Number-space mapping in the newborn chick resembles humans' mental number line

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ABSTRACT: Humans represent numbers along a mental number line (MNL), where smaller values are located on the left and larger on the right. The origin of the MNL and its connections with cultural experience are unclear: Pre-verbal infants and nonhuman species master a variety of numerical abilities, supporting the existence of evolutionary ancient precursor systems. In our experiments, 3-day-old domestic chicks, once familiarized with a target number (5), spontaneously associated a smaller number (2) with the left space and a larger number (8) with the right space. The same number (8), though, was associated with the left space when the target number was 20. Similarly to humans, chicks associate smaller numbers with the left space and larger numbers with the right space.

Number knowledge and processing are fun- damental to everyday life. There is now considerable empirical evidence that num- bers may be represented along a continuous, left-to-right—oriented, mental number line (MNL) (1); however, the origin of this orien- tation is debated. In humans (2) and nonhuman animals (3, 4), numerical judgments become easier as the difference between the numbers increases (the distance effect) and harder as the magnitude of numbers increases (the size effect). Interspecific similarities suggest a continuous and analogical nonverbal representation of nu- merical magnitude (3). This indicates that nu- merical competence did not emerge de novo in linguistic humans but was probably built on a precursor nonverbal number system (1, 5).

The size and distance effects, though, are not informative about the origin of the orientation of the MNL. Indeed, the MNL has been, up to now, demonstrated solely among humans (6–8), where its orientation may be influenced by cul- tural factors, such as reading direction. People primarily educated in Arabic show an inverted

spatial-numerical association of response codes (SNARC) (9) effect (10), whereas people with mixed reading habits (such as Israelis) show no SNARC at all (11). It remains unclear whether the MNL orienta- tion is simply modulated or entirely produced by educational factors. Seven-month-old infants prefer increasing (e.g., 1-2-3) to decreasing (e.g., 3-2-1) magnitudes displayed from left to right, (12), showing that spatial-numerical association does exist before mathematics and linguistic education. A tendency to count from left to right has also been found in domestic chicks (13), adult Clark's nutcrackers (14), and adult Rhesus macaques (15). In these studies, animals were trained to identify a target element in a sagitally oriented series of identical elements. When required to repeat the task with an identical series of ele-ments rotated by 90°, animals identified as cor-rect the target positioned from the left end (14). However, this left-sided preference could de-pend on a general bias in the allocation of spa-tial attention (16). Both humans (17) and birds (18, 19) primarily attend to objects in the left side of space, a phenomenon termed "pseudoneglect." When a different paradigm was used, adult chimpanzees were trained to touch in ascendant order Arabic numerals (1 to 9) ran-domly displayed on a computer screen. At test- ing, they were presented with only two numerals (1 and 9) displayed horizontally, one on the left and the other on the right; chimpanzees responded faster to the left-right (1-9) than to the right-left condition (9-1) (20). However, these results are not conclusive concerning the spon- taneous mapping of magnitudes onto space, be-cause apes required intensive sequential learning during training.

The spatial arrangement of numbers is high- ly flexible in humans: A fundamental charac- teristic of the human MNL is its relativity. In the 1-9 range, for instance, responding to 9 is faster when responses are executed on the right; but in the 9-18 range, responding to 9 is faster when re- sponses are executed on the left (1). No evidence of this has been reported in nonhuman species.

To avoid the influence of pseudoneglect and to ascertain the relativity of the MNL and its depen- dence on the number magnitude, we devised a new experimental paradigm (21). Three-day- old domestic chicks (Gallus gallus) learned to circumnavigate a panel to reach a food reward (fig. S1). At training, the panel depicted a target number of elements (5 in experiment 1; Fig. 1A). At testing, we presented each chick with two panels, one on its left side and one on its right side, both depicting the same number of ele- ments, which was, however, a different

number from the target. Each chick underwent two tests: a small number test in which the panels depicted a number of elements smaller than the target (2 in experiment 1; Fig. 1B), and a large number test in which the number of ele-ments was larger than the target (8 in experi- ment 1; Fig. 1C). The test stimuli looked identical. Moreover, birds could not rely on familiar in-formation concerning their spatial position or appearance to choose which panel to approach first when looking for food. Any facilitation in processing a number smaller than the target to the left (or larger to the right), resulting in a coherent preferential choice for one side, would support the hypothesis of a left-to-right-oriented spatial numerical association. On each of five testing trials, for each test, we scored the first panel (left or right) inspected by the chick (fig. S2). In the small number test (2 versus 2), chicks chose the left panel 70.67% and the right panel 29.33% of the times. In the large number test (8 versus 8), the chicks chose the left panel 29% and the right panel 71% of the times (Fig. 3). In ex- periment 2, a new group of chicks was presented with the target number "20" (Fig. 2A). Now 8 versus 8 constituted the small number test (Fig. 2B), and chicks chose the left panel 70% and the right panel 30% of the time. In the large number test, 32 versus 32 (Fig. 2C), chicks chose the left panel 22.5% and the right panel 77.5% of the times (Fig. 3). The association of a certain num- ber on the left or on the right was not absolute but depended on the relative magnitude of the number with respect to the target. Chicks that had experienced the number "5" as the target, associated the number "8" with the right side of space. On the contrary, chicks that had experi- enced the number "20" as the target, associated the number "8" with the left side of the space. These results were confirmed in experiment 3, in which we controlled for the effect of the fol-lowing non-numerical cues on number-space mapping: condition 1: shape, color, and size of each element; condition 2: overall area (summa-tion of the areas of all elements depicted in each stimulus); condition 3: overall perimeter (sum- mation of the perimeters of all elements depicted in each stimulus) and density (the mean distance among the elements). Moreover, in condition 3, there was a negative correlation between overall area and number: The overall area of the 8 elements was larger than that of the 32 elements. Furthermore, the elements of each stimulus occupied the same overall spatial frame in conditions 2 and 3. If the overall area, in the presence of the same perimeter, was the crucial factor underlying number-space mapping, chicks would have chosen the right panel in the small number test and the

left panel in the large number test. The results showed that in the small number test (8 versus 8), chicks chose the left panel 69.46% and the right panel 30.54% of the times. In the large number test (32 versus 32), chicks chose the left panel 25.27% and the right panel 74.73% of the times (Fig. 3). Therefore, the results of experiment 3 demonstrate that spatial mapping relates to the abstract numerical magnitude, indepen- dently of non-numerical cues.

Our results indicate that a disposition to map numerical magnitudes onto a left-to-right— oriented MNL exists independently of cultural factors and can be observed in animals with very little nonsymbolic numerical experience, sup- porting a nativistic foundation of such orien- tation. Spatial mapping of numbers from left to right may be a universal cognitive strategy avail- able soon after birth. Experience and, in humans, culture and education (e.g., reading habits and formal mathematics education) may mod- ulate or even be modulated by this innate num- ber sense.

During evolution, the direction of mapping from left to right rather than vice versa, although in principle arbitrary, may have been imposed by brain asymmetry, a common and ancient trait in vertebrates (22), prompted by a right hemisphere dominance in attending vis- uospatial and/or numerical information. Recent studies have suggested that numerical knowl- edge constitutes a domain-specific cognitive abil- ity, with a dedicated neural substrate located in the inferior parietal cortices (1, 23). Moreover, number-space mapping is implemented in hu- mans through a topographical representation in the right posterior parietal cortex (24). Such topography has not yet been found in neurons responding to number in animals (25, 26).

Because nonverbal numerical cognition is shared by many animal classes (1, 27, 28), we suggest that a similar predisposition to map numbers onto space is embodied in the archi- tecture of the animal neural systems.

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Figures and captions

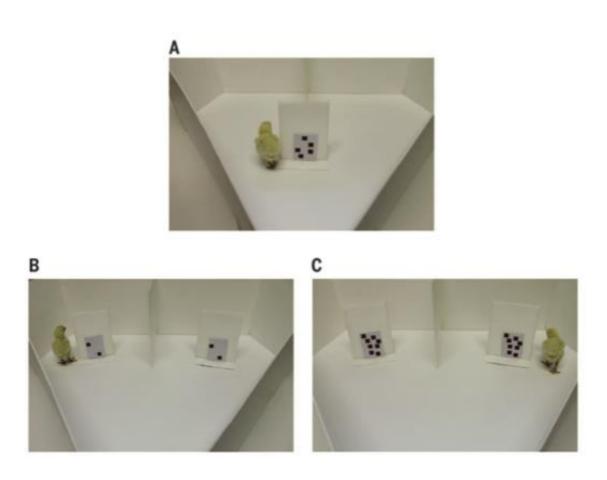


Fig. 1. Experimental settings of experiment 1. Chicks were trained to circumnavigate a panel, lo- cated in the center of the apparatus, depicting 5 identical elements (i.e., the target number). (A) In all experiments, we used 20 different training stimuli, differing in the spatial disposition of the elements. The training finished whenever the chick circum- navigated the screen and reached the food reward 20 consecutive times. After training, each chick underwent two tests in random order: a small number test (2 versus 2) (B) and a large number test (8 ver- sus 8) (C). In all experiments, each test consisted of five nonreinforced trials (a novel

pair of stimuli was employed on each trial). On each test trial, we scored the panel first inspected by the chick and computed the mean percentage of choices for the left panel.

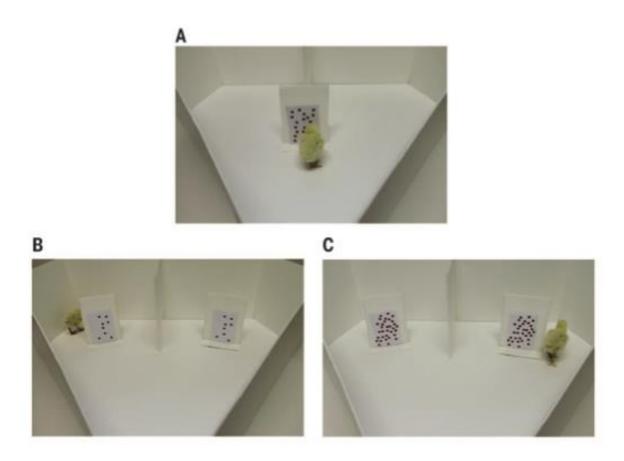


Fig. 2. Experimental settings of experiment 2. We trained a new group of chicks on the target number 20 (A). Birds then underwent both a small number test (8 versus 8) (B) and a large number test (32 versus 32) (C).

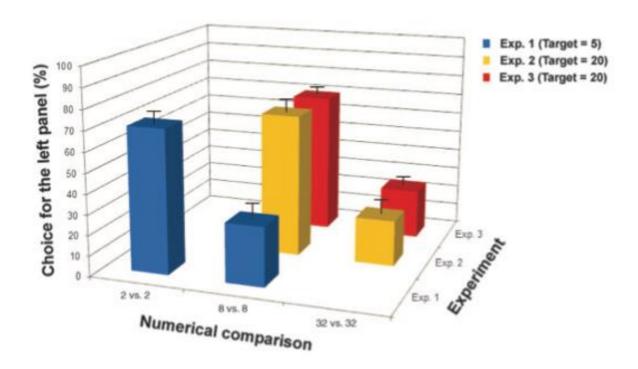


Fig. 3. Results of all the experiments. For each experiment, we calculated the percentage of the times each chick chose the left panel [range: 0 (left panel never chosen) – 100 (left panel always chosen)]. Experiment 1: A Mann-Whitney U test on the percentage of choices for the left panel did not reveal any difference between chicks that underwent the small number test first (n = 8) or second (n = 7) (U = 24.50, P = 0.66), nor between chicks that underwent the large number test first (n = 7) or second (n = 8) (U = 24.50, P = 0.68). Data were merged and compared with chance level (50%) with a t test. In the small number test, chicks preferred the left panel (n = 15 chicks, mean = 70.67%, SE = 5.81, t(14) = 3.56, P < 0.01). In the large number test, chicks preferred the right panel (n = 15, mean = 29%, SE = 7.37, t(14)

= -2.85, P = 0.01). Experiment 2: A Mann-Whitney U test did not reveal any difference between chicks that underwent the small number test first (n = 6) or second (n = 6) (U = 18, P = 1), nor between chicks that underwent the large number testfirst(n=6)orsecond(n=6)(U=16,P=0.72).

In the small number test, chicks preferred the left panel (n = 12, mean = 70%, SE = 5.77, t(11) = 3.46, P < 0.01). In the large number test, chicks preferred the right panel (n = 12, mean = 22.5%, SE = 6.53, t(11) = -4.21, P < 0.01). In experiment 3, we ran a two-way mixed analysis of variance [between-subjects factor: condition (1, 2, 3); within-subjects factor: number (8 versus 8, 32 versus 32)] to control for the effect of non-numerical cues. Only the main effect of number was significant [F(1, 34) = 98.71, P < 0.01, partial eta squared = 0.74]. In the small number test, chicks preferred the left panel (n = 37, mean = 69.46%, SE = 2.94, t(36) = 6.61, P < 30.01). In the large number test, chicks preferred the right panel (n = 37, mean = 25.27%, SE = 3.36, t(36) = -7.35, P < 30.01).