

RESEARCH ARTICLE

Neural association between non-verbal number sense and arithmetic fluency

Mengyi Li^{1,2,3} | Dazhi Cheng^{1,2,4} | Yujie Lu^{1,2,3} | Xinlin Zhou^{1,2,3} 

¹State Key Laboratory of Cognitive Neuroscience and Learning, IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing, China

²Advanced Innovation Center for Future Education, Beijing Normal University, Beijing, China

³Siegler Center for Innovative Learning, Beijing Normal University, Beijing, China

⁴Department of Pediatric Neurology, Capital Institute of Pediatrics, Beijing, China

Correspondence

Xinlin Zhou, State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875, China.

Email: zhou_xinlin@bnu.edu.cn

Funding information

Advanced Innovation Center for Future Education, Grant/Award Number: 27900-110631111; Chinese Academy of Medical Sciences Initiative for Innovative Medicine, Grant/Award Number: 2016-I2M-1-008; Higher Education Discipline Innovation Project, Grant/Award Number: BP0719032; National Natural Science Foundation of China, Grant/Award Numbers: 31671151, 31700977

Abstract

Non-verbal number sense has been shown to significantly correlate with arithmetic fluency. Accumulated behavioral evidence indicates that the cognitive mechanism relies on visual perception. However, few studies have investigated the neural mechanism underlying this association. Following the visual perception account, we hypothesized that there would be a neural association in occipital areas of the brain between non-verbal number sense, arithmetic fluency, and visual perception. We analyzed event-related potentials that are sensitive to neural responses while participants performed five cognitive tasks: simple addition, simple subtraction, numerosity comparison, figure matching, and character rhyming. The single-trial ERP-behavior correlation approach was used to enhance the statistical power. The results showed that the N1 component significantly correlated with reaction time at occipital electrodes on all tasks except for character rhyming. The N1 component for arithmetic fluency (simple addition and subtraction) and character rhyming correlated with the reaction time for numerosity comparison and figure matching. The results suggest that there are neural associations between arithmetic fluency, non-verbal number sense, and visual perception in the occipital cortex, and that visual perception is the shared mechanism for both non-verbal number sense and arithmetic fluency.

KEYWORDS

arithmetic fluency, event-related potentials, non-verbal number sense, single-trial ERP-behavior correlation, visual perception

1 | INTRODUCTION

Non-verbal number sense is the ability to perceive the number of items in a typical visual or auditory array with more than three items. Several lines of evidence suggest that skill in this ability correlates with mathematics achievement (e.g., Halberda, Mazocco, & Feigenson, 2008; Libertus, Feigenson, & Halberda, 2011; Lyons &

Beilock, 2011). First, non-verbal number sense has been linked to individual differences in mathematics achievement in typically developing children (e.g., Bonny & Lourenco, 2013; Halberda et al., 2008; Halberda, Ly, Wilmer, Naiman, & Germine, 2012; Inglis, Attridge, Batchelor, & Gilmore, 2011; Libertus et al., 2011; Libertus, Feigenson, & Halberda, 2013; Mazocco, Feigenson, & Halberda, 2011; Mundy & Gilmore, 2009). Second, children with developmental dyscalculia show severe impairment in numerosity judgment (e.g., Cheng, Xiao, Chen, Cui, & Zhou, 2018; Geary, Bailey, &

Mengyi Li and Dazhi Cheng contributed equally to this study.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2020 The Authors. *Human Brain Mapping* published by Wiley Periodicals LLC.

Hoard, 2009; Landerl, Bevan, & Butterworth, 2004; Piazza et al., 2010). Specifically, they had deficits in counting dots (Butterworth, 2005; Landerl et al., 2004; Zhang et al., 2016). Third, training on non-verbal number sense can facilitate mathematical development (e.g., Hyde, Khanum, & Spelke, 2014; Park & Brannon, 2013).

Domain-specific explanations for the association emphasize shared processing of quantity (Hyde et al., 2014; Landerl et al., 2004; Park & Brannon, 2013). The processing of numerical quantity has thus been proposed to underlie the association between non-verbal number sense and arithmetic fluency (e.g., Halberda et al., 2008). Evidence for this idea comes from neuroimaging studies which showed that processing numerosity and doing arithmetic problems activated the same brain areas (i.e., bilateral intraparietal sulcus) (e.g., Ansari & Dhital, 2006; Izard, Dehaene-Lambertz, & Dehaene, 2008).

In contrast, a domain-general hypothesis provides an alternative explanation for the association between numerosity processing and arithmetic fluency from the viewpoint of general cognitive processing. Visual perception, as measured by a geometric figure-matching task, has emerged as a critical general cognitive mechanism that is shared between non-verbal number sense and arithmetic fluency (Cheng et al., 2020; Cui, Zhang, Cheng, Li, & Zhou, 2017; Wang, Sun, & Zhou, 2016; Zhou, Hu, Yuan, Gu, & Li, 2020; Zhou, Wei, Zhang, Cui, & Chen, 2015). For example, Zhou et al. (2015) showed that visual perception measured with such a task could fully account for the association between non-verbal number sense and arithmetic fluency. Cheng et al. (2018) and Zhou and Cheng (2015) found that the children with developmental dyscalculia had concurrent deficits in visual perception processing and non-verbal number sense, and that the visual perception deficit accounted for the non-verbal number sense deficit.

Although some behavioral evidence points toward an association between non-verbal number sense, arithmetic fluency, and visual perception, the neural mechanisms underlying such an association remains unclear. The aim of the current investigation was to determine a neural mechanism underlying the association between non-verbal number sense and arithmetic fluency. Based on the visual perception hypothesis, we expected the association in the brain to be located in the occipital cortex.

Event-related potentials (ERPs) recorded from the scalp are an ideal tool for investigating potential neural mechanisms that link non-verbal number sense and arithmetic fluency. First, ERPs over the occipital cortex can demonstrate that visual perception has occurred. For example, a study combining electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) found that visual stimuli presented in the left or right visual fields induced larger N1 ERP components over the contralateral side than over the ipsilateral side of the occipital cortex, corresponding to greater activation in the contralateral middle occipital gyrus than in the ipsilateral middle occipital gyrus (Novitskiy et al., 2011). Second, ERPs can be recorded at high temporal resolution, allowing visual perception to be detected at very early stages of cognitive processing, which is important when studying perception during arithmetic fluency and character rhyming.

Associations between non-verbal number sense and arithmetic fluency can be found using a correlation approach based on individual differences (e.g., Cui et al., 2019; Halberda et al., 2008; Zhou et al., 2015). Indeed, ERP-behavior correlations have been used to determine the neural mechanisms underlying associations, with single-trial interindividual correlation typically being applied to greatly enhance statistical power (Zhou, Li, Zhou, Li, & Cui, 2018).

To maintain consistency with the procedures used in previous behavioral studies of the association between non-verbal number sense and arithmetic fluency (e.g., Cheng et al., 2018; Cui et al., 2017; Cui et al., 2019; Wang et al., 2016; Zhang, Liu, Chen, & Zhou, 2019; Zhou et al., 2015; Zhou & Cheng, 2015), we used similar tasks in the current study, including numerosity comparison, figure matching, simple addition, simple subtraction, and character rhyming.

According to the visual perception hypothesis, we predicted that when measuring non-verbal number sense or arithmetic fluency, a correlation between an ERP component and task behavior should be observed at the occipital electrodes. Then, the arithmetic ERP at occipital electrode(s) should correlate with the reaction time and/or error rate for both non-verbal number sense and visual perception.

2 | MATERIALS AND METHODS

2.1 | Participants

Forty healthy right-handed university students (19 males and 21 females) were recruited from Peking University, Tsinghua University, and Beijing Geely University. Participants majored in a wide range of disciplines other than mathematics. Their average age was 19.8 years (range: 18–23 years). Participants self-reported having normal or corrected-to-normal eyesight and normal hearing. All procedures were approved by the institutional review boards (IRBs) of Beijing Normal University. Participants gave their written informed consent before the experiment and were compensated 200 RMB (about 30 USD) for their time.

2.2 | Procedures

The experiment had five tasks: figure matching, numerosity comparison, simple addition, simple subtraction, and character rhyming. The task order was balanced across participants using a Latin-square design. The experiment was performed on a computer and tasks were presented using E-prime software (Carnegie Mellon University, Pittsburgh, PA). In each trial, a 200–400 ms fixation was presented followed by a blank screen for 300 ms. Target stimuli were then presented for 100 ms followed by another black screen that lasted until participants used the keyboard to choose an answer. When participants chose the answer, the next trial began automatically after a fix intertrial interval (ITI) for 1,000 ms. The experimental procedure and task paradigm are shown in Figure 1.

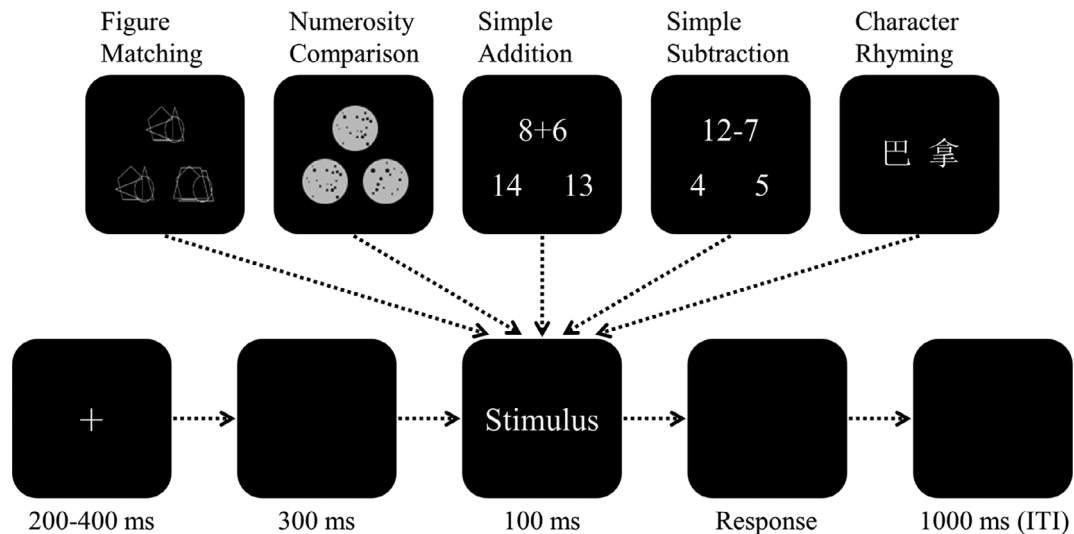


FIGURE 1 Example stimuli for each task (figure matching, numerosity comparison, simple addition, simple subtraction, and character rhyming tasks) and a schematic depicting the experimental procedure. ITI, intertrial interval

2.3 | Tasks

2.3.1 | Figure matching

This task was adapted from the picture test in Ekstrom, French, Harman, and Dermen (1976). Each trial containing one target picture in the center of the monitor and two candidate pictures beneath the target. The pictures were constructed from 240 abstract line figures. Participants were asked to judge which of the two candidate pictures was the same as the target. Choices were made by pressing the “Q” (left candidate) and “P” (right candidate) keys on the keyboard. The task comprised 120 trials that were divided into two 60-trials blocks.

2.3.2 | Numerosity comparison

Three dot arrays were presented simultaneously on the screen. The target array was presented in upper part of the screen, and two candidate arrays were presented in the lower half of the screen. Participants were asked to judge which candidate array contained the same number of dots as the target array. However, as this was not a matching task, the layout of the dots differed even when the number of dots was the same. For half of the trials, the total area taken up by the dots was the same for all three arrays. For the other half, the average area for a single dot (total area/number of dots) was the same for all three arrays. Dot size varied and dots were randomly distributed within a circle. Choices were made by pressing the “Q” (left candidate) and “P” (right candidate) keys on the keyboard. The task comprised 120 trials that were divided into two 60-trials blocks.

2.3.3 | Simple addition

We used a simple single-digit addition task. For each trial, an addition problem was presented in the middle of the upper part of the screen

and two candidate answers, one of which was correct, were presented side by side in the lower part of the screen. Participants were asked to choose the correct answer by pressing the “Q” (left candidate) and “P” (right candidate) keys on the keyboard. There are 81 possible single-digit addition problems starting from $1 + 1$ and ending at $9 + 9$. To avoid repeating the same problem more than once, this test only had 81 trials.

2.3.4 | Simple subtraction

The subtraction problems were the reversed calculations from the single-digit addition. Thus, there are 81 possible problems starting from 2 to 1 and ending at 18 to 9. Again, to avoid repeating problems, this test only had 81 trials. All other aspects of the task were the same as the simple addition task.

2.3.5 | Character rhyming

Two Chinese characters were presented simultaneously on the screen. Participants were asked to judge whether they rhymed or not. This test had 120 trials.

2.4 | ERP recording and preprocessing

EEGs were recorded using a 32-channel NeuroScan recording system (Neurosoft Inc., Sterling, VA). Scalp electrodes were online referenced to the left mastoid and off-line algebraic re-referenced to the average of the left and right mastoids. The distribution of electrodes was set according to the international 10–20 system. Vertical electrooculograms (EOGs) were recorded supra- and infra-orbitally at the left eye and horizontal EOGs were recorded from the left vs. right orbital rim.

Impedances for all electrodes were kept below 5 k Ω . EEG and EOG signals were filtered with a 0.05–100 Hz bandpass filter and continuously sampled at 1000 Hz/channel.

The ERP data were analyzed using NeuroScan EDIT software Version 4.3 (Neurosoft Inc., Sterling, VA) and Matlab R2015a (Mathworks Inc., Natick, MA). Offline, a direct current (DC) correction was applied, and ocular artifacts were then corrected. The trigger threshold for ocular artifacts was set to 10%. The minimum number of sweeps that were required to construct an averaged vertical EOG artifact was 20. The duration of the average artifact was 400 ms. After correcting for ocular artifacts, the continuous EEG data were segmented into epochs starting from 200 ms before stimulus onset and continuing until 1,500 ms after stimulus onset. A 200-ms pre-stimulus period served as the baseline. EEG data were detrended and baseline corrected. Epochs outside the range of -100 to 100 μ V at any channel except for the horizontal and vertical EOGs were rejected as artifacts.

2.5 | ERP analysis

After preprocessing, data from remaining trials with correct responses were averaged for each task and for each participant. The mean number of valid trials (epochs) included in the averaged ERPs were 87.2 ± 11.3 (SD) for figure matching, 82.5 ± 13.8 for numerosity comparison, 72.1 ± 6.0 for simple addition, 70.2 ± 8.1 for simple subtraction, and 99.6 ± 15.3 for character rhyming. The averaged waveform was low-pass filtered at 30 Hz (zero-phase, 12 dB/octave). The grand average for each task was obtained by averaging across the individual participant averages, separately for each task.

2.6 | ERP-behavior correlation analysis

An ERP-behavior correlation analysis can determine how non-verbal number sense, arithmetic fluency, and visual perception are associated in brain. We applied a single-trial (item-wise) interindividual correlation that has been used in a previous functional neuroimaging study (Zhou et al., 2018). In this two-step process, first, an interindividual correlation was performed on each trial. Then, a one-sample *t* test was conducted on the *r*-values for all trials. The traditional mean-trial interindividual correlation simply performs a correlation on the averaged responses. The single-trial correlation can be more effective than the mean-trial correlation because it can filter out much of the noise that exists after the first step (Zhou et al., 2018).

In the single-trial interindividual correlation approach in the current ERP study, first we computed the correlation between the ERP (i.e., magnitude of the potential) and behavior (i.e., reaction time or error rate) for each trial of a task after rejecting artifacts during preprocessing. And only correct trials were included in the correlation analysis between ERP and reaction time. Then we performed a one-sample *t* test on the correlation coefficients obtained for all trials of the task against zero. The analysis was performed separately for each task.

This technique can also be used to assess ERP-behavior correlations across two different tasks (e.g., the ERP for simple addition and the behavioral responses for numerosity comparison). This correlation can indicate whether the ERPs are generally associated with a certain type of cognitive processing. There are no one-to-one corresponding relationships between the ERPs and the behavioral responses in the correlation analysis. Therefore, the ERPs for each trial within a task (e.g., task A) were first correlated with the behavioral response for each trial of another task (e.g., task B). For example, if task B had 30 trials, there would be 30 *r*-values for each trial from task A. The *r*-values were then averaged and represented the correlation coefficient for that trial in task A. After calculating the average *r*-values for each trial in the task A, we then performed a one-sample *t* test on all the average *r*-values against zero.

The traditional mean-trial interindividual correlation was also used. This involved first computing the mean ERP across trials and the mean performance for each task for each participant. Then, we performed a correlation analysis between the mean ERP magnitudes and the behavioral data across participants. These results were compared with those from the single-trial correlation.

3 | RESULTS

3.1 | Behavioral results

Table 1 shows the mean reaction times for correct trials and the error rates for figure matching, numerosity comparison, simple addition, simple subtraction, and character rhyming. The mean-trial Pearson correlation coefficients for the five tasks are also listed. The correlations were typically weak.

3.2 | ERP component N1

The early N1 component of the ERP occurred at bilateral occipital electrodes for all five tasks (figure matching, numerosity comparison, simple addition, simple subtraction, and character rhyming) around 75 ms after stimulus onset and with a peak at around 150 ms. Figure 2 (red lines) shows the grand averaged ERP waveforms of the whole interval (from 200 ms before stimulus onset to 1,500 ms after stimulus onset) at bilateral occipital electrodes for the five tasks. The time interval of the N1 component (between 75 ms to 150 ms after stimulus onset) is marked with vertical dotted lines.

3.3 | Interindividual ERP-behavior correlation for the five tasks

We first analyzed the single-trial and mean-trial interindividual ERP-behavior correlations for figure matching, numerosity comparison, simple addition, simple subtraction and character rhyming. The

TABLE 1 Pearson's correlations between behavioral measures among the five tasks. Mean reaction times for correct trials (millisecond and SE in brackets) and their correlations are above the diagonal. Error rate (% and SE in brackets) and their correlation are below the diagonal

| Task | | 1 | 2 | 3 | 4 | 5 |
|--------------------------|------------|------------|----------|----------|------------|-------------|
| | | 1,009 (65) | 973 (56) | 906 (40) | 1,053 (72) | 1,428 (104) |
| 1. Figure matching | 25.0 (1.3) | – | .82** | .01 | .03 | .13 |
| 2. Numerosity comparison | 29.5 (1.9) | .57** | – | .20 | .19 | .33* |
| 3. Simple addition | 7.9 (1.2) | .24 | .26 | – | .91** | .76** |
| 4. Simple subtraction | 10.7 (1.6) | .39* | .24 | .73** | – | .73** |
| 5. Character rhyming | 14.8 (2.1) | .29 | .15 | .51** | .60** | – |

Abbreviations: ER, error rate; RT, reaction time.

* $p < .05$.

** $p < .01$.

magnitude of the potential at each time point for each electrode was used as the ERP data and reaction time was used as the behavioral data.

The single-trial ERP-behavior correlations waveforms for the whole interval and the topographic t -value maps for the correlation between the N1 component and behavior are presented in Figure 2 for the five tasks (blue lines, correlations waveforms; blue box, topographic t -value map). At left/right occipital electrodes, we observed significant positive ERP-behavior correlations ($p < .05$, Bonferroni corrected) between the N1 component and reaction time for figure matching, numerosity comparison, simple addition, and simple subtraction, but not for character rhyming. When correcting a p -value of .05 using the Bonferroni method, .05 is divided by the number of electrodes and the number of time points. Thus the corrected p -value was 9.80×10^{-7} (.05/30/1701). For figure matching and numerosity comparison, significant positive ERP-behavior correlations ($p < .05$, Bonferroni corrected) were observed at the right occipital electrode (O2), with the highest t -values being 6.86 and 8.30, respectively. For simple addition and simple subtraction, significant positive ERP-behavior correlations ($p < .05$, Bonferroni corrected) were observed at bilateral occipital electrodes (O1 and O2), with the highest t -values being 6.95 and 6.91 for simple addition, and 7.69 and 5.70 for simple subtraction, respectively.

We also analyzed the single-trial ERP-behavior correlation between the N1 component (mean magnitude of the potential between 75 ms to 150 ms after stimulus onset) at whole brain electrodes and reaction time for each task. The significant positive correlations ($p < .05$, Bonferroni corrected) were only observed at occipital electrodes. Table 2 shows the t -values for the correlation at occipital, parietal, central, and frontal electrodes.

The traditional mean-trial ERP-behavior correlations waveforms for the whole interval and the topographic t -value maps for the correlation between the N1 component and behavior are presented in Figure 2 for the five tasks (cyan lines, correlation waveforms; cyan box, topographic t -value map). We compared the results with those from the single-trial ERP-behavior correlation. At right/left occipital electrodes, we again observed positive ERP-behavior correlations between the N1 component and reaction time for figure matching, numerosity comparison, simple addition, and simple subtraction, but

not for character rhyming. Although the uncorrected p -values were significant (less than .05), those after Bonferroni correction were not. For figure matching and numerosity comparison, positive ERP-behavior correlations ($p < .05$ uncorrected) were observed at the right occipital electrode (O2), with the highest t -values being 2.38 and 4.08, respectively. For simple addition and simple subtraction, positive ERP-behavior correlations ($p < .05$, uncorrected) were observed at bilateral occipital electrodes (O1 and O2), with the highest t -values at O1 and O2 electrodes being 2.92 and 2.63 for simple addition, and 2.96 and 2.37 for simple subtraction, respectively.

In addition to reaction time, we performed the same series of analyses for error rate. We did not find any significant correlations at occipital electrodes between the N1 component and error rate for any task, regardless of whether we used the single-trial or mean-trial ERP-behavior correlation. Table 3 shows the mean t -values at the O2 electrode for single-trial and mean-trial ERP-behavior correlations between 75 ms to 150 ms after stimulus onset for the five tasks.

3.4 | ERP-behavior correlation between the academic ERP and cognitive behavior

To determine the neural mechanism underlying the association between non-verbal number sense and arithmetic fluency and the role of visual perception in this context, we analyzed the single-trial ERP-behavior correlation between the ERPs for the three academic tasks (simple addition, simple subtraction, and character rhyming) and reaction times for the two cognitive tasks (figure matching and numerosity comparison). Figure 3 shows the single-trial ERP-behavior correlations waveforms at occipital electrodes (O1 and O2) for the whole interval and the topographic t -value maps for the correlation between the N1 component and behavior.

For the single-trial ERP-behavior correlation between academic ERPs and reaction time for figure matching, we observed significant positive correlations ($p < .05$, Bonferroni corrected) for all three academic tasks between the N1 component and reaction time at right/left occipital electrodes. Positive correlations were observed at bilateral occipital electrodes (O1, O2) for simple addition, with the highest t -values being 7.18 and 5.90, respectively. A positive correlation at

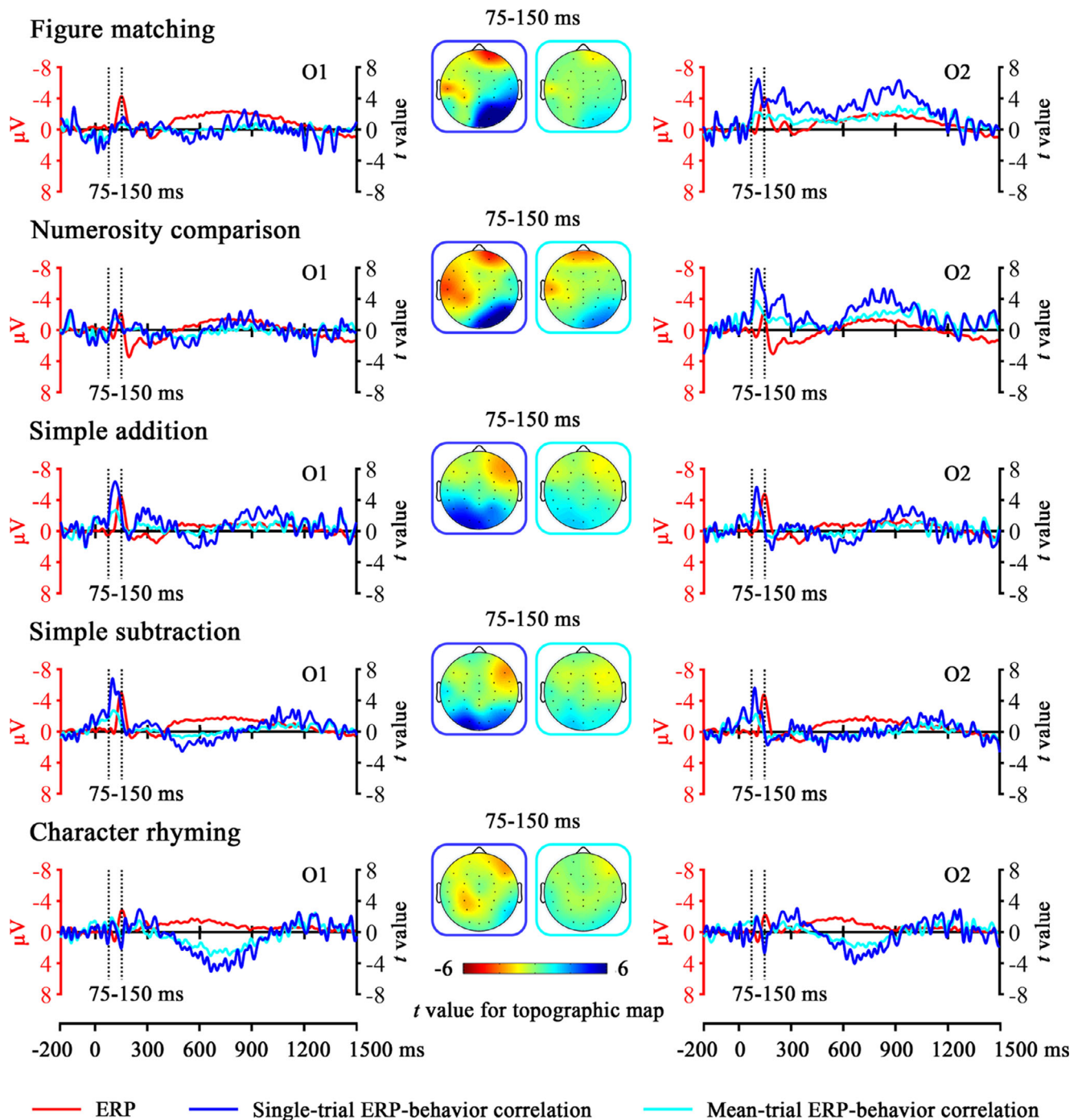


FIGURE 2 The ERP waveforms, the ERP-behavior correlations waveforms at occipital electrodes (O1 and O2), and topographic t -value maps for the five tasks. The ERP waveforms are presented with red lines (left-side y-axis). The single-trial ERP-behavior correlations waveforms are presented with blue lines (right-side y-axis). The traditional mean-trial ERP-behavior correlations waveforms are presented with cyan lines (right-side y-axis). The topographic t -value maps for the single-trial correlations between the N1 component and behavior are presented in the blue box. The topographic t -value maps for the mean-trial correlations between the N1 component and behavior are presented in the blue box

the right occipital electrode (O2) was observed for simple subtraction, with the highest t -value being 8.72. We also observed a positive correlation at the left occipital electrode (O1) for character rhyming, with the highest t -value being 5.51.

For the single-trial ERP-behavior correlation between academic ERPs and reaction time for the numerosity comparison, we observed

significant positive correlations ($p < .05$, Bonferroni corrected) between the N1 component and reaction time at the right occipital electrode (O2) for simple addition and simple subtraction, with the highest t -values being 7.71 and 9.43, respectively. We also found a positive correlation at the left occipital electrode (O1) (181 ms after stimulus onset) for character rhyming, with the highest t -value being 6.96.

TABLE 2 The *t*-values for single-trial ERP-behavior correlation between the N1 component at different electrodes and reaction time for each of the five tasks

| Task | Occipital | | | Parietal | | | Central | | | Frontal | | |
|-----------------------|-----------|-------|-------|----------|-------|-------|---------|-------|-------|---------|-------|-------|
| | O1 | Oz | O2 | P3 | Pz | P4 | C3 | Cz | C4 | F3 | Fz | F4 |
| Figure matching | 0.76 | 5.59* | 6.92* | -0.25 | 1.81 | 4.56 | -1.27 | -0.06 | 0.85 | -0.47 | -0.04 | -0.36 |
| Numerosity comparison | 1.75 | 6.64* | 9.07* | -2.25 | -0.98 | 3.27 | -2.91 | -1.71 | -0.41 | -2.01 | -0.90 | -1.05 |
| Simple addition | 8.08* | 7.58* | 5.50* | 4.95 | 1.94 | 4.07 | 0.81 | 0.55 | -0.56 | -1.01 | -0.91 | -2.59 |
| Simple subtraction | 7.14* | 5.62* | 5.05 | 2.87 | -0.50 | 2.23 | -0.28 | 0.12 | -1.21 | -0.89 | -0.13 | -1.78 |
| Character rhyming | 0.19 | 0.15 | 0.61 | -2.85 | -2.21 | -0.46 | -2.70 | -0.23 | -1.33 | -0.84 | -0.69 | -1.09 |

**p* < .05, Bonferroni corrected.

| Task | ERP-RT correlation | | ERP-ER correlation | |
|-----------------------|--------------------|------------|--------------------|------------|
| | Single-trial | Mean-trial | Single-trial | Mean-trial |
| Figure matching | 4.67 | 1.81 | 1.01 | 0.23 |
| Numerosity comparison | 5.74 | 2.85 | -1.05 | -0.18 |
| Simple addition | 3.34 | 1.48 | -0.61 | 0.29 |
| Simple subtraction | 3.10 | 1.25 | 0.78 | 0.09 |
| Character rhyming | 0.17 | 0.92 | -0.79 | 0.33 |

TABLE 3 Mean *t*-values for single-trial and mean-trial ERP-behavior correlations (75–150 ms after stimulus onset) at electrode O2 for each of the five tasks

Abbreviations: ER, error rate; RT, reaction time.

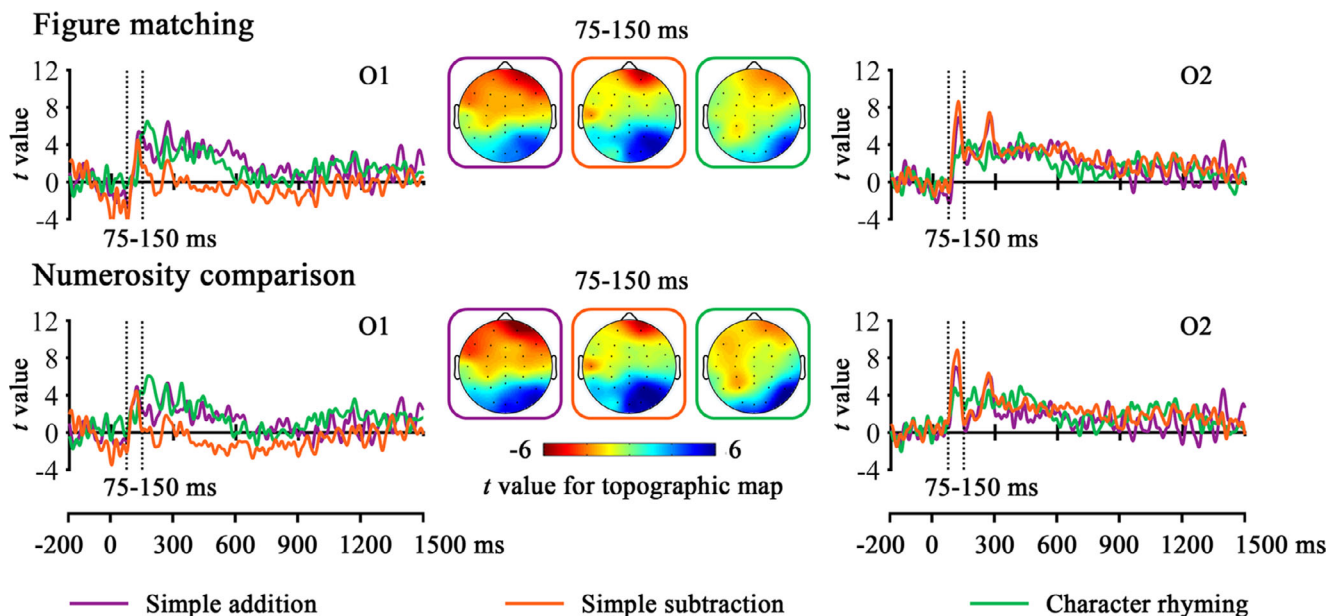


FIGURE 3 Single-trial correlations waveforms between the three academic ERPs and the two cognitive behaviors at occipital electrodes (O1 and O2) and topographic *t*-value maps for the correlation between the N1 component and behavior

To compare results, we then analyzed the mean-trial ERP-behavior correlation between the ERPs for the same three academic tasks and reaction times for the two cognitive tasks. Figure 4 shows the mean-trial ERP-behavior correlations waveforms at

occipital electrodes (O1 and O2) for the whole interval and the topographic *t*-value maps for the correlation between the N1 component and behavior. We found only positive correlations (*p* < .05, uncorrected) between the three academic ERPs and the two

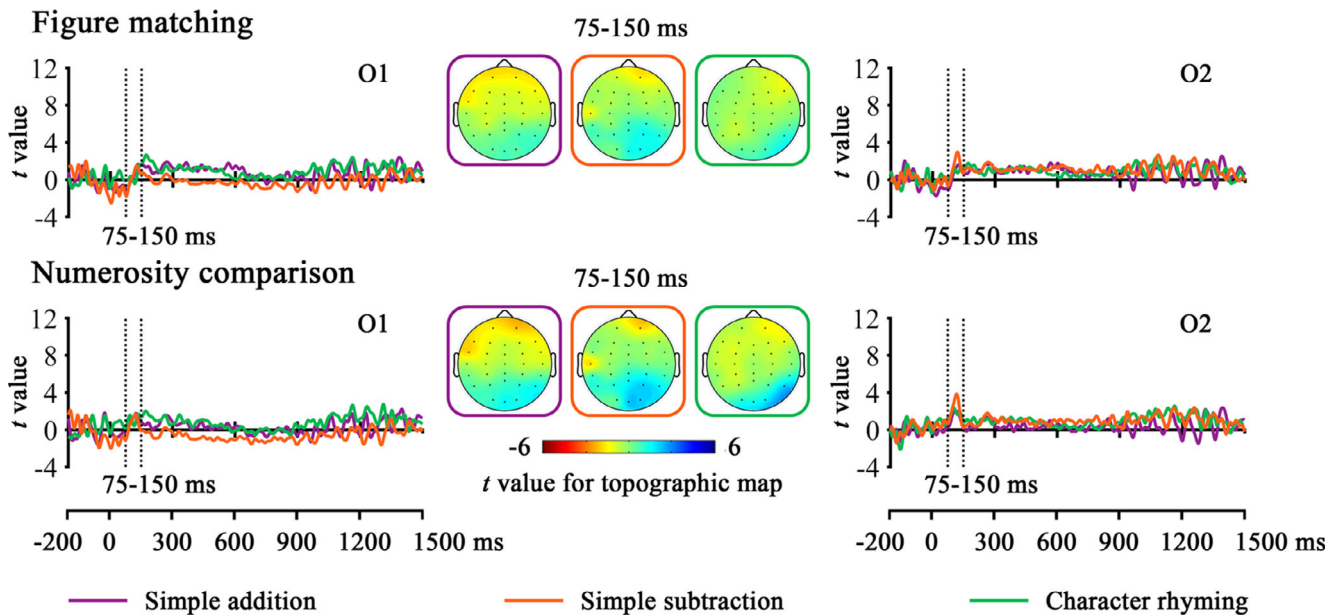


FIGURE 4 Mean-trial correlations waveforms between the three academic ERPs and the two cognitive behaviors at occipital electrodes (O1 and O2), and topographic t -value maps for the correlation between the N1 component and behavior

cognitive behaviors for the N1 component at right/left occipital electrodes.

4 | DISCUSSION

Numerous studies have been devoted to understanding the relationship between non-verbal number sense and mathematics achievement. However, little is known about the neural correlates for this association. The aim of current study was to apply a single-trial ERP-behavior interindividual correlational approach to examine the neural mechanism underlying the association between non-verbal number sense and arithmetic fluency. This analysis revealed significant ERP-behavior correlations on 4 of the 5 tasks (figure matching, numerosity comparison, simple addition, and simple subtraction) between the N1 component at right/left occipital electrodes (typically O2 and O1) and reaction time. Further, the N1 component at the occipital electrodes during arithmetic fluency tasks (simple addition and subtraction) and character rhyming correlated with reaction time during figure matching and numerosity comparison. These results suggest that occipital areas might support the association between non-verbal number sense and arithmetic fluency.

4.1 | The N1 component in visual perception

The N1 component is characterized by the first negativity at the lateral occipital electrode sites. It has been consistently revealed with a peak around 150 ms (Luck, 2005). It is highly sensitive to variations in stimulus parameters, including location, color, luminance, and length. For example, even if the task were to detect the color of the stimuli,

location-repeated stimuli would elicit larger N1 amplitudes than presented in variable locations (Yang, Fan, Wang, Fogelson, & Li, 2017). Additionally, bright stimuli have been shown to induce shorter peak latencies and larger N1 amplitudes than do dim stimuli (Johannes, Munte, Heinze, & Mangun, 1995). Further, stimulus size can also modulate N1; longer stimuli were shown to elicit larger N1 amplitudes than shorter stimuli (Wydell, Vuorinen, Helenius, & Salmelin, 2003). Moreover, the N1 component is sensitive to the level of expertise. When participants have some expertise or familiarity related to the stimuli, N1 is larger than when they do not. For instance, letters or words evoked larger N1 components than did symbols or form strings in the left hemisphere (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999). In another study, objects within participants' domain of expertise aroused larger N1 amplitudes than did objects outside of their expertise (Tanaka & Curran, 2001). Further, skilled adult readers exhibited significantly larger N1 components for words than for symbolic strings, while kindergarten children who could not yet read very well failed to show any differences in N1 based on the word/non-word string stimuli (Maurer, Brem, Bucher, & Brandeis, 2005). Lastly, N1 is also sensitive to the direction of spatial attention (see review by Hillyard, Vogel, & Luck, 1998) and to the participant's state of arousal (Vogel & Luck, 2000).

Studies using visually evoked potentials, structural and functional MRI, and retinotopic mapping of visual cortical areas all support the idea that the N1 component originates from extrastriate visual cortex (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Jeffreys & Axford, 1972), reflecting early visual perception. The early visual processing of shapes can elicit the N1 component. In a recent ERP study, unattended changes in shape elicited significant, gradual adaptation effects in the range of the early N1 visual component, indicating the fast and automatic processing of shapes (Soltesz &

Szucs, 2014). All types of visual object processing elicit the N1 component, including but not limited to geometric-figures, dots, Arabic digits, Chinese characters, and faces (e.g., Chen et al., 2007; Fornaciai, Brannon, Woldorff, & Park, 2017; Park, Chiang, Brannon, & Woldorff, 2014; Rossion, Joyce, Cottrell, & Tarr, 2003; Xue, Jiang, Chen, & Dong, 2008). In the current study, we similarly found that the N1 component was elicited by figure matching, numerosity comparison, simple addition, simple subtraction, and even character rhyming. This is not surprising as all tasks required visual perception processing.

Additionally, significant ERP-behavior correlations for simple addition, simple subtraction, numerosity comparison, and figure matching were observed for the early N1 component (actually the rising branch) at occipital electrodes. The time window was typically 75–150 ms. The correlations we found generally show that an electrophysiological index of visual perceptual processing can reflect behavioral performance, and more specifically the importance of visual processing during the four tasks. We did not find any correlation between N1 amplitude and reaction time in the character rhyming task. We propose two explanations for this finding. First, the character rhyming task was more difficult than the simple addition and subtraction tasks, as evidenced by the slower reaction time and poorer error rate. Second, judging character rhyming typically includes phonological processing, even when stimuli are visual (Booth et al., 2006; Wei et al., 2012). Reaction time could also reflect phonological processing, which might weaken the correlation during early visual perception.

Although we found significant correlations at occipital electrodes between the N1 component and reaction time, we did not observe any significant correlations between N1 and error rate/accuracy for any task. This could have been because the tasks used in current study were relatively simple for adults. In cases like that, the reaction time can better reflect individual differences. A second explanation considers that the reaction time is the sum of the time used for each mental process used to complete the task. As such, it varies depending on individual variation in all the component mental processes. In contrast, accuracy can only be one of two values (correct or incorrect). Previous studies have also shown that reaction time correlated with the amplitude of the N1 component, while accuracy did not (e.g., Korinth, Sommer, & Breznitz, 2012; Wiegand et al., 2014).

4.2 | The significance of single-trial ERP-behavior correlation

The traditional mean-trial ERP-behavior interindividual correlation approach did not consistently result in any significant correlations. Although some correlations were significant before correcting for multiple comparisons, the same has found when using the pre-stimulus interval (e.g., from –200 to 0 ms as baseline). The single-trial ERP-behavior correlation approach that has been used in fMRI neuro-imaging data analysis (Zhou et al., 2018) consistently showed the involvement of both/right lateral occipital cortex for simple arithmetic

(addition and subtraction), numerosity comparison, and figure matching.

However, the mean-trial correlation approach might not efficiently remove enough of the noise and the traditional mean-trial correlation approach cannot result in a high correlation coefficient (Meyer et al., 2001). The single-trial ERP-behavior correlation approach can avoid the influence of noise on statistical analyses. That is, this approach removes much of the noise (i.e., residuals) during the correlation analysis of each trial, and then reference test is conducted on the weak but possibly stable correlation coefficients filtered much of the noise. Thus, the statistical power is greatly enhanced. Note that after correcting for multiple comparisons, we were still able to find significant correlations with this method.

This approach could be used extensively in ERP and fMRI studies. Reaction time reflects a sum of mental processes. The correlation shows how the time-locked neural responses reflect the behavioral performance. The reaction time of a simple task might be helpful for detecting synchronized neural responses. The single-trial correlation also provides the opportunity to compare the correlations from different time windows or conditions.

4.3 | The neural mechanism underlying the association between non-verbal number sense and arithmetic fluency

From a domain-specific perspective, numerical quantity processing might underly the association between non-verbal number sense and arithmetic fluency (e.g., Halberda et al., 2008). Both numerosity processing and arithmetic processing activate the same brain areas (i.e., bilateral intraparietal sulcus) (e.g., Ansari & Dhital, 2006; Izard et al., 2008). However, some recent studies have questioned the domain-specific hypothesis (e.g., Gilmore et al., 2013; Inglis et al., 2011; Park, DeWind, Woldorff, & Brannon, 2016; Sasanguie, De Smedt, Defever, & Reynvoet, 2012; Sasanguie, Gobet, Moll, Smets, & Reynvoet, 2013; Vanbinst, Ghesquiere, & De Smedt, 2012). Early N1 components peaking at 180 ms over bilateral occipitoparietal sites is sensitive to changes in numerosity presentation, which demonstrates the existence of a human visual pathway for rapidly and directly extracting numerosity information (Park et al., 2016). Moreover, visual perception can account for the association between approximate number system (ANS) acuity and arithmetic fluency (e.g., Cui et al., 2019; Zhou et al., 2015). This idea is called the visual perception hypothesis, which is a type of domain-general hypothesis. Arithmetic is based on symbols (Arabic digits) and signs consisting of lines, which also require visual perception. Perceiving numerosity also involves visual perception such that apparent numerosity was shown to decrease through adaptation to large numbers of dots and to increase through adaptation to small numbers of dots. This is similar to adaptation mechanisms for other primary visual properties of a scene such as color, contrast, size, and movement speed (Burr & Ross, 2008; Tibber, Greenwood, & Dakin, 2012).

The present study has provided psychophysiological evidence that visual perception is the mechanism underlying the association between non-verbal number sense and arithmetic fluency. We found that the N1 component at occipital electrodes during arithmetic computation (simple addition and subtraction) was correlated with reaction time on figure matching and numerosity comparison tasks. The correlation with figure matching behavior and the correlation with numerosity comparison behavior show a similar pattern. Visuospatial processing in general (e.g., Berg, 2008; Hubbard, Piazza, Pinel, & Dehaene, 2005; Krajewski & Schneider, 2009; Simmons, Willis, & Adams, 2012; van der Ven, van der Maas, Straatemeier, & Jansen, 2013), and visual perception in particular (Kurdek & Sinclair, 2001; Rosner, 1973; Sigmundsson, Anholt, & Talcott, 2010), have been shown to be important for mathematics achievement. For example, Rosner (1973) showed that visual perception was correlated with mathematics achievement even after controlling for auditory perception. Sigmundsson et al. (2010) also found that compared with age-matched controls, children with low mathematics achievement were less sensitive to visually coherent motion (i.e., objects moving consistently in the same direction rather than randomly). The early ERP component response (N1) and the N1-behavior correlation suggested that visual perceptual processing was the common mechanism underlying both arithmetic and numerosity processing.

In addition, single-trial ERP-behavior correlation analysis revealed a positive correlation between the N1 amplitude during character rhyming and reaction time to stimuli in the figure matching and numerosity comparison tasks, although the correlation occurred later in time than the cross-task correlation for arithmetic fluency. Written language processing should involve visual perception (e.g., Cui et al., 2019; Vidyasagar & Pammer, 2010). For example, children's scores in a rapid visual temporal processing task correlated with oral reading fluency (McLean, Stuart, Coltheart, & Castles, 2011). It is widely assumed that phonological deficits cause the reading difficulties in dyslexia. However, emerging evidence has provided an alternative hypothesis for developmental dyslexia, holding that the reading impairment arises from poor visual coding (Vidyasagar & Pammer, 2010). Thus, when we used behavioral data from the figure matching or numerosity comparison tasks as a probe (instead of complex behavioral data that comes with character rhyming), we were able to show a positive single-trial ERP-behavior correlation between N1 amplitude and reaction time during character rhyming.

The relatively late correlation might be associated with the complex structure of Chinese characters. The visual configuration of a character plays an important role in Chinese character identification. Visual perception processing (e.g., low-spatial-frequency sensitivity, geometric-figure processing) can affect the recognition and encoding of Chinese characters during reading in typically developed children and adults (Yang et al., 2013; Zhao, Kwok, Liu, Liu, & Huang, 2017; Zhao, Qian, Bi, & Coltheart, 2014). Chinese language is a logographic writing system. This means that Chinese character processing primarily involves visual complexity, which was evidenced by a significant effect of stimulus length on the N1 response (Wong, Gauthier,

Woroch, DeBuse, & Curran, 2005; Xue et al., 2008). In addition, the N1 component during arithmetic fluency tasks also correlated with behavioral performance on numerosity comparison and figure matching tasks. For visually complex symbols (e.g., Arabic digits, Chinese character), the N1 component is mainly modulated by visual complexity. These results indicate that there are common neuronal associations between arithmetic, language, and visual perception in the occipital areas. The N1 component of visual perception over occipital areas likely underlies the neural association between non-verbal number sense and arithmetic fluency. This result further strengthens our understanding of how individual differences in achievement in school mathematics are related to individual differences in the acuity of approximate number sense.

5 | CONCLUSION

In summary, the current study recorded ERPs and performed single-trial ERP-behavior interindividual correlations to investigate the neural mechanism underlying the association between non-verbal number sense and arithmetic fluency. We found significant correlations between the N1 component at occipital electrodes and behavior during figure matching, numerosity comparison, simple addition, and subtraction, but not for character rhyming. Further, the N1 component at occipital electrodes during the arithmetic fluency and character rhyming tasks also correlated with reaction times on the figure matching and numerosity comparison tasks. The results suggest a neural association between arithmetic fluency, non-verbal number sense, and visual perception in the occipital cortex, with visual perception being the mechanism shared by both non-verbal number sense and arithmetic fluency.

ACKNOWLEDGMENTS

This research was supported by grants from the National Natural Science Foundation of China to XZ (grant number 31671151), DC (grant number 31700977), the 111 Project to XZ (grant number BP0719032), a grant from the Advanced Innovation Center for Future Education to XZ (grant number 27900-110631111) and a grant from the Chinese Academy of Medical Sciences Initiative for Innovative Medicine to DC (grant number 2016-I2M-1-008).

CONFLICT OF INTEREST

The authors declare no competing interests.

ETHICS STATEMENT

This research was approved by the institutional review boards (IRBs) of Beijing Normal University. Participants gave their written informed consent before the experiment.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on reasonable request from the corresponding authors.

ORCID

Xinlin Zhou  <https://orcid.org/0000-0002-3530-0922>

REFERENCES

- Ansari, D., & Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: An event-related functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, 18(11), 1820–1828. <http://doi.org/10.1162/jocn.2006.18.11.1820>
- Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience*, 11(3), 235–260. <http://doi.org/10.1162/089892999563373>
- Berg, D. H. (2008). Working memory and arithmetic calculation in children: The contributory roles of processing speed, short-term memory, and reading. *Journal of Experimental Child Psychology*, 99(4), 288–308. <http://doi.org/10.1016/j.jecp.2007.12.002>
- Bonny, J. W., & Lourenco, S. F. (2013). The approximate number system and its relation to early math achievement: Evidence from the preschool years. *Journal of Experimental Child Psychology*, 114(3), 375–388. <http://doi.org/10.1016/j.jecp.2012.09.015>
- Booth, J. R., Lu, D., Burman, D. D., Chou, T. L., Jin, Z., Peng, D. L., ... Liu, L. (2006). Specialization of phonological and semantic processing in Chinese word reading. *Brain Research*, 1071(1), 197–207. <http://doi.org/10.1016/j.brainres.2005.11.097>
- Burr, D., & Ross, J. (2008). A visual sense of number. *Current Biology*, 18(6), 425–428. <http://doi.org/10.1016/j.cub.2008.02.052>
- Butterworth, B. (2005). The development of arithmetical abilities. *Journal of Child Psychology and Psychiatry*, 46(1), 3–18. <http://doi.org/10.1111/j.1469-7610.2004.00374.x>
- Chen, A. T., Luo, Y. J., Wang, Q. H., Yuan, H. J., Yao, D. Z., & Li, H. (2007). Electrophysiological correlates of category induction: PSW amplitude as an index of identifying shared attributes. *Biological Psychology*, 76(3), 230–238. <http://doi.org/10.1016/j.biopsycho.2007.08.007>
- Cheng, D. Z., Xiao, Q., Chen, Q., Cui, J. X., & Zhou, X. L. (2018). Dyslexia and dyscalculia are characterized by common visual perception deficits. *Developmental Neuropsychology*, 43(6), 497–507. <http://doi.org/10.1080/87565641.2018.1481068>
- Cheng, D. Z., Xiao, Q., Cui, J., Chen, C. S., Zeng, J. Y., Chen, Q., & Zhou, X. L. (2020). Short-term numerosity training promotes symbolic arithmetic in children with developmental dyscalculia: The mediating role of visual form perception. *Developmental Science*, 23, e12910. <https://doi.org/10.1111/desc.12910>
- Cui, J. X., Zhang, Y. Y., Cheng, D. Z., Li, D. W., & Zhou, X. L. (2017). Visual form perception can be a cognitive correlate of lower level math categories for teenagers. *Frontiers in Psychology*, 8, 1–17. <http://doi.org/10.3389/fpsyg.2017.01336>
- Cui, J. X., Zhang, Y. Y., Wan, S. R., Chen, C. S., Zeng, J. Y., & Zhou, X. L. (2019). Visual form perception is fundamental for both reading comprehension and arithmetic computation. *Cognition*, 189, 141–154. <http://doi.org/10.1016/j.cognition.2019.03.014>
- Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping*, 15(2), 95–111. <http://doi.org/10.1002/hbm.10010>
- Ekstrom, R. B., French, J. W., Harman, H. H., & Dermen, D. (1976). *Manual for kit of factor-referenced cognitive tests*. Princeton, NJ: Educational Testing Service.
- Fornaciai, M., Brannon, E. M., Woldorff, M. G., & Park, J. (2017). Numerosity processing in early visual cortex. *NeuroImage*, 157, 429–438. <http://doi.org/10.1016/j.neuroimage.2017.05.069>
- Geary, D. C., Bailey, D. H., & Hoard, M. K. (2009). Predicting mathematical achievement and mathematical learning disability with a simple screening tool the number sets test. *Journal of Psychoeducational Assessment*, 27(3), 265–279. <http://doi.org/10.1177/0734282908330592>
- Gilmore, C., Attridge, N., Clayton, S., Cragg, L., Johnson, S., Marlow, N., ... Inglis, M. (2013). Individual differences in inhibitory control, not non-verbal number acuity, correlate with mathematics achievement. *PLoS One*, 8(6), e67374. <http://doi.org/10.1371/journal.pone.0067374>
- Halberda, J., Ly, R., Wilmer, J. B., Naiman, D. Q., & Germine, L. (2012). Number sense across the lifespan as revealed by a massive Internet-based sample. *Proceedings of the National Academy of Sciences of the United States of America*, 109(28), 11116–11120. <http://doi.org/10.1073/pnas.1200196109>
- Halberda, J., Mazocco, M. M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, 455(7213), 665–668. <http://doi.org/10.1038/nature07246>
- Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 353(1373), 1257–1270. <http://doi.org/10.1098/rstb.1998.0281>
- Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, 6(6), 435–448. <http://doi.org/10.1038/nrn1684>
- Hyde, D. C., Khanum, S., & Spelke, E. S. (2014). Brief non-symbolic, approximate number practice enhances subsequent exact symbolic arithmetic in children. *Cognition*, 131(1), 92–107. <http://doi.org/10.1016/j.cognition.2013.12.007>
- Inglis, M., Attridge, N., Batchelor, S., & Gilmore, C. (2011). Non-verbal number acuity correlates with symbolic mathematics achievement: But only in children. *Psychonomic Bulletin & Review*, 18(6), 1222–1229. <http://doi.org/10.3758/s13423-011-0154-1>
- Izard, V., Dehaene-Lambertz, G., & Dehaene, S. (2008). Distinct cerebral pathways for object identity and number in human infants. *PLoS Biology*, 6(2), 275–285. <http://doi.org/10.1371/journal.pbio.0060011>
- Jeffreys, D. A., & Axford, J. G. (1972). Source locations of pattern-specific components of human visual evoked-potentials. 2. Component of extrastriate cortical origin. *Experimental Brain Research*, 16(1), 22–40. <http://doi.org/10.1007/BF00233371>
- Johannes, S., Munte, T. F., Heinze, H. J., & Mangun, G. R. (1995). Luminance and spatial attention effects on early visual processing. *Cognitive Brain Research*, 2(3), 189–205. [http://doi.org/10.1016/0926-6410\(95\)90008-X](http://doi.org/10.1016/0926-6410(95)90008-X)
- Korinth, S. P., Sommer, W., & Breznitz, Z. (2012). Does silent reading speed in normal adult readers depend on early visual processes? Evidence from event-related brain potentials. *Brain and Language*, 120(1), 15–26. <http://doi.org/10.1016/j.bandl.2011.08.003>
- Krajewski, K., & Schneider, W. (2009). Exploring the impact of phonological awareness, visual-spatial working memory, and preschool quantity-number competencies on mathematics achievement in elementary school: Findings from a 3-year longitudinal study. *Journal of Experimental Child Psychology*, 103(4), 516–531. <http://doi.org/10.1016/j.jecp.2009.03.009>
- Kurdek, L. A., & Sinclair, R. J. (2001). Predicting reading and mathematics achievement in fourth-grade children from kindergarten readiness scores. *Journal of Educational Psychology*, 93(3), 451–455. <http://doi.org/10.1037/0022-0663.93.3.451>
- Landerl, K., Bevan, A., & Butterworth, B. (2004). Developmental dyscalculia and basic numerical capacities: A study of 8-9-year-old students. *Cognition*, 93(2), 99–125. <http://doi.org/10.1016/j.cognition.2003.11.004>
- Libertus, M. E., Feigenson, L., & Halberda, J. (2011). Preschool acuity of the approximate number system correlates with school math ability. *Developmental Science*, 14(6), 1292–1300. <http://doi.org/10.1111/j.1467-7687.2011.01080.x>
- Libertus, M. E., Feigenson, L., & Halberda, J. (2013). Is approximate number precision a stable predictor of math ability? *Learning and Individual Differences*, 25, 126–133. <http://doi.org/10.1016/j.lindif.2013.02.001>

- Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, MA: The MIT Press.
- Lyons, I. M., & Beilock, S. L. (2011). Numerical ordering ability mediates the relation between number-sense and arithmetic competence. *Cognition*, 121(2), 256–261. <http://doi.org/10.1016/j.cognition.2011.07.009>
- Maurer, U., Brem, S., Bucher, K., & Brandeis, D. (2005). Emerging neurophysiological specialization for letter strings. *Journal of Cognitive Neuroscience*, 17(10), 1532–1552. <http://doi.org/10.1162/089892905774597218>
- Mazzocco, M. M. M., Feigenson, L., & Halberda, J. (2011). Impaired acuity of the approximate number system underlies mathematical learning disability (dyscalculia). *Child Development*, 82(4), 1224–1237. <http://doi.org/10.1111/j.1467-8624.2011.01608.x>
- McLean, G. M. T., Stuart, G. W., Coltheart, V., & Castles, A. (2011). Visual temporal processing in dyslexia and the magnocellular deficit theory: The need for speed? *Journal of Experimental Psychology-Human Perception and Performance*, 37(6), 1957–1975. <http://doi.org/10.1037/a0024668>
- Meyer, G. J., Finn, S. E., Eyde, L. D., Kay, G. G., Moreland, K. L., Dies, R. R., ... Reed, G. M. (2001). Psychological testing and psychological assessment – A review of evidence and issues. *American Psychologist*, 56(2), 128–165. <http://doi.org/10.1037//0003-066x.56.2.128>
- Mundy, E., & Gilmore, C. K. (2009). Children's mapping between symbolic and nonsymbolic representations of number. *Journal of Experimental Child Psychology*, 103(4), 490–502. <http://doi.org/10.1016/j.jecp.2009.02.003>
- Novitskiy, N., Ramautar, J. R., Vanderperren, K., De Vos, M., Mennes, M., Mijovic, B., ... Wagemans, J. (2011). The BOLD correlates of the visual P1 and N1 in single-trial analysis of simultaneous EEG-fMRI recordings during a spatial detection task. *NeuroImage*, 54(2), 824–835. <http://doi.org/10.1016/j.neuroimage.2010.09.041>
- Park, J., & Brannon, E. M. (2013). Training the approximate number system improves math proficiency. *Psychological Science*, 24(10), 2013–2019. <http://doi.org/10.1177/0956797613482944>
- Park, J., Chiang, C., Brannon, E. M., & Woldorff, M. G. (2014). Experience-dependent hemispheric specialization of letters and numbers is revealed in early visual processing. *Journal of Cognitive Neuroscience*, 26(10), 2239–2249. http://doi.org/10.1162/jocn_a_00621
- Park, J., DeWind, N. K., Woldorff, M. G., & Brannon, E. M. (2016). Rapid and direct encoding of numerosity in the visual stream. *Cerebral Cortex*, 26(2), 748–763. <http://doi.org/10.1093/cercor/bhv017>
- Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., ... Zorzi, M. (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition*, 116(1), 33–41. <http://doi.org/10.1016/j.cognition.2010.03.012>
- Rosner, J. (1973). Language arts and arithmetic achievement, and specifically related perceptual skills. *American Educational Research Journal*, 10(1), 59–68. <http://doi.org/10.3102/00028312010001059>
- Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *NeuroImage*, 20(3), 1609–1624. <http://doi.org/10.1016/j.neuroimage.2003.07.010>
- Sasanguie, D., De Smedt, B., Defever, E., & Reynvoet, B. (2012). Association between basic numerical abilities and mathematics achievement. *British Journal of Developmental Psychology*, 30(2), 344–357. <http://doi.org/10.1111/j.2044-835X.2011.02048.x>
- Sasanguie, D., Gobet, S. M., Moll, K., Smets, K., & Reynvoet, B. (2013). Approximate number sense, symbolic number processing, or number-space mappings: What underlies mathematics achievement? *Journal of Experimental Child Psychology*, 114(3), 418–431. <http://doi.org/10.1016/j.jecp.2012.10.012>
- Sigmundsson, H., Anholt, S. K., & Talcott, J. B. (2010). Are poor mathematics skills associated with visual deficits in temporal processing? *Neuroscience Letters*, 469(2), 248–250. <http://doi.org/10.1016/j.neulet.2009.12.005>
- Simmons, F. R., Willis, C., & Adams, A. M. (2012). Different components of working memory have different relationships with different mathematical skills. *Journal of Experimental Child Psychology*, 111(2), 139–155. <http://doi.org/10.1016/j.jecp.2011.08.011>
- Soltesz, F., & Szucs, D. (2014). Neural adaptation to non-symbolic number and visual shape: An electrophysiological study. *Biological Psychology*, 103, 203–211. <http://doi.org/10.1016/j.biopsycho.2014.09.006>
- Tanaka, J. W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychological Science*, 12(1), 43–47. <http://doi.org/10.1111/1467-9280.00308>
- Tibber, M. S., Greenwood, J. A., & Dakin, S. C. (2012). Number and density discrimination rely on a common metric: Similar psychophysical effects of size, contrast, and divided attention. *Journal of Vision*, 12(6), 1–19. <http://doi.org/10.1167/12.6.8>
- van der Ven, S. H. G., van der Maas, H. L. J., Straatemeier, M., & Jansen, B. R. J. (2013). Visuospatial working memory and mathematical ability at different ages throughout primary school. *Learning and Individual Differences*, 27, 182–192. <http://doi.org/10.1016/j.lindif.2013.09.003>
- Vanbinst, K., Ghesquiere, P., & De Smedt, B. (2012). Numerical magnitude representations and individual differences in children's arithmetic strategy use. *Mind Brain and Education*, 6(3), 129–136. <http://doi.org/10.1111/j.1751-228X.2012.01148.x>
- Vidyasagar, T. R., & Pammer, K. (2010). Dyslexia: A deficit in visuo-spatial attention, not in phonological processing. *Trends in Cognitive Sciences*, 14(2), 57–63. <http://doi.org/10.1016/j.tics.2009.12.003>
- Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, 37(2), 190–203. <http://doi.org/10.1017/S0048577200981265>
- Wang, L., Sun, Y. H., & Zhou, X. L. (2016). Relation between approximate number system acuity and mathematical achievement: The influence of fluency. *Frontiers in Psychology*, 7, 1–9. <http://doi.org/10.3389/fpsyg.2016.01966>
- Wei, W., Lu, H., Zhao, H., Chen, C. S., Dong, Q., & Zhou, X. L. (2012). Gender differences in children's arithmetic performance are accounted for by gender differences in language abilities. *Psychological Science*, 23(3), 320–330. <http://doi.org/10.1177/0956797611427168>
- Wiegand, I., Tollner, T., Dyrholm, M., Müller, H. J., Bundesen, C., & Finke, K. (2014). Neural correlates of age-related decline and compensation in visual attention capacity. *Neurobiology of Aging*, 35(9), 2161–2173. <http://doi.org/10.1016/j.neurobiolaging.2014.02.023>
- Wong, A. C. N., Gauthier, I., Woroch, B., DeBuse, C., & Curran, T. (2005). An early electrophysiological response associated with expertise in letter perception. *Cognitive, Affective, & Behavioral Neuroscience*, 5(3), 306–318. <http://doi.org/10.3758/Cabn.5.3.306>
- Wydell, T. N., Vuorinen, T., Helenius, P., & Salmelin, R. (2003). Neural correlates of letter-string length and lexicality during reading in a regular orthography. *Journal of Cognitive Neuroscience*, 15(7), 1052–1062. <http://doi.org/10.1162/089892903770007434>
- Xue, G., Jiang, T., Chen, C., & Dong, Q. (2008). Language experience shapes early electrophysiological responses to visual stimuli: The effects of writing system, stimulus length, and presentation duration. *NeuroImage*, 39(4), 2025–2037. <http://doi.org/10.1016/j.neuroimage.2007.10.021>
- Yang, L. Y., Guo, J. P., Richman, L. C., Schmidt, F. L., Gerken, K. C., & Ding, Y. (2013). Visual skills and Chinese reading acquisition: A meta-analysis of correlation evidence. *Educational Psychology Review*, 25(1), 115–143. <http://doi.org/10.1007/s10648-013-9217-3>
- Yang, P., Fan, C. G., Wang, M., Fogelson, N., & Li, L. (2017). The effects of changes in object location on object identity detection: A simultaneous EEG-fMRI study. *NeuroImage*, 157, 351–363. <http://doi.org/10.1016/j.neuroimage.2017.06.031>

- Zhang, H., Chen, C. S., Sun, Z. H., Lin, J. L., Zhou, W. J., & Zhou, X. L. (2016). Early occipital injury affects numerosity counting but not simple arithmetic. *Neurocase*, 22(1), 12–21. <http://doi.org/10.1080/13554794.2015.1023316>
- Zhang, Y. Y., Liu, T. J., Chen, C. S., & Zhou, X. L. (2019). Visual form perception supports approximate number system acuity and arithmetic fluency. *Learning and Individual Differences*, 71, 1–12. <http://doi.org/10.1016/j.lindif.2019.02.008>
- Zhao, J., Kwok, R. K. W., Liu, M. L., Liu, H., & Huang, C. (2017). Underlying skills of oral and silent reading fluency in Chinese: Perspective of visual rapid processing. *Frontiers in Psychology*, 7, 1–11. <http://doi.org/10.3389/fpsyg.2016.02082>
- Zhao, J., Qian, Y., Bi, H. Y., & Coltheart, M. (2014). The visual magnocellular-dorsal dysfunction in Chinese children with developmental dyslexia impedes Chinese character recognition. *Scientific Reports*, 4, 1–7. <http://doi.org/10.1038/srep07068>
- Zhou, X. L., & Cheng, D. Z. (2015). When and why numerosity processing is associated with developmental dyscalculia. In S. Chinn (Ed.), *The Routledge international handbook of dyscalculia and mathematical learning difficulties* (pp. 78–89). New York: Routledge.
- Zhou, X. L., Hu, Y. W., Yuan, L., Gu, T. A., & Li, D. W. (2020). Visual form perception predicts 3-year longitudinal development of mathematical achievement. *Cognitive Processing*. <http://doi.org/10.1007/s10339-020-00980-w>
- Zhou, X. L., Li, M. Y., Zhou, H. T., Li, L. N., & Cui, J. X. (2018). Item-wise interindividual brain-behavior correlation in task neuroimaging analysis. *Frontiers in Neuroscience*, 12, 1–17. <http://doi.org/10.3389/fnins.2018.00817>
- Zhou, X. L., Wei, W., Zhang, Y. Y., Cui, J. X., & Chen, C. S. (2015). Visual perception can account for the close relation between numerosity processing and computational fluency. *Frontiers in Psychology*, 6, 1–13. <http://doi.org/10.3389/fpsyg.2015.01364>

How to cite this article: Li M, Cheng D, Lu Y, Zhou X. Neural association between non-verbal number sense and arithmetic fluency. *Hum Brain Mapp*. 2020;41:5128–5140. <https://doi.org/10.1002/hbm.25179>