

## Effects of Internal and External Grouping Cues on Grouping Strategies in Numerical Perception: Evidence from fMRI

**Authors:** Pan Yun, Yang Huanyu, Jia Liangzhi, Zhu Jun, Yu Fangwen, Zhang Di, Yang Ping, Pan Yun

**Date:** 2024-07-27T00:00:00+00:00

### Abstract

This study employed a numerical estimation task combined with fMRI technology to deeply investigate the respective influences of internal and external grouping cues on numerical perceptual grouping strategies, and to reveal the neural mechanisms underlying numerical perceptual grouping strategies. The results revealed that, compared to the ungrouped condition, the grouped condition exhibited more significant activation in calculation-related brain regions such as the left intraparietal sulcus, angular gyrus, and superior frontal gyrus; external grouping cues showed more significant activation in topology-related brain regions such as the middle frontal gyrus and inferior temporal gyrus compared to internal grouping cues. These findings indicate that participants were more inclined to employ calculation-related strategies for numerical perception under grouped conditions, and that external grouping cues possess topological properties, thereby supporting topological perception theory.

### Full Text

## The Influence of Intrinsic and Extrinsic Grouping Cues on Numerosity Perception Grouping Strategies: Evidence from fMRI

### Abstract

Numerosity perception refers to the cognitive ability to extract numerical information from various stimuli, serving as a fundamental basis for understanding the world and processing information that guides human behavior and decision-making. Current research on the cognitive mechanisms of numerosity perception has primarily focused on strategic processing, including subitizing (accurate and

rapid reporting of up to 4 objects), counting (slower reporting of more than 4 objects requiring coordination of numerical symbols and visuospatial processing), and estimation (rapid but approximate processing of large quantities when insufficient time is available for counting).

Unlike these three strategies, “groupitizing” involves organizing objects into sets or groups during numerosity perception to enable rapid and effective estimation, particularly when presentation times are short and quantities are large. This strategy not only expands the subitizing range and facilitates understanding of how small numbers combine to form larger concepts but also allows individuals to use simple mental arithmetic (addition and multiplication) during grouping, thereby improving numerosity perception efficiency.

Since Starkey et al. (2014) first proposed groupitizing in numerosity perception research, it has become a focal point in the field. Ciccione and Dehaene (2020) found that participants estimated arrays grouped by color similarity and proximity more quickly. Groupitizing strategies can enhance numerosity perception performance in elementary school children and predict their mathematics achievement. Similar to subitizing, Maldonado et al. (2020) discovered that when grouped stimuli are presented, individuals with stronger arithmetic abilities automatically group array items into subitizable sets, improving numerosity perception performance. However, these studies have predominantly examined groupitizing from the perspective of intrinsic grouping cues (e.g., proximity, color similarity).

According to Gestalt theory, Palmer (1992, 1999) distinguished between intrinsic grouping principles (based on intrinsic relationships among element properties such as shape, position, and color, like proximity and similarity) and extrinsic grouping principles (based on external relationships among elements, such as common region and connectedness). Unlike intrinsic principles, researchers consider extrinsic grouping principles to be based on the topological properties of connectedness and enclosure. Therefore, compared to intrinsic grouping cues, the mechanisms of extrinsic grouping cues may be related to topological properties and can be explained through the Theory of Topological Perception. Within this framework, connectedness and common region as important extrinsic grouping cues possess topological properties. Connectedness describes the relational connections between objects, while common region emphasizes associations among elements within enclosed spaces, both influencing each other through topological principles to form perceptions of environmental structure. This highlights the importance and priority of topological structure in shape perception.

Cognitive neuroscience evidence indicates that key brain regions for topological properties include the inferior temporal cortex. In visual and numerosity perception domains, existing research supports that extrinsic grouping cues demonstrate advantages over intrinsic grouping cues. For instance, Luna et al. (2016) showed that participants responded faster to stimuli with extrinsic grouping cues, while Palmer et al. (2007) found faster discrimination responses for in-

terconnected elements. Pan et al. (2021) similarly reported higher perceptual precision and faster reaction times for extrinsic versus intrinsic grouping cues. Therefore, to deeply investigate the processing mechanisms of groupitizing in numerosity perception, it is necessary to compare the effects of intrinsic and extrinsic cues on numerosity perception groupitizing to reveal its functional role and neural mechanisms, providing empirical evidence for existing theories of numerical processing.

Revealing the neural mechanisms of numerosity perception strategies is crucial for understanding how humans comprehend and process quantities. Previous neuroimaging research suggests that subitizing involves the parietal cortex and primary visual cortex, with the parietal cortex receiving visual input and performing initial quantity perception, while the primary visual cortex handles initial separation and encoding of quantity information. Estimation strategies involve the intraparietal sulcus (IPS) and prefrontal cortex, with the IPS responsible for approximate quantity estimation and the prefrontal cortex integrating external stimuli with internal representations. Counting strategies similarly involve the IPS and prefrontal cortex, with functional connectivity between the IPS and visual/temporal cortices closely related to converting visual input into numerical counts. However, only Maldonado et al. (2021) have found that grouped conditions during numerosity perception activate the frontoparietal network, angular gyrus, and left IPS—regions proven to be computation-related. Thus, research on the neural mechanisms of groupitizing strategies remains limited and warrants deeper investigation.

In summary, this study employs a numerosity estimation task to examine the effects of intrinsic and extrinsic grouping cues on numerosity perception groupitizing and reveal its neural mechanisms. Based on topological perception theory and previous research on groupitizing strategies, we hypothesize that: (1) groupitizing strategy use will activate more arithmetic-related regions such as the IPS, angular gyrus, and superior frontal gyrus; (2) the processing mechanisms of extrinsic grouping cues, potentially related to topological properties, will activate more topology-related regions such as ventral temporal cortex, frontal gyri, and IPS compared to intrinsic cues.

## 2.1 Participants

Based on previous groupitizing effect studies and reported effect sizes (0.25) with desired statistical power (0.8), we used G\*Power 3.1 software for sample size estimation, determining a minimum requirement of 15 participants. We recruited 21 participants (mean age =  $21 \pm 3.4$  years, range = 18-24 years). Due to excessive head motion in one participant (translation > 3 mm, rotation >  $2.5^\circ$ ), the final sample comprised 20 valid participants. All participants were right-handed university students with normal or corrected vision, no neurological or psychiatric disorders, and no color blindness. Before entering the scanner, participants completed a magnetic resonance safety screening form to exclude those with non-removable metal implants. The study was approved by the Ethics Com-

mittee of a university in Guizhou (approval number: \*\*PSY202111005), and all participants signed informed consent forms before the formal experiment.

## 2.2 Experimental Materials

Intrinsic grouping cues included color similarity and proximity based on previous research, while extrinsic grouping cues comprised connectedness and common region. Each stimulus measured  $0.4^\circ \times 0.4^\circ$ . For color similarity cues, grouped stimuli consisted of red, blue, yellow, and green squares (RGB: 255 0 0; 0 0 255; 255 255 0; 0 255 0) randomly distributed, while ungrouped stimuli were white squares with black borders randomly distributed in a large grid. As shown in [Figure 1: see original paper]F, the left side shows the grouped condition and the right side shows the ungrouped condition.

Proximity stimuli consisted of white squares with black borders ( $0.4^\circ \times 0.4^\circ$ ). In the grouped condition, stimuli were divided into four groups with 12 possible positions each, distributed within the same quadrant (maximum area per quadrant =  $4^\circ \times 2^\circ$ , center distance from screen center =  $5^\circ$ ) (see [Figure 1: see original paper]C). In the ungrouped condition, each stimulus was randomly distributed in the large grid ([Figure 1: see original paper]C, G).

Connectedness stimuli consisted of white squares with black borders randomly distributed in a grid. In the grouped condition, squares within each group were connected by a black line segment joining their centers ([Figure 1: see original paper]B, D). The ungrouped condition lacked connecting lines, with stimuli randomly distributed ([Figure 1: see original paper]B).

Common region stimuli also consisted of white squares with black borders. In the grouped condition, the grid was divided into four quadrants, with stimuli randomly distributed within boxes ( $2.5^\circ \times 2.5^\circ$ ) in each quadrant. For example, [Figure 1: see original paper]A shows an array with three subgroups (3, 3, 3), thus only three boxes appeared. The ungrouped condition had no boxes, with stimuli randomly distributed ([Figure 1: see original paper]E).

[Figure 1: see original paper] shows example stimulus materials. Note: A-C show distribution diagrams for common region, connectedness, and proximity stimuli; D-G show schematic diagrams for extrinsic and intrinsic grouping cue stimuli, with grouped conditions on the left and ungrouped conditions on the right (stimuli not drawn to actual scale for viewing convenience).

## 2.3 Experimental Procedure

The task fMRI imaging employed a block design with two runs, each containing eight blocks: connectedness/grouped, connectedness/ungrouped, common region/grouped, common region/ungrouped, color similarity/grouped, color similarity/ungrouped, proximity/grouped, and proximity/ungrouped ([Figure 2: see original paper]). Based on previous research, we selected numerosities 6, 9, 12, and 16, which show the strongest groupitizing effects. Each condition was re-

peated three times, with 12 trials per block. Each trial lasted 6 seconds, with 18-second rest periods between blocks, resulting in an 11-minute 7-second run duration.

The experimental task was a numerosity estimation task requiring participants to estimate the number of target stimuli presented. The procedure ([Figure 2: see original paper]) began with a black fixation cross (+) for 1 second, followed by target stimulus presentation for 500 ms, a 500 ms blank screen, and then a rectangular input box where participants used a special keyboard to enter their estimated number. Participants had 4 seconds to respond, after which they rested until the next trial began.

Stimuli were presented and responses recorded using MATLAB's PsychToolbox (version R2016b). Before the formal experiment, participants practiced in a preparation room to familiarize themselves with the task and response keys. Stimuli were projected via LCD onto a screen in front of the scanner, viewed through a tilted mirror on the head coil. In the scanner, participants held a magnet-compatible response box with four keys corresponding to the numerosities 6, 9, 12, and 16. After ensuring familiarity with the procedure, experimenters used a metal detector to scan for metal objects. Participants lay in the MRI scanner, keeping head and body stable while wearing earplugs and specialized glasses. They were instructed to remain quiet but could press a stop key if uncomfortable or wishing to terminate.

## 2.4 fMRI Data Acquisition

Brain imaging data were collected using a Siemens 3.0T MRI scanner. Task-state functional images were acquired using echo-planar imaging (EPI) with parameters: field of view = 192 mm, repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, resolution =  $64 \times 64$ ,  $voxelsize = 3 \times 3 \times 2mm$ ,  $flipangle = 52^\circ$ ,  $slices = 72$ . Following functional scans, T1 structural images were acquired using a T1-weighted 3D gradient echo pulse sequence with parameters:  $TR = 2530ms$ ,  $TE = 1.94ms$ ,  $slicethickness = 1mm$ ,  $flipangle = 7^\circ$ ,  $fieldofview = 256mm$ ,  $voxelsize = 1 \times 1 \times 1mm$ ,  $slices = 176$ .

### 2.5.1 Behavioral Data Analysis

Following previous research, we combined common region and connectedness as extrinsic grouping cues, and color similarity and proximity as intrinsic grouping cues. SPSS 25.0 was used for  $2 \times 2$  repeated measures ANOVA on grouping cue (extrinsic, intrinsic) and grouping condition (grouped, ungrouped) to compare reaction times and perceptual precision. Perceptual precision was measured by coefficient of variation (CV), a classic psychophysical parameter reflecting sensory noise during numerosity estimation, where higher CV values indicate greater noise and less precise estimation (see Formula 1, where  $N_i$  is the analyzed numerosity and  $i$  is its standard deviation).

### 2.5.2 fMRI Data Analysis

Data preprocessing was performed using SPM12 in MATLAB, including: conversion from DICOM to NIFTI format; slice timing correction; head motion correction; coregistration of high-resolution structural T1 images to MNI standard space; structural-to-functional image coregistration; segmentation into gray matter, white matter, and cerebrospinal fluid; normalization to standard space; and spatial smoothing with a 6 mm full-width at half-maximum (FWHM) Gaussian kernel.

First-level analysis used a general linear model (GLM) at the whole-brain voxel level. The design matrix included five regressors: four grouping cue types (connectedness, common region, proximity, color similarity) and one ungrouped condition. Time series vectors were convolved with the hemodynamic response function (HRF), with six head motion parameters included as nuisance regressors. After standardization and multicollinearity checks, the GLM was fitted using least squares. Contrast images were used for second-level analysis with voxel-level uncorrected  $p < 0.001$  and cluster-level FDR-corrected  $p < 0.05$  thresholds.

Based on peak activation coordinates from whole-brain analysis, 6-mm spherical ROIs were created. ROI analysis using the Rex toolbox extracted beta values for each participant in grouped vs. ungrouped conditions (IPS, angular gyrus, superior frontal gyrus) and extrinsic vs. intrinsic cue conditions (IPS, middle frontal gyrus, inferior temporal gyrus). Paired  $t$ -tests were performed in SPSS 25.0.

For generalized psychophysiological interaction (gPPI) analysis, the CONN toolbox was used to examine functional connectivity patterns. Six-mm spherical seed regions were created based on whole-brain activation peaks in bilateral IPS, angular gyrus, superior frontal gyrus, middle frontal gyrus, and inferior temporal gyrus.  $t$ -tests assessed connectivity strength differences between conditions, with seed time series representing physiological variables and grouping conditions/cues representing psychological variables.

### 3.1 Behavioral Results

Independent  $t$ -tests on connectedness and common region showed no significant differences in perceptual precision ( $t(19) = 0.0776$ ,  $p = 0.940$ ) or reaction time ( $t(19) = 1.325$ ,  $p = 0.224$ ), supporting their combination as extrinsic grouping cues. Similarly, color similarity and proximity showed no differences in precision ( $t(19) = 0.869$ ,  $p = 0.390$ ) or reaction time ( $t(19) = 0.277$ ,  $p = 0.783$ ), justifying their combination as intrinsic grouping cues.

For perceptual precision,  $2 \times 2$  repeated measures ANOVA revealed a significant main effect of grouping condition ( $F(1, 38) = 49.533$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.559$ ), with grouped conditions showing higher precision than ungrouped ( $t(19) = 3.610$ ,  $p < 0.001$ , Cohen's  $d = 0.219$ ). The main effect of grouping cue was non-significant ( $F(3, 17) = 1.049$ ,  $p =$

0.382), but the interaction was significant ( $F(3, 17) = 3.539$ ,  $p = 0.024$ ,  $\eta^2 = 0.223$ ). Post-hoc tests showed extrinsic cues yielded higher precision than intrinsic cues in grouped conditions ( $t(19) = 4.050$ ,  $p_{\text{Bonferroni}} < 0.001$ , Cohen's  $d = 0.896$ ), with no difference in ungrouped conditions ( $t(19) = 0.502$ ,  $p_{\text{Bonferroni}} = 0.609$ , Cohen's  $d = 0.112$ ) ([Figure 3: see original paper]A).

For reaction time, ANOVA showed only a significant main effect of grouping condition ( $F(1, 19) = 12.963$ ,  $p < 0.001$ ,  $\eta^2 = 0.249$ ), with grouped conditions faster than ungrouped ( $t(19) = 3.245$ ,  $p = 0.036$ , Cohen's  $d = 0.767$ ) ([Figure 3: see original paper]B). These results replicate previous findings, demonstrating stronger groupitizing effects for grouped vs. ungrouped conditions and superior performance for extrinsic vs. intrinsic grouping cues.

## 3.2 fMRI Results

### 3.2.1 Whole-Brain Analysis

**3.2.1.1 Activation in Grouped vs. Ungrouped Conditions** Single-sample t-tests examined activation patterns. Grouped conditions activated bilateral IPS, left angular gyrus (AG), left middle frontal gyrus (MFG), left inferior temporal gyrus (ITG), left lingual gyrus (LG), and left supramarginal gyrus (SMG). Ungrouped conditions activated left superior parietal lobule (SPL), left AG, left SMG, left MFG, right IPS, and right MFG ([Figure 4: see original paper], ).

To identify groupitizing-specific activation, we contrasted grouped > ungrouped conditions. Grouped conditions showed additional activation in left IPS, left ITG, left LG, and bilateral AG/SMG ([Figure 4: see original paper]C, ). No significant activation was found for ungrouped > grouped.

**3.2.1.2 Activation in Extrinsic vs. Intrinsic Grouping Cues** Single-sample t-tests for extrinsic and intrinsic cues showed extrinsic cues activated left IPS, left AG, left MFG, left SMG, left supplementary motor area (SMA), left LG, right SPL, right ITG, right MFG, and right fusiform gyrus (FG). Intrinsic cues activated left IPS, left SMG, left AG, left SMA, left MFG, right IPS, right AG, and right anterior insula (AI) ([Figure 5: see original paper], ).

Contrasting extrinsic > intrinsic cues revealed additional activation in left IPS, left SMA, left MFG, left LG, and bilateral ITG ([Figure 5: see original paper]C, ). No significant activation was found for intrinsic > extrinsic.

### 3.2.2 ROI Analysis

**3.2.2.1 Grouping Condition Effects** Six-mm spherical ROIs were created from peak activation coordinates. Beta values were extracted for IPS, AG, and superior frontal gyrus in grouped vs. ungrouped conditions. Paired t-tests showed significantly greater activation in grouped vs. ungrouped conditions in

left IPS ( $t(19) = 3.336$ ,  $p = 0.003$ , Cohen's  $d = 6.646$ ), left AG ( $t(19) = -0.548$ ,  $p = 0.020$ , Cohen's  $d = 14.614$ ), and left MFG ( $t(19) = 3.046$ ,  $p = 0.007$ , Cohen's  $d = 5.369$ ). Right hemisphere activation differences were non-significant ([Figure 6: see original paper]).

**3.2.2.2 Grouping Cue Effects** ROIs were created from peak coordinates for extrinsic vs. intrinsic cues. Beta values were extracted for IPS, MFG, and ITG. Extrinsic cues showed significantly greater activation than intrinsic cues in left IPS ( $t(19) = 3.071$ ,  $p = 0.006$ , Cohen's  $d = 6.909$ ), left MFG ( $t(19) = 2.665$ ,  $p = 0.015$ , Cohen's  $d = 4.735$ ), and left ITG ( $t(19) = 3.038$ ,  $p = 0.007$ , Cohen's  $d = 3.434$ ). Right hemisphere differences were non-significant ([Figure 7: see original paper]).

### 3.2.3 gPPI Analysis

**3.2.3.1 Grouping Condition Connectivity** With left IPS as a seed region, grouped conditions showed enhanced functional connectivity with bilateral IPS, bilateral AG, bilateral superior frontal gyrus, and left MFG compared to ungrouped conditions (, [Figure 8: see original paper]A). Other seed regions showed no significant condition-modulated connectivity differences.

**3.2.3.2 Grouping Cue Connectivity** With left ITG as a seed region, extrinsic cues showed stronger functional connectivity with left superior frontal gyrus, left AG, left IPS, and bilateral ITG compared to intrinsic cues (, [Figure 8: see original paper]B). Other seed regions showed no significant cue-modulated connectivity differences.

## Discussion

This fMRI study manipulated intrinsic and extrinsic grouping cues to investigate their neural mechanisms in numerosity perception groupitizing. Results showed that both grouped and ungrouped conditions activated numerosity estimation-related regions including prefrontal cortex, IPS, and ITG. Grouped conditions additionally activated computation-related regions such as superior frontal gyrus, IPS, and AG, showing left hemisphere lateralization. Compared to intrinsic cues, extrinsic cues additionally activated topology-related regions including middle frontal gyrus and ITG. These findings support our hypotheses that participants employ arithmetic and retrieval strategies under grouped conditions to enhance efficiency, and that extrinsic grouping cues operate through topological invariance mechanisms, providing direct neural evidence for topological perception theory.

Humans can employ different strategies depending on task context. In numerosity perception groupitizing, ungrouped arrays engage the approximate number representation system important for estimation strategies, whereas grouped arrays automatically employ more precise computational and retrieval strategies.

Research shows distinct brain activity patterns for different task types: approximate estimation activates prefrontal cortex, parietal cortex, hippocampus, striatum, and thalamus, while exact calculation activates frontal cortex, parietal cortex, and anterior temporal cortex. Our findings show both conditions activated superior frontal gyrus and IPS—regions known as visual number form areas—indicating estimation strategies were used in both conditions.

Superior groupitizing performance likely results from participants employing computational and retrieval strategies in grouped conditions. Pan et al. (2021) found higher precision for grouped vs. ungrouped conditions, particularly for numerosities 6, 9, 12, and 16, suggesting these values facilitate mental calculation (e.g.,  $3+3=6$ ,  $3\times 3=9$ ). Ciccione et al. (2020) similarly argued that composite numbers show stronger groupitizing effects because participants can directly apply mental arithmetic or retrieval strategies (e.g., recalling multiplication tables). fMRI studies show left prefrontal and parietal activation is higher during fact retrieval, with left AG and IPS showing stronger activation during combined exact calculation and retrieval tasks. Our results showing additional activation in left IPS, AG, and superior frontal gyrus during grouped conditions confirm that participants employed computational and retrieval strategies for higher-level quantity representation, making groupitizing more efficient.

Organizing scattered visual elements requires considering holistic element properties. Topological perception theory posits that topological properties are the starting point for object perception, maintaining holistic properties invariant across transformations—an invariance explainable through topological invariants where connectedness and enclosure are preserved. For example, a rubber band maintains its holistic properties through stretching, squeezing, or twisting as long as it remains uncut, because its ends connect to form a closed loop. Thus, connectedness and enclosure are significant topological features in visual perception. Key brain regions for topological properties include ventral temporal cortex, frontal gyri, and IPS. Our findings show both cue types activated bilateral IPS and AG, indicating both engaged groupitizing strategies and estimation/computation regions. Additionally, extrinsic cues activated middle frontal gyrus and ITG—regions associated with topological properties—further confirming that extrinsic grouping mechanisms involve topological invariance.

Neuroscience research demonstrates hemispheric lateralization advantages, with the left hemisphere preferentially processing holistic information (overall shape, contour, spatial layout) and the right hemisphere processing local features (details, edges, structure). Studies support left hemisphere advantages in processing topological properties, with left frontal and temporal cortices showing greater activity for holistic topological information. Our results show left hemisphere lateralization for extrinsic cues, with enhanced functional connectivity in left middle frontal gyrus and ITG, and stronger left hemisphere activation in ROI analyses, confirming the topological invariance mechanism. Grouped conditions also showed left lateralization, with stronger left hemisphere activation in IPS, AG, and superior frontal gyrus, consistent with the left hemisphere's

important role in arithmetic.

In conclusion, this study innovatively examined the effects of intrinsic and extrinsic grouping cues on numerosity perception groupitizing, filling a gap in neural mechanism research. Notably, by focusing on extrinsic grouping cue mechanisms, we addressed previous limitations of focusing solely on intrinsic cues, enriching understanding of groupitizing strategies and providing new directions for future research. However, limitations exist. First, we used a numerosity estimation task with only four values due to fMRI constraints. Future studies should employ numerosity discrimination tasks with broader numerical ranges to investigate neural mechanism differences across values. Second, our study focused only on spatial dimensions, whereas magnitude theory suggests time, space, and quantity share neural mechanisms. Future research should examine temporal dimensions to explore cross-dimensional groupitizing mechanisms. Finally, Piaget's "topological primacy theory" describes spatial concept development in children as progressing from topological to Euclidean and projective geometry. Future studies should examine whether similar "topological priority" patterns exist in children's numerosity perception to reveal developmental characteristics of groupitizing strategies under different grouping cues.

Under our experimental conditions, we conclude: (1) Bilateral IPS is a critical brain region for numerosity perception; (2) Both grouped and ungrouped conditions activate cortical regions related to quantity estimation, emphasizing their importance; (3) Groupitizing activates computation-related regions including superior frontal gyrus, IPS, and AG with left hemisphere lateralization, indicating computational/retrieval strategy use for efficiency; (4) Extrinsic grouping cues additionally activate middle frontal gyrus and ITG, revealing topological invariance characteristics and priority in numerosity perception and information processing.

## References

- Anobile, G., Castaldi, E., Maldonado Moscoso, P. A., Arrighi, R., & Burr, D. (2021). Groupitizing Improves Estimation of Numerosity of Auditory Sequences. *Frontiers in Human Neuroscience*, 15. <http://doi.org/10.3389/fnhum.2021.687321>
- Anobile, G., Castaldi, E., Moscoso, P. A. M., Burr, D. C., & Arrighi, R. (2020). "Groupitizing": a strategy for numerosity estimation. *Scientific Reports*, 10(1) <http://doi.org/10.1038/s41598-020-68111-1>
- Arsalidou, M., Pawliw-Levac, M., Sadeghi, M., & Pascual-Leone, J. (2018). Brain areas associated with numbers and calculations in children: Meta-analyses of fMRI studies. *Developmental Cognitive Neuroscience*, 30, 239-250. <http://doi.org/10.1016/j.dcn.2017.08.002>
- 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>

- Cai, Y., Hofstetter, S., Harvey, B. M., & Dumoulin, S. O. (2022). Attention drives human numerosity-selective responses. *Cell Reports*, 39(13), 111005. <http://doi.org/10.1016/j.celrep.2022.111005>
- Cai, Y., Hofstetter, S., van Dijk, J., Zuiderbaan, W., van der Zwaag, W., Harvey, B. M., & Dumoulin, S. O. (2021). Topographic numerosity maps cover subitizing and estimation ranges. *Nature Communications*, 12(1) <http://doi.org/10.1038/s41467-021-23785-7>
- Cao, M., Wang, J., Dai, Z., Cao, X., Jiang, L., Fan, F., Song, X., Xia, M., Shu, N., Dong, Q., Milham, M. P., Castellanos, F. X., Zuo, X., & He, Y. (2014). Topological organization of the human brain functional connectome across the lifespan. *Developmental Cognitive Neuroscience*, 7, 76-93. <http://doi.org/10.1016/j.dcn.2013.11.004>
- Caponi, C., Maldonado, M. P., Castaldi, E., Arrighi, R., & Grasso, P. A. (2023). EEG signature of grouping strategies in numerosity perception. *Front Neurosci*, 17, 1190317. <http://doi.org/10.3389/fnins.2023.1190317>
- Chen, L. (1982). Topological Structure in Visual Perception. *Science (New York, N.Y.)*, 218, 699-700. <http://doi.org/10.1126/science.7134969>
- Cicchini, G. M., Anobile, G., Burr, D. C., Marchesini, P., & Arrighi, R. (2023). The role of non-numerical information in the perception of temporal numerosity [Journal Article]. *Frontiers in Psychology*, 14, 1197064. <http://doi.org/10.3389/fpsyg.2023.1197064>
- Ciccione, L., & Dehaene, S. (2020). Grouping Mechanisms in Numerosity Perception. *Open Mind*, 4, 102-118. [http://doi.org/10.1162/opmi\\_a\\_00037](http://doi.org/10.1162/opmi_a_00037)
- Czarnecka, M., Raczy, K., Szewczyk, J., Paplinska, M., Jednorog, K., Marchewka, A., Hesselmann, G., Knops, A., & Szwed, M. (2023). Overlapping but separate number representations in the intraparietal sulcus-Probing format- and modality-independence in sighted Braille readers. *Cortex*, 162, 65-80. <http://doi.org/10.1016/j.cortex.2023.01.011>
- Dehaene, S., & Changeux, J. (1993). Development of Elementary Numerical Abilities: A Neuronal Model. *Journal of Cognitive Neuroscience*, 5, 390-407. <http://doi.org/10.1162/jocn.1993.5.4.390>
- Fornaciai, M., & Park, J. (2018). Early numerosity encoding in visual cortex is not sufficient for the representation of numerical magnitude. *Journal of Cognitive Neuroscience*, 30(12), 1788-1802. [http://doi.org/10.1162/jocn\\_a\\_01320](http://doi.org/10.1162/jocn_a_01320)
- Grasso, P. A., Anobile, G., Arrighi, R., Burr, D. C., & Cicchini, G. M. (2022). Numerosity perception is tuned to salient environmental features. *iScience*, 25(4), 104104. <http://doi.org/https://doi.org/10.1016/j.isci.2022.104104>
- Grotheer, M., Herrmann, K., & Kovács, G. (2016). Neuroimaging evidence of a bilateral representation for Visually presented numbers. *The Journal of Neuroscience*, 36(1), 88-97. <http://doi.org/10.1523/JNEUROSCI.2129-15.2016>

- Guillaume, M., Roy, E., Van Rinsveld, A., Starkey, G., Uncapher, M., & McCandliss, B. (2022). Groupitizing reflects conceptual developments in math cognition and inequities in math achievement from childhood through adolescence. *Child Development*, 94. <http://doi.org/10.1111/cdev.13859>
- Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic representation of numerosity in the human parietal cortex. *Science*, 341(6150), 1123-1126. <http://doi.org/10.1126/science.1239052>
- He, L., Zhang, J., Zhou, T., & Chen, L. (2009). Connectedness affects dot numerosity judgment: Implications for configural processing. *Psychonomic Bulletin & Review*, 16(3), 509-517. <http://doi.org/10.3758/PBR.16.3.509>
- He, L., Zhou, K., Zhou, T., He, S., & Chen, L. (2015a). Topology-defined units in numerosity perception. *Proceedings of the National Academy of Sciences of the United States of America*, 112. <http://doi.org/10.1073/pnas.1512408112>
- He, L., Zhou, K., Zhou, T., He, S., & Chen, L. (2015b). Topology-defined units in numerosity perception. *Proceedings of the National Academy of Sciences*, 112(41), E5647.
- He, S. (2008). Holes, objects, and the left hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, 105(4), 1103-1104. <http://doi.org/10.1073/pnas.0710631105>
- Kluth, T., & Zetzsche, C. (2016). Numerosity as a topological invariant. *Journal of Vision*, 16(3), 30. <http://doi.org/10.1167/16.3.30>
- Kragel, P., Čeko, M., Theriault, J., Chen, D., Satpute, A., Wald, L., Lindquist, M., Barrett, L., & Wager, T. (2021). A human colliculus-pulvinar-amygdala pathway encodes negative emotion. *Neuron*, 109. <http://doi.org/10.1016/j.neuron.2021.06.001>
- Luna, D., Villalba-Garcia, C., Montoro, P. R., & Hinojosa, J. A. (2016). Dominance dynamics of competition between intrinsic and extrinsic grouping cues. *Acta Psychologica*, 170, 146-154. <http://doi.org/10.1016/j.actpsy.2016.07.001>
- Luna, D., & Montoro, P. R. (2011). Interactions between intrinsic principles of similarity and proximity and extrinsic principle of common region in visual perception. *Perception*, 40(12), 1467-1477. <http://doi.org/10.1068/p7086>
- Maldonado Moscoso, P. A., Castaldi, E., Burr, D. C., Arrighi, R., & Anobile, G. (2020). Grouping strategies in number estimation extend the subitizing range. *Scientific Reports*, 10(1) <http://doi.org/10.1038/s41598-020-71871-5>
- Maldonado, M. P., Greenlee, M. W., Anobile, G., Arrighi, R., Burr, D. C., & Castaldi, E. (2021). Groupitizing modifies neural coding of numerosity. *Human Brain Mapping*. <http://doi.org/10.1002/hbm.25694>
- Malone, S. A., Pritchard, V. E., Heron-Delaney, M., Burgoyne, K., Lervåg, A., & Hulme, C. (2019). The relationship between numerosity discrimination and arithmetic skill reflects the approximate number system and cannot be explained

by inhibitory control. *Journal of Experimental Child Psychology*, 184, 220-231. <http://doi.org/10.1016/j.jecp.2019.02.009>

Montoro, P. R., Villalba-García, C., Luna, D., & Hinojosa, J. A. (2017). Common region wins the competition between extrinsic grouping cues: Evidence from a task without explicit attention to grouping. *Psychonomic Bulletin & Review*, 24(6), 1856-1861. <http://doi.org/10.3758/s13423-017-1254-3>

Palmer, S. E. (1992). Common region: a new principle of perceptual grouping. *Cognitive Psychology*, 24(3), 436.

Palmer, S. E., & Beck, D. M. (2007). The repetition discrimination task: an objective method for studying perceptual grouping. *Perception & psychophysics*, 69(1), 68.

Palmer, S., & Rock, I. (1994). Rethinking perceptual organization: The role of uniform connectedness [Journal Article]. *Psychon Bull Rev*, 1(1), 29-55. <http://doi.org/10.3758/BF03200760>

Pan, Y., Yang, H., Li, M., Zhang, J., & Cui, L. (2021). Grouping strategies in numerosity perception between intrinsic and extrinsic grouping cues. *Scientific Reports*, 11(1) <http://doi.org/10.1038/s41598-021-96944-x>

Pennock, I. M. L., Schmidt, T. T., Zorbek, D., & Blankenburg, F. (2021). Representation of visual numerosity information during working memory in humans: An fMRI decoding study. *Human Brain Mapping*, 42(9), 2778-2789. <http://doi.org/10.1002/hbm.25402>

Piazza, M., Mechelli, A., Butterworth, B., & Price, C. J. (2002). Are subitizing and counting implemented as separate or functionally overlapping processes? *Neuroimage*, 15(2), 435-446. <http://doi.org/10.1006/nimg.2001.0980>

Piazza, M., & Izard, V. (2009). How humans count: numerosity and the parietal cortex. *Neuroscientist*, 15(3), 261-273. <http://doi.org/10.1177/1073858409333073>

Polspoel, B., Peters, L., Vandermosten, M., & De Smedt, B. (2017). Strategy over operation: neural activation in subtraction and multiplication during fact retrieval and procedural strategy use in children. *Human Brain Mapping*, 38(9), 4657-4670. <http://doi.org/10.1002/hbm.23691>

Simon, T., & Vaishnavi, S. (1996). Subitizing and counting depend on different attentional mechanisms: Evidence from visual enumeration in afterimages. *Perception & Psychophysics*, 58, 915-926. <http://doi.org/10.3758/BF03205493>

Skagenholt, M., Skagerlund, K., & Träff, U. (2021). Neurodevelopmental differences in child and adult number processing: An fMRI-based validation of the triple code model. *Developmental Cognitive Neuroscience*, 48, 100933. <http://doi.org/10.1016/j.dcn.2021.100933>

Starkey, G. S., & McCandliss, B. D. (2014). The emergence of “groupitizing” in children’s numerical cognition. *Journal of Experimental Child Psychology*, 126, 120-137. <http://doi.org/10.1016/j.jecp.2014.03.006>

- Tschemtscher, N., & Hauk, O. (2014). How are things adding up? Neural differences between arithmetic operations are due to general problem solving strategies. *Neuroimage*, 92, 369-380. <http://doi.org/10.1016/j.neuroimage.2014.01.061>
- Tsouli, A., Harvey, B. M., Hofstetter, S., Cai, Y., van der Smagt, M. J., Te, P. S., & Dumoulin, S. O. (2022). The role of neural tuning in quantity perception. *Trends in Cognitive Sciences*, 26(1), 11-24. <http://doi.org/10.1016/j.tics.2021.10.004>
- Wang, B., Zhou, T. G., Zhuo, Y., & Chen, L. (2007). Global topological dominance in the left hemisphere. *Proceedings of the National Academy of Sciences of the United States of America*, 104(52), 21014-21019. <http://doi.org/10.1073/pnas.0709664104>
- Wang, L., Li, M., Yang, T., Wang, L., & Zhou, X. (2022). Mathematics meets science in the brain. *Cerebral Cortex*, 32(1), 123-136. <http://doi.org/10.1093/cercor/bhab198>
- Wang, W., Zhou, T., Chen, L., & Huang, Y. (2023). A subcortical magnocellular pathway is responsible for the fast processing of topological properties of objects: A transcranial magnetic stimulation study. *Human Brain Mapping*, 44(4), 1617-1628. <http://doi.org/10.1002/hbm.26162>
- Wege, T., Trezise, K., & Inglis, M. (2021). Finding the subitizing in groupitizing: Evidence for parallel subitizing of dots and groups in grouped arrays. *Psychonomic Bulletin & Review*, 29. <http://doi.org/10.3758/s13423-021-02015-7>
- Whalen, J., Gallistel, C. R., & Gelman, R. (2016). Nonverbal Counting in Humans: The Psychophysics of Number Representation. *Psychological Science*, 10(2), 130-137. <http://doi.org/10.1111/1467-9280.00120>
- Wurm, M. F., Tagliabue, C. F., & Mazza, V. (2021). Decoding location-specific and location-invariant stages of numerosity processing in subitizing. *European Journal of Neuroscience*, 54(3), 4971-4984. <http://doi.org/10.1111/ejn.15352>
- Yeo, D., Wilkey, E., & Price, G. (2017). The Search for the Number Form Area: A Functional Neuroimaging Meta-Analysis. *Neuroscience & Biobehavioral Reviews*, 78. <http://doi.org/10.1016/j.neubiorev.2017.04.027>
- Zhang, D., Zhou, L., Yang, A., Li, S., Chang, C., Liu, J., & Zhou, K. (2023). A connectome-based neuromarker of nonverbal number acuity and arithmetic skills. *Cerebral Cortex*, 33(3), 881-894. <http://doi.org/10.1093/cercor/bhac108>
- Zhou, K., Luo, H., Zhou, T., Zhuo, Y., & Chen, L. (2010). Topological change disturbs object continuity in attentive tracking. *Proceedings of the National Academy of Sciences*, 107(50), 21920-21924. <http://doi.org/10.1073/pnas.1010919108>

*Note: Figure translations are in progress. See original paper for figures.*

*Source: ChinaXiv — Machine translation. Verify with original.*