

The use of proportion by young domestic chicks (*Gallus gallus*)

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Abstract We investigated whether 4-day-old domestic chicks can discriminate proportions. Chicks were trained to respond, via food reinforcement, to one of the two stimuli, each characterized by different proportions of red and green areas ($\frac{1}{4}$ vs. $\frac{3}{4}$). In Experiment 1, chicks approached the proportion associated with food, even if at test the spatial dispositions of the two areas were novel. In Experiment 2, chicks responded on the basis of proportion even when the testing stimuli were of enlarged dimensions, creating a conflict between the absolute positive area experienced during training and the relative proportion of the two areas. However, chicks could have responded on the basis of the overall colour (red or green) of the figures rather than proportion per se. To control for this objection, in Experiment 3, we used new pairs of testing stimuli, each depicting a different number of small squares on a white background (i.e. 1 green and 3 red vs. 3 green and 1 red or 5 green and 15 red vs. 5 red and 15 green). Chicks were again able to respond to the correct proportion, showing they discriminated on the basis of proportion of continuous quantities and not on the basis of the prevalent colour or on the absolute amount of it. Data indicate that chicks can track continuous quantities through various manipulations, suggesting that proportions are information that can be processed by very young animals.

Keywords Proportion · Numerical cognition · Numerical discrimination · Number sense · Visual discrimination learning · Domestic chick

Introduction

A wealth of behavioural studies has shown that humans share with non-human animals an implicit understanding of numerical reasoning. Such a non-verbal ‘number sense’ is thought to be available soon after birth, and it is considered to be the ancient evolutionary foundation of more complex numerical reasoning (Kinzler and Spelke 2007; de Hevia and Spelke 2010; Cantlon 2012; Vallortigara 2012; McCrink et al. 2012; Haun et al. 2010). Up to now, the majority of the comparative studies have focused on a comprehension of numerosness that is based on the capability to reason with discrete units. This ability can support different kinds of mathematical reasoning, such as numerical discrimination, ordinal identification and arithmetic calculation (for review, see Gallistel and Gelman 1992; Roberts 1997; Dehaene 1997; Feigenson 2007; Vallortigara et al. 2010a, b).

Numerical discrimination is defined as the ability to make judgments of difference in the quantity of individual items between two and more sets (Davis and Pérusse 1988). That capability has been found in 10-month-old human infants (*Homo sapiens sapiens*, Xu et al. 2005), apes (*Pongo pygmaeus*, Call 2000; *Pan troglodytes*, Beran 2001); monkeys (*Macaca mulatta*, Hauser et al. 2000), Asian elephants (*Elephas maximus*, Irie-Sugimoto et al. 2009), horses (*Equus caballus*, Uller and Lewis 2009), domestic dogs (*Canis lupus familiaris*, Ward and Smuts 2007), coyotes (*Canis latrans*, Baker et al. 2011), the African Grey parrot Alex (*Psittacus erithacus*, Pepperberg

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1987), north island robins (*Petroica longipes*, Gerland et al. 2012), domestic chicks (*Gallus gallus*, Rugani et al. 2008, 2010a, 2013a, b), salamanders (*Plethodon cinereus*, Uller et al. 2003; Krusche et al. 2010), fish (*Xenotoca eiseni*, Stancher et al. 2013; *Pterophyllum scalare*, Gómez-Laplaza and Gerlai 2013), frogs (*Bombina orientalis*, Stancher et al. 2014) and mealworm beetles (*Tenebrio molitor*, Carazo et al. 2009).

Ordinality can be considered to be the ability to identify an object on the exclusive basis of its position in a series of identical objects. Rats are capable of learning to enter a target tunnel solely on the basis of its ordinal position in an array of six (Davis and Bradford 1986) or 18 (Suzuki and Kobayashi 2000) tunnels. Honey bees are able to find a food source located between the third and the fourth position along a series of four identical, equally spaced landmarks (Chittka and Geiger 1995); they can also identify the fourth position in a series of five and generalize it to a novel series of objects (Dake and Srinivasan 2008). Young domestic chicks (*Gallus gallus*, Rugani et al. 2007, 2011a) and adult Clark's nutcrackers (*Nucifraga Columbiana*, Rugani et al. 2010b) can identify the fourth and the sixth element in a series of identical elements, even when the possible use of spatial information was controlled (Rugani et al. 2011a, b).

Ordinality is also referred to the ability to sort in ascending (or descending) order sets representing different numerosness. Rhesus monkeys, (*Macaca mulatta*, Brannon and Terrace 1998; Cantlon and Brannon 2006), hamadryas baboons (*Papio hamadryas*), squirrel monkeys (*Saimiri sciureus*, Smith et al. 2003) and brown capuchin monkeys (*Cebus apella*, Judge et al. 2005) trained to touch numbers from one to four, in ascending order, could then generalize to new numbers from five to nine. Up until the present, the only evidence that determined a more abstract ordinal comprehension in non-human animals comes from a study on the African Grey parrot (*Psittacus erithacus*) Alex. After being trained to label vocally the numbers seven and eight and to order them with respect to the number six, Alex inferred the use of the appropriate label for the cardinal values of seven and eight items, suggesting that he constructed the cardinal meanings of seven and eight from his knowledge of the ordinal meanings (Pepperberg and Carey 2012).

Some arithmetic capability, i.e. the capacity to summate or subtract two or more sets of items, has been demonstrated in 6-month-old human infants (Wynn 1992; Simon et al. 1995; McCrink and Wynn 2007), chimpanzees (*Pan troglodytes*, Rumbaugh et al. 1987, 1988; Boysen and Berntson 1989; Boysen et al. 1995), rhesus monkeys (*Macaca mulatta*, Washburn and Rumbaugh 1991; Olthof et al. 1997; Brannon and Terrace 1998; Merritt et al. 2009), cotton-top tamarins (*Saguinus oedipus*, Uller et al. 2001), the African Grey parrot

Alex (*Psittacus erithacus*, Pepperberg 2006), day-old domestic chicks (*Gallus gallus*, Rugani et al. 2009, 2011a, b, 2013c, 2014) and ants (Reznikova and Ryabko 2011).

Usually the main challenge of all these kinds of investigation consists of demonstrating that subjects had based their responses solely on numerical cues and not on any other quantitative information. Changes in number correlate with changes in other quantitative variables (e.g. volume, surface area, distance, perimeter, area) that co-vary with numbers—also called 'continuous physical variables'. The use of heterogeneous elements, changing in size, colour, shape and spatial disposition, over trials, has allowed the purely numerical information to be isolated from other continuous variables, therefore demonstrating that non-verbal subjects can rely on numerical cues only (Brannon and Terrace 1998; Scarf et al. 2011; Rugani et al. 2013a, b, c). This evidence has led to the understanding that animals use numerical information not solely as a 'last resort' when no other properties differentiate stimuli (Davis and Pérusse 1988), but instead that numerical cues are salient information that is promptly and spontaneously processed.

Discrete numerical estimation, however, is not informative enough to guide decisions in all circumstances. In a natural environment, events requiring two interconnected quantitative-numerical evaluations occur frequently. For example, a situation may exist in which two sources of the same type of food are available with equal effort. According to optimal foraging strategy, the best choice would be to select the alternative that would allow access to the larger quantity of food (Krebs 1974). If the animal is alone, this choice can be based simply on a quantitative-numerical discrimination. However, whenever other conspecifics are exploiting these resources, the best choice/strategy will be based on two interrelated evaluations: an estimation of the quantity of food that the two alternatives offer connected with a second evaluation of the number of animals that are feeding at the two sites. In the above case, the best choice would take both quantitative dimensions into account by assessing, for each patch, the amount of available food relatively to the numbers of competitors.

One of the first observations that described the implicit use of proportional reasoning in animals was a field observation by Harper (1982). Harper wanted to investigate how individuals, in this case mallards *Anas platyrhynchos*, distribute themselves between resource patches when competing for food. In each trial, two experimenters, positioned at opposite sides of a lake, offered different and pre-established quantities of food (pieces of bread). The distribution of ducks between the two food patches was proportional to the amount of food offered at each side. Although in the original paper the author did not speculate about the underlying computation of proportions, it was

later suggested that the ducks had used information regarding the overall amount of food in relation to the amount given by either source to guide their foraging behaviour (Gallistel 1990). In another study, five chimpanzees (*Pan troglodytes*) were trained to discriminate proportions (1/4, 1/2, 3/4, 1) in a match-to-sample task. The stimuli were paintings of three kinds of objects: spherical food items (apple, grapefruit, potato), circular wood discs and cylindrical water containers. At test, one of the five subjects successfully matched exemplars of all proportions, also when the sample and the alternatives differed in kind. The only chimpanzee that succeeded in the task was the only one that had received intensive language training. Thus, the authors concluded that prior practice with symbol-like labels might be a necessary prerequisite to understanding abstract proportions (Woodruff and Premack 1981). More recently, however, the capacity to discriminate proportions has been reported in rhesus monkeys (*Macaca mulatta*) that had not been previously exposed to any kind of language training, using different kinds of stimuli (each composed of two black lines on a white background (Vallentin and Nieder 2008). In a delayed match-to-sample task, the monkeys were able to judge length ratios (1/4, 2/4, 3/4 and 4/4). When, in the same study, the monkeys' performance was compared with that of adult humans, tested under specific experimental conditions to prevent language use, the two species showed a similar performance. Such striking similarities have been considered as proof of an evolutionary ancient cognitive system for understanding of proportion (Vallentin and Nieder 2008). From this perspective, it would be interesting to investigate how early animals can start to use this kind of information. Moreover, the use of very young and inexperienced animals may enlighten us with regard to core knowledge mechanisms (Spelke 2000, 2003) in the vertebrate brain, in particular, concerning the extent to which the capacity to use proportional information depends on acquired experience versus inborn predispositions (Val-lortigara 2012).

So far all the studies on this topic have been conducted in adult subjects, with the exception of humans. A study using the habituation-dishabituation paradigm showed that 6-month-old infants represent the ratios between two sets of blue and yellow dots. Infants were firstly habituated to arrays containing blue and yellow dots in a single specific ratio to each other. Then, when presented with the same and a new ratio of blue and yellow dots, they looked longer at the new one. These results are consistent with infants' ability to process non-symbolic numerical ratios (McCrink and Wynn 2007).

The aim of the present research was to enlarge the investigation of this issue to a young animal model, the domestic chick (*Gallus gallus*).

Experiment 1

The goal of the first experiment was to investigate whether chicks can discriminate proportions (1/4 vs. 3/4) of continuous quantities.

Materials and methods

Subjects

We used twenty 'Hybro' domestic chicks (*Gallus gallus*), a local variety of the White Leghorn breed. These were obtained weekly, every Monday morning when they were a few hours old, from a local commercial hatchery (Agricola Berica, Montegalda, Vicenza, Italy). On arrival, the chicks were housed individually in standard metal cages (28 × 32 × 40 cm) in a rearing room.

The rearing room was constantly monitored for temperature (28–31 °C) and humidity (68 %) and was continuously illuminated by fluorescent lamps (36 W) located 45 cm above the floor of each cage. Water and food, placed in transparent glass jars (5 cm in diameter, 5 cm high) in the corners of the cages, were available ad libitum. Twice a day chicks were also allowed to eat some mealworms (*Tenebrio molitor* larvae) in order to familiarize them with this food which was used as reinforcement during test. An artificial imprinting object (a red capsule measuring 2 × 3 cm) was suspended (at the chick's head height) in each rearing cage to prevent social isolation. Artificial imprinting objects are effective social substitutes for real social partners: after about one to two hours of exposure, chicks respond to the artificial object with a range of behavioural responses which are clearly identifiable as socio-affiliative (Bolhuis 1991; Bateson 2000; Regolin et al. 2005a, b; Fontanari et al. 2011, 2014). Chicks were reared in these conditions from Monday morning (11 a.m.) to Wednesday morning (8 a.m.), and when the food jars were removed from the home cages (water was left available), and after a couple of hours (10 a.m.), chicks underwent shaping. At the end of shaping, chicks were placed back in their home cages, and two hours later, they underwent training individually. At the end of training, each chick was caged overnight with food and water available ad libitum.

Apparatus

Shaping, training and testing took place in a separate room (experimental room) located near the rearing room. In the experimental room, temperature and humidity were controlled for (at 25 °C and 70 %, respectively) and the lighting was provided by four 58-W lamps (placed on the ceiling, 194 cm above the floor of the experimental apparatus).

The experimental apparatus (see Fig. 1) consisted of an equilateral triangular arena (60 cm of side, 20 cm high) made of uniformly white plastic panels. The floor consisted of a white plastic board.

A ‘starting’ area was positioned at about 10.0 cm from one vertex of the arena. This was delimited by a transparent removable partition (10.0 × 20.0 cm) and, over it, an opaque plastic removable partition (10.0 × 20.0 cm) that allowed subjects to be confined during the inter-trial period. The opaque partition was used to prevent chicks seeing the experimenter during the changing of the stimuli. The transparent partition was used to confine subjects for a few seconds before the beginning of each trial, in order to give them the possibility of seeing the inner apparatus and the stimuli.

Depending on the experimental phase, we used one or two identical white plastic screens (16.0 × 8.0 cm; with 3.0 cm). Screens were provided with 3.0 cm sides bent back to prevent the chicks from looking behind the screen (where the *Tenebrio molitor* mealworm was hidden) before having walked around it. During shaping, we used a single screen, positioned in the centre of the arena and 30.0 cm away from the transparent partition. During training, retraining and testing, we used two screens, located symmetrically with respect to the confining area, spaced 6.0 cm apart and located 30.0 cm away from the transparent partition.

Stimuli

Shaping and training stimuli Stimuli consisted of six pairs of static 2D images, depicting a certain proportion of colours (red and green) printed on identical square plastic

boards (4.0 × 4.0 cm; see Fig. 2a), created using MATLAB R2010a. For each pair, one stimulus was coloured $\frac{3}{4}$ (12 cm²) of the area in red and the remaining $\frac{1}{4}$ (4.0 cm²) of the area in green; the other stimulus was coloured $\frac{1}{4}$ (4.0 cm²) red and $\frac{3}{4}$ green (12.0 cm²). We decided to use red and green because previous experiments showed that chicks can accurately discriminate between these two colours (Osorio et al. 1999). Chicks have four types of single-cone photoreceptors sensitive to ultraviolet, short-, medium- or long-wavelength light. The outputs of these photoreceptors are encoded by three opponency mechanisms: the first compares the outputs of ultraviolet-sensitive and short-wavelength-sensitive receptors, the second compares the outputs of medium- and long-wavelength receptors, and the third compares the outputs of short- and long- and/or medium-wavelength receptors. Therefore, chicks have tetrachromatic colour vision (Kelber et al. 2003).

To prevent the chicks from learning to identify the stimuli only by the specific pattern depicted on the screens, we used six different pairs of patterns.

Testing stimuli In Test 1, we used six new (in terms of the pattern pictured on them) pairs of stimuli, characterized by the same dimensions (4.0 × 4.0 cm) and of the same proportions $\frac{1}{4}$ (4.0 cm²) and $\frac{3}{4}$ (12.0 cm²) of colours (red and green). Stimuli differed from one another and also from the shaping and training stimuli with regard to the patterns.

In Test 2, six new pairs of stimuli were used. In this phase, the stimuli differed from the ones experienced during shaping and training both in terms of the patterns depicted on them and also in their dimensions (7.75 × 7.75 cm). As in the previous phases, all pairs were



Fig. 1 Apparatus used in all of the experiments; both screens are present in the apparatus just as they were during the testing session

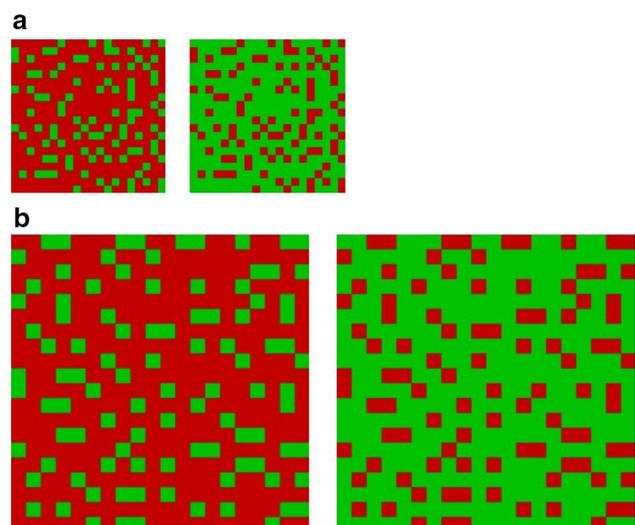


Fig. 2 Two pairs of stimuli used during Test 1

composed of complementary stimuli, depicting the same proportions $\frac{1}{4}$ (15.0 cm²) and $\frac{3}{4}$ (45.0 cm²) of the area being red or green (Fig. 2b).

Procedures

Shaping On the morning of the third day (i.e. the testing day), each chick underwent shaping. Initially, a single screen depicting a stimulus (in this phase stimuli were used depicting the proportion that will become associated with food through training), was located between the starting area and the screen. The chick was at first placed within the arena, in the starting area, for a couple of minutes, free to move around and to get acquainted with the novel environment (no partition was used to confine the bird in this experimental phase). Five mealworms were subsequently offered to the subject, whilst in the arena, to get it used feeding in this new environment.

Following this acclimation, the subject underwent a shaping procedure. Initially, a piece of mealworm was positioned in view in front of the screen (for each trial, a single stimulus associated with food was used). Thereafter, the food reinforcement was progressively moved behind the screen, requiring the bird to go behind the screen to retrieve the hidden mealworm. Once the chick had gone directly behind the screen and obtained the food reinforcement three consecutive times, it then passed to the next experimental session (i.e. training). Overall, depending on the chick's behaviour, the shaping phase could last from 10 to 20 min. Chicks that showed little interest in the food reinforcement (i.e. poor mealworm following behaviour), chicks that were too anxious in the new environment and chicks that were inattentive to the experimental stimuli were discarded from the study: this occurred in about 25 % of cases and such chicks are not included in the number of subjects described below.

Training Training took place immediately after the end of shaping.

For ten subjects, the stimulus associated with food (i.e. the one that indicated the presence of the food reinforcement behind the screen) was the $\frac{3}{4}$ *Red proportion stimulus* ($\frac{3}{4}$ *Red Group*); for this group, the $\frac{3}{4}$ *Green proportion stimulus* was the stimulus not associated with food (behind the screen depicting the stimulus not associated with food there was nothing). For the other ten subjects, the stimulus associated with food was the $\frac{3}{4}$ *Green* ($\frac{3}{4}$ *Green Group*); for this group, the stimulus not associated with food was the $\frac{3}{4}$ *Red stimulus*.

At the beginning of each trial, the chick was confined to the starting area, behind the transparent partition, from where it could see the two screens positioned in the arena. On the front part of each screen (facing the starting area)

was the stimulus. In each trial, a pair of training stimuli was used. The left–right (L–R) position of the stimulus associated with food with respect to the stimulus not associated with food was changed from trial to trial according to a semi-random sequence (e.g. L–R–L–R–L–L–R–R–L–R–L–R–L–R–L–L–R–R–L–R; Fellows 1967). The chick remained confined in the starting area for about 5 s so that it could see the two stimuli, after which the transparent partition was removed and the chick was left free to move around and search for food reinforcement within the arena. When the chick had placed its head and about $\frac{3}{4}$ of its body behind a screen, it was deemed to have made a choice, at which point the trial was considered to be over (only the first screen chosen was taken into consideration). If the first screen approached corresponded to the one depicting the stimulus associated with food, the response was considered as 'correct', otherwise it was considered 'incorrect'. At the end of each trial when the chick had emitted a correct response, it was given a reward which consisted of a mealworm.

Training trials were scheduled in a maximum of 20 blocks made of a maximum of 20 trials each. To pass the training phase, each chick had to reach the learning criterion: choosing the stimulus associated with food at least 17 times within 20 valid trials (Rugani et al. 2008). Whenever a chick made 4 errors within the same training block, that block was considered over (this could happen before reaching 20 trials) and a new block was started. When the learning criterion was reached, the training was considered successful and the chick was placed back in its home cage until Test 1 commenced. Overall, depending on the chick's behaviour, the training phase could last from 60 to 120 min.

Retraining Immediately before the beginning of test, each chick was first retrained, to ascertain whether they had actually learned the task. The experimental setting and the stimuli used in this phase was exactly identical to those previously described for training. The learning criterion was three consecutive correct trials, which was obtained in about ten trials. All of the chicks that reached the training criterion also reached the retraining criterion. Retraining lasted 5–10 min. At the end of the retraining, chicks directly proceeded to Test 1.

Test All subjects underwent two tests.

Test 1 At the beginning of each testing trial, the chick was confined in the starting area behind the transparent partition, from where it could see the two screens positioned in the arena. In each trial, one screen depicted a stimulus associated with food and the other the stimulus not associated with food. The left–right (L–R) position of

the stimulus associated with food with respect to the stimulus not associated with food was changed from trial to trial according to a semi-random sequence described above (see ‘Training’ paragraph). The chick remained confined to the starting area for about 5 s, in order to let it see the two stimuli, then the transparent partition was removed and the chick was left free to move around within the arena. A choice was defined as when at least the head and $\frac{3}{4}$ of the chick’s body had entered the area behind one of the two screens (beyond the side edges). Only the choice of the first screen visited was scored, and the trial was concluded as soon as a choice had been made. At the end of each trial, chicks were placed back in the starting area with both the transparent and the opaque partition in place. During testing, the food reinforcement was available behind the correct screen only in some pre-established trials (i.e. trial number 4, 5, 7, 10, 13, 14, 16 and 19), and chicks could gain it only by emitting a correct choice in those trials. The use of the opaque partition was necessary to allow the experimenter to change the screens and the stimuli without letting the subject see the inner apparatus (about 15 s were necessary for the experimenter to set up the apparatus for the next trial). As soon as the new pair of stimuli was in place, the opaque partition was removed and the chick remained confined behind the transparent partition for another 5 s, after which the transparent partition was removed and the new trial begun. This procedure was carried out such that each chick underwent a complete testing session of 20 valid trials.

All trials were video-recorded allowing chicks’ behaviour to be scored both online and later offline. The chicks’ behaviour was observed and scored from a monitor connected to a video camera so as not to disturb the chicks by direct observation. Their behaviour was fully video-recorded so that a second experimenter, blind to the hypotheses, could score the chicks’ performance offline. Online and offline scoring was found to be highly consistent with one other (100 % consistency).

Test 2 The procedure used during this session was exactly the same as that described for Test 1 with the exception of the stimuli used; see ‘Stimuli’ paragraph above.

Results and discussion

The number of trials during which each chick chose the screen depicting the stimulus associated with food (regarded as the correct choice) was calculated, and the percentages were computed as: (number of correct choices/20) \times 100. The Mann–Whitney U test was used to compare the performance of the different groups. The mean

(\pm SEM) of the experimental groups was compared with the chance level (50 %) using a Wilcoxon test.

Test 1 The percentages of correct responses registered did not reveal any significant difference between the two groups ($U = 32.0$; $P = 0.19$; $\frac{3}{4}$ Red Group: $n = 10$; mean = 85 %, SEM = 2.7; $\frac{3}{4}$ Green Group: $n = 10$; mean = 80 %, SEM = 2). The data of the two groups were therefore merged, and the resulting mean ($n = 20$; mean = 82 %; SEM = 1.8) was significantly different from chance level ($T^+ = 210.00$; $P < 0.01$), as shown in Fig. 3. We also considered the performance of each subject using a binomial test: 18 chicks scored 15 or more correct choices out of 20 (two-tailed binomial test $P < 0.05$), and two chicks scored 14 correct choices out of 20 (two-tailed binomial test $P = 0.12$).

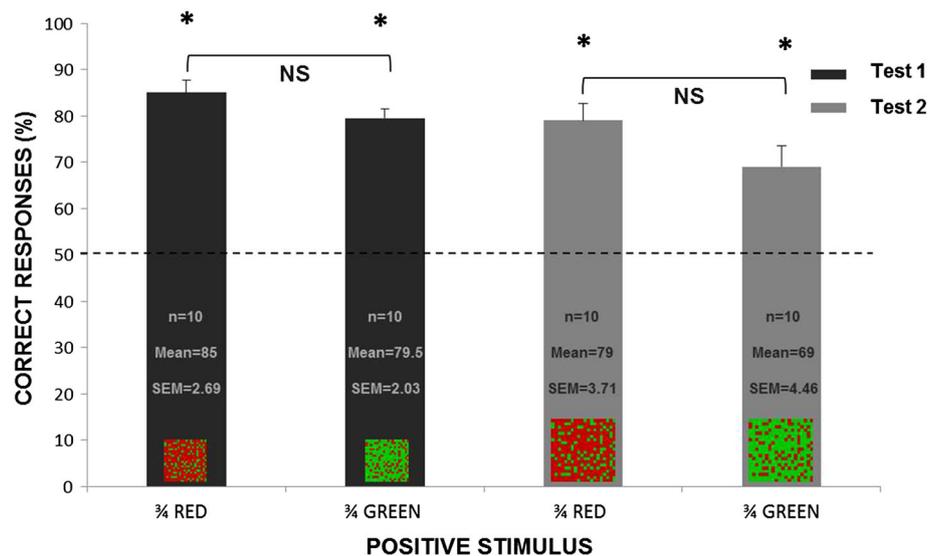
Test 2 The percentages of correct responses registered by the two groups did not reveal any significant difference ($U = 30.0$; $P = 0.14$; $\frac{3}{4}$ Red Group: $n = 10$; mean = 79 %, SEM = 3.7; $\frac{3}{4}$ Green Group: $n = 10$; mean = 69 %, SEM = 4.5). The data of the two groups were therefore merged, and the resulting mean ($n = 20$; mean = 74 %; SEM = 3.1) was significantly different from chance level ($T^+ = 207.50$; $P < 0.01$). For this test, we also considered the performance of each subject using a binomial test: 12 chicks scored 15 or more correct choices out of 20 (two-tailed binomial test $P < 0.05$), three chicks scored 14 correct choices out of 20, two chicks scored 13 correct choices under 20, one chick scored 12, another 11 and another 8 correct choices out of 20 (two-tailed binomial test $P > 0.05$).

The first experiment showed that both groups of chicks approached the proportion associated with food, even if at test the spatial disposition of the two areas were novel with respect to what had been experienced at training (Test 1) and even when the dimensions of the stimuli had been changed (Test 2).

Experiment 2

The aim of Experiment 2 was to disentangle whether chicks use the absolute or relative area in the identification of proportions. Because in Experiment 1 no difference was found between the $\frac{3}{4}$ Red Group and the $\frac{3}{4}$ Green Group, in Experiment 2 only the $\frac{3}{4}$ Red stimulus was used as the stimulus associated with food. At test, the chicks were required to generalize to new and larger stimuli. The dimensions of the new testing stimuli were calculated so that the overall amount of the $\frac{1}{4}$ Red testing stimulus was identical to the red area of the $\frac{3}{4}$ Red Training stimulus. In

Fig. 3 Results of Test 1 and Test 2 of Experiment 1. Choice (means with SEM) displayed at testing by the chicks, expressed as a preference for the stimulus associated with food. The dotted line represents the chance level



this way we created a conflict between the absolute red area and the relative green and red areas.

Subjects, apparatus and procedure

A new group of ten chicks was used. The rearing conditions, shaping and training procedures were the same as those described above. All the chicks were trained to respond to the $\frac{3}{4}$ Red stimulus. The same pairs of stimuli employed in Experiment 1 were used (for stimulus descriptions, see the ‘Stimuli’ paragraph of Experiment 1). It is important to note that for these stimuli, the overall area (16.0 cm²) was coloured $\frac{3}{4}$ (12.0 cm²) red and $\frac{1}{4}$ (4.0 cm²) green.

At test, six new pairs of stimuli were used. These stimuli differed from the ones used during shaping and training in Experiment 1 both in terms of the patterns depicted upon them and in their dimensions. The new dimensions (6.9 cm × 6.9 cm; area 48.0 cm²) were calculated to create a conflict between the absolute positive-red area (12.0 cm²) experienced during training on the $\frac{3}{4}$ Red stimulus (that for this group of subjects corresponded to the stimulus associated with food), and the correct relative proportion ($\frac{1}{4}$ vs. $\frac{3}{4}$) between the two areas. Indeed, considering the new dimensions of the stimuli, the $\frac{3}{4}$ Red stimulus (that corresponded to the stimulus associated with food) was $\frac{3}{4}$ red, now an area of 36 cm², and $\frac{1}{4}$ (12.0 cm²) green with the $\frac{3}{4}$ Green stimulus (i.e. the stimulus not associated with food) $\frac{3}{4}$ green (36.0 cm²) and $\frac{1}{4}$ red (12.0 cm²). Therefore, the absolute area (12.0 cm²) experienced during training on the stimulus associated with food—i.e. the $\frac{3}{4}$ Red stimulus with an area of 12.0 cm² associated with the reinforcement—was also now depicted on the stimulus not associated with food ($\frac{3}{4}$ Green stimulus, i.e. still with 12.0 cm² area in red).

Results and discussion

The percentage of correct responses shown by chicks ($\frac{3}{4}$ Red Group: $n = 10$; mean = 78 %, SEM = 2.7) was significantly different from chance ($T^+ = 55.00$; $P < 0.01$).

As regards the individual performance, 6 chicks scored 15 or more correct choices out of 20 (two-tailed binomial test $P < 0.05$), three chicks scored 14 correct choices out of 20 and one chick scored 13 correct choices out of 20 (two-tailed binomial test $P > 0.05$).

Results demonstrated that chicks did not rely on the absolute amount of area. Nevertheless, they could select the stimulus that, in a specific trial, depicted the larger red area. To control for this objection, we conducted the Experiment 3.

Experiment 3

The aim of the Experiment 3 was to control for the use of absolute versus proportional information. Chicks were trained to respond to the stimulus with $\frac{3}{4}$ of its area red (stimulus associated with food), ignoring the complementary (stimulus not associated with food) stimulus having $\frac{1}{4}$ of its total area red. During training, three different dimensions of stimuli were used. In each training trial, both stimuli have the same dimensions. However in Test 1, chicks were presented, with stimuli (again one $\frac{3}{4}$ Red and one $\frac{1}{4}$ Red) of different dimensions to one another. In this way, we avoided the possibility that chicks relied on the absolute red area. Moreover, in this case, differing from Experiment 2, the red area in the stimulus associated with food ($\frac{3}{4}$ Red) could be either smaller or larger than the red area in the stimulus not associated with food ($\frac{1}{4}$ Red).

In Test 2, all the stimuli were changed, in order to avoid chicks responding on the basis of the overall colour of the figure. Stimuli consisted of different numbers of small (red and green) squares on a white background.

Subjects, apparatus and procedure

A new group of ten chicks was used. The rearing conditions, shaping and training procedures were the same as those described for previous experiments, except where otherwise noted.

All the chicks were trained to respond to the $\frac{3}{4}$ Red stimulus. Training stimuli were similar to those used in Experiments 1 and 2 except in terms of their dimensions: here, we used squares of three different dimensions (Small, Medium and Large).

Small stimuli measured 4.0×4.0 cm, and the overall area was therefore 16.0 cm^2 . The stimuli associated with food had an area of 12.0 cm^2 coloured red and 4.0 cm^2 coloured green. The stimuli not associated with food were complementary to the reverse, stimuli associated with food: 4.0 cm^2 red area and 12.0 cm^2 green area.

Medium stimuli measured 6.9×6.9 cm. The overall area was therefore 48.0 cm^2 . Stimuli associated with food had an area of 36.0 cm^2 coloured red and 12.0 cm^2 coloured green. Stimuli not associated with food were complementary to the stimuli associated with food: 12 cm^2 coloured red and 36 cm^2 green.

Large stimuli measured 12.0×12.0 cm. The overall area was therefore 144.0 cm^2 . Stimuli associated with food had an area of 108.0 cm^2 coloured red and 36.0 cm^2 coloured green. Stimuli not associated with food were complementary to the stimuli associated with food: 36.0 cm^2 in red and 108.0 cm^2 in green.

In each training trial, stimuli of the same dimension were used. The stimulus dimensions (Small, S; Medium, M; or Large, L) were changed from trial to trial according to a semi-random sequence (i.e. L, M, S, L, L, S, M, M, S, L, M, M, L, S, S, L, M, S, S, M, L).

At Test 1, we used 21 new pairs of stimuli (seven for each dimension), differing from the training stimuli in the pattern depicted on them. In each trial, we used a stimulus of Medium dimension, paired with either a Large or a Small one (see Fig. 4), according to the following sequence: L–M, S–M, S–M, L–M, S–M, L–M, L–M, S–M, S–M, L–M, S–M, L–M, S–M, L–M, S–M, L–M.

At Test 2, we used completely different stimuli. All stimuli were composed of static 2D images representing a given number of elements (each element being either a red or a green square) printed on identical white square plastic boards (12.0×12.0 cm).

In a subgroup of stimuli (Small Numbers Stimuli, SN), a small number of red and green squares (1.5×1.5 cm)

were depicted. Therefore, a $\frac{3}{4}$ Red stimulus consisted of three red squares and one green square, and a $\frac{3}{4}$ Green stimulus consisted of three green squares and one red square, as shown in Fig. 5a. In a second subgroup of stimuli (Large Numbers Stimuli, LN) a larger number of red and green squares of a smaller size (1.0×1.0 cm) were depicted. Therefore, a $\frac{3}{4}$ Red stimulus consisted of 15

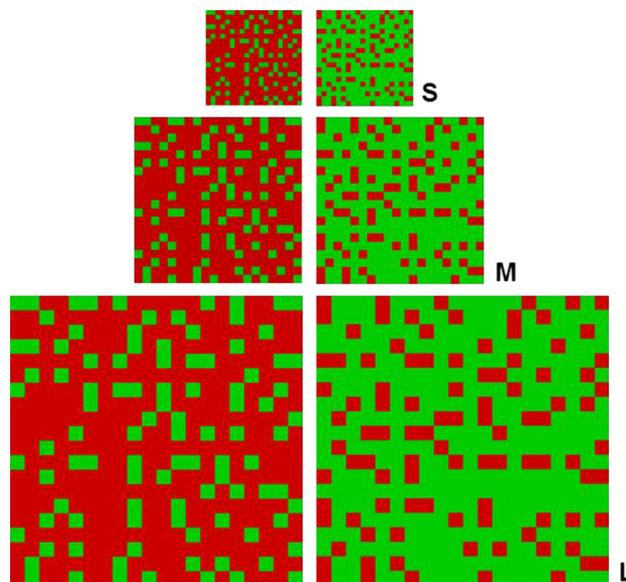


Fig. 4 An example of the three dimensions (S Small, M Medium, L Large) of the stimuli used in Test 1 of Experiment 3

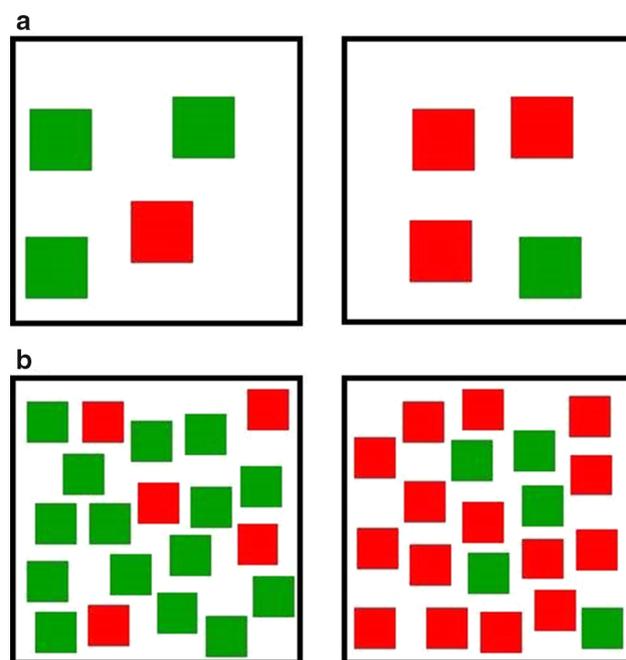


Fig. 5 Results of Test 1 and Test 2 of Experiment 3. Choice (means with SEM) displayed at testing by the chicks, expressed as a preference for the stimulus associated with food. The dotted line represents the chance level

red squares and five green squares, and a $\frac{3}{4}$ Green stimulus consisted of 15 green squares and five red squares, as shown in Fig. 5b.

During Test 2, Small and Large Numbers Stimuli were mixed, accordingly with the following sequence: SN, LN, SN, LN, SN, SN, LN, LN, SN, LN, SN, LG, SN, LN, SN, SN, LN, LN, SN, LN.

Results and discussion

Test 1

The percentage of correct responses shown by chicks ($n = 10$; mean = 89 %, SEM = 1) was significantly different from chance level ($T^+ = 55.00$; $P < 0.01$). All chicks ($n = 10$) scored 15 or more correct choices out of 20 (two-tailed binomial test $P < 0.05$).

Test 2

The percentages of correct responses shown by chicks with Small and Large Numbers Stimuli were not statistically different ($T^+ = 5.00$; $P = 1.00$; Small Numbers: $n = 10$; mean = 81 %, SEM = 2.3; Large Numbers: $n = 10$; mean = 81 %, SEM = 3.2). Data were therefore merged together and the resulting mean (mean = 81 %, SEM = 2.6) was statistically greater than chance ($T^+ = 55.00$; $P < 0.01$), as shown in Fig. 6. Eight chicks scored 15 or more correct choices out of 20 (two-tailed binomial test $P < 0.05$), and two chicks scored 14 correct choices out of 20 (two-tailed binomial test $P > 0.05$). Data obtained in Test 1 confirmed the results from Experiment 2 in supporting the idea that chicks primarily use proportions in preference to absolute area as a cue. Moreover, data in Test 2 demonstrated that birds actually used proportions

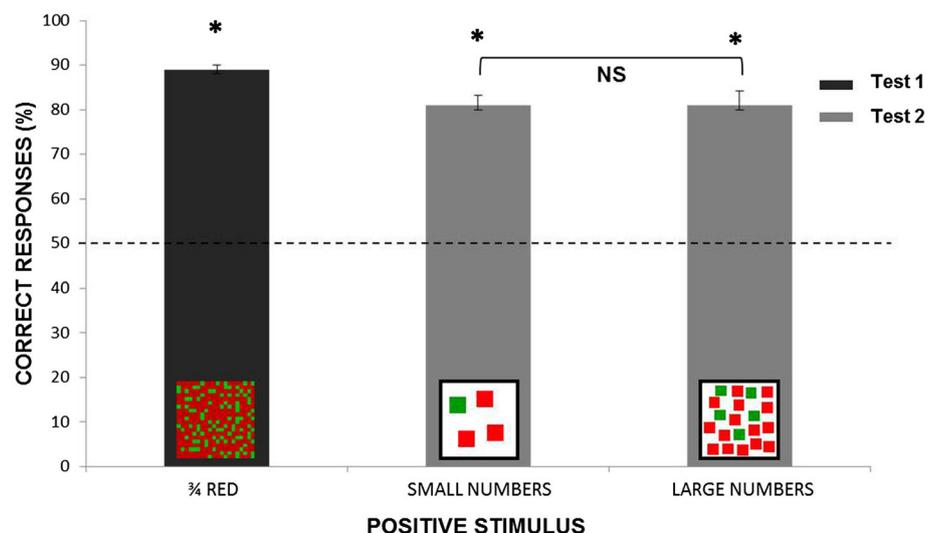
rather than overall colour for their assessment of the visual cue.

Conclusions

The aim of the present research was to investigate whether day-old domestic chicks can discriminate between proportion and absolute quantities. Results suggest that chicks are able to track proportions of continuous quantities through various manipulations.

In Experiment 1, chicks demonstrated an ability to discriminate at test between new and larger stimuli than those used in training. In Experiment 2, chicks continued to discriminate on the basis of proportional information, even when we equated the amount of red area of the stimulus associated with food ($\frac{3}{4}$ Red) during training and the amount of the red area depicted on the stimulus not associated with food ($\frac{1}{4}$ Red) during testing. If chicks based their choice on the overall amount of red area, their choices would be incorrect in their test; but this was not the case. This indicates that chicks did not rely on the absolute amount of the red area, but that they could compare the proportion of the red and of the green areas. In Experiment 3, we controlled for the use of absolute versus proportional information by changing, during testing, the dimensions of the two stimuli so that the positive (red) area of the stimulus associated with food could be either smaller or larger than the red area of the stimulus not associated with food. Unlike Experiment 2, where the control for the overall positive-red area was conducted between the training and the testing stimuli, Experiment 3 controlled for the overall amount of red area during testing, equating the overall amount of red area depicted in the two stimuli in each trial. Chicks again continued to rely on proportional information

Fig. 6 **a** An example of the Small Numbers Stimuli (SN) used in Test 2 of Experiment 3. **b** An example of the Large Numbers Stimuli (LN) used in Test 2 of Experiment 3



and not on the absolute area. This indicates that chicks did not rely on the ‘more red’ information, but that they could compare the two stimuli, extracting the proportions between the two areas. The second test of Experiment 3 showed that chicks did not use the cue provided by the overall colour of the stimuli. Indeed, in this experiment, chicks could discriminate between different numbers of discrete items (squares; i.e. 1 green and 3 red vs. 3 green and 1 red or 5 green and 15 red vs. 5 red and 15 green) on a white background. This indicates that chicks can identify the correct proportion also when it was presented with completely new stimuli, depicting different numbers of elements.

Overall, these results show that even when very young, animals can use proportional/analogical information, an ability that has been sparsely investigated within the field of numerical cognition. The majority of research in this area has considered the capacity of animals to use numerical information that varied from numerical discrimination (Call 2000 and other studies cited in the “Introduction”), ordinal abilities (Brannon and Terrace 1998 and other studies cited in the “Introduction”) and arithmetic abilities (Rumbaugh et al. 1987 and other studies cited in the “Introduction”). The main focus of this research work was to ascertain whether animals can represent number abstractly (when the perceptual-quantitative features, such as cumulative surface area or contour length, were controlled for) and whether non-numerical quantitative features could be extracted more readily from the external world than number. In contrast, the capacity to extract purely quantitative information in the absence of discrete numerical cues has seldom been investigated. Initially, such an ability was considered to be strictly connected with symbol-like labels training (Woodruff and Premack 1981). In their pioneering study, Woodruff and Premack (1981) found that the only chimpanzee that succeeded in discriminating proportions was the only one that had received intensive language training. More than 10 years later, the capacity to discriminate proportions has been studied in rhesus monkeys and compared with those of humans. The authors found that monkeys that had not been previously exposed to any kind of language training could use proportional information and that their performance was similar to that of adult humans when tested under specific experimental conditions to prevent language use (Vallentin and Nieder 2008). This similarity suggests that an evolutionary ancient cognitive system for proportional understanding might be shared by animals (Vallentin and Nieder 2008).

Vallentin and Nieder (2010) also investigated the response properties of single neurons in the lateral prefrontal cortex and the inferior parietal lobe in rhesus monkeys performing a lengths-proportion-discrimination task. They found neurons in both these areas that showed

peaked tuning functions with preferred proportions. Whether a similar machinery does exist in the avian brain is currently unknown but deserves to be investigated.

Recently, de Hevia et al. (2014) have shown that 0- to 3-day-old neonates, after being familiarized with correlations of both number and duration with spatial length, expected these dimensions to change in the same direction (number or duration increase as length increases), but not in opposite directions (number or duration increase and length decreases). These findings provide evidence that representations of number, space and time are interrelated at the beginning of post-natal life, suggesting that the predisposition to relate these magnitudes might be present at or soon after birth, as part of the evolutionary endowment of cognition (de Hevia et al. 2014).

Our results extend the comparative research on the representation of proportion. We believe that this finding provide striking support to the ‘core knowledge’ hypothesis (Pica et al. 2004; Spelke and Kinzler 2007; Vallortigara et al. 2010a, b; Vallortigara 2012) according to which mental representations of analogue proportion of quantities (as well as other basic representations such as those of number, physical objects, animate objects and geometry) would be in place at birth and shared among vertebrates. Indeed to the best of our knowledge, this is the first evidence showing that proportions discrimination can be successfully performed by very young animals. The next step of the present research, already ongoing in our laboratory, will be to investigate whether animals can rely on abstract proportion when all non-numerical quantitative cues are controlled for, and whether they can choose a specific proportion over other smaller and larger proportions.

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Ethical standard The experiments complied with all applicable national and European laws concerning the use of animals in research and were approved by the Italian Ministry of Health (permit number: 5/2012 B emitted on 10 January 2012). All procedures employed in the experiments were examined and approved by the Ethical Committee of the University of Padua (Comitato Etico di Ateneo per la Sperimentazione Animale—C.E.A.S.A.) as well as by the Italian National Institute of Health (N.I.H).

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