

Numerical competence in animals, with an insight from ants

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Summary

We survey a variety of experimental paradigms for studying animal abilities to count, to understand numerical information and to perform simple arithmetic operations. There is a huge body of evidence that different forms and elements of quantitative judgement and numerical competence are spread across a wide range of species, both vertebrate and invertebrate. Here we pay particular attention to the display of numerical competence in ants. The reason is that most of the existing experimental schemes for studying numerical processing in animals, although often elegant, are restricted by studying subjects at the individual level, or by the use of artificial communicative systems. In contrast, the information-theoretic approach that was elaborated for studying number-related skills in ants employs their own communicative means and, thus, does not require the subjects to solve any artificial learning problems, such as learning intermediary languages, or even learning to solve multiple choice problems. Using this approach, it was discovered that members of highly social ant species possessed numerical competence. They were shown to be able to pass information about numbers and to perform simple arithmetic operations with small numbers. We suggest that applying ideas of information theory and using the natural communication systems of highly social animals can open new horizons in studying numerical cognition.

Keywords: numerical competence, arithmetic, animals, ants, chimpanzees, birds, communication, information theory.

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1. Introduction

Basic number-related skills, that is, knowledge of quantities and their relations, are one of the most interesting domains of animal behaviour. Perhaps, no field of ethological and cognitive science is based on comparison between animal and human abilities to such a great extent as the field of studying reasoning about numbers. However, we are still lacking an adequate ‘language’ for a comparative analysis. Apparently, all experimental paradigms and criteria for the comparison of number-related skills in animals and humans are derived from developmental psychology, that is, from studying human infants. Recent approaches to studying numerical processing in animals are mainly based on criteria suggested by Gelman & Gallistel (1978; see also Gallistel & Gelman, 2000) for children and then adopted for animal studies by Davis & Pérusse (1988). Based primarily on the animal literature, these authors described four major processes involved in numerical competence — counting, subitising, estimation and relative numerosness judgements. From these, counting was regarded as the most complex process. The authors defined counting as a formal enumerative process used to discriminate the absolute number of a set of items.

Until recently it was widely believed that the main difficulty in comparing numerical abilities in humans and other species is that number-related skills in our species are closely connected with our capacity for language and symbolic representation. However, not all human cultures possess linguistic means for number representation. The language of an Amazonian indigenous group Mundurucu lacks words for numbers beyond 5, and these people fail in exact arithmetic with numbers larger than 4 or 5 (Pica et al., 2004; Dehaene et al., 2008). Besides, recent studies that combine behavioural and neurobiological methods have changed our picture of numerical reasoning in animals. An important idea emerging from this research is that adult humans share with non-human animals a system for representing numbers as language-independent mental magnitudes, and that this system emerges early in development (Brannon, 2006)

Development of cognitive ethology and behavioural ecology has given rise to a growing body of evidence that members of many species can judge about proportions and numbers of things, sounds, time intervals, smells, and so on. In nature, being able to perceive quantities is helpful in many situations, for example, in tracking predators, selecting the best foraging grounds

or the best chance to mate. Different kinds of cognitive processes, including counting, can be understood in terms of the ways in which species are cognitively adapted to their different ecological niches. It is known that some species, both vertebrate and invertebrate, are capable of intellectual feats within narrow limits of solving certain vital problems. Specific cognitive adaptations include extraordinary classificatory abilities in pigeons (Herrnstein & Loveland, 1964; Huber, 1995) and honey bees (Mazokhin-Porchyakov & Kartsev, 2000; Menzel & Giurfa, 2001), the ability to memorize and recognize many mates by facial features in chimpanzees (Parr & deWaal, 1999), monkeys (Pokorny & deWaal, 2009) and paper wasps (Tibbetts & Dale, 2007); huge data storage in food caching birds and mammals (Clayton & Dickinson, 1998; Shettleworth, 1998), extraordinary spatial abilities reflected in maze learning in rats (Hodges, 1996), and so on. Some species demonstrate, within specific fields, cognitive abilities superior to those of humans. For example, pigeons achieve higher scores in some tasks demanding recognition of 3-D reorganized objects (review in Spetch & Friedman, 2006). Humans have more difficulties in some tasks than animal ‘species genius’, for example, in memorising locations (far lesser than food caching birds and mammals) and in orienting in complex labyrinths (poorer than rats).

Recent studies revealed the capacity for numerical discrimination in a wide variety of species, from honey bees (Dacke & Srinivasan, 2008), salamanders (Krusche et al., 2010), fish (Agrillo et al., 2008; Gómez-Laplaza & Gerlai, 2010) and birds (Emmert, 2001) to dogs (Cooper et al., 2003), elephants (Irie-Sugimoto et al., 2009), horses (Uller & Lewis, 2009) and other species including primates (Call, 2000; Anderson et al., 2005; Santos et al., 2005; Nikitin et al., 2006; Harris et al., 2007; Beran, 2007, 2008, 2010; Chernikova et al., 2008; Banerjee, 2009).

It is intuitively clear that number-related skills can be divided into ‘higher’ and ‘lower’ cognitively demanding levels, and many researchers suggested using different terms for them (Thomas et al., 1980). Summarising modern concepts of number representation in animals and humans (Brannon & Roitman, 2003; Reznikova, 2007a; Beran, 2009; Cantlon et al., 2009; Evans et al., 2009; Premack, 2010), we suggest a distinction between quantitative judgement (quantitative but not necessarily numerical) and numerical competence which is based on the ability to solve truly numerical tasks.

In this survey we consider the main ideas and experimental results in the field of studying quantitative judgement and numerical abilities of different

levels in a wide variety of species. The literature in this field is so vast that the review provided here is necessarily biased and incomplete. We are focusing mainly on empirical accounts concerning what animals can do numerically, and how that is separate from other quantification skills they may have. We also describe an original experimental paradigm for investigating numerical competence in social animals exploiting their own communicative means. This paradigm is based on fundamental ideas of information theory and has already allowed to reveal the ability to perform simple arithmetic tasks in certain highly social ant species (Reznikova & Ryabko, 1994, 2001), which appeared to be comparable to the corresponding skills of primates (Boysen et al., 1996; Hauser et al., 2000) and some tribes of humans (Dehaene et al., 2008). This could be related to ants' 'species genius' within the narrow domain of solving problems based on their complex and flexible communication which possibly surpasses honey bees' symbolic language (Reznikova, 2008). However, we suggest that this experimental approach can be applied to other social species of animals that possess individual recognition, and that need to pass and memorise complex 'messages'.

2. Quantitative judgement in animals

There are many examples in the history of studying cognition in animals when the finding of a new, more adequate, experimental method has essentially changed the picture of the intellectual abilities of the animals under study, in particular of their numerical skills. Thus, applying a method of sample-choice to a chimpanzee revealed its ability to count within limits of two objects only (Ladygina-Kohts, 2002/1935). The use of sequential responding task allowed researchers to show a subject of the same species to be able to respond adequately to Arabic numerals between 1 and 9 (Matsuzawa, 1985).

The earliest attempts to find experimental evidence of quantitative judgements and numerical competence in animals were made in the beginning of the 20th century. Porter (1904) tested the response of house sparrows to numbers by hiding food under, say, the third container in a row, then recording which container a bird flew to first on repeated trials. Then he changed the number of the baited pot and tested the birds' ability to redirect its choices. After extensive testing, Porter concluded that the sparrows based their choice

on the relative distance of the baited container from the end of the row. Kinnaman (1902) examined two rhesus monkeys. He aligned 21 boxes and trained monkeys to choose the boxes in the requested order. One of Kinnaman's subjects successfully mastered this task and searched for bait in six positions, whereas the second subject learned to find the goal only within three positions after many attempts. For comparison, Kinnaman trained two children of 5 and 3 years old to solve the same task using marbles as rewards, and both displayed results were worse than those of monkeys.

The real progress in the field of studying quantitative judgement and numerical competence in animals was made by Otto Koehler (1941, 1956). He established a number of experimental paradigms, such as simultaneous or successive stimulus presentation, as well as matching-to-sample and oddity matching procedures. The experiments were performed on a variety of animals, including squirrels, pigeons, jackdaws, a raven, an African grey parrot and budgerigars. These experiments had been so much appreciated that historical development of this field was subdivided in pre- and post-Koehler developments. Koehler concluded that animals have two basic numerical abilities. One, based on a visual-spatial sense, enables them to assess the number of items presented simultaneously in a group, while the other allows them to assess the number of events that occur successively, or spread out in time. Many of experimental procedures elaborated by Koehler are included in modern experimental techniques.

There is a growing body of evidence that adult humans, developing humans, and non-human animals share a language-independent analogue magnitude system for representing numbers. This system of representing numbers obeys Weber's law (Weber, 1834/1996), which states that the size of a just noticeable difference in stimulus intensity is a constant proportion of the original stimulus magnitude (see review in: Jordan & Brannon, 2006).

2.1. Relative numerosness judgements

Judgements on relative numerosness involve only a simple decision process, in which no knowledge of an absolute number is required. Davis & Pérusse (1988) described relative numerosness judgements as a dichotomous judgement of numerical inequality that may be ordered in magnitude (e.g., a more versus less comparison). The ability to make decisions based on relative numerosness discrimination has been tested in many species, using

different types of experimental paradigms and stimuli of different modalities. It is now well established that human babies, as well as members of many animal species, can compare two quantities, when the difference between them is large enough. For instance, using a classic method of habituation and recovery of looking time, Xu & Spelke (2000) reported that 6-month old infants can discriminate between 8 and 16 items, but not between 8 and 12.

In many experiments animals demonstrated that they perceive one stimulus as having 'more' items compared with another that has 'fewer'. Carrying on the dialogue with language-trained animals, it became possible to ask them directly about the dichotomy 'more versus less'. One of such subjects, a chimpanzee Lana, was presented with two sets of objects consisting of one to five items that varied in size to prevent labelling based on relative area. During testing, Lana was able to label with a lexigram the larger or the smaller set of quantities (Dooley & Gill, 1977). Similar results have been obtained with 'non-speaking' animals by means of conditional discrimination and matching-to-sample experimental procedures, in particular with chimpanzees (Rumbaugh et al., 1987), monkeys (Olthof et al., 1997), pigeons (Emmerton et al., 1997), hooded crows (Smirnova et al., 2000) and dolphins (Kilian et al., 2003).

It has been demonstrated in many experiments that animals could recognize which of the two numbers of stimuli was greater. Such experiments were conducted on different types of stimuli, including smells, sounds, and visual stimuli. For example, beetles (*Tenebrio molitor*) were trained by using a spontaneous two-choice procedure in which males were exposed to substrates bearing odours from different numbers of females in increasing numerosity ratios (1:2, 1:3 and 1:4). Males discriminated sources of odours reflecting 1 versus 4 and 1 versus 3 females, but not 2 versus 4 or 1 versus 2 (Carazo et al., 2009). So, the beetles demonstrated the ability to discriminate between 'more or less smells' within the limit of four with an operational signature ratio of 1:2. The similar results have been obtained on meadow voles (Ferkin et al., 2005). Experiments with rats showed that animals possess an abstract, amodal representation of number. Rats that were initially trained on distinct auditory and visual numerosity discrimination task could later generalise to novel sequences in which auditory and visual sequences were mixed (Church & Meck, 1984).

It seems natural that, although accurate distinguishing between similar large quantities demands extensive training in animals (Pepperberg, 2006),

even after such training performance is much lower when compared to the performance on tasks involving only small quantities. For example, it seems likely that primates could easily discriminate between a tree with 60 items on it and a one with 20. Moyer & Landauer (1967) first showed that when human adults are required to compare the relative magnitudes represented by two Arabic numerals, their reaction time is systematically influenced by both the linear distance and the absolute magnitude of the values compared. In other words, reaction time decreases with increasing numerical distance between two values (e.g., people are faster at 2 versus 9 than 2 versus 5 tasks), and if distance is held constant, reaction time increases with numerical magnitude (e.g., people are faster at 2 versus 3 than 4 versus 5 tasks). Recent experiments revealed similar regularities in rhesus monkeys, thus demonstrating similarities in the representation of magnitude in human- and non-human animals which does not demand language-related skills (Cantlon & Brannon, 2007).

2.2. *Subitising*

Subitising is a form of pattern recognition that is used to rapidly assess small quantities of simultaneously presented items. British economist and logician Jevons (1871) was the first to note that when making rapid estimates of the number of black beans tossed into a dish, he never made errors for bean numbers up to four, but did for larger numbers, with the standard deviation of the estimates increasing in direct proportion to the physical number of beans. The term has been coined by Kaufman et al. (1949) from the Latin word 'subitus' meaning 'sudden'. Subitising can be described as an innate perceptual process through which a certain number of items can just be 'seen' without the need for counting it. The extensive review of Davis & Pérusse (1988) postulates that, being a perceptual automatic pre-attentive process, subitising can account for much of the animal 'counting' literature.

To distinguish between subitising and other forms of numerical competence, the reaction time displayed by a subject is important. This criterion was originally derived from the reaction time displayed by humans in psychological experiments (Kaufman et al., 1949). This parameter was used in experiments of Matsuzawa (1985, 2003) with a female chimpanzee, Ai. She was trained to select an Arabic numeral corresponding to the number of objects within the quantity of 10. Ai showed quite an accurate and fast responding from 1 to 4. This was considered to be the same process as subitising in humans.

2.3. Estimation

Estimation in humans refers to the ability to assign a numerical label to a large array of items with a poor precision. When we judge at a glance that there are about 50 ducks on the lake we are ‘estimating’. Animals’ judgements about large arrays have not been systematically studied yet. The chimpanzee Ai mentioned above, being presented with the number of items more than 5, showed monotonically increasing reaction time and decreasing accuracy as a function of number. An apparent increase in reaction time from 5 to the largest numbers suggests that a process different from counting was taking place. This hypothesis was supported by an expressive behavioural indicator. Ai often looked back and forth at the item display. The authors considered this ‘looking-back’ behaviour as reflecting decision processes, that is, estimation rather than counting (Tomonaga & Matsuzawa, 2002).

Undoubtedly, all forms of quantitative judgement have a great adaptive value in the context of natural life. For example, fish use number estimation in order to join to a greater shoal (Agrillo et al., 2008), female lions can judge about number of possible intruders by ‘counting’ unfamiliar roars within the limit of four (McComb et al., 1994), New Zealand robins (*Petroica australis*) uses numerical judgements when retrieving and pilfering cached food (Hunt et al., 2008), and ants of several species are able to estimate quite precisely numbers of encounters with members of other colonies on their feeding territories (Reznikova, 1999; Gordon, 2010).

Overall, the described experiments, conducted in a variety of species, demonstrate that animals enjoy different forms of quantitative judgement. Members of many species can compare two quantities when the differences between the quantities are big enough, and they are also capable of subitising, as well as of estimation of sets of stimuli.

3. Numerical competence in animals

Advanced numerical abilities — exact counting and arithmetic operations — have been considered for a long time to be uniquely human and based on our language symbolic representation. Recent studies provide intermediary links between numerical abilities in human and non-human animals. The central issue in studying numerical cognition is counting. Gelman & Gallistel (1978) list five criteria that formally define the process of counting and have been widely accepted in comparative studies. They are:

1. The one-to-one principle. Each item in a set (or event in a sequence) is given a unique tag, code or label so that there is a one-to-one correspondence between items and tags.
2. The stable-order principle (ordinality). The tags or labels must always be applied in the same order (e.g., 1, 2, 3, 4 and not 3, 2, 1, 4). This principle underlies the idea of ordinality: the label '3' stands for a numerosity greater than the quantity called '2' and less than the amount called '4'.
3. The cardinal principle (cardinality). The label that is applied to the final item represents the absolute quantity of the set. In children, it seems likely that the cardinal principle presupposes the one-to-one principle and the stable-order principle and, therefore, should develop after the child has some experience in selecting distinct tags and applying those tags in a set.
4. The abstraction principle (property indifference). Counting can be applied to heterogeneous items. In experiments with children, a child should be able to count such different items as toys of different kinds, colour or shape and to demonstrate skills of counting even actions or sounds. There are indications that many 2 or 3 year old children can count mixed sets of objects.
5. The order irrelevance: the order in which objects are counted is irrelevant.

3.1. Proto-counting and understanding of numerical information

Most researchers define 'true counting' as a formal enumerative process that conforms to the principles proposed by Gelman & Gallistel (1978), and use the term 'proto-counting' as a more flexible one, thus leaving open the question of whether or not animals can count in the same sense that humans can count. However, there is some evidence of similarities between processes of counting in human- and non-human animals. For example, chimpanzees, like young children, tend to touch or point to each item when judging the number of items in an array (Boysen et al., 1996). These gestures, known as indicating acts, may help the child or animal coordinate the tagging process involved in the application of the one-to-one correspondence principle.

In other studies, capuchin monkeys and rhesus monkeys trained to associate Arabic numerals with the corresponding number of food pellets were

able to order correctly arrays of up to five numerals (Beran et al., 2008). This behaviour suggests that they understand the order of the symbols, as required by the stable order principle. In addition, there is evidence that chimpanzees can reliably apply the correct Arabic numeral to arrays of familiar and novel objects. This evidence suggests that monkeys understand the special status of the last number in a numerical sequence, as described by the cardinality principle (Boysen & Berntson, 1989). Chimpanzees can also select the number of dots on a computer screen equal to an Arabic numeral cue and then indicate the end of the count by contacting the numeral. This behaviour further demonstrates the use of the cardinality principle (Beran et al., 1998).

There is a great deal of experimental results supporting the hypotheses that members of many species can recognize the ordinal character of numbers (Boysen, 1993; Xia et al., 2000; Pepperberg, 2006). This principle may be well illustrated by the results of Brannon & Terrace (1998) obtained on two rhesus monkeys. It was shown that monkeys represent the numerosity of visual stimuli and detect their ordinal disparity. The exemplars were constructed from various abstract elements (e.g., circles, squares, triangles, bananas, hearts, etc.). As a control for non-numerical cues, exemplars were varied in size, shape, and colour. The monkeys were first trained to respond to exemplars of the numerosities 1 to 4 in ascending numerical order (1, 2, 3, 4). To reveal the subject's ability for ordering stimuli, four exemplars, one from each set, were displayed simultaneously on a touch-sensitive video monitor. The configuration of the exemplars was varied randomly between trials. The subjects' task was to touch each exemplar in the ascending numerical order. The monkeys had to learn the required sequence by trial and error and by remembering the consequences of their responses to each stimulus. The monkeys were later tested, without reward, on their ability to order stimulus pairs composed of the novel numerosities 5 to 9. Both monkeys responded in the ascending order to the novel numerosities. These results clearly demonstrate that rhesus monkeys represent the numerosities 1 to 9 on the ordinal scale.

There are only a few experiments devoted to animals' ability to discriminate the number of objects in the context of their vital situations, as well as their ability to detect the number of biologically relevant sequential events. Experiments of Chittka & Geiger (1995) suggested that honey bees can count landmarks or at least use the number of landmarks as one of the criteria in searching for food sources. Researchers worked with honey bees in a large

meadow which was practically devoid of any natural landmarks that could be used by bees. The experimenters then set up their own landmarks, which consisted of large yellow tents. The bees were trained to take sugar syrup from a feeder that was placed between the third and fourth tents. In the tests, the number of landmarks between hive and feeder were altered. It is interesting to note that individual foragers in a hive used different cues in their searching. Many bees continued to rely only on flying distance between the hive and the feeder. Anyway, the distance estimation of the bees as a group depended notably on the number of landmarks. If some family members encountered more landmarks on their way from the hive to the feeder than they had during training, they landed at a shorter distance than during control tests with the training landmark set up. If they encountered fewer landmarks, they flew significantly further. Discussing their results, the authors consider it unlikely that their bees meet the abstraction principle of 'true counting'. As it was noted above, this principle states that after having learnt to perform a given behavioural unit assigned to a certain number of objects counted, the subject should be able to transfer this knowledge to a set of objects of a different quality. Since transfer of the counting performance on different objects is unlikely to occur in honeybees, the observed behaviour is referred by the authors to as *proto-counting*. Dacke & Srinivasan (2008) obtained further results on counting in honey bees training them to forage from a tunnel. Bees received a food reward after they have passed a specific number of landmarks. They appeared to be able to count up to four objects when these objects were encountered sequentially during flight. Bees trained in this way were able to count novel objects which they have never previously encountered, thus demonstrating that they are capable of object-independent counting.

Capaldi & Miller (1988) tested rats' ability to detect absolute number by using biologically important events — the number of reinforced runs followed by a non-reinforced run — and found that the rats ran significantly slower on the non-reinforced run, and they distinguish between 'numbers' of runs. Rayburn-Reeves et al. (2010) used a procedure similar to that of Capaldi & Miller in their experiments with pigeons. The birds were given a sequence of trials in which responding on the first three trials ended in reinforcement but responding on the fourth trial did not (RRRN). When the response requirement on each trial was a single peck, no significant increase in latency to peck on the fourth trial was found. When the response

requirement was increased to 10 pecks, however, the time to complete the peck requirement was significantly longer on the non-reinforced trial than on the reinforced trials. Tests for control by time, number of responses, and amount of food consumed indicated that the pigeons were using primarily the number of reinforcements obtained in each sequence as a cue for non-reinforcement.

Thus, we can see that the five criteria listed by Gelman & Gallistel (1978) were used in the experiments on counting in animals described above only as a very general guideline, with some of the principles verified for some species and others for others (perhaps, all the five principles were established only for chimpanzees that have used Arabic numerals). Therefore, for the sake of clarity of definitions, and to comply with the established terminology, we say that in these experiments (excluding some of those with chimpanzees) it was only proto-counting that was demonstrated.

3.2. *Arithmetic skills*

One of the most interesting fields in cognitive ethology is studying arithmetic abilities in non-human animals and human infants. Wynn (1992) explored whether five-month old infants can solve addition and subtraction problems taking advantage of the human infants' capacity for understanding object permanence (*sensu* Piaget, 1936). As many development psychologists who work with pre-linguistic infants, she used 'looking time' (the expectancy violation technique) as a relevant measure to judge about subject's understanding of a problem. The idea was that if infants keep track of the numbers of toys they see being placed behind a screen, they should look longer at a screen that, when lowered, reveals an outcome that violates their expectations. For example, in the ' $(1 + 1) = 1$ or 2 ' task, one doll was placed on a stage, covered with a screen, and then another doll was visibly introduced behind the screen. A further manipulation occurred out of sight of the subjects, where either another doll was added, or one of the existing ones was removed. When the screen was removed, infants looked longer at the 'impossible' outcomes of either one doll or three dolls, suggesting that they expected two dolls. The same kind of result emerges from an experiment involving subtraction instead of addition. Wynn concluded that infants have an innate capacity to do simple arithmetic.

Hauser et al. (2000) set up Wynn's $1 + 1 = 2$ task for the free-living rhesus monkeys. In the first series of experiments subjects watched as an experimenter placed two eggplants behind a screen and then removed the screen. Subjects looked longer when the test outcome was one or three eggplants than when it was the expected two. Like human infants, rhesus monkeys appear to understand that $1 + 1 = 2$. Rhesus monkeys also appear to understand that $2 + 1 = 3$, $2 - 1 = 1$, and $3 - 1 = 2$. It is worth noting that this technique allows to reveal what animals 'think' spontaneously, in the absence of training. Comparable results have been obtained with cotton-top tamarins (Uller et al., 2001) and lemurs (Santos et al., 2005).

Using other experimental schemes, researchers have demonstrated animals' abilities for active mental manipulations with quantities. Summation has been demonstrated in tasks where animals were required to compute and choose the larger of two quantities. For example, chimpanzees were presented with two sets of two food wells, each of which contained a number of chocolate chips (up to four). To choose the set with the overall larger quantity, the chimpanzee had to sum the chocolates in each of the two sets and then compare the two summed values. The chimpanzees consistently selected the pair of quantities with the greater combined total (Rumbaugh et al., 1987). Boysen & Berntson (1989) provided an impressive demonstration of arithmetic abilities in non-humans. A chimpanzee Sheba, experienced with Arabic numerals, was led around a room to three different hiding places that could contain 1, 2, 3, or 4 pieces of orange. Subsequently, Sheba was required to choose the Arabic numeral that corresponded to the sum of number of items she had met before. She chose the correct sum from the first session of test in both cases, showing mastery of this ability without any explicit training.

Cantlon & Brannon (2007) tested two rhesus monkeys and college students in a task where two sets of dots were shown in succession on a computer screen, and participants had to add the sets and then find a matching option that had the same total number of dots. For example, subjects could have been shown two dots and four dots, followed by a choice of six dots — the right answer — or, say, eight dots — a wrong answer. While the college students were correct 94% of the time and the monkeys 76%, the average reaction time for both monkeys and humans was about 1 s. The performance of both the monkeys and the college students worsened when the two choices were closer.

In experiments of Adessi et al. (2007) capuchin monkeys (*Cebus apella*) appeared to be able to use tokens as symbols to represent and combine quantities in rather complex tasks. The experimental paradigm involved choices between various combinations of tokens A and B, worth one and three rewards (pieces of peanuts), respectively. Pay-off maximisation required making simple computations. In particular, in the first series of experiments capuchins were presented with choices between one token B and one to five tokens A. Four out of ten capuchins relied on a flexible strategy that allowed maximising their pay-off, i.e., they preferred one token B against one and two tokens A, and they preferred four or five tokens A against one token B. In the second series of experiments they had to choose between two tokens B and three to six tokens A; therefore, the value of each type of token needed to be summed with the value of tokens of the same type, and the sums obtained to be compared. Capuchins faced three new conditions (2B versus 4A, 2B versus 5A, and 2B versus 6A) interspersed with three familiar conditions (1B versus 5A, 1B versus 4A, and 1B versus 3A). In these conditions two out of six capuchins successfully performed summation over representation of quantities, which is similar to multiplication.

There are only a few studies on arithmetic skills beyond primates. For example, in experiments with pigeons Brannon et al. (2001) found that they are able to discern correct from incorrect outcomes of a subtraction task. Pigeons were required to compare a constant number with the number remaining after a numerical subtraction. The birds appeared to be able to subtract one set of light flashes from another and, subsequently, peck the estimated number of flashes that are left after subtraction. Pigeons successfully solved different tasks including '12 - 6'. The language-trained grey parrot Alex, able to quantify sets of 6 or fewer items by using English labels, was tested on tasks involving addition of quantities up to 6. He was, without explicit training, asked 'How many total X?' for two sequentially presented collections and required to answer with a vocal English number label. His accuracy suggested that his addition abilities are comparable to those of non-human primates and young children (Pepperberg, 2006).

Recent experiments on newly hatched domestic chicks (Rugani et al., 2010; Vallortigara et al., 2010) enable researchers to appreciate core components of animals' numerical cognition, that is, a set of building block systems that emerge early in ontogeny and show characteristic limits of domain and task specificity (sensu Spelke, 2000). Chicks were reared with five identical

objects (small balls). On days 3 or 4, chicks underwent free-choice tests in which two sets containing three and two balls disappeared (either simultaneously or one by one), each behind one of two opaque identical screens. Chicks spontaneously inspected the screen occluding the larger set. In the next experiment, after the initial disappearance of the two sets, some of the objects were visibly transferred, one by one, from one screen to the other. Thus, computation of a series of subsequent additions or subtractions of elements that appeared and disappeared, one by one, was needed in order to perform the task successfully. Chicks chose the screen, hiding the larger number of elements at the end of the event, irrespective of the directional cues provided by the initial and final displacements.

Thus, not only primates but some birds including newly hatched domestic chicks displayed the ability to add and subtract small numbers. In this context, it is worth of noting that demonstrating the animals' ability to simple arithmetic does not require demonstrating (as a prerequisite) their ability to count.

Overall, although many impressive results concerning sophisticated forms of numerical cognition in animals have been obtained, our knowledge is restricted by the use of artificial communicative systems elaborated specifically for communication with animals, or by the use of experimental paradigms for examining individual cognitive capacities in rather sophisticated situations of solving complex learning problems. In this respect, we encounter a methodological paradox. It is evident that in humans high levels of number-related skills are closely connected with the development of language. At the same time, all known experimental paradigms for studying numerical competence in animals do not exploit the phenomenon of close relations between intelligence, sociality and natural communication. Even in the honey bee studies mentioned above (Chittka & Geiger, 1995; Dacke & Srinivasan, 2008), cognitive capacities of these social insects have been tested individually, and the facilities of honey bees' extraordinary symbolic language were not included into the experimental schemes. In the next section of the review we will consider a principally different approach for studying numerical competence in animals, which harnesses their natural communication. The suggested experimental paradigm reveals ants' ability to elaborate a new code in order to optimise their messages. It is then shown that the usage of this new code has to be based on simple arithmetic operations.

4. An insight from ants: flexibility of communication as a basis for numerical competence

The complexity of communication systems in animals is closely connected with their intelligence (Reznikova, 2007a). Ants can serve a good example because several highly social ant species (such as red wood ants) are able to pass exact information to their nest mates by means of distant homing (see review in Reznikova, 2007b, 2008). Distant homing here means that messages about remote events come from the scouting individual, without other cues such as scent trail or direct guiding. The classic example of distant homing is the honey bee Dance Language (von Frisch, 1967). Distant homing in ants was firstly discovered in *Formica polyctena* Foerster (Reznikova & Ryabko, 1994) belonging to red wood ants species. This group of highly social ant species is characterised by a complex system of division of labour among workers (Dobrzanska, 1959; Rosengren, 1977). Later, the existence of a system of task allocation basing on team fidelity and individual recognition was demonstrated (Reznikova & Ryabko, 1994; Reznikova, 2007a,b). We suggest that this system distinguishes highly social group-foraging ant species from many other ant species with more simple foraging systems, where worker allocation to tasks is unrelated to their ability to perform them (for reviews, see Hölldobler & Wilson, 1990; Dornhaus, 2008). It turned out that distant homing in red wood ants is based on a scout-foragers recruitment system: ants work in constant teams for many days, and a scout shares the information about the discovered food only with members of its team (for review, see Reznikova, 2008).

The experimental paradigm for studying ants' numerical competence using their own communication skills is based on the information-theoretic approach (Reznikova & Ryabko, 1994, 2001; Ryabko & Reznikova, 1996, 2009). The main idea of this approach is that experimenters force animals to transfer a predetermined quantity of information to each other, and then measure the duration of time spent by subjects for the transmission of this information. Comparing time durations required for information transfer in different situations, one can reason about certain key characteristics of the communication system under study. We suppose that this approach is applicable not only to ants but to other highly social animals.

In the described experiments scouting ants actively manipulated with quantities, as they had to transfer to foragers in a laboratory nest the information about which branch of a 'counting maze' they had to go to in order

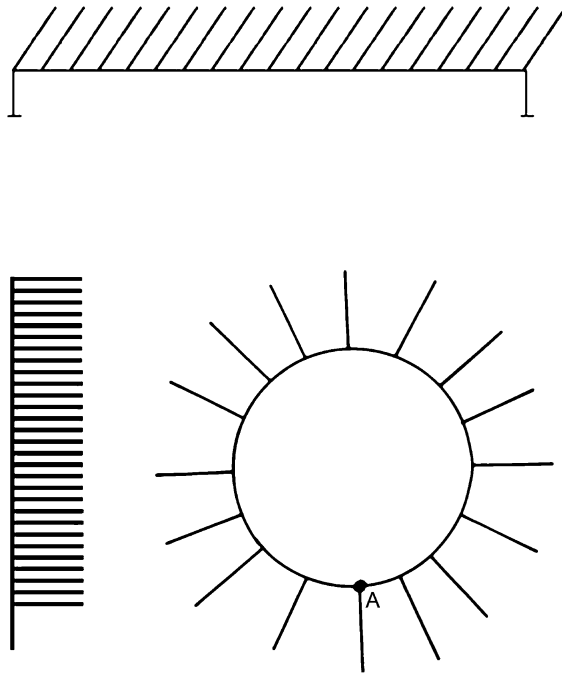


Figure 1. The comb-like set-ups for studying numerical competence in ants: a vertical trunk, a horizontal trunk and a circle.

to obtain syrup. ‘Counting maze’ is a collective name for several variants of set-ups. The first variant of the counting maze is a comb-like set-up consisting of a long horizontal plastic trunk with 25–60 equally spaced plain plastic branches, each of them 6 cm in length (Figure 1).

Each branch ended with an empty trough, except for one filled with syrup. Ants came to the initial point of the trunk over a small bridge. The second variant is a set-up with 60 vertically aligned branches. In order to test whether the time of transmission of information about the number of a branch depends on its length as well as on the distance between the branches, one set of experiments was carried out on a similar vertical trunk in which the distance between the branches was twice as large, and the branches themselves were three times and five times longer (for different series of trials). The third variant was a circular trunk with 25-cm-long branches.

Ants were housed in a laboratory arena divided into two parts, one containing a plastic nest with a laboratory ant colony and the other containing one of the variants of the counting maze. The laboratory colonies consisted

of about 2000 individuals each. All actively foraging ants were individually marked with coloured paint. Each series of experiments was preceded by the run-up stage consisting of familiarization trials. In order to force a scout to transfer the information about food to its nest mates the experimenters showed it the trough containing syrup (placing the scout directly on the trough) and then let it return to the nest. The time, which the scouting ants spent on the information contacts with their teams in order to transfer the information about which 'branch' contained the feeder, was measured (in seconds). The information contact included fast movements of antenna and legs, what myrmecologists call 'antennal code' after Wasmann (1899) who first hypothesized that ants can use this way of information transmission for distant homing. The duration of each information contact in the described experiments was considered to begin when the scout touched the first forager ant, and to end when the first two foragers left the nest for the maze. After allowing it to contact the foragers within the nest, the scout was removed and isolated for a while, so that the foragers had to search for the food by themselves, without their guide (for details, see Reznikova, 2008).

The experiments were devised so as to eliminate all possible ways for the members of each foraging team to find the goal, except by an information contact with their scout. The set-up was replaced with a fresh one, with all troughs filled with water, while the scout was in the nest; if the foraging team reached the correct branch in a compact group, then the water-filled trough was replaced with a one with syrup. It is worth noting that in these series of experiments ants had to face a rather complex life-or-death task: they could obtain food only in the maze and only once every 2–3 days.

4.1. *The ants' ability to transfer information about numbers of objects*

The findings described below concerning number-related skills in ants are based on comparisons of duration of information contacts between scouts and foragers that preceded successful trips by the foraging teams. Two laboratory colonies of red wood ants *F. polyctena*, were used in this set of experiments. In total, 32 scout-foragers teams worked in three kinds of set-ups. The teams left the nest after they were contacted by scouts and moved towards the trough by themselves on 152 trials. In 117 cases the team immediately found the correct path to the trough. In the remaining cases, ants came to the empty troughs, and began looking for food by checking neighbouring

branches. It was proofed statistically that the success ratio which was obtained experimentally could only be explained by information transmission from the scouts. In addition, in control experiments ants, including scouts placed in the set-up, without information on which trough contained food usually failed to find the food, even though they actively searched for it.

It turned out that, when the rewarded branch was randomly selected by the experimenters, the relation between the number of the branch (i) and the duration of the contact between the scout and the foragers (t) was well described by the equation $t = ai + b$ (where a and b are constant) for different set-ups which were characterised by different shapes, distances between the branches and lengths of the branches. The parameter b is introduced, since ants can transmit information not related directly to the task, for example, the additional signal 'food'. Besides, it is not ruled out that a scout ant transmits, in some way, the information on its route to the nest, using acoustic or some other means of communication. In this context, it is important that the route from the maze to the nest on the arena was in all experiments approximately the same. Being highly motivated, scouts hurried on to the nest in a beeline and, therefore, the time before they made antennal contact with the foragers in the nest, which the scout could hypothetically use for message transmission, was approximately the same and did not depend either on the lengths of the branches or on other features of set-ups. The values of parameters a and b appeared to be close for all set-ups, and did not depend on their physical characteristics. The correlation coefficient between t and i was high for different kinds of counting mazes. In turn, it proves the hypothesis that the connection between t and i is close to linear (see details in Ryabko & Reznikova, 2009).

The likely explanation of the results concerning ants' ability to find the 'right' branch is that they can evaluate the number of the branch in the sequence of branches in the maze and transmit this information to each other. Presumably, a scout could pass messages not about the number of the branch but about the distance to it or about the number of steps and so on. What is important is that even if ants operate with distance or with the number of steps, this shows that they are able to use quantitative values and pass on exact information about them.

It is worth to note that, in other series of experiments made by a similar procedure with five colonies of *F. polycтена*, these ants were demonstrated

as being able to transmit information on the ordinal number of a given side-branch in a linear maze (a 'lattice' set-up) and on the numerical coordinates in a grid-type maze of a node (a 'globe' set-up). The results of these experiments showed that the ants are able to memorise and transmit information regarding the location of the goal on the plane or on the globe surface (Reznikova & Ryabko, 2001).

All these data based on the analysis of the time spent by ants for transmitting the coordinates of objects in different situations enable us to conclude that these insects can encode and transmit information about quantitative parameters of objects.

As in the experiments with other species (described in the first part), in ants it was only proto-counting that was established, since adherence to all of the five principles of counting listed by Gelman & Gallistel (1978) was not demonstrated.

4.2. *The ants' ability to add and subtract small numbers*

The experimental paradigm of studying ants' 'arithmetic' skills is based on a fundamental idea of information theory, which is that in a 'reasonable' communication system the frequency of usage of a message and its length must correlate. The informal pattern is quite simple: the more frequently a message is used in a language, the shorter is the word or the phrase coding it. Professional slang, abbreviations, etc. can serve as examples. This phenomenon is manifested in all known human languages as well as in technical systems of information transmission.

The main experimental procedure was similar to other experiments with counting mazes (Reznikova & Ryabko, 2000; Ryabko & Reznikova, 2009). In various years four colonies of red wood ants were used. The scheme of the experiments is as follows. Ants were offered a horizontal trunk with 30 branches. Each experiment was divided into three stages, and at each of them the regularity of placing the trough with syrup on branches with different numbers was changed. At the first stage, similarly to the previous set of experiments, the branch containing the trough with syrup was selected randomly, with equal probabilities for all branches. So the probability of the trough with syrup being placed on a particular branch was $1/30$. Thus, the first stage of the 'arithmetic' experiments did not differ from 'counting' experiments described above. At the second stage two 'special' branches A

and B were chosen (N 7 and N 14; N 10 and N 20; and N 10 and N 19 in different years) on which the trough with syrup was placed much more frequently than on the rest of the branches: with the probability $1/3$ for 'A' and 'B', and $1/84$ for each of the other 28 branches. In this way, two 'messages' to be transmitted, namely, 'the trough is on branch A' and 'the trough is on branch B', had a much higher probability than the remaining 28 messages. In one series of trials we used only one 'special' point A (the branch N 15). On this branch the food appeared with the probability of $1/2$, and $1/58$ for each of the other 29 branches. At the third stage of experiments the number of the branch with the trough was again chosen at random.

Now let us consider the relationship between the time which the ants spent to transmit the information about the branch containing food, and its number (for details, see Ryabko & Reznikova, 2009). The information obtained at the first and third stages of the experiments are shown on the graph (Figure 2) in which the time of the scout's contact with foragers (t) is plotted against the number (i) of the branch with the trough. At the first stage

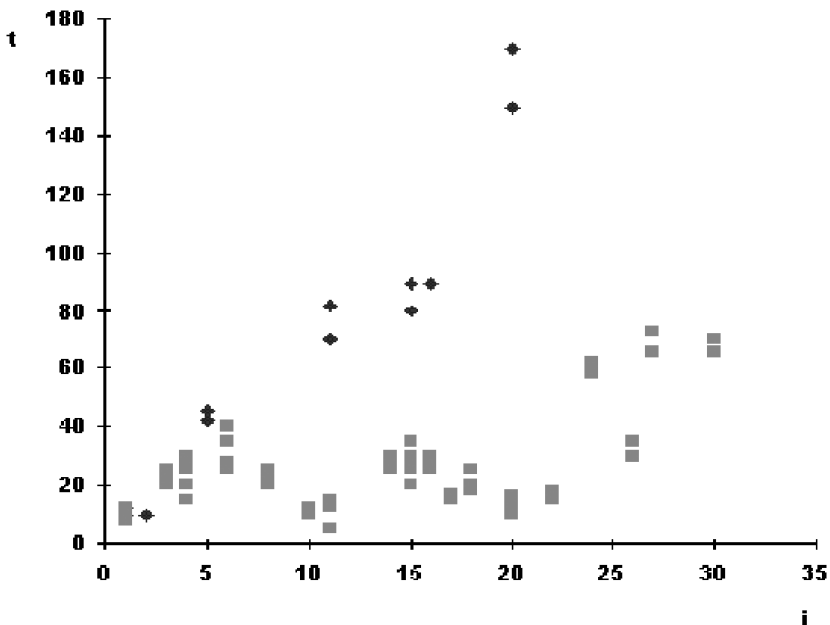


Figure 2. Dependence between the time (t , measured in seconds) of transmission of information about the number of the branch having food and its ordinal number (i) in the first and the third series of experiments in the ant *Formica polyctena*. Diamonds indicate the time taken for transmission of information at the first stage, squares the same at the third stage.

the dependence is close to linear. At the third stage, the picture was different: first, the information transmission time was very much reduced, and, second, the dependence of the information transmission time on the branch number is obviously non-linear: a depression can be seen in the vicinities of the 'special' points (A and B). So the experimental data demonstrate that the patterns of the dependence between the time of information transmission and the index number of the food-containing branch at the first and third stages of experiments are considerably different. Moreover, in the vicinities of the 'special' branches, the time taken for transmission of the information about the number of the branch with the trough is, on the average, much shorter. For example, in the first series, at the first stage of the experiments the ants took 70–82 s to transmit the information about the fact that the trough with syrup was on branch N 11, and 8–12 s to transmit the information about branch N 1. At the third stage it took 5–15 s to transmit the information about branch N 11 (nearest to the 'special' branch N 10). These data enable us to suggest that the ants have changed the mode of presenting the data about the number of the branch containing food.

The statistical analysis of the results (for details, see Ryabko & Reznikova, 2009) supports the hypothesis that at the third stage of the experiment the time of transmission of a message about the number of the branch is shorter when this branch is close to either of the special ones. Our interpretation is that at this stage of the experiment the ants used simple additions and subtractions, achieving economy in a manner reminiscent of the human numerical system. Note that when using numerical systems, people have to perform simple arithmetical operations, for example, $13 = 10 + 3$. It is particularly obvious in Roman numerals, for example, $VII = V + II$.

Let us now consider ants' arithmetic skills in more details. Analysis of the time duration of information transmission by the ants raises the possibility that at the third stage of the experiments the scouts' messages consisted of two parts: the information about which of the 'special' branches was the nearest to the branch with the trough, and the information about how many branches away is the branch with the trough from a certain 'special' branch. Informally, the ants were forced to develop a new code based on simple arithmetic operations, that is, to perform an operation similar to passing the 'name' of the 'special' branch nearest to the branch with the trough, followed by the number which had to be added or subtracted in order to find the branch

with the trough. A good illustration here is that ants spend, for example, 25–30 s to transmit the message ‘a trough is on the branch 4’ at the first stage of the experiment, and they spend the same time to transmit a message that says ‘a trough is on the forth branch after the branch 10’ at the third stage. That ant teams went directly to the ‘correct’ branch enables us to conclude that they performed correctly whatever ‘mental’ operation was to be made.

Let us show that the mental operations that the scouts had to perform can be considered the operations of addition and subtraction. Indeed, we have shown that what the scout had to do was to transmit the name of one of the ‘special’ branches plus the directions (how many branches backwards or forwards) from this special branch. However, in these experiments the ‘special’ branches could only be referred to by their numbers. That is, there was no possibility to associate some visual (olfactory, etc.) mark with them. In the absence of any such mark, what scout had to do when placed on, say, the branch 17, when the branch 20 was ‘special’, was to calculate correctly that 17 is 3 branches away from 20 (the ‘special’ one). In other words, it had to perform subtraction. Similarly, when placed on the branch (say) 23, the scout had to correctly compute that this branch is 3 branches away from the ‘special’ branch 20, which, in the absence of any mark on the branch 20, requires addition.

The foragers then had to correctly interpret this information, which does not necessarily mean that they have actually performed exactly the same mental operation. For example, if the information from the scout was of the form ‘ $20 + 3$ ’, then the foragers could, when passing the branch 20, start ‘counting’ to 3 to reach the target. This does not require performing the operation of addition.

The obtained results also demonstrate that red wood ants possess a communication system that has a great degree of flexibility. Until the frequencies with which the food was placed on different branches started exhibiting regularities, the ants were ‘encoding’ each number i of a branch with a message of length proportional to i . Subsequent changes of the code in response to special regularities in the frequencies are in line with one of the basic information-theoretic principles that states that in an efficient communication system the frequency of use of a message and the length of the message are related. The complexity and flexibility of ants’ communication can be considered an evidence of their intelligence.

5. Conclusion

Apparently, the fact that different forms and elements of numerical competence are spread across a wide variety of species, both vertebrate and invertebrate, as well as that these abilities emerge early in ontogeny, support the idea of evolutionary psychology inspired by Darwin (1871a,b) that the human mind is a collection of special-purpose mechanisms, each shaped by evolution to perform a particular function. A huge body of experimental data includes demonstrations of animals' abilities to count, to understand numerical information and to perform simple arithmetic operations. Not only primates but also ants, honey bees, pigeons, and even newly hatched domestic chicks demonstrate some forms of numerical competence. More simple (but also cognitively demanding) forms of quantity judgement, such as relative numerosness judgements, estimation and subitising have been revealed in a variety of species, from beetles, fish and salamanders to rodents, dogs, cats, horses, elephants and primates.

There is much work to be done to extend our understanding of whether at least some species share advanced characteristics of numerical cognition with humans, or whether animals think about the quantitative parameters of the world in a way radically different from ours. Although our knowledge about advanced forms of animal numerical competence have been much enlarged by applying new experimental paradigms and elaborating new concepts, we are still far from having an integrative measure of animal numerical competence. New approaches are needed, and in this aspect the insight from ants is indicative.

The information-theoretic experimental paradigm described in this review has been used to show that members of highly social ant species are able to pass information about numbers of objects (at least within 30), and, moreover, they can add and subtract small numbers and use these operations for optimising their messages. The scheme of the experiments is based on the information-theoretic idea that in a 'reasonable' communication system the frequency of usage of a message and its length must correlate. Facing a new task in which a food source appeared on a 'special' branch of a counting maze much more frequently than on other ones, scouting ants were forced to develop a new code based on arithmetic operations.

The obtained results do not mean that within the animal kingdom ants possess outstanding cognitive skills. First, it is likely that these cognitive

abilities lie within a narrow domain of ants ‘species genius’ and concern their complex and flexible communication system which has much in common with the honey bee ‘Dance Language’ and serves for transferring information about food. Second, which is particularly important, the described situation is, as far as we know, the first case when animals’ own communicative means are used for studying their numerical cognition. The experimental paradigm based on the information-theoretic approach does not require the subjects to solve any artificial learning problems, such as learning intermediary languages, or even learning to solve multiple-choice problems. The main principle of this scheme of experiments is to force animals to transfer a piece of information known exactly to the researchers, and to measure and analyse the time of information transmission.

It can be suggested that the scheme of experiments used to study ants’ numerical competence can be directly used on other animals, including mammals, and, in particular those whose intellectual abilities are most studied — the chimpanzees. Using this scheme on such animals as chimpanzees would require the use of cooperative tasks. For example, two subjects can be involved, one of which is shown the food source, but has to communicate its location to the other, in order for both of them to get it. The food can be placed in one out of (say) 20 containers, which play the same role as the branches of the comb-like maze in the experiments with ants. The numerical abilities of the subjects can then be studied by analysing the time the first subject (that has seen the food) spends on transferring the information on its location to the other, exactly as in the experiments with ants.

Therefore, we suggest that the use of communication systems of highly social animals and application of ideas of information theory can open new horizons for studying numerical competence in non-human animals.

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