratensis*, almost all “naive” foragers were able to find food on their own, but they spent 10–15 times more than those ants that entered the maze after the contact with the successful scout. Average values and amounts of sampling are given in Table 1. For every trial, Wilkoxson’s non-parametric test was used (see Hollander and Wolf 1973) to test the hypothesis H_0 (data from both samples follow the same distribution) against H_1 (they follow different distributions) at significance level 0.01. It turns out that the duration of searching time is essentially greater in those ants that previously contacted with the successful scout.

In sum, the obtained data confirm information transmission in three species belonging to subgenus *Formica* s.str., whereas the experimental design eliminates any other orientation mechanism, except the use of information transmission by the scouts.

No information transmission based on distant homing was observed in the other two species. In singly foraging *F. cunicularia*, the foragers learned the way towards the maze, whereas making up to 30 trips per day, but they did not try to recruit other members of their colony. Not more than five

ants were active in the maze per day. *M. rubra* workers used olfactory cues, but when we changed the maze, they had to cope with the task without odour trails. In these cases, they resorted to only solitary foraging, just as *F. cunicularia*.

Evaluation of information transmission rate in ants is based on the fact that the quantity of information (in bits), necessary for choosing the correct way towards the maze, equals i , the number of forks (Ryabko and Reznikova 1996). One can assume that the duration of the contacts between the scouts and foragers (t) is $ai+b$, where i is the number of forks, a is the coefficient of proportionality, equal the rate of information transmission (bit/min), and b is an introduced constant, since ants can transmit information not related directly to the task, for example, the simple signal “food”. Besides, it is not ruled out that a discovering ant transmits, in some way, the information on its route to the nest, using acoustic or some other means of communication (Hickling and Brown 2000). In this connection, it is important that the way from the maze to the nest was in all experiments approximately the same and, therefore, the time before the antennal contact with the foragers in the nest, which the scout could hypothetically use for the message transmission, was approximately the same and did not depend on the number of forks.

From the obtained data, the parameters of linear regression and the sample correlation coefficient (r) can be evaluated. The rate of the information transmission (a) derived from the equation $t=ai+b$, was 0.738 for *F. sanguinea* and 1.094 for *F. rufa*. These values are not considered species-specific constants; they probably vary. Note that the rate of information transmission is relatively small in ants.

To estimate the potential productivity of ants “language”, let us count the total number of different possible ways to the trough. In a simplest binary tree with one fork, there are two leaves and therefore two different ways. In a tree with two forks, there are 2^2 ways, with three forks, 2^3 ways, and with six forks, 2^6 ways; hence, the total number of different ways is equal to $2+2^2+2^3+...+2^6=126$. This is the minimal number of messages the ants must possess to pass the information about the food placed on any leaf of the binary tree with six forks.

Another series of experiments was based on a basic concept of Kolmogorov complexity and was aimed to check whether highly social ant species possess such an important property of intelligent communicators as the ability to quickly grasp the regularities and to use them for coding and “compression” of information. Thus, the length of the text should be proportional to the complexity of the information. This idea is the basic concept of Kolmogorov complexity. This concept is applied to words (or text) composed of the letters of an alphabet, for

Table 1 Comparison of duration of search for the trough by “uninformed” (U) *F. pratensis* ants and individuals that previously contacted with the successful scout (“informed”, I); July–August, 2003

Sequence of the turns	Ants (U/I)	Mean	Amounts of sampling	P value
RRRR	U	345,7	9	<0,01
	I	36,3	9	
LLLL	U	508,0	9	<0,01
	I	37,3	9	
LRRL	U	118,7	7	<0,01
	I	16,6	7	
RLLR	U	565,9	7	<0,01
	I	16,3	7	

example, of an alphabet, consisting of two letters, L and R. Informally, the complexity of a word (and its uncertainty) equals the length of its most concise description, according to Kolmogorov (1965). For example, the word “LLLLLLL” can be represented as “8L” and the word “LRLRLRLR” as “4LR”, whereas the “random” word of shorter length “LRRLLR” probably cannot be expressed more concisely, and this is the most complex of the three and has the greatest uncertainty.

The question was analysed of whether ants can apply simple “text” regularities for compression (here, “text” means the sequence of the turns towards the maze). As proven by Kolmogorov (1965), there is no algorithmically computable quantitative measure of text complication. Therefore, strictly speaking, we can only verify whether ants have the “notion” of simple and complex sequences. In the special series of experiments, ants *F. sanguinea* were presented with different sequences of turns. Comparison of the main hypothesis H_0 (the time of the information transmission does not depend on the text complexity) with hypothesis H_1 (this time actually depends on it) showed that the more time ants spent on the information transmission, the more information—by Kolmogorov—was contained in the message. It is interesting that the ants began to use regularities to compress only quite large “texts”. Thus, they spent from 120 to 220 s to transmit information about random turn patterns on the maze with five and six forks and from 78 to 135 s when turn patterns were regular. On the other hand, there was no essential significance when the length of sequences was less than four (Table 2).

These results enable us to suggest that ants’ communication system meets Hockett’s criterion of productivity because ants not only produce the great number of messages but can change them by the use of rule extraction. Besides, seemingly with honeybees, ants are able to inform their nestmates about remote events. This feature of their communication meets the criterion of displacement. One can consider ants’ communication system rational and flexible. From the view of Information Theory, at least two important standards should be added to a list of criteria characterising a language. First, the length of a message should correlate with the quantity of information contained in this message. Second, the ability to grasp the regularities and to use them for coding and “compression” of information should be considered one of the most important properties of language and its carriers’ intellect.

Conclusion

During the last decades, common efforts of ethologists applying different experimental approaches revealed some

Table 2 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	Sequences	Mean duration (s)	SD	Numbers of experiments
1	LL	72	8	18
2	RRR	75	5	15
3	LLLL	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	LRLR	100	11	10
11	RLLR	120	9	6
12	RRLRL	150	16	8
13	RLRRRL	180	22	6
14	RRLRRR	220	15	7
15	LRLRLR	200	18	5

From Ryabko and Reznikova 1996

features of communication systems of non-human species that were earlier attributed exclusively to humans. Among them, one can list animals’ ability to use referential signals organised by “proto-grammar” rules to transfer messages in abstract “symbolic” form and to compress regular messages, to create messages about things and events distant in time and space, to “translate” messages of other species and to extract meaningful parts from strangers’ signals. However, one can find many points of discontinuity of what the communicative practice of animals. Although members of several species demonstrate understanding of grammatical rules when using artificial intermediary languages, there is no evidence of syntax in the natural communication of animals. There is also little evidence for learning and modification in the natural signals of animals. There is much to be done to complete a complex picture of animals’ natural language behaviour.

Each of three methodological approaches that have been discussed in this review has its specific power. Direct deciphering of animals’ communication is the oldest of the considered methods. By now, some of the researchers who have tried to crack wild codes by means of recording signals and playback experiments became masters of at least segments of *King Solomon’s Ring*. Dictionaries, although very fragmentary, have been compiled for several species of mammals, birds and insects. The decoded “words” concern alarm calls, calls for cohesion and signals about food. The honeybees’ dance language remains the most complex among animals’ communication system that was decoded up to date. However, we are still far from complete understanding of bees’ language behaviour. It is

worth to note that discoveries of elements of flexibility of bees' communication are based on experiments with hive as "black box"; there are no special signals revealed in their dance language that may correspond to changes in bees' behaviour. Besides this unique system, other communications are difficult to decipher because of many methodological barriers, among which low repeatability of standard living situations in wild life seems to be the bottleneck.

A number of studies with captive animals that have been trained with human-designed artificial communication systems has revolutionarily changed our imagination about animals' linguistic abilities and language-related cognitive skills. Language-training experiments are of great help for discovering potentials of animal language behaviour and for studying roots of human predisposition for the development of sophisticated language. Animals from very far systematic taxa that were taught very different artificial languages have met the same criteria of language rules and demonstrated their competence in syntax and semantics. At the same time, only narrow and limited syntactic abilities discovered in natural communicative systems restrict our possibilities to judge about potential power of species' language behaviour and related cognitive abilities.

For this, the use of ideas of Information Theory opens new horizons. This approach is designed to study quantitative characteristics of natural communicative systems and important properties of animal intelligence. Applying this method, there is no need to crack animals' codes. All we need is to ask animals to pass messages of definite lengths and complexities. By measuring time duration that the animals spend on transmitting messages with desired conditions, we can judge about potentials of their communicative system. This experimental paradigm first of all allows demonstrating the fact of information transmission between animals. The most likely situation to observe task distribution and behavioural flexibility at the individual level and to evaluate potential properties of communication social animals is to force them to solve a complex search problem. In this situation, hidden processes of information transmission would become observable. Furthermore, this approach allows evaluating important characteristics of natural communication systems, which we were not able to study before, and among them are the rate of information transmission, the complexity of transferred information and the potential flexibility of communication systems. It is a challenge to apply the Information Theory approach for studying communication in a wide variety of social animals.

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