Numerical abilities in non-humans: the perspective of comparative studies

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Abstract

The history of the study of animal numerical cognition is characterized by an unfortunate start: the Clever Hans story, which caused a widespread scepticism across the scientific community. In the last decades, a growing body of evidence demonstrates numerical skills in non-humans; nonetheless, studies have focused on adult subjects. Here, we discuss numerical comprehension in day-old chicks, a model species that allows an insight on the early development of cognitive abilities. Newborn chicks discriminate between diverse numbers, solve arithmetic calculations and use ordinal information. This animal model allowed us to also unveil another peculiar aspect of numbers: their association with space. This ordered representation of numbers in space is known in humans as the mental number line (MNL) and refers to an ascending mapping of numbers from left to right. Chicks associate smaller numbers with the left and larger numbers with the right space. The paradigm used to test spatial numerical association (SNA) in chicks has been proficiently used to also assess this association in human newborns, providing a suggestive example of animal research inspiring developmental studies. Overall findings from 1- or few-day-old chicks, virtually naïve or reared under strictly controlled conditions, constitute a strong case for the claim that numbers are a primitive and inherent information processed by animals.

Keywords: numerical cognition, numerical skills, number sense, numerical discrimination, ordinality, ordinal information, arithmetic, spatial numerical association, mental number line, domestic chick.

THE LINK BETWEEN HUMAN AND ANIMAL NUMERICAL COGNITION

Mathematics includes abstract and complex operations based on the use of specific symbols and rules, which only educated humans are able to master (Gallistel and Gelman 1992; Dehaene 1997; Carey 2004; Hauser and Spelke, 2004). In spite of this, all adult humans are still able to master "non-symbolic" numerical tasks. This can be tested under specific experimental conditions. Syllable repetition prevents language use while solving non-symbolic numerical tasks, which could consist of estimating which of the two arrays depicts a larger number of dots (Cordes et al. 2001). The extrapolation of numerical information from a visual or auditory stimulation, without any possible support from the symbolic system, is defined as a non-symbolic ability (Feigenson et al. 2004; Rugani et al. 2017). Non-symbolic processing is preserved in educated humans and can be compared to the performance of non-symbolic individuals such as preverbal infants and non-human animals (Cordes, et al. 2001; Cantlon and Brannon 2007).

Intriguingly, similarities have been found in the non-symbolic numerical system across species. When the difference between two numbers increases, the task becomes easier (*distance effect*). For example, it is easier to decide that an array depicting eight dots is larger than another depicting two dots, and it is more difficult to assess that an array of eight dots is larger than one depicting seven dots. Another effect, the *size effect*, describes an increase of performance as the magnitude decreases. This means that, keeping the distance constant between two numbers, it is easier to deal with smaller magnitudes rather than larger ones. For example, it is easier to discriminate between 2 vs. 3 dots than 80 vs. 81 dots. The distance and side effect have been described in

humans (Moyer and Landaeuer 1967) and non-human animals (Cantlon and Brannon 2007; Scarf 2011). As a result of combining the two effects, the ease of distinguishing two numbers depends on their ratio and not their absolute magnitudes. A numerical task becomes easier as the ratio between two numbers decreases. This is directly measured both as increased accuracy and as a reduction of response times. On the other side, the task becomes more difficult whenever the ratio increases: accuracy declines and response times increase (Gallistel and Gelman 1992). Since similar effects have been shown in a variety of animals, humans included, the presence of an ancient non-symbolic numerical system, shared across species and able to deal with numerical and quantity estimation, has been hypothesized (Cantlon and Brannon 2007). Even if the link between the non-symbolic and symbolic numerical system is still unclear, it seems that the first could serve as a building block onto which the abstract and purely symbolic knowledge may develop (Spelke 2000). In support of this view, it has been proven that non-symbolic number sense in 6-month-old infants can predict mathematical ability in first graders (Starr et al. 2013) and that training the non-symbolic number sense increases proficiency in mathematics (Park and Brannon 2013). Non-symbolic mathematics appears to be deeply connected to an ontogenetically precocious and evolutionarily ancient "number sense" (Butterworth 2005; Butterworth 2010; Dehaene 1997), which arises in the first days of life (Mussolin et al. 2012). Non-symbolic number sense would play a primary role in achieving abstract and symbolic mathematical thinking. A deeper knowledge of the non-symbolic number system could allow for early identification of children who may develop an impaired mathematical comprehension and thus pave the way for educational interventions to increase their number sense, even before formal schooling.

HISTORICAL BACKGROUND OF ANIMAL NUMERICAL ABILITIES

Animal numerical cognition attracted scientific interest in the twentieth century (Rilling 1993); nevertheless, a substantial growth in knowledge of comparative numerical abilities has occurred in the last three decades (Haun et al. 2010). The huge gap of interest in animal numerical studies was mainly caused by an unlucky beginning. In the early twentieth century, a horse, known as Clever Hans, was trained by his owner, Wilhelm von Osten, to solve several calculations, which comprised additions, subtractions, divisions and square roots. In a typical examination, Hans stood in front of its owner, or another interviewer, who showed him a mathematical operation. Hans answered by tapping his hoof on the ground the exact number of times. Initially the horse convinced a large majority of scientists of his arithmetic skills. A few years later, it turned out that Hans responded correctly only if he could see his interviewer while performing the task, so his answers were wrong when the interviewer was hidden. Moreover, if the interviewer knew a wrong answer for a specific mathematical question and Hans could observe his face while responding, he tapped his hoof on the ground the wrong number of times (Pfungst 1907). Hans's intelligence was not mathematical but social: even if he did not master mathematical reasoning, he was amazingly skilled at detecting and interpreting minimal behavioural gestures, subconsciously produced by his interviewer, upon reaching the correct number of taps. Such new evidence revolutionized Hans' reputation, and he was no longer considered an intelligent animal. At the same time, an impressive scepticism towards animal numerical skills pervaded the scientific community,

which was no longer predisposed to believe in animals' numerical capabilities. Scientists aligned with the Aristotelian thought, which postulated that logic, represented in its higher form to numerical comprehension, was strictly intertwined with language. Thus, "logos" was considered a prerogative of human minds (Houndé and Tzourio-Mazoyer 2003). Language and symbols were the prerequisites for cognition, and all creatures unable to grasp them, principally infants and animals, were considered incapable of any numerical comprehension. For several decades, only very few researchers were still persuaded that animals could possess basic but adaptive numerical understandings. They performed rigorous and elegant tests, avoiding face-to-face contacts, and controlled for several non-numerical cues onto which animals could base their responses.

The German zoologist Otto Koehler, around 1941, was the first to study numerical abilities in various bird species. He showed that a pigeon, *Columba livia*, could learn to select a set containing a certain number of grains to receive a food reward. For example, pigeons could chose the set containing four grains when it was paired with another set comprising either a smaller or larger number of grains. A jackdaw, *Corvus monedula*, succeeded in identifying a given number in a matching-to-sample task. The bird was initially presented with a card depicting a "sample" number of dots. Then the bird faced two dishes each covered by a lid. One lid illustrated the sample number of dots, and the other illustrated a different number. The jackdaw correctly matched the sample number with the corresponding one on the lid; in other words, the bird selected the lid depicting the number shown on the card, especially when the dimensions of the dots depicted on the card differed from those illustrated on the lid. Koehler also investigated action enumeration in pigeons and budgerigars, *Melopsittacus undulatus*. The birds learned to

peck only a pre-established number of times; for example, if they were trained to peck only four times, they ate only four seeds when presented with 10. From his experiments, Koehler concluded that the birds had mastered simple abilities such as number discrimination and action enumeration. Moreover, he noted that various species exhibited incredible similarities in the upper numbers they could deal with: they mastered the tasks only when evaluations of about five or six items were required (Koehler 1943). In all his studies, Koehler accurately avoided providing animals with any cue that may have triggered the infamous Clever Hans effect. To avoid direct contact between birds and the experimenter, he hid himself behind a panel and out of the birds' sight. To prevent the experimenter from unconsciously biasing the birds' behaviour, he used mechanical devices to dispense rewards. Moreover, these were filmed to provide objective records of the experiments. However, despite his experimental rigor, Koehler's evidence, as well as other researchers', was criticized for its lack of controls on quantitative cues, among others: odour, brightness, size, colour, shape, texture and similar (Wesley 1961). It is worth mentioning that the numerical skills investigated by Koehler were much easier than the mathematical calculations presented to Clever Hans. The numerical magnitudes were smaller, and the required numerical computations were simpler; likewise, there was a discrimination of various numbers of dots in Koehler's experiments vs. symbolic arithmetic operation in Hans' tasks. Koehler's tasks involved more ecologically relevant numerical estimations, which can improve animals' fitness in their natural environments. Different from Hans' symbolic calculations, Koehler's findings fall into the non-symbolic category. Nevertheless, scepticism towards animal numerical competences persisted, and the general belief was that although animals could learn to deal with numerical problems,

they would only use numbers as a last-resort strategy. Thus, animals were considered able to process numerical cues only when all other non-numerical cues such as odour, brightness, size, colour, shape, texture and similar were prevent. Moreover, animals were considered incapable of a spontaneous use of numbers—instead, this was possible only after extensive trainings (Davis and Pérusse 1988).

In the last three decades, growing evidence has proven various kinds of non-symbolic numerical competences in non-human species. Interestingly, some of these can also be shown in the absence of specific numerical training. Lions use sounds to decide whether to attack a potential troop of rivals. Hearing recorded sounds of potential rivals during controlled trials, lions decided to attack only if their own troop was double their rivals. Such behaviour requires initial numerical estimation of their own and external troops and then a numerical discrimination between these to evaluate if the attack could be a convenient strategy (McComb et al. 1994). Breeding and nesting behaviours are other ecological contexts in which animals use numerical cues. American coots, *Fulica americana*, compute the number of their own eggs, neglecting the parasitic ones, to reach an optimal number of their nested eggs. This implies a certain kind of enumeration: they could "count" the number of their own eggs, separating them from the parasitic ones (Lyon 2003).

Also, foraging has been used to assess animal numerical comprehension and to compare across species. Facing diverse food options, animals choose the one ensuring the highest energetic gain (Krebs 1974). This spontaneous behaviour has been exploited to explore numerical discrimination in the absence of any numerical trainings. When facing two foraging alternatives, each containing the same food but in differing quantities (e.g., one

comprised of two and the other three bites of food), diverse species chose the bigger one (see Rugani 2017 for a review and the proto-numerical and numerical discrimination of this chapter for a detailed description). These outcomes suggested that various species share the capability of discriminating two "numerousnesses." We specifically refer to these sets not as "numbers" but as numerousness, since the number of food pieces co-varies with several quantitative cues in these studies. Whenever a rigorous control for the possible use of quantity information was not performed, animals could equally use numerical and quantitative cues. Thus, it is appropriate to consider these abilities as proto-numerical. Nevertheless, their scientific relevance is high, since they proved that animals, in various contexts, spontaneously use proto-numerical cues to optimize their fitness in the absence of any numerical training.

On the basis of these and other evidence, it has been proposed that numerousness estimation is one of the core knowledge systems that might have developed, under specific evolutionary pressures, to better interact with the natural environment. A current challenge in numerical cognition consists of disambiguating the relative role and importance of numerical versus quantitative cues and the way they interact in making numerical estimation. It is worth noticing that these are two sides of the same coin. The assessment of abstract numerical abilities requires controlling for all non-numerical variables that can affect performance. On the flip side, the inner essence of non-symbolic numbers is intrinsically related to their physical dimensions. A deeper understanding of this aspect requires reflection on what a non-symbolic number is, namely the extraction of numerical information from a perceptual stimulus (Feigenson et al. 2004; Rugani et al. 2017). Being that perceptual entities, mainly objects and sounds, exist in the physical

world in a specific time and space, they come together with volume, mass, surface area and other quantitative measures. From this perspective, non-symbolic numbers can be considered as a portion of a general system that estimates quantities, whether continuous, such as area and volume, or discrete, such as numbers (Gallistel 2011).

A large majority of researches have been conducted on altricial animals, which are almost impossible to test early in life, limiting the comprehension of developmental aspects of numerical cognition. Nevertheless, a peculiar animal model, the domestic chick, *Gallus gallus,* permits to disentangle "nature" from "nurture". Such a precocious bird has shown a variety of numerical cognitions that animals can master from their first days of life, which we will describe in the rest of this chapter.

PROTO-NUMERICAL AND NUMERICAL DISCRIMINATION

A very basic numerical ability displayed by animals is the capacity to compare two sets and judge their relative difference in magnitude—that is, which is "more" and which is "less" (Vallortigara et al. 2010). Such relative numerical discrimination (Davis and Pèrusse 1988) leads animals to make a choice in favour (usually) of the larger amount (of resources). In the laboratory, this ability is assessed by placing the animal in front of a choice among two stimuli featuring different numerousness of relevant objects (e.g., prey, conspecifics, and food items). In this paradigm, non-numerical (quantitative) variables correlate with numerical cues, and choice of the larger number is confounded with choice of the larger amount. An interesting solution to control for non-numerical cues

has been that of presenting to the animals sets in which some of the elements were not fully visible, as they were partly hidden by occluders. This way the elements could still be perceived in full (through the perceptual process of amodal completion), but it was possible to manipulate and equalize at once the physical amount of their surface. For example, in the 2 vs. 1 comparison, one object was fully visible on one side, whereas on the other side of the choice area, where the two objects should be presented, these were masked so that only half of each could actually be seen. Chicks, like humans and many other species, have the ability to complete the missing parts of objects when these are hidden behind other objects (occluders). As a result, the object that is only partly physically visible is still perceived as a whole object. This perceptual mechanism, deemed "amodal completion," was first described in our own species (Grossberg and Mingolla 1985; Kanizsa 1979; Michotte 1963; Michotte et al. 1964): a circle with a missing sector, or even a missing half, is still perceived as a full circle, and we can effortlessly recognize the letters in a word/sentence even after they have been masked. The same mechanism is also well attested in non-human species (review in Vallortigara, 2004), including the (very young) domestic chicken (Regolin and Vallortigara 1995; Lea et al. 1996; Regolin et al. 2004). By exploiting amodal completion to control for non-numerical cues, it was possible to demonstrate that day-old chicks discriminate sets of objects by relying on non-quantitative cues to solve the task (Rugani et al. 2008). In this study, young chicks were trained to peck onto a small panel to retrieve some food reinforcement. Chicks had to discriminate between 1 vs. 2 or betweem 2 vs. 3 elements, and the elements were identical shapes depicted onto two different panels. For each comparison (e.g., 1 vs. 2), one group of chicks was reinforced for selecting one element and ignoring the two

elements' stimulus, and the other half of chicks was only reinforced when pecking onto the panel depicting two elements. During training, the birds could make use of numerical "as well as" quantitative (overall area or perimeter) cues to discriminate among the two stimuli. Thereafter, in a number of tests, chicks had to choose among the two stimuli experienced during training, but this time the quantitative cues were controlled. For example, when the elements presented during the test were displaced in various positions on the panel, this control for spatial distribution did not affect the chicks' ability to select the stimulus that had been reinforced during training. In spite of the fact that most trials were unrewarded during the tests, this result was clear cut (i.e., they were "in extinction"). A key control consisted of equalizing at once both the contour length and the overall surface that could be seen in each of the two compared stimuli. In the stimulus depicting the smaller number of elements, these were entirely visible, whereas some of them could only be seen partially in the larger set of elements (but were visually and amodally completed by the observer). Basically, the exceeding area or perimeter that should have been present in the larger stimulus corresponded exactly to its occluded, hence missing, parts. For example, in the 1 vs. 2 comparison, the occluder hid exactly half of each of the two dots of the stimulus representing 2 (the same occlude was also present in the other stimulus, but it did not overlap the single dot). Even in this case, chicks successfully identified the stimulus that had been reinforced during training (S+) in the 1 vs. 2 and 2 vs. 3 comparisons. However, with a larger set of comparisons (3 vs. 4 or 4 vs. 6), chicks failed to acquire the discrimination during training, in spite of the available possibility to use both numerical and non-numerical cues at once (Rugani et al. 2008). Therefore, the ability of very young domestic chicks is attested to spontaneously encode the numerical

cue during training (at least for sets up to three elements), in spite of the fact that quantitative cues were also available and could by themselves suffice to solve the discrimination learning task. In fact, chicks could still perform the discrimination successfully when, during the test, all other non-numerical cues were controlled. This means that numerical cues are a natural and significant cue for animals: they are rather easily encoded and effectively used, even early in life, by the young chicks and possibly by other species.

In this first set of experiments, a brief training of about 1 hour was required to unveil chicks' abilities to process numerical cues. However, would the young chicks be able to encode numbers truly spontaneously (i.e., in the absence of any training at all)? Animals do discriminate between various amounts of relevant objects, such as food patches, and usually prefer to go for the larger quantity. Several studies showed that animals prefer the more abundant source of food or energy according to what was predicted by an optimal foraging strategy (Krebs 1974). For example, salamanders prefer 2 to 1 and 3 to 2 mosquitos (Uller et al. 2003). Frogs prefer 2 to 1, 3 to 2, 6 to 3 and 8 to 4 prey (Stancher et al. 2015). Similar evidence was reported for birds (robins discriminating 6 vs. 8, 8 vs. 64, and 16 vs. 64, Garland et al. 2012) and for a range of mammals: coyotes 2 vs. 5, 1 vs. 3, and 1 vs. 4 (Baker et al. 2011); dogs 1 vs. 4, 1 vs. 3, 2 vs. 4, 3 vs. 5, 1 vs. 2, 2 vs. 3, 3 vs. 4, 4 vs. 5, and 5 vs. 6 (Ward and Smuts 2007); and elephants 4 vs. 1, 3 vs. 1, 4 vs. 2, 5 vs. 3, 2 vs. 1, 3 vs. 2, 4 vs. 3, 5 vs. 4, and 6 vs. 5 (Irie et al. 2009). Some studies also assessed discrimination in non-human apes (orang-utans, with comparisons of sets in a range from 1 to 6, Call, 2000) and human infants (1 vs. 2 and 2 vs. 3, Feigenson et al. 2002). Recently, numerical discrimination abilities have also been described in a

variety of invertebrate species (Bortot et al. 2021), confirming how these abilities likely confer an evolutionary advantage to all living species.

In this kind of study, differences in number co-varied with differences in non-numerical (also deemed "continuous" or "quantitative") cues, such as volume, surface area, contour length, occupancy, density and so on. This renders it impossible to prove that animals can process numerical information by itself. Some studies have attempted to run controls for continuous cues, but in all cases, at least some of the non-numerical variables remained available to the subjects, offering an alternative explanation for the results. For example, animals may have relied on the perimeter when the total surface had been equated, and they may have relied on the surface when the overall perimeter had been equated.

In an attempt to find a method to test the truly spontaneous abilities of animals in the absence of any extensive or supervised formal training and to convincingly control for the non-numerical variables at the same time, we designed a new paradigm for newly hatched domestic chicks, exploiting the phenomenon of filial imprinting. Chicks in fact remember the fine features of the relevant social objects they have been reared together with soon after hatching (a few hours of exposure usually suffice to create a strong social bond and memory for those objects). These objects in the natural condition are real conspecifics (the mother hen or the siblings), but, in the laboratory, chicks can socially attach (imprint onto) artificial objects (e.g., 3D objects with surface, volume etc. can be effectively controlled experimentally). We reared newly hatched chicks for 2 days with various numbers of objects and then tested them on Day 3 of their life for their spontaneous choice among the familiar and novel numerousness of those same objects.

Chicks could freely choose which set to approach during the 6 minutes of the test. Chicks showed a preference not for the familiar but rather for the larger numerosity in the two sets presented. This means that chicks that had familiarized with the smaller set during the test chose the larger set. Interestingly, the choice was not based on the absolute numerosity of the test stimuli; rather, choice was based on the numerosity of the familiar object, which emerged when the number of novel objects was introduced so that the numerosity of the two possible alternative sets during the test was equalized (1 novel object was added to the group of 3 and 3 novel objects to the group of 1). The novel objects were identical in size and shape and only differed slightly for their colour shade. Chicks obviously discriminated the familiar objects and chose the larger group of those objects.

In this type of experiment, discrimination could of course be based either on numerical or non-numerical cues because the overall surface area and volume co-varied with the set size. To disentangle this issue, objects of varying size were used so that in each comparison (1 vs. 4, 1 vs. 6 and 1 vs. 3), either volume or surface area was equalized (it was unfortunately impossible to control for all continuous variables at once within the same condition). This also means that the size of the one object presented in the smaller stimulus was always larger than the size of the objects presented in the larger sets used as comparisons. In all these tests, chicks were shown to discriminate, but they approached the single larger object, possibly because this provided some sort of supernatural stimulus, resulting as more interesting or attractive than the other sets.

An alternative strategy to control for non-numerical cues (and avoid the presence of larger objects in one set) is to use sets made up of all heterogeneous objects (each

differing from all others in terms of colour, shape and size). The first group of chicks was familiarized with two objects and another group with three objects. During the test, objects employed were completely different from those used during rearing in terms of their colour, shape and size. The overall surface and volume of the two groups presented during the test were also equalized. Under these conditions, both groups of chicks preferred the set comprising the familiar numerosity, and this also means that chicks reared with the smaller set (i.e., two objects) approached the set containing two objects being tested and not the set with the larger numerosity. We concluded that no other cues are available in the case and that the chicks do rely on numbers to discriminate between two sets (and choose the familiar numerosity).

To summarize, chicks familiarized with a given number of objects then

- approached the larger set with objects all identical in size,

- approached the set with the single larger object, and

- approached the familiar number of objects when the use of non-numerical cues had been prevented through the use of all heterogeneous objects both at rearing and during the test.

In chicks, the information onto which their choice is based (number vs. quantity) seems to be induced by the rearing and testing conditions. This is not surprising. In fact, it echoes that which was reported in the developmental psychology literature. Infants in some studies were shown to discriminate between arrays of numbers when the overall perimeter is controlled (Xu et al. 2005; Libertus and Brannon 2010; Starr and Brannon 2015), but in other studies they showed higher sensitivity to the non-numerical, rather

than numerical, variables (e.g., perimeter and area, Clearfield and Mix, 1999, 2001; Feigenson, Carey and Spelke, 2002).

Based on all of the mentioned studies, it appears that young chicks can discriminate sets of elements on the basis of numerical information but only up to 3-4 elements. On the basis of such evidence, it was originally hypothesized that young chicks only possessed a small number system, in spite of the fact that discrimination of large numbers had not been investigated in this species.

Two separate systems have been put forward to explain non-symbolic number cognition:

- A system capable of representing small numbers, deemed Object File System (OFS), and

- A system to represent large numerical magnitudes, deemed Analogue Magnitude System (AMS).

The first system, the OFS, seems to be an attentional-driven mechanism to represent and process the objects we perceive as individual files (a new file is created for each object) within working memory. The original purpose of this system may serve to represent objects, not enumerate them. However, since there is a 1:1 correspondence between objects and files, the system also implicitly leads to representing the number of objects "individuated" in the visual scene. The signature of the OFS is its capacity: a maximum of (usually) ≤ 4 files/objects can be simultaneously held in working memory (Trick and Pylyshyn 1994). Processing of numerousness larger than 4 therefore needs to be supported by the second system: the AMS. This second system does not appear to have an upper limit, but it operates according to Weber's function: as the ratio between

the two numbers to be discriminated increases, response time decreases and accuracy increases (Gallistel and Gelman 1992).

In spite of this clear-cut separation between the two systems, later evidence supported the idea that the AMS would actually also process numbers in the range of the small magnitudes (Brannon and Terrace 1998; Cantlon and Brannon 2007; Pepperberg 2012; Rugani et al. 2013). However, other studies maintained that small magnitudes are selectively processed by the OFS (Feigenson et al. 2002; Feigenson and Carey 2005). The central issue in this debate is what kind of information prompts processing via either system: whether it is numerosity *per se* (OFS with less than 4 objects and AMS with numbers larger than 4) or another kind of contextual information.

This second possibility was first elaborated by Hyde and Spelke (2011), who highlighted the role of attentional processes: attention to the whole group of elements (triggered, for example, by simultaneous presentation of the sets) would activate AMS processing; and attention focused onto individual objects (prompted by sequential/one-by-one presentation of the elements) would activate OFS processing.

The time was come to challenge the limits of number processing of day-old chicks. Their ability to succeed in the small and large numerical range by employing the AMS was assessed (Rugani et al. 2014). Comparisons used during the test involved just small numbers (less than 3) or just large numbers (larger than 4), or a direct comparison between one small and one large numerousness. This last test was devised to investigate whether a processing gap existed when bridging across the two domains was required. Chicks had learned to associate food to numbers during spontaneous foraging and feeding (no supervised training required). During their regular rearing, for about 2 days,

chicks learned that food was always located behind salient environmental stimuli (vertical panels depicting a specific numerosity). The panel hiding food depicted a given number of red squares. Other similar panels were there in the cage and depicted a different number of identical elements, which was not associated with food (nothing could be found behind such panels). The position of all panels was changed regularly during rearing for each chick so that food could not be located through association with a spatial location, and the only relevant cue to the food was the number of red elements on the panel. On Day 3 of life, a 6-minute free-choice test was run, during which chicks could freely choose to approach a panel depicting the previously reinforced numerosity or a second panel depicting the familiar but never reinforced numerosity. Chicks discriminated and approached the number associated with food in all circumstances: when both numbers confronted were small (2 vs. 3) or large (6 vs. 9, 8 vs. 12, and 8 vs. 14) and even when one number was small and one was large (2 vs. 8). Chicks' performance was confirmed also when the non-numerical variables (overall area and perimeter) had been controlled. The results of this study (Rugani et al. 2014) offer additional support to the fact that animals can spontaneously encode numerical information and that at least some species can do so remarkably early in life. As already mentioned, no supervised training was required in this paradigm. The association among food and the landmark cue represented by the number of elements pictured on the vertical panel took place naturally during autonomous foraging behaviour. Moreover, the fact that chicks were smoothly responding also in the 2 vs. 8 comparison (1 small vs. 1 large numerousness) seems to favour the hypothesis that the same system, the AMS, operates along the whole numerical continuum. This would be coherent with previous evidence on adult humans engaged in

non-symbolic numerical tasks (Cordes et al. 2001), children (de Hevia and Spelke 2009), infants (Cordes and Brannon 2009) and non-human species such as gorilla (Hanus and Call 2007); macaque monkey (Cantlon and Brannon 2007; Brannon and Terrace 1998; Jordan and Brannon 2006; Beran 2007); baboon and squirrel monkey (Smith et al. 2003); capuchin monkey (Judge et al. 2005); dog (Ward and Smuts 2007); coyote (Baker et al. 2011); parrot (Pepperberg 2012); and robin (Garland et al. 2012).

In Rugani et al. (2014), why did the baby chicks appear to be capable of processing numerosities larger than 3? We hypothesized that a key element relied on the fact that, in previous studies, the pecking response had been actively shaped (during conditioning procedures) onto a specific stimulus. The birds, in order to coordinate the pecking response (which is some sort of grasping action) towards a specific target, likely needed to focus their attention on the features of that stimulus. However, when chicks are not formally trained to peck for food, but learn spontaneously to associate the food to a nearby environmental feature, they tend to perceive the stimulus more globally. Therefore, pecking onto the stimulus, required in some paradigms, triggered processing by the OFS, and as a result the chicks missed the discrimination of sets larger than four elements. To prompt processing of the whole collection of elements, in subsequent experiments, we located the stimuli more distantly and made them clearly visible by presenting the sets onto vertical panels. Previous studies, in fact, used this paradigm to encourage configural processing—for example, when testing the discrimination between possible and impossible objects (Regolin et al. 2010) or chicks' sensitivity to the Ebbinghaus illusions, also known as Titchener circles (Rosa-Salva et al. 2013).

In all, the findings presented are in line with the idea that attentional mechanisms can differentially activate the processing systems (Hyde and Spelke 2011). Whenever attention is focused on the individual elements, processing would be supported by the OFS; whenever attention is directed to the overall set, processing would be undertaken by the AMS.

ARITHMETIC ABILITIES

Besides representing numbers, adult humans can also manipulate numerical representations to perform arithmetic calculations. For a long time this was considered a distinctive capacity of our own species, which had to be culturally framed and was only possible following a long and specific education (Gallistel and Gelman, 1992; Dehaene 1997; Hauser and Spelke 2004; Carey 2004).

In recent years, scientists started to wonder whether arithmetic could be performed at a non-symbolic level. This issue has been tackled by studying non-human species and young infants. The aim of those studies (reviewed in Gallistel 1990; Dehaene 1997; Spelke and Dehaene, 1999; Brannon and Roitman 2003) was to ascertain whether non-symbolic (animals) or pre-symbolic (infants) subjects can perform simple calculations such as adding/subtracting elements from a numerical representation to obtain a new mathematically correct representation.

Not surprisingly, the first demonstrations that animals can add two or more numerousnesses came from studies that looked at our closest relatives: apes and other

primates. Chimpanzees, for example, were able to choose the more advantageous (larger) combination of two smaller amounts. Each of the four subsets was constituted by a number of chocolates from 0 to 4, and to solve the task, the chimps had to sum the chocolates of two specific subsets and compare the result with the sum of the chocolates in the other two subsets. Subjects solved the task even when the correct (i.e., the overall larger) combination did not include the single larger subset as in 3+0 vs. 2+2, ruling out the possibility that animals were using a simpler strategy (Rumbaugh et al. 1988).

Another chimpanzee, named Sheba, confirmed these results in a different paradigm. To obtain the food she had previously seen during three different hidings (each concealing from 1 to 4 orange pieces), Sheba was required to choose the Arabic number corresponding to the summation of the three sets. Sheba solved the task even when food items were replaced with symbols (Arabic numbers).

Thereafter, two macaque monkeys were trained (Washburn and Savage-Rumbaugh 1991) to respond to symbols representing numbers. Animals were shown two combinations of two numbers and were allowed to eat an equivalent number of food pieces as the combination they selected. Monkeys chose the larger overall number even when confronted with novel combinations. Similar evidence was obtained from squirrel monkeys (Olthof et al. 1997).

Other paradigms involved training capuchin monkeys to associate tokens to numbers of food items. Capuchins were able to select the higher number among two combinations of tokens (Addessi et al. 2008).

Some bird species also displayed remarkable mathematical skills. Pigeons learned to choose the combination of two visual symbols leading to the larger reward. However, they

chose on the basis of the larger total amount of food and not on the basis of the larger number of food items (Olthof and Roberts 2000). The grey parrot Alex, who was famously able to understand and respond to many vocal requests, could answer questions such as "How many blue objects plus yellow objects?" with sets of up to six objects. Alex extracted the two relevant numerical values from a complex scene containing other differently coloured objects and correctly combined the two representations (Pepperberg 2006).

Besides the abovementioned studies on adult individuals of non-human species, convincing evidence of non-symbolic arithmetic came from developmental studies. A seminal paper (Wynn 1992) showed that 5-month-old infants mastered simple summations (1+1) and subtractions (2-1). For example, infants who saw two toys, one at a time, being positioned behind a single panel, expected to see exactly two objects once the panel was removed; in fact, infants stared significantly longer at the unexpected outcomes (which overtly violated their expectations) of either one or three objects. This result demonstrated that infants master the simple addition 1+1, expecting exactly 2 as the result. Similarly, after having seen two toys being placed behind the panel, and then one of them being removed (i.e., the 2-1 operation), infants looked longer at the incorrect outcome of two toys found behind the panel rather than at the correct outcome (one toy). This first study did not control for non-numerical variables, such as volume or surface area; therefore, infants might have based their responses on the numerical result and on other continuous cues that co-varied with the number. An interesting control was employed in a later study employing the same paradigm (Simon et al. 1995). In this study, the identity of the toys was manipulated so that the characters found after the panel was removed were novel, even if they corresponded in number to the arithmetical calculation.

This study therefore assessed whether infants react to unexpected object identity or to numerically unexpected events. Infants showed surprise (i.e., they looked longer) only at the numerically unexpected outcome, whereas the object identity switch did not violate their expectations. This interestingly indicates that subjects represented the numerical information stripped from other non-numerical features.

The same paradigm was used to investigate arithmetic abilities in non-humans, showing that monkey species looked longer at arithmetically incorrect outcomes (e.g., 1+1=1 or 1+1=3, or 2-1=2). This led to the conclusion that monkeys were expecting exactly that 1+1=2 and 2-1=1 (Hauser et al. 1996; Uller et al. 1999; Sulkowski and Hauser 2001).

Summation of items over time (i.e., tracking and adding items one by one) was specifically demonstrated in chimpanzees and macaques (Beran and Beran, 2004; Beran 2007), as well as in 12-month-old human infants. Infants chose the larger set in 1vs.1+1, 1vs.1+1+1 and 1+1vs.1+1+1. Remarkably, they chose at random in the comparison of a small vs. a large number (1vs.1+1+1+1; Feigenson et al. 2002). Although non-numerical variables were not controlled in the studies just mentioned, it was demonstrated that infants as young as 9 months old can add and subtract larger numbers (5+5=10 rather than =5; and 10-5=5 rather than =10) and that their performance is maintained even when the overall area and perimeter are carefully controlled by employing computer-presented stimuli (McCrink and Wynn 2004). Computer-presented stimuli were also successfully employed to control for non-numerical variables in adult monkeys. They were able to select, among two arrays of dots equalized for quantitative cues, the one array which corresponded to the numerical summation of two sets previously seen (Cantlon and Brannon 2007).

Non-symbolic arithmetical abilities assessed in non-human adult individuals could not be directly compared with developmental studies in human infants. The only exception to the study of non-human adults was the work on domestic chicks.

Arithmetic in baby chicks was studied by exploiting chicks' tendency to approach the larger group of siblings or, in laboratory conditions, familiar objects (Rugani et al. 2010a). The chicks had been reared, upon hatching, one per cage, together with five identical objects, and the test took place on Day 3. During the test, each chick was presented with a series of events featuring their five familiar objects moving around one by one and hiding in either of the two identical locations (two vertical panels). If two objects went behind one panel and three behind the other one, chicks preferred to approach the panel hiding three objects in an attempt to re-join the larger number of familiar objects, even in the case where the objects' size had been manipulated so as to control for the overall area or overall perimeter of the two groups. Interestingly, when the overall perimeter was equalized, an inverse correlation was apparent between the number and overall area: the larger area belonging to the smaller number set. As a result, chicks' choice for the larger set could not be based on the overall area or perimeter.

These results showed for the first time that even extremely young organisms could combine a representation of multiple elements individually experienced. Day-old chicks created and updated two distinct representations, corresponding, respectively, to the number of objects present behind each of the two panels, and then compared these representations to find the larger group (Rugani et al. 2009).

Chicks could also perform simple addition or subtraction. To this purpose, they were presented with two sequences of events, such as (4-1) vs. (1+1) (or, in other conditions,

5-2 vs. 0+2, 4-2 vs. 1+2, or 5-3 vs. 0+3). The result of the first series of object displacements (in bold) could be reversed by the second series of displacements so that the panel hiding the larger number of elements may or may not be the one that hid the smaller number at the end of the first part of the events. In all conditions at the end of all events, one panel hid two objects and the other hid three objects. Other possible cues were also controlled, such as the panel where the first or last object was seen to hide, the left-right position of either displacement, and where each final numerosity was to be found. The only tenable hypothesis to explain chicks' behaviour is that the subjects created and updated two mathematically correct representations of the object in each location (Rugani et al. 2009).

Notably, representations of small numerousness would not suffice in this study because some of the comparisons involved numerousness higher than 4. These findings seem therefore to support that the AMS also processes small numbers or that the two systems may be integrated (Cordes and Brannon 2009; Brannon and Terrace 1998; Cantlon and Brannon 2007; Judge et al. 2005; Cordes et al. 2001; Pepperberg 2012).

This would be in contrast with evidence already reported above from infants who could choose the larger set in a series of comparisons involving one, two and three elements, but they chose at random when confronted with 1 vs. 4 (retrieving 1 biscuit from one box vs. 4 biscuits from a second box). This surprising result has been considered as evidence of a distinct system dedicated to represent small numbers (Feigenson et al. 2002). Since infants are capable of adding a large number (5+5, McCrink and Wynn 2004, see above), for infants, it generally seems that two separate and independent systems to represent numbers are there: one for values up to 4 and the other for values > 4. Nevertheless, on

this topic, scientific literature has reported contrasting evidence. On the one hand, some data suggest that small numbers can be treated solely via OFS (Starkey and Cooper 1980; Hauser et al. 2000; Barner et al. 2008).

Domestic chicks offered to this purpose a good model for the comparative analysis of the 1vs.1+1+1+1 dilemma. Would baby chicks also fail in the 1 vs. 4 discrimination? It seems this was not the case. Chicks that presented with sequential events involving social objects or food objects succeeded in locating the larger set of the 1 vs. 4 comparison. Chicks in the same study also succeeded in the 2 vs. 4 discrimination, even when the non-numerical cues had been controlled. Overall, the evidence obtained from domestic chicks in this task supports a continuity in the processing of small and large numbers (Rugani et al. 2014). However, when presented with large numbers (sequential presentation of objects and final choice with 5 vs. 10 or 6 vs. 9), chicks were only successful when all objects had the same size and not whenever the non-numerical cues had been controlled for (Rugani et al. 2011a).

It was concluded that with more difficult tasks, animals need to rely on a convergence of multiple cues. This would be in line with that reported for human infants employing a different paradigm (Suanda et al. 2008) and other vertebrates (Stancher et al. 2015), thus introducing the need to investigate the coordinated role of numerical and quantitative cues in non-symbolic numerical processing.

SPATIAL NUMERICAL ASSOCIATION

One of the most outstanding characteristics of number processing, which is apparently shared between humans and animals, is their tendency to associate numbers onto space. A peculiar characteristic of numbers is their intrinsic association with space: educated humans typically represent numbers along a left-right continuum, where small numbers are associated with their left and large numbers with their right space: the mental number line (MNL) (Galton 1880; Restle 1970; Dehaene et al. 1993). Traditionally, the MNL has been considered a by-product of culture and education, mainly writing and reading habits (Zebian 2005; Shaki and Fischer 2008; Shaki et al. 2009). More recently, an association between numbers and space has been reported in preverbal infants and non-human animals (for a review see Rugani and de Hevia 2017; Vallortigara 2018). The increasing quantity of evidence of a spatial numerical association (SNA), in nonverbal subjects, opens a scientific debate on its possible evolutionarily ancient and shared origin. Below, we will discuss the SNA and specify how it was first reported in animal species, specifically domestic chicks. We will describe two central sources of evidence of the SNA, each based on peculiar numerical competences: ordinality and magnitude processing.

2. NON-HUMAN ANIMALS ASSOCIATE NUMBERS WITH SPACE

2.1. Ordinality

Ordinality refers to the capability to identify a target element in a series of identical elements on the basis of its ordinal position. In a seminal study aimed at testing if young animals could use ordinal information, an unexpected bias in counting directionality has been surprisingly found, which paved the way for a new perspective according to which non-human animals associate numbers and space. To be more precise, these studies

indicated that young and inexperienced birds are perhaps also predisposed to "count from left to right."

Domestic chicks learned to select an item based on its ordinal position within a series of identical items (Rugani et al. 2007). During training, 5-day-old chicks gradually learned that a food reinforcement was always located in the container that occupied a target ordinal position (e.g., the fourth one), in a series of 10 identical and equidistant containers, which were sagittally displayed with respect to the chicks' starting position. The ordinal location of the target varied for various groups of chicks: a group learned to find the food in the third, another in the fourth and one more in the sixth container. Chicks took a few hours to learn such spatial/ordinal strategies to locate the food. During the test, they faced the same displacement of containers, and each group selected above chance only their target container. Nevertheless, given that the location of the containers was always identical, this evidence could not yet demonstrate that chicks processed serial/ordinal cues. In fact, chicks could have relied on spatial cues rather than ordinal ones. A variety of other usable cues were available. For example, chicks could have merely memorized either the distance separating the target container from the first container or from their starting position. Thus, a series of control experiments were fundamental to excluding these and other similar alternative explanations. One of these controls was designed to determine the distance of the target from the starting position, as well as to determine if its specific spatial location was indispensable to solving this task. Birds were initially trained to select the fourth container in a series of 10 sagittally oriented ones (Figure Rugani.1a). During training, chicks always experienced the target in the same location, and, with the distance between the containers being constant, the

target was always at the same distance from the starting point. During testing, the series was maintained as identical, but it was rotated by 90 degrees, becoming fronto-parallel oriented with respect to the birds' starting position (Figure Rugani.1b). In this test displacement, chicks actually had two possible correct choices: the fourth left or the fourth right containers. Despite both options being in the same way consistent with the reinforcement contingencies learned during training, chicks significantly chose the fourth left element, neglecting the right one. This was the first proof of a preferential left-to-right "counting" in non-human animals (Rugani et al. 2007). Such a left asymmetry is now considered a robust phenomenon, and it has been replicated in subsequent studies. Young domestic chicks and adult Clark's nutcrackers, once trained to select either the fourth or sixth containers in a series of identical and equidistant containers, sagillaty oriented with respect to the bird's starting point, showed the same left asymmetry in the fronto-parallel test (Rugani et al. 2010b).

Figure Rugani.1 about here

Figure Rugani.1 a) Overhead view of the experimental apparatus and of the series of items, sagittaly displaced with respect to the bird's starting position. During training and the test, the items looked identical; here for illustrative purposes, the target item, the fourth one, has been filled. b) The series of items as they were displaced during the fronto-parallel test. The filled circles show the two correct items.

Although intriguing, this left bias could be interpreted in several ways. A lateral preference for targets located on the left side could reflect a phenomenon similar to the human "pseudoneglect" (Albert, 1973). The pseudoneglect describes that humans preferentially allocate their attention on one side of the extracorporeal space, which typically is their left one. In a free foraging task, similar behavioural asymmetries had been reported in chicks and pigeons. Chicks and pigeons faced a symmetrical grid of cells, each containing a grain of food, and were allowed to feed themselves for a limited amount of time. Both species ate the left grains while neglecting the right ones, showing a non-learned asymmetrical behaviour in a simple spatial task (Diekamp et al. 2005). Similarly, chicks show a left bias also in a line-bisection task. Birds were presented with a series of three aligned beads and learned to peck the central one for a food reward. When they faced larger numbers of beads during the test (i.e., 5, 7 or 9), they continued to peck the central one; nonetheless, their errors were mainly concentrated on their left side (Regolin 2006). It has been proposed that all of these biases in spatial tasks as the researchers mentioned, could reflect a right-hemispheric specialization for processing spatial information. In chicks, in fact, a right-hemispheric specialization for spatial processing has been well documented (Tommasi and Vallortigara 2001; Tommasi et al. 2003; Regolin et al. 2005a; Rashid and Andrew 1989; review in Vallortigara et al. 2010; Rugani et al. 2015c). In the ordinal experiments described above, the distance between the items (hereafter inter-item distance) was kept constant; thus, the overall length of the series was also identical during the training and test. This way, chicks could rely on ordinal/numerical information as well as various kinds of metric cues. Between the other

metric cues available in this version of the task, the one that more likely played a crucial role in determining the left bias was the distance of the target from the beginning of the series (in identifying the fourth containers – fourth left, fourth right – chicks anchor their counting to the fist container; see Rugani et al. 2007 for a broader discussion). This regular displacement could have prompted the birds to preferentially rely on spatial cues to resolve the task, eliciting a processing with the right hemisphere. The tendency to count from left to right can be considered a consequence of an allocation of attention to the left space.

To test the influence of the metric cues in determining the left bias, a new study was designed. In various experiments, chicks were prevented from using metric cues during training or during the test. In one experiment, chicks were trained to select the fourth container in a sagittal series of 10 identical containers, which were kept in a fixed location (Figure Rugani.2a). At the fronto-parallel test, the inter-element distances were either increased for one group of animals or reduced for a second group. In both cases, the new inter-item distances were calculated to conflict between the spatial and ordinal cues; more precisely, whenever the distance was increased, the third container was in the location occupied during training by the fourth container. When the distance was reduced, the fifth container was in the location previously occupied by the fourth one (Figure Rugani.2b and 2c). This test allowed the disentanglement of the use of the spatial *versus* numerical information.

Fig Rugani.2 about here

Figure Rugani.2 Overhead view of the experimental apparatus and of the items' displacements with respect to the bird's starting position. In all training and testing trials, the items looked alike. Here, to better illustrate the procedure, the target items are filled. a) the displacement of the series during training. The distance (d) of the target item from the closest end of the series, which was identical in each training trial. b) The items' displacement in the fronto-parallel series in which the inter-item distances were increased. c) The items' displacement in the fronto-parallel series in which the inter-item distances were reduced.

In these tests, chicks pecked at the fourth element and almost neglected those located at the correct distance from the beginning of the series. However, they did not show any left bias, choosing the left and right targets almost with the same frequency (Rugani et al. 2011b). This indicates that even if both cues were accessible and identically reliable during training, chicks used the numerical rather than the spatial one. The availability of the spatial cue seemed therefore to play a crucial role in the determination of the left-to-right counting direction. This hypothesis was also corroborated in another experiment. In this case, during training, the inter-element distances were changed (i.e., either reduced or increased). This way, the numerical/ordinal cue was reliable, whereas the spatial one was not, thus forcing chicks to rely only on numerical information. Also, during the test, the inter-element distances were changed at each trial. Birds properly selected the target element. However, they did not display any spatial asymmetry (Rugani et al. 2011b). This demonstrates that chicks can solve an ordinal task by relying solely on numerical/ordinal cues, supporting the idea that the integrated processing of numerical and spatial

information is indispensable to show a preferential counting from left to right. An alternative explanation could be that this lack of left bias may be caused by a general novelty effect that can be triggered by some kind of modification of the test series with respect to the training one.

Another experiment was designed to investigate this possibility. Chicks learned to find the reward in a sagittally oriented series of green containers, always maintained at static distances. During the fronto-parallel test, the metric features of the series remained identical, but the containers were red. In this case, chicks correctly selected the target item (the fourth one), and, interestingly enough, they showed a left bias (Rugani et al. 2011b). This shed light on the fact that it is not a generic novelty effect that affects the left bias—instead, it was clearer that a specific spatial change was the relevant aspect that could disrupt the tendency to count from left to right.

Overall, these findings suggested that, while both cerebral hemispheres equally process numerical/ordinal information, spatial ones should be represented in the right hemisphere. To disentangle the engagement of each hemisphere in dealing with the ordinal task and determining the leftward bias, the monocular occlusion technique was used. This consists of restricting the visual input to one eye by placing a patch over it. Since the avian brain has no corpus callosum and displays a virtually complete decussation of fibres at the optic chiasm (Csillag and Montagnese 2005), by restricting the visual input to a single eye, it is possible to determine the functioning of the contralateral hemisphere.

The chicks were binocularly trained to peck at the fourth container in a series of 10 identical and static containers, which were sagittaly aligned with respect to the chick in its starting position. The fronto-parallel test was then conducted in three vision conditions:

binocular, right monocular and left monocular. In the right monocular condition, the chicks identified as correct the fourth container from the right. In both the left monocular condition and the binocular condition, the chicks solely selected the fourth left container. These results indicated that ordinal information is bilaterally represented in the cerebral hemispheres. Whenever both hemispheres process this information, the extra-activation of the right hemisphere takes place. This leads to the allocation of attention to the left hemispace and thus produces a bias to ''count'' selectively from left to right (Rugani et al. 2016). For fostering a better understanding of the involvement of the hemispheres in dealing with spatial *versus* numerical-ordinal cues, the monocular occlusion technique was used in a fronto-parallel test, characterized by a conflict between number and space. Again, the chicks learned to peck at the fourth container in a sagittal series of identical containers, maintained in static positions, to allow the birds to rely on both spatial and numerical cues. In the fronto-parallel tests, the inter-item distance was increased so that the third container was at the distance where the fourth one was training, thus compelling the chicks to use either a spatial cue or an ordinal cue. When seeing binocularly, the chicks selected the fourth left and right containers. In both monocular tests, the chicks equally chose the third and fourth containers selectively in their clear spaces, indicating that both hemispheres can process spatial as well as ordinal information. However, the hemispheres also interact to integrate both types of information (Rugani and Regolin 2020). This perhaps allows us to speculate on a model—which assumes the two hemispheres' differential encoding, processing and integration of numerical and spatial information—to determine a specific SNA's left-to-right orientation.

The domestic chick and Clark's nutcrackers (birds showing left-to-right-oriented counting strategies), together with the avian species characterized by laterally placed eyes, are recognized as unique models for investigating the effect of cerebral lateralization on behavioural functions. The neural substrates of these species are characterized by a complete decussation of visual fibres at the optic chiasm (Weidner et al. 1985; Ocklenburg and Güntürkün 2012), as well as by a lack of any substantial inter-hemispheric connection tracts analogous to the mammalian corpus callosum (even though other smaller tracts allow for inter-hemispheric communication, e.g., Hardy et al. 1984; Robert and Cunéond 1969; Theiss et al. 2003; Zeier and Karten 1973). As a consequence, in these species, behavioural lateralization is particularly noticeable (e.g., Daisley et al. 2009; Rogers et al. 2013), as information from each eye (and thus each spatial side) is mainly elaborated by the contralateral hemisphere (Deng and Rogers 1998). Such peculiarities of the avian brain anatomy could determine the left asymmetry observed in the fronto-parallel tests, making it difficult to generalize findings for chicks to humans (Drucker and Brannon 2014). Nevertheless, rhesus macaques, which are characterized by a less asymmetrical brain, also showed a similar leftward lateralization in ordinal processing (Drucker and Brannon 2014). Rhesus monkeys learned to select a target dot (the fourth from the bottom) in a series of identical vertically aligned dots. As in the fronto-parallel test used with the chicks, the monkeys faced a series rotated by 90 degrees during their test. They selected the fourth dot from the left and not the fourth one from the right. Such a left bias was also maintained when the whole series was displaced on the screen in such a way that the fourth left dot was actually to their right (Drucker and

Brannon 2014). This indicates that left bias is not related to a tendency to respond to left stimuli but rather to count from left to right.

A similar facilitation to order numerosities according to a left-to-right orientation was demonstrated in chimpanzees while they were performing a different task (Adachi 2014). Chimpanzees were trained to touch Arabic numerals (in the interval of 1-9) in ascending order. During training, the numerals appeared in random locations; thus, no specific relation existed between each numeral and a spatial position. During the test, when they faced only the smallest (1) and the largest numeral (9) presented side by side, with one on the left and one on the right side of the screen, their speed was faster if 1 was on the left and 9 was on the right than when the spatial positions of the numerals were shifted (9 on the left and 1 on the right). This indicates that chimpanzees mapped the learned sequence in a left-to-right-oriented sequence (Adachi 2014). These data on chimpanzees are parallel to those reported for monkeys in Drucker and Brannon (2014). Together, they suggest that the asymmetrical processing of ordinal information is not a prerogative of the highly lateralized bird brain. Instead, it is a more general phenomenon that potentially reflects the mechanism shared between distant species. The numerical biases reported for different animal species challenge the primary role of education in determining the left-to-right-oriented association between numbers and space. They also emphasize the non-linguistic nature of this association.

2.2 Number-space association in magnitude-estimation tasks

Associations between numbers and space have been reported in domestic chicks not only in ordinal tasks but also in tasks requiring magnitude estimations. A limitation of the

ordinal task that we described above is related to the constant left bias. Nevertheless, the human MNL is not only characterized by a tendency to count from left to right but also is reported to be in an association of larger numbers with the right space. The first study to show an association of a large numerical magnitude with the right space in animals, in the absence of any specific numerical training, is the work by Rugani, Rosa-Salva and Regolin (2014). To their aim, these authors exploited chicks' tendency to re-join a bigger group of artificial social companions (Regolin et al. 2005a; Regolin et al. 2005b; Rugani et al. 2009; Rugani et al. 2010a; 2011a, Rugani et al. 2013; Fontanari et al. 2011; 2014). All of these studies share a rearing procedure: chicks were exposed since their very first hours of life to a set of objects—for example, three identical red squares. After this type of brief exposure, birds will consider these objects to be their social companions and will be motivated to stay close to them. If they see two objects disappear behind a panel (P1) and only one object disappear behind another panel (P2), the birds will circumnavigate the panel, P1, to re-join the larger group of social companions (Rugani et al. 2009). This experimental procedure has demonstrated that day-old birds can master simple arithmetic in a range of small numerousness (Rugani et al. 2009) and in a range of large numerousness (Rugani et al. 2011).

In the study by Rugani, Rosa-Salva and Regolin (2014), chicks were exposed for a few days to a set of identical objects. During the test, the birds faced two identical panels, one on their left and one on their right. They also observed some objects disappear behind the left panel, whereas other objects disappeared behind the right panel. For example, five objects disappeared behind the left panel and 10 behind the right panel. Then, the birds could freely approach either panel. The crucial manipulation involved the location

where the larger group disappeared, which was randomized and balanced between trials: for half of the time, the larger group was hidden behind the left panel, and during the other half of the time, it was behind the right panel. The study's rationale was that if larger numbers were preferentially associated with the right space, the chicks should perform better when the larger group was hidden in the right space. This is actually what happened: the chicks found the larger group of artificial social companions more easily when these were on the right side. Such a right advantage in remembering where the larger group was has been consistently reported in two numerical conditions (5 vs. 10 and 6 vs. 9). Nevertheless, an alternative explanation is still possible: the intrinsic motivation to join the larger group of social companions (a category that the left hemisphere usually processes) could have biased chicks' behaviours towards the right space. With the goal of ruling out this alternative, in a control experiment, the same number of artificial companions (2 vs. 2) was hidden behind the two panels. Interestingly enough, in this case, the chicks did not show a directional bias, thus excluding any intrinsic motivational effect related to the social nature of the stimuli (Rugani et al. 2014). The innovative aspect of the results of the latter study was to clarify the presence of a right spatial bias in responding to a large numerical magnitude. Nevertheless, so far, all of the studies have been able to solely demonstrate either an association of small numbers with the left or an association of bigger numbers with the right. Thus, the need still existed for a paradigm that would allow for the simultaneous demonstration of both small and large numerical associations, respectively, with the left and right spaces—an aspect that was intrinsically impossible in the design previously described.

Moreover, the human MNL is characterized by another essential feature: relativity. In our species, the direction of the association of a given number with the left or with the right space is determined by the relation of a number with a reference number, which functions as an anchor value onto which all of the following numbers will be compared. As a consequence, the same number can be associated with the left space or the right space, with the anchor value simply being changed. For example, if our anchor value is 4, the number 6 will be on the right, but if the anchor value is 8, the number 6 will be associated with the left. In other words, the human MNL—and likewise, the number magnitude—is not absolute but rather relative (Dehaene 2011; Rugani and Rosa-Salva, in press).

To summarize, for clearly proving that other species show a number-space association that is analogous to the human MNL, an experimental paradigm should simultaneously assess two main aspects: i) a magnitude-related bidirectional bias: a left bias for small numbers and a right bias for large ones, and ii) the SNA "relativity": changing the anchor value, with the bias switching sides. To the best of our knowledge, so far, only a few studies in nonverbal subjects have met these criteria.

In a seminal study, 3-day-old chicks showed left responses when dealing with relatively smaller numerical magnitudes and right responses when dealing with relatively bigger numbers (Rugani et al. 2015a). The same numerical magnitude was associated with the left or with the right side depending on whether the anchor value was, respectively bigger or smaller, thus providing the first direct evidence on the SNA's relativity in animals (Rugani et al. 2015a). Considering its scientific relevance, we will describe this study in further detail.

During the study, chicks were initially familiarized with a certain number, which became the anchor value. To this aim, the chicks underwent training during which they faced a panel, which was always located in the centre of the apparatus, exactly in front of the chicks' starting position. The panel always depicted the same numerical magnitude (five or 20 squares for different groups of animals), but this was presented in different forms: the spatial organization of the squares was unique for each stimulus. In each trial, the panel hid a piece of food that the birds could reach by circumnavigating the panel. Once the chicks learned to promptly circumnavigate the central panel to reach the reward, they underwent two tests: a small number test and a large number test. In both tests, the chicks faced two identical panels located in two new locations: one on the chicks' left and one on the chicks' right. The panels depicted the same number of squares. In the small number test, the panels represented a number smaller than the one experienced during training, and in the large number test, the number was bigger than that experienced at training. For example, the chicks that experienced five squares during training (Figure Rugani.3a) were presented with two squares (Figure Rugani.3b) in the small number test and with eight squares in the large number test (Figure Rugani.3c). Meanwhile, the chicks that experienced 20 squares during training (Figure Rugani.4a) were presented with eight squares in the small number test (Figure Rugani.4b) and with 32 squares in the large number test (Figure Rugani.4c). In this way, the same number of 8 corresponded to a large numerical magnitude for the first group of chicks and to a small one for the second group. As a consequence, if chicks do associate numerical magnitudes with space, the birds that had been formerly trained with five squares should have preferentially associated the exact same stimulus depicting eight squares with the right side. Likewise,

the birds trained with 20 squares should have done this with the left side, thus allowing the relativity of the SNA to be tested.

Figure Rugani.3 and Figure Rugani.4 about here

Figure Rugani.3 a) Schematic illustration of the training setup: only one panel, depicting five items, was in the centre of the experimental apparatus, in front of the chicks' starting position. b) Schematic illustration of the setup used for the small number test (2 vs. 2). Two panels were in novel positions, one on the left and one on the right side of the experimental apparatus. Chicks preferentially approached the left one. c) The setup for the large number test (8 vs. 8). As in the small number test, the two identical panels were on the left and right sides. Chicks preferentially approached the right panel.

Figure Rugani.4 a) Schematic illustration of the training setup. The chicks from their starting point faced a single central panel depicting 20 elements. b) Schematic illustration of the setup for the small number test (8 vs. 8). Between the two identical lateral panels, chicks approached the left one. c) The setup for the large number test (32 vs. 32). Between the two identical lateral panels, the chicks approached the left one.

To explore the occurrence of such number-space associations, Rugani et al. (2015a) recorded whether birds circumnavigated the left or right panels in their attempt to gain the reward that was never present during the test. The predictions were that during the small number test, the chicks would preferentially look for food behind the left panel, whereas during the large number test, they would prefer to direct their searches behind the right

panel. Consistently with these predictions, the chicks trained with five squares circumnavigated the left panel when the stimuli depicted two squares (Figure Rugani.3b), and they circumnavigated the right panel when the stimuli depicted eight squares (Figure Rugani.3c). Remarkably, chicks trained with 20 squares preferentially circumnavigated the left panel when the stimuli represented eight squares (Figure Rugani.4b), and they circumnavigated the right panel when both stimuli represented 32 squares (Figure Rugani.4c).

Additional control experiments showed that such asymmetrical behaviour stemmed from numerical information and not other continuous physical cues, such as the overall perimeter, area or density, which co-varied with the number whenever the dimensions of the squares were identical in the stimuli's set. For example, if we imagine that the squares in the stimuli were identical in size, the overall area and perimeter of the three-square stimuli would be smaller than those of the five-square stimuli. For the purpose of controlling for these two variables (overall area and perimeter), three control experiments were designed. In one experiment, the stimuli, instead of representing identical red squares, consisted of heterogeneous elements, each characterized by a peculiar shape, colour and size. In the second experiment, the elements were always red squares in each numerical stimulus. Nevertheless, their sizes varied in the stimuli so that they covered an identical overall red area. Finally, in the third experiment, the stimuli depicted red squares of different sizes. These stimuli were characterized by an identical overall perimeter, density (mean distance between the elements) and occupancy (overall surface covered by each square's array). By maintaining an identical overall perimeter, in this last experiment, the stimuli also presented an inverse correlation between the overall area

covered by the red squares and the number of squares; in other words, the total red area was smaller in the stimuli depicting eight squares than in a stimulus depicting two squares. See Rugani et al. (2018) for the mathematical formula that describes the variation of the overall area when the perimeter is constant. Consistently, in all of these control experiments, the chicks circumnavigated the left panel when facing smaller numbers and the right panel when facing larger numbers. This demonstrated that the asymmetrical number-space association was based on the numerical information and not on other continuous physical variables, such as the overall perimeter, area, colour, light, occupancy and density (Rugani et al. 2015a; 2015b; 2015c).

This evidence has literally unleashed a firestorm of controversy about the origin of the association between number and space among members of the scientific community. Psychologists, biologists, linguists and cognitive scientists are divided into two opposite counterparties. On one side are those who believe that early SNA in chicks is unrelated to the human phenomenon and can simply be explained by individual bias or by preference for novelty. On the opposite side are those welcoming the new evidence, mainly coming from newborn humans and non-human species. In support of the latter hypothesis, in a more recent study, 3-day-old chicks were trained to circumnavigate a central panel that depicted five identical red squares. Then, the chicks underwent three tests: a small number test, in which the two stimuli on the lateral panels depicted two squares; a large number test, in which the two stimuli depicted eight squares; and a control test, in which the stimuli depicted five squares—the number they experienced during training. The left-sided choice (LC) was then computed on each chick's performance in each test. Interestingly, the LC was explained by the number of squares

and not by an individual lateral bias in the spatial task. Moreover, we found a linear trend with three points of reference (LC2vs.2 > LC5vs.5 > LC8vs.8), which provided for the first time convincing evidence in domestic chicks that the numerical magnitude of the stimuli and not individual bias drives the asymmetrical displacement of numbers into space. Overall, these studies concluded that chicks do associate small numbers with their left and larger ones with their right spaces. This evidence, together with that reported in human newborns, indicate that side biases similar to the ones observed in humans and driven by the MNL can be observed in illiterate and almost naïve subjects. This impacts the investigation on the origin of the SNA towards its neural representation (Brugger 2015; Vallortigara, 2018; Rugani and Rosa-Salva, in press).

Using a similar paradigm, the SNA also has been shown in gorillas and orangutans (Gazes et al. 2017). Although present in most apes, the SNA was not equally oriented onto space in all individuals. Various animals showed either left-to-right- or right-to-left-oriented SNA. Distinctive experiences—for instance, the interactions with caregivers, rather than differences linked to species or handedness—have been identified as the central factors that might regulate the SNA's orientation at an individual level (Gazes et al. 2017, but see Beran et al. 2019 for information on the failure of the replication of the SNA in rhesus monkeys). No SNA evidence has been found in a cleaner fish species (Triki and Bshary 2018). This may indicate the presence of specific evolutionary factors in developing the SNA in only some vertebrate lineages. For example, the mechanisms underlying the spatial asymmetries in numerical processing perhaps evolved with amniotes, i.e., after the last common ancestor of the fish and reptiles. Nevertheless, any conclusions regarding this cannot be based on the idea of solitary evidence, especially

considering the huge taxonomic and neuroanatomical diversity reported between fish species (Triki and Bshary 2018; Rugani and Rosa-Salva, in press). Follow-up studies on the SNA in various fish species may be dedicated to disentangling these open issues.

More successful and intriguing findings were obtained in two studies that replicated Rugani and colleagues' paradigm in newborns (di Giorgio et al. 2019, de Hevia et al. 2018). These studies exploring human newborns under minimal to no exposure to adults' scanning biases clearly assessed how precocious the association between number and space is in humans. Newborns were first habituated to a numerical value—for example, a group of 12 items—that was presented in two identical copies, one on their left and one on their right on a monitor. Immediately after the habituation, they were presented with two identical stimuli—again, one on the left and one on the right. These could represent either a smaller (four) or a larger (36) number of items. When they faced a smaller number, they looked longer at the left copy of the stimulus, but when facing a larger number, they looked longer at the right one. Moreover, the SNA was not absolute but rather relative: the same number "12" was associated with the left when newborns previously experienced a larger number—for example, "36"—but it was associated with the right side when they were habituated to a smaller number, like "4" (di Giorgio et al. 2019). These findings demonstrate that a disposition to associate numbers on a left-to-right-oriented MNL exists independently of cultural factors and with little, if any, early exposure to directional cues. This supports the hypothesis that it is perhaps biologically predisposed in the brain.

CONCLUSIONS

Some very early attempts to ascertain the presence of mathematical understanding in non-humans were a clamorous failure (Pfungst 1907). This was probably linked to the pervasive anthropocentric perspective of those times and approaches. It was also responsible for the subsequent trail of scepticism and mistrust towards the possibility of objectively investigating cognitive functions in non-humans. Animals were thereafter regarded as being capable of acquiring only number-response-conditioned associations following intensive training. The key feature is that animals were considered to be incapable of responding to purely numerical information (Davis and Pérusse 1988). According to this view, only adult humans could grasp the numbers. To them, these symbols were meaningful, and no calculations would be possible in the absence of language or other symbolic representations.

This position is, of course, no longer tenable, as a huge number of demonstrations have been accumulating during the past few decades concerning the fact that many species can master numerical tasks. In some instances, animals successfully deal with purely numerical information. Notably, animals can encode a number even when other, non-numerical cues are also available. This means that number processing is not employed as a last-resort strategy—for example, only when the non-numerical cues are unavailable (Berkay et al. 2016; Kawai and Matsuzawa 2000; Biro and Matsuzawa 2001; Benson-Amram et al. 2011; Vallortigara 2010). In the natural environment, though, usually numerical cues co-vary with other continuous information. Therefore, not surprisingly, when both types of cues are available, animals exploit them to solve more complex numerical tasks (Rugani et al. 2017).

Parallel to the comparative evidence, a growing number of studies have demonstrated the presence of numerical skills in very young human infants as well, well before language and culture could be claimed as being responsible. The domestic chicken (*Gallus gallus*) has offered a unique model for bridging the comparative studies (carried out invariably in adult individuals) and the developmental evidence. Research on very young chicks, in fact, was able to assess early predispositions for number processing with strict controls over the role of experience. Chicks spontaneously discriminated the numerousness of sets of familiar objects and approached the larger set. Chicks even solved simple arithmetic computations with sequential presentations of objects, such as 1+1+1 judged as larger (hence preferred) than 1+1. Chicks seemingly operated based on representations of objects that were no longer visible in each set, and based on representations of their overall numerosities. These fine numerical abilities demonstrated that number processing is an inherent ability of animals that is crucial for survival, and these skills emerge even in the presence of an extremely reduced amount of experience. The sense of number (Dehaene 2011) would be shared across species—obviously preceding school and cultural education—and it would constitute the core knowledge supporting successful interactions with the environment (Feigenson et al. 2004). Even in humans, the non-symbolic numerical abilities are considered to be the foundations of more complex numerical reasoning (Starr et al. 2013; Park and Brannon 2013; Burr and Ross 2008; Anobile et al. 2019; Castaldi et al. 2020).

Another inherent property that appears (to the surprise of many) in animal species concerns the integration of two domains: numerical and spatial. A leftward bias has been described when animals locate a target by its ordinal position within a series of identical

targets oriented from left to right in front of the subject. This bias was confirmed in three animal species: domestic chicks (Rugani et al. 2007), Clark's nutcrackers (Rugani et al. 2010b) and rhesus monkeys (Drucker and Brannon 2014). It remains unclear whether such bias depends on the same (homologous) mechanism shared across species or whether we are looking at similar but analogous mechanisms (developed separately in the different species) for number-spatial processing. The bias seems to be specific for the integrated use of numerical and spatial information: chicks manifest a left-bias when ordinal and spatial information are both available, but they do not do this when the numerical information is all that is available (Rugani et al. 2011; Rugani and Regolin 2020). This bias seems to be linked to the spatial representation of various (increasingly large from left to right) numerical quantities. Newborn chicks display a left-spatial bias when exploring a numerosity smaller than expected, and a right-spatial bias when exploring a numerosity larger than expected (Rugani et al. 2015; 2020). Such space-number association was also confirmed in human infants (Bulf et al. 2015 and Rugani and de Hevia, 2017 de Hevia et al. 2016) and in newborns (de Hevia et al. 2018; di Giorgio et al. 2019). Clearly, the processing (and possibly the neurobiology) of numerical versus other types of dimensions are intertwined. The direction of the association is consistent across species: smaller numbers are associated with the left space, and larger numbers are associated with the right space. This fact is rather suggestive of a common origin of the underlying mechanisms at least in humans, other mammals and other vertebrates (i.e. birds).

The neural basis of non-symbolic numerical cognition in general, and of number-space mapping mechanism in particular, is currently being studied in avian species. In humans

and monkeys, the intraparietal sulcus seems to be involved in number processing, and topographically organized neurons responsive to small numerousness were found in the human parietal cortex (Piazza et al. 2004; Eger et al. 2009; Harvey et al. 2013). Neurons that are responsive to numbers have been found in the *nidopallium caudolaterale* of crows, an associative area of the avian pallium engaged in higher cognitive functions. These neurons are thought to represent the analogues of the mammalian prefrontal-cortex (Ditz and Nieder 2015). It has been proposed that this neural organization may determine the organization of magnitudes along a left-to-right-oriented space. A right hemisphere dominance in processing numerical and spatial information may prompt animals to start to count from left to right (Rugani et al. 2010a). Alternatively, the two hemispheres may be differently involved in processing small (right hemisphere) or large magnitudes (left hemisphere) (Vallortigara, 2018). Recent evidence in chicks showed that no one hemisphere preferentially deals with small or large numerical magnitudes (Rugani et al. 2020). Instead, the proficient use of numerical/ordinal information requires simultaneous processing by both hemispheres (Rugani and Regolin 2020). How this integration occurs in the brain remains to be discovered. Overall, this pattern of results seems to suggest that educational factors could not be the only factor determining the development of the number-space associations. This does not mean that experience cannot affect the SNA. Recent data on newborn chicks demonstrated that experience can indeed modulate the strength of the SNA (Rugani et al. 2020). Nevertheless, the integration of brain numerical representation and experience with determining the direction of the SNA remains one of the greatest challenges.

Acknowledgments

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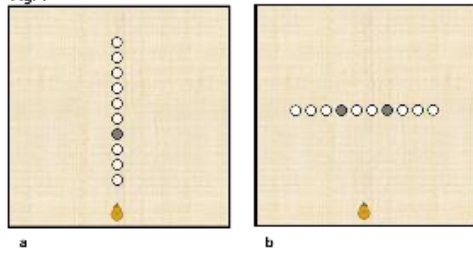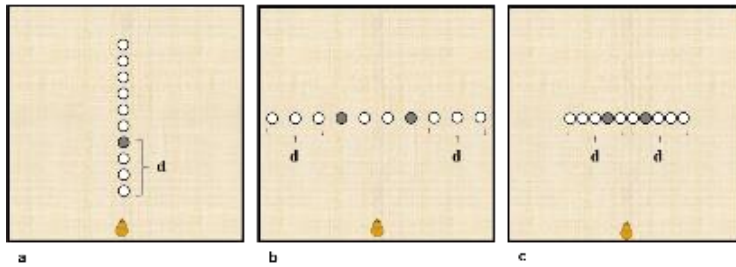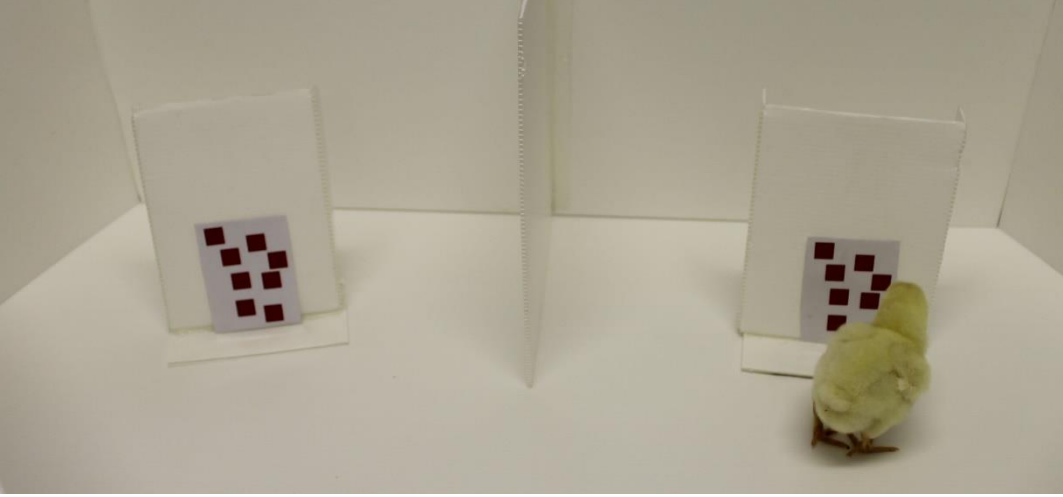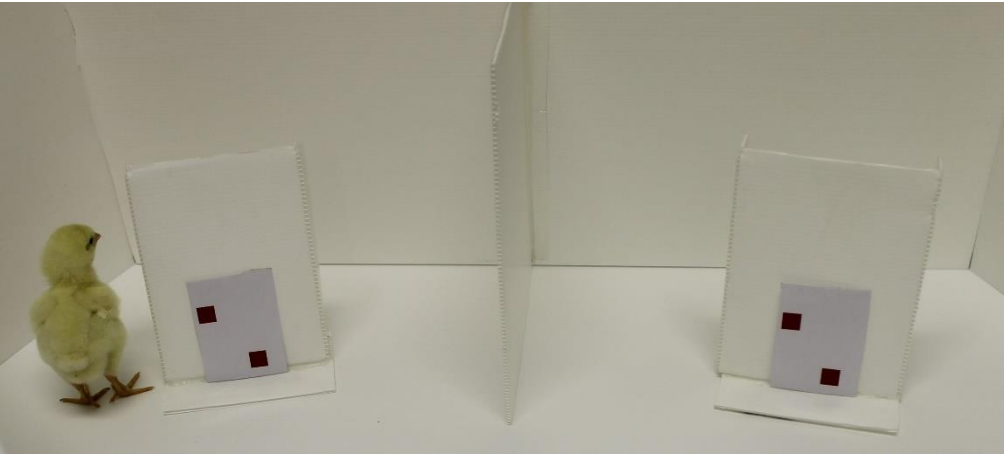
Fig. 1

Fig. 2

Fig. 4 a

Fig. 4 b

Fig. 4 c