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## Rudiments of mind: Insights through the chick model on number and space cognition in animals

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Studies on human infants, focused on the ontogenetic origins of knowledge, have provided evidence for a small set of separable systems of core knowledge dealing with the representation of objects, number, and space. We investigated core knowledge systems from a comparative perspective, making use of the domestic chick as a model system, and filial imprinting as a key to animal mind. Here, we discuss evidence showing precocious abilities in the chick for representing: (i) the cardinal and ordinal/sequential aspects of numerical cognition, and (ii) the distance, angle, and sense relations among extended surfaces in the surrounding layout. Some of the abilities associated with core knowledge systems of number and space were observed in the absence of (or with very reduced) visual experience, supporting a nativistic account of the origins of knowledge.

Keywords: number, space, geometry, avian cognition, chick.

### Introduction

According to a prominent view in current cognitive sciences, human knowledge is composed of a set of core systems – a tool-kit of cognitive mechanisms – for representing significant aspects of the environment (Spelke, 2000; Carey, 2009). These core knowledge systems would serve to facilitate the mental representations of physical and social objects, spatial relationships, and number. Core systems would be available at birth and shared by other animals. However, there is scant evidence for these last two claims.

The idea that core knowledge systems would be available at birth is difficult to prove in human infants because of practical and ethical limitations. Human newborns are very

immature at birth, and any precise control of their early experiences is very hard to accomplish. To take an example: Are mechanisms that preferentially orient the attention of neonates to human faces inborn? It is unfeasible to provide a complete absence of face stimulation even in neonates studied a few hours after birth (Johnson, 2005; Rosa-Salva et al., *subm.*). Similar limitations are also present with other animals with an altricial pattern of development (e.g., Sugita, 2008). Here is where the importance of comparative studies becomes most readily apparent. Animals' models are useful not only in testing for the generality of core knowledge systems in different species (as mentioned above, at present much of the extant evidence is only available for number cognition and largely confined to primates, see e.g. Hauser & Spelke, 2004). The advantage of animal models is that there are species, such as the domestic chick, which are extremely precocial with regard to their pattern of motor development, making possible both sophisticated behav-

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journal analyses at an early age (i.e., soon after hatching), and enabling very precise control on the effects of past (even *in ovo*) sensory experience. In the latter case, such an approach may even demonstrate the complete lack of a tangible influence of such experience.

The domestic chick has been a very successful animal model system in neurobiology and in the study of early learning, particularly for studies on memory consolidation, brain asymmetries, and the neural bases of memory (Andrew, 1991; Rogers, 1996; Rogers & Andrew, 2002; Horn, 2004; Matsushima et al., 2003; Rose, 2000; Vallortigara, 2000; 2006a). In addition, we believe it may prove to be an excellent model to adopt in order to tackle some classical issues in developmental psychology, offering a novel battle-ground for the empirical investigation of nature-nurture issues on the origins of knowledge. We used the domestic chick to investigate social cognition, looking for innate predispositions to respond to face-like stimuli (Rosa-Salva et al., 2010), biological motion (Vallortigara et al., 2005; Regolin & Vallortigara, 2006), and causal agency associated with self-propulsion (Mascalzoni et al., 2010; and see Vallortigara, 2006b; 2009b for general reviews). Here, we review our studies on core knowledge of number and geometry in very young chicks.

## Number

Since Aristotle argued that the “logos” is the essence of the human mind, logic and language were considered strictly interdependent (Houndé & Tzourio-Mazoyer, 2003). From this perspective, all of cognition and consequently, even mathematical thinking, was believed to be firmly related to language. Doubtless, the ability to represent number and selected numerical concepts, such as real numbers, logarithms, and square roots, is only performed by a subset of human beings, who have received specific mathematical instruction. Nonetheless, in the last decades, there has been an increasing interest in the study of numerical competences in nonverbal creatures – namely pre-verbal infants and non-human species – in an attempt to better understand the role of language in such processes. The availability of behavioural tests suitable to nonverbal subjects provides a unique opportunity to compare numerical abilities among species, and to investigate the development and evolutionary origin of these abilities (reviews in Gallistel & Gelman, 1992; Dehaene, 1997; Hauser & Spelke, 2004).

In the variety of numerical competences mastered by non-verbal-creatures, the most basic one is proto-numerosity, defined as the ability to make judgements of size differences between two or more sets, i.e. “more than...”, “less than...”, (Davis & Pérusse, 1988).

## Numerical discrimination

Numerical discrimination is also often found in ecological situations whenever an animal chooses the larger or smaller between two alternative sets of food items. Such an ability would conceivably be the basis for efficient foraging strategies (Krebs, 1974). Several species prefer the larger amount of food in a spontaneous forced-choice discrimination task (Anderson, 2003; Call, 2000; Boysen, Bertson & Mukobi, 2001). For example, rhesus monkeys (*Macaca mulatta*) can discriminate between 1 vs. 2; 2 vs. 3; 3 vs. 4, and 3 vs. 5 (in this instance referring to pieces of apple) but not between 4 vs. 5; 4 vs. 6; 4 vs. 8, and 3 vs. 8 (Hauser, Carey & Hauser, 2000). Infants are able to discriminate between 1 vs. 2 and 2 vs. 3 cookies, but not between 3 vs. 4 and 3 vs. 6. (Feigenson, Carey & Spelke, 2002). When salamanders (*Plethodon cinereus*) were presented with two different quantities of live fruit flies (*Drosophila virilis*) placed in two identical plastic transparent tubes positioned 20 cm apart, and these subjects were required to choose between quantities of 1 vs. 2, and 2 vs. 3, they tended to choose the set that maximised their net energy gain. The salamanders were allowed to approach one of the tubes; in order to make their choice, flies remained visible throughout the duration of the trial. Thus, salamanders were not required to memorize the two different quantities of food available in each container, but instead to make a decision on the basis of what they were seeing in front of them (Uller, Jaeger & Guidry, 2003). In this kind of situation in which several different numbers of items are employed at test, changes in number correlate with changes in quantitative variables (e.g. volume and surface area) that co-vary with numerosness – also called ‘continuous physical variables’. Since these continuous variables were not controlled for in the experiment by Uller et al., it is impossible to conclude that subjects’ choices were based solely on numerical information. Indeed, only when the possibility of the subject using non-numerical cues is ruled out or controlled for, can we meaningfully discuss proper cardinal abilities.

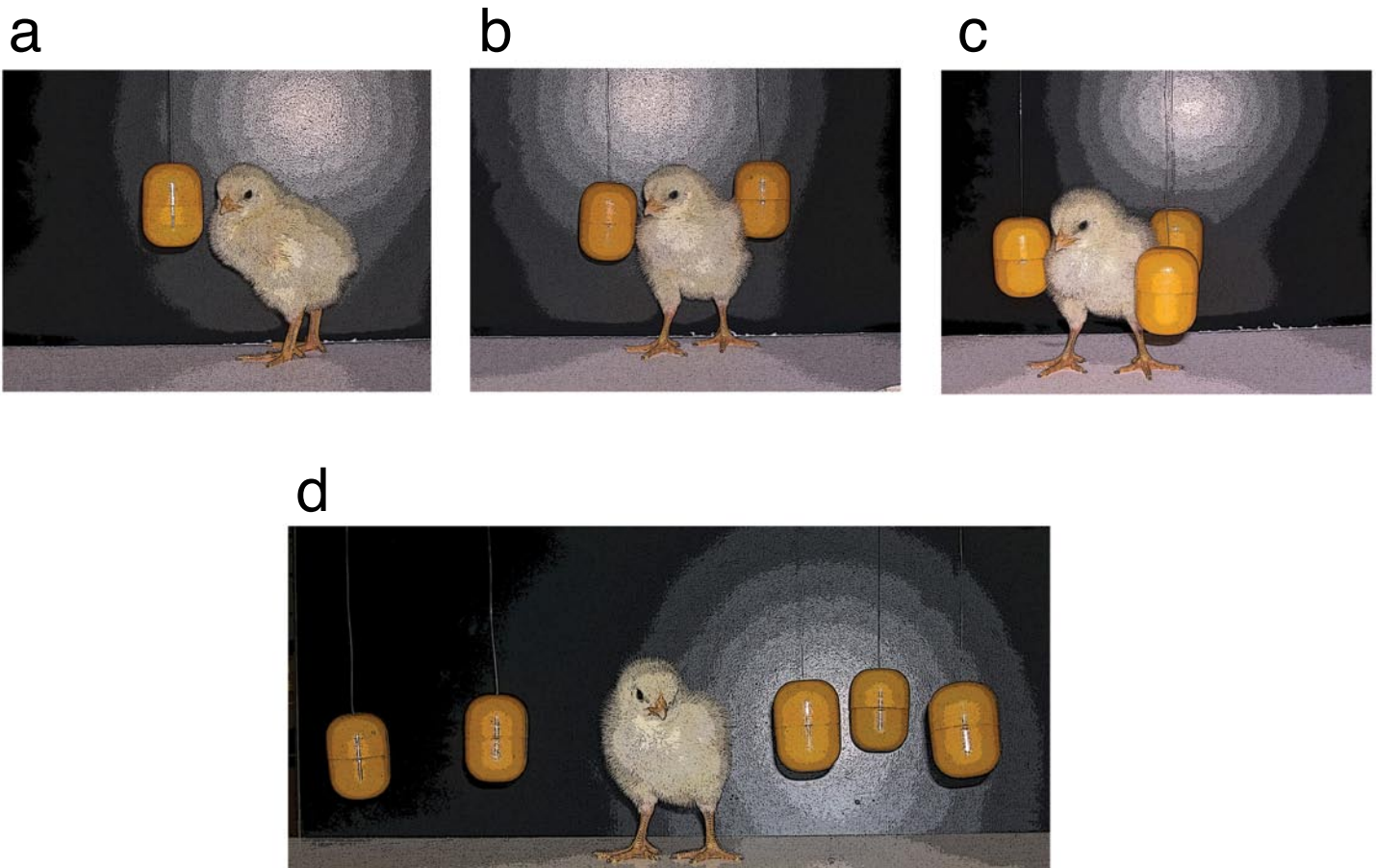
In the comparative literature, the issue of determining the instances during which animals and pre-verbal infants differentially rely on number vs. continuous extent has been poorly considered (Cantlon & Brannon, 2007). Some data on infants showed that subjects were unable to represent variation in numbers of items without also unavoidably considering the correlated continuous variables (Moore, Mix, Levine & Huttenlocher, 1997). However, there does appear to be some difference in how these influences are weighted: It seems reasonable that infants should be able to discriminate sets solely on the basis of their numerosness, yet they seem to prefer to do it on the basis of continuous variables (Wynn, 1996). The little amount of research that has been carried out specifically investigating this issue has not provided a clear account of when animals would be shown to rely on num-

ber or continuous extent. Hauser, Carey & Hauser (2000) showed individual monkeys some pieces of apple that were placed by the experimenter into one box, and a different number of pieces that the experimenter placed into another box. Monkeys approached the box with the larger quantity for 2 vs. 1, 3 vs. 2, 4 vs. 3, and 5 vs. 3 sets of elements. To address the possibility that monkeys were attending to volume rather than number, in a control condition, Hauser, Carey & Hauser (2000) placed 3 pieces of apple in one box, and placed 1 piece of apple equal in volume to those three pieces in the other box. Monkeys chose the box with the larger number of apple pieces.

Spontaneous number discrimination was investigated in very young animals by taking advantage of chicks' sensitivity towards fine visual characteristics of their own imprinting object (Rugani, Regolin & Vallortigara, *in press*). Chicks (*Gallus gallus*) of separate experimental groups were reared for 3 days while isolated from one another in single cages, and were each exposed to artificial stimuli of different numerosness. The testing phase consisted of a 6-minute free choice between the familiar stimulus and a novel stimulus,

with stimuli differing in the number of items present. In the first experiment, individual groups of chicks were maintained for the first three days of life in different conditions of rearing (i.e. reared with either one, two, three identical small imprinting balls, or with no object at all). Thereafter, at test, all chicks underwent a 2 vs. 3 discrimination (see Fig. 1a, 1b, 1c, and 1d). Though we were expecting that chicks would prefer to approach the familiar stimulus, it should be noted that any unambiguous and consistent preference expressed by birds implies that they are able to detect a physical difference between testing stimuli.

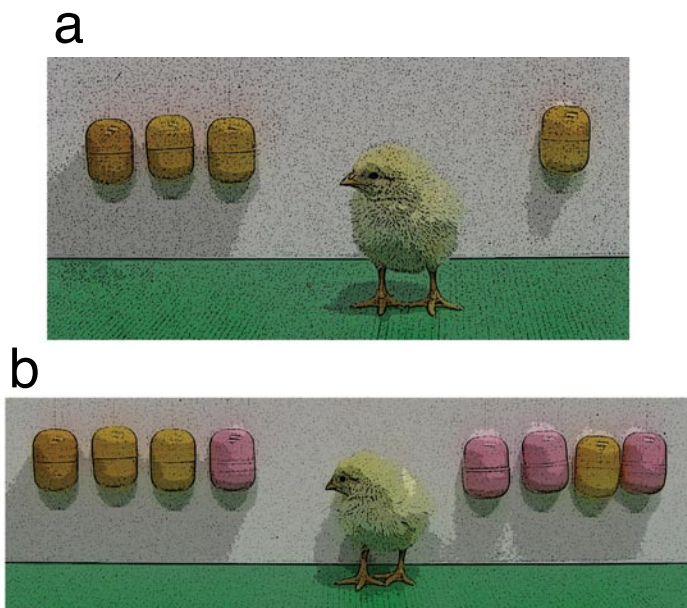
Only chicks reared together with at least one imprinting object (1, 2, or 3) were able to discriminate between those numbers of objects at test, and these chicks preferred the larger number of items. In contrast, chicks not exposed to any imprinting object did not show any preference for either of the two stimuli used at test. Irrespective of the numerosness of the imprinting objects, chicks subsequently preferred to associate with the stimulus set containing three objects, which implies, as mentioned, that chicks are able to discriminate the physical difference between the stimuli. Moreover,



**Figure 1.** An example of the stimuli used to rear chicks with one (a), two (b) or three (c) imprinting objects. d) Illustrative representation of the 2 vs. 3 discrimination test.

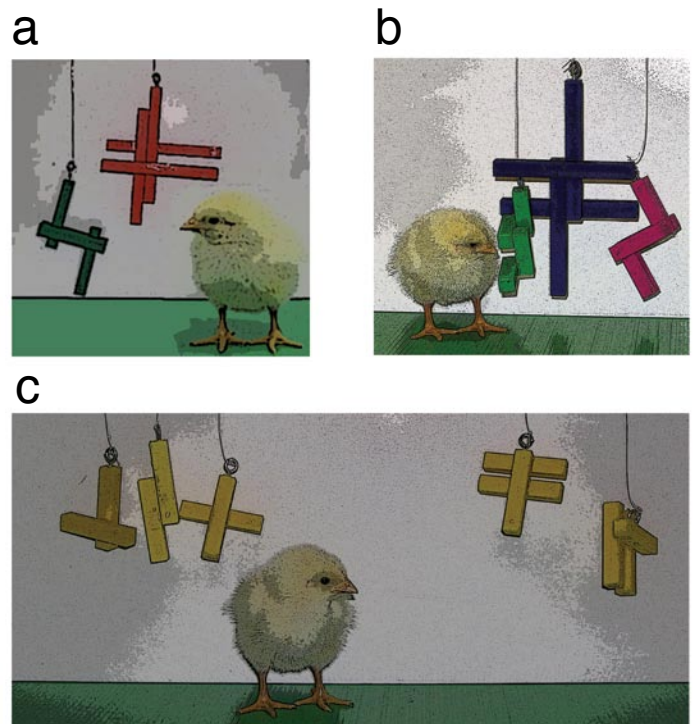
the lack of choice reported for chicks that have been reared with no imprinting object suggests that imprinting is a necessary process in the experimental investigation of spontaneous number discrimination abilities in chicks. We wondered, however, whether such a preference was a specific outcome of the imprinting procedure or whether it reflected a generic preference for larger collections of objects.

In an experiment designed to address this question, a similar procedure as before was employed with two new groups of chicks, one reared with a single imprinting object, and the other with three imprinting objects. In addition, half of the chicks in the test phase had to choose from three objects vs. one object (this procedure was referred to as “absolute” number discrimination, see Fig. 2a). The other half of the subjects had to choose between two sets of identical overall numerosness, i.e. comprising 4 items each, but of which either one or three objects were of the same colour as the training stimulus (this procedure was termed “relative” number discrimination, see Fig. 2b). The remaining objects in that condition were of a slightly different and non-familiar colour. Results confirmed that, when exposed to sets of objects of different numbers of items, comprised of objects identical to each other and to the objects present during familiarization, chicks chose on the basis of the larger quantity of items present in the set. There being no difference between the two test conditions (absolute vs. relative number discrimination), it appears that when faced with identical overall numbers of items, chicks could base their choice on the relative amount of familiar objects – which were identifiable only through a difference in colour.



**Figure 2.** An illustrative representation of the two stimuli used in the Absolute Discrimination (a). An illustrative representation of the two stimuli used in the Relative Discrimination (b).

Overall, the data described above can be accounted for in terms of a preference in choice for the larger set of objects present at test, rather than for the actual number of objects experienced during familiarization. We wondered whether, comparable to human infants (Feigenson, 2005), the use of objects that are different from one another may promote individual item processing, favouring judgements based on the numerosness of the set. To this end, sets of objects which were very different from each other (in shape, colour, area, and volume), rather than being identical as in the previous experiments, were used for imprinting (see Fig. 3a and 3b). At test, chicks faced a situation very different from that described for the previous experiments, as birds were now required to discriminate between two sets made of novel objects, in comparison with the stimuli that the chicks had become familiar with during exposure. As before, at test, one set was comprised of two objects and the other of three. The testing stimuli were different from those used during imprinting in the dimensions of colour, shape, and size. The two sets used in the test phase were equalized with each other for both overall surface and volume (see Fig. 3c). In this way, any visual characteristic of the original imprinting set (apart from number of items) was either not present (colour, shape) or equalized (volume, surface) in the testing



**Figure 3.** An example of the two element stimulus used to rear a group of chicks. Each element differed from the others in shape, colour and dimension. b) An example of the three-element stimulus used to rear a group of chicks. The elements were different in colour, shape and dimension. c) An example of the two sets of element used at test. The overall surface area and volume of the two stimuli were identical.

sets. With regard to object number, only one of the test sets was identical to that of the familiar (imprinting) set. Within these conditions, chicks reared with three objects chose the set comprising three objects, while chicks reared with two objects chose the set comprising two objects (Rugani, Regolin & Vallortigara, *in press*).

On the whole, results showed that when exposed to homogeneous sets, i.e. sets composed of otherwise identical objects, chicks prefer a larger quantity of items to a familiar quantity. This means that, irrespective of the amount of elements present during imprinting, chicks preferred to associate with the greater quantity of objects at test. Presumably, this preference emerged because imprinting stimuli are considered by chicks as possible social companions and when presented with a new environment (for example, the testing apparatus), chicks preferred to stay nearer to the larger number of mates. However, when chicks were exposed to sets of different and heterogeneous familiarization objects and then faced, at test, with two sets of novel objects with identical overall volume and contour length, they chose to associate with the set of familiar numerosness; when reared with three objects, they preferred sets of three novel objects to sets of two novel objects and when reared with two objects, they preferentially chose sets of two novel objects over sets of three novel objects (Rugani, Regolin & Vallortigara, *in press*).

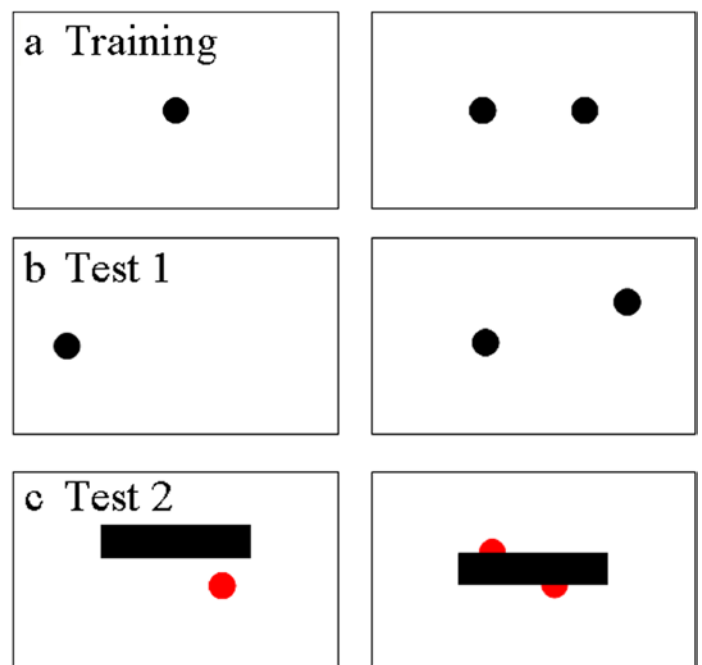
These results are similar to those obtained, employing different procedures, in experiments with human infants. Although a series of studies found that infants represent total continuous extent rather than numerosness in small object arrays (Clearfield & Mix, 1999; Feigenson, Carey & Spelke, 2002), there is also evidence showing that infants may respond to the number of objects in the arrays, rather than to their overall continuous extent. This finding was reported when heterogeneous objects were used (Feigenson, Carey & Spelke, 2002; Feigenson, Carey & Hauser, 2002; Feigenson, 2005). Similarly, chicks seem to rely on continuous extent when small arrays of identical objects are used, but turn to use of numerosness when presented with object sets of contrasting properties. Even honey bees (*Apis mellifera*) trained to discriminate between two versus three elements could generalize the discrimination between three versus four elements using numerical information and not other cues, such as when elements differing in colour, shape, and dimensions were used (Gross et al., 2009).

Number discrimination can also be assessed by employing conditioning procedures. We performed this in a separate set of experiments with week-old-chicks (a training period is required in this case). In these experiments, control for continuous variables was obtained with a different procedure than before, by exploiting chicks' ability to recognize partly

occluded objects as corresponding whole objects. Such a process is known as "amodal completion" and was originally described in human perception studies (Grossberg & Mingolla, 1985; Kanizsa, 1979; Michotte, 1963; Michotte, Thinès & Crabbé 1964), but the phenomenon has been also shown in a number of animal species, including domestic chicks (review in Vallortigara, 2004). Chicks seem to perceptually complete the "missing parts", just as humans do (Regolin & Vallortigara, 1995; Lea, Slater & Ryan, 1996; Regolin, Marconato & Vallortigara, 2004).

Chicks were trained to discriminate pictures representing small sets of identical elements in order to obtain food reinforcement. They were then tested for choices (which were unrewarded) between sets of similar numerosness, while continuous physical variables such as spatial distribution, contour length, and overall surface area were equalized (Rugani, Regolin & Vallortigara, 2008).

In the first experiment, chicks' ability to discriminate one versus two elements was assessed by testing birds that had been previously trained to discriminate and selectively peck at stimuli depicting either one or two identical elements. Half of the birds were trained to select the one-element-stimulus, and the other half trained to select the two-element-stimulus. During training, a single pair of stimuli was used: a cardboard which represented one black circle and another cardboard representing two black circles, each identical to



**Figure 4.** Stimuli employed in the discrimination between 1 vs. 2 elements. The pair of stimuli used during the training (a). An example of a pair of stimuli used in Test 1 (b). An example of a pair of stimuli used in Test 2 (c). Letters in the figure refer to both illustrations in each row

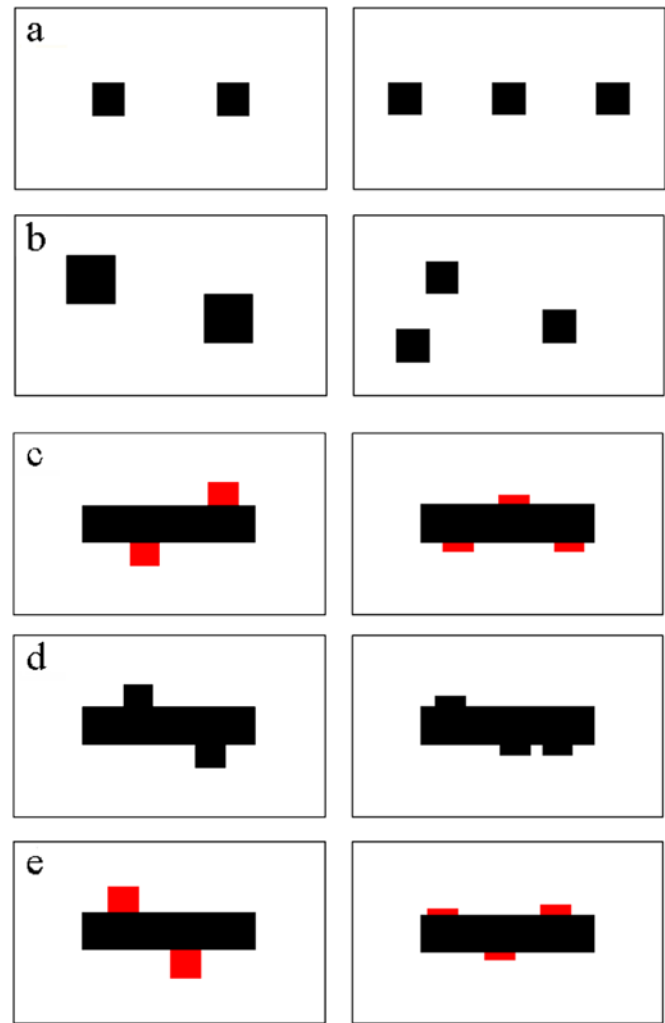
the first one (see Fig. 4a). Birds then underwent two testing sessions.

The objective of the first testing session was to check for the possible use of spatial information. Ten different pairs of stimuli were used. In each pair, one stimulus consisted of one circle, and the other consisted of two circles identical in dimension and colour to the circles used at training. The only difference between stimuli was in the spatial position of the circles over the paperboard, which was randomly determined for each stimulus (see Fig. 4b for an example of a pair of stimuli used in this phase). Chicks succeeded at discriminating between 1 vs. 2 elements, pecking at the previously reinforced number of elements even when the position of the single items was changed from trial to trial.

An interesting observation arose from the second testing session, in which animals were presented with pieces (i.e., two halves) of the single elements, hidden by an occluder; to the human observer, the pieces would amodally complete into two separate whole and identical objects (see Fig. 4c). Nine different pairs of stimuli, drawn on identical white rectangular plastic paperboards, were used. Each pair was comprised of a stimulus made of one red circle and a second stimulus made of two red circles. One black occluding bar was present in both types of stimuli. The size of the circles was the same as for those used in the previous training and testing. Their spatial positions varied randomly from stimulus to stimulus (therefore, from trial to trial). For the stimuli with two circles, the black bar overlapped the circles so that it occluded exactly one half of each circle. In the stimuli with one single circle, the bar was positioned above or beyond the circle itself, but without occluding it. In this way, the total overall area of the elements present in each stimulus was identical (see Fig. 4c). Nevertheless, due to the perceptual process of amodal completion, the two occluded elements were perceived as two whole and separate elements in one stimulus, whereas in the other stimulus, a single unoccluded element was perceived. Consistent discrimination between item quantities acquired during training was maintained for these new and peculiar stimuli, in which surface and outline of the visible sections of the two elements were actually congruent with that of the single element. Nonetheless, the chicks perceived the occluded items as being greater in number, in accordance with the concept of amodal completion.

In a new group of birds, the ability to discriminate between 2 vs. 3 items was investigated, employing a procedure similar to the one described above. In this experiment, a control was used for the possible influence of contour length on discrimination, using both physically-completed and amodally-completed stimuli. Half of the chicks were trained to find food by pecking at the two-element display, and the other half at the three-element display.

Stimuli used at training consisted of two identical paperboards over which either two or three black elements had been printed (Fig. 5a). The elements consisted of black-filled squares aligned along the midline of the cardboard. In this experiment, squares were used rather than circles (as in the previous experiments) in order to facilitate the construction of modified stimuli that were used for the control of the overall outline. After training, chicks underwent four testing



**Figure 5.** Stimuli employed in 2 vs. 3 discrimination tasks. The pair of stimuli used at training (a). Example of a pair of stimuli used in Test 1, when the overall perimeter was controlled for, by modifying the dimension of the three element-stimuli (b); An example of a pair of stimuli used in Test 2 where the control for the perimeter was obtained considering three sides of the occluded squares (c). An example of a pair of stimuli used in Test 3 where the control of the perimeter was obtained by considering all four sides of the occluded squares (d). An example of a pair of stimuli used in Test 4 (controlled for the perimeter considering three sides of the occluded squares and also controlled for the overall perimeter of bar plus squares (e). Letters in the figure refer to both illustrations in each row.

sessions. In each session, ten different pairs of stimuli were used, in which all of the possible use of spatial information was controlled for by changing the position of the elements drawn on the cardboards between trials. In the first test, the perimeter was controlled for by manipulating the dimensions of the squares and composing the sets in such a way that the perimeter length of the two sets was exactly the same (see an example in Fig. 5b).

In the subsequent three tests, different kinds of control over the contour-length were obtained by using partly occluded objects. In the second test, for example, control over the perimeter length was obtained by manipulating three sides of the occluded squares because during the perceptual process of figure-background segregation, margins shared by two configurations are perceived as belonging to only one of the two objects (Rubin, 1921). The same process also occurs during amodal completion. In this case, the contour is attributed to the configuration perceived as being in front of the other. This means that in our stimuli, the side boundary shared between the bar and any of the elements should be perceived as part of the occluder (the bar itself). Each pair of the ten stimuli was comprised of a stimulus made of two red squares and a second stimulus made of three red squares. The size of the squares prior to occlusion was the same as that used at training. One black bar was present in both types of stimuli. All stimuli were placed in the middle of the paperboard. For both the stimuli with two squares and with three squares, the black bar overlapped the squares so that it partly occluded them (the amount of occluded surface could vary from square to square and from trial to trial). In this way, the total visible perimeter (considering 3 sides) of the squares was identical in the two stimuli presented in each trial (Fig. 5c).

In the third test, control of the perimeter length was achieved by manipulating all four sides of the elements (i.e. the three visible outline edges plus the edge between the occluder and the occluded elements; see Fig. 5d). Each stimulus pair was comprised of one stimulus made of two red squares and a second stimulus made of three red squares. In both stimuli, the black bar overlapped the squares so that it occluded part of each of them, and the amount of occlusion was variable from square to square and from trial to trial.

In the final test, perimeteric control was achieved by equalizing the overall outline in the two stimuli, taking into account the three sides of the occluded squares as well as the overall outline of the occluding bar. Each pair of stimuli was comprised of a stimulus made of two black squares and a second stimulus made of three black squares, with one black bar present in each stimulus. For both the stimuli with two black squares and with three black squares, the black bar overlapped some amount of the squares so that it occluded

part of them (Fig. 5e). The visible surface was variable from square to square and from trial to trial, but was within the same range of the visible surface presented in the stimuli of the previous (third) test. This final type of perimeteric control would provide a response to any potential objections concerning the role of the part of the perimeter in which the bar overlaps the squares. This is because in the stimuli just described, the relevant section of the perimeter would simply not be physically existent, as both the squares and the occluding bar are of identical colour, i.e. black. In this situation, the perceptual rule stated by Petter (1956) would hold. 'Petter's Rule' states that the object with the shorter contours in the region where the surfaces look superimposed has a greater probability of appearing in front of the other object (see also Singh, Hoffman & Albert, 1999; Tommasi, Bressan & Vallortigara, 1995; Vallortigara & Tommasi, 2001).

In all of these tests, chicks consistently and significantly selected the stimulus depicting the same number of elements previously reinforced during training, showing them to be able to discriminate 2 vs. 3 items even when the length of the contour was controlled for, and furthermore, they did so even when the elements were partly occluded.

Overall, the results described would support evidence collected in a variety of other species, showing that non-verbal creatures are capable of discriminating sets of 1 vs. 2 and 2 vs. 3 elements.

What should be noted in these findings is that, although the young chicks were trained with only one specific set of stimuli (in which number co-varied with several continuous physical variables such as density of the elements, surface area, and contour length), chicks seemed to be encoding number rather than, or as well as, physical variables. When tested with changes in the positions of the elements and with equalized overall surface area and contour length, chicks consistently maintained the discrimination on the basis of number that they acquired at training. These data strongly suggest that for some animals, number is a natural, important, and spontaneously encoded cue. Rhesus monkeys (*Macaca mulatta*) are also shown to require no training in order to attend to numerical values (Cantlon & Brannon, 2007), which runs contrary to the hypothesis that animals represent number only as a last resort when no other properties were available (Davis & Pérusse, 1988).

### *Ordinal reasoning*

Another central aspect of number cognition is the ability to represent ordinal (serial) relations, which is based on mastering the rule that when one element is added to a certain set, the new set becomes larger than the previous one and smaller than the next. Eleven month-old infants are sensitive to the ordinal relations between numerical values (Brannon,

2002), while nine month-old infants demonstrate such sensitivity only when cues provided by continuous variables are also available (Suanda, Thompson & Brannon, 2008). Rhesus monkeys (*Macaca mulatta*, Brannon & Terrace, 1998; 2000), hamadryas baboons (*Papio hamadryas*), squirrel monkeys (*Saimiri sciureus*, Smith, Piel & Candland, 2003), and brown capuchin monkeys (*Cebus paella*, Judge, Evans & Vyas, 2005), when trained to touch, in ascending order, stimuli depicting one to four elements, were then able to generalise this behaviour to new stimuli depicting larger and novel numbers of elements (e.g. from five to nine). Monkeys (*Macaca mulatta*) trained to respond (in ascending or descending order) to pairs of stimuli representing item numbers from one to nine, spontaneously generalised in the same direction when new pairs of larger values (i.e., 10, 15, 20, 30) were employed, demonstrating that there is not an easily reached upper limit to the ability (Cantlon & Brannon, 2006).

Ordinal reasoning also refers to 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 6 (Davis & Bradford, 1986) or 18 (Suzuki & Kobayashi, 2000) items. 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 & Geiger, 1995). These insects can also identify the fourth position in a series of five, and generalize it to a novel series of objects (Dacke & Srinivasan, 2008).

The next experiments that we describe focused on the investigation of ordinal abilities of five day old domestic chicks (Rugani, Regolin & Vallortigara, 2007).

In the first of these experiments, different groups of chicks were trained to peck either at the 3<sup>rd</sup>, 4<sup>th</sup>, or 6<sup>th</sup> position in a series of ten identically spaced locations, sagittally aligned in front of the subjects' starting point. During subsequent parametric testing, the results showed that chicks could accurately identify a given position. In all cases, chicks chose the correct location well above chance (i.e. 10%). Selections exhibiting trained/tested congruence broke down as follows: chicks trained on the 3<sup>rd</sup> position: N=20, Mean=64.000, ES=4.710;  $t(19)=2.972$ ,  $p=0.008$ ; 4<sup>th</sup> position: N=20, Mean=63.229, ES=1.052;  $t(19)=12.575$ ,  $p<0.001$ ; 6<sup>th</sup> position: N=22, Mean=78.409, ES=2.065;  $t(21)=13.757$ ,  $p<0.001$ .

Of course, chicks in this experiment could have relied on information other than numerical (ordinal) cues – for example, they could have used relational spatial (metric) information provided by the experimental apparatus, or simply computed the absolute distance from the walking time of the

correct position from the starting point (or from the beginning of the sequence). In order to check for these possible alternative explanations, we ran a series of control experiments on new groups of chicks of the same age.

The second experiment aimed to ascertain, at test, if chicks would correctly identify the target based on whether it was located at the same absolute distance as in the training apparatus, or in the correct ordinal position. A new group of birds was trained to peck at the fourth position, as in the first experiment, and was then required, at test, to generalise the learned response to a new sequence in which the distance from the starting point to each position had been experimentally manipulated in such a way that ordinal position and distance from the starting point were different than in the training apparatus. Chicks demonstrated the ability to generalise their behavioural response in the new apparatus, by correctly pecking at the 4<sup>th</sup> serial position, even if that position was now located much farther away than before. If chicks had taken into account the actual distance from the starting point, they would have pecked at the second position in the series.

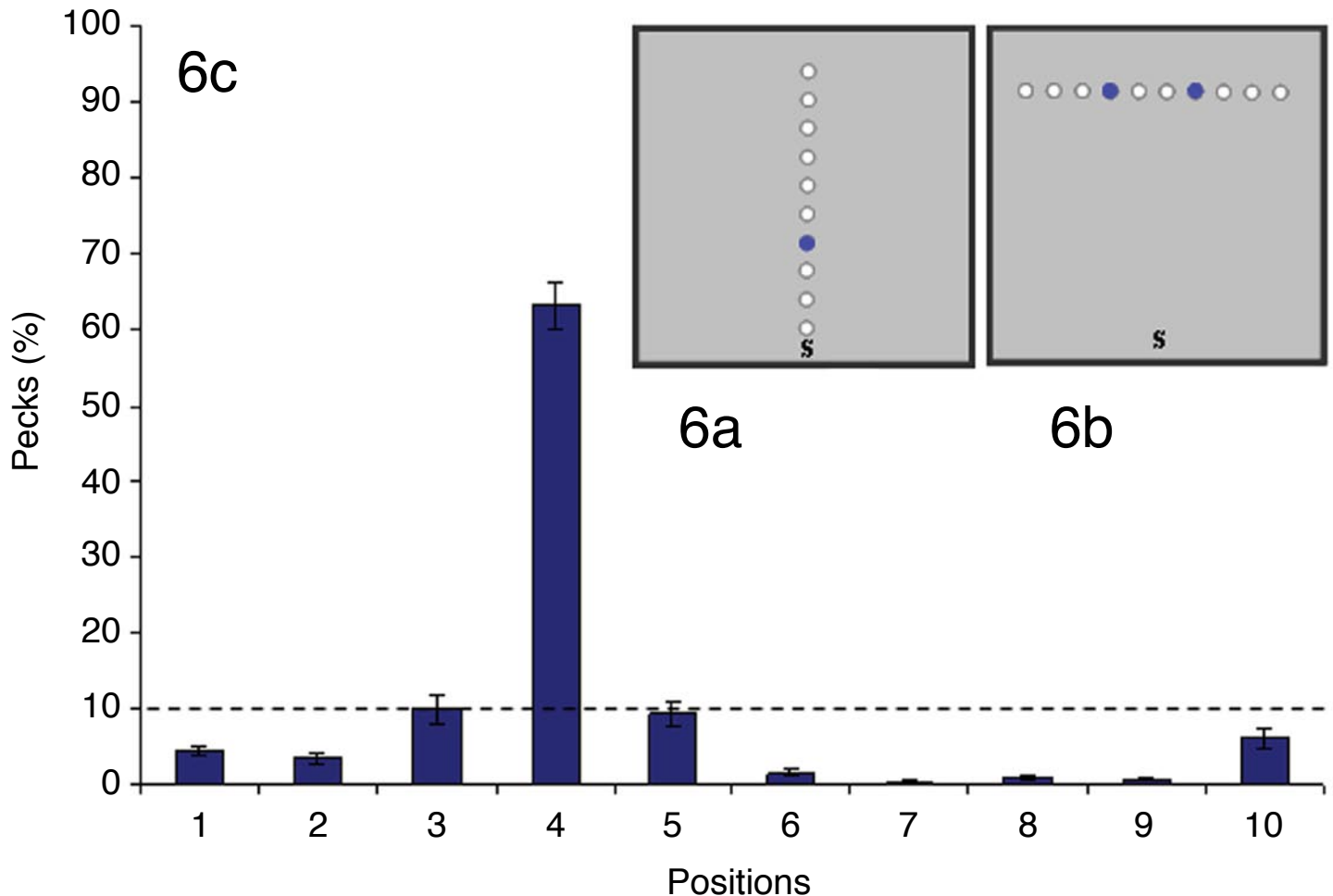
From these first two experiments, it seems that chicks' behaviour is best accounted for by assuming that they can learn and use ordinal information in order to identify the position reinforced at test. A possible issue concerning the results described so far is that, in all apparatus, the sequences were made of fixed target positions, i.e. they never changed throughout the 20 testing trials. In the third experiment, we addressed this problem by devising a new apparatus, and an ordinal stimulus series made of detached and singly displaceable objects. Some of the animals were trained on the 3<sup>rd</sup> position from the left end (in a line of 7 identical items), and the other subjects were trained on the corresponding 3<sup>rd</sup> position from the right end. This was done to control for the possibility of chicks' preferences to rely on one of either end-side in order to locate the correct position (as side preferences did emerge in the previous experiment). At test, from trial to trial, the reciprocal distance between the positions, the location of the entire stimulus array within the arena, and the ordinal position of each position was altered (i.e. all positions were swapped so that any item (in this case, a jar) changed by at least one position). Furthermore, on some of the testing trials, a new jar was used to replace the one in the correct position, in order to prevent the possibility that chicks' choice could depend on unique characteristics of the jar itself, rather than by its ordinal position. No difference was noticed during training in the two groups of animals (trained on the 3<sup>rd</sup> from the left or trained on the 3<sup>rd</sup> from the right), and both of the groups successfully mastered the task.

A serendipity bias for a hemispace was instead found in one of the space-controlled groups where birds were trained to peck at a selected position in a sagittally-oriented series of



identical elements, and were then required to generalise to an identical series, but rotated by 90°. This series was oriented in a fronto-parallel manner with respect to the chick's starting point; hence, the correct position could not be located on the basis of absolute distances from the starting point. In the fourth experiment, a different group of chicks was trained to peck at the 4<sup>th</sup> position in a series of ten identical, equispaced and sagittally oriented (with respect to the starting point of the chicks, see Fig. 6a) locations. Chicks were then required to respond to a different apparatus, where the correct position had to be identified within a series identical to the one used at training, but rotated by 90° (see Fig. 6b). The new series was horizontally positioned in front of the chick's starting point; hence, the correct position could not be located on the basis of absolute distances from the start-

ing point. On the basis of the results from the second experiment, chicks seem able to generalise the learned response to a new sequence where the target must be identified on the basis of its position in the series, without relying on the absolute distance from the starting point or on geometrical information. However, a very interesting finding concerns the fact that chicks identified as correct only the 4<sup>th</sup> position from the left end, and not the 4<sup>th</sup> position from the right end, which was chosen at chance level (see Fig. 6c). This preference for targets located on the left hemispace could be ascribed to a bias in the allocation of attention, somewhat similar to that shown by humans and dubbed as "pseudoneglect" (Jewell & McCourt, 2000; Albert, 1973). Nevertheless, chicks' performance is also undeniably reminiscent of the human mental number line (Dehaene, 1993).



**Figure 6.** a) Schematic representation of the apparatus used for training. The filled circle indicates the reinforced position and S indicates the chick's starting point. b) schematic representation of the apparatus used for generalization test (the filled circles indicate the two possible correct positions for the chick). c) Results of generalization test: Mean values ( $\pm$  SEM) are shown of the pecks directed to each position in the series used for the generalization. The dotted line ( $y=10$ ) represents chance level.

In conclusion, the understanding of ordinal information does not seem to require complex training or sophisticated mental skills, but can be seen in species very different from man and other primates, and is already available very early during ontogeny, having probably been selected due to its high adaptive value.

### *Arithmetic abilities*

A more complex non-verbal numerical ability consists in the manipulation of numerical representations in simple arithmetic operations such as additions and subtractions. Summation has been demonstrated in tasks where primates were required to compute and choose the larger of two quantities. Chimpanzees (*Pan troglodytes*) were presented with two sets of two food wells, each of which contained a number of chocolates. To choose the set with the overall larger quantity, the chimpanzee had to sum the chocolates in each of the two sets and then compare the two summed values. On the critical trial, the largest set of wells did not contain the larger summed value. Even in this case, subjects preferred the larger quantity (Rumbaugh, Savage-Rumbaugh & Pate, 1988). In 1989, Boysen and Bertson provided a very impressive demonstration of arithmetic animal ability. An adult chimpanzee (named Sheba) was led around a room to three different hiding places that could contain 1, 2, 3, or 4 pieces of orange. Subsequently, Sheba was required to choose the Arabic number that corresponded to the number of items she had met before. She chose the correct sum from the first session of test in both cases, showing mastery of this ability without any explicit training.

Using the violation of expectancy looking time method, Hauser and Carey (2003) have shown that free-ranging rhesus macaques (*Macaca mulatta*) are spontaneously able to solve simple additions. Each animal watched as eggplants were sequentially placed behind a screen, after which the screen was removed, revealing an outcome that either did match or did not match the number placed there. Macaques looked longer at impossible outcomes, such as when after the presentation of (1+1) eggplants, the screen revealed 3 eggplants instead of 2, or when following the disappearance of (2+1) eggplants, the screen revealed 4 eggplants instead of 3. Even when the subjects were presented with the sum (1 small + 1 small), they were surprised that the screen revealed a single big eggplant and not 2 small ones, showing that macaques probably based their decision on the number of objects and not on the total amount of volume.

In another approach to the same issue, Washburn and Rumbaugh (1991) trained two rhesus monkeys (*Macaca mulatta*) to choose between two Arabic numbers on a touch-sensitive screen. The animals received the corresponding number of pellets as a reward. Monkeys always chose the larger num-

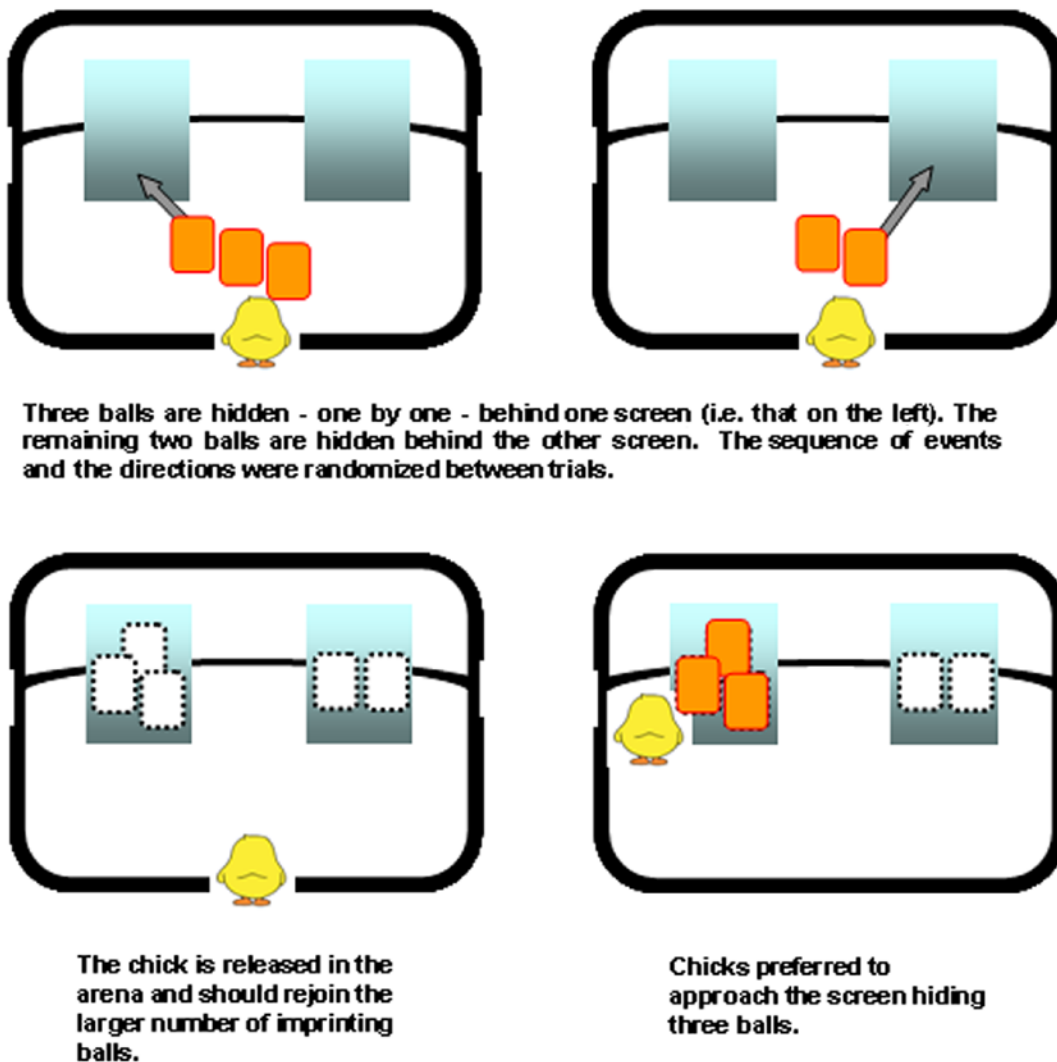
ber even when they were presented with new combinations of numbers. A similar paradigm was used to test squirrel monkeys (*Saimiri sciureus*) on problems where they were required to choose between pairs or triplets of Arabic numerals. Monkeys chose the larger sum and their performance could neither be attributed to choosing the largest single value nor to avoiding the single smallest value. (Olthof, Iden & Roberts, 1997). The famous gray parrot, Alex, was able to correctly respond to the question “How many x”? or “How many y”? and even to “How many x + y?” when the question was referring to a set of  $\leq 6$  objects (Pepperberg, 2006). Even pigeons (*Columba livia*) trained to discriminate between 2 visual symbols learned to choose the symbol corresponding to the larger reward, and performed successfully on summation tests. However, when the number of food elements was varied but the physical mass of reward was held constant, they chose the pair of symbols that summed to the larger total amount of reward and not to the larger number (Olthof & Roberts, 2000).

Using the methodology of violation of expectancy, Karen Wynn (1992) showed that 5-month-old human infants can solve some simple arithmetic operations. The idea was that if infants keep track of the numbers of toys they see being placed behind a screen, they should look longer at a screen that, when lowered, reveals an outcome that violates their expectations. For example, in the “(1 + 1) = 1 or 2” task, one object was placed on a stage, covered with a screen, and then another object was visibly introduced behind the screen. A further manipulation occurred out of sight of the subjects, where either another object was added, or one of the existing ones was removed. When the screen was removed, infants looked longer at the impossible outcomes of either one object or three objects, suggesting that they expected two objects. In the original studies, continuous variables, such as volume or surface area, were not controlled for; therefore, it is possible that infants might have attended to the number of dolls behind a screen or to the amount (volume, area) of the dolls’ physical characteristics. Wynn’s data were duplicated by other studies where continuous variables were partially controlled for. Simon, Hespos and Rochat (1995) adapted Wynn’s paradigm to include the use of ‘Elmo’ dolls in the initial phase of the trials, and then surreptitiously replaced ‘Elmo’ dolls with ‘Ernie’ dolls. The infants’ expectations were not violated by this identity switch. They looked longer at only the numerically unexpected outcome, without paying attention to the physical characteristics of the unexpected outcome’s objects. This indicates that, in some sense, infants represent the number of objects stripped of non-numerical features. Wynn’s paradigm was also adapted to test arithmetic reasoning in monkeys (*Macaca mulatta*). Subjects first viewed food items and then, a screen was raised to obscure the items on the stage. At this point, some items were visibly

added or removed from behind the screen. Finally, the screen was lowered to reveal the expected or unexpected number of objects and looking time was measured. Monkeys looked longer when the unexpected outcome was revealed for  $(1 + 1) = 1$  or  $2$ , and  $(2 - 1) = 1$  or  $2$  operations (Hauser, MacNeilage & Ware, 1996; Sulikowski & Hauser, 2001). Cotton-top tamarins (*Saguinus oedipus*), if presented with the  $(1 + 1)$  operation, also looked longer at the unexpected outcome of 3 or 1, compared to the expected outcome of 2 (Uller et al., 1999).

Using a paradigm inspired by the one devised by Wynn, it was demonstrated that five-day-old domestic chicks are able to perform addition and subtraction operations, to a total of 5 objects (Rugani et al., 2009). Chicks were reared, in their first 3 days of life, with five identical objects (imprinting balls). Thereafter, at test, each chick was confined to a holding box behind a transparent partition, from where it could see two identical opaque screens positioned within the arena. The chick saw two sets of elements, one made of three of

the five imprinting objects and the other made of two such objects; each set disappeared (either simultaneously, or one-by-one) behind one of the two screens. Immediately after the disappearance of both sets, the transparent partition was removed and the chick was left free to move around and search for its imprinting balls within the arena. Chicks spontaneously inspected the screen occluding the larger set (see Fig. 7). Results were confirmed under conditions controlling for continuous variables; the dimensions of each object in the set of three, and separately, two elements were computed so as to equate either the overall contour length or the overall area between the two sets. When chicks were presented with subsequent displacements of objects that appeared and disappeared behind the two screens, they successfully kept track of which screen eventually hid the larger number of objects, and they did so by performing subsequent addition or subtraction operations on the objects. In the final experiment, after the initial disappearance of two sets (e.g. 4 objects disappeared behind a screen and 1 behind the other),



*Figure 7. Illustrative representation of the number discrimination task which was preliminary to the arithmetic task.*

some of the objects were visibly transferred, one by one, from one screen to the other before the release of the chick in the arena. Even in this case, chicks spontaneously chose the screen hiding the larger number of elements, and did so irrespective of the directional cues provided by the initial and final displacements. Therefore, young and relatively inexperienced chicks could compute a series of subsequent additions or subtractions of elements that appeared and disappeared over a certain period of time, suggesting impressive and proto-arithmetic capacities with early availability.

Overall, chicks possess a broad range of numerical abilities, and in some cases, such abilities are already available from their first days of life. They are able to learn to discriminate between small sets characterised by different number of elements, as well as to identify a certain position solely on the basis of its ordinal position in a series of identical ones. Chicks are even able to discriminate between different numbers of imprinting objects, as well as demonstrating the ability to solve some simple arithmetic problems spontaneously. Even though a variety of mathematical abilities has been demonstrated in many animal species, no other animal model has thus far been used to show such abilities in very young and inexperienced animals. Their availability so early in the chicks' development would suggest that numerical competences are probably in place at birth. Moreover, evidence coming from comparative research, involving this species as well as many other species, has convincingly shown that number cognition, in its full variety of expressions, is widespread in the animal kingdom. Understanding numbers must have provided a precious tool to aid survival, shaped through natural selection to best suit the needs of the different species.

### *Geometry*

It is really challenging to demarcate the separation between space from number. Space is inextricably linked to number: distances are numerically expressed, numbers are spatially ordered, and the notion of measurement permeates both domains.

Therefore, spatial processing proceeds along metrically expressed distances and directions. Of course, places can be described in either topological or metric terms, and organisms are sensitive to both types of spatial information. Topology, in its specific meaning within geometry, expresses the possibility of defining a place (in Greek terms: *τόπος* place, and *λόγος* definition) devoid of all metric attributes, but comprising the concepts of order, enclosure, and adjacency. Topology was a key-concept in Piaget's theory of children's cognitive development of space. In the original formulation of this idea by Piaget and Inhelder (1956), it was proposed that children initially represent space only in

topological terms: spatial and geometric reasoning between 2 and 7 years of age would be operating on topological representations of spatial relations with no conception of metric, which would emerge instead only after the shift from an egocentric to an allocentric representation. We now know that this idea is incorrect, since it has been demonstrated that even young infants, early in development, represent and respond to metric information (for a review, see Newcombe & Huttenlocher, 2000). A representation that only encompasses topology would be fairly useless for locomotion (except in some very specific and human-made environment such as navigation on an underground railway system where in map representations, distances and directions are completely ignored and only the important information for travellers – order, enclosure, and adjacency – is preserved). It is really doubtful that animals' navigation is topological (but see Poucet, 1984) because notions of direction, distance, or size are used to move from and towards important places (see for examples Gallistel, 1990). In fact, even the most simple navigation is expressed by metric: to locate a goal signalled by the presence of a landmark while moving and approaching it from different perspectives, an animal has to perceive the distance and the direction of its own position with respect to the landmark, to remember the distance between the landmark and the goal as well as the intervening direction between those points and then, to implicitly calculate the distance and direction from its position to the goal. In this sense, there is an inherently metric concept that leads to topography. As a drawing of a place (in Greek terms: *τόπος*, place and *γράμμα*, drawing), it adds the idea of distances, directions, and elevations, which are all metric concepts that would be indefinable within a topological framework. It would be really impossible to imagine biological adapted organisms that would not use metric estimation for evaluating distances (e.g., before jumping from one branch to the next). Metric is an essential – and it could be argued “natural” – spatial cognitive tool. The literature on the subject is full of evidence that corroborates this idea: several species have been shown to be capable of determining the centre of an environment, or identifying a position on the basis of its relative location to other salient points (chicks: Tommasi, Vallortigara & Zanforlin, 1997; rats: Tommasi & Thinus-Blanc, 2004; pigeons: Gray, Spetch, Kelly & Nguyen, 2004). This is functionally equivalent to saying that animals are capable of reasoning within a geometrical framework.

When artificial walls conjoin and define a space, the layout composition of axes, surfaces, and incident joint points (geometric information) gives the organism the possibility to re-align itself with the surroundings after losing its bearing, and eventually to reorient by using integrated left-right directional sense (Cheng, 1986; Vallortigara, Zanforlin & Pasti, 1990; Hermer & Spelke, 1994; Cheng & Spetch, 1998).

Here, the metrical distribution of surfaces and egocentric left-right discrimination are fundamental. A common experimental situation makes use of a rectangular enclosure to test geometry in animals. By simply relying on metric (length of contiguous surfaces) and the sense of left and right, several vertebrate species appear to be able to reorient and relocate a target position (reviewed in Cheng & Newcombe, 2005). In such an environment, the symmetry is such that with a turn of 180°, another position is defined with the very same distribution of geometric information. All species which have been investigated appear to mistake the target location with this rotationally equivalent position (reviewed in Vallortigara, 2009a). Very recently, even ants (*Gigantiops destructor*) have been proven capable of reorienting in a rectangular enclosure, displaying the same rotational errors of vertebrate species (Wystrach & Beugnon, 2009). The authors of this last study explained their findings within a view-based matching strategy, arguing that ants would match a view-based representation, stored and captured while moving, to the current view without encoding any geometry. However, the fact that ants display choices for the correct position as well as for the diagonally opposite equivalent clearly calls for metric to be (implicitly) encoded in the snapshot (chicks have also been shown recently to use view-based geometric representations, Pecchia & Vallortigara, *in press*).

As noted above, when animals are trained to locate a position in a rectangular environment, they succeed in reorienting. Furthermore, when they are trained in the presence of salient visual features that would be sufficient for piloting towards the correct position (through a cue-guided orientation), they appear to spontaneously encode some geometry; when features are removed, they still reorient using the residual environmental geometry (e.g., chicks: Vallortigara, Zanforlin & Pasti, 1990; pigeons: Kelly, Spetch & Heth, 1998; fish: Sovrano, Bisazza & Vallortigara, 2003). That metrical information is “naturally special” is sustained also by data arising from the investigation of the role of slope information during reorientation. Ecologically, environments extend in the vertical as well as horizontal dimension, with bumps and hollows providing important kinaesthetic and vestibular signals for navigation. For this reason, along with visual cues, slopes can be retained as extremely salient information in reorientation. Pigeons have been trained to retrieve a reward in a particular position defined not only by metrical information, as in the original paradigm, but also by slope; when subjects were tested in a flat environment, they were shown to be able to distinguish the correct corner on the basis of the right association of lengths with left and right distinction (Nardi & Bingman, 2009), demonstrating once again the primacy of metric encoding.

The predominant use of the “geometry” of the environment seems ubiquitous among species, and it can be taken

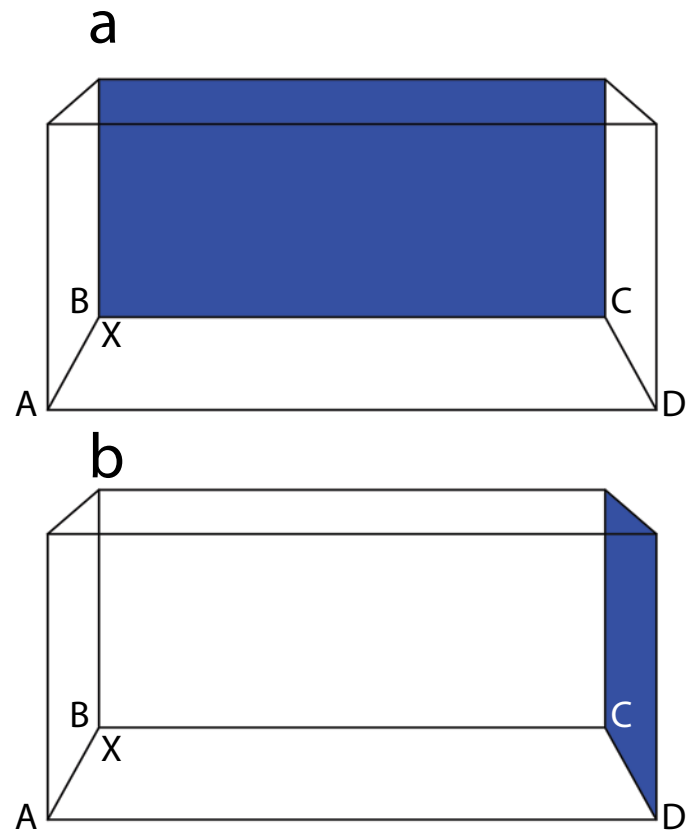
to be somewhat “predisposed to” in the brain. Thus, one could wonder whether some rudimentary concept of geometry would be already available at birth. The ability to reason about metric information, so rooted in navigation systems, could be a pre-existent hard-wired function utilised in dealing with space.

The idea of an innate system for the synthesis of metric information seems to fall on the thorny problem of the unsolvable nurture-nature controversy. The ability of vertebrate species tested in a rectangular enclosure to reorient with respect to the geometric shape of an environment (the geometric module task; Cheng, 1986) has been suggested to depend on the fact that the animals used in these studies were raised (and selected) in the laboratory and hence, exposed to artificial (geometric) environments (Gray, Bloomfield, Ferrey, Spetch & Sturdy, 2005). This hypothesis may be opportunely tested in animal models, for instance, by comparing the behaviour of wild-caught to laboratory-kept animals. Gray et al. (2005) trained mountain chickadees (*Poecile gambeli*) in a rectangular enclosure in the presence of a distinctive coloured wall. Wild-caught animals were found to be unable to spontaneously encode the geometry of the arena when the feature was near the goal (Gray, et al., 2005). This finding was interpreted as evidence that experience with geometric information may subsequently affect the source of information preferred for reorientation. However, more recent results have challenged this hypothesis. Black-capped chickadees (*Poecile atricapillus*), a closely-related family to the species tested by Gray and collaborators (2005), resorted to geometry in the geometric test, despite specific previous experience, or more accurately, a lack of it (Batty, Bloomfield, Spetch & Sturdy, 2009). The critical condition in Gray and collaborators’ work (training in the near-feature wall) was presented here with a slight change. In both experiments, training occurred in the presence of an entire wall painted blue; Gray et al. tested animals for reorientation with geometry only after removing the coloured wall, while Batty et al. tested subjects by placing short blue panels on one side of each corner, making all corners appear featurally identical. In the Batty et al.’s experiment, mountain chickadees [the species tested by Gray et al. (2005)], were equally able to use the geometry to reorient, and being wild-caught, this contradicts the experimental concerns of previous data. Both black-capped and mountain chickadees were shown to perform the test in the same way with regard to the ability to rely on geometry independent of subject experience; the only notable difference found was that mountain chickadees were less inclined to use geometry. However, such a pattern of results may be accounted for by invoking a species-specific difference in the primacy of geometry rather than an effect of early experience.

A viable alternative to cross-species comparisons may be

supplied by controlled-rearing studies: the idea in this type of paradigm is to provide animals with different rearing conditions in order to rigorously check the kind of geometric experience or ability they have. Fish (*Archocentrus nigrofasciatus*) have been raised in a circular (absence of geometry) or a rectangular (presence of geometry) tank, and then tested in a rectangular environment in different situations (Brown, Spetch & Hurd, 2007). Overall, there was no effect of rearing condition, with fish being able to spontaneously rely on geometry, both when reorientation occurred in a rectangular featureless environment, and when some features were provided within it. However, when geometric and featural cues were set in conflict, with a displacement of features from training to test in order to obtain incongruent information about the target position (see Fig. 8), fish raised in a circular tank showed less use of geometric information than fish raised in a rectangular tank. Thus, early experience during rearing did not affect the fishes' general ability to encode geometrical or featural information, though it influenced the relative weight of either one cue or other cue in adulthood. Moreover, it has been demonstrated that there are species-specific differences in the relative weight attributed to different sources of information (Sovrano, Vallortigara & Bisazza, 2002) and in different situations. For instance, the size of the experimental space determines which source of information is retained as the most reliable (reviewed in Chiandetti & Vallortigara, 2008a): salient visual characteristics are preferred for reorientation in larger spaces, whereas metric information is favoured in smaller spaces (Chiandetti, Regolin, Sovrano & Vallortigara, 2007). When chicks are trained in a rectangular environment with a blue wall and tested after a shift in the position of the coloured wall, they combined left-right sense with geometry much more in the small arena, and left-right sense with colour in the large arena (Sovrano & Vallortigara, 2006). In the same vein, the ecological demands associated with inhabiting different ecological niches may require different kinds of information to be taken into consideration (e.g., Shettleworth, 1998; Sovrano, Bisazza & Vallortigara, 2007; Brydges, Holmes & Braithwaite, 2008). Another example of this phenomenon comes in the form of demonstrated species-specific differences based on the type of disorienting procedure used. Usually, in order to disorient the subject, a viewer-rotation is applied: the aim being to disrupt the positional links between the subject itself and the external environment. An alternative strategy, that is formally equivalent in the disruption of the alignment between the subject and the surroundings, is the environment-rotation that occurs while the subject stays still as the experimenter limits the subject's possibility of noticing any external change. Children display a different pattern of choice while reorienting with these particular disorienting procedures (Lourenco & Huttenlocher, 2006). After a disorientation involving a viewer-movement procedure, they are able to find

the target hidden in every corner and remarkably, this occurs at the first attempt; after the environment-rotation, they systematically confuse the equivalent corners. In this last condition, only when given the possibility of repeated trials, infants may learn to reorient. Chicks, in contrast, either self- or environment-disoriented, equally appear to be able to reorient, resorting from the beginning to the same mechanism. A species-specific difference is likely to be at work here since precocial species, such as chicks, may be tuned to use the more stable external geometric features to reorient (Chiandetti & Vallortigara, 2010a), whereas human infants, being altricial, would need some sort of training to adopt the rule of observing the external layout in order to reorient.



**Figure 8.** The geometric module task in the blue-wall version: animals are trained to locate a goal in a particular corner (X) of the rectangular environment - as shown in a) - and are subsequently tested after a displacement of the coloured wall - as depicted in b); different choices are available depending on the combination of long-short and white-blue information with left-right sense.

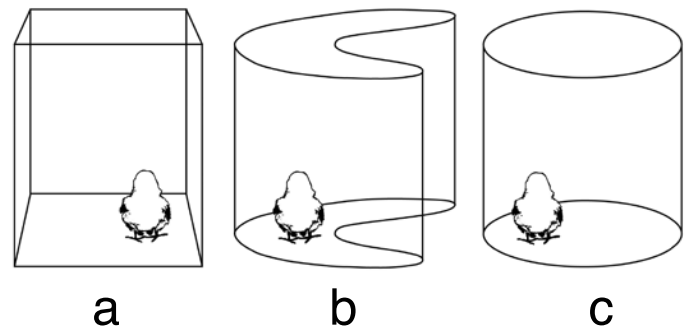
The choice of the most adequate system to address the issue of the innateness of metricity depends upon the contingent presence of different co-occurring characteristics, and the domestic chick (*Gallus gallus*) seems to represent an optimal compromise in its performance strategy. Belonging to precocial species, the chick goes through a rapid motor de-

velopment that allows it to display, immediately after hatching, a complete behavioural repertoire typical of its species. For these reasons, it is possible to test the chick in very sophisticated cognitive tasks that, together with the rigorous experimental control that can be exerted on sensorial experiences, both pre- and post-hatching, allows for an optimal investigation of the ontogenesis of cognitive functions (review in Vallortigara, 2009b). The chick can be tested following deprivation of certain sensory stimulation without incurring the problem of having an unnatural or inadequate development that would impede any reliable experimental inference. It is not by chance that it has been dubbed by Steven Rose “the God’s organism” for studies about the neurobiology of learning and memory (Rose, 2000). Furthermore, considering that several studies have been carried out on the chick’s ability to reorient in the first two weeks of life (review in Vallortigara, 2009a), this species may become a particularly well-suited model for investigating the “innateness” of cognitive functions, and in this specific case, the innateness of metric sense.

Naïve chicks, hatched under controlled conditions in darkness and devoid of any visual exposure or stimulation after hatching, were reared in isolation in either rectangular or circular cages (Fig. 9). Different from the study with fish previously discussed, each chick was singly exposed (or not exposed) to angled surfaces of different length and major axis of elongation for the first 3 days of life (Chiandetti & Vallortigara, 2008b). Chicks underwent training in a rectangular environment, and the testing conditions were chosen to investigate the possible effects of rearing experience. Circular- and rectangular-reared chicks proved to be identically able to reorient even in the very early phases of training, showing the same pattern of choice when tested in the presence of featural information, after its removal, and when using enclosures of different sizes. Most importantly, in conflict tests (Fig. 10) similar to those carried out with fish, rectangular-reared chicks showed no difference in utilising environmental geometry in comparison with circular-reared chicks (Chiandetti & Vallortigara, 2010). Thus, for chicks, it can be clearly asserted that no environmental triggering is necessary either for dealing with geometry or for attributing differential reliability to multiple sources of information. Although it can be argued that animals were unavoidably exposed to geometry while learning the task, chicks were shown to behave identically between early training and subsequent test conditions (Vallortigara, Sovrano & Chiandetti, 2009). In conclusion, rearing exposure does not interfere with animals’ ability to encode geometry.

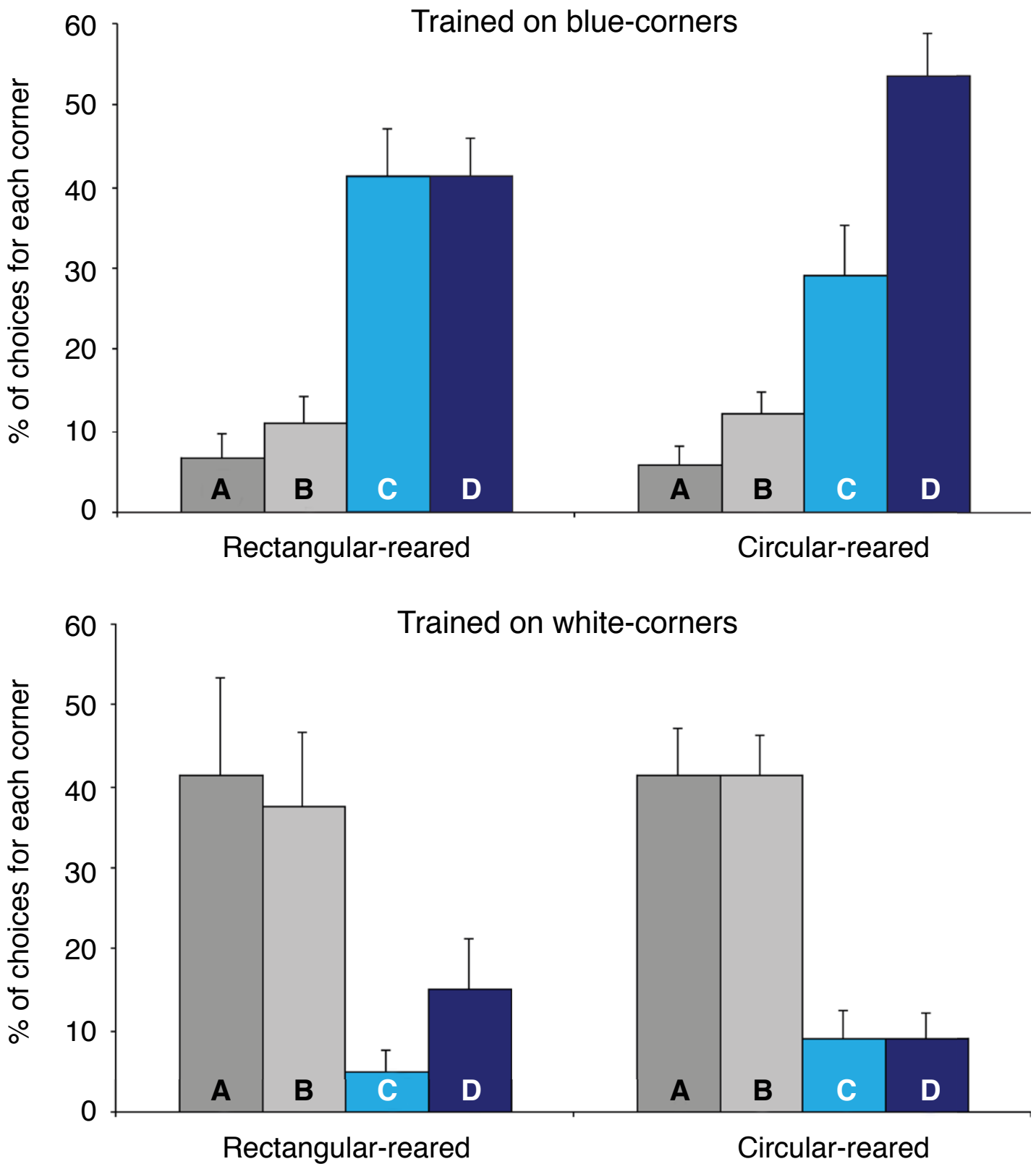
Studies concerning the human development of spatial abilities have shed light on the fact that tribal populations deal successfully with rudimentary geometric intuitions, even in the absence of particular training at school, specific maps

or other graphic symbols, or even a precise vocabulary for geometrical terms (Dehaene, Izard, Pica & Spelke, 2006).



**Figure 9.** An illustrative representation of the rearing condition used to raise single chicks: a) rectangular, b) c-shaped, and c) circular home-cages.

This seems to hold true for both infants and adults. It can be asserted that education largely determines our refinement in geometric skill: this is what makes us able to solve the most complex geometrical problems, and engage in symbolic, exact manipulation of geometric concepts and measurements. However, the relevant point here is, again, that basic metric and geometric reasoning emerges from a type of non-symbolic ability that is spread across species and developmental level: ontogenetically and phylogenetically preserved (Spelke & Kinzler, 2009) and not really experience-dependent (Newcombe & Uttal, 2006). Further support for this view derives from the fact that when such a core-knowledge (Spelke, 2000) system is not working in the proper way, the use of geometry alone may be severely compromised. This is the case in William’s syndrome, a genetic disorder in which patients exhibit impaired spatial abilities, with relatively preserved language abilities (Lakusta, Dessalegn & Landau 2010). The use of simple animal models that allow scientists to perform controlled-rearing studies may open the door to research linking specific genes (Osborne, 2006) and elderly-related spatial detriments to reorientation impairment (Fellini, Schachner & Morellini, 2006). Comparative research investigating the role of the hippocampus as a crucial area for representing space is long established (O’Keefe & Nadel, 1978); however, hippocampal involvement in the geometric module paradigm remains controversial (Burgess, 2008; Vargas, Bingman, Portavella & Lopez, 2006; Vargas, Petruso & Bingman, 2004; Bingman, Erichsen, Anderson, Good & Pearce, 2006). Different families of cells strictly related to specific spatial demands have been discovered in the parahippocampal circuit (place cells: O’Keefe & Dostrovsky, 1971; head direction cells: Taube, Muller & Ranck, 1990; grid cells: Fyhn, Molden, Witter, Moser & Moser, 2004), but we are still far from comprehending their exact role in coordinating navigation and orientation; future investigation will be required before resolving this issue. In fact, a



**Figure 10.** Results of blue-wall version of the geometric module conflict test in rectangular- and circular-reared chicks trained on corners B or C (all transformed in B - top) or A or D (all transformed in A - bottom): Mean values ( $\pm$  SEM) of the choices for each corner at test are shown.



particularly well-suited class of cells for the metric analysis of an environment has been recently added to the spatial neural circuit: the border cells (Solstad, Boccara, Kropff, Moser & Moser, 2008). These cells seem to encode obstacles and borders of the surroundings, thereby allowing for the definition of the perimeter of an environment. Whether or not they represent the firing expression of the capture of distances and directions from surfaces, border cells may be an instrumental step in deepening our understanding of spatial cognition of geometry. Their existence was first posited in computational models as boundary vector cells (Barry, Lever, Hayman, Hartley, Burton, O'Keefe, Jeffery & Burgess, 2006), which demonstrates the power of an integrated disciplinary approach that tackles the issue of spatial cognition from different perspectives. For instance, an associative model of geometric learning, developed to study reorientation in a geometric environment (Miller & Shettleworth, 2007), may reproduce the behavioural data obtained previously, while being independent of the potential size of the environment, by its ability to simply adjust the salience of either geometric or featural information (or both) resulting from the change in environmental size (Miller, 2009). This represents a further example of the diverse disciplines by which investigation of the putative geometric module can be approached from, each of which promise to yield unprecedented insights into the neural mechanisms of either spatial cognition processing *per se*, or its evolution.

### Conclusion

Apparently, rudimentary cognition of number and space requires very little experience and interaction with the environment, being available at birth (we believe) in newly-hatched chicks as well as in human newborns (see Spelke, 1998; Platt & Spelke, 2009). This of course does not subtract from the powerful effects that learning in a social, and for humans, a cultural environment, may exert on initial knowledge. Nonetheless, we believe that the type of core knowledge available to biological organisms at birth is, in a sense, the *necessary* knowledge – the *sine qua non* for learning and subsequent development of knowledge. Moreover, the basic similarity of core knowledge of number and space (not to mention object, agency, and cause, which were not discussed here) between humans and other animals should not make us oblivious to the fact that humans alone engage in a series of activities which have no obvious equivalents in other species – arts, religion, law, politics, architecture, cooking, theatre, etc. What is peculiar to human cognition that make us capable of all these activities is at present unclear, though it seems likely that language, and the cognitive abilities associated with it, should be crucial in some way (Spelke, 2003). In this vein, comparative studies on animals, in association with cognitive anthropological studies, may be enlightening. Pica et al. (2004) studied numerical cognition among

Mundurukú, an Amazonian tribe with a very small lexicon of number words. Although the Mundurukú lack words for numbers beyond 5, they are able to compare and add large approximate numbers that are far beyond their naming range. However, in exactly the same way as our chicks, they fail in arithmetic involving numbers larger than 4 or 5. These findings suggest a distinction between nonverbal systems that allow either number approximation or exact arithmetic up to a set limit of about 3-4 elements, and a language-based counting system for exact number and arithmetic, which has no upper limit. Mundurukú, of course, do possess (differently from our chicks) the cognitive capabilities to learn words for numbers beyond 4-5 and to learn a precise arithmetic for numbers beyond 4-5. Trying to explain how and why humans (and not chicks or other animals) developed these capacities would represent an important challenge for cognitive neuroscience.

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