

Mapping number to space in the two hemispheres of the avian brain



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ABSTRACT

Pre-verbal infants and non-human animals associate small numbers with the left space and large numbers with the right space. Birds and primates, trained to identify a given position in a sagittal series of identical positions, whenever required to respond on a left/right oriented series, referred the given position starting from the left end. Here, we extended this evidence by selectively investigating the role of either cerebral hemisphere, using the temporary monocular occlusion technique. In birds, lacking the corpus callosum, visual input is fed mainly to the contralateral hemisphere. We trained 4-day-old chicks to identify the 4th element in a sagittal series of 10 identical elements. At test, the series was identical but left/right oriented. Test was conducted in right monocular, left monocular or binocular condition of vision. Right monocular chicks pecked at the 4th right element; left monocular and binocular chicks pecked at the 4th left element. Data on monocular chicks demonstrate that both hemispheres deal with an ordinal (sequential) task. Data on binocular chicks indicate that the left bias is linked to a right hemisphere dominance, that allocates the attention toward the left hemisphere. This constitutes a first step towards understanding the neural basis of number space mapping.

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1. Introduction

It is well known from the classical work of Galton (1880) that humans represent numbers on a left to right oriented continuum, the so-called Mental Number Line, MNL (see for recent studies Dehaene, 2011).

The first experimental evidence regarding the left-to-right orientation of the MNL was reported by Dehaene, Bossini, and Giraux (1993). They showed that participants are faster in responding to small numbers when responses are executed on the left side of space, and to large numbers when responses are executed on the right side of space (Spatial-Numerical Association of Response Code, SNARC effect). Interestingly, in populations that read from right to left the SNARC effect is attenuated or even reversed, suggesting that the left to right orientation emerges as a result of exposure to formal instruction - i.e., it may be linked to writing and reading rules (Shaki, Fischer, & Petrusic, 2009; Zebian, 2005). Although the specific orientation of the MNL varies with the influences of cultural conventions, its presence across all cultures suggests that the spatial numerical association is an universal cognitive strategy (Göbel, Shaki, & Fischer, 2011).

Pre-verbal children (Bulf, de Hevia, & Macchi-Cassia, in press; de Hevia, 2011; de Hevia, Girelli, Addabbo, & Macchi Cassia, 2014; de Hevia & Spelke, 2010; McCrink & Opfer, 2014;) and non-human animals (Adachi, 2014; Drucker & Brannon, 2014; Rugani, Rosa Salva, & Regolin, 2014b; Rugani, Vallortigara, & Regolin, 2015a; Rugani, Vallortigara, Priftis, & Regolin, 2015a) also show left to right orientation in non-symbolic numerical tasks, indicating that number-space association could occur in absence of language. By scoring 8–9 month-old infants' eye movements, Bulf et al. (in press) showed that a small numerosity (e.g. 2 dots) oriented infants' visual attention toward the left and a large numerosity (e.g. 9 dots) toward the right. This suggests that the link between numbers and oriented spatial codes occurs in humans before any exposure to formal education. Day-old domestic chicks (*Gallus gallus*), trained to respond to a target number (5), then associated a smaller number (2) to the left and a larger number (8) to the right. Interestingly enough this spatial-numerical association could be reversed by changing the numerical interval. When the target was 20, chicks associated the number 8 to the left and 32 to the right. Control experiments ruled out other non-numerical features of the visual displays (such as overall area, overall perimeter, density and occupancy) that might have influenced chicks' choices (Rugani, Vallortigara, Priftis, & Regolin, 2015a, 2015b, 2016a, 2016b). Chimpanzees trained to touch in ascending order Arabic numerals, shown in random locations on a monitor screen, when

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presented with only two numerals (1 and 9) horizontally arranged, responded more quickly when 1 was on the left and 9 on the right (Adachi, 2014).

Different species (domestic chicks, Rugani, Regolin, & Vallortigara, 2007; Rugani, Vallortigara, Vallini, & Regolin, 2011; adult Clark's nutcrackers, Rugani, Kelly, Szelest, Regolin, & Vallortigara, 2010 and adult rhesus macaques, Drucker & Brannon, 2014) also showed a similarity in preferentially representing the sequential aspects of identical objects as oriented from left to right. In this task animals were trained to select a target element (e.g. the 4th) in a series of identical ones, sagittally oriented with respect to the animals' starting point. When required to repeat the task with a series identical to the first one, but rotated by 90°, therefore fronto-parallel oriented with respect to the animals' starting point (i.e. from left to right), they identified as correct the target element from the left end, neglecting the right one. This left-sided bias could depend on numerical as well as on spatial cue. In fact the target, in both the sagittal and the fronto-parallel series, was located at the same distance from the closest end of the series. In another study, chicks learned to identify the target element (the 4th in a series of 10) in a condition in which spatial and numerical information were both available. In fact during training the elements were maintained in fixed positions and therefore the distances between elements were identical. Then at fronto-parallel test, a conflict between spatial and numerical information was created, manipulating the distance between elements. Half chicks took part in a fronto-parallel test in which the distance between elements was increased (but kept identical throughout the line), in such a way that the 3rd position was in the position previously occupied by the 4th element. For the other half of the birds the distance between elements was reduced in such a way that the 5th position was in the position previously occupied (at training) by the 4th element. Interestingly, chicks neglected the element located at the correct distance from the beginning of the series (Rugani, Vallortigara, et al., 2011). In spite of the fact that spatial information would permit target identification, chicks relied onto ordinal information. In this case, however, chicks chose identically the left and the right target element (Rugani, Vallortigara, et al., 2011). Even when the possible use of spatial information was disrupted by changing from trial to trial, both during training and during fronto-parallel test, the distance between the elements, chicks identified as correct both the left and the right target element. Interestingly enough a change not involving a spatial manipulation - using elements of a different color between training and test - did not affect the presence of the left-bias. These findings suggested three main points. First chicks could use purely numerical information for solving the task. Second they preferably relied on numerical over spatial cues. Third, and more important for the aim of this study, the left-bias occurred solely when chicks could rely on both spatial and numerical information (Rugani, Vallortigara, et al., 2011). The authors claimed that left bias, in such a serial ordering task, could be due to a selective allocation of attention in the left hemifield as a consequence of a right hemisphere dominance in processing spatial information. However, no direct evidence for this has been provided.

Here, we studied for the first time the effect of hemispheric asymmetries in non-human animal spatial-numerical processing. We took advantage of the fact that the avian brain presents a complete decussation of fibres at the optic chiasm (Ocklenburg & Güntürkün, 2012; Weidner, Reperant, Miceli, Haby, & Rio, 1985) and lacks of a structure homologous to the *corpus callosum* (even though other smaller tracts allow inter hemispheric communication, e.g. Hardy, Leresche, & Jassik-Gerschenfeld, 1984; Robert & Cuénod, 1969; Theiss, Hellmann, & Güntürkün, 2003; Zeier & Karten, 1973). Thus, each eye projects mainly to the visual system of the contralateral hemisphere (Deng & Rogers, 1998). Method-

ologically speaking, this means that by restricting the visual input to a single eye, it is possible to investigate the functioning of the contralateral hemisphere in the intact animal to discern hemisphere specializations (Gülbetekin, Güntürkün, Dural, & Çetinkaya, 2007; Rogers, 1997). We tested chicks in a serial ordinal task, in which spatial and numerical cues were available during sagittal training as well as during fronto-parallel test. We trained chicks binocularly and then, under monocular testing conditions, we restricted the visual input to one eye, using a patch over the other eye (Rogers, 1997; Vallortigara & Andrew, 1991; for a review see Daisley, Mascalzoni, Rosa-Salva, Rugani, & Regolin, 2009).

2. Methods

2.1. Subjects

Subjects were 13 (Experiment 1), 12 (Experiment 2) and 10 (Experiment 3) male domestic chicks (*G. gallus*). Chicks a few hours old were placed in standard cages (28 × 40 × 32 cm) at controlled temperature (28–31 °C) and humidity (68%). Food and water were available ad libitum. Testing began when they were 4 days old, because of yolk sac reserve chicks are unmotivated to peck for food reward before day 4 post-hatching. Two hours before each experimental session (training, re-training and tests), chicks were food deprived to avoid testing chicks that had just fed, which are usually sleepy (Regolin, Rugani, Pagni, & Vallortigara, 2005). Moreover two hours of food deprivation maintain chicks' motivation sufficiently high to look for food in all testing trials. In a previous experiment in which we used the experimental procedure also employed in the present experiment, we found that chicks' performance remained stable throughout all test trials, and that chicks' performance was above chance already in the first block of trials (trials 1–5) up to the very last trials (16–20) (Rugani et al., 2007; but see also Rugani, Regolin, & Vallortigara, 2011).

2.2. Apparatus

Pre-training, training, re-training, sagittal test and fronto-parallel test took place in an experimental room located near to the rearing room. During experimental phases temperature was maintained at 25 °C. The room was lit by four 58 W lamps, placed on the ceiling, 148 cm above the experimental apparatus. This consisted in a wooden square-shaped arena (80 × 80 × 40 cm), with the floor covered with wood-shaving. Subjects could enter the arena through two openings (7 × 11 cm) positioned at the midline of two opposing walls. Each opening connected the arena with a starting box (7 × 11 × 11.5 cm) located outside of the arena itself (Fig. 1). The side of the starting box, facing the openings was



Fig. 1. The apparatus and the sagittal disposition of the elements used for training. One of the two opposite entrances is visible in the back wall.

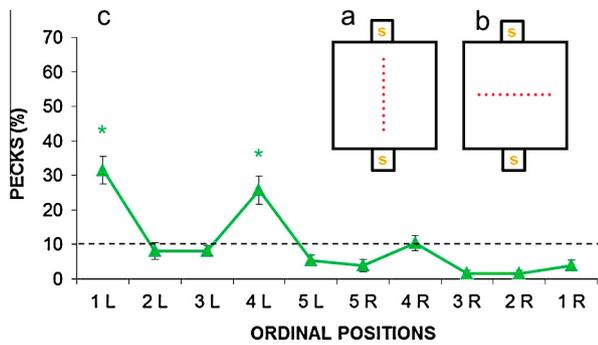


Fig. 2. (a) Schematic illustration of the arena setup during training and sagittal test in all the experiments. “S” represents the chick’s starting points (subjects could enter the arena through either openings positioned at the midline of two opposing walls). (b) Schematic representation of the apparatus and the left–right disposition of the series of elements in the fronto-parallel test (S = chick’s starting points). (c) Results of fronto-parallel test of Experiment 1: The graph represents the mean percentage with SE (number of pecks to each position/ 20×100) of pecks directed to each element. Only the target element and the first element from the left (4L and 1L) were pecked statistically above chance level (represented by the dotted line: $y = 10$). In this as well as in the subsequent figures the labels on the x-axis indicate the ordinal position from the closest end (L = left end and R = right end), asterisks (*) indicated $p < 0.05$.

usually covered by a removable, opaque plastic partition (12×12 cm). Along the midline of the arena’s floor was a series of 10 identical and aligned elements (i.e. plastic bottle tops, 3.2 cm in diameter and 0.4 cm height), spaced 1 cm from one another, for an overall length of 41 cm (19.5 cm apart from the openings and 38.4 cm from the side walls; Figs. 1 and 2a). During pre-training, training, re-training and sagittal test the series was sagittally aligned, with respect to the chick’s starting point (Figs. 1 and 2a), while during fronto-parallel test it was left-right oriented (Fig. 2b). All elements were filled with wood-shaving, so that at the beginning of each trial, all elements appeared identical. Only the 4th element hid a piece of mealworm. This occurred in each pre-training, training and re-training trial. During testing (both sagittal and fronto-parallel) the food reinforcement was available only in some pre-established trials (trial number 4, 5, 7, 10, 13, 14, 16 and 19; Rugani, Regolin, & Vallortigara, 2008; Rugani, Vallortigara, & Regolin, 2015b), and chicks could gain the food only by choosing correctly in those trials. All other trials were unrewarded. During testing, the position of the elements into the series was systematically manipulated, in order to ensure that a chick identified the correct element by its ordinal position, rather than any other cues. Moreover, from trial to trial the apparatus was randomly rotated in the experimental room, to avoid any possible use of external cues.

3. Experimental procedures

3.1. Pre-training

On Day 4 of life, each chick underwent a pre-training. At the beginning of each trial the subject was confined in the starting box for about 3 s. Then, by sliding the partition, it could enter the apparatus, where for about 2 min it could freely move around and get acquainted with the novel environment. In the first trials a piece of mealworm was visibly positioned (not covered by wood-shaving) into the niche of the 4th element. The mealworm remained completely visible until the subject have learned to promptly go toward the target element eating the mealworm for three consecutive times. In subsequent trials the food reinforcement was progressively occluded by wood-shaving requiring the birds to dig in the container to retrieve the hidden mealworm. In this way chicks gained the reinforcement only searching at the

target element. Learning criterion was three consecutive correct trials.

3.2. Training

Training took place 2 h after pre-training. All chicks (13 in Experiment 1, 12 in Experiment 2 and 10 in Experiment 3) were binocularly trained to identify the 4th element in the sagittal series of 10 identical and equidistant elements (Figs. 1 and 2a). The distances between elements were maintained identical throughout training, therefore, chicks, in identifying the target element, could use both spatial and numerical information (Fig. 2a). At the beginning of each trial, the chick was in the starting box for about 3 s; then the removable partition was lifted up from above permitting the chick to walk towards and peck at any element. Only one peck on each trial was allowed. A trial was considered correct when the chick pecked at the 4th element. The trial was considered null and thus terminated after 180 s in the absence of a response. All chicks produced at least eight correct responses across 20 valid trials and thus, progressed to the subsequent phase.

3.3. Sagittal test

Two hours after the end of training, to assess whether chicks had learned the task, they underwent a sagittal test. This consisted of 20 consecutive trials. In sagittal test the disposition of the series was maintained identical to the training one. During each trial, the chick was allowed one peck. If no response occurred within 60 s, the trial was terminated. At the end of each trial, the chick was gently placed back at the starting box and after approximately 3 s it was given a new trial.

3.4. Fronto-parallel tests

Two hours after completion of the sagittal test, chicks underwent the fronto-parallel test. During this test, on the floor of the apparatus was a series of 10 elements all identical to those previously described. The new test series was rotated by 90° when compared with the training series, and placed fronto-parallel in front of the chick’s starting point (at 38.4 cm from either openings; Fig. 2b).

Immediately before the beginning of the fronto-parallel test chicks underwent a binocular brief re-training with the sagittal series. Learning criterion was three consecutive correct trials. In Experiments 1 and 2 each chick took part at a single fronto-parallel test in a monocular condition of vision: left monocular in Experiment 1 (Left Eye in Use - Right Hemisphere Processing) and right monocular in Experiment 2 (Right Eye in Use - Left Hemisphere Processing).

In Experiment 3 (All conditions of vision: Binocular, Left Monocular and Right Monocular) the fronto-parallel test was conducted in three different conditions of vision: binocular, left monocular and right monocular. Chicks firstly underwent the fronto-parallel test binocularly and thereafter in both monocular conditions of vision, either the left ($N = 5$) or the right ($N = 5$) as first monocular test.

The interval between two consecutive testing phases (each consisting in 20 trials) was of two hours. Before each test chicks underwent a re-training session. Each re-training trial was performed as in the training phase and lasted 5–10 min. As soon as the chicks reached the learning criterion, fixed at 3 consecutive correct trials, they immediately underwent the test.

Monocular testing was carried out by means of temporary eye patches made of special, removable paper tape, worn by the chicks 20 min before testing to get them acquainted to the new situation (binocular chicks were not eye-patched but received an equivalent

amount of handling and acquainting time as did monocular chicks).

3.4.1. Analysis

On each test trial, we scored the first element inspected by the chick and computed the mean percentage of choices for any of the 10 elements in the series, using this formula: number of pecks to a given element/ 20×100 . We used parametric paired *t*-tests to compare pecks emitted to target elements (4th left and 4th right), and one-sample *t*-tests to assess significant departures from chance level, i.e. 10%.

4. Results

4.1. Experiment 1, left eye in use - right hemisphere processing

Chicks in the sagittal test pecked the 4th element well above chance (10%): $N = 13$, Mean = 42.69, ES = 2.75; $t(12) = 11.88$, $p < 0.01$. Any other element was pecked at or below chance level.

In the fronto-parallel test, in left monocular condition of vision, they pecked the 4th element from the left: Mean = 25.77, ES = 4.12, $t(12) = 3.83$, $p < 0.01$; the 4th element from the right was chosen at chance: Mean = 10.39, ES = 2.23, $t(12) = 0.17$, $p = 0.87$ (Fig. 2c). A statistically significant difference was found between left vs. right target element (paired *t*-test: $t(11) = 2.90$; $p = 0.01$). Chicks pecked all other elements at or below chance, with the only exception of the 1st from the left: Mean = 31.54, ES = 4.02, $t(12) = 5.36$, $p < 0.01$.

4.2. Experiment 2, right eye in use - left hemisphere processing

Chicks in the sagittal test selected the 4th element above chance ($N = 12$, Mean = 42.08, ES = 2.92; $t(11) = 10.99$, $p < 0.01$), all other elements were pecked at or below chance.

Birds in fronto-parallel test, in right monocular condition of vision, pecked at the 4th element from the right: Mean = 20.17, ES = 3.61, $t(11) = 2.76$, $p = 0.02$; the 4th element from the left was chosen at chance: Mean = 14.17, ES = 2.60, $t(11) = 1.60$, $p = 0.14$ (Fig. 3). No statistically significant difference was found between the pecks given at the left vs. right target element (paired *t*-test: $t(11) = 1.32$; $p = 0.21$). Birds pecked all other elements at or below chance, with the only exception of the 1st from the right: Mean = 23.42, ES = 5.32, $t(11) = 2.53$, $p = 0.03$.

These findings prove that the left hemisphere can identify a target element on the basis of spatial-numerical information. As in the previous experiment, chicks pecked above chance the first element in the hemifield homolateral to the eye in use. This behavior had been already described in rats (Davis & Bradford, 1986) and in domestic chicks (Rugani, Vallortigara, et al., 2011), and it was

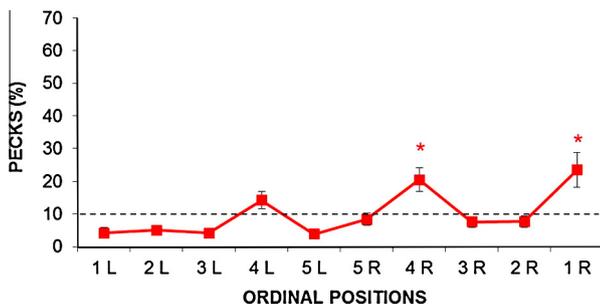


Fig. 3. Results of Experiment 2: Mean values (\pm SE) of the pecks emitted by subjects to each element in the fronto-parallel series are shown. The dotted line ($y = 10$) represents chance level. Only the target element and the first element from the right (4R and 1R) were pecked statistically above chance. Asterisks (*) indicated $p < 0.05$.

explained by the tendency of animals to search for food in the most salient possible location, whenever placed in front of elements totally identical to the target.

4.3. Experiment 3, all conditions of vision: Binocular, left monocular and right monocular

Chicks in the sagittal test pecked selectively the 4th element: $N = 10$, Mean = 45.50, ES = 2.73; $t(9) = 12.99$, $p < 0.01$; while all others were pecked at or below chance. Thereafter chicks underwent the fronto-parallel test in three different conditions of vision (Fig. 4a–c). All birds firstly underwent the fronto-parallel test binocularly, then they underwent the monocular tests in random order.

4.3.1. Binocular

Chicks selectively chose the target element significantly above chance only when locating it from the left end: Mean = 26.00, ES = 2.87, $t(9) = 5.57$, $p < 0.01$, while the 4th element from the right was chosen at chance: Mean = 13.00, ES = 2.00, $t(9) = 1.50$, $p < 0.17$ (Fig. 4d). A statistically significant difference was found between left vs. right target element (paired *t*-test: $t(9) = 6.30$; $p < 0.01$). All other elements were pecked at or below chance.

4.3.2. Right monocular

Chicks that underwent the fronto-parallel test in right monocular condition of vision as first or second test did not differ in the responses given at the 4th left element, Wilcoxon test, $p = 0.564$ (First: Mean = 11.00, ES = 1.00; Second: Mean = 10.00, ES = 1.58), neither in the pecks emitted at the 4th right element, Wilcoxon test, $p = 0.214$ (First: Mean = 31.00, ES = 4.58; Second: Mean = 24.00, ES = 1.00). Data of the two groups were therefore

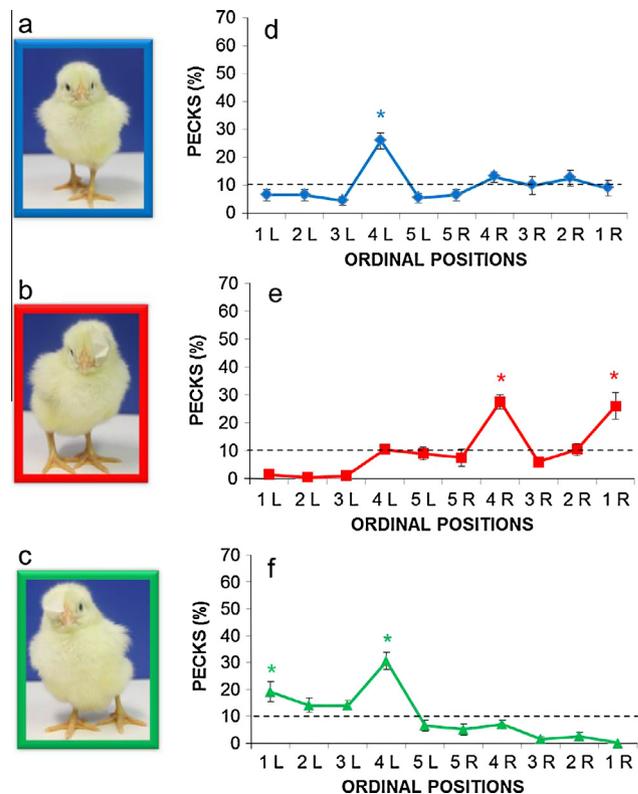


Fig. 4. Pictures of chicks in binocular (a), right monocular (b) and left monocular (c) condition of vision. Results (Mean values \pm SE) of Experiment 3 in binocular (d), right monocular (e) and left monocular (f) condition of vision.

merged. Chicks identified as correct the 4th element from the right $N = 10$, Mean = 27.50, ES = 2.50, $t(9) = 7.00$, $p < 0.01$; the 4th element from the left was chosen at chance: $N = 10$, Mean = 10.50, ES = 0.89, $t(9) = 0.56$, $p = 0.58$ (Fig. 4e). A statistically significant difference was found between left vs. right target element (paired t -test: $t(9) = 5.85$; $p < 0.01$).

Chicks pecked all other elements at or below chance, with the only exception of the 1st element from the right $N = 10$, Mean = 26.00, ES = 4.78, $t(9) = 3.35$, $p = 0.01$.

4.3.3. Left monocular

Chicks that underwent the fronto-parallel test in left monocular condition of vision as first or second test did not differ in the responses given at the 4th left element, Wilcoxon test, $p = 0.713$ (First: Mean = 30.00, ES = 3.54; Second: Mean = 31.00, ES = 5.79), neither in the pecks emitted at the 4th right element, Wilcoxon test, $p = 0.655$ (First: Mean = 8.00, ES = 3.00; Second: Mean = 6.00, ES = 1.00). Data of the two groups were therefore merged. Chicks identified as correct solely the 4th element from the left: $N = 10$, Mean = 30.50, ES = 3.20, $t(9) = 6.41$, $p < 0.01$; the 4th element from the right was chosen below chance: $N = 10$, Mean = 7.00, ES = 1.53, $t(9) = 1.96$, $p = 0.08$ (Fig. 4f). A statistically significant difference was found between left vs. right target element (paired t -test: $t(9) = 3.03$; $p = 0.01$).

Chicks pecked all other elements at or below chance, with the only exception of the 1st element from the left $N = 10$, Mean = 19.00, ES = 3.71, $t(9) = 2.43$, $p = 0.04$.

These data confirm previous results, showing that chicks exploring the environment with both eyes manifest a left-bias in an ordinal task that allows the use of ordinal and spatial cues. After this binocular experience, in the two monocular conditions of vision, chicks continued to be able to identify the target element. As in the previous experiments, birds tested with the left eye in use generalized to the left target element; birds tested with the right eye in use generalized to the right target element. Interestingly enough, birds behavior was not influenced by their previous experience with the fronto-parallel series, alternating their choice in the left and right space.

5. Discussion

In all conditions of vision chicks performed successfully at fronto-parallel test, choosing the correct 4th element in the series (either left or right) significantly above chance. In monocular conditions of vision, however, chicks generalized at the target element located in their unobstructed hemifield. When the left eye was in use, chicks chose the 4th element from the left end and when the right eye was in use they chose at the 4th element from the right end (i.e. the 7th element, counting from left to right). This shows that the serial-ordinal information acquired during binocular training can be correctly represented, and independently used by each hemisphere though with a different starting point for each hemisphere. The bilateral hemispheric representation of numerical processing found here is coherent with scientific literature (for a review see Piazza & Eger, 2016).

The fact that, in the monocular test, responses were limited to the visible hemifield is likely due to the fact that chicks could only see the hemispace homolateral to the eye in use. As a consequence only one end of the series, either left or right, was clearly seen, and used by chicks as benchmark to start to “count”. This is also supported by the fact that chicks, in fronto-parallel test, pecked significantly at the first element selectively in the visible part of the series: right monocular chicks pecked at the first right element and left chicks pecked at the first left element (see also Rugani, Vallortigara, et al., 2011). Another consideration relating to the fact

that pecks emitted at the first left and at the first right positions were above chance solely when chicks were tested in monocular condition of vision, but not when chicks were tested in binocular condition. This may also suggest that suppression of response to the first element is possible only in the binocular condition. Nevertheless chicks' left or right bias depended uniquely on the condition of vision. The bias was not influenced by previous binocular or monocular experiences with the fronto-parallel series, showing that the preceding responses do not influence the following ones (Experiment 3).

When binocularly tested, chicks showed a left-hemisphere bias, selecting the left target element. This confirms the previously documented tendency to start to “count” from left to right, whenever both spatial and numerical information are accessible (Rugani et al., 2007, 2010, Rugani, Vallortigara, et al., 2011). The left bias would occur because of availability of the spatial information, that in the chick forebrain is represented in the right hemisphere (Rashid & Andrew, 1989; Regolin, Garzotto, Rugani, & Vallortigara, 2005; Tommasi, Gagliardo, Anrew, & Vallortigara, 2003; Tommasi & Vallortigara, 2001; review in Vallortigara, Chiandetti, Sovrano, Rugani, & Regolin, 2010). When both hemispheres are processing the information, availability of spatial cues, coherent with the numerical cues, would result in control by the right hemisphere, that drives chicks' behavior. This would favor the preferential allocation of attention into the left hemispace, producing a bias to “count” selectively from left to right.

Up to now there is no sufficient evidence to indicate which explanation best describes the origin of number space mapping. An essential question is indeed how and where number magnitude is represented in the brain. Comparative studies on numerical processing have suggested that numerical knowledge constitutes a domain-specific cognitive ability (Cantlon, 2012; Pepperberg & Carey, 2012; Rugani, Vallortigara, & Regolin, 2013, 2014a; Scarf, Hayne, & Colombo, 2011; Stancher, Rugani, Regolin, & Vallortigara, 2015; Wang, Uhrig, Jarraya, & Dehaene, 2015; Xia, Emmerton, Siemann, & Delius, 2001) with a dedicated neural substrate located in the parietal cortices (Nieder, Freedman, & Miller, 2002; Vallentin & Nieder, 2008; Dehaene, 2011). Recently neurons selective to numbers have been found in a brain association area (*nidopallium caudolaterale*, NCL) of crows (Ditz & Neider, 2015). This allows future investigations of the neural basis of the numerical cognition in brains lacking the six-layered neo-cortex, that for a long time has been considered an essential prerequisite for high cognition. Nevertheless, how this neural substrate can determine a left-to-right mapping of numbers remains to be understood. Future studies on the neural codes of space and number will shed light on the origin of the number mapping.

Authors' contribution

Designed the study: all authors. Testing and data collection were supervised by R.R. and L.R. and R.R. performed the data analysis and wrote the manuscript. L.R. and G.V. provided critical revision. All authors approved the final version of the manuscript for submission.

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