Animal Cognition
https://doi.org/10.1007/s10071-019-01244-7

ORIGINAL PAPER

Precise relative-quantity judgement in the striped field mouse *Apodemus agrarius* Pallas

Zhanna Reznikova[1,2] · **Sofia Panteleeva**[1,2] · **Nataliya Vorobyeva**[3]

Received: 24 July 2018 / Revised: 14 January 2019 / Accepted: 23 January 2019

Abstract

Applying the classical experimental scheme of training animals with food rewards to discriminate between quantities of visual stimuli, we demonstrated that not only can striped field mice *Apodemus agrarius* discriminate between clearly distinctive quantities such as 5 and 10, but some of these mice also exhibit high accuracy in discriminating between quantities that differ only by one. The latter include both small (such as 2 versus 3) and relatively large (such as 5 versus 6, and 8 versus 9) quantities of elements. This is the first evidence of precise relative-quantity judgement in wild rodents. We found striking individual variation in cognitive performance among striped field mice, which possibly reflects individual cognitive variation in natural populations. We speculate that high accuracy in differentiating large quantities is based on the adaptive ability of wild rodents to capture subtle changes in their environment. We suggest that the striped field mouse may be a powerful model species to develop advanced cognitive tests for comparative studies of numerical competence in animals and for understanding evolutionary roots of quantity processing.

Keywords Numerical competence · Relative-quantity judgement · Training · Two-choice discrimination · Visual stimuli · Rodents · Behavioural flexibility · Individual cognitive variation

Introduction

The fundamental nature and the adaptive value of basic number-related skills in animals have been thoroughly documented. The club of 'numerically competent' animals already includes many species, from insects, spiders, salamanders, lizards and fishes to birds, rodents, dogs, cats, horses, dolphins, elephants and primates (for reviews see: Cantlon et al. 2009; Reznikova and Ryabko 2011; Agrillo and Beran 2013; Beran and Parrish 2016; Beran et al. 2016; Benson-Amram et al. 2018), and continues to accept species whose numerical abilities have been underestimated before. Animal abilities to judge about proportions and numbers of things and events, sounds, time intervals, and smells have been considered a reliable tool for studying intelligence (Reznikova 2007). However, the cognitive mechanisms of animal numerical abilities are still poorly understood. The vast majority of studies are devoted to animal abilities to perform 'more versus fewer' comparisons, and to estimate small numbers within the limits of subitising, typically four. Judgements on relative numerousness involve only a simple decision process, in which no knowledge of the absolute number is required (Davis and Pérusse 1988). Subitising is a form of pattern recognition that is used to rapidly assess small quantities (up to four) of simultaneously presented items. The term has been coined by Kaufman et al. (1949) from the Latin word 'subitus' meaning 'sudden'. Subitising can be described as the innate perceptual process through which a certain number of items can just be 'seen' without

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10071-019-01244-7) contains supplementary material, which is available to authorized users.

✉ Zhanna Reznikova
zhanna@reznikova.net
http://www.reznikova.net

Sofia Panteleeva
psofia@mail.ru

Nataliya Vorobyeva
vorobyeva.nataliya.s@gmail.com

[1] Institute of Systematics and Ecology of Animals, Siberian Branch RAS, Frunze 11, Novosibirsk 630091, Russia

[2] Novosibirsk State University, Pirogova 2, Novosibirsk 630090, Russia

[3] National Research Center Kurchatov Institute, 1, Akademika Kurchatova pl, Moscow 123182, Russia

the need for counting them. Being a perceptual automatic pre-attentive process, subitising can account for much of the 'animal counting' literature (Dehaene 2011).

It is intuitively clear that number-related skills can be divided into 'higher' and 'lower' cognitively demanding levels, and some researchers suggested using different terms for them (Thomas et al. 1980). Reznikova and Ryabko (2011) 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 such as ordering of the numerosities, operating on discrete quantities, and performing simple arithmetic operations. Basing on an experimental paradigm for investigating numerical competence in social animals that exploits animals' own communicative means, they revealed in certain highly social ant species the ability to memorise and pass the information about numbers within the limit of 30, as well as to perform subtraction and addition within the limit of 5 (see details in: Reznikova 2017, 2018). Displays of 'higher' capacities in operating with numbers have been found in ants (Reznikova and Ryabko 1994, 2011), pigeons (Brannon et al. 2001), a grey parrot (Pepperberg 2012), crows (Smirnova et al. 2000), rats (Burns et al. 1995; Capaldi and Miller 1988; Taniuchi et al. 2016), monkeys (Cantlon and Brannon 2007; Addessi et al. 2008; Beran et al. 2015), apes (Boysen and Berntson 1989; Call 2000; Anderson et al. 2007; Tomonaga 2008; Beran et al. 2013) and some other animals.

Studies on spontaneous arithmetic capacities in ants (Reznikova and Ryabko 2001, 2011) and newly hatched domestic chicks (Rugani et al. 2010, 2013), together with numerical competence in honeybees (Pahl et al. 2013; Howard et al. 2018), spatial representations of numbers, such as the left-to-right-oriented mental number line in 3-days-old domestic chicks (Rugani et al. 2015), and precocious quantitative cognition in monkeys (Ferrigno et al. 2016) enable one to suggest that animals possess a core system of processing numerical information. Even more surprisingly, humans in some tribal populations appear to cope with numbers more poorly than ants (Pica et al. 2004; Dehaene et al. 2008; Reznikova 2017). Studies that combine behavioural and neurological methods lead to the idea that humans share with non-human animals a system for representing numbers as language-independent mental magnitudes, and that this system emerges early in their development (Brannon and Merritt 2011; Nieder 2018).

It is still being debated whether quantification skills that are the basis for mathematical competencies are predicated on one system or two systems for representing and judging quantity or number (Beran and Parrish 2016). In the first core system of number, that has been seen in a wide variety of animals and is often called the approximate number system (Gallistel and Gelman 2000; Brannon and Roitman 2003; Cantlon et al. 2009), quantities are represented inexactly, with increasing variance in discriminating or estimating set sizes as the true set sizes increase. This system produces the well-established distance and size effects, whereby performance in discriminating sets is best predicted by the ratio of those sets to each other (e.g., Beran 2007), an outcome that reflects the workings of Weber's law. The second system operates very differently, for highly precise representation of only small numbers of items within the limit of subitising, and cannot accommodate numbers greater than four because of limits in attention and working memory capacity. Some reports have suggested that fish may show evidence of these two systems (Agrillo et al. 2012), as do humans (Feigenson et al. 2004), birds (Garland et al. 2012), salamanders (Krusche et al. 2010) and some other vertebrate species, whereas much of the primate studies show ratio effects indicative of the approximate number system only (see Beran and Parrish 2016).

All these results and ideas shape the multifaceted panorama of numerical reasoning in animals.

Limits of numerical skills in different species, and the ways they correlate with ecologically relevant problems are still unclear. Extensive comparative studies in this field are needed at different levels of numerical competence to analyse the evolutionary roots of quantity processing.

Small rodents are good candidates for assessing the adaptive role of numerical reasoning. These animals share with primates a diverse set of behavioural and cognitive functions such as behavioural flexibility, social behaviour, evaluating expected outcomes and working memory (Hamilton and Brigman 2015). However, although laboratory strains of mice and rats have been used for studying different forms of cognitive abilities over the past century, the knowledge about quantity judgement in 'wild' rodents until recently has been restricted to the studies on meadow voles which displayed the ability to discriminate between 'more or less smells' within the limit of four (Ferkin et al. 2005; Ferkin and Hobbs 2014). Cognitive abilities of striped field mice *A. agrarius*, to our knowledge, have never been studied before. This species inhabits a wide range of habitats including the edges of woodlands, grasslands and marshes, pastures and gardens, and urban areas (Chelkowska et al. 1985). In heterogeneous landscapes these mice move distances of more than 1000 m and pass through different biotopes (Szacki and Liro 1991). In an urban environment, *A. agrarius* flexibly alters its habitat preferences and life-history parameters (Łopucki et al. 2013). Compared to many small wild rodents, this species is rather bold and explorative and surprisingly easy to handle in the laboratory (Reznikova et al. 2017). All these displays of behavioural flexibility suggest *A. agrarius* may engage cognitive mechanisms frequently.

In our previous study on this species, we presented the first experimental paradigm based on the evaluation of quantity judgements in the context of risk/reward decision-making where the animals face a trade-off between the hedonistic value of the prey and the danger it presents (Panteleeva et al. 2013). In our experiments, mice had to choose between different quantities of ants placed in two transparent tunnels. Ants here served both as food items and as a source of danger. We found that when mice have to choose between 5 versus 15, 5 versus 30, and 10 versus 30 ants, they always tend to prefer the smaller quantity, thus displaying the capacity for distinguishing more from less in order to ensure comfortable hunting. That fact that *A. agrarius* appeared to be able to use approximate quantity judgement to choose optimal amounts of dangerous prey items provoked our curiosity about their capacities of precise relative-quantity judgement.

In this study, we investigate whether striped field mice are capable of precise relative-quantity judgements: specifically, whether they are able to discriminate between quantities of arbitrary visual stimuli that differ by one item only. While in our previous study we applied the spontaneous choice tests studying mice reactions to artificial food patches (Panteleeva et al. 2013), in the current experiments we use the training paradigm to investigate the cognitive aspects of numerical processing in wild rodents. To examine whether striped field mice possess a core system of quantitative competence we tested both laboratory-reared and wild-caught individuals.

We set up a procedure that consists of training animals to discriminate between sets containing different numbers of geometric figures while controlling for the perceptual non-numerical variables. Similar experimental schemes were applied to monkeys (Brannon and Terrace 1998; Judge et al. 2005), hooded crows (Smirnova et al. 2000), pigeons (Brannon et al. 2001), dolphins (Kilian et al. 2003), fishes (Agrillo et al. 2009), bears (Vonk and Beran 2012), honey bees (Mazokhin-Porshnyakov and Kartsev 2000; Giurfa et al. 2001; Gross et al. 2009), and some other animals. Like in some bird studies (Smirnova et al. 2000; Hunt et al. 2008), in our experiments animals had to deal with a card that covered a box containing food items. However, in contrast to birds, rodents are strongly smell-guiding. That is why we applied the 'examination' paradigm (described in the "Methods" section) following the bee studies of Mazokhin-Porshnyakov and Kartsev (2000).

In the present work, we demonstrated that not only can striped field mice *A. agrarius* discriminate between clearly distinctive quantities such as 5 and 10, but some of these mice also exhibit high accuracy in discriminating between quantities that differ only by one. The latter include both small (such as 2 versus 3) and relatively large (such as 5 versus 6, and 8 versus 9) quantities of elements. This is the first evidence of precise relative-quantity judgement in wild rodents.

Methods

Subjects and housing

In all series of experiments we used 37 striped field mice *A. agrarius* (22 males and 15 females); 8 animals were taken from the wild, and the others were the first and the second generation descendants of those captured in a mixed-pine forest near Novosibirsk. Wild-caught mice only participated in the Control experiment-1 (see below). All animals were naive, that is, lacking any experimental history. Mice were housed singly in clear plastic cages (40 × 30 × 20 cm) that contained cotton nesting material. Mice were fed each day with mixed seeds, fruits, boiled eggs and mealworms (*Tenebrio molitor* larvae), and they had free access to water. Subjects were tested once a day 2–3 times per week on the laboratory arena. Animals were not deprived of food before testing. In order to promote engagement with the trials, small pieces of walnut were used as rewards. In our experience, walnuts are a highly preferred food for mice, and are attractive at any food-deprivation level including full repletion. It is worth noting that studying cognitive skills in small rodents should be organised so as to minimise their anxiety and to ensure engagement with the chosen task. Striped field mice are relatively bold, and they usually allow handling straight after being caught in a living trap in the wild. In our study, home cages were placed in the laboratory area frequently visited by researchers. All animals readily entered the plastic coffee-cup that we used to manipulate them, and they showed no signs of distress while being tested.

Apparatus, stimuli and procedure

In order to investigate whether striped field mice can successfully learn to discriminate between numbers of arbitrary static visual stimuli, we applied the 'examination' paradigm based on the special schedule of reinforcement that differed essentially both from the intensive training used in experiments on numerical competence in rodents (Fernandes and Church 1982; Inman et al. 2016) and the spontaneous choice paradigm (Agrillo and Bisazza 2014) also applied to small rodents (Cox and Montrose 2016). In our study, each series contained the pre-training phase, the training phase and the 'exams', that is, the critical phase which was characterised by the absence of a food reward and served to prevent the animal from using food odour as a cue (Mazokhin-Porshnyakov and Kartsev 2000). The pre-training and training phases were intended to shape the association between the visual stimulus and reward. During the pre-training phase, the animal was allowed to explore two feeders that differed visually, until it finds the food placed in one of them, whereas during the training phase only one choice was allowed (see details below). During exams both feeders were empty, and the subject received a reward from the experimenter immediately after making the correct choice. Since we do not know when and how the association is shaped, we consider the possibility that a mouse can associate first the smell and then the taste of the desired food with the rewarded visual stimulus during the pre-training and the training phases.

The details of the experimental procedure were as follows. Animals were provided with pairs of identical feeders that differed by the array of visual stimuli drawn on their surfaces. Mice were tested one by one in a circular arena (33 cm in diameter, 35 cm high) with two opaque plastic boxes (8.5 cm × 8.5 cm × 2 cm) attached to its sides. Each box was covered by a changeable ‘curtain’ made of white paper with an array of geometric figures (elements) drawn on their surfaces, similar with the crow study by Smirnova et al. (2015) (Fig. 1). We used heterogeneous graphic arrays of different quantities of simple geometric elements (5 and 10 elements in the first experiment; 2 and 3 in the second one, etc.), black on white background (Fig. 2). Geometric figures had approximately the same linear dimensions (diameter, side). The differences in the overall amount of black image in the two arrays decreased as the number of geometric figures increased. For example, in the case of eight elements on one picture and nine on the other, the difference between the total areas covered by black images on the two different pictures was 11%, and, in the case of 5 and 6 elements, the difference was 17%. Thus, total area of black in the images co-varied with the numerical difference between arrays. Elements varied in position and were selected randomly from a large pool. The choice of a certain number of elements (for example, 10 versus 5 in Experiment 1) was rewarded. Different tests were carried out by four people to randomise difference in experimenters’ behaviour and experience.

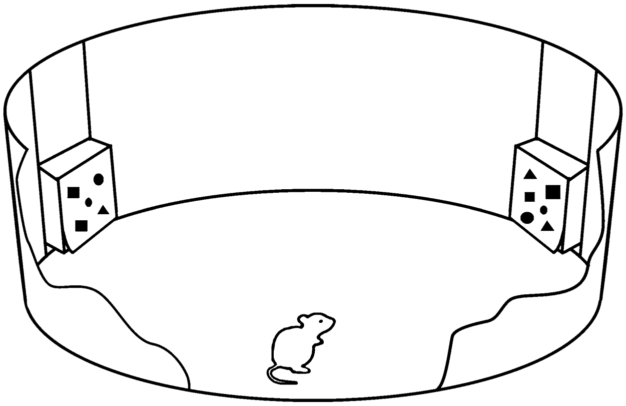

Fig. 1 Apparatus used to train mice

The mice were subjected to one series of experiments per day. Each series consisted of a pre-training phase, a training one, and an exam. Both the pre-training phase and the exam included one trial, and the training phase included three trials. In the beginning of each trial, the mouse was carefully placed in the centre of the arena with the help of a plastic coffee cup (suppl. 1, 2). An animal could freely choose to

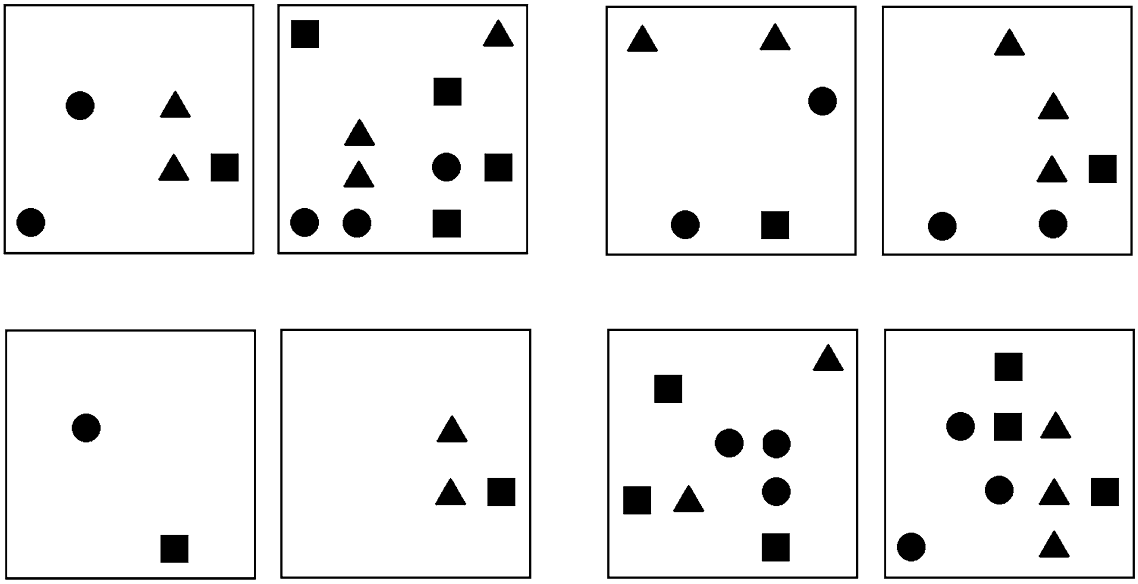

Fig. 2 Schematic representation of the stimuli used in the experiments. Elements varied in shape and position, and were randomly selected from a large pool. Sizes of elements: squares (side = 9 mm, area = 81 mm^2), circles (diameter = 10 mm, area = 78.5 mm^2) and triangles (side = 10 mm, area = 45 mm^2)

visit one of the two boxes present. During the pre-training phase the mice were allowed to choose between two boxes covered with the curtains with different numbers of elements drawn on them. During this phase, a bait was placed inside the box covered with a curtain with a certain number of elements drawn on it. For example, in the first experiment the choice of ten elements was rewarded. Number of choices was unlimited, until the animal found and ate the bait. After that we captured the mouse and placed it in its home cage. During the second, training phase, the animal, being again placed in the centre of the arena, was allowed to make only one choice between two boxes. If the choice was correct (say, ten elements in the first experiment), then the mouse was allowed to enter the box and eat the bait. We considered the choice to be made if the animal threw back the paper curtain by its head or got into the box with its whole body (suppl. 1, 2). Sniffing the curtain was not considered a choice. When the wrong choice was made (five elements in the first experiment), the 'punishment' came, which consisted in the mouse being captured and placed into a separate dark arena for 1 min. During the training phase each subject received three training trials, with intervals of 5–7 min between them. For each trial we used fresh boxes and a fresh arena. To reduce the issues associated with side-bias, the location of the correct stimulus (left versus right) was determined randomly each time. The arrays of elements drawn on the curtains were also changed each time to randomise the localisation of the visual stimuli and thus prevent animals from memorising character pictures. After three training trials, the mouse passed to the exam stage, which was the key phase of the experiment. During the exam again fresh boxes were used; however, at this time they did not contain food. The intervals between trials were 5–7 min. Figure 3 shows the time course of the entire study, with intervals between the tests.

In most of the trials, mice made their choice very quickly, straight after jumping out of the cup (see suppl. 1), and likely they made their decision already when looking out of the cup. In some cases, animals ran between the boxes several times before making their choice.

We analysed the data at the group and individual levels. In the first case, we checked whether the total number of correct choices in the exams of all mice in each experiment differed from random. In the second case, we tested whether each animal chose by chance. To test whether the number of choices of the correct quantity during the exams deviated from chance level, we applied 2-tailed binomial tests. The learning criterion was a statistically significant frequency of the correct choice made by the animal during the exams only, estimated with two-tailed binomial tests.

Results

Experiment 1: Relative numerosity judgements: 5 versus 10

Mice had to choose between 5 and 10 geometric figures; the choice of 10 was rewarded. 24 animals were tested, and after one year we repeated the experiments with the same animals. In total, 1223 exams were held. In the first series of Experiment 1, 18 (75.0%) mice learned to discriminate between 5 and 10, and 17 (70.8%) learned to do this in the second series after a year (Table 1). Two individuals (N 61, 47) learned to choose the rewarded stimulus only in the second series, whereas one animal (N 27) that was successful in the first series, failed in the second one. 17 (70.8%) individuals were successful both in the first and the second series of the experiment 1.

Experiment 2: Discriminating between quantities of visual stimuli within the limit of subitising: 2 versus 3

Mice had to discriminate between 2 and 3. This experiment included two series: in the first one the choice of 3 was rewarded, whereas in the second series the rewarded choice was 2. There were 24 mice that participated in the first series of the experiment, and 22 in the second (Table 2). In total, 913 exams were held. In the first series of Experiment 2, 14

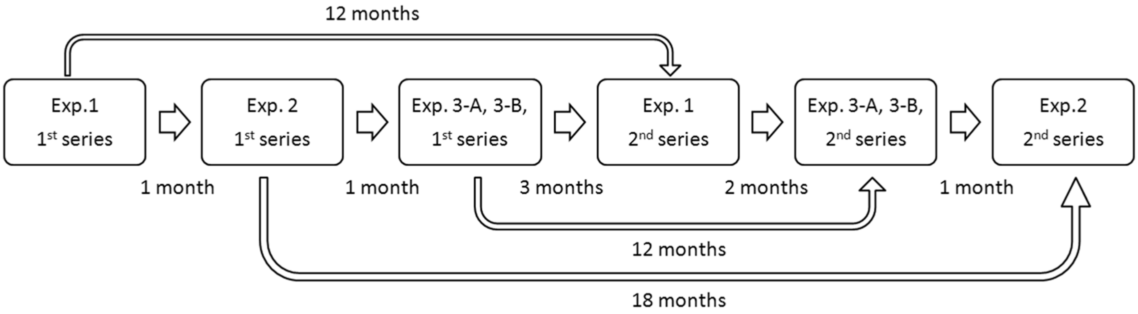

Fig. 3 The time course of the entire study, with intervals between the tests

Table 1 Exam outcomes: the number of correct choices made in Experiment 1 (“5 versus 10”); the last column shows the *p* value of the 2-tailed binomial test

Individuals	Percentage of times the number 10 was chosen (first series)	*p*	Percentage of times the number 10 was chosen (second series)	*p*
1 ♂	90.2% (46 out of 51)	< 0.0001*	95.0% (19 out of 20)	< 0.0001*
11 ♂	90.0% (45 out of 50)	< 0.0001*	95.0% (19 out of 20)	< 0.0001*
14 ♂	78.4% (40 out of 51)	< 0.0001*	95.0% (19 out of 20)	< 0.0001*
16 ♂	76.5% (39 out of 51)	< 0.0002*	90.0% (18 out of 20)	0.0004*
18 ♂	70.6% (36 out of 51)	0.0046*	95.0% (19 out of 20)	< 0.0001*
21 ♀	68.8% (33 out of 48)	0.0133*	90.0% (18 out of 20)	0.0004*
22 ♀	70.6% (36 out of 51)	0.0046*	85.0% (17 out of 20)	0.0026*
23 ♀	47.1% (24 out of 51)	0.7798	40.0% (8 out of 20)	0.5034
24 ♀	94.1% (48 out of 51)	< 0.0001*	95.0% (19 out of 20)	< 0.0001*
27 ♂	85.0% (18 out of 20)	0.0004*	70.0% (14 out of 20)	0.0577
29 ♂	85.0% (17 out of 20)	0.0026*	80.0% (16 out of 20)	0.0599*
46 ♀	89.5% (17 out of 19)	0.0028*	90.0% (18 out of 20)	0.0004*
47 ♂	63.2% (12 out of 19)	0.3593	80.0% (16 out of 20)	0.0599*
48 ♂	88.9% (16 out of 18)	0.0013*	90.0% (18 out of 20)	0.0004*
49 ♀	95.0% (19 out of 20)	< 0.0001*	95.0% (19 out of 20)	< 0.0001*
58 ♀	83.3% (15 out of 18)	0.0075*	75.0% (15 out of 20)	0.0414*
59 ♀	85.0% (17 out of 20)	0.0026*	90.0% (18 out of 20)	0.0004*
61 ♀	68.4% (13 out of 19)	0.1671	75.0% (15 out of 20)	0.0414*
62 ♂	10.0% (8 out of 20)	0.5035	50.0% (10 out of 20)	1.1762
63 ♂	80.0% (16 out of 20)	0.0118*	80.0% (16 out of 20)	0.0599*
64 ♀	55.6% (10 out of 18)	0.8145	55.0% (11 out of 20)	0.8238
65 ♀	85.0% (17 out of 20)	0.0026*	90.0% (18 out of 20)	0.0004*
67 ♂	31.6% (6 out of 19)	0.1671	45.0% (9 out of 20)	0.8238
68 ♂	88.9% (16 out of 18)	0.0013*	85.0% (17 out of 20)	0.0026*

Numbers mean individuals

*The number of correct choices that significantly differ from the chance level, $p \leq 0.01$

(58.3%) animals learned to choose the rewarded stimulus, and in the second series, 12 (54.6%) animals were successful, out of which 9 (40.9%) individuals achieved success in both series.

Experiment 3: Distinguishing between quantities of visual stimuli beyond the limit of subitising: 5 versus 6 (Experiment 3-A) and 8 versus 9 (Experiment 3-B)

Experiment 3-A included two series. In the first series the choice of 6 was rewarded, whereas in the second one the rewarded choice was 5. Experiment 3-B also included two series. In the first series the choice of 9 was rewarded, and in the second one the rewarded choice was 8. In total, 1009 exams were held. In both series of Experiment 3-A, and the first series of Experiment 3-B, 11 mice were tested, and in the second series of Experiment 3-B, the number of animals was 22 (Table 3). In the first series of Experiment 3-A, 7 (63.7%) out of 11 animals learned to discriminate between 5 and 6; in the second one 8 (80.0%) out of 11 animals were successful. In the first series of Experiment 3 B, 7 (70.0%) out of ten animals learned to discriminate between 8 and 9, and in the second one, 12 (54.6%) out of 22 animals were successful. All four individuals (N 1, 11, 14, 24) that successfully learned in Experiment 2, also reached success in both two series of Experiment 3.

Control Experiment 1: are there any extraneous stimuli?

We carried out Control Experiment 1 after Experiments 1–3, to check whether animals formed associations between the reward and any extraneous stimuli out of our consideration. To do this, we changed the condition of the training phase, that is, both stimuli were rewarded. This paradigm is similar to ‘non-differential reinforcement’ used by Smirnova et al. (2015) in their experiments with the crows. Our assumptions were the following: in our experiments described above, some animals during the exams performed the correct choice of the visual stimulus that was rewarded at the training stage. Was this just the differential reinforcement which influenced their choice? We excluded the possible influence of the experimenter himself, as well as possible

Table 2 Exam outcomes: the number of correct choices made in Experiment 2 (“2 versus 3”); the last column shows the *p* value of 2-tailed binomial test

Individuals	Percentage of times the number 3 was chosen (first series)	*p*	Percentage of times the number 2 was chosen (second series)	*p*
1 ♂	81.3% (26 out of 32)	0.0005*	100.0% (14 out of 14)	0.0001*
11 ♂	84.4% (27 out of 32)	0.0001*	92.9% (13 out of 14)	0.0018*
14 ♂	78.1% (25 out of 32)	0.0021*	100.0% (14 out of 14)	0.0001*
16 ♂	81.3% (26 out of 32)	0.0005*	×	×
18 ♂	75.0% (24 out of 32)	0.0070*	×	×
21 ♀	75.0% (24 out of 32)	0.0070*	92.9% (13 out of 14)	0.0018*
22 ♀	50.0% (16 out of 32)	1.1399	85.7% (12 out of 14)	0.0129*
23 ♀	81.3% (26 out of 32)	0.0005*	85.7% (12 out of 14)	0.0129*
24 ♀	90.6% (29 out of 32)	<0.0001*	100.0% (14 out of 14)	0.0001*
27 ♂	65.6% (21 out of 32)	0.1102	64.3% (9 out of 14)	0.4210
29 ♂	76.0% (19 out of 25)	0.0146*	92.9% (13 out of 14)	0.0018*
46 ♀	60.0% (12 out of 20)	0.5034	85.7% (12 out of 14)	0.0129*
47 ♂	45.0% (9 out of 20)	0.8238	64.3% (9 out of 14)	0.4210
48 ♂	75.0% (15 out of 20)	0.0414	85.7% (12 out of 14)	0.0129*
49 ♀	25.0% (5 out of 20)	0.0414	42.9% (6 out of 14)	0.7905
58 ♀	80.0% (16 out of 20)	0.0118*	92.9% (13 out of 14)	0.0018*
59 ♀	90.0% (18 out of 20)	0.0004*	78.6% (11 out of 14)	0.0574
61 ♀	70.0% (14 out of 20)	0.0577	71.4% (10 out of 14)	0.1796
62 ♂	50.0% (10 out of 20)	1.1762	57.1% (8 out of 14)	0.7905
63 ♂	90.0%(18 out of 20)	0.0004*	64.3% (9 out of 14)	0.4210
64 ♀	85.0% (17 out of 20)	0.0026*	71.4% (10 out of 14)	0.1796
65 ♀	60.0% (12 out of 20)	0.5034	71.4% (10 out of 14)	0.1796
67 ♂	45.0% (9 out of 20)	0.8238	78.6% (11 out of 14)	0.0574
68 ♂	80.0% (16 out of 20)	0.0118*	92.9% (13 out of 14)	0.0018*

*The number of the correct choices significantly differs from chance level, $p \leq 0.01$

‘×’—not tested because the animal died

associations with side-bias and the smell of different places of the arena and of the food itself. However, we had to consider the possibility that there were some other extraneous stimuli which could impact animals’ choice. Had it been so, the mice would show a preference for a certain visual stimulus at the exam phase, even under the circumstances of non-differential reinforcement during the training phase. Otherwise, mice would choose randomly.

We carried out Control Experiment 1 with a subset of 13 new individuals, eight of which were caught in nature and five were reared in the laboratory. First, we checked whether these animals can learn to choose the rewarded visual stimuli. To do this, we performed two series of tests. In the first series 10 versus 5 was rewarded, and in the second one 6 versus 5, with the use of the same protocol as before. The third series was the Control per se, and the protocol differed. There were 2 and 8 elements on the pictures, that is, the stimuli were easily distinguishable. In contrast to all previews experiments, both boxes contained bait during both the first (pre-training) and the second (training) phases. So, any choice was rewarded. During the exams, as always, both boxes were empty. In total 796 exams were held.

The results were as following. In the first series (5 versus 10) nine animals (69.2%) learned to choose the rewarded stimulus (10). In the second series 11 animals (84.5%) were successful, out of which nine were the same as in the first series. In the control per se experiment (the third series) all mice chose a box randomly (Table 4). In the first (5 versus 10) and second (5 versus 6) Control-1 experiment series, the average share of correct choices for wild (78.6 ± 12.0%) and laboratory (85.0 ± 4.7%) mice was not significantly different (*t* test, $t_{\text{emp}}. = 1.6$; $p > 0.05$).

Control Experiment 2: spontaneous choice

To check whether mice possess the spontaneous preference for pictures with more elements, or vice versa, we performed Control experiment 2 in which pairs of stimuli were presented to animals randomly, without any reward: 3 versus 5, 4 versus 6, 2 versus 7, 3 versus 8, 4 versus 8, 3 versus 6, 4 versus 7, 2 versus 8, 3 versus 7, 6 versus 8, 6 versus 9, 2 versus 6, and 4 versus 9. In total, 9 animals were tested, each one in 20 trials (Table 5). In total 180 trials were held. We tested the Hypothesis H_0 (mice choose the stimulus

Table 3 Exam outcomes: the number of correct choices made in Experiments 3-A ("5 versus 6") and 3-B ("8 versus 9"); given is the *p* value of 2-tailed binomial test

	Percentage of times the number 6 was chosen (the first series of Experiment 3 A)	*p*	Percentage of times the number 5 was chosen (the second series of Experiment 3 A)	*p*	Percentage of times the number 9 was chosen (the first series of Experiment 3 B)	*p*	Percentage of times the number 8 was chosen (the second series of Experiment 3 B)	*p*
1 ♂	100.0% (11 out of 11)	0.0010*	88.9% (40 out of 45)	< 0.0001*	(93.8% 15 out of 16)	0.0005*	100.0% (14 out of 14)	0.0001*
11 ♂	100.0% (11 out of 11)	0.0010*	77.8% (35 out of 45)	0.0002*	(93.8% 15 out of 16)	0.0005*	100.0% (14 out of 14)	0.0001*
14 ♂	90.9% (10 out of 11)	0.0117*	91.1% (41 out of 45)	< 0.0001*	(87.5% 14 out of 16)	0.0042*	92.9% (13 out of 14)	0.0018*
16 ♂	90.9% (10 out of 11)	0.0117*	×	×	×	×	×	×
18 ♂	100.0% (11 out of 11)	0.0010*	87.0% (20 out of 45)	0.0005*	(81.3% 13 out of 16)	0.0213	×	×
21 ♀	45.5% (5 out of 11)	1.2461	88.4% (38 out of 43)	< 0.0001*	(87.5% 14 out of 16)	0.0042*	92.9% (13 out of 14)	0.0018*
22 ♀	36.4% (4 out of 11)	0.7539	90.7% (39 out of 43)	< 0.0001*	(81.3% 13 out of 16)	0.0213	92.9% (13 out of 14)	0.0018*
23 ♀	90.9% (10 out of 11)	0.0117*	48.8% (21 out of 43)	1.0000	(87.5% 14 out of 16)	0.0042*	85.7% (12 out of 14)	0.0129*
24 ♀	100.0% (11 out of 11)	0.0010*	88.9% (40 out of 45)	< 0.0001*	(93.8% 15 out of 16)	0.0005*	92.9% (13 out of 14)	0.0018*
27 ♂	81.8% (9 out of 11)	0.0654	60.5% (26 out of 45)	0.2221	(93.8% 15 out of 16)	0.0005*	64.3% (9 out of 14)	0.1210
29 ♂	45.5% (5 out of 11)	1.2461	88.9% (40 out of 45)	< 0.0001*	(75.0% 12 out of 16)	0.0768	92.9% (13 out of 14)	0.0018*
46 ♀	–		–		–		85.7% (12 out of 14)	0.0129*
47 ♂	–		–		–		64.3% (9 out of 14)	0.1210
48 ♂	–		–		–		85.7% (12 out of 14)	0.0129*
49 ♀	–		–		–		42.9% (6 out of 14)	0.7905
58 ♀	–		–		–		92.9% (13 out of 14)	0.0018*
59 ♀	–		–		–		78.6% (11 out of 14)	0.0574
61 ♀	–		–		–		78.6% (11 out of 14)	0.0574
62 ♂	–		–		–		57.1% (8 out of 14)	0.7905
63 ♂	–		–		–		71.4% (10 out of 14)	0.1796
64 ♀	–		–		–		71.4% (10 out of 14)	0.1796
65 ♀	–		–		–		78.6% (11 out of 14)	0.0574
67 ♂	–		–		–		78.6% (11 out of 14)	0.0574
68 ♂	–		–		–		92.9% (13 out of 14)	0.0018*

*The number of the correct choices significantly differs from chance level, $p \leq 0.01$

'×'—not tested because the animal died, '–'—not tested because of an accident

randomly) against H_1 (the choice differs from the random one). All animals appeared to make a random choice.

Group-level analysis

We analysed the data at the group level to check whether the total number of correct choices in the exams of all mice in each experiment differs from random. The results are shown in Table 6.

Discussion

In our experiments, more than half of the individuals learned not only to discriminate with high accuracy between quantities at the ratio 1:2, but also between such quantities as 5 versus 6 and 8 versus 9, making the correct choice in more than 90% of the exams. The results of two control experiments enable us to assume that this was the differential reinforcement that influenced animals' choice, and neither any extraneous stimuli nor a spontaneous preference for the bigger quantities played a role here. It is clear that striped field mice come to learn reasonably rapidly to discriminate between specific quantities at a level that is far beyond subitising.

One can consider two hypotheses about which clues mice use to distinguish between stimuli. The first hypothesis is that that the mice were using the number of items, and the second one is that the overall amount of black image is a predictor of which container should be selected. In experiment 3-B (8 versus 9) the difference between total areas of black images was 11%, that is, both ratios between the number of items and the overall amounts of black figures were about 9:8. This situation is comparable with the dramatic story of inducing experimental neurosis in dogs in the Pavlov's lab. Shenger-Krestovnikova (1921) conditioned a dog to respond to a circle but not to an ellipse. Then, in a five-trial series, different ellipses were projected on the screen in a dark

Table 4 Exam outcomes: the number of correct choices made in Control 1 Experiment ("5 versus 10", "5 versus 6" and "2 versus 8"); the last column shows the *p* value of a 2-tailed binomial test

Individuals	Percentage of times the number 10 was chosen (first series)	*p*	Percentage of times the number 5 was chosen (second series)	*p*	Percentage of times the number 2 was chosen (third series)	*p*
72 ♂	90.0% (18 out of 20)	0.0004*	90.0% (18 out of 20)	0.0004*	70.0% (14 out of 20)	0.1153
81 ♀	80.0% (16 out of 20)	0.0118*	80.0% (16 out of 20)	0.0118*	65.0% (13 out of 20)	0.2630
82 ♂	85.0% (17 out of 20)	0.0026*	85.0% (17 out of 20)	0.0026*	60.0% (12 out of 20)	0.5034
91 ♂	80.0% (16 out of 20)	0.0118*	80.0% (16 out of 20)	0.0118*	45.0% (9 out of 20)	0.8238
92 ♀	90.0% (18 out of 20)	0.0004*	90.0% (18 out of 20)	0.0004*	55.0% (11 out of 20)	0.8238
343 ♀	77.3% (17 out of 22)	0.0169	80.0% (16 out of 20)	0.0118*	70.0% (14 out of 20)	0.1153
344 ♀	72.7% (16 out of 22)	0.0525	75.0% (15 out of 20)	0.0414	45.0% (9 out of 20)	0.8238
515 ♂	81.8% (18 out of 22)	0.0043*	85.0% (17 out of 20)	0.0026*	65.0% (13 out of 20)	0.2632
552 ♂	68.2% (15 out of 22)	0.1338	65.0% (13 out of 20)	0.2632	65.0% (13 out of 20)	0.2632
613 ♂	86.4% (19 out of 22)	0.0009*	90.0% (18 out of 20)	0.0004*	60.0% (12 out of 20)	0.5034
649 ♂	45.5% (10 out of 22)	0.8318	75.0% (15 out of 20)	0.0414	35.0% (7 out of 20)	0.2632
745 ♂	86.4% (19 out of 22)	0.0009*	90.0% (18 out of 20)	0.0004*	30.0% (6 out of 20)	0.1153
748 ♂	90.9% (20 out of 22)	0.0001*	90.0% (18 out of 20)	0.0004*	50.0% (10 out of 20)	1.1762

Mice that have a three-digit number are wild-caught

*The number of the correct choices significantly different from chance level, $p \leq 0.01$

Table 5 The number of choices made in Control 2 experiment: the last column shows the *p* value of a 2-tailed binomial test

Individuals	Percentage of times pictures with more elements were chosen	*p*
1 ♂	75.0% (15 out of 20)	0.0414
11 ♂	75.0% (15 out of 20)	0.0414
14 ♂	40.0% (8 out of 20)	0.5034
18 ♂	55.0% (11 out of 20)	0.8238
21 ♀	50.0% (10 out of 20)	1.1762
22 ♀	35.0% (7 out of 20)	0.2632
23 ♀	45.0% (9 out of 20)	0.8238
24 ♀	70.0% (14 out of 20)	0.1153
29 ♂	40.0% (8 out of 20)	0.5034

room. The proportion of vertical to horizontal diameters of the ellipses were 2:1, 3:2, 4:3, 5:4, and 9:8. When a dog had to differentiate a circle from a 9:8 ellipse, its behaviour became disorganised: the dog whined, yelped, and became very excited. In our experiment, the mice coped with a similar task rather quickly without any agitation, although their task was not just to compare two geometric figures, but to sum up the total area of 8 items and 9 ones. However, with that dog story in mind, one can suggest that 'counting' the number of items is more accessible for mice than 'measuring' their total areas. Studies on laboratory strains of mice and rats have shown that these animals view the world at extremely low resolution (for the reviews see: Huberman and Niell 2011; Djurdjevic et al. 2018). Even horses, with their wide visual field, were able to discriminate between circles that differed by up to 14% in size but not less (Tomonaga et al. 2015). We consider both hypotheses plausible, but in either case we can conclude that striped field mice exhibit precise relative-quantity judgement in our experiments.

We still do not have enough data to form an opinion about whether striped field mice possess one system or two systems for representing and judging quantity. However, the fact that mice in our experiments do not show privileged capacities for dealing with small numbers of items, just as capuchin monkeys showed no such privilege (Beran and Parrish 2016), suggests that there may be similarities between quantity representations in rodents and primates.

The fact that laboratory-reared naive mice performed well in all tasks enables us to suggest that their abilities to distinguish between numbers of visual stimuli with high accuracy can be attributed to their species-specific cognitive capacities and do not depend on their current experience in the wild.

We found striking individual variation in cognitive performance among striped field mice. Out of 24 animals tested in the experiments 1–3, four individuals (N 1, 11, 14, 24) reached success in all of the tests but made some mistakes, four (N 47, 61, 62, 67) failed all of them, and four (N 1, 11, 18, and 24) passed the exams in all six series without any mistakes. One of these advanced subjects (N 1) lived to be 4 years old, which is extraordinary for mice. It is likely that the individual differences in cognitive performance found in our experiments reflect variations in the cognitive abilities in natural populations.

It is of particular interest in our study that, although we used sufficiently long intervals between series of

Table 6 Exam outcomes: the number of correct choices made in the experiments; the last column shows the *p* value of the 2-tailed binomial test

Experiment	Number of mice	Total number of correct choices made in exams by all mice	Total number of exams	*p*
Experiment 1				
The first series	24	557	743	< 0.0001*
The second series	24	386	480	< 0.0001*
Experiment 2				
The first series	24	434	605	< 0.0001*
The second series	22	248	308	< 0.0001*
Experiment 3-A				
The first series	11	97	212	< 0.0001*
The second series	10	340	420	< 0.0001*
Experiment 3-B				
The first series	10	140	160	< 0.0001*
The second series	22	251	308	< 0.0001*
Control 1 Experiment				
The first series	13	219	276	< 0.0001*
The second series	13	215	260	< 0.0001*
The third series	13	143	260	0.1209
Control 2 Experiment	9	97	180	0.3326

*The number of correct choices that significantly differ from the chance level, $p \leq 0.01$

experiments, such as 12 months in one case and 18 months in another one, no deterioration of the accuracy was revealed in the subjects. We do not assume that our animals keep the memory about a task during an 18-, 12-, or even a 1-month period, the latter being the typical interval between series. However, in contrast to many studies carried out on laboratory mice (for a review see: Webster et al. 2014), our results demonstrate the lack of ageing effect in performing a cognitively demanding task in the striped field mouse. Although in many laboratory studies cognitive performance is influenced by age, sex, rearing conditions and previous experience (for a review see: Thornton and Lukas 2012), this was not found to be the case in our experiments.

The results obtained raise the question about the core system of spontaneous numerosity in rodents and its possible evolutionary roots. We speculate that high accuracy in differentiating large quantities is based on the adaptive ability of wild rodents to capture subtle changes in their environment. That the striped field mouse possesses high accuracy in distinguishing between large numbers of items at a level comparable with monkeys is possibly caused by peculiarities of their visual discrimination and neuronal organisation. Recent studies on laboratory mice and rats have revealed that, although the murine cortex is indeed performing similar computations to those in other species, these animals have severe limitations in visual processing, as well as in some types of large-scale orientation. Mice and rats have poor spatial resolution and they are non-foveal, and, as a result, they may rely on head movements more than eye movements to view specific portions of visual space. It remains unclear what types of higher order visual processing and cognitive decisions mice can perform (for a review see Huberman and Niell 2011). Recent findings on laboratory rats (Djurdjevic et al. 2018) indicate that rats are capable of advanced processing of shape information. It is worth noting that subjects in this study displayed a high variability in visual object recognition, similar to striped field mice in our experiments. Variability in rats is accounted for by the diversity of rat perceptual strategies. Animals building richer perceptual templates achieve higher accuracy. The most advanced individuals discriminate a reference object from 11 distractors, which spanned a spectrum of image-level similarity to the reference. It is likely that some rats can compensate for the limitations of their visual processing with cognitive abilities.

Peculiarities of perceptual and cognitive processing in wild rodents remains to be determined. It is known that laboratory strains of mice and rats can differ dramatically in terms of their visual ability. For example, rearing mice from birth in an enriched environment leads to a conspicuous acceleration of visual system development as ascertained at behavioural, electrophysiological, and molecular levels (Cancedda et al. 2004). One can suggest even more striking differences in information processing and behavioural responses in diverse rodent species. It has been recently revealed on African mole rats that the high number of forebrain neurons likely endows solitary species with improved cognitive abilities and increased behavioural flexibility compared to social ones (Kverková et al. 2018) *A. agrarius* is a solitary living species inhabiting very changeable habitats including urban environment, which may be cognitively demanding. We suggest that the striped field mouse may be a powerful model species for developing advanced cognitive tests for comparative studies of numerical competence in animals, as well as for understanding evolutionary roots of quantity processing.

Acknowledgements We are grateful to Daniil Ryabko for the helpful discussion and useful comments. We thank Veronika Aculich for the help in conducting experiments. We appreciate the efforts and valuable comments of two anonymous reviewers that helped us to improve the manuscript.

Funding The study was funded by Russian Fund for Basic Research (No. 17-04-00702) and by The Federal Fundamental Scientific Research Program for 2013–2020 No. VI.51.1.10. (AAAA-A16-116121410120-0) (Grant no. 0-109-2018-0074).

References

Addessi E, Crescimbene L, Visalberghi E (2008) Food and token quantity discrimination in capuchin monkeys (*Cebus apella*). Anim Cogn 11(2):275–282. https://doi.org/10.1007/s10071-007-0111-6

Agrillo C, Beran MJ (2013) Number without language: comparative psychology and the evolution of numerical cognition. Front Psychol 4:295. https://doi.org/10.3389/fpsyg.2013.00295

Agrillo C, Bisazza A (2014) Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals. J Neurosci Meth 234:82–91. https://doi.org/10.1016/j.jneumeth.2014.04.027

Agrillo C, Dadda M, Serena G, Bisazza A (2009) Use of number by fish. PLoS One 4(3):e4786. https://doi.org/10.1371/journal.pone.0004786

Agrillo C, Piffer L, Bisazza A, Butterworth B (2012) Evidence for two numerical systems that are similar in humans and guppies. PLoS One 7(2):e31923. https://doi.org/10.1371/journal.pone.0031923

Anderson US, Stoinski TS, Bloomsmith MA, Maple TL (2007) Relative numerousness judgment and summation in young, middle-aged, and older adult orangutans (*Pongo pygmaeus abelii* and *Pongo pygmaeus pygmaeus*). J Comp Physiol 121(1):1–11

Benson-Amram S, Gilfillan G, McComb K (2018) Numerical assessment in the wild: insights from social carnivores. Phil Trans R Soc B 373(1740):20160508. https://doi.org/10.1098/rstb.2016.0508

Beran MJ (2007) Rhesus monkeys (*Macaca mulatta*) enumerate large and small sequentially presented sets of items using analog numerical representations. J Exp Psychol Anim Behav Proc 33(1):42–54. https://doi.org/10.1037/0097-7403.33.1.42

Beran MJ, Parrish AE (2016) Going for more: discrete and continuous quantity judgments by nonhuman animals. In: Henik A (ed) Continuous issues in numerical cognition: How many or how. Academic Press, San Diego, pp 175–192. https://doi.org/10.1016/C2014-0-00082-2

Beran MJ, McIntyre JM, Garland A, Evans TA (2013) What counts for 'counting'? Chimpanzees, *Pan troglodytes*, respond appropriately to relevant and irrelevant information in a quantity judgment task. Anim Behav 85(5):987–993. https://doi.org/10.1016/j.anbehav.2013.02.022

Beran MJ, Perdue BM, Evans TA (2015) Monkey mathematical abilities. In: Kadosh RC, Dowker A (eds) The Oxford handbook of numerical cognition. Oxford University Press, Oxford, pp 237–257

Beran MJ, Menzel CR, Parrish AE, Perdue BM, Sayers K, Smith JD, Washburn DA (2016) Primate cognition: attention, episodic memory, prospective memory, self-control, and metacognition as examples of cognitive control in nonhuman primates. Wiley Interdiscip Rev Cogn Sci 7(5):294–316. https://doi.org/10.1002/wcs.1397

Boysen ST, Berntson GG (1989) Numerical competence in a chimpanzee (*Pan troglodytes*). J Comp Psychol 103(1):23

Brannon EM, Merritt DJ (2011) Evolutionary foundations of the approximate number system. In: Dehaene S, Brannon E (eds) Space, time and number in the brain: searching for the foundations of mathematical thought. Academic Press, San Diego, pp 207–224. https://doi.org/10.1016/B978-0-12-385948-8.00014-1

Brannon EM, Roitman JD (2003) Nonverbal representations of time and number in animals and human infants. In: Meck WH (ed) Functional and neural mechanisms of interval timing. CRC Press, Boca Raton, pp 143–182. https://doi.org/10.1201/9780203009574.ch6

Brannon EM, Terrace HS (1998) Ordering of the numerosities 1 to 9 by monkeys. Science 282(5389):746–749. https://doi.org/10.1126/science.282.5389.746

Brannon EM, Wusthoff CJ, Gallistel CR, Gibbon J (2001) Numerical subtraction in the pigeon: evidence for a linear subjective number scale. Psychol Sci 12(3):238–243. https://doi.org/10.1111/1467-9280.00342

Burns RA, Goettl ME, Burt ST (1995) Numerical discrimination with arrhythmic serial presentations. Psychol Rec 45(1):95–104

Call J (2000) Estimating and operating on discrete quantities in orangutans (*Pongo pygmaeus*). J Comp Psychol 114(2):136

Cancedda L, Putignano E, Sale A, Viegi A, Berardi N, Maffei L (2004) Acceleration of visual system development by environmental enrichment. J Neurosci 24(20):4840–4848. https://doi.org/10.1523/JNEUROSCI.0845-04.2004

Cantlon JF, Brannon EM (2007) Basic math in monkeys and college students. PLoS Biol 5(12):e328. https://doi.org/10.1371/journal.pbio.0050328

Cantlon JF, Platt ML, Brannon EM (2009) Beyond the number domain. Trends Cogn Sci 13(2):83–91. https://doi.org/10.1016/j.tics.2008.11.007

Capaldi EJ, Miller DJ (1988) Counting in rats: its functional significance and the independent cognitive processes that constitute it. J Exp Psychol Anim Behav Proc 14(1):3–17. https://doi.org/10.1037/0097-7403.14.1.3

Chelkowska H, Walkowa W, Adamcszyk K (1985) Spatial relationship in sympatric population of the rodents: *Clethrionomys glareolus*, *Microtus agrestis* and *Apodemus agrarius*. Acta Ther 30(2):51–78

Cox L, Montrose VT (2016) Quantity discrimination in domestic rats, *Rattus norvegicus*. Animals 6(8):46. https://doi.org/10.3390/ani6080046

Davis HP, Pérusse R (1988) Numerical competence in animals: definitional issues, current evidence, and a new research agenda. Behav Brain Sci 11(4):561–615. https://doi.org/10.1017/S0140525X00053437

Dehaene S (2011) The number sense: how the mind creates mathematics. Oxford University Press, New York

Dehaene S, Izard V, Spelke E, Pica P (2008) Log or linear? Distinct intuitions of the number scale in Western and Amazonian indigene cultures. Science 320(5880):1217–1220

Djurdjevic V, Ansuini A, Bertolini D, Macke JH, Zoccolan D (2018) Accuracy of rats in discriminating visual objects is explained by the complexity of their perceptual strategy. Curr Biol 28(7):1005–1015. https://doi.org/10.1016/j.cub.2018.02.037

Feigenson L, Dehaene S, Spelke E (2004) Core systems of number. Trends Cogn Sci 8(7):307–314. https://doi.org/10.1016/j.tics.2004.05.002

Ferkin MH, Hobbs NJ (2014) Female meadow voles, *Microtus pennsylvanicus*, respond differently to the scent marks of multiple male conspecifics. Anim Cogn 17(3):715–722. https://doi.org/10.1007/s10071-013-0703-2

Ferkin MH, Pierce AA, Sealand RO (2005) Meadow voles, *Microtus pennsylvanicus*, can distinguish more over-marks from fewer over-marks. Anim Cogn 8(3):182–189. https://doi.org/10.1007/s10071-004-0244-9

Fernandes DM, Church RM (1982) Discrimination of the number of sequential events by rats. Anim Learn Behav 10(2):171–176

Ferrigno S, Hughes KD, Cantlon JF (2016) Precocious quantitative cognition in monkeys. Psychon Bull Rev 23(1):141–147. https://doi.org/10.3758/s13423-015-0893-5

Gallistel CR, Gelman R (2000) Nonverbal numerical cognition: from reals to integers. Trends Cogn Sci 4(2):59–65. https://doi.org/10.1016/S1364-6613(99)01424-2

Garland A, Low J, Burns KC (2012) Large quantity discrimination by North Island robins (*Petroica longipes*). Anim Cogn 15(6):1129–1140. https://doi.org/10.1007/s10071-012-0537-3

Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of 'sameness' and 'difference' in an insect. Nature 410(6831):930. https://doi.org/10.1038/35073582

Gross HJ, Pahl M, Si A, Zhu H, Tautz J, Zhang S (2009) Number-based visual generalisation in the honeybee. PLoS One 4(1):e4263. https://doi.org/10.1371/journal.pone.0004263

Hamilton DA, Brigman JL (2015) Behavioral flexibility in rats and mice: contributions of distinct frontocortical regions. Genes Brain Behav 14(1):4–21. https://doi.org/10.1111/gbb.12191

Howard SR, Avarguès-Weber A, Garcia JE, Greentree AD, Dyer AG (2018) Numerical ordering of zero in honey bees. Science 360(6393):1124–1126. https://doi.org/10.1126/science.aar4975

Huberman AD, Niell CM (2011) What can mice tell us about how vision works? Trends Neurosci 34(9):464–473. https://doi.org/10.1016/j.tins.2011.07.002

Hunt S, Low J, Burns KC (2008) Adaptive numerical competency in a food-hoarding songbird. Proc R Soc B Biol Sci 275(1649):2373–2379. https://doi.org/10.1098/rspb.2008.0702

Inman RA, Honey RC, Eccles GL, Pearce JM (2016) Asymmetry in the discrimination of quantity by rats: the role of the inter-trial interval. Learn Behav 44(1):67–77. https://doi.org/10.3758/s13420-015-0191-0

Judge PG, Evans TA, Vyas DK (2005) Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*). J Exp Psychol Anim Behav Proc 31(1):79–94. https://doi.org/10.1037/0097-7403.31.1.79

Kaufman EL, Lord MW, Reese TW, Volkmann J (1949) The discrimination of visual number. Am J Psychol 62(4):498–525. https://doi.org/10.2307/1418556

Kilian A, Yaman S, von Fersen L, Güntürkün O (2003) A bottlenose dolphin discriminates visual stimuli differing in numerosity. Anim Learn Behav 31(2):133–142. https://doi.org/10.3758/BF03195976

Krusche P, Uller C, Dicke U (2010) Quantity discrimination in salamanders. J Exp Biol 213(11):1822–1828. https://doi.org/10.1242/jeb.039297

Kverková K, Bělíková T, Olkowicz S, Pavelková Z, O'Riain MJ, Šumbera R, Burda H, Bennett NC, Němec P (2018) Sociality does not drive the evolution of large brains in eusocial African mole-rats. Sci Rep 8(1):9203. https://doi.org/10.1038/s41598-018-26062-8

Łopucki R, Mróz I, Berliński Ł, Burzych M (2013) Effects of urbanization on small-mammal communities and the population structure of synurbic species: an example of a medium-sized city. Can J Zool 91(8):554–561. https://doi.org/10.1139/cjz-2012-0168

Mazokhin-Porshnyakov GA, Kartsev VM (2000) Learning in bees and wasps in complicated experimental tasks. In: Cruse H, Dean J, Ritter H (eds) The cognitive development of an autonomous behaving operational intelligence: adaptive behavior and intelligent systems without symbols and logic. Springer, Dordrecht, pp 908–926. https://doi.org/10.1007/978-94-010-0870-9_56

Nieder A (2018) Evolution of cognitive and neural solutions enabling numerosity judgements: lessons from primates and corvids. Phil Trans R Soc B 373(1740):20160514. https://doi.org/10.1098/rstb.2016.0514

Pahl M, Si A, Zhang S (2013) Numerical cognition in bees and other insects. Front Psychol 4:162. https://doi.org/10.3389/fpsyg.2013.00162

Panteleeva S, Reznikova Z, Vygonyailova O (2013) Quantity judgments in the context of risk/reward decision making in striped field mice: first 'count', then hunt. Front Psychol 4:53. https://doi.org/10.3389/fpsyg.2013.00053

Pepperberg IM (2012) Further evidence for addition and numerical competence by a Grey parrot (*Psittacus erithacus*). Anim Cogn 15(4):711–717. https://doi.org/10.1007/s10071-012-0470-5

Pica P, Lemer C, Izard V, Dehaene S (2004) Exact and approximate arithmetic in an Amazonian indigene group. Science 306(5695):499–503. https://doi.org/10.1126/science.1102085

Reznikova Z (2007) Animal intelligence: from individual to social cognition. Cambridge University Press, Cambridge. https://doi.org/10.1016/j.intell.2009.04.004

Reznikova Z (2017) Studying animal language without translation: an insight from ants. Springer, Switzerland. https://doi.org/10.1007/978-3-319-44918-0

Reznikova Z (2018) Ants. Individual and social cognition. In: Bueno-Guerra N, Amici F (eds) Field and laboratory methods in animal cognition: a comparative guide. Cambridge University Press, Cambridge, pp 8–30

Reznikova Z, Ryabko B (1994) Experimental study of the ants' communication system with the application of the Information Theory approach. Mem Zool 48:219–236

Reznikova Z, Ryabko B (2001) A study of ants' numerical competence. Comput Inf Sci 6(15):111–126

Reznikova Z, Ryabko B (2011) Numerical competence in animals, with an insight from ants. Behaviour 148(4):405–434. https://doi.org/10.1163/000579511X568562

Reznikova Z, Levenets J, Panteleeva S, Ryabko B (2017) Studying hunting behaviour in the striped field mouse using data compression. Acta Ethol 20(2):165–173. https://doi.org/10.1007/s10211-017-0260-9

Rugani R, Regolin L, Vallortigara G (2010) Imprinted numbers: newborn chicks' sensitivity to number vs. continuous extent of objects they have been reared with. Dev Sci 13(5):790–797. https://doi.org/10.1111/j.1467-7687.2009.00936.x

Rugani R, Cavazzana A, Vallortigara G, Regolin L (2013) One, two, three, four, or is there something more? Numerical discrimination in day-old domestic chicks. Anim Cogn 16(4):557–564. https://doi.org/10.1007/s10071-012-0593-8

Rugani R, Vallortigara G, Priftis K, Regolin L (2015) Number-space mapping in the newborn chick resembles humans' mental number line. Science 347(6221):534–536. https://doi.org/10.1126/science.aaa1379

Shenger-Krestovnikova NR (1921) On the differentiation of visual stimuli and on the limits of differentiation in the visual analyzer of a dog. Bull Lesgaft Inst Petrograd 3:1–43

Smirnova AA, Lazareva OF, Zorina ZA (2000) Use of number by crows: investigation by matching and oddity learning. J Exp Anal Behav 73(2):163–176. https://doi.org/10.1901/jeab.2000.73-163

Smirnova A, Zorina Z, Obozova T, Wasserman E (2015) Crows spontaneously exhibit analogical reasoning. Curr Biol 25(2):256–260. https://doi.org/10.1016/j.cub.2014.11.063

Szacki J, Liro A (1991) Movements of small mammals in the heterogeneous landscape. Landsc Ecol 5(4):219–224. https://doi.org/10.1007/BF00141436

Taniuchi T, Sugihara J, Wakashima M, Kamijo M (2016) Abstract numerical discrimination learning in rats. Learn Behav 44(2):122–136. https://doi.org/10.3758/s13420-016-0209-2

Thomas RK, Fowlkes D, Vickery JD (1980) Conceptual numerousness judgments by squirrel monkeys. Am J Psychol 93:247–257. https://doi.org/10.2307/1422230

Thornton A, Lukas D (2012) Individual variation in cognitive performance: developmental and evolutionary perspectives. Phil Trans R Soc B 367(1603):2773–2783. https://doi.org/10.1098/rstb.2012.0214

Tomonaga M (2008) Relative numerosity discrimination by chimpanzees (*Pan troglodytes*): evidence for approximate numerical representations. Anim Cogn 11(1):43–57. https://doi.org/10.1007/s10071-007-0089-0

Tomonaga M, Kumazaki K, Camus F, Nicod S, Pereira C, Matsuzawa T (2015) A horse's eye view: size and shape discrimination compared with other mammals. Biol Lett 11(11):20150701. https://doi.org/10.1098/rsbl.2015.0701

Vonk J, Beran MJ (2012) Bears 'count' too: quantity estimation and comparison in black bears, *Ursus americanus*. Anim Behav 84(1):231–238. https://doi.org/10.1016/j.anbehav.2012.05.001

Webster SJ, Bachstetter AD, Nelson PT, Schmitt FA, Van Eldik LJ (2014) Using mice to model Alzheimer's dementia: an overview of the clinical disease and the preclinical behavioral changes in 10 mouse models. Front Genet 5:88. https://doi.org/10.3389/fgene.2014.00088