

One, two, three, four, or is there something more? Numerical discrimination in day-old domestic chicks

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Abstract Human adults master sophisticated, abstract numerical calculations that are mostly based on symbolic language and thus inimitably human. Humans may nonetheless share a subset of non-verbal numerical skills, available soon after birth and considered the evolutionary foundation of more complex numerical reasoning, with other animals. These skills are thought to be based on the two systems: the object file system which processes small values (<3) and the analogue magnitude system which processes large magnitudes (>4). Infants' ability to discriminate 1 vs. 2, 1 vs. 3, 2 vs. 3, but not 1 vs. 4, seems to indicate that the two systems are independent, implying that the conception of a continuous number processing system is based on precursors that appear to be interrupted at or about the number four. The findings from the study being presented here indicating that chicks are able to make a series of discriminations regarding that borderline number (1 vs. 4, 1 vs. 5, 2 vs. 4) support the hypothesis that there is continuity in the number system which processes both small and large numerosness.

Keywords Number cognition · Object file system · Analogue magnitude system · Number sense · Arithmetic · Domestic chick · Human infant · Large numbers · Continuous variables

Introduction

Although human adults typically solve mathematical problems using numerical language, they are able to master some numerical tasks when, under specific experimental conditions, language is prevented (Cordes et al. 2001). Pre- or non-verbal numerical skills (i.e. those calculations that could be solved in the absence of numerical words) do exist in humans and can be compared with those found in other non-linguistic creatures such as preverbal infants and non-human animals (Cordes et al. 2001). The similar performance by individuals of different species, including human adults, compared qualitatively and quantitatively, suggests that an ancient, non-verbal numerical mechanism could be shared by all (Cantlon and Brannon 2006).

A variety of experimental studies have demonstrated that this mechanism is based on two separate systems: one regarding small values (the object file system, *OFS*) and one concerning large numerical magnitudes (the analogue magnitude system, *AMS*). The *OFS* is an object-based attention mechanism according to which each element present in a real scene is represented by a unique symbol called an “object file” that is stored in the working memory. That system may have originally evolved to represent objects, and its functioning implies the capability of individuating each new object that is introduced into a scene to which a new file in the working memory is dedicated. Spatio-temporal information and property/kind changes are thus tracked by the *OFS*. Although the system is not specific to a number representation, numbers are implicitly represented. The signature of the system is that there is a limit to the quantity (usually ≤ 3) of object-files that can be simultaneously tracked and stored in the working memory (Trick and Pylyshyn 1994).

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Processing larger sets (i.e. ≥ 4) seems to be entrusted to the *AMS*, which, according to Weber's law, is ratio-dependent. As the ratio then between the numbers to be discriminated becomes larger, response times decrease and accuracy increases (Gallistel and Gelman 1992). The *AMS* is also involved in discriminating between small numbers and shows greater sensitivity as the ratio became smaller: it is easier, in fact, to distinguish between 1 vs. 2 than between 2 vs. 3. From this perspective, it is possible that the inexact discrimination between 3 vs. 4 could be explained by a difficult (too large) ratio and not by the absolute number of elements in each set. The minimum discernible ratio, in fact, has been found to narrow with human development going from 1/3 in new-borns, to 1/2 at 6 months, to 2/3 at 9 months and 3/4 for preschool children (Izard et al. 2009; Feigenson et al. 2004; Halberda and Feigenson 2008). Critical data on how the two systems function independently and relate to one another have been provided by experimental findings on human infants who seem to process small numbers via *OFS* (Feigenson and Carey 2005) and large numbers via *AMS* (Xu et al. 2005). This would imply that there could be a gap in processing values at the boundary between the two domains. Greater imprecision in discrimination has, in fact, been reported when the comparison includes 4 (Le Corre and Carey 2007). When 12- to 14-month-old infants were made to choose between two sets of crackers concretely placed in front of them one by one in one of two opaque containers, they chose the larger set when the choice was between 1 vs. 2, 1 vs. 3 and 2 vs. 3 but not when faced with 1 vs. 4. The infants' failure to discriminate between numbers (1 vs. 4) even though the ratio fell within the *AMS* jurisdiction coupled with their failure to track more than 3 objects at a time suggests that a different representation system operates with regard to small numbers (Feigenson et al. 2002; for similar data obtained on infants employing other experimental procedures, see Starkey and Cooper 1980).

Taken together, these data suggest that the *OFS* processes small numbers, with its limit being at or around 3–4 elements per set. Inaccurate discrimination between 1 vs. 4 has been considered evidence that the non-verbal numerical systems are processed by distinct domains (Feigenson et al. 2002). Differences at the upper limit, 3 in the case of children and chicks (Rugani et al. 2008) and 4 in the case of adult monkeys (Hauser et al. 2000; Barner et al. 2008), have been attributed to maturational factors (Carey 2009).

Other experimental evidence, instead, suggests that there is continuity in processing small and large numbers. Seven-month-old infants were able to discriminate between small and large sets when the choice was between 1 vs. 4 and 2 vs. 8 (Cordes and Brannon 2009). Rhesus monkeys (*Macaca mulatta*; Brannon and Terrace 1998; Cantlon and Brannon 2007), hamadryas baboons (*Papio hamadryas*),

squirrel monkeys (*Saimiri sciureus*; Smith et al. 2003) and brown capuchin monkeys (*Cebus apella*; Judge et al. 2005) were able to master numerical tasks involving numbers from 1 to 9, showing that discrimination of a numerical comparison depends on the ratio of the numbers needed to be discriminated, regardless if these are small or large. Even human adults when prevented from using numerical words seem to rely on *AMS* to process both small and large numbers (Cordes et al. 2001). Continuity in processing small and large numbers also seems to exist in the avian species. A grey parrot (*Psittacus erithacus*) was able to sum two sets of items (up to 6) and to use English labels to order numbers from 1 to 8 (Pepperberg 2012).

Sensitivity to numerosness has been studied in domestic chicks exploiting their spontaneous tendency to gravitate towards objects they were reared with (imprinted onto). Their spontaneous tendency to prefer a larger group has, moreover, been used to test their arithmetic abilities. When a group of identical objects were presented to day-old chicks, they chose the larger set when the choice was between 1 vs. 2 or 2 vs. 3, irrespective of the number of objects (considered social companions), they were familiar with (Rugani et al. 2010). The findings from that study demonstrated that the chicks were not only able to solve simple addition problems (1 + 1 vs. 1 + 1 + 1)—when quantitative variables were being controlled—but that they could also perform sequential addition and subtraction problems to finally identify the larger group, such as in “(4 – 1) vs. (1 + 1)”, “(5 – 2) vs. (0 + 2)”, “(4 – 2) vs. (1 + 2)” and “(5 – 3) vs. (0 + 3)” comparisons. During the first sequence of trials (shown in **boldface**), the task needed to be completed was to calculate a “large” number of elements (up to 4 or 5) within a single set and a small number within another one. During a subsequent series of trials (in *italics*), one or more elements was/were moved from behind one screen to behind another one. The chicks were thus constrained to update their representation of the two sets in order to finally discriminate between 2 vs. 3 elements (Rugani et al. 2009). In that case, the chicks needed to discriminate between small and large numbers in order to solve the task. On the other hand, it is also unlikely that the discrimination was based on the *OFS*, because this would imply a storage capacity larger than 4, usually considered as the upper limit of the *OFS* both for humans and non-human animals.

Contrasting evidence has until now been reported in the scientific literature. On the one hand, according to some findings, small numbers can be computed via *AMS*, suggesting that there is a continuity in processing small and large numbers (see above with regard to the performance in ordinal tasks by monkeys and in summation tasks by birds). On the other, some data suggest that small numbers can be treated solely via *OFS* (see children and

monkeys who can discriminate between 1 vs. 2, 1 vs. 3 and even between 2 vs. 3 but not between 1 vs. 4 food items, Hauser et al. 2000; Barner et al. 2008). Nevertheless in some circumstances, great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus*, *Gorilla gorilla*; Hanus and Call 2007; Uher and Call 2008), chimpanzees (*Pan troglodytes*; Beran, 2001; Beran and Beran, 2004), monkeys (*Macaca mulatta*; Jordan and Brannon 2006a, b; Beran, 2007), orangutans (*Pongo pygmaeus*; Call, 2000), capuchin monkeys (*Cebus apella*; Evans et al., 2009), black bears (*Ursus americanus*; Vonk and Beran 2012), domestic dogs (*Canis lupus familiaris*; Ward and Smuts 2007), asian elephants (*Elephas maximus*; Irie-Sugimoto et al. 2009; Perdue et al., 2012), coyotes' (*Canis latrans*; Baker, Shivik and Jordan, 2011), South American sea lions (*Otaria flavescens*; Abramson et al., 2011), mosquitofish (Dadda et al. 2009), guppies (Piffer et al. 2012) and robins (*Petroica longipes*; Garland et al. 2012) did not show the *OFS* limitations.

A series of numerical comparisons, employing a procedure similar to the one already utilized and described elsewhere (Rugani et al. 2009) in which newly hatched domestic chicks were reared with five identical objects, were utilized in the study being described here. Comparisons between 1 vs. 4 and 1 vs. 5 were assessed to evaluate the chicks' *OFS* storage capacity. To exclude the possibility that the chicks' performance could be explained by a mechanism distinguishing a singular versus a plural set, a

comparison between 2 vs. 4 was also employed. Controls for quantitative cues were also performed to exclude the possibility that the discrimination could be based on non-numerical, continuous, physical variables, such as the overall amount of surface area or perimeter rather than on numerosness. On the fourth day, the chicks underwent free-choice tests comparing two sets, each composed of a different number of objects. The chicks, as expected, preferred the larger set.

Materials, methods and results

The subjects and rearing conditions

The subjects were 55 female chicks (*Gallus gallus*) obtained weekly when they were only a few hours old. One group of the chicks was reared and tested with social attractors (social-attractor group, *SAG*). There was also a control group with which food attractors were used (food-attractor group, *FAG*; see Fig. 1 for the number of subjects in each experimental group). Food, in addition to social attractors (already employed in experiments with chicks), was used to make our data more comparable with those obtained with infants (who were tested with crackers used as both the stimuli and the reward).

Each chick in the *SAG* was reared together with an imprinting stimulus composed of 5 identical objects in a

Fig. 1 For each comparison carried out in this study (1 vs. 4, 1 vs. 5 and 2 vs. 4), the experimental group, the number of chicks and the statistical significance of *t* are outlined for each group and compared with the chance level

Testing Comparisons	Rearing	Experimental Group	n	p
1 vs. 4		Social attractor (<i>SAG</i>) (3 <i>D</i> - <i>NCG</i>)	8	<.001
		Food attractor (<i>FAG</i>)	8	<.001
1 vs. 5		Social attractor (<i>SAG</i>) (3 <i>D</i> - <i>NCG</i>)	8	<.001
2 vs. 4		Social attractor (<i>SAG</i>) No Control (3 <i>D</i> - <i>NCG</i>)	8	<.001
		Social attractor (<i>SAG</i>) No Control (2 <i>D</i> - <i>NCG</i>)	8	
		Social attractor (<i>SAG</i>) Perimeter Control (2 <i>D</i> - <i>PCG</i>)	8	
		Social attractor (<i>SAG</i>) Area Control (2 <i>D</i> - <i>ACG</i>)	7	

standard metal cage (28 cm wide \times 32 cm long \times 40 cm high) at a controlled temperature (28–31 °C) and humidity (68 %), with food and water available ad libitum in transparent glass jars (5 cm in diameter, 5 cm high). The cages were constantly (24 h/day) lit by fluorescent lamps (36 W) located 45 cm above the cage floor. The chicks in the *FAG* were also reared in individual cages under the same standard conditions, but in absence of any imprinting objects. The *FAG* chicks were fed from day 1 twice a day on live mealworms.

All the chicks (both study and control) were kept in those conditions from the morning (11.00 am) of the first day to the morning of the third day, when they underwent training, and, approximately 1 h later, testing during which they were presented with one of three numerical comparisons (1 vs. 4, 1 vs. 5 and 2 vs. 4).

The apparatus

Training and testing took place in an experimental room in which the temperature and humidity were maintained, respectively, at 25 °C and 70 %. The room was kept dark, except for the light coming from a 40 W lamp placed approximately 80 cm above the centre of the apparatus which (Fig. 2) consisted in a circular arena (95 cm diameter, 30 cm outer wall height) whose floor was uniformly lined with white plastic sheets. Adjacent to the outer wall of the arena, there was a holding box (10 \times 20 \times 20 cm) where each chick was confined for a short time before the trial was begun. The side walls of the box were covered with opaque plastic sheets, and the ceiling was open, so it was possible to place the chicks inside. The side of the holding box, facing the centre of the arena, consisted of a removable, clear glass partition (20 \times 10 cm), so that while the chicks were kept there, they could see the inside of the arena. During the training phase, one single vertical cardboard screen (16 \times 8 cm) was used, positioned in the centre of the arena, in front of and 35 cm away from the holding box. During testing, two identical screens were

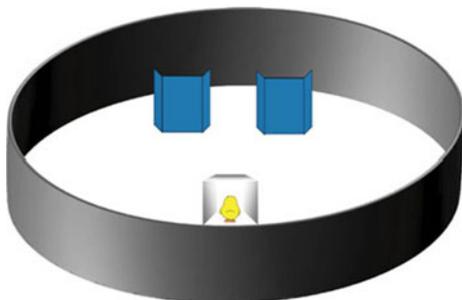


Fig. 2 The apparatus employed in all of the experiments. The holding box and both screens are present in the arena just as they were during the testing session

used, positioned symmetrically with respect to the front of the confining box (i.e. 35 cm away from it and 20 cm apart from one another, see Fig. 2).

The experimental setting was identical during the training and testing phases for all the numerical comparisons (1 vs. 4, 1 vs. 5 and 2 vs. 4).

The procedure

Training

The chicks underwent a preliminary training session on day three. Each chick, together with a single attractor (a single imprinting element for the *SAG* and a mealworm for the *FAG*), was placed in front of the screen in the testing arena. The attractor was held at the height of the chick's head via a fine thread and kept visible to the chick during its stay in the holding box and while it was left free in the testing arena for about five min to move around to get acquainted with the environment. Then, the experimenter slowly moved the attractor in the direction of the screen and, finally, behind it, until it completely disappeared from the chick's sight. This sequence was repeated a few times, until the chick responded by following and catching up with the attractor. The chick was then confined in the holding box, and the transparent partition was put in place. The chick could see the attractor being moved behind the screen from where it was in the holding box. As soon as the attractor had completely disappeared from sight, the chick was set free by lifting the transparent partition and every time it caught up with the attractor it was allowed to spend a few seconds together with it (*SAG*) or to eat a mealworm (*FAG*). The sequence was then begun again, and the training session was concluded when the chick caught up with the attractor for three consecutive times. The training session was identical for all the chicks.

Testing

A complete testing session was made up of 20 trials. At the beginning of each trial, the chick was confined to the holding box with the transparent partition in place, from where it could see the two screens in the arena. The chick was presented with only one element at a time and could not see either set as a whole. Every element of the first set was placed about 10 cm from the front of the holding box and then made to disappear behind one of the screens. Immediately after it disappeared the next element was introduced into the arena. In this way, all the elements of the first set were made to disappear one by one behind the same screen. Then, the identical procedure was repeated for the second set behind the other screen. Five seconds after both sets were complete (behind the screens), the

transparent partition was removed, and the chick was left free to move about within the arena. The order the two sets were presented (which one was presented first) as well as the position (left or right screen) where they disappeared was counterbalanced within each chick's testing trials.

When the chick pointed its head behind the screen was defined as the moment of choice and when that took place that trial was considered over (only the first screen chosen was taken into consideration). At the end of each trial during which the chick chose the larger set, it was given reinforcement which consisted in spending 1–2 s with the "social companions" behind the screen for the *SAG* and eating a mealworm for the *FAG*.

The chicks' behaviour was observed and scored by a monitor connected to a video camera so as not to disturb the chicks by direct observation. Their behaviour was entirely video-recorded so that a second, blind experimenter could score the chicks' performance off-line. On-line and off-line scoring was found to be highly consistent with one other (100 % consistency).

Stimuli

As explained above, the rearing and experimental stimuli for the *FAG* were live mealworms (*Tenebrio molitor larvae*). The stimuli for the *SAG* consisted in five objects that were always present in the rearing cage. For the majority of the chicks, those consisted of three-dimensional (3D) yellow plastic capsules $4 \times 3 \times 3$ cm which were separately suspended in the centre of the cage by a fine thread, arriving at approximately 4–5 cm from the floor at about the height of the chick's head. The stimuli were about 2 cm from one another, and overall, they occupied a maximum area of about 23×23 cm in the centre of the cage. Objects identical to the ones used during the imprinting stage were employed during testing.

A subgroup of *SAG* was reared and tested with 2D stimuli in the attempt to ensure a precise control of the quantitative variables (Perimeter and Area). Whenever the comparison was between two plural sets (2 vs. 4), the quantitative variables could be controlled by manipulating the objects dimensions. We avoided comparisons between comparisons between a single big object and several smaller ones. When, in fact, one big object was compared with 3, 4 or 6 smaller ones (in conditions in which perimeter, volume and surface area were controlled), chicks tend to choose the former (Rugani et al. 2010).

To control for quantitative variables, the objects used during the rearing and testing phases had different dimensions. The rearing stimuli were identical for all the subgroups and consisted of a set of five, 2D (approx. 1 mm thick), red plastic squares (4×4 cm). The testing stimuli also consisted in red squares. For some chicks (No Control

Group, *2D-NCG*), the dimensions of the rearing stimuli were the same as those used during testing, so the squares in the sets of 4 and 2 elements were all identical. At testing, the dimension of the squares in the set made up of 2 elements was larger for the Perimeter Control group (*2D-PCG*) and for the Area Control Group (*2D-ACG*) (8×8 cm squares for the *former* and 5.657×5.657 cm squares for the *latter*).

Results and discussion

The number of trials during which each chick chose the screen hiding the larger number of objects (regarded as the correct choice) was calculated, and the percentages were computed as: (Number of Correct Choices/20 \times 100). The mean (\pm SEM) of each experimental group was compared with the chance level (50 %) using one-sample *t* tests (see Fig. 3). Unpaired *t* tests were used to compare the performance of the different groups.

It was found that all the chicks groups almost always succeeded in selecting the correct answer which was to choose the larger numerosness. In particular, it was seen that:

1 vs. 4: A significant difference was found between the *SAG* and the *FAG*: ($t(14) = 2.620$; $p = 0.020$), with *SAG* performing better than the *FAG*. Both groups, in fact, performed significantly above the chance level: *SAG* ($n = 8$; mean = 81.250, SEM = 4.092; $t(7) = 7.638$; $p < 0.001$), effect-size: $r = 0.945$; *FAG* ($n = 8$; mean = 68.750, SEM = 2.455; $t(7) = 7.637$; $p < 0.001$), $r = 0.945$. In order to assess whether the overall performance depended on learning that took place during testing, the percentage of correct responses on the first five trials was compared with chance level (*SAG*: mean = 77.500,

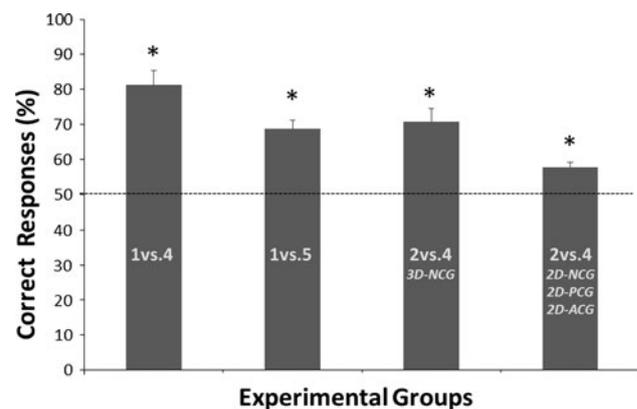


Fig. 3 Choice (means with SEM) displayed at test by *SAG* chicks, expressed as preference for the larger stimulus. In all comparisons (1 vs. 4, 1 vs. 5, 2 vs. 4) chicks of all experimental groups (*3D-NCG* 3D-no control group, *2D-NCG* 2D-no control group, *2D-PCG* 2D-perimeter control group, and *2D-ACG* 2D-area control group) performed statistically above chance as indicated by asterisks

SEM = 5.901; $t(7) = 4.660$; $p = 0.002$; *FAG*: mean = 67.500, SEM = 3.536; $t(7) = 4.950$; $p = 0.002$). To compare more directly the performance of chicks with that of human infants, which was scored over three trials, we also focused on chicks' initial trials and computed the proportion of correct responses. Overall, chicks in the first three trials preferred the larger set (*SAG*: mean = 87.500, SEM = 6.099; $t(7) = 6.148$; $p < 0.001$; *FAG*: mean = 70.834, SEM = 5.892; $t(7) = 3.536$; $p = 0.001$).

Each chick's performance was assessed using a non-parametric (one-tail) Binomial test. Five *FAG* chicks performed above chance level, scoring 15 or more correct responses out of 20 ($p = 0.021$); and 3 performed marginally not significantly, with 14 correct responses out of 20 ($p = 0.058$). Three of the *SAG* subjects gave 15 or more correct responses out of 20 ($p = 0.021$), while the performance of all the other chicks was at chance level (4 chicks gave 13 and one 12 correct responses out of 20).

1 vs. 5: ($n = 8$; mean = 73.750, SEM = 3.750; $t(7) = 6.333$; $p < 0.001$, $r = 0.923$). Even at the first five trials (mean = 75.000, SEM = 7.319; $t(7) = 3.416$; $p < 0.011$), the chicks showed a preference for the large set.

Three chicks performed above chance level at the binomial test (with 15 or more correct responses out of 20), 2 performed marginally not significantly (14 correct responses out of 20) and 3 gave 13 correct responses out of 20.

2 vs. 4: An ANOVA analysis with Group as an independent variable (*3D-NCG*, *2D-NCG*, *2D-ACG*, *2D-PCG*) was made. The dependent variable was the percentage of choice for the larger group. A significant effect of Group was found ($F(3, 27) = 7.724$; $p < 0.001$), depending on the difference in behaviour of chicks belonging to the *3D-NCG* ($n = 8$; mean = 70.855, SEM = 2.311; $t(7) = 9.024$; $p < 0.001$, $r = 0.960$) who performed better with respect to the three 2D Groups.

In fact, an ANOVA limited to the 2D Groups uncovered no difference ($F(2, 20) = 0.574$; $p = 0.572$) between the 2D Groups (*2D-NCG*: $n = 8$; mean = 57.500, SEM = 1.637; *2D-PCG*: $n = 8$; mean = 56.250, SEM = 1.830; *2D-ACG*: $n = 7$; mean = 60.000, SEM = 3.780). Data concerning the 2D Groups were therefore merged, and the resulting mean ($N = 23$; mean = 57.826, SEM = 1.400) was significantly above chance level ($t(22) = 5.590$; $p < 0.001$).

When the analysis was limited to the first five trials, the chicks belonging to the *3D-NCG* preferentially chose the larger set (mean = 70.000, SEM = 5.345; $t(7) = 3.742$; $p = 0.007$). At the ANOVA, limited to the percentage of correct responses given by the three 2D Groups during the first five trials, no difference ($F(2, 20) = 0.921$; $p = 0.416$) was found between the three Groups (*2D-NCG*: $n = 8$; mean = 60.000, SEM = 3.780; *2D-PCG*: $n = 8$; mean = 60.000, SEM = 6.547; *2D-ACG*: $n = 7$; mean =

68.571, SEM = 4.041). These data were therefore merged, and the resulting mean (mean = 62.609, SEM = 2.896) was significantly above chance level ($t(22) = 4.354$; $p < 0.001$).

The binomial test revealed that 2 out of the *3D-NCG* chicks performed statistically above chance level (15 correct responses out of 20), 4 performed marginally not significantly (2 subjects scored 13 correct out of 19 valid trials, $p = 0.083$ and 2 subjects scored 14 correct responses out of 20, $p = 0.058$); 2 chicks performed at chance level (13 correct out of 20 valid trials).

With regard to the 2D groups, 1 chick gave 15 correct responses out of 20 ($p = 0.021$); 1 chick gave 14 correct responses out of 20 ($p = 0.058$) and the remaining 21 subjects gave 13 or less correct responses out of 20.

A larger proportion of chicks did not perform significantly better than the chance level, when quantitative variables were no longer available. No chick, however, scored less than 50 % and, in fact, all of the chicks scored at least 60 % correct responses. This results can only not be explained by the fact that the attention required by the task was quite high as the location of the "correct" stimulus was alternated from trial to trial. Indeed under similar conditions, we expected a percentage of error of about 20 %, as reported by previous works (Regolin et al. 2005a, b).

General discussion

The data outlined here support the hypothesis that there is a continuity in processing small and large numbers. Our findings do not concord with those of studies concerning developmental psychology. While infants between 12 and 14 months (Feigenson et al. 2002) failed to discriminate between 1 vs. 4 crackers, chicks can distinguish between sets of 1 vs. 4 objects. The diversity in performance cannot be explained by motivational factors linked to the kind of attractors that were used, since the chicks mastered the task when food as well as social attractors was utilized. The chicks' discrimination between 1 vs. 4 could suggest that an *OFS* is able to process larger groups, including up to 4 elements for each set. If that would be the case, the chicks should have failed when they were presented with the 1 vs. 5 comparison. The fact that the chicks were able to discriminate between 5 and 1 disproves this hypothesis, leaving two different alternative explanations: the discrimination could be supported by an *OFS* with a larger capacity capable of processing up to 5 elements per set. This seems unlikely because the signature limit of that system in animals has been reported at around 3 or, at most, 4 (Feigenson and Carey 2005). Consistent with these findings, chicks have been found able to discriminate up to 3 items per set during a task in which discrimination was

presumably based on *OFS* (Rugani et al. 2008). With regard to the second possible explanation, the chicks' performance could be explained by a mechanism that discriminates between sets composed, on the one hand, by a singular entity and, on the other, by plural entities. A system that allows discrimination of numerical values only when singular and plural sets (1 vs. 2 and 1 vs. 5) and not when two plural sets (2 vs. 3, 2 vs. 4 and 2 vs. 5) are compared has been described in rhesus monkeys (Barner et al. 2008). The chicks, however, succeeded in comparing 2 vs. 4, thus disproving this hypothesis. The fact that the chicks' performance remained above chance levels even when continuous physical variables were being controlled indicates that this type of discrimination could be based on numerical cues. For what concerns the 2D stimuli, it should be noted that even if the performance remained statistically above chance, the percentage of correct responses are actually lower. This is due to the nature of the stimuli employed and not on a lack of discrimination. A decrement of the performance was indeed found also in our experiments on arithmetic abilities in chicks (Rugani et al. 2009). Such an evidence was also supported by similar data collected in this species, for example, it has been shown that chicks prefer two-dimensional pictures depicting possible three-dimensional objects rather than impossible versions of those same objects (Regolin et al. 2011).

Neither the *OFS* nor the singular versus plural system seem to be capable of explaining all of our data, suggesting that the *AMS* is involved in making the 2 vs. 4 discrimination. A collection of data on chicks (Rugani et al. 2007, 2008, 2009, 2010, 2011; Garland et al. 2012), elephants (Irie-Sugimoto et al. 2009; Perdue et al. 2012), bears (Vonk and Beran 2012), fish (Dadda et al. 2009; Piffer et al. 2012), sea lions (Abramson et al. 2011), non-human primates (Beran 2001; Beran and Beran 2004; Jordan and Brannon 2006a, b; Beran 2007; Cantlon and Brannon 2007; Hanus and Call 2007; Uher and Call 2008; Evans et al. 2009; Merritt et al. 2009), 7-month-old infants (Cordes and Brannon 2009), preschool and school children (De Hevia and Spelke 2009) supports this hypothesis.

It is possible that all these experimental findings can be explained by a recent work showing that it is the modality of stimulus presentation that can trigger activation of one or the other numerical systems. When attention is focused on the distinct identity of the elements, the *OFS* is activated and does the processing, but when the attention is directed towards the whole collection, the *AMS* is activated and does the data elaboration (Hyde and Spelke 2011). According to that hypothesis, the rearing experience of our chicks with a whole group of imprinting elements could have elicited subsequent processing of those elements by *AMS*, even if they were presented one by one during the testing session. The infants' lack of experience with an

overall group of crackers and the fact that these were presented one by one could, instead, have triggered processing by *OFS* in that case.

The data gathered during our experiments with chicks do not clarify by themselves the exact functioning of non-verbal numerical representations, although they support the hypothesis that the numerical system is not specialized in processing small or large numbers. Instead, a pre-attentional selection would activate analysis by the *AMS* or the *OFS*.

To summarize, we are still convinced that the domain of the *OFS* is limited to the smallest numbers, but it is possible that in some circumstances, those same small numbers could be processed by the *AMS*, meaning that there could be a partial overlapping of the two. Nonetheless sometimes, the processing of both small and large numbers seems to be based solely on the *AMS*, as shown by performing ordinal task by *Macaca mulatta* (Brannon and Terrace 1998; Merritt et al. 2009), *Papio hamadryas* and *Saimiri sciureus* (Smith et al. 2003) and *Cebus apella* (Judge et al. 2005).

Although originally the *OFS* may not have been a numerical system, we can compare its action to that of a magnifying glass on the number line which focuses attention on first small numbers allowing comprehension of their exact value while the *AMS* permits an overall view of numerical magnitudes on the whole number line. In humans, the *OFS* allows comprehension of exact small values and interacts with the *AMS* through language creating an ever more exact representation of large numbers. This pre-verbal numerical base could serve as the foundation for more sophisticated numerical concepts which are uniquely human.

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References

- Abramson JZ, Hernandez-Lloreda V, Call J, Colmenares F (2011) Relative quantity judgments in South American sea lions (*Otaria flavescens*). Anim Cogn 14:695–706
- Barner D, Wood J, Hauser M, Carey S (2008) Evidence for a non-linguistic distinction between singular and plural sets in rhesus monkeys. Cognition 107(2):603–622
- Beran MJ (2001) Summation and numerosness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). J Comp Psychol 115:181–191
- 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 Process 33:55–63
- Beran MJ, Beran MM (2004) Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. Psychol Sci 15:94–99

- Brannon EM, Terrace HS (1998) Ordering of the numerosities 1 to 9 by monkeys. *Science* 282(5389):746–749
- Cantlon JF, Brannon EM (2006) Shared system for ordering small and large numbers in monkeys and humans. *Psychol Sci* 17:401–406
- Cantlon JF, Brannon EM (2007) Basic math in monkeys and college students. *PLoS Biol* 5(12):2912–2919
- Carey S (2009) *The origin of concepts*. Oxford University Press, New York
- Cordes S, Brannon E (2009) Crossing the divide: infants discriminate small from large numerosities. *Dev Psychol* 45(6):1583–1594
- Cordes S, Gelman R, Gallistel CR, Whalen J (2001) Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychon Bull Rev* 8(4):698–707
- Dadda M, Piffer L, Agrillo C, Bisazza A (2009) Spontaneous number representation in mosquitofish. *Cognition* 112:343–348
- De Hevia MD, Spelke E (2009) Spontaneous mapping of number and space in adults and young children. *Cognition* 110:198–207
- Evans TA, Beran MJ, Harris EH, Rice D (2009) Quantity judgments of sequentially presented food items by capuchin monkeys (*Cebus apella*). *Anim Cogn* 12:97–105
- Feigenson L, Carey S (2005) On the limits of infants' quantification of small object arrays. *Cognition* 97:295–313
- Feigenson L, Carey S, Hauser M (2002) The representations underlying infants' choice of more: object files versus analog magnitudes. *Psychol Sci* 13(2):150–156
- Feigenson L, Dehaene S, Spelke E (2004) Core systems of number. *Trends Cogn Sci* 8:307–314
- Gallistel CR, Gelman R (1992) Preverbal and verbal counting and computation. *Cognition* 44:43–74
- Garland A, Low J, Burns KC (2012) Large quantity discrimination by North Island robins (*Petroica longipes*). *Anim Cogn* 15(6):1129–1140
- Halberda J, Feigenson L (2008) Developmental change in the acuity of the 'number sense': the approximate number system in 3-, 4-, 5-, 6-year-olds and adults. *Dev Sci* 44(5):1457–1465
- Hanus D, Call J (2007) Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): the effect of presenting whole sets versus item-by-item. *J Comp Psychol* 121:241–249
- Hauser MD, Carey S, Hauser LB (2000) Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proc R Soc Lond B* 267(1445):829–833
- Hyde DC, Spelke ES (2011) Neural signatures of number processing in human infants: evidence for two core systems underlying numerical cognition. *Dev Sci* 14(2):360–371
- Irie-Sugimoto N, Kobayashi T, Sato T, Hasegawa T (2009) Relative quantity judgment by Asian elephants (*Elephas maximus*). *Anim Cogn* 12:193–199
- Izard V, Sann C, Spelke ES, Steri A (2009) Newborn infants perceive abstract numbers. *Proc Natl Acad Sci USA* 106(25):10382–10385
- Jordan KE, Brannon EM (2006a) A common representational system governed by Weber's law: nonverbal numerical similarity judgments in 6-year-olds and rhesus macaques. *J Exp Child Psychol* 95:215–229
- Jordan KE, Brannon EM (2006b) Weber's Law influences numerical representations in rhesus macaques (*Macaca mulatta*). *Anim Cogn* 9:159–172
- Judge PG, Evans TA, Vyas TK (2005) Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*). *J Exp Psychol Anim Behav Process* 31(1):79–94
- Le Corre M, Carey S (2007) One, two, three, four, nothing more: an investigation of the conceptual sources of the verbal counting principles. *Cognition* 105:395–438
- Merritt D, Rugani R, Brannon E (2009) Empty sets as part of the numerical continuum: conceptual precursors to the zero concept in rhesus monkeys. *J Exp Psychol Gen* 138(2):258–269
- Pepperberg MI (2012) Further evidence for addition and numerical competence by a Grey parrot (*Psittacus erithacus*). *Anim Cogn*. doi:10.1007/s10071-012-0470-5
- Perdue BM, Talbot CF, Stone A, Beran MJ (2012) Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Anim Cogn* 15:955–961
- Piffer L, Agrillo C, Hyde DC (2012) Small and large number discrimination in guppies. *Anim Cogn* 15:215–221
- Regolin L, Garzotto B, Rugani R, Vallortigara G (2005a) Working memory in the chick: parallel and lateralized mechanisms for encoding of object- and position-specific information. *Behav Brain Res* 157:1–9
- Regolin L, Rugani R, Pagni P, Vallortigara G (2005b) Delayed search for a social and a non-social goal object by the young domestic chick (*Gallus gallus*). *Anim Behav* 70:855–864
- Regolin L, Rugani R, Stancher G, Vallortigara G (2011) Spontaneous discrimination of possible and impossible objects by newly hatched chicks. *Biol Lett* 7:654–657
- Rugani R, Regolin L, Vallortigara G (2007) Rudimental competence in 5-day-old domestic chicks (*Gallus gallus*): identification of ordinal position. *J Exp Psychol Anim Behav Process* 33(1):12–20
- Rugani R, Regolin L, Vallortigara G (2008) Discrimination of small numerosities in young chicks. *J Exp Psychol Anim Behav Process* 34(3):388–399
- Rugani R, Fontanari L, Simoni E, Regolin L, Vallortigara G (2009) Arithmetic in newborn chicks. *Proc R Soc Lond B* 276:2451–2460
- 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* 13:790–797
- Rugani R, Regolin L, Vallortigara G (2011) Summation of large numerosity by newborn chicks. *Frontiers Comp Psychol*. doi:10.3389/fpsyg.2011.00179 (online first)
- Smith BR, Piel AK, Candland DK (2003) Numeracy of a socially housed hamadryas baboon (*Papio hamadryas*) and a socially housed squirrel monkey (*Saimiri sciureus*). *J Comp Psychol* 117(2):217–225
- Starkey P, Cooper RG (1980) Perception of numbers by human infants. *Science* 210(4473):1033–1035
- Trick LM, Pylyshyn ZW (1994) Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychol Rev* 101(1):80–102
- Uher J, Call J (2008) How the great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus*, *Gorilla gorilla*) perform on the reversed reward contingency task II: transfer to new quantities, long-term retention, and the impact of quantity ratios. *J Comp Psychol* 122:204–212
- Vonk J, Beran MJ (2012) Bears "count" too: quantity estimation and comparison in black bears (*Ursus americanus*). *Anim Behav* 84:231–238
- Xu F, Spelke ES, Goddard S (2005) Number sense in human infants. *Dev Sci* 8(1):88–101