Rhesus monkeys show no preference for a left-to-right number-space mapping

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Abstract

Humans who use a left-to-right writing system often associate smaller numbers with the left side of space and larger numbers with the right. Whether this left-to-right number-space mapping is innate or culturally learned is unclear. Here, we test whether monkeys who lack human cultural practices show a left-to-right number-space mapping. Previous work in monkeys has found mixed evidence on whether monkeys show a left-to-right bias in their number-space mappings. Replicating the methods of Drucker and Brannon (2014), monkeys were trained to touch the fourth circle from the bottom in a vertical array of five circles. Then, they were tested with a horizontal array of five circles. Overall, monkeys showed no preference for the fourth circle from the left compared to the fourth from the right. This suggests monkeys may not have a directionality bias for number-space mappings. Therefore, the left-to-right bias in humans may be due to specific cultural practices.

Keywords: mental number line; numbers; space; monkeys; language; culture

Introduction

Humans use spatial position to mentally represent and manipulate numbers, often mapping small numbers on the left and larger numbers on the right (Walsh, 2003). This linear spatial representation of numbers is often referred to as a "mental number line" (Dehaene & Changeux, 1993; Galton, 1880; Moyer & Landauer, 1967). More specifically, left-to-right number space associations are often seen in Western adults with left-to-right writing systems. This was initially reported in experiments testing for a SNARC effect, or Spatial Numerical Association of Response Codes Effect (Dehaene, Bossini, & Giraux, 1993). French subjects, whose language is written left to right, were asked to click one of two keys located on either side of a keyboard to report whether a given number was less than five (small) or greater than five (large). They showed faster reaction times to smaller numbers when they clicked a key on the left side of the keyboard and faster reaction times to larger numbers when they clicked a key on the right side. This pattern of response times suggests that the French subjects were spatially representing numbers in order from left to right. A similar study (Shaki, Fischer, & Petrusic 2009) looked at Arabic speakers, whose language is written right to left, and they showed a trend in the opposite direction: they had faster reaction times for smaller numbers when they clicked a key on the *right* side, and faster reaction times for larger numbers when they clicked a key on the *left* side. This pattern suggests that Arabic speakers spatially represented numbers in order from right to left. A host of other studies support that: 1) Western adults with a left-to-right writing system associate smaller numbers with the left side and larger numbers with the right side (Dehaene & Cohen, 1997; Loetscher et al., 2008; Vuilleumier, Ortigue, & Brugger, 2004; Wood et al., 2008; Zorzi, Priftis, & Umiltà, 2002), and 2) adults with a right-to-left writing system associate smaller numbers with the right side and larger numbers with the left side (Shaki, Fischer, & Göbel, 2012; Zebian, 2005; although this evidence is somewhat mixed, see Pitt & Casasanto, 2020). These studies suggest that specific cultural practices can influence the directionality of number-space mappings. It is unclear if cultural experience is the only factor though. One proposal suggests that humans (and other animals) do not have an inherent directionality to their number-space mapping, and that directionality is developed through specific cultural practices (Pitt & Casasanto, 2019; Pitt et al., 2021). Another proposal is that humans and animals have an innate bias to represent numbers from left-to-right. This hypothesis proposes that this innate bias (which may also be present in other animals) is then reinforced or reversed based on specific cultural practices (Bulf, de Hevia, & Macchi Cassia, 2016; de Hevia et al., 2014; Rugani et al., 2007).

Number-space mappings in humans with different cultural practices

One way to test these theories is by studying number-space mapping in humans in the process of learning specific cultural practices: children. English-speaking children show evidence of a left-to-right mental number line at ages 9-10 years (Berch et al., 1999), ages 6-7 years, (Cooney et al., 2021; Van Galen & Reitsma, 2008; White et al., 2012), and ages 4-5 years (Opfer et al., 2010). There is some evidence

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that even newborn infants may show a left-to-right number-space mapping (de Hevia et al., 2014; de Hevia et al., 2017). These studies showing early left-to-right number-space mapping suggest that the left-to-right number-space mapping either develops very early or is potentially innate.

However, these findings are at odds with what has been found in populations with limited literacy and a lack of Western cultural practices such as Tsimane' adults. The Tsimane' live in a largely isolated, farmer-forager society and many Tsimane' adults do not learn to read or write. When Tsimane' adults were asked to order quantities in a linear fashion, they did so according to magnitude, but, as a group, showed no bias for a leftward or rightward direction. This suggests that Tsimane' adults do not have a left-to-right bias (Pitt et al., 2021). By contrast, using the same methods, U.S. adults showed a clear left-to-right bias when ordering quantities by increasing magnitude. This contrast suggests that U.S. adults' left-to-right bias may be culturally dependent, potentially due to the directionality of the English writing system or some other cultural practice not present in Tsimane' culture. U.S. children (ages 3-5 years) were also tested on the same task and, like the Tsimane' adults, showed no overall leftward or rightward directionality when ordering quantities by magnitude. Notably, a bias for a leftward directionality emerged in older children (Pitt et al., 2021). The results of both the Tsimane' adults and young U.S. children taken together suggest that there may not be an innate left-to-right bias but instead a left-to-right bias dictated by cultural practices.

Number-space mapping in nonhuman animals

Another way to test if there is an innate bias to represent numbers from left to right is to measure if animals (with no human-specific cultural practices) show the same bias. If nonhuman species show a left-to-right number-space mapping, it would suggest that a left-to-right mapping is not just due to human-specific cultural practices. Several studies of number space-mapping directionality have been conducted by Rugani and colleagues (2007; 2010; 2015) in chicks, using two different methods.

The first method used a comparison task of different dot arrays. Chicks were trained to walk to a center panel with a five-square array and were then tested with pairs of panels with either two-square or eight-square arrays. Given that both arrays on a given trial were the same, chicks with a left-to-right number-space mapping should choose the two-square array on the left (associating 'two' to the left of 'five') and the eight-square array on the right (associating 'eight' to the right of 'five'). Indeed, chicks tended to walk towards the two-dot array on the left and the eight-dot array on the right, showing evidence for a left-to-right number-space mapping. In the second method, Rugani et al. trained chicks to attend to the ordinal position (e.g., first, second) of an element within an array (2007; 2010). Chicks were given a vertical array of ten elements and trained to walk to and peck at the fourth element from their starting position at the bottom of the array. When presented with a horizontal array in testing, they pecked at the fourth element from the left significantly above chance. This suggests that chicks may have assigned ordinal position in a left-to-right direction during testing, which suggests chicks have a left-to-right number-space mapping. Notably, both types of studies were conducted on three-day-old chicks, suggesting that the directionality of the number-space mapping in chickens is innate, and not due to environmental exposure.

However, there are alternative explanations for these effects. First, birds show a phenomenon called "pseudoneglect" in which they visually attend to stimuli on the left side more than the right side (Diekamp et al., 2005; Wilzeck & Kelly, 2012). Second, birds have lateralized visual fields, such that information from the left side of space is processed in the right hemisphere of the brain, and vice versa (Rogers, 2008). This lateralization of visual fields, as well as left-biased head turning behaviors (Tommasi, Andrew, & Vallortigara, 2000) in chickens may explain the observed effects, even in the absence of any number-space mapping. Humans and other primates, conversely, intake visual information from both sides of space and process across both hemispheres, which are connected via the corpus callosum and other interhemispheric connections not found in birds (Howard, Rogers, & Boura, 1980). Therefore, nonhuman primates may offer more insight on factors underlying the left-to-right number-space mapping found in Western humans.

Beran and colleagues (2019) tested for an inherent directionality of number-space mapping in capuchins and rhesus monkeys, adapting the comparison method from Rugani and colleagues (2015). Monkeys were trained to choose either the larger or the smaller of two arrays of dots shown side by side. They were then tested on arrays containing the same number of dots, either two or eight. If these monkeys had a left-to-right number-space mapping, we would expect them to associate small numbers on the left and large numbers on the right. Therefore, we would expect them to pick the two-dot array on the left and the eight-dot array on the right. Monkeys did not select an array on one side more than the other, failing to show evidence of either a left-to-right or a right-to-left number-space mapping.

Drucker and Brannon (2014) also tested for an inherent directionality of number-space mapping in nonhuman primates, adapting the array method from Rugani and colleagues (2007; 2010). They trained four rhesus monkeys to tap the fourth circle from the bottom in a five-circle vertical array. To encourage the monkeys to map ordinal position in a bottom-to-top direction, they had to begin every trial by tapping a box below where the array would later appear. They then presented monkeys with the same five circles, now in a horizontal array. Monkeys selected the fourth circle from the left significantly more often than the other circles. This suggests that they assigned ordinal position in a left-to-right direction and may have a left-to-right number-space mapping.

Given the mixed results on the directionality of a number-space mapping in monkeys (Drucker & Brannon, 2014;

Beran et al., 2019), we sought to replicate the methods of Drucker and Brannon with a larger sample of ten rhesus monkeys. We trained monkeys to tap the fourth circle in a vertical five-circle array, then presented them with a horizontal five-circle array. If monkeys have a left-to-right number-space mapping, they should transfer the fourth circle from the bottom to the fourth circle from the left. If monkeys have a right-to-left number-space mapping, they should pick the fourth circle from the right. If instead we find similar rates, this would suggest that the directionality of number-space mappings is not innate and may be culturally learned.

Methods

Subjects

We tested ten rhesus monkeys (*Macaca mulatta*, mean age = 6 years, range = 4-8 years) from the Harlow Primate Laboratory. Monkeys were pair-housed and separated for testing within their home enclosure. All monkeys were experimentally naive. All animals were socially housed in the Harlow Center for Biological Psychology, and all procedures were approved by the Institutional Animal Care and Use Committee at the University of Wisconsin-Madison.

Materials

Monkeys used a touch screen system consisting of a hollow metal box (19.5" x 15.25" x 10") outfitted with a 15.6" touch screen frame, containing a 15.6" touch screen computer (HP Envy x360 Convertible) and an automated food pellet delivery system (Med Associates) with nutritionally complete primate food pellets (190mg, Dustless Precision Pellets Primate, Purified, Bio-Serv).

Procedure

We closely followed Drucker and Brannon's (2014) procedure. Monkeys were shown a vertical array of five ovals on the screen. Ovals measured 1 9/16" x 7/8" and were evenly spaced apart by 5/8". Following Drucker and Brannon (2014), all trials in both training and testing began with a red "start box" displayed on the bottom of the screen that the monkey needed to select to move on. This start box at the bottom of the screen was included to encourage monkeys to think of the target oval in relation to the start box, and thus as the fourth oval from the bottom, not the second oval from the top. After a two second delay, a vertical array of five ovals (or, in the last phase, circles) was shown. Monkeys were rewarded with a food pellet for tapping the fourth oval from the bottom.

All training sessions consisted of 200 trials. The goal of the first six training phases was to orient the monkey to the target fourth oval from the bottom. In training phase one, monkeys were presented with an array of five ovals in which all ovals were black except the target fourth oval, which was green with three white horizontal stripes. As the phases progressed, this target fourth oval gradually faded until it was black in the sixth training phase, matching the rest of the oval array. An oval was considered selected when monkeys tapped the invisible rectangular space enclosing the oval on all sides. Correct responses resulted in a positive sound, a green screen shown for two seconds, and a food pellet reward. Incorrect responses resulted in a negative sound, a red screen shown for four seconds, and no food reward. We used an intertrial interval of two seconds for all training phases.

The criterion to pass Training Phase One was to tap the fourth oval from the bottom on 80% of all trials in a session. Selecting any other oval was considered an incorrect response. Criterion to pass Training Phases Two and Three was 70% accuracy on one session, to pass Phases Four and Five was 60% accuracy on one session, and to pass Training Phase Six (when all ovals were black) monkeys needed 50% accuracy on two consecutive sessions. The last training phase was Training Phase Circle, in which the stimuli were switched to circles to avoid cueing rotation later in testing. Monkeys passed by completing one session at 80% accuracy or five consecutive sessions at 60% accuracy. All training phases consisted of 100 trials, whereas Drucker and Brannon (2014) ran 50 trials per session. Drucker and Brannon required two sessions of Training Phase Circle, including one at 80% accuracy, so the training was comparable across both studies.

Testing sessions were comprised of a subset of testing trials mixed in with additional training trials. Training trials were the same as those from Training Phase Circle (see Fig. 1A). Testing trials consisted of five black circles in a horizontal array (see Fig. 1B), instead of a vertical array. Testing trials were non-differentially reinforced; monkeys always earned positive feedback (pellet, positive sound, green screen) for any choice on these trials. Testing sessions had 24 testing trials interleaved with 48 training trials. Sessions began with three training trials and then continued randomly between training and testing trials. Each monkey ran on ten testing sessions, for a total of 240 testing trials and 480 training trials per monkey.

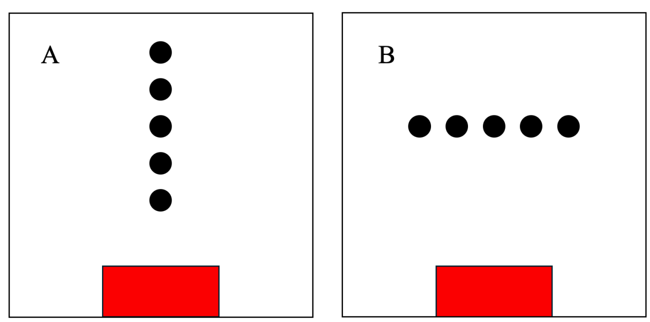

Figure 1: Stimuli for the training phase (A) and the testing phase (B). In all trials, the red "start box" appears and disappears before the array is shown.

Results

On the final phase of training (Train Phase Circle), monkeys picked the fourth circle from the bottom on 87.4% of trials, and this was significantly higher than chance levels of 20% (two-sided one-sample binomial, $p < 0.001$). They maintained these levels of high accuracy on training trials throughout the testing sessions, both as a group (84.2%, two-sided one-sample binomial, $p < 0.001$; Fig. 2, triangles) and individually (63.3 – 98.3%, two-sided one-sample binomials, all p's < 0.001; Fig. 3, triangles).

To test if monkeys had a spontaneous bias to represent ordinal position from left to right, we analyzed the first twelve testing trials for each monkey, following Drucker and Brannon (2014). We used two-sided one-sample binomial tests to determine if the monkeys picked a specific circle above chance levels of 20%. As a group, monkeys chose the fourth circle from the left (13.3%) and the fourth circle from the right (19.2%) less often than chance (Fig. 2, squares). Neither of these differences were significant (two-sided one-sample binomials, 4th from left: $p = 0.068$, 4th from right: $p = 0.909$) . Instead, overall monkeys picked the first circle from the left significantly above chance (39.2%, two-sided one-sample binomial, $p < 0.001$). In fact, most monkeys picked the first circle from the left on the first testing trial. Additionally, we tested if there was a significant difference in the number of fourth from the left and fourth from the right choices. If monkeys prefer a left-to-right number-space mapping compared to a right-to-left number-space mapping, we should see a preference for the fourth circle from the left. However, we did not find a significant preference of the fourth circle from the left over the fourth from the right (Fisher's exact test, $p = 0.307$). Taken together, these results suggest that monkeys overall do not show evidence for a left-to-right (or a right-to-left) number-space mapping.

We then looked at monkeys' individual performance (Fig. 3). We found mixed evidence of a directional number-space mapping. Only one monkey picked the fourth circle from the left significantly above chance (Subject 9: 66.7%, two-sided one-sample binomial, $p < 0.001$) and only two monkeys picked the fourth circle from the right significantly above chance (two-sided one-sample binomials; Subject 4: 50.0%, binomial, $p = 0.0194$; Subject 6: 50.0%, binomial, $p = 0.0194$). Notably, four monkeys chose the first circle from the left significantly above chance and more often than any other circle (two-sided one-sample binomials; Subjects 1, 2, 3, and 7: 50.0 – 100%, all binomial tests, all p's < 0.05). This suggests that some monkeys applied a number-space mapping of ordinal position when choosing a circle on test trials, and others did not.

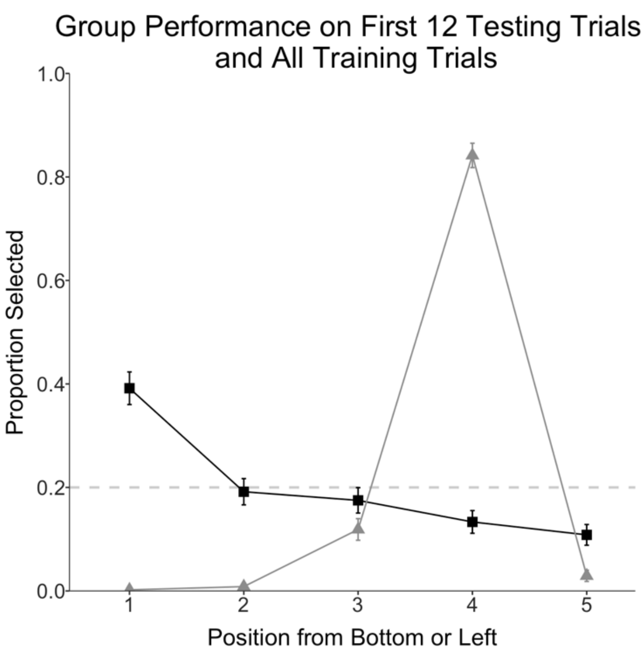

Figure 2: Group performance on the first 12 testing trials (squares) and all training trials (triangles). Error bars represent standard error of the mean. The dotted line represents chance levels of 20%.

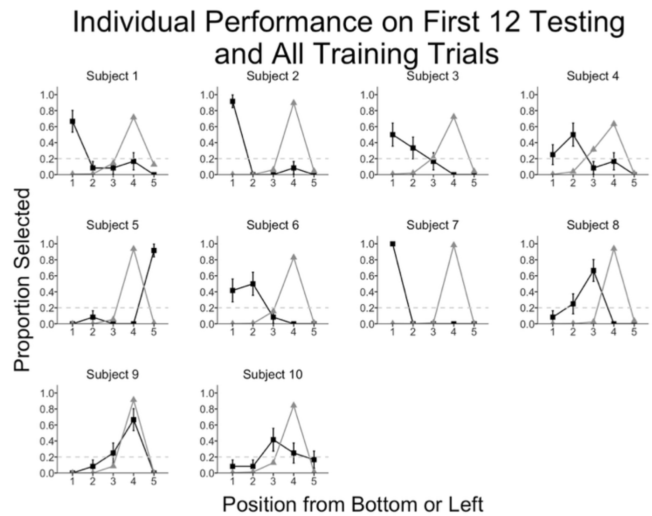

Figure 3: Individual performance on the first 12 testing trials (squares) and all training trials (triangles). Error bars represent standard error of the mean. Dotted line represents chance levels.

To further test if our monkeys had a direction-specific number-space mapping, we analyzed testing trials from all testing sessions (n = 240, per monkey). As a group, monkeys chose the fourth circles from the left (10.2%) and the right (13.5%) below chance levels of 20% (two-sided one-sample binomials, 4th from left: $p < 0.001$, 4th from right: $p < 0.001$). Furthermore, monkeys as a group chose the first circle from the left significantly above chance (41.1%, all two-sided one-sample binomial tests, all p's < 0.001). This suggests that monkeys had no inherent directionality to their number-space mappings.

We also looked for direction-specific number-space mapping in individual monkeys across all testing trials (Fig. 4). Six monkeys had no preference for the fourth circles from the left or the right above chance levels of 20%. Two monkeys picked the fourth circle from the left significantly above chance (two-sided one-sample binomials; Subject 4: 33.3%, binomial, $p < 0.001$; Subject 10: 30.4%, binomial, $p < 0.001$). Two monkeys picked the fourth circle from the right significantly above chance (two-sided one-sample binomials; Subject 3: 59.6%, binomial, $p < 0.001$; Subject 9: 28.3%, binomial, $p < 0.001$). Finally, of the six monkeys that picked neither the fourth circles from the right or left above chance, five monkeys picked the first circle from the left significantly above chance (Subjects 1, 2, 3, 6, and 7: 25.4 – 99.6%, all two-sided one-sample binomial tests, all p's < 0.05). Overall, after expanding our dataset we still find no clear evidence for an inherent directionality in the number-space mapping of rhesus monkeys.

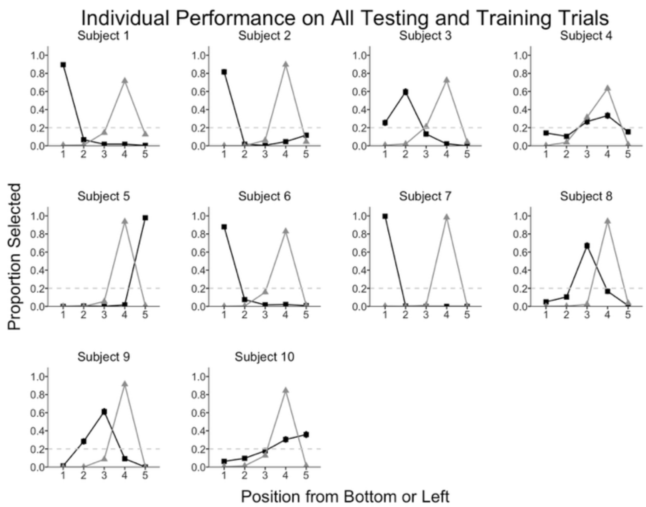

Figure 4: Individual performance on all testing trials (squares) and training trials (triangles). Error bars represent standard error of the mean. Dotted line represents chance levels of 20%.

Discussion

We investigated whether monkeys show directionality in their number-space mapping, which has previously been taken as evidence that left-to-right number-space mapping is not solely due to human cultural practices. Our goal was to replicate the findings from Drucker & Brannon (2014). They found that their four monkeys, as a group and individually, preferred the fourth circle from the left, providing evidence for a left-to-right number-space mapping. The results from our replication were quite different. Only one of our ten monkeys picked the fourth circle from the left significantly above chance, while two monkeys picked the fourth circle from the right significantly above chance. When we analyzed all 240 trials from each monkey, we found similar results: two monkeys picked the fourth circle from the left significantly above chance and two monkeys picked the fourth circle from the right significantly above chance.

We found that monkeys most often chose the first circle from the left. None of the monkeys studied by Drucker and Brannon (2014) showed this preference for the first circle from the left. That our ten monkeys most often chose the first circle from the left can be explained in two ways, both of which would require further testing. First, monkeys may have picked the leftmost circle because they demonstrate a "pseudoneglect", focusing more of their attention to stimuli on their left than their right, a phenomenon also reported in humans (Friedrich, Hunter, & Elias, 2018). A pseudoneglect of the right side in favor of the left side has been attributed as an alternate explanation for a left-to-right number-space mapping for studies in rhesus monkeys (Rugani et al., 2024) and chicks (Rugani et al., 2007; Rugani et al., 2010). Second, the pellet dispenser on our touch screen device is located below and to the left of the screen displaying the task. The leftmost circle in the array is closest to the pellet dispenser, so monkeys may have chosen this circle due to its proximity to the reward. However, it is important to note that if there is a directionality to number-space mapping in rhesus monkeys that could be influenced by a feature like the placement of the pellet dispenser, then any bias could not be very strong.

Resolving differences between our results and those of Drucker & Brannon. Drucker and Brannon report that all study subjects had previous experience on touch-screen tasks unrelated to their study of number-space mapping. However, there is a chance that the Western adult bias of a left-to-right number-space mapping was imposed *unknowingly* through the design of these other touch-screen tasks. Given that the monkeys tested in the current study were either completely experimentally naïve or had very minimal experience with cognitive testing (<1 year), this could account for the differences in results.

Conclusions

There is a wealth of evidence suggesting that the left-to-right mental number line found in Western humans is influenced by culture-specific practices such as the left-to-right writing system (Dehaene et al, 1993; Shaki et al., 2009; Zebian, 2005). However, the evidence for an innate left-to-right bias is much less clear. Here, we chose to study the directionality of number-space mapping in rhesus monkeys because they are neurally (Diamond, 1990) and cognitively (Malkova, Heuer, & Saunders, 2006) similar to humans, more so than other animals like birds (Rugani et al., 2007) or bees (Giurfa et al., 2022). Here, we were unable to replicate one of the strongest findings (Drucker & Brannon, 2014) for a left-to-right mental number-space mapping in nonhuman primates and instead find no preference for a left-to-right or a right-to-left mental number-space mapping in our sample of ten monkeys. Our work supports the theory that the direction of a direction-specific number-space mapping is not innate. Instead, our evidence suggests that it is dictated just by human cultural practices. Taken together, the lack of inherent direction-specificity in monkeys (in the present study), adults from a non-Western, non-literate culture (Pitt et al., 2021), and young children suggests that there may not be an innate left-to-right number-space mapping. Instead, these results suggest that the directionality of number-space mapping develops according to specific cultural practices.

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