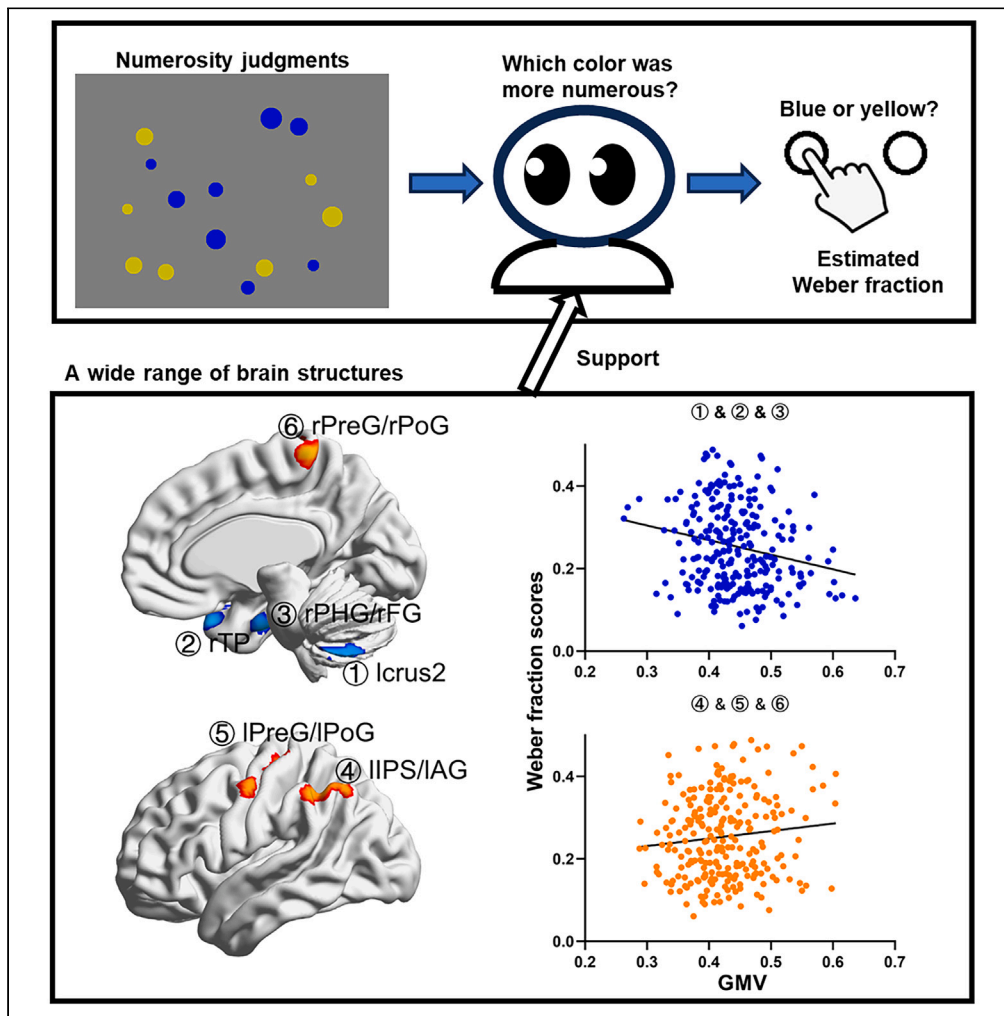


Article

The neural correlates of individual differences in numerosity perception: A voxel-based morphometry study



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Highlights

Unveils neuroanatomical basis of numerosity perception

Discovers positive and negative greater GMV correlations

Links GMV in a wide range of brain regions to numerical sensitivity

Supports the network view of the neural representation of numerosity perception

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Article

The neural correlates of individual differences in numerosity perception: A voxel-based morphometry study

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SUMMARY

Numerosity perception is a fundamental cognitive function in humans and animals. Using an individual difference approach with a comprehensive dataset (N = 249), we performed a voxel-based morphometry analysis to unravel the neuroanatomical substrates associated with individual differences in numerosity perception sensitivity, measured by a classical non-symbolic numerical judgment task. Results showed that greater gray matter volume (GMV) in the left cerebellum, right temporal pole, and right parahippocampal was positively correlated to higher perceptual sensitivity to numerosity. In contrast, the GMV in the left intraparietal sulcus, and bilateral precentral/postcentral gyrus was negatively correlated to the sensitivity of numerosity perception. These findings indicate that a wide range of brain structures, rather than a specific anatomical structure or circuit, forms the neuroanatomical basis of numerosity perception, lending support to the emerging network view of the neural representation of numerosity. This work contributes to a more comprehensive understanding of how the brain processes numerical information.

INTRODUCTION

Numerosity could be conceived as the quantity of a collection of things, such as a crowd of people.¹ Perception of numerosity is a cognitive ability to represent nonverbal information of quantity without counting.^{2,3} The number sense theory proposed that numerosity perception is a fundamental innate skill, which is independent of other properties (e.g., size) of items.²⁻⁴ In contrast, some researchers regarded numerosity perception as a sense of magnitude, which suggests that continuous magnitude representation such as density and field area is more fundamental and automatic than numerosity.^{5,6} While there is an ongoing debate about the nature of numerosity perception, it is widely accepted that numerosity perception is vital for both humans and many animal species.⁷⁻¹² Research has shown that numerosity perception plays a crucial role in the survival of animals by aiding in foraging, avoiding predators, and courtship.^{7,12,13} For humans, there is also evidence showing that children's ability of numerosity perception can predict their mathematics performance in school.^{14,15} Thus, this shared ability has evolutionary and developmental advantages for both animal species and human beings.

Previous research has made great progress in unraveling the neural basis of numerosity perception. Studies using the neurophysiological and functional magnetic resonance imaging (fMRI) techniques have indicated that a parietal-frontal network, including the intraparietal sulcus (IPS) and the dorsal lateral prefrontal cortex (DLPFC), played a key role in numerosity perception.¹⁶⁻²⁹ Recently, emerging new evidence suggested that other brain areas were also involving the perception of numerosity. For example, in the medial temporal lobe (MTL), a study on neurosurgical patients utilized the single-cell recording to show that the numerical information of stimuli could be robustly decoded from the neural activities of neurons there, suggesting the existence of the number neurons.³⁰ Other studies also revealed the involvement of other brain regions in numerosity processing, such as the visual cortex, inferior temporal gyrus (ITG), fusiform gyrus, angular gyrus, parietal lobe, and prefrontal cortex.³¹⁻³⁴ Most of the previous neuroimaging studies focused on the functional aspect of the neural processing in numerosity perception, i.e., brain function-behavior associations measured by fMRI, electroencephalogram (EEG), magnetoencephalography (MEG), and electrophysiology, such as regional brain activity, activity profiles/patterns, and functional connectivity. However, little attention has been devoted to the structural basis of numerosity perception, e.g., of brain

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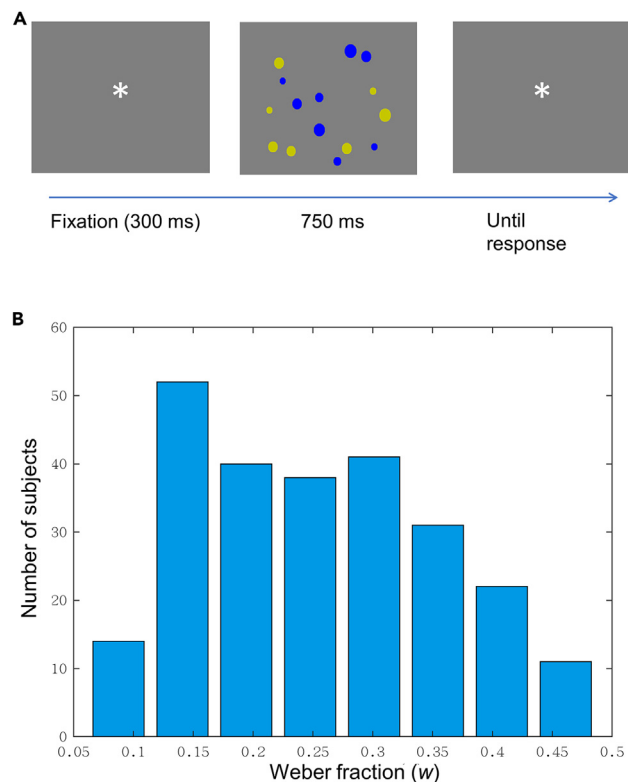


Figure 1. Experimental procedure and group performance of the non-symbolic numerosity task

(A) Schematic illustration of the number judgment task.

(B) Distribution of the Weber fractions (i.e., non-symbolic numerosity acuity, as determined by using a psychophysical procedure) of all participants ($n = 249$).

structure-behavior associations based on neuroimaging measures, e.g., grey matter volume (GMV). Understanding the brain structure-behavior associations is essential for further delineating structure-function relationships, elucidating the neural mechanisms underlying numerosity perception, and providing valuable insights into brain development, maturation, and longitudinal alterations.^{35–38}

Furthermore, from a methodological perspective, previous studies have primarily focused on identifying common patterns of brain structure/function across individuals through group-level analyses, which assumes that the manner in which information is processed is invariant across individuals given a particular experimental context. In contrast, the individual differences approach accounts for the variability in brain structure/function across individuals and identifies the neural correlates of specific cognitive abilities that vary across individuals, which thus can provide a more refined understanding of brain structure/function and their relationship with cognitive abilities.^{39,40} Considering that substantial individual differences existed in numerosity perception,¹⁴ here in the present study, we adopted an individual difference approach to explore the structural basis of numerosity perception. Specifically, in a large sample of 249 participants, we employed a behavioral numerosity judgment task to assess their sensitivity to numerosity (Figure 1),⁴¹ and used MRI scans to obtain their structural brain imaging data. We then performed a voxel-based morphometry (VBM) analysis on these images to identify brain regions that showed significant correlations with the individual difference in the sensitivity to numerosity.

RESULTS

Summary of participants' demographic characteristics

For all participants, measures of numerosity, age, and total GMV were shown in Table 1. There was no significant difference in numerosity performance ($t_{247} = 1.66, p > 0.09$) and age ($t_{247} = -0.26, p > 0.79$) between the female and male groups. The total GMV in the female group was significantly smaller than that in the male group ($t_{247} = -9.55, p = 1e-18$).

Table 1. Summary of the participants' demographic characteristics

Metric	Mean ± SD			Gender difference
	All participants	Females (n = 132)	Males (n = 117)	
Numerosity	0.254 ± 0.101	0.264 ± 0.098	0.243 ± 0.103	$t_{247} = 1.662, p = 0.098$
Age	21.641 ± 0.999	21.625 ± 0.993	21.659 ± 1.009	$t_{247} = -0.264, p = 0.792$
Total GMV	71571 ± 5662	68808 ± 4643	74688 ± 5070	$t_{247} = -9.551, p = 1e-18$

Data are represented as mean ± SD. GMV, gray matter volume; SD, standard deviation.

Structure basis of individual differences in numerosity

Pearson's partial correlation analysis revealed that six spatially separated clusters showed significant correlations between the GMV and Weber fraction (3dClustSim corrected, AFNI, $\alpha = 0.01, p < 0.05$, cluster size >307 voxels) (Figure 2; Table 2).

Three clusters, including the left cerebellum crus II, right temporal pole, and right parahippocampal/fusiform, exhibited significantly negative correlations between the GMV and Weber fraction ($r = -0.2210, p = 4.78e-4$; $r = -0.2080, p = 0.001$; and $r = -0.2221, p = 4.49e-4$, respectively) (Figure 3, upper panel). The other three clusters, i.e., left IPS/angular gyrus, left precentral/postcentral gyrus, and right precentral gyrus/paracentral lobule, exhibited significantly positive correlations between the GMV and Weber fraction ($r = 0.1825, p = 0.0041$; $r = 0.1818, p = 0.0042$; and $r = 0.2295, p = 2.83e-4$, respectively) (Figure 3, lower panel). Note that a positive partial correlation of a brain area indicates that the larger GMV in that area corresponds to a larger Weber fraction (i.e., poor numerosity acuity). On the contrary, a negative partial correlation indicates that the larger GMV corresponds to better numerosity acuity.

DISCUSSION

Using the VBM analysis in a large sample of participants, the present study investigated the neuroanatomical basis of numerosity perception. Our results showed that the GMV in brain regions, including the left

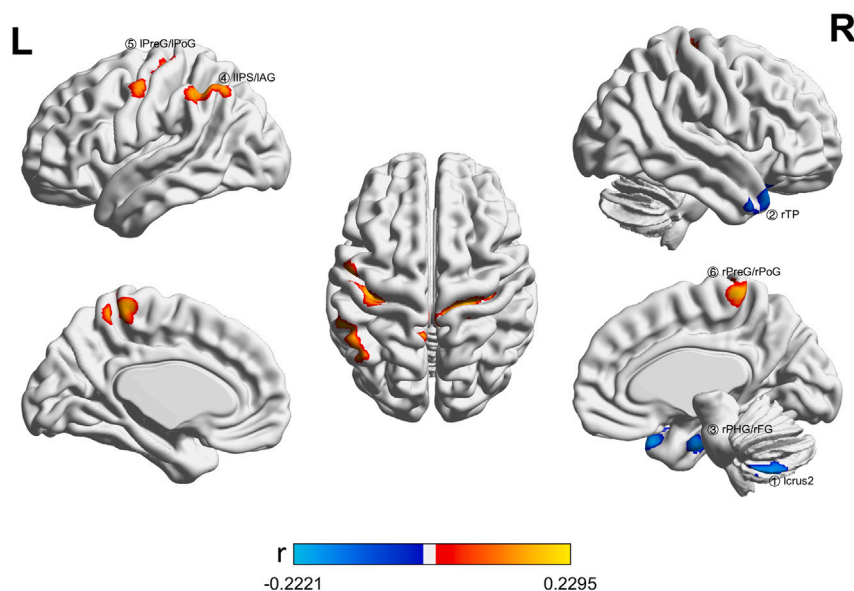


Figure 2. Brain regions showing significant correlations between GMV and Weber fraction

The red and blue colors indicate the positive and negative correlations between the GMV and Weber fraction, respectively. Numerals within circles represent six distinct brain clusters, listed in the following order as that in the Table 2: left cerebellum crus II (lcrus2), right temporal pole (rTP), right parahippocampal/fusiform gyrus (rPHG/rFG), left intraparietal sulcus/angular gyrus (lIPS/AG), left precentral/postcentral gyrus (lPreG/IPoG), and right precentral/postcentral gyrus (rPreG/rPoG). r represents the Pearson correlation coefficient.

Table 2. MNI coordinates of the clusters showing significant correlations between GMV and Weber fraction

Cluster #	Cluster size	Peak MNI coordinate	Peak <i>r</i> value	Brain region name
1	477	[-46, -48, -50]	-0.2210**	Left cerebellum crus II
2	358	[34, 20, -28]	-0.2080**	Right temporal pole
3	333	[26, -14, -32]	-0.2221**	Right parahippocampal/fusiform
4	325	[-54, -46, 46]	0.1825*	Left intraparietal sulcus/angular gyrus
5	412	[-40, -22, 50]	0.1818*	Left precentral/postcentral gyrus
6	772	[24, -22, 60]	0.2295**	Right precentral/postcentral gyrus

*: $p < 0.01$; **: $p < 0.001$.

cerebellum crus II, right temporal pole, and right parahippocampal/fusiform was positively correlated to the numerosity acuity (i.e., higher perceptual precision). In contrast, the GMV in the left IPS/angular gyrus, and bilateral precentral/postcentral gyrus were negatively correlated to the numerosity acuity. Therefore, our findings clearly indicated that neural representation of the non-symbolic number was not confined to one particular anatomical structure or circuit, but rather suggested the involvement of a group of brain structures, which forms the neuroanatomical basis of numerosity perception.

The six brain structures we found exhibited distinct associations with individual differences in numerosity judgment. Less GMV in one group of regions (i.e., left IPS and bilateral precentral/postcentral gyrus) was associated with better numerosity acuity, while more GMV in the other group of regions (i.e., left cerebellum, right temporal pole, and right parahippocampal/fusiform) may lead to better numerosity acuity. From a developmental perspective, in general, the development of a cognitive ability involves changes in the strength and effectiveness of connections between neurons in the brain. This can be achieved through both synaptic pruning and synaptogenesis. Synaptic pruning removes unnecessary or underused synapses between neurons to optimize the brain's connections and allow it to function more efficiently,⁴² whereas synaptogenesis formats new synapses between neurons to learn and adapt to new experiences.⁴⁰ By modifying the connections between neurons, both of these processes help to fine-tune the brain's connections and improve its overall efficiency, but they have opposite effects on brain structure over

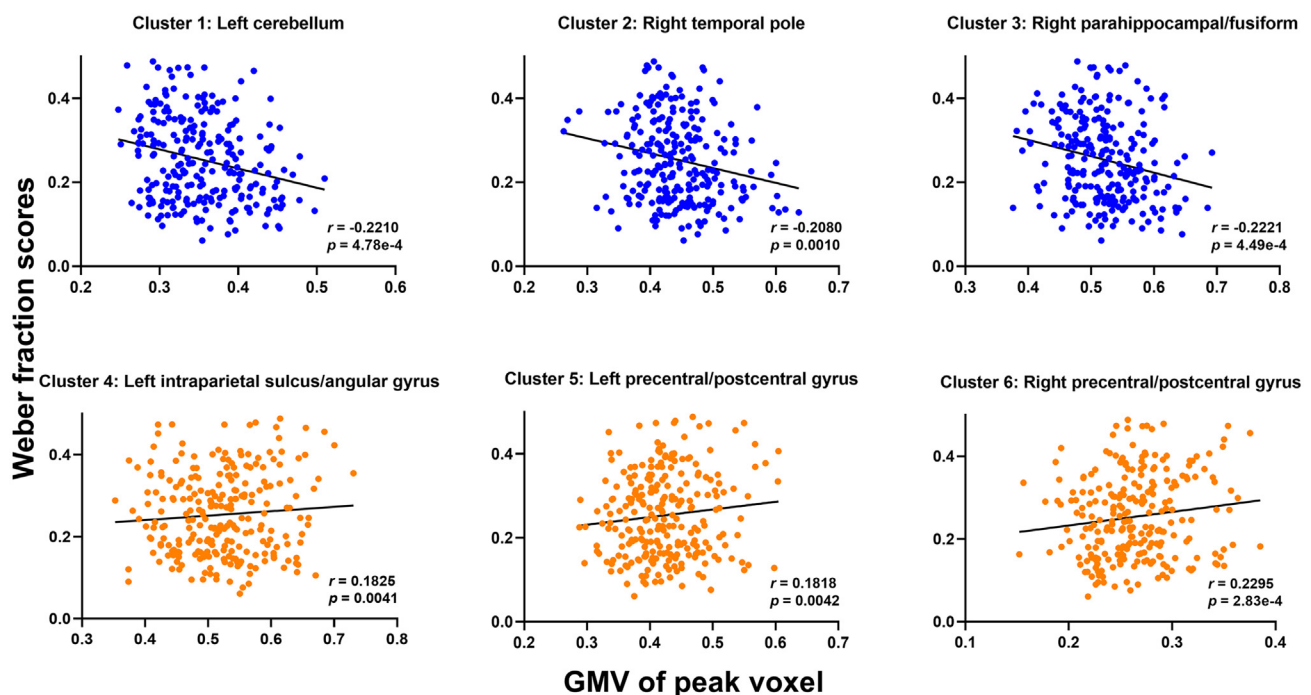


Figure 3. Scatterplot illustrating the relationship between GMV at peak voxels within each cluster and corresponding Weber fraction scores

development. Considering the fact that the numerosity acuity became progressively more precise during development,⁴³ we thus speculated that, assuming that the GMV is an indirect measure of synaptic density,⁴⁴ the improvement of numerosity acuity could be reflected in both the reduction of GMV due to the synaptic pruning and the increase of GMV due to synaptogenesis, the extent of which determine the individual differences of numerosity acuity in adult age. That is, both synaptic pruning and synaptogenesis contribute to the development of numerosity representation. It should be noted that the relationship between GMV and cognitive function is complex and may be influenced by various factors, such as genes and environment.⁴⁵ And the GMV reflects mixed contributions from various structural components within a voxel, such as glia, dendrites, and neurons, the exact cellular processes that underlie GMV change cannot be easily determined. Therefore, further research is needed to fully understand the relationship between GMV in these regions and numerosity representation.

In the literature on the neural correlates of numerosity representation, earlier functional imaging studies have suggested that a parieto-frontal network, including the IPS and DLPFC, was involved in the representation and processing of non-symbolic numerical information.^{17,23,26,46} However, recent research has identified the involvement of other brain regions in the processing of non-symbolic numbers, e.g., the early visual areas,^{47–51} ITG and fusiform gyrus,¹⁸ and sensorimotor cortex.^{52,53} The present results echoed these findings, at the structural-anatomical level, suggesting that the non-symbolic number representation involved multiple widely distributed brain regions.

It should be noted that, in contrast to the existing literature, we did not find any significant correlation in the right IPS or DLPFC between GMV and numerosity acuity. Although several previous studies also failed to reveal the involvement of right IPS in numerosity processing,^{48,50,54,55} we had to acknowledge that this discrepancy is so far difficult to explain and would require further studies to test the robustness of our findings, as well as the contribution of methodological differences, such as stimulus design, task measure, sample size, and most importantly, imaging methodology (i.e., the sensitivity of macrostructural gray matter measures). In fact, diverse structural components within a voxel may affect brain function distinctly and accordingly change MR signals in opposite directions.⁵⁶ Therefore, both synaptic pruning and synaptogenesis may take place in the right IPS, which could explain the absence of a significant correlation between the right IPS GMV and numerosity performance. Future study is thus needed to clarify this important issue.

Instead, we found a significant correlation in the individual differences between the GMV of the left IPS and the numerosity acuity. This result was in line with the findings of previous studies examining the causal relationship between IPS and numerosity perception. For instance, participants showed impairments in numerosity perception after disrupting the left IPS by applying low-frequency transcranial magnetic stimulation (TMS).⁵⁷ Patients with damage in the left IPS also exhibited deficits in numeral tasks, which provided further evidence for the vital role of the left IPS in numerosity processing.⁵⁸

A novel and interesting finding in our study was that GMV in the precentral/postcentral gyri that are responsible for processing sensory information and controlling movements,^{59,60} was significantly correlated to the numerosity acuity. It thus suggested a key role of these regions in numerosity perception. Recently, Anobile et al.⁶¹ proposed that the number sense is closely linked to action, and there is a "sensorimotor numerosity system" that encodes the number of both self-generated actions and external stimuli. Several empirical findings seemed to support such a link between number sense and motor function. For example, one electrophysiological study has suggested the existence of motor number neurons (i.e., neurons in the sensorimotor area which respond to a specific number of self-produced actions).⁵³ In children with learning disabilities, the deficiency in their mathematics was positively correlated to the lag in their motor performance.⁶² Here, our findings might provide the direct neuroanatomical evidence supporting the existence of the sensorimotor numerosity system.

Another novel finding was the significant correlation between GMV in the left cerebellum Crus II and numerosity acuity. So far, little is known about the contribution of the cerebellum to numerosity-related information processing, although several previous studies have found the involvement of the cerebellum in numerosity processing.^{52,63–65} According to the sequence detection hypothesis (Vandervort, 2017), the development of number sense involves the cerebro-cerebellar collaboration but is prominently driven by the predictive sequence-detecting computations of the cerebellum. Specifically, the cerebellum detects and simulates repetitive patterns of temporally or spatially structured events to create internal models of

dynamics and inverse dynamics,^{66,67} which can be used to make a prediction of future internal or external events. Hence the ability to detect sequences is deemed as the foundation of numerosity perception. Consistent with this hypothesis, it was shown that cerebellum Crus II contributed to the accurate temporal prediction of absolute timing,⁶⁸ and was involved in the processing of automated counting during a number addition task in verbal working memory.⁶⁹ Moreover, previous studies also found that cerebellum Crus II was involved in observing, memorizing, and reproducing the sequences of movement.^{70,71} On the other hand, beside the cerebellum, the precentral gyrus was also found to be related to sequence learning and processing,⁷² and reciprocal anatomical connections existed between the motor cortex and cerebellum.⁶⁹ Here in the present study, because significant correlations were found between GMV in the sensory-motor cortex and numerosity acuity, and GMV in the left cerebellum Crus II and numerosity acuity, we further hypothesized that the cerebro-cerebellar collaboration, especially the interaction between sensory-motor and cerebellum Crus II may serve as the foundation of the development of number sense.

Conclusions

In summary, our study demonstrated a link between neuroanatomical brain structure and numerosity perceptual ability. Our findings, together with previous functional imaging studies, would produce a more comprehensive understanding of how the brain processes numerical information.

Limitations of the study

However, there are also several limitations of our study. First, we only measured the spatial numerosity acuity. Previous research has demonstrated that temporal numerosity, compared to spatial numerosity, is more closely linked to action, and its acuity does not necessarily correlate with the acuity of spatial numerosity.⁷³ Therefore, it is necessary to carry out a comprehensive investigation to examine whether our findings can be generalized to temporal numerosity. Second, the representativeness of our sample may be subject to evaluation, as all participants were within a similar age range. To address this issue, future studies should consider recruiting subjects across a wider age range. Third, we employed only one behavioral paradigm in this study. Since previous research⁷⁴ has demonstrated that various number comparison paradigms targeted different aspects of non-symbolic numerosity perception, it thus remains debatable whether the Weber fraction measures numerosity acuity or merely general comparison and response processes. Future investigations adopting behavioral paradigms that are specifically designed to measure numerosity perception acuity are necessary to validate our findings. Finally, it is no doubt that combining structural analysis and functional connectivity analysis in brain research provides a more integrative perspective on brain function and organization.³⁵ Future investigations focusing on the interindividual variability of structure-function coupling at both regional or network levels will provide valuable information about the relationship between brain structure/function and numerosity perception.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

Conceptualization, K.Z and D.Z.; Methodology, D.Z.; Investigation, X.Y., L.N., and H.L.; Writing – Original Draft, X.Y. and D.Z.; Writing – Review & Editing, K.Z.; Funding Acquisition, K.Z.; Supervision, K.Z.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Peak GMV of ROIs and numerosity acuity data	This paper	https://github.com/Dzhang1989z/numGMV
Software and algorithms		
MATLAB2018a	The MathWorks Software	https://www.mathworks.com ; RRID:SCR_001622
AFNI	Cox et al. ⁷⁵	https://afni.nimh.nih.gov ; RRID:SCR_005927
BrainNet Viewer	Xia et al. ⁷⁶	https://www.nitrc.org/projects/bnv ; RRID: SCR_009446
Custom code and algorithms	This paper	https://github.com/Dzhang1989z/numGMV

RESOURCE AVAILABILITY

Lead contact

Further information requests should be directed to and will be fulfilled by the lead contact, Ke Zhou (kzhou@bnu.edu.cn).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Peak grey matter volume data within each cluster, behavior results, and custom codes has been deposited at GitHub: <https://github.com/Dzhang1989z/numGMV>.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The behavioral and MRI data were collected from 249 college students (mean age, 21.64 years; standard deviation, 0.99 years; range, 18–24 years, 117 males). This study is part of an ongoing project (gene, environment, brain, and behavior).⁷⁷ Participants completed the MRI scan first and finished the behavioral tests within several weeks. None of the participants had a history of neurological disorders (e.g., mental retardation or traumatic brain injury) or psychiatric illness. The Institutional Review Board of Beijing Normal University approved the experimental protocol and written informed consent was obtained from all participants before MRI and behavioral testing.

METHOD DETAILS

Numerosity judgment task

Following Halberda et al.,⁴¹ we adopted a classical more/less numerosity judgment task to measure the non-symbolic number acuity of each participant. In each trial, a display containing spatially intermixed blue and yellow dots was shown at the center of the screen for 750 ms (Figure 1 A). The ratio between the two sets of colored dots varied randomly among 11 levels, i.e., 12:11, 11:10, 10:9, 9:8, 8:7, 7:6, 6:5, 10:8, 8:6, 9:6, and 12:6. The average total-dot-area of yellow dots was equal to that of the blue dots. The color of the more numerous set was randomly assigned in each trial and counterbalanced across trials. The participants were instructed to indicate which color was more numerous by pressing a key. After finishing five practice trials, participants completed 40 test trials.

Each participant's non-symbolic number acuity, also known as the Weber fraction, was calculated as the ratio between the just noticeably different amounts of blue and yellow dots to detect a difference. For each participant, the Weber fraction was estimated using a QUEST procedure,^{78,79} which provides a given number of sequential trials and updates the probability distribution function (PDF) of the Weber fraction based on the participant's current-trial response and previous-trial PDF, according to the Bayes' Rule. Using the Quest procedure, at the end of the last trial, a mean PDF value was recorded as the participant's Weber fraction, representing the participant's perceptual sensitivity for numerosity discrimination. A lower Weber fraction score corresponded to a higher perceptual sensitivity to numerosity.

MRI data acquisition

The structural MRI data were acquired using a Siemens 3T Trio scanner (MAGENTOM Trio, a Tim system) with a 12-channel phased-array head coil at the Imaging Center for Brain Research of the Beijing Normal University. T1-weighted structure images were acquired with a 3D magnetization-prepared rapid gradient-echo (3D MPRAGE) sequence (TR/TE/TI = 2.53 s/3.45 ms/1.1 s; FA = 7°; voxel size = 1 × 1 × 1 mm³; slice thickness = 1.33 mm) for each participant.

QUANTIFICATION AND STATISTICAL ANALYSIS

Pre-processing

Structural MR data were analyzed using the VBM analysis in SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>). First, T1-weighted anatomical images of all participants were segmented into GM, white matter, and cerebrospinal fluid using the unified segmentation method.⁸⁰ Second, the obtained GM images were rigidly aligned and resampled to 2 × 2 × 2 mm³. Third, a study-specific GM template was created using the Exponential Lie Algebra registration method.⁸¹ Each GM image was normalized to the template in Montreal Neurological Institute (MNI152) space. Fourth, the GM values of each voxel were modulated by multiplying the Jacobian determinants derived from the normalization procedure to preserve the tissue volume of each structure. Finally, the modulated GM images were smoothed with an 8-mm FWHM isotropic Gaussian kernel and masked using an absolute threshold of 0.2. Further analysis was conducted using these masked-modulated images.

Whole brain correlation analysis

To explore the neuroanatomical correlates of individual differences in the non-symbolic numerosity, we calculated the Pearson's partial correlations between the GMV of each voxel and the Weber fraction after controlling for the gender, age, and total GM volume. Only clusters with a voxel-wise intensity threshold of $p < 0.01$ and a minimal cluster extent of 307 contiguous voxels (determined by 3dclustSim in AFNI; $\alpha = 0.01$, 26 nearest neighbor voxels), were considered to be significant.