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THE CALCULATING BRAIN

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KEY WORDS

arithmetic; fact knowledge; mathematics; number; procedural strategy

CLINICAL HIGHLIGHTS

- Numeracy, the ability to comprehend and manipulate numbers, is indispensable for daily functioning, influencing tasks from financial management to medication dosing. Its impact surpasses that of literacy, serving as a pivotal determinant of individual efficacy and economic prosperity at large.
- Low numeracy can also stem from acquired deficits obtained through brain injuries, known as acalculia. Unlike language impairments (aphasias), individuals with acalculia encounter difficulties with basic arithmetic operations.
- Developmental dyscalculia, a learning disorder, impairs mathematical abilities due to brain areas dedicated to numerical processing affected from birth. Although symptoms typically manifest in childhood, adults may remain unaware of their condition. With prevalence estimates ranging from 5% to 7%, dyscalculia poses a greater hindrance to personal and societal well-being than low literacy.
- To devise educational interventions and rehabilitation procedures, the initial step involves precisely identifying the characteristics of the defect and delineating the calculation abilities that are compromised or preserved. To delineate clinical syndromes and devise tailored interventions, comprehension of distinct brain processing systems underlying numerical cognition is imperative.

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REVIEW ARTICLE

THE CALCULATING BRAIN

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Abstract

The human brain possesses neural networks and mechanisms enabling the representation of numbers, basic arithmetic operations, and mathematical reasoning. Without the ability to represent numerical quantity and perform calculations, our scientifically and technically advanced culture would not exist. However, the origins of numerical abilities are grounded in an intuitive understanding of quantity deeply rooted in biology. Nevertheless, more advanced symbolic arithmetic skills require a cultural background with formal mathematical education. In the past two decades, cognitive neuroscience has seen significant progress in understanding the workings of the calculating brain through various methods and model systems. This review begins by exploring the mental and neuronal representations of nonsymbolic numerical quantity and then progresses to symbolic representations acquired in childhood. During arithmetic operations (addition, subtraction, multiplication, and division), these representations are processed and transformed according to arithmetic rules and principles, leveraging different mental strategies and types of arithmetic knowledge that can be dissociated in the brain. Although it was once believed that number processing and calculation originated from the language faculty, it is now evident that mathematical and linguistic abilities are primarily processed independently in the brain. Understanding how the healthy brain processes numerical information is crucial for gaining insights into debilitating numerical disorders, including acquired conditions like acalculia and learning-related calculation disorders such as developmental dyscalculia.

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1. BEGINNINGS: THE STUDY OF... 267
2. NONSYMBOLIC NUMBER REPRESENTATIONS 268
3. SYMBOLIC NUMBER REPRESENTATIONS 279
4. THE SPECIAL NUMBER ZERO 282
5. PROPORTIONS, RATIOS, AND FRACTIONS 284
6. ARITHMETIC 284
7. ADVANCED MATHEMATICS DISSOCIATED... 296
8. CONCLUSIONS 298

1. BEGINNINGS: THE STUDY OF MATHEMATICALLY GIFTED BRAINS

The mastery of numbers and arithmetic has long been seen as a formidable task. When individuals demonstrate exceptional skill in calculations and mathematics, it is often interpreted as a sign of remarkable intelligence; such individuals are assumed to possess exceptional cognitive abilities. Consequently, it comes as no surprise that scientists have been studying gifted brains since early times, aiming to understand, albeit with varying degrees of success, the neural underpinnings of extraordinary cognitive abilities and talents relative to the general population.

The study of gifted brains began with the examination of Carl Friedrich Gauss' brain after his death in 1855. Researchers compared the brains of gifted individuals to those of ordinary people, influenced by the phrenology of the time (1). Contrary to expectations, Gauss' brain, weighing 1.492 kg, was only slightly larger than average, challenging early notions that brain size correlates with intellectual ability (2). To make matters worse, in 2014 an

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- To devise educational interventions and rehabilitation procedures, the initial step involves precisely identifying the characteristics of the defect and delineating the calculation abilities that are compromised or preserved. To delineate clinical syndromes and devise tailored interventions, comprehension of distinct brain processing systems underlying numerical cognition is imperative.

analysis of MRI images and original drawings revealed that the brain labeled as Gauss' actually belonged to medical scholar C. H. Fuchs (3).

Even today, the belief in simple gross anatomical specializations for mathematical talent persists, as shown by the case of Albert Einstein. After Einstein's death, his brain was photographed and sliced into histological sections (4) (**FIGURE 1**). Decades later, studies of these tissue slices and photographs attempted to find anatomical traits linked to his mathematical abilities. Findings included a higher count of glia cells (5), greater neuronal density, an absence of the parietal operculum (6), an extraordinary prefrontal cortex and unusual parietal lobes (7), and a thicker corpus callosum (8). Despite media attention, these studies have not provided a credible anatomical basis for Einstein's genius, relying on the simplistic notion that brain structure directly correlates with intellect (9).

With the advent of functional imaging, researchers can now localize mathematical functions in the brains of living individuals. Mathematical prodigies like Rüdiger Gamm, who can perform complex calculations quickly and accurately, have been studied to understand gifted brains. A positron emission tomography (PET) study revealed that Gamm's expertise was not due to increased activity in number-processing areas but involved additional brain areas related to long-term memory, such as the medial temporal lobe (MTL) (10). This suggests that prodigies use enhanced long-term memory capacity and exhibit brain plasticity from extensive training (11, 12). These findings indicate that prodigies' skills are more about advanced memory techniques than innate mathematical ability (13).

This article begins with a more humble question: how are numbers represented in the brain? Here, one emphasis is on the distinction between nonsymbolic and symbolic number representations. It then proceeds to discuss calculations with numbers in arithmetic. Toward the end of the article, the study of gifted brains is revisited from a more modern perspective, when examining the brains of professional mathematicians.

2. NONSYMBOLIC NUMBER REPRESENTATIONS

2.1. Two Ways to Represent Number

Numbers are the foundational mathematical entities used for counting, measuring, and performing calculations such as addition, subtraction, multiplication, and division. Humans understand and process numerical information in two ways: through nonsymbolic and symbolic representations (**FIGURE 2**). Nonsymbolic and symbolic representations of numbers are conceptually distinct but neurally interconnected systems in the human brain.

Nonsymbolic number representation refers to the innate and intuitive ability to assess and discriminate numerical quantities (e.g., arrays of dots or sequences of sounds) directly, or analogically, without relying on symbols (**FIGURE 3*A***). This capacity shared by humans and animals has been conceptualized as "number sense" (19, 20) or "number instinct" (21). Since infants and animals can already judge numerical quantity nonsymbolically, this capability is considered phylogenetically and

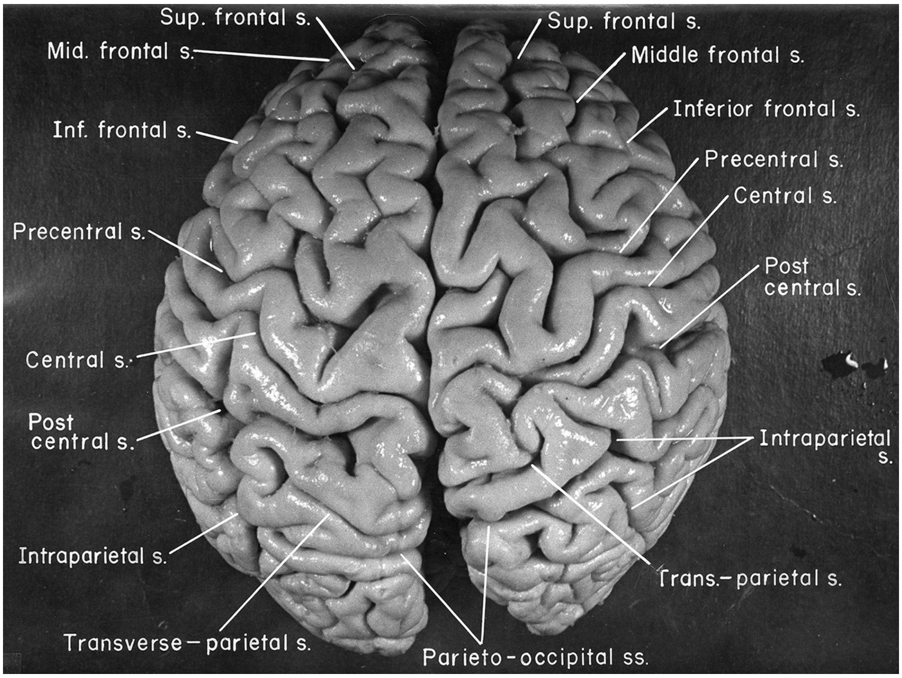


FIGURE 1. The brain of mathematical genius Albert Einstein. In search of his genius, the brain's structure was studied extensively. Before Einstein's brain was sliced, the brain was photographed from various angles, including this dorsal view (*top* is anterior). Image is courtesy of the Otis Historical Archives at the National Museum of Health and Medicine and used with permission.

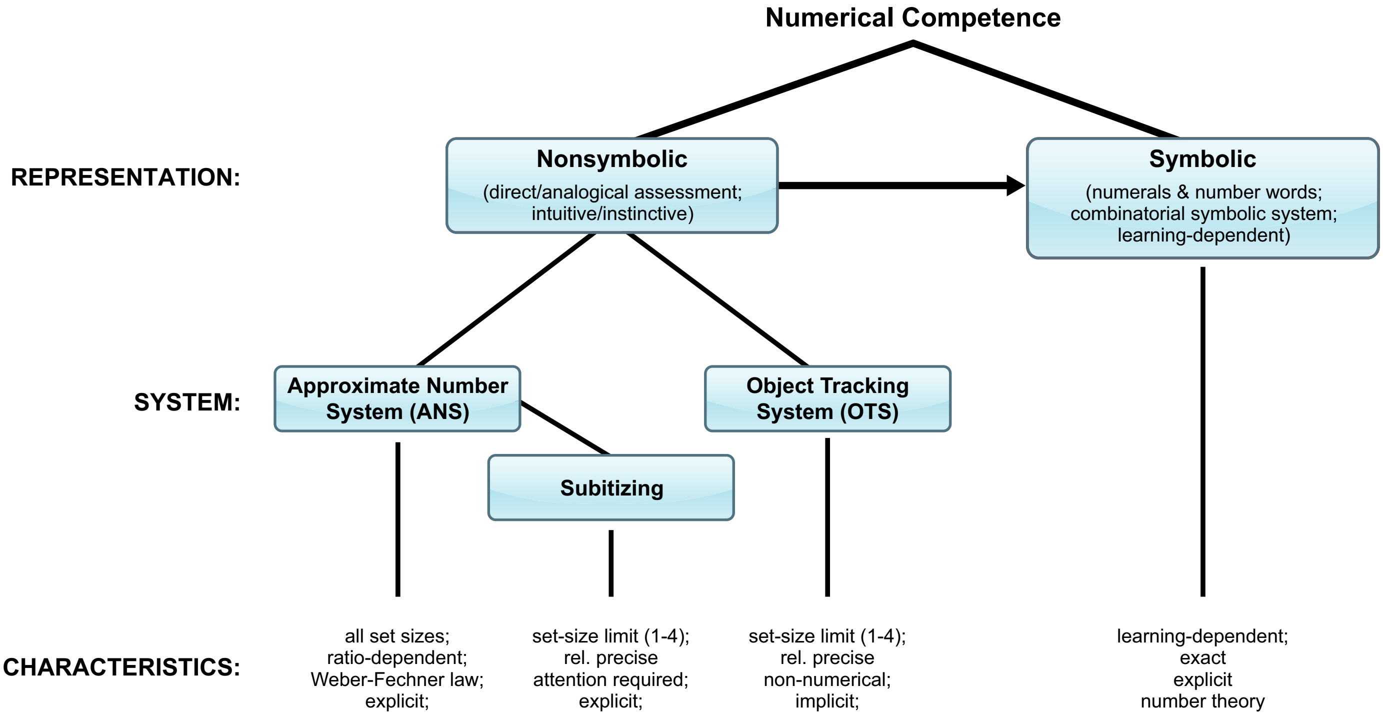


FIGURE 2. Taxonomy of representations and systems in numerical competence.

ontogenetically primordial. Studies with indigenous populations show that nonsymbolic number representations remain fundamental in the absence of formal counting education, even in adults (22–24). Nonsymbolic number representations form the basis for culturally learned symbolic number representations, as they inform what a numerical quantity means and how rudimentary operations on them can be performed. Three different representational systems are available to grasp nonsymbolic number: the approximate number system (ANS), the object tracking system (OTS), and subitizing. They are introduced in the following.

Building on nonsymbolic number representations, humans can learn and use symbolic number representations. They involve number symbols such as numerals (“5”) and number words (“five”), as part of a combinatorial symbolic system (25, 26). Numbers are used in various ways to describe objects and events: cardinal numbers represent quantity (e.g., “5 apples”), ordinal numbers denote the order in a sequence (e.g., “he finished third”), and nominal numbers identify specific objects (e.g., “runner number 456”). We assign numbers to measure a wide range of properties, providing information about both discrete and continuous quantitative aspects such as volume, length, temperature, time, and more (25). Symbolic number representations rely on learned associations between symbols and quantities, facilitated by a symbolic mental faculty enabling precise counting, arithmetic operations, and advanced mathematical reasoning unique to humans.

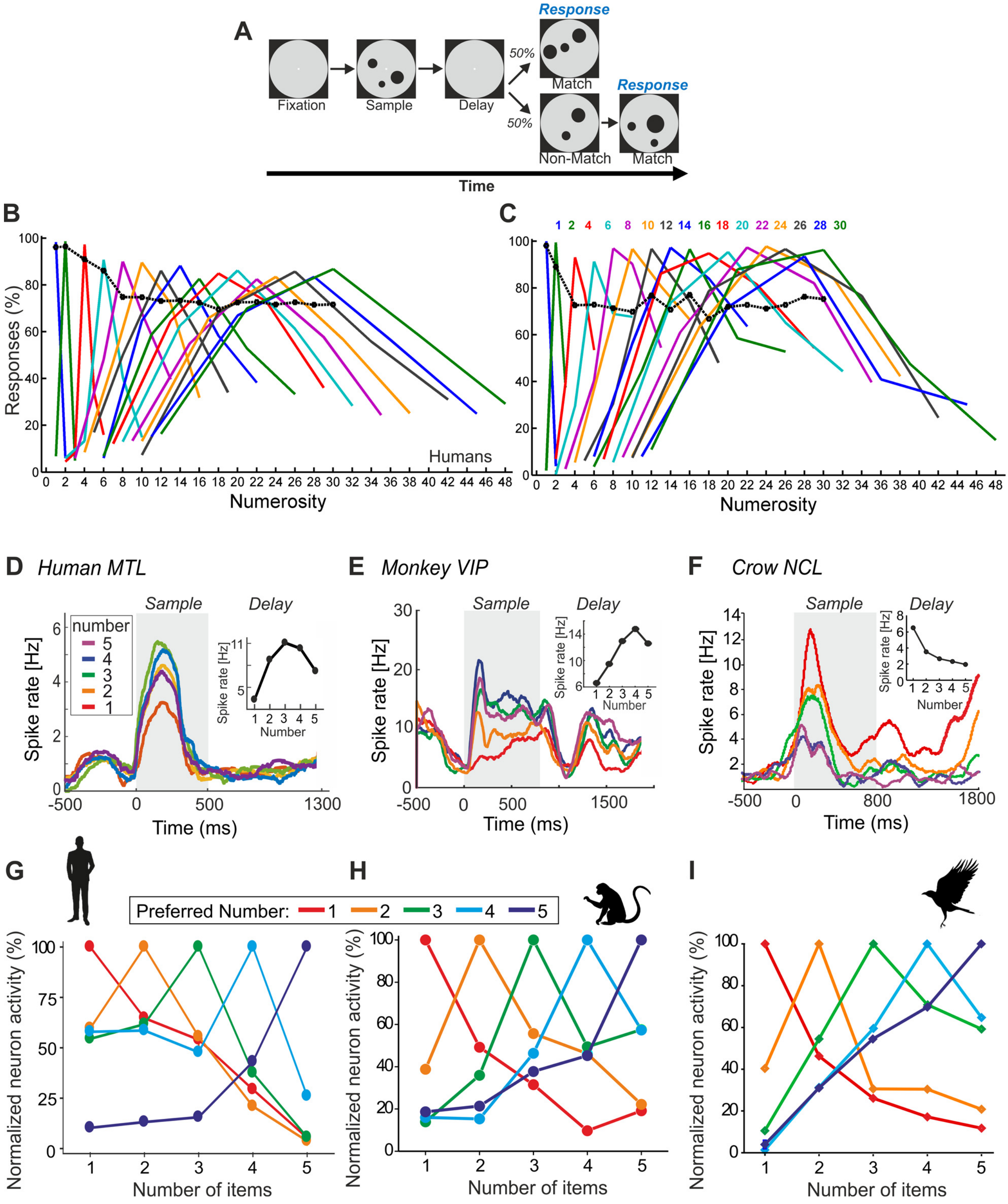
2.2. The Approximate Number System

2.2.1. Behavior.

The first system allowing the representation and manipulation of nonsymbolic numerical quantity is the approximate number system (ANS) (27) (**FIGURE 2**). This system enables the estimation of small and large numerosities in an approximate way (**FIGURE 3*B***). Similar numerical values are difficult to discriminate, but discrimination performance systematically enhances the more different (or distant) two values are (an effect called “numerical distance effect”). Moreover, discrimination of two sets becomes systematically less precise in proportion to increasing numbers (termed “numerical size effect”), in other words, the perception of the difference between two sets is influenced by their ratio (27, 28). Both distance and size effects are captured by Weber’s law, stating that the just-noticeable difference (ΔI) divided by the reference value (I) is a constant ($\Delta I/I = c$) (29). In addition, the subjective sensation of number (S) is proportional to the logarithm of the objective stimulus magnitude (I) [$S = k \times \log(I)$], a phenomenon encapsulated by Fechner’s law (30). Consequently, as objective numerical values increase, numerical representations remain equidistant in mental number space (14).

The ANS emerges ontogenetically as the first cognitive system in children (27). Approximate number discriminations, even across visual and auditory numbers of items/events, have been demonstrated in neonates as early as

50 h after birth (31). Newborns can only discriminate a 1:3 ratio (4 vs. 12) but not a 1:2 ratio (4 vs. 8). By the age of 5 mo, infants can discriminate between numbers differing in a 1:2 ratio when presented with arrays of dots (32, 33), sequences of sounds (34), or sequences of actions (35). Careful controls confirm that the number of objects is a parameter infants readily detect (36). With age, the precision of numerical discrimination improves. By 20 mo, infants can discriminate numerosities with a 2:3 ratio but not yet a 4:5 ratio (37). Six-year-olds can discriminate a 5:6 ratio, and adults can even discriminate a ratio of 9:10 (38). This enhancement could be due to brain maturation, an improvement driven by learning and experience with numbers, or a combination of both.



Indigenous people living in cultures with only rudimentary counting abilities and minimal symbolic number words exemplify the ability to perform arithmetic without formal mathematical training. The Munduruku, an indigenous group from the Amazon rainforest in Brazil, possess only a limited set of number words, using them more as estimates (“one,” “two,” “three-ish,” “four-ish,” and “five-ish”) rather than precise numerical terms (23). The Pirahã, indigenous people of the Amazon rainforest, have an even more reduced system, with number words for one (“hói”), approximately two (“hoí”), and many (“baágiso” or “aibaagi”) (22). When tested on nonsymbolic number discrimination tasks, the Pirahã were accurate for sets of 1 or 2, but their performance systematically deteriorated from 3 to 10, particularly when they had to memorize the target number. However, their performance for larger numbers was not random: With increasing target numbers, the average answers increased as a rough approximate of the correct number, and, in accordance with Weber’s law, the distribution of the answers became broader with increasing target numbers (24).

Not only in humans, but also across the animal kingdom, numerical competence is a widespread cognitive ability. Species from diverse zoological groups, ranging from primates to birds and from fish to insects, can discriminate the number of elements in a set, known as numerosity (14, 39–45) (**FIGURE 3C**). Animals estimate numerosity approximately rather than precisely. Discriminating similar numbers is difficult, but performance improves as the difference between numbers increases, a phenomenon known as the “numerical distance effect.” Additionally, as the numbers get larger, discrimination becomes less precise, known as the “numerical size effect.” For animals to tell sets apart, the numerical difference between them must usually increase in proportion to their size, making quantity discrimination “ratio-dependent.” These effects are explained by Weber’s law, which indicates the presence of an internal “approximate number system” (ANS) in various animal species (46).

2.2.2. Neurons selective to numerosity.

Single-neuron recordings from the cerebral cortex of behaving macaque monkeys were instrumental in deciphering the neuronal code for nonsymbolic numerical quantity representations (**TABLE 1**) (18, 47–50). These studies identified numerosity-selective neurons in the posterior parietal cortex (PPC), particularly the intraparietal sulcus (IPS), and prefrontal association cortices (PFC) as the anatomical and physiological units of number representation. A numerosity-selective neuron exhibits its strongest firing rate to a specific numerosity; it is tuned to a preferred numerosity but also responds more weakly to numerosities adjacent to the preferred one, resulting in a bell-shaped tuning function (**FIGURE 3*E***). Different neurons are tuned to different numerosities (18, 47, 48, 50–53), and, as a population, they thus cover the entire number line. Like behavioral performance functions (**FIGURE 3*H***), the resulting bell-shaped neuronal tuning functions adhere to the Weber–Fechner law characteristic for the ANS: the tuning functions become systematically less selective (i.e., broader) with increasing preferred numerosities, and they are better represented on a logarithmic than a linear number scale (54, 55). Numerosity-selective neurons respond to the number of items in a set abstractly, irrespective of the sensory attributes of the items (48), and for numbers distributed in space (dot displays) or across time (item sequences) (56). These neurons integrate items of a set across the visual field, even independently from, and outside of, their classical

FIGURE 3. Behavioral and neuronal representations of the approximate number system. *A*: delayed match-to-number task used to explore the representation of numbers in humans and animals. A trial begins when the subject grasps a lever and fixates a central target on a screen. After fixation, the sample stimulus displays a varying number of dots, which the subject has to memorize during a delay period. The subject has to respond whenever the numerosity displayed in the sample phase is shown again in the test phase. The first test stimulus was a match in 50% of the cases. Trials are pseudorandomized, and each numerosity is shown with many different dot patterns. Changes of nonnumerical parameters with changes in numerosity were controlled for. *B*: behavioral numerosity discrimination functions of humans performing the task in *A* for sample numerosities 1–30. The curves indicate whether the participants judged the first test stimulus (after a delay) as containing the same number of items as the sample display. The function peaks (and the color legend) indicate the sample numerosity at which each curve was derived (from Ref. 14). *C*: behavioral numerosity discrimination functions of a rhesus monkey performing the task in *A* for sample numerosities 1–30. Same layout as in *B*. Image is from Ref. 14 and used with permission from *Journal of Cognitive Neuroscience*. *D*: single-neuron activity in human medial temporal lobe (MTL) as response to numerosity. This example MTL neuron shows the preferred numerosity 3, it is tuned to numerosity 3. Every colored line represents the time course of the average momentary firing rate of the neuron to the five tested numerosities 1–5 during sample and delay periods. The first 500 ms represents the fixation period (baseline). Gray shading represents the sample period in which the numerosity display was shown. The tuning curve *inset* indicates the mean activity of the neurons to the numerosities in the sample period. Image is from Ref. 15 and used with permission from *Neuron*. *E*: example neuron in rhesus monkey ventral intraparietal areas (VIP) tuned to numerosity 4. Same layout as in *D*. Image is from Ref. 16 and used with permission from *Current Biology*. *F*: example neuron in the nidopallium caudolaterale (NCL) of a carrion crow tuned to numerosity 1. Same layout as in *D*. Image is from Ref. 17 and used with permission from *Proceedings of the National Academy of Sciences USA*. *G*: the normalized activity of all numerosity-selective neurons in human MTL averaged according to individual preferred numerosities (indicated by same color) form overlapping neuronal numerosity representations covering the entire number line. *H*: neuronal numerosity representations in monkey intraparietal sulcus (IPS). Layout as in *G*. Image is from Ref. 18 and used with permission from *Proceedings of the National Academy of Sciences USA*. *I*: neuronal numerosity representations in crow NCL. Layout as in *G*. Image is from Ref. 17 and used with permission from *Proceedings of the National Academy of Sciences USA*.

Table 1. ***Neuroscientific techniques***

Recording methods

Single-neuron recording is an electrophysiological technique where microelectrodes are inserted into specific brain tissue to directly record action potentials from individual neurons. Although primarily utilized in animal studies, it can also be conducted in rare cases in neurosurgical patients who have chronic depth electrodes implanted for diagnostic purposes.

Electrocorticography (ECoG) is an electrophysiological recording technique where blunt surface electrodes are placed directly on the brain surface of neurosurgical patients. Each electrode captures electrophysiological signals emanating from a population of neurons estimated to encompass several hundred thousand neurons.

Functional magnetic resonance imaging (fMRI) is a noninvasive method to study brain activity. It detects changes in blood flow, indirectly revealing neural activity while participants are scanned in an MRI machine. The technique relies on the blood oxygen level-dependent (BOLD) signal, which reflects alterations in blood flow linked to neuron activity across brain regions.

Positron emission tomography (PET) is a neuroimaging technique. It measures local radioactivity of radioactive tracers (metabolites such as glucose) that have been injected into the bloodstream. Active brain areas metabolize and accumulate these compounds, showing increased radioactivity in PET scans, which correlates with brain activity.

Magnetoencephalography (MEG) is a noninvasive neuroimaging technique that measures magnetic fields generated by synchronized neuron activity. It offers high temporal resolution (milliseconds) but lower spatial resolution compared to fMRI. MEG is most sensitive to cortical activity near the brain's surface.

Perturbation methods

Lesion studies used in neuropsychology involve investigating the effects of brain damage or injury on cognitive and behavioral functions in individuals that perform specific tasks.

Direct electrical stimulation in neurosurgery applies controlled currents via blunt electrodes to map brain function on the cortical surface. In areas related to numbers and language, it temporarily halts these functions, aiding precise localization during surgery.

Transcranial magnetic stimulation (TMS) is a noninvasive neuromodulation technique that involves the application of brief magnetic pulses to specific regions of the brain. In associative brain areas, TMS typically causes a transient disruption of numerical functions.

visual receptive fields (57). These findings show that neurons in frontal and parietal association cortices encode global and spatially released number representations as required for number perception.

The highest abundance of numerosity-selective neurons in monkeys is found in the lateral PFC, followed by the ventral intraparietal area (VIP) (18), a polymodal association zone in the fundus of the IPS (58). Neurons in the IPS exhibit the shortest response latencies to numerosity among all tested brain areas. This suggests that the IPS functions as the initial site in the primate brain where numerical information is first extracted (18, 59, 60). This information is then distributed to other active brain areas, including the PFC, through well-established direct anatomical (61–64) and functional (65, 66) connections. The relatively high prevalence of neurons tuned to numerical information in the IPS aligns with the regular identification of the IPS as a primary hub for representing both approximate and exact numerical quantity in humans (67, 68). This observation suggests homologous brain areas for number processing in both human and nonhuman primates (69, 70).

In the monkey PFC, where the highest proportion of numerosity-selective neurons exists (18), numerical information is encoded more abstractly and working memory-related compared to the IPS. PFC neurons demonstrate minimal sensitivity to the sensory appearance of set items (18, 48), encode preferred numerosity regardless of sensory modalities (71), display heightened working memory activity related to numerosity (18), and can establish semantic links between dot numerosities and associated visual shapes, represented as Arabic numerals (72). When monkeys need to process numerical information during the course of time in a task, a sequential transformation of neuronal signals from representation of numerical values to representation of abstract decision (such as the binary judgment of "same number" vs. "different number") is seen (73). All these findings suggest that coding beyond the IPS is becoming more relevant for cognitive processing and behavioral output.

Despite the importance of the lateral PFC and VIP, numerosity-selective neurons have also been identified in other associative cortical areas of the nonhuman primate brain. These areas comprise other intraparietal areas (18), the superior parietal lobule of the posterior parietal cortex (47), as well as the premotor cortex and the cingulate cortex within the frontal lobe (74). There is also suggestive evidence of numerosity tuning in the macaque hippocampus in the medial temporal lobe (MTL) (75).

Although the MTL is often not considered part of the core number network, recent neuroimaging studies in humans have increasingly demonstrated its involvement in representing numerical information, particularly during the developmental stages when children learn to count and perform arithmetic (76–79). It is therefore plausible that the first study reporting single neurons responding to specific numerical values was based on direct recordings in the MTL (15). In this study, patients undergoing treatment for pharmacologically intractable epilepsy were implanted with chronic depth electrodes in regions of the MTL, including the hippocampus, parahippocampal cortex, entorhinal cortex, and amygdala. During the experiment, participants performed simple sequential addition and subtraction tasks using dot numerosities as operands. A substantial 16% of the recorded MTL neurons exhibited responses correlated with the number of items in the first operand, regardless of the arrangement of the dot arrays (15). Each of these selective neurons demonstrated a preference for a particular numerosity, as illustrated by bell-shaped number tuning curves (**FIGURE 3, *D* AND *G***). These numerosity-selective neurons were relatively broadly tuned, resulting in rather coarse discriminability between numerosities and thus large numerical distance effects for the comparison of nonsymbolic numerosities. This finding correlates with behavioral studies and neural modeling, which show that the distance effect is substantial for the comparison of nonsymbolic numerosities but minimal for judgments of exact number symbols (80, 81). The broad tuning of these neurons suggests that, although they are effective for approximate numerical comparisons, they lack the precision required for exact symbolic number judgments. Computational decoding analyses further revealed that numerosities could reliably be predicted from the activity of a population of MTL neurons. Interestingly, the numerical code present in the human brain closely resembled the approximate number code previously identified in monkeys (48) (**FIGURE 3, *E* AND *H***). The same numerosity code is found in crows (17, 82–84), birds with which humans share a last common ancestor already 320 Mio years ago (**FIGURE 3, *F* AND *I***). This suggests an evolutionarily conserved mechanism for representing numerosity.

Animal studies support the notion that the basic neuronal circuitries enabling number representations are hardwired in the brain. One line of evidence is the finding that numerosity-tuned neurons exist already in numerically naive monkeys (60) and birds (85, 86) that have never been trained to discriminate numerosity. A second line of evidence comes from neural modeling simulating brain processing: deep learning networks that mimic the visual system, spontaneously and without number training, develop network units tuned to numerosity (87, 88). Such network units exhibit the same Weber–Fechner characteristics as real neurons. The inherent capacity of the brain to represent numerical quantity explains why neonates (31) and animals across diverse taxa (89–91) can spontaneously and readily assess numbers in their environments. Of course, this does not mean that numerosity tuning of neurons could not be shaped and sharpened through experience and behavioral relevance. In fact, putative pyramidal cells, the cortex's excitatory projection neurons, in the prefrontal cortex (PFC) exhibit higher numerosity selectivity when monkeys explicitly discriminate the number of dots compared to discriminating the color of dots (16).

To sculpt numerosity tuning curves at the level of local microcircuits, the interactions between the two major cell classes in the cerebral cortex, excitatory pyramidal projection neurons and inhibitory interneurons, play a crucial role (92–94). More selective, i.e., narrower tuning functions are generally associated with better discriminability of stimulus features (95–97). Analyses of response properties of adjacent and functionally coupled neurons suggest that the tuning of pyramidal cells is sharpened by lateral inhibition exerted via inhibitory interneurons, which typically exhibit inverted tuning profiles compared to the coupled pyramidal cell (98). Such basic circuit operations appear to be necessary for the representation of categorical numerical information, as they also exist in anatomically distinct and independently evolved endbrains of phylogenetically distant birds (99, 100).

2.2.3. Neuroimaging of nonsymbolic number.

In neuroimaging studies using functional magnetic resonance imaging (fMRI) (**TABLE 1**), the PPC has been identified repeatedly as a crucial area for representing the nonsymbolic number of visual items in a collection (101–104). To measure activity related to numerical values per se rather than to cognitive task factors such as response selection that inevitably occur when participants are engaged in number tasks, a method called fMRI adaptation was employed (101). This approach exploits the finding that single neurons in monkeys adapt to repeatedly presented stimuli they are tuned to by showing progressively decreased firing rates (105). This decrease in neuronal firing rate is expected to be mirrored in declining blood oxygen level-dependent (BOLD) activity with repeated stimulus presentations in fMRI, offering a chance to find out if neurons in the human brain also would be tuned to numerosity (**FIGURE 4*A***).

It was found that repeated presentation of one fixed visual numerosity resulted in the expected decline of BOLD activity in the IPS (101) and in the lateral PFC (107). When immediately after adaptation a deviant numerosity

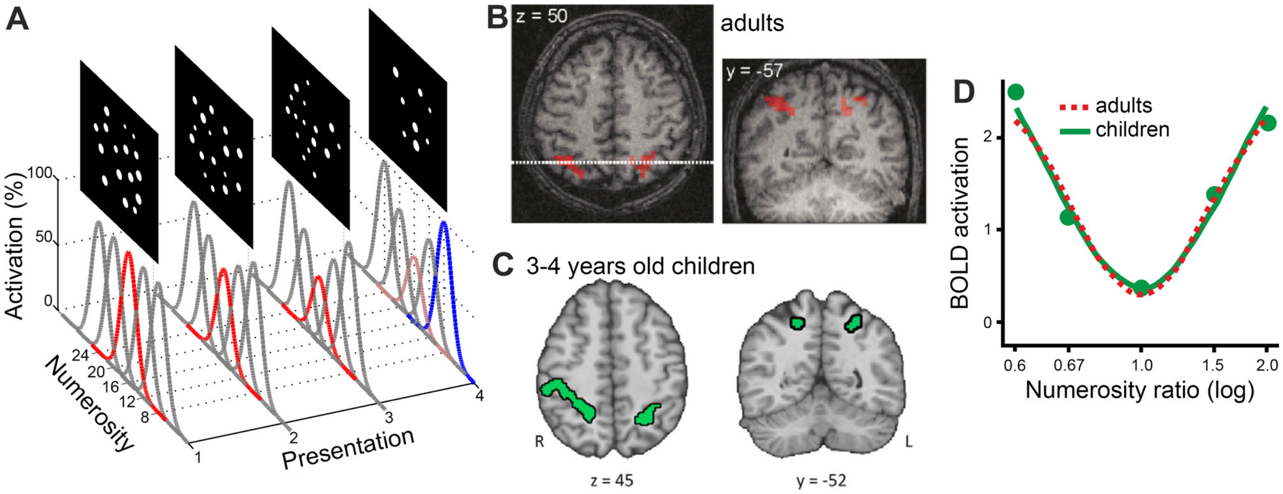


FIGURE 4. Functional MRI (fMRI) adaptation used to indirectly demonstrate populations of numerosity-tuned neurons underlying blood oxygen level-dependent (BOLD) activation in adults and children. *A*: principle of fMRI adaptation with numerosities. Subjects are repeatedly presented with a fixed numerosity (for example, 16 dots). If any region of the brain contains numerosity-selective neurons tuned to a specific numerosity (illustrated by Gauss functions below the dot patterns), neurons should habituate (that is, decrease discharge) with repeated numerosity presentations. In this example, neurons tuned to numerosity 16 (represented by red Gaussian) should habituate, whereas neurons tuned to other numerosities should not be affected. This habituation effect is "read out" by recording the relative increase in fMRI activation to a single deviant numerosity presented at the end of a sequence (represented by blue Gaussian). *B*: regions of interest (red) in the right and left intraparietal sulcus (IPS) of adults who showed a monotonically decreasing effect of fMRI adaptation and a preference for numerical changes. Image is from Ref. 101 and used per Open Access CC-BY 4.0 terms. *C*: regions of interest (green) in the right and left IPS of children. Image is from Ref. 106 and used per Open Access CC-BY 4.0 terms. *D*: BOLD tuning curves in right IPS of adults (*B*) and children (*C*) passively viewing dot numerosities. Original data points from the children are shown together with the best fits of a model simulating an inverted symmetric tuning curve. Ratio 1.0 signifies the habituation numerosities that is repeated several times before the deviant numerosity at ratio 0.5, 0.87, 1.5, and 2.0 are presented. After BOLD activation was suppressed to the habituation numerosity and set to activation 0.0 as reference, a release from suppression represented by an increase in activation was seen for deviant numerosities as a function of numerical distance. Note that the curves are plotted on a logarithmic ratio scale as this scale described the curves better than a linear number line. Adult data were rescaled to match the amplitude range of the children's data. Child data are redrawn from Ref. 106, and adult data are from Ref. 101; both are used per Open Access CC-BY 4.0 terms.

was shown, a recovery of the BOLD signal in the same brain area of the IPS and PFC was detected (**FIGURE 4*B***). This recovery from habituation was stronger for deviants more distant from the habituation numerosity, which resulted in a peak recovery tuning function similar to single-neuron tuning functions (**FIGURE 4*D***). These BOLD signal recovery functions followed Weber's law and even showed logarithmic compression, providing a connection to numerosity-tuned single neurons (101, 107).

Already 4-yr-old children exhibited the same parieto-frontal adaptation patterns as seen in adults (**FIGURE 4C**). In the parietal lobe, activation was observed in the right IPS, right superior parietal lobule (SPL), and left inferior parietal lobule (IPL) (108). In the frontal lobe, stronger activation was noted in the left precentral gyrus, the left superior frontal gyrus (SFG), and the right middle frontal gyrus (MFG). With the abovementioned fMRI adaptation protocol, BOLD tuning functions could be measured even in the IPS of 3- to 4-yr-old preschoolers (109) (**FIGURE 4*D***). These BOLD tuning functions were again best described on a logarithmic number scale, mirroring findings in adults (101, 107) and in monkey number neurons (110). Moreover, the sensitivity of young children's neural tuning to number in the right IPS was comparable to their behavioral discrimination sensitivity observed outside of the scanner. Children with sharp neural tuning curves in the right IPS were better at differentiating numbers (106). With other neuroimaging techniques, similar parieto-frontal adaptation patterns have even been observed in 6-mo-old (111) and even 3-mo-old (112) children. These findings suggest that, anatomically and mechanistically, the brain's primordial number-processing capacity based on the ANS precedes formal number training and counting. As a consequence, atypical development of the brain areas involved in representing numerical quantity leads to dyscalculia (BOX 1).

High-field fMRI studies in adults passively viewing dot numerosities indicate that nonsymbolic numerosity values are organized in a topographic manner on the cortical surface. In the human SPL, activation sites responsive to passively viewed small numerosities are organized as a numerosity map (126) (**FIGURE 5*A***). Adjacent to the activation site for one, the activation spot for two was located, and this pattern continued for higher numerosities. Along this numerosity map, the amount of cortical space devoted to representation was highest for the smallest numerosities and progressively decreased for higher numerosities (**FIGURE 5*B***).

BOX 1: DYSCALCULIA

"Dyscalculia" describes poor calculation abilities. Developmental dyscalculia is a learning disorder involving difficulty in acquiring arithmetic skills, unrelated to intelligence, schooling, emotional stability, motivation, or neurological deficits like brain injury. (113). Dyscalculia is diagnosed with standardized arithmetic tests. Significant underachievement in these tests compared to expected levels based on age, education, and intelligence serves as an objective criterion for identifying developmental dyscalculia (114) The specific learning disorder for impairments in mathematics is classified under DSM-5 diagnostic code 315.1 (F81.2) by the American Psychiatric Association (115).

The estimated prevalence of developmental dyscalculia is between 5% and 7% (116). This is approximately the same prevalence as developmental dyslexia, a much more recognized disability in reading (117). Numeracy skills are crucial for daily functioning, impacting tasks like managing finances and understanding medical instructions. A significant United Kingdom study revealed that low numeracy poses greater challenges than low literacy: dyscalculic individuals earn less, spend less wisely, face more health and legal issues, and require increased educational support (118).

Neuroimaging studies highlight structural changes in brain regions like the posterior parietal cortex (PPC), prefrontal cortex (PFC), temporooccipital cortices, and subcortical areas in individuals with developmental dyscalculia (106, 119–124). Understanding these brain differences is crucial for addressing this challenging learning disorder. Treatment and intervention approaches for developmental dyscalculia are informed by diverse neurocognitive models (125). These models suggest that dyscalculia arises from various factors such as deficits in basic numerical quantity, visuospatial processing, working memory, attention, and broader executive functions. The specific nature and severity of these deficits vary widely among individuals, resulting in diverse manifestations and degrees of impairment in mathematical abilities. This complexity poses significant challenges in developing effective interventions, with current outcomes demonstrating only modest success. Progress hinges on a detailed understanding of the neurocognitive systems involved, including variations in how dyscalculia manifests. This understanding is crucial for designing targeted rehabilitation methods for this disabling neurodevelopmental disorder.

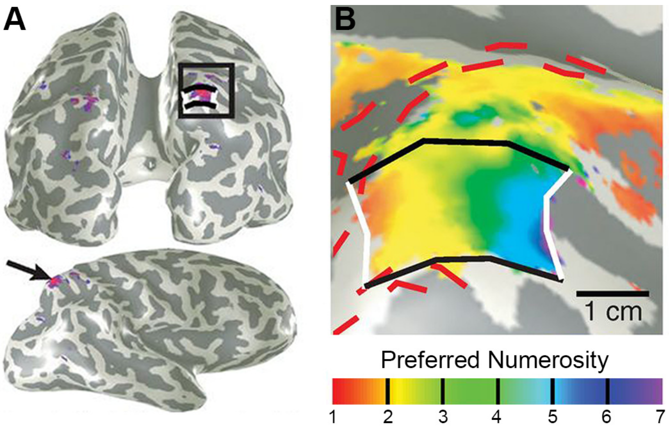


FIGURE 5. A functional MRI (fMRI) map for numerosity. *A*: posterior-dorsal view of the human brain showing the region in the right parietal cortex where fMRI numerosity tuning in various dot numerosity arrangements (constant dot area, constant dot size, constant circumference, constant density) was found. The area indicated by the black square is enlarged in *B*. *B*: topographic representation of preferred numerosities (color coded) averaged for all dot numerosity arrangements. The preferred numerosity of 1 to 7 is increasing from the medial to lateral ends (white lines) of the region of interest (black and white lines). Image is from Ref. 126 and used with permission from *Science*.

Thus, small numerosities have more neurons available for encoding, which could be one factor for better behavioral discrimination of small compared to large numerosities. Subsequent studies discovered an entire network of six numerosity maps that covers the temporal, parietal, and frontal cortices (127–129).

The PPC is not only involved in encoding numerosity during passive viewing but also during active discrimination such as in a delayed match-to-sample task. In one study, the participants' BOLD activation patterns in the parietal lobe resulting from different numerosities were used to train a statistical classifier [support vector machine (SVM)] (130). For instance, the classifier could learn that four dots produced a distinct distribution of BOLD activation on the cortical surface, differing from the pattern caused by eight dots. Based on what the classifier had learned about these activation patterns in the bilateral intraparietal cortex, it could accurately decipher the numerosity participants had seen in novel trials (130), confirming the reproducibility of neural activation patterns for nonsymbolic numbers.

Numerosity representation studies predominantly employed visual dot arrays as simultaneous presentation format, yet a few also explored sequential presentation formats. In tasks involving classifying both linear arrays of dots (simultaneous numerosity presentation) and flashed dot sequences (sequential numerosity presentation), the simultaneous numerosity presentations induced bilateral activations in various areas of the intraparietal sulcus (IPS) and the inferior temporal gyrus (131). In contrast, sequential numerosity presentations revealed a different activation pattern, with activations confined to the right hemispheric IPS and the inferior frontal gyrus. Simultaneous and sequential numerosities appear to be processed differently in the brain. However, these networks are not entirely segregated but showed overlap in two regions: the right IPS and the right precentral gyrus extending into the frontal gyrus (131).

The unexpected involvement of the precentral gyrus, housing the motor cortex, suggests a potential connection to the use of hands and fingers in tracking numerical magnitude. This observation may also explain why another fMRI study identified the lateral premotor cortex as consistently activated during sequential enumeration of sensory items and counting motor movements (132). Moreover, a PET study found that the left precentral gyrus and the anterior IPS (AIP), a premotor area, were more strongly activated during multiplication compared to reading. This activation pattern has been interpreted as these areas being involved in finger counting-based representations (133). Indeed, finger counting is known to be a useful tool for numerical development across cultures, allowing individuals to alleviate working memory load and thus perform better in complex numerical tasks (134–137).

As an abstract quantity, the number of items should be represented irrespective of sensory modality. To explore a potential cross-modal numerical representation, researchers investigated whether neural representations of the quantity of sequentially presented items in one modality (visual) could be identified from brain activation patterns evoked by quantities presented in another modality (auditory). The study revealed that quantities of visual dots were recognizable by a classifier trained on neural patterns evoked by quantities of auditory tones, and vice versa (138). Brain regions supporting cross-modal quantity classification included the bilateral frontal (precentral, superior frontal, and inferior frontal regions) and parietal (inferior and superior parietal lobules, intraparietal sulci, and postcentral regions) lobes. This study demonstrated stable neural representations of sequential numerosities across visual and auditory modalities, emphasizing the crucial role of the PPC and PFC in numerical quantity representation.

Damage to these areas in the frontal and posterior parietal association cortices consequently causes deficits in processing numerical quantity (e.g., acalculia) (BOX 2). For instance, a patient with a focal lesion to the left posterior parietal lobe demonstrated a severe slowness in estimating dot numerosities extending to Arabic numerals (139). The selective numerical deficits following lesions in patients point to the causal involvement of brain areas such as the IPS in processing numbers.

2.3. The Object Tracking System

The second nonsymbolic system available for numbers is the object tracking system (OTS) (27, 28, 140, 141) (**FIGURE 2**). This system enables the automatic and perceptual individuation, tracking, and memorization of a limited number of three or four items at a time. The individuation of single objects has been conceptualized to occur through object files, serving as a temporary memory representation (142), or a limited number of object markers called FINSTs (FINgers of INSTantiation) that are automatically attached to targets in the visual field for later processing (143, 144). As the OTS focuses on individuating discrete items rather than sets, the resulting mental representation is precise but not inherently numerical (28, 141).

Nevertheless, the OTS appears to allow arithmetic-like computations through representation of the exact equality of two sets through one-to-one correspondence (141, 145). That is, individual items can be mentally aligned to determine whether the same items persist or to judge whether two sets have the same or different number of items. For instance, preschool children can match or align small sets of items accurately by number for smaller quantities up to ~3 or 4, but not larger quantities (146). Even more, when 5-mo-old infants witness two stuffed animals being placed sequentially behind a screen (1 + 1), they exhibit heightened visual attention when the screen is lifted to reveal only one stuffed animal (1 + 1 = 1) compared to when the correct arithmetical outcome of two stuffed animals is revealed (1 + 1 = 2) (147, 148). Preschool children aged 18 mo to 4 yr also demonstrate the capability to utilize object tracking for precise addition or subtraction outcomes with small sets (fewer than 4) of objects (149–153). As a characteristic of the OTS, these abilities begin to fail when the quantities involved exceed the limit of 4 items.

Compared to evidence for the ANS, evidence supporting the existence of an OTS in animals is rarer and primarily comes from wild animals spontaneously choosing between item sets (of food, for instance). During numerosity discrimination in taxonomically diverse species, a set size limit of up to 4 has been observed in such tasks (154–159).

Despite more than four decades of theorizing, attempts to neuronally identify object pointers as part of an object tracing system in the visual brain remain challenging (160). As object pointers are supposed to provide object permanence, i.e., objects continue to exist and ought to be signaled by neurons even when they are out of sight, neuronal correlates of object permanence are currently the best indicators of a realization of object pointers. Indeed, neurons in monkey temporal cortex signal hidden objects for seconds after occlusion (161, 162), a capacity that seems to be based on object pointers. However, such object permanence neurons are selective for the identity of the occluded objects, whereas neurons that act as object pointers should abstract from specific object features (160). Where in the brain and how the OTS could be implemented has yet to be discovered.

2.4. Subitizing

When numerate adults are asked to judge the number of briefly presented items in a set, they show a behavioral dichotomy that is unexpected based on the assumption of a single ANS (163): participants respond fast and accurately for small numbers up to ~4, a process termed "subitizing" (164) (**FIGURE 2**). For larger numbers beyond 4, participants use the ANS and show increasingly slower and more imprecise number "estimation" exhibiting number ratio dependency based on the ANS (**FIGURE 3C AND FIGURE 6*A***) (164, 166, 167). Subitizing of small numbers plays a crucial role in children's early stages of learning to count and seems to function as a developmental stepping stone in acquiring the meaning of the initial number words (168). The subitizing system, initially identified in numerate adults, has also been observed in animals, including nonhuman primates (169–171).

The explanation of the behavioral effects of subitizing is a subject of ongoing debate. Some argue that the observed judgment differences arise from a single approximate estimation system (the ANS), where the negligible ratio-dependent imprecision for small numbers creates a seeming dichotomy in underlying mechanisms (172–174). In contrast, others claim that subitizing and estimation represent two distinct mechanisms for assessing small versus large numbers (164, 166, 167).

Subitizing exhibits similarities with the OTS, but if and how both processes are related is unclear. On one hand, the effortless assessment of up to 4 items is an important characteristic shared by both, arguing for fundamental commonalities. Subitizing has therefore been proposed to depend on the OTS for representing and tracking small numbers of individuals (143). Whereas the OTS allows for the selection and tracking of individual objects, subitizing may be considered the process of extracting the numerical value from the input of the OTS, and this value can then be associated with a symbolic label (175). On the other hand, fundamental mechanistic differences between subitizing and the OTS exist. Although subitizing has traditionally been considered preattentive (176), more recent research indicates that attention plays a crucial role in numerosity processing within the subitizing range. If attention is diverted from numerosity assessment, subitizing is significantly compromised (177–182). While the estimation of larger quantities hardly changes as a function of attentional load, subitizing emerges only with attention placed on numerosities (183, 184). In the absence of attention required for the subitizing system to surface, the ANS continues to function, enabling numerosity estimates also for small numbers, albeit with less precision. Thus, the significance of attention in subitizing highlights it as a distinct small-number mechanism separate from the OTS.

Despite explorations into underlying brain mechanisms of subitizing using blood flow imaging or electroencephalography, the results remain inconclusive; while some studies advocate for a single underlying system (126, 128, 185–187), others propose two separable number systems (188–190). Recent single-neuron recordings in the medial temporal lobe of neurosurgical patients engaged in judging numerosities reveal that two distinct neuronal mechanisms underlie the representation of small and large numbers (**FIGURE 6*B***) (165). Within the subitizing range of small numbers, neurons exhibit superior tuning selectivity accompanied by suppression effects (**FIGURE 6C**). This suggests neuronal surround inhibition as a mechanism for increasing selectivity of neurons' approximate numerosity tuning curves (191, 192). In contrast, tuning selectivity decreases with increasing numbers beyond 4, indicating the workings of a ratio-dependent ANS (**FIGURE 6*D***). Neuronal population analyses using statistical classifiers (**FIGURE 6*E***) and state-space analysis further confirm the existence of these two coding mechanisms delineated by a coding boundary at the level of neuronal populations (165) (**FIGURE 6*F***). This study establishes a clear boundary in neuronal coding around the number 4, corresponding to the behavioral transition from subitizing to estimation. Because the participants actively assessed numerical information to solve the behavioral task, the hypothesis is that the small-number coding characteristics and boundary emerged because of activation of attention-demanding subitizing.

The strong impact of attention on numerosity-selective responses in the brain has been supported by neuroimaging studies in humans (193). Attention seems to have a specific influence on the representations of small numbers. Brain areas thought to be involved in stimulus-driven attention (194), such as the right temporoparietal junction, are activated during a quantity-comparison task, but only for small numbers of items, typically up to 3 or 4 (195, 196). These findings suggest an attention-assisted boost in the performance of numerosity judgments within the subitizing range. As subitizing and large number estimation based on the ANS are differently influenced by attentional load, the conclusion is that they depend on different processes and potentially operate through distinct systems. If this holds true, subitizing may share fundamental mechanistic similarities with other capacity-limited attention-based processes, such as working memory (197, 198), which shows precisely the set size limit of 4 found for subitizing (199).

2.5. Views on the Origin of Number Sense

The origin and development of the number system are conceptualized through two contrasting viewpoints: the "nativist" and "emergentist" perspectives. According to the nativist viewpoint, number sense is primarily innate, domain specific, and shaped by biological evolution (20, 21). These inherent cognitive capacities are believed to have evolved through natural selection over evolutionary history, providing adaptive advantages crucial for

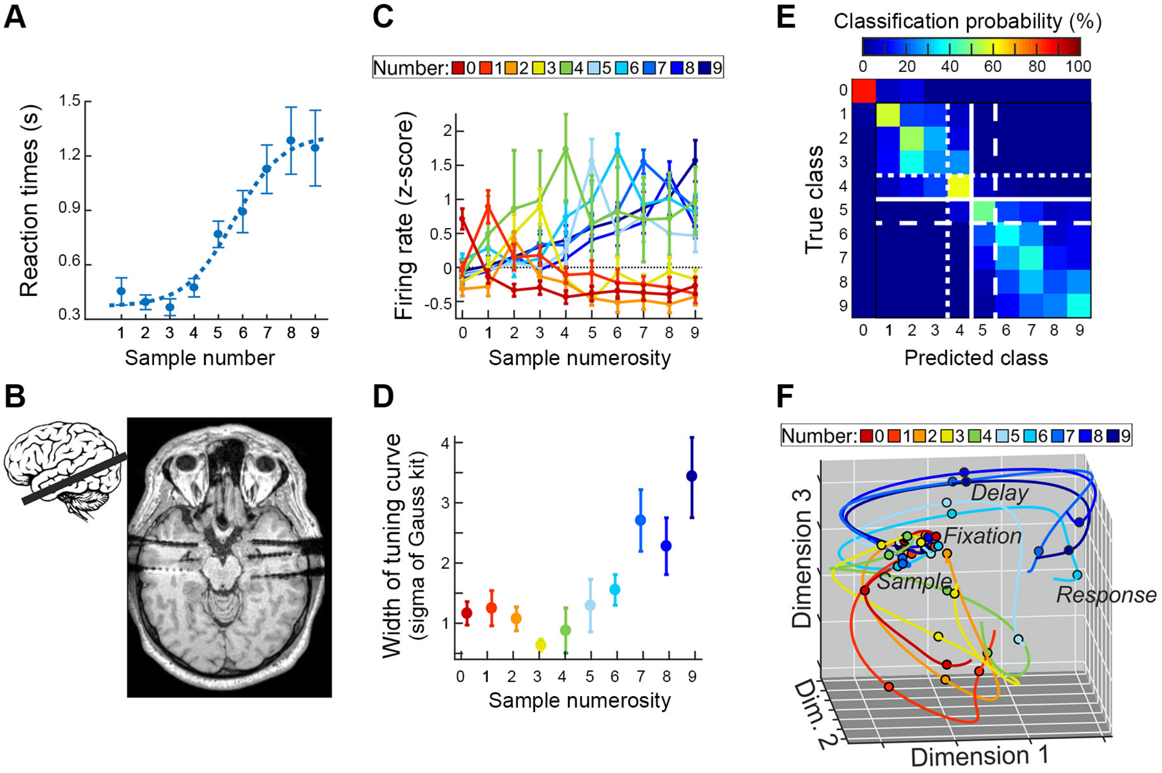


FIGURE 6. Small vs. large number tuning of numerosity-selective neurons during a parity judgment task. *A*: when subjects judged the parity (odd/even) of dot numerosities, they showed the well-known behavioral effects indicative of 2 different representational systems: Small countable numerosities from 1 to 4 were equally effortlessly judged with short reaction times (and few errors), as expected for subitizing. In contrast, numbers 5 and higher were judged with noticeably increasing reaction times indicative of number estimation via the approximate number system (ANS). *B*: electrode implantation sites in the human brain. *Left*: lateral view of a human brain. The black line indicates the temporally angulated brain section (magnetic resonance image on *right*) from an example patient at the transversial level. *Right:* magnetic resonance image with several electrodes implanted bilaterally in areas of the medial temporal lobe (MTL). Electrodes appear thicker than they are because of imaging artifacts. *C*: average *z*-scored tuning curves of number-selective neurons tuned to the 10 numbers (color-coded as depicted in *B*). Error bars denote SE. *D*: average sharpness of tuning curves per preferred number as measured by sigma from Gauss fits to tuning curves. Error bars denote SE. Sigmas were small and constant for small numbers but increased in proportion with the value of large numbers. *E*: population classification analysis using support vector machines (SVMs): confusion matrix derived from training an SVM classifier on firing rates averaged across the presentation and brief memorization of dot numerosities. White lines depict the significant boundaries (highest significance for the solid thick line) that divide the number range into small and large number categories. *F*: population state-space analysis. At any moment in time during a trial, the activity of a population of MTL neurons is represented by an *n*-dimensional vector in *n*-dimensional space grouped according to the 10 numerosities. Reducing this state space to the 3 principal dimensions for visualization results in state-space trajectories of number-selective neurons for all number conditions. Each trajectory depicts the temporal evolution in the trial time window from trial onset to the beginning of the choice period. The state space shows a gap between trajectories for numbers 0–4 vs. 5–9. Circles indicate boundaries between task phases. Image is from Ref. 165 and used with permission from *Nature Human Behavior*.

survival and reproduction (46). The numerical distance effect provides greater dissimilarity between quantities, which enhances discrimination. In foraging, for instance, this ensures substantial energy benefits in distinguishing between dissimilar numbers of food items. Moreover, the numerical size effect enables animals to benefit more from detecting small absolute numerical differences than large ones, for instance, doubling the gain when distinguishing between 2 and 1 food item, compared to a modest 1.1-fold increase from 10 to 11 items. Support for nativism includes the discovery of numerical abilities that emerge very early in ontogeny (31, 200) and are present across a diverse range of species, from primates to bees (14, 39–43) (**FIGURE 3C**). These abilities share foundational properties, suggesting a common evolutionary origin underlying numerical cognition in various organisms, including humans. Furthermore, there are putatively homologous brain areas, such as the intraparietal sulcus, that process numbers in both humans and nonhuman primates (18, 69, 201). Additionally, corresponding neural mechanisms of numerosity-selective neurons are found in diverse species such as chicks (86), crows (17), monkeys (47, 48), and humans (165), which are dedicated to processing numerical information (89).

On the other hand, the emergentist perspective posits that numerical abilities arise from an interplay of learning experiences, domain-general processes, neural architecture, and evolutionary pressures (202). This viewpoint proposes that number sense develops gradually through developmental processes rather than being solely innate or genetically predetermined. Evidence supporting emergentism comes from computer simulations using neural networks, which demonstrate how network architecture and learning biases contribute to the progressive development of number sense (203). Additionally, the rapid and precise extraction of numerosity information in the early human visual pathway is evidence that number sense emerges almost as a by-product from sensory analysis mechanisms within the neural architecture of sensory brain areas (204–206).

Despite the nativist view emphasizing innate cognitive structures and the emergentist view focusing on learning and environmental interactions, both acknowledge the existence of number sense, its early development, the role of biology, the importance of experience, the reliance on neural mechanisms, and the implications for education. An integrative approach would bridge these views by considering the interplay between innate predispositions and experiential learning.

3. SYMBOLIC NUMBER REPRESENTATIONS

3.1. Acquiring Number Symbols

Building upon these nonsymbolic numerical systems (ANS, OTS, and subitizing), or in conjunction with them, children leverage their developing understanding of symbolic number words and counting to enhance exact arithmetic skills before formal schooling (207–210) (**FIGURE 2**). Starting as early as 2 yr of age, the development of symbolic number knowledge progresses through systematic stages in preschool (141, 211). Children begin by reciting the words of the count list, initially without an understanding of the meaning of the number words. Later, they gradually acquire the meanings of the first few numbers, learning the significance of “one,” followed by “two,” and then “three”: they become “subset knowers.” Children are considered to understand the meaning of a specific number word if they can accurately produce the corresponding quantity in “give-a-number tasks” (207, 211). In the give-a-number task, an experimenter prompts a child by asking them to provide a certain number of items (“Give me one,” “Give me two,” and so forth). Upon grasping the meaning of “four,” children undergo a conceptual leap, comprehending the cardinal principle: children become cardinal principle knowers. This understanding enables them to grasp the workings of the counting system and apply counting to determine the cardinality of larger sets of items (141).

The comprehension of the cardinal principle, and, consequently, the logic of natural numbers, inherently incorporates some basic arithmetic logic (212–216). After all, successive counting entails an iterative process of addition (+1). Likewise, recognizing that altering a set by adding or taking away items (e.g., +1, −1) results in a change in the number is crucial for a comprehension of cardinal numbers and is inherently arithmetic. Supporting this notion, comprehension of the numerical consequences of arithmetic set transformations is evident only in children who have managed to understand the cardinal principle, and not before (217, 218).

Unlike sets or numerosities, number symbols, such as numerals and number words, permit most precise representation of numerical quantity. Number symbols are part of a combinatorial sign system, enabling counting and ultimately the formation of a full-blown number theory. To arrive at symbolic number representations, the ANS is thought to play a key role because no other system can convey the meaning of numerical quantity (219). Indeed, behavioral evidence suggests that symbolic counting is, at least partly, grounded in nonsymbolic quantity representations. For instance, both nonsymbolic and symbolic number judgments exhibit numerical distance and the size effect, which are captured by Weber’s law, albeit the symbolic system does so in much more subtle ways (80, 220–222).

3.2. Neuroimaging of Symbolic Number

3.2.1. Numerals in the adult brain.

In the adult human brain, neuroimaging provides strong evidence that the IPS in conjunction with prefrontal areas represent the semantic meaning conveyed by numerical symbols. Modulation of brain activation in the IPS and frontal cortex has been observed in tasks where participants choose the larger or smaller numeral (223–225). Significant IPS activation also occurs in calculation tasks involving number symbols, such as mentally subtracting a single digit from a fixed reference number (226, 227). Further evidence shows that the IPS is active in tasks where adults estimate a number’s position on a number line (228) and in fMRI adaptation tasks responding to numerical deviants (229, 230).

Beyond the IPS-prefrontal areas, accumulating evidence indicates that temporal regions also play a critical role in representing number symbols. The posterior inferior temporal gyri (pITG), known as the “number form area,” has been shown to be selective to number symbols compared to letters and false fonts (231–236). This number-processing region in the pITG is anatomically distinct from other category-selective regions in the ventral temporal cortex (VTC), such as the fusiform face area (FFA) and the visual word form area (VWFA) (237). Building upon previous findings of numerosity maps (126), an fMRI study found that a numerosity map in the temporal-occipital cortex also responded to symbolic numbers, suggesting a shared role in representing nonsymbolic and symbolic numbers, although the preferred tuned responses to symbolic numbers were uncorrelated with those to numerosity (238). This combined numerosity-numeral map is located in a different area from the number form area of the pITG.

The number representations in the temporal lobe are influenced by, or rely on, their functional connectivity with classical number-related areas in the parietal and frontal regions (233, 239). That this preference for number symbols over other types of linguistic symbols emerges via connections with parieto-frontal number areas that provide information about the meaning of numerical quantity, and is independent from visual input, is supported by similar findings in blind individuals (240). In an fMRI study where individuals blind from birth judged which of two sequences of beeps were more numerous, BOLD activity in the IPS differed between numerosities in a ratio-dependent manner, even better than in blindfolded sighted participants (241). In fact, the classic frontoparietal number network is preserved in the total absence of visual experience in congenitally blind individuals (241). These findings suggest that nonvisual experience with sets is sufficient for typical development of number representations in the IPS. The alternative interpretation is that number representations have innate precursors.

The specific connections between the human frontoparietal number network have been identified based on imaging methods (242, 243). The inferior part of IPL comprising the angular gyrus (AG) is strongly connected to lateral and medial PFC, ventral premotor cortex, cingulate cortex, hippocampus, and parahippocampal cortex. The superior part of the IPL including the IPS showed two distinct connection patterns: the anterior IPS projects to the inferior frontal cortex and insula, whereas the posterior part of the IPS is more strongly connected with posterior occipital (visual) cortex. This distinction is consistent with macaque anatomical studies, which have shown strong connections between the anterior IPS (AIP) and ventral premotor cortex and between the posterior IPS (CIP) and visual cortices (244). Overall, this examination of functional and structural connectivity of the human inferior parietal lobule (IPL) showed connections that broadly correspond to those of non-human primates.

3.2.2. Linking symbolic and nonsymbolic number representations.

Acquiring a grasp of symbolic numbers as an adult involves brain reorganization. The big question is whether these symbols arise de novo or build upon earlier, nonsymbolic quantity representations. If symbolic number understanding does stem from preexisting nonsymbolic representations, one would expect to see shared brain activity, cross-influence between these representations, and similar brain patterns across different number formats.

Initially, studies using conjunction analysis have identified activation in the IPS for both symbolic and nonsymbolic representations, and thus overlapping brain area (122, 245). In addition, cross-activation implied that processing one format (e.g., symbolic) influences the activation of the other (e.g., nonsymbolic). fMRI adaptation studies have shown bilateral activation in frontal-parietal regions when participants adapt to one format and then encounter deviations in the other (246). This recovery of activation in the IPS and frontal regions for deviant numbers in both notations occurred regardless of transitions between numerals and dots. Moreover, number representations in the IPS appear largely independent of sensory modality: stronger responses to numerals over letters and colors were observed in a bilateral region in the horizontal IPS across visual and acoustic presentations (247). A comprehensive review of 52 brain imaging studies comparing activations when participants evaluated nonsymbolic and symbolic numbers revealed significant overlap primarily in the posterior parietal lobe (SPL, IPS, IPL), as well as in the superior, medial, and inferior frontal gyri, the precentral gyrus, the cingulate gyrus, the insula, and the left fusiform gyrus (68). Activations were also observed in regions of the cerebellum and basal ganglia.

However, as more studies emerge, coding differences have also become apparent. Whereas the left IPS demonstrates precise coding of numerical values across formats including Arabic numerals, number words, and mixed formats, the right IPS shows selective adaptation to quantity primarily with Arabic numerals, indicating a notation-dependent representation in the right hemisphere (229, 230, 246, 248). Even more, with high-resolution 7-T fMRI it was shown that viewing sets of dots activated the IPS differently compared to viewing numerals. Nonsymbolic numbers activated the superior/medial parts of the IPS and SPG more, whereas symbolic numbers activated the angular gyrus and superior temporal sulcus more (249).

Additionally, multivoxel pattern analysis (MVPA), which correlates activation patterns of multiple voxels across conditions, has shown that both dot sets and numerals are decodable in various brain regions, yet there is limited overlap in their representations, indicating a potential absence of an abstract numerical magnitude representation (250, 251). An examination of the correlation between multivoxel pattern (an analysis called "representational similarity analysis") also failed to show significant correlations between activation patterns of individual symbolic and nonsymbolic numbers (252). Moreover, when exploring map-like arrangements of numerical values, no responses to symbolic numbers were found in the original topographic numerosity map in the SPL (126). Similarly, although tuned BOLD responses to numerosity were found in multiple cortical sites in a follow-up study, only one numerosity map in the left temporal-occipital cortex responded to symbolic numbers (238). These findings suggest a link between numerosity representation and symbolic number processing in the ventral temporal-occipital cortex but also reveal different functions of the numerosity maps.

In summary, although there is evidence of some shared brain activation between symbolic and nonsymbolic numerical representations, recent neuroimaging advancements underscore distinct neural substrates for each. This could imply that symbolic representations may depend only partially on cognitive mechanisms supporting nonsymbolic quantity processing. However, it is crucial to recognize that the adult brain represents the culmination of developmental reorganization seen in children, where the connection between nonsymbolic representations and newly acquired number symbols may be more pronounced during earlier stages of ontogeny.

3.2.3. Young children transitioning to symbolic numeracy.

Children initially view numerical symbols as meaningless shapes but eventually develop rich semantic representations of these symbols and their relationships as they learn their meanings. In young children transitioning to symbolic numeracy, developmental imaging studies indicate a reorganization in the brain's functional neuroanatomy for processing symbolic numbers. When processing number symbols, children initially activate prefrontal regions more than adults do, whereas adults primarily rely on parietal regions, especially the intraparietal sulcus (IPS) (225, 253). For instance, the neural correlates of the numerical distance effect, measured with a number comparison task with numerals, were present in bilateral parietal cortex regions and middle frontal gyrus in adults, whereas children primarily activated frontal cortex regions, specifically right precentral gyrus and right inferior frontal gyrus (225). This frontal-to-parietal shift is often interpreted as an age-related improvement in the efficiency of processing symbolic numerical magnitudes. It reflects strengthened associative connections between numerical symbols and their semantic meanings (numerical magnitudes), accompanied by reduced prefrontal activation due to decreased reliance on resources supporting the initial weak representations of symbolic numerical magnitudes in children. Two meta-analyses on the development of numerical processing have confirmed this trend (254, 255).

The intraparietal sulcus (IPS) in children undergoes age-related changes in ratio-dependent brain activation with number symbols. fMRI adaptation studies demonstrated that the right IPS is active early and remains stable in young children, consistent with the finding that nonsymbolic numerical magnitudes (e.g., dot arrays) cause early activation of the right IPS in preverbal infants and young children (111, 122, 125). In contrast, the left IPS develops gradually alongside improvements in numerical discrimination skills (256, 257), and symbolic number values start to elicit activations in bilateral posterior parietal regions (255). Interestingly, children use somatomotor-related areas, including the anterior IPS and parts of the somatosensory cortex on the postcentral gyrus, for processing nonsymbolic numbers, which suggests a potential link to children's early use of finger counting in numerical tasks (258, 259).

Together, these findings suggest that while the right IPS is involved in processing nonsymbolic numerical information from infancy, the left IPS, along with other posterior parietal areas, becomes increasingly engaged in processing symbolic numerical symbols with age and proficiency, leading to distinct anatomical specializations in the brain.

3.3. Neurons for Symbolic Number in the Human Brain

To learn about how single neurons represent symbolic numbers, single-cell recordings in humans are required. In the recording study mentioned above (15), simple calculation tasks were presented to epileptic patients who were implanted with chronic depth electrodes in their MTLs. During recordings, the patients performed simple calculation tasks not only with operands involving the numerosity of sets of dots (nonsymbolic format) but also with Arabic numerals (symbolic format). Many neurons responded to nonsymbolic numerosities, whereas a small but significant proportion of neurons (3%) encoded numbers signified by numerals (15). Although numerical information could be decoded robustly from the population of neurons tuned to nonsymbolic numbers, and with lower accuracy also from the population of neurons selective to number symbols, these groups of neurons represented either nonsymbolic or symbolic numbers but not both number formats simultaneously. Thus, neurons did not abstract across nonsymbolic and symbolic notation. Whether the representation of nonsymbolic and symbolic number information by two distinct populations of tuned number neurons is a special feature of the human MTL or representative of general neuronal number representations is currently unknown. In prefrontal neurons, at least in monkeys trained to associate visual shapes with varying numbers of items, the neurons reflected the associated numerical value (72). Moreover, PFC neurons in monkeys were observed to generalize across visual and auditory numerosity (71). Although monkeys are confined to nonsymbolic representations, this could suggest the existence of more abstractly responding number neurons in the human prefrontal cortex.

Whereas activity dropped off gradually with numerical distance from the preferred numerosity for neurons tuned to nonsymbolic numerosity, the decline of activity from the preferred to the nonpreferred value was brisk and categorical for neurons tuned to symbolic numerals. This aligns with behavioral findings demonstrating a large numerical distance effect for the comparison of nonsymbolic numerosities but a small one for judgments of exact number symbols (80). These correlations between neuronal tuning and behavioral discrimination performance suggest that number neurons serve as the neuronal basis for human number representations.

The presence of a (minute) distance effect for number symbols in human number neurons, thought to be inherited from basic nonsymbolic number representations (80, 220, 246), supports the hypothesis that high-level human numerical abilities are rooted in biologically determined mechanisms. This, in turn, suggests that number symbols acquire their numerical meaning by linking to evolutionarily conserved numerosity representations during cognitive development (38, 260). Hence, symbolic number cognition is likely grounded in neuronal circuits dedicated to approximate numerosity representations (261).

Besides MTL, recent single-neuron recordings also provide suggestive evidence for number-selective neurons in the posterior parietal cortex in humans. When two human patients implanted with anterior intraparietal sulcus (aIPS) electrodes verbally reported numbers (1 to 6), some neurons coarsely differentiated between two groups of numbers (1–3 vs. 4–6); however, the representation of specific numbers was not investigated in this study (262). In another intracranial recording study with a single patient, some neurons in the inferior parietal lobule (IPL) showed tuning to both nonsymbolic numerosity and symbolic numerals (263). As a proof of concept, these findings establish a welcome connection between neuronal activity in the parietal cortex and other more indirect measures, such as synchronous activity of neural populations using electrocorticography (ECoG) (**TABLE 1**) (233) and blood flow modulation in functional imaging studies (101, 246, 264). They also link neuronal processing in the human parietal cortex with numerosity-selective neurons that have been characterized in detail in nonhuman primates (18, 47, 48, 51, 56).

4. THE SPECIAL NUMBER ZERO

Zero is a remarkable number, representing emptiness or nothingness while playing a crucial role in the development of numerical systems. It serves as the gateway to negative numbers and is essential for the formulation of a comprehensive number theory. Despite its significance, zero also introduces challenges such as arithmetic paradoxes, including the inability to perform operations like division by zero or raising zero to the power of zero, the latter being usually undefined in mathematical analysis.

Throughout history, the recognition and appreciation of zero have grown gradually. It took humanity a considerable amount of time to understand and acknowledge zero's importance (265, 266) (**FIGURE 7*A***). Similarly, children typically grasp the concept of zero later than positive integers, indicating a developmental progression in numerical understanding (268–270) (**FIGURE 7*B***). In the animal kingdom, only cognitively advanced animals demonstrate rudimentary comprehension of zero, suggesting a primitive form of numerical cognition shared across species (267, 271–273).

Absence becomes a meaningful behavioral category when it is relevant to a specific task. It requires a task where the position of an empty set in this numerical continuum is task relevant, such as comparing the empty set to sets with countable values (274). The ability to conceive of empty sets, or "nothing," as a meaningful category represents a remarkable cognitive feat. Because brains have evolved primarily to process sensory stimuli and make sense of the world around us, this evolutionary focus on processing "something" poses a challenge when it comes to understanding and conceptualizing "nothing."

The emergence of zero involves four distinct stages or representations across various realms: history, ontogeny (individual development), phylogeny (evolutionary history), and brain processing (275). Initially, the absence of a stimulus is perceived as a mental or neural resting state without specific characteristics. Subsequently, this absence is recognized as a meaningful behavioral category "nothing" but lacks quantitative significance. In the third stage, "nothing" gains quantitative meaning and is represented as an empty set on a numerical continuum or number line. Finally, this empty set representation evolves into the concept of zero, that is integrated into a symbolic number system used for mathematical calculations.

Insights into the neuronal basis of nonsymbolic empty set representations come from macaque monkeys. In monkeys trained to discriminate the empty set from other countable numerosities, neurons in the primate parieto-frontal cortex (50, 267, 276) are tuned to numerosity zero (**FIGURE 7, *C–E***). Such single neurons were

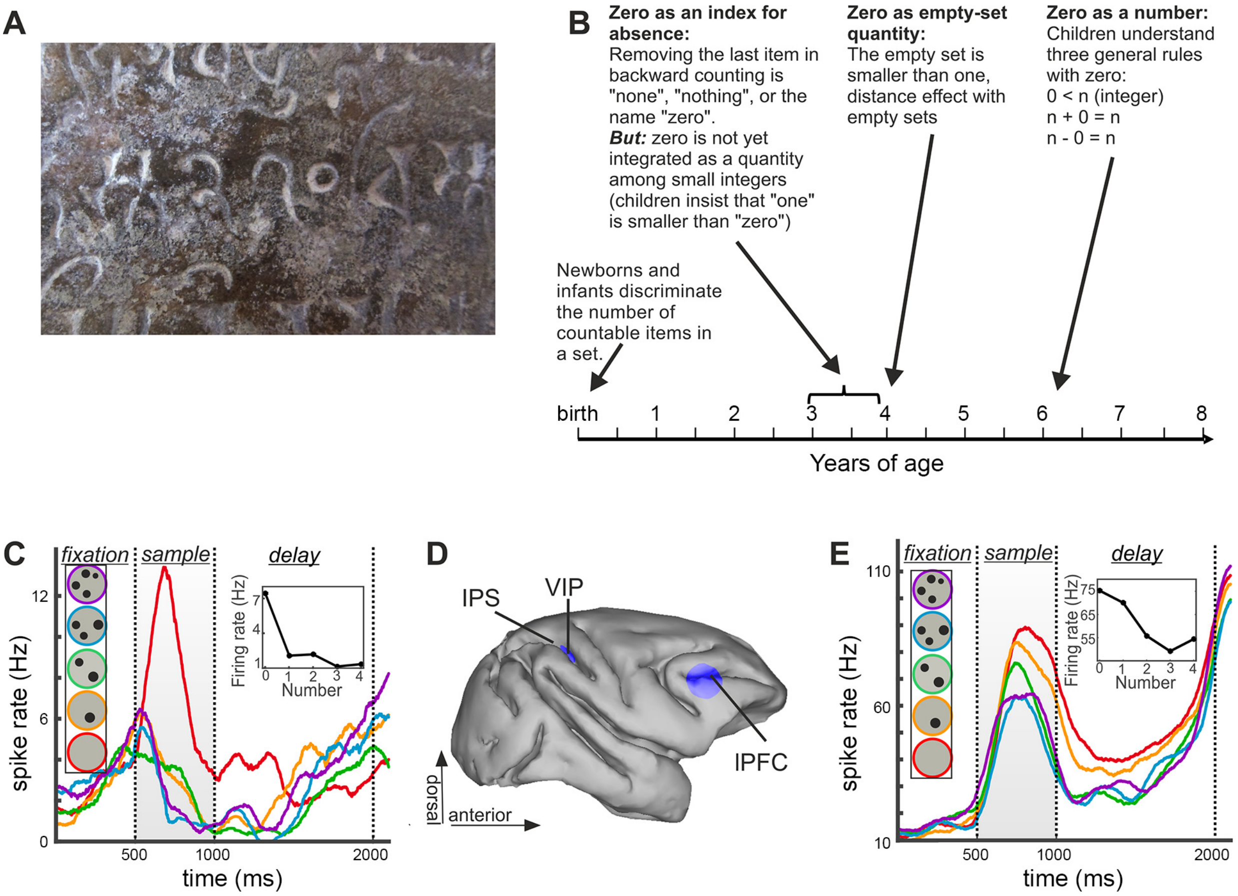


FIGURE 7. Emergence of the special number zero. *A*: the first written record of numeral 0 in ninth century inscription in Gwalior, India: the number 270 is in the middle of the image. Photograph by courtesy of Alex Bellos. *B*: stages of zero representation in children's development. *C*: ventral intraparietal area (VIP) neurons encoded empty sets as categorically distinct stimuli. This example VIP neuron was tuned to empty sets but showed no progressive decrease of activity toward larger numerosities. Spike-density histograms of the neuronal responses are shown. The sample numerosity was shown after 500 ms, followed by a memory delay. Colors of the spike density functions correspond to the numerosity of the sample stimulus. *Inset* in the spike-density histogram shows the neuron's numerosity tuning function. (from Ref. 267). *D*: a lateral view of a monkey brain shows the recording sites in VIP and prefrontal cortex (PFC) from which empty-set representations were recorded. *E*: PFC neurons responded to empty sets as part of the numerosity continuum. This example PFC neuron was tuned to empty sets and showed a progressive decrease of activity toward larger numerosities. Image is from Ref. 267 and used with permission from *Current Biology*.

tuned to empty sets just as other neurons were tuned to countable numerosities, and therefore represented empty sets as conveying a quantitative null value.

However, the encoding of empty sets differed between two key brain regions: VIP neurons primarily encoded empty sets as a distinct category separate from other numerosities (267) (**FIGURE 7C**). In contrast, PFC neurons represented empty sets more similarly to numerosity 1 than to larger numerosities. Thus, PFC neurons exhibited numerical distance and size effects when encoding empty sets (**FIGURE 7*E***). Moreover, prefrontal neurons represented empty sets abstractly and independently of stimulus variations, and their activity correlated more strongly with the behavioral outcome of empty-set trials compared to VIP neurons (267). This suggests a hierarchical processing pathway from VIP to PFC, where empty sets are gradually detached from visual properties and positioned within a numerical continuum.

Besides nonhuman primates, neurons tuned to the empty set have also been found in the telencephalic avian pallium of numerosity-discriminating crows (273). Additionally, a deep learning neural network trained solely for object discrimination spontaneously developed units tuned to zero (277). These findings suggest an evolutionary predisposition of brain networks to represent nothingness as a numerical quantity, serving as a potential evolutionary precursor for symbolic zero representations unique to humans (275).

The representation of zero in the human brain is largely unexplored. After suffering a left frontal contusion, a patient exhibited a selective impairment in solving arithmetic problems involving zero (0-based computational rule), whereas problems with two nonzero operands were largely intact (278). Another case report presented a brain-damaged patient who showed moderate deficits in arithmetical fact retrieval (279). This patient displayed a striking dissociation between preserved "n + 0" problems and impaired

"0 + n" problems, whereas most other arithmetical rules were fully preserved. These neuropsychological studies highlight the importance of specific brain regions, particularly the frontal and parietal cortex, in understanding and processing numerical concepts, including the role of zero in arithmetic computations (513, 514).

5. PROPORTIONS, RATIOS, AND FRACTIONS

Two nonsymbolic quantities frequently need to be related to create a more complex measure of magnitude: a proportion. Nonsymbolic proportions and ratios serve as abstract quantities that relate the values of different kinds of magnitudes (including size, number, duration, and loudness) and across various sensory modalities in both humans (280) and animals (281). For example, proportions of body parts are linked to mate attractiveness (282–284), whereas proportions of social groups influence fight-or-flight decisions in social encounters (285, 286). Thus, even before a formal understanding of fractions, judgments of proportions are biologically relevant.

In symbolic mathematics, a fraction represents a numerical quantity expressed as the ratio of two integers, denoted by a numerator (a) and a denominator (b): the standard notation for a fraction is a/b. Symbolic fractions hold a key position in mathematics learning, both theoretically and educationally (287). Theoretically, fractions demand a deeper comprehension of numbers beyond the familiarity with whole numbers (288). Educationally, fractions are crucial because of their integral role in advanced mathematics and their predictive value for later mathematical achievement (289, 290). Even before formal instruction, an intuitive understanding of division is present in children. Children entering school who are not familiar with division symbols or basic division equations can already perform both symbolic (with numeral formats) and nonsymbolic (with sets of dots) approximate division (291). The dependency of these children's nonsymbolic division performance on the ratio between the target and quotient, coupled with the correlation between accuracy on division tasks and children's acuity in discriminating dots, implies a grounding of nonsymbolic division in the ANS.

Neuroimaging studies in adults have revealed that brain regions typically associated with natural number representations are also involved in processing fractions. In adults, the processing of nonsymbolic proportions (e.g., dot patterns) and symbolic fractions (numeral displays) both activate comparable segments of the bilateral intraparietal sulcus (IPS) (292–294). This activation of the IPS occurs automatically, simply by looking at fractions (292). Because the BOLD signal is modulated by the distance between the numerical values of the two fractions, the IPS appears to represent the numerical values of fractions as a whole rather than the values of their constituents (292, 293). Compared to activation accompanying whole number comparisons, BOLD activity for the active evaluation of fractions is greater in several brain regions, including the bilateral intraparietal sulcus (IPS), left precentral gyrus, left superior and middle frontal gyri, and the left inferior and middle temporal gyrus (294, 295). These imaging findings indicate a shared neural basis for both whole number and fraction knowledge.

To unveil the neuronal code for magnitude ratios at the single-cell level, electrophysiological recordings were conducted in the frontal and parietal cortex of behaving rhesus monkeys. The monkeys were trained to discriminate the proportions (1:4, 2:4, 3:4, and 4:4) of the lengths of two parallel lines. In both the prefrontal cortex (PFC) and the inferior parietal cortex (area 7a), many neurons were tuned to specific proportions (296, 297). The neurons' tuning showed a distance effect, resembling the coding scheme observed for other abstract quantities, such as dot numerosities (discrete quantity) and line length (continuous quantity) (59, 298). As an indication of the neurons' significance for behavior, the neurons' activity predicted the monkeys' success or failure in the proportion discrimination task. Parietal neurons exhibited a tendency to respond earlier than PFC neurons (297). Just as for numerosity representations, this finding suggests information relay from the parietal cortex to the PFC.

6. ARITHMETIC

6.1. Calculation with Nonsymbolic Numerical Representations

The ANS seems to facilitate nonsymbolic arithmetic computations prior to a formal number system (e.g., Refs. 299–301). Infants and young children can approximate the sum or difference in nonsymbolic arithmetic tasks, wherein animations depict objects being added to or subtracted from an initial set (299, 301). For instance, after watching animations of two sets of 8 items entering a box (8 + 8), 9-mo-old infants exhibit surprise, as indicated by increased visual attention and looking time, when the box reveals only 8 items (8 + 8 = 8), compared to scenarios where the box contains 16 items (8 + 8 = 16) (301). This arithmetic ability, akin to the underlying numerosity representation, is approximate and ratio dependent; hence, infants' looking times do not distinguish comparable scenarios with closer ratios (8 + 8 = 12 vs. 8 + 8 = 16).

Despite the ANS operating over nonsymbolic sets and being inherently approximate, traces of the ANS become evident in behavioral responses to symbolic number, too. Children aged 5–6 yr, having acquired verbal counting skills and approaching formal arithmetic instruction, utilize the ANS to approximate solutions for addition and subtraction problems presented symbolically with number words (302). This suggests an inherent association between approximate numerical meanings and symbolic numbers (245, 302, 303), so that the features of the ANS are reflected in symbolic number tasks. Several studies demonstrate a positive correlation between acuity in discriminating nonsymbolic set sizes and symbolic math ability. Children who can discriminate small differences of set sizes, on average, are better at symbolic mathematical achievement scores later in life (38). Such advantages are specific to numbers and mathematics, as they are not related to other cognitive capabilities, such as intelligence and verbal skills. Today, three meta-analyses have found support for a modest but significantly positive relationship between approximate numerosity estimation and math ability in children, although this correlation weakens with age and with the possible emergence of more abstract concepts of number (304–306). Although correlations do not establish causality, these results suggest that the ANS may at least partly govern the understanding of symbolic arithmetic later in life.

The ANS also allows adults without formal schooling to perform approximate calculations. The indigenous Munduruku with their reduced number system can approximately add and subtract sets of dots in computer animations (23). Compared to French adults engaging in similar additions and subtractions with large sets of dots, the Munduruku exhibit a level of precision equivalent to that of their numerate counterparts. However, distinctions emerge in small-number calculations, particularly in subtractions; in tasks involving small numbers, where the Munduruku still rely on approximate representations governed by Weber's law, they are outperformed by French control subjects who execute precise calculations using number symbols with minimal errors (23).

As a sign of evolutionary rooting of nonsymbolic calculation, animals use approximate number representations not only for discrimination but also for rudimentary arithmetic. When free-ranging rhesus macaques were tested with food items disappearing behind occludes, they looked longer at the impossible outcome relative to the expected one, suggesting that they spontaneously added such items (307). Trained rhesus monkeys can approximately add two sets of dots shown on a computer screen and choose a subsequent display that shows the correct sum of the two sets (308). The monkeys were as proficient as college students relying on estimation. Using a manipulandum, Japanese macaques can learn to add dots to a display, or remove dots from a display, to match a target numerosity (309).

When macaques watched movies showing implicit calculation operations, they added or subtracted items (310). In these movies, dots were moving behind occludes in some trials (addition) and dots were moving out from behind occludes in other trials (subtraction), and the monkeys were required to indicate the outcome of these observed dot operations in a forced-choice situation. The monkeys not only succeeded with novel set sizes but also showed some of the classic psychological characteristics of calculations that have sometimes been considered unique to humans: the problem size effect and the tie effect (311–314). The problem size effect manifests as a systematic decline in both accuracy and response time as the magnitude of the operands in an arithmetic problem increases. For instance, solving $5 + 7$ is more challenging than $3 + 4$. The tie effect indicates superior performance in addition problems where the two operands are identical, e.g., $2 + 2$ is easier than $1 + 3$. Unlike humans, however, monkeys did not exhibit a practice effect: the monkeys showed no improvements in performance with repeated exposure to a given problem. These findings suggest that, at least in primates, basic arithmetic capabilities precede symbolic calculations in evolutionary history.

Apart from primates, studies with imprinted chicks have reported behaviors suggestive of early proto-arithmetic addition and subtraction capacities (200). Further research is needed to ascertain whether insects such as bees (315) and fish (316), which, based on a color cue, choose a target numerosity that is either one item greater or smaller compared to a reference numerosity, engage in a form of calculation.

6.2. Neural and Neuronal Representations of Arithmetic Rules

Work in nonhuman primates has shown that the brain possesses rule-selective neurons that respond when a subject follows one rule but not the other. In the PFC, rule-selective neurons represent abstract principles, such as "same" or "different" applied to perceptual categories (317, 318). In the number domain, mastering "greater-than" and "less-than" rules is fundamental and one of the first quantitative rules children learn in school. Monkeys can also master such numerical relationships (319, 320).

To investigate the neuronal processing of numerical rules, rhesus monkeys were trained to flexibly switch between "greater-than" and "less-than" rules (320, 321). In each trial, a sample stimulus indicated the reference numerosity the monkey had to remember over a brief time interval. Subsequently, a rule cue instructed the monkey to follow either a "greater-than" or a "less-than" rule (**FIGURE 8*A***). After a second delay, the monkey had to respond according to the currently valid rule cue to more or fewer numbers of dots, respectively, than it had previously seen in the sample display. The monkeys performed this task with varying numbers of items and generalized to novel numerosities, indicating their acquisition of an abstract numerical principle. Electrophysiological recordings during performance of the "greater-than/less-than" rule-switching task revealed that 20% of the monkeys' PFC neurons were rule selective, with about half favoring the "greater-than" rule and the other half favoring the "less-than" rule (320). These rule-selective neurons demonstrated a robust response to the preferred rule during a delay period, regardless of the specific sample numerosity the rule applied to and irrespective of the sensory appearance of the rule cue (**FIGURE 8, *C* AND *D***). These rule-selective responses were linked to the encoding of an abstract numerical principle and could not be attributed to motor preparation, as the comparison number was still unknown, preventing the monkey from anticipating the required response.

The activity of these rule-selective neurons correlated with the monkeys' behavior; when the animals made incorrect decisions, the neurons' responses to the preferred rule were significantly reduced (320). This suggests a direct link between the neurons' rule selectivity and task performance. Such rule-selective neurons were primarily located in the frontal lobe, encompassing prefrontal and premotor cortex, but were also, albeit less frequently, observed in area VIP of the IPS (322) (**FIGURE 8*B***).

The coding properties of numerical rule-selective neurons are under the influence of the neuromodulator dopamine (323–325). Experiments combining single-cell recordings and microiontophoretic drug applications revealed that Dopamine-1 and Dopamine-2 receptor families cooperatively enhance number coding by employing distinct physiological mechanisms (326).

In human imaging studies, corresponding brain activation during calculation is observed in prefrontal activity, particularly in children, in addition to posterior parietal activity (68, 327–329). In the posterior parietal cortex, intracranial ECoG recordings in patients with epilepsy (**TABLE 1**) who were engaged in solving additions with numerals showed a significantly higher increase in high-frequency broadband (HFB) power, compared to a non-arithmetic task, in selected areas around the intraparietal sulcus (IPS) (see sect 6.2.1) (330). Some, but not all, of the selective sites also exhibited HFB activity when participants read, heard, or spoke words with numerical content. In a subsequent study, it was shown that when subjects actively manipulated numerals in addition operations, not only the superior parietal lobule (SPL) but also the anterior intraparietal sulcus (aIPS) in both

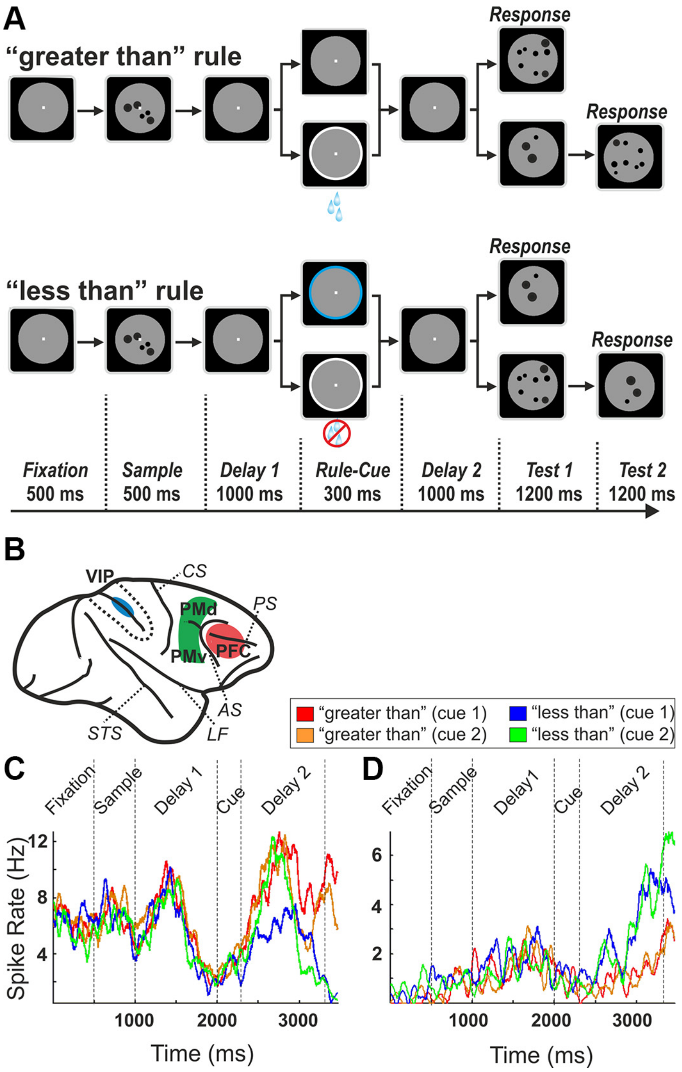


FIGURE 8. Numerical rule-selective neurons in the monkey cortex. *A*: numerical rule-switching task used to investigate how monkeys process numerical quantity according to principles. Here, monkeys had to choose more or less dots than presented in a sample display (5 different numerosities). A cue showed in the delay phase indicated whether the "greater-than" rule (*top*) or the "less-than" rule (*bottom*) was correct (the probability of each rule being displayed was 0.5). Each rule was signified by 1 of 2 pairs of different sensory cues in alternating trials. *B*: lateral view of a rhesus monkey brain (*right* is anterior) depicting brain areas ventral intraparietal area (VIP), PMd/v (dorsal/ventral premotor cortices), and prefrontal cortex (PFC) from which numerical rule-selective neurons have been recorded (STS, superior temporal sulcus; LF, lateral fissure; CS, central sulcus; AS, arcuate sulcus; PS, principal sulcus). *C*: rule neuron selective to the "greater than" rule irrespective of the rule cue. The spike-density histogram shows the time course of the average activity of this neuron that was systematically higher toward the end of the rule delay (*delay 2*) when the "greater than" rule was cued, irrespective of the sensory features of the rule cue ("greater than" activity coded by warm colors). The plot is temporally correlated to the task layout that is shown in *A*. *D*: rule neuron selective to the "less than" rule. Same layout as in *C*. Images in *A*, *C*, and *D* from Ref. 320 and used with permission from *Proceedings of the National Academy of Sciences USA*.

hemispheres was more engaged during arithmetic processing than during reading sentences or memory retrieval (233).

Consistent with the general role of the PFC in executive functions, lesions in this area can result in complex deficits in numbers and calculations in humans (331) (see sect 6.2.1). Patients with frontal lesions often exhibit cognitive estimation deficits, linked to executive deficits hindering the translation of number representations to structured output (332–334). A unique deficit, "task-switching acalculia" (BOX 2), was reported in a stroke patient with left ventral and dorsolateral frontal lobe lesions (335). Although calculation ability remained intact, the patient exhibited a specific deficit in switching between different operations in simple calculations, indicating weakened top-down control from frontal lesions.

Mental calculation is a classic working memory task engaging the PFC as the core site for working memory processes. At the same time, working memory functions are embedded in a larger network spanning several associative telencephalic brain areas. Recent data show that one of these areas is the MTL, which is traditionally thought to support long-term memory (336–338). Human intracranial recording studies showed that a selection of MTL neurons show feature-selective sustained delay activity, correlate with memory load, and predict the successful retrieval of working memory contents (339, 340).

In the single-neuron recording study mentioned above, human neurosurgical participants performed a sequential calculation task encompassing a rule delay period in which the participants processed the cued addition versus subtraction instruction (352) (**FIGURE 9, *A* AND *B***). During this working memory period, a significant proportion of 6% of MTL neurons were modulated by the arithmetic rule. Neurons selectively responding to addition exhibited increased firing when an addition was instructed, irrespective of whether the operation was cued by a word ("add") or a sign (+) (**FIGURE 9*A***). In contrast, subtraction-selective neurons showed a specific increase in activity when a subtraction was instructed by either cue ("minus", "−") (**FIGURE 9*B***). The activity of the population of neurons enabled a statistical classifier [support vector machine (SVM)] to accurately read out the participants' chosen arithmetic rule. Information about the calculation rules was encoded regardless of the rule cues for addition and subtraction, respectively (**FIGURE 9, C AND *D***). Such neurons may allow humans to decode the operation type (addition vs. subtraction) found in magnetoencephalography (MEG; **TABLE 1**) signals (353).

In recent years, it has become clear that neurons in the brain use different coding strategies to represent information over time, especially in working memory tasks (354–356). In the classical static code, neurons maintain a consistent firing rate or activity pattern over time to encode specific information, like remembering an arithmetic rule. In contrast, neurons can also exhibit a dynamic code where they rapidly and transiently change their activity patterns to encode information flexibly. To distinguish between these codes, researchers use cross-temporal classifier (decoder) analysis. In this method, classifiers are trained to identify patterns of brain activity associated with a particular memory or task at one time point. Then, they are tested to see if they can accurately recognize similar activity patterns at different time points. With time-resolved decoding analyses, significant coding differences emerged across different MTL brain areas (352). A static code was found in the hippocampus, relying on persistently active rule-selective neurons (**FIGURE 9*E***). In contrast, a dynamic code was observed in the parahippocampal cortex, originating from neurons carrying rapidly changing rule information (**FIGURE 9*F***). The implementation of abstract arithmetic codes suggests distinct cognitive functions of medial temporal lobe regions in arithmetic (352).

BOX 2: ACALCULIA

"Acalculia" denotes the acquired loss or impairment of numerical processing and calculation abilities, often resulting from acquired brain damage. (341). Originally described in 1908 (342), acalculia refers to challenges with basic arithmetic operations unrelated to language impairments (aphasias) (343, 344). Early research highlighted left hemispheric specialization: the third frontal convolution for speaking numbers, angular gyrus and intraparietal sulcus for reading numbers, angular gyrus for writing numbers, and inferior parietal areas for mental calculation (345).

"Primary acalculia" involves a specific loss of numerical concepts and an inability to perform basic operations, distinct from "secondary acalculia," where calculation abilities are impaired because of deficits in general cognitive functions like attention, memory, language, and spatial abilities (346). Neuropsychological studies in patients have been crucial in developing modular models of number processing and calculation (347). The triple-code model, comprising three interrelated major internal mental representations (or codes) for numbers, is the most influential framework in numerical cognition (348, 349). Central semantic representations of numbers include the analog magnitude code supported bilaterally by the intraparietal sulcus (IPS). This domain-specific region aids tasks like number comparison and approximate calculation. Additionally, two domain-general parietal systems assist: the bilateral posterior superior parietal lobule (PSPL) attention system and the left angular gyrus (AG) verbal number system. The visual Arabic code in the left AG provides a semantic-free visual representation of Arabic numerals. The verbal code in the left inferior frontal gyrus (IFG) supports prephonological processing of numerical information, facilitating comprehension and expression of numerical concepts through language.

Patients with lesions in the left posterior parietal cortex, particularly the intraparietal sulcus (IPS), exhibit deficits in processing nonsymbolic numerical magnitudes, such as slowed estimation, impaired subitizing, and difficulties in numerical comparisons with dot arrays or Arabic numerals (139, 350). Damage to the IPS also hampers both approximate (351) and exact calculation of multidigit arithmetic problems, highlighting its pivotal role in fundamental numerical functions.

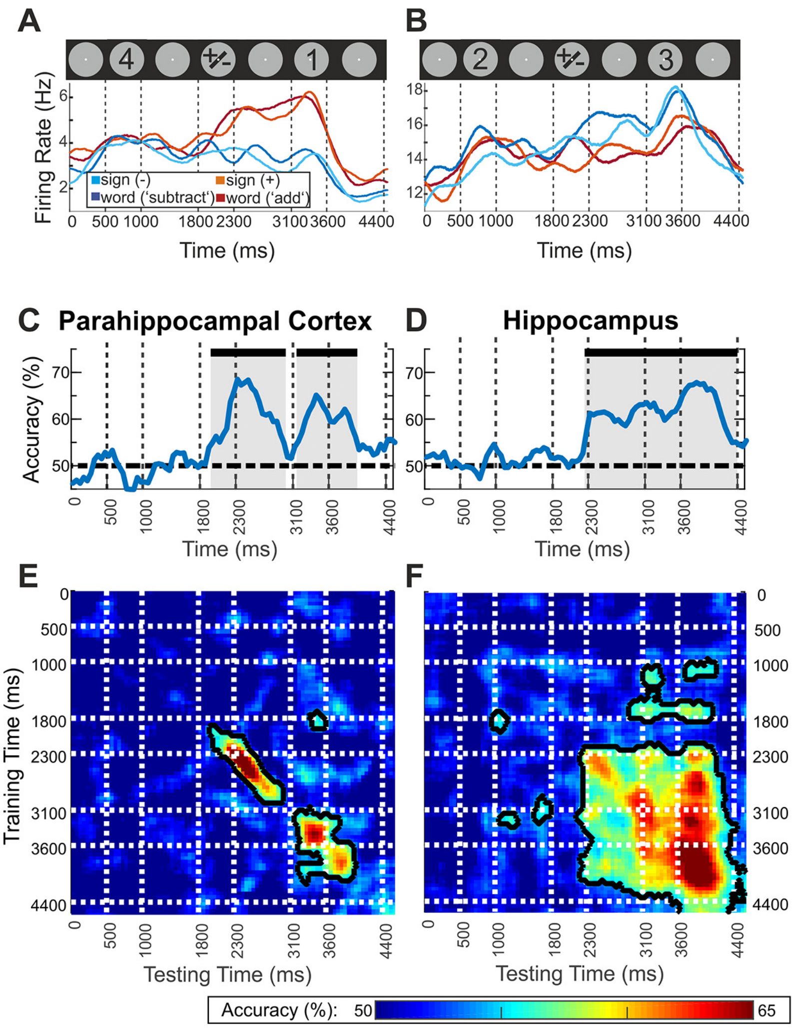


FIGURE 9. Responses of neurons selective to arithmetic rules in the human medial temporal lobe (MTL). *A*: across-trial averaged instantaneous firing rates (spike-density histogram) of an example neuron selective to the addition rule by increased firing rates after the onset of the rule cue and regardless of the concrete cue (sign or word) indicating the rule. Blueish colors depict subtraction (for 2 different rule cues); reddish colors correspond to addition. Neuronal activity is temporally aligned to the calculation trial sequence at *top* showing exemplary number displays as operands. *B*: example neuron selective to the subtraction rule. Same layout as in *A*. *C*: based on the population of neurons from the parahippocampal cortex, a statistical classifier [support vector machine (SVM)] can decode the arithmetic rule: classification accuracy for decoding arithmetic rule information when training an SVM classifier on the instantaneous firing rates across the trial period. The dashed line represents chance level (2 classes). Black bars above the data and gray shaded areas indicate significance ($P < 0.05$) when testing against performance for SVMs trained on shuffled data in a permutation test. *D*: classifier decoding accuracy based on the population of hippocampal neurons. Same layout as in *C*. *E*: cross-temporal decoding in the population of parahippocampal neurons: accuracy when training an SVM classifier at a given time point of the trial and testing it on another time point (the main diagonal of the matrix corresponds to the curve in *C*). Black contours indicate significance ($P < 0.05$) in a permutation test. *F*: cross-temporal decoding in the population of hippocampal neurons. Same layout as in *E*. All data from Ref. 352.

Recordings from neurons in both humans (339, 340, 357) and nonhuman primates (358–360), along with computational modeling (361–363), suggest distinct cognitive functions for the two codes involved in working memory. A dynamic code appears sufficient for short-term maintenance of implicit information, whereas intense mental manipulation of attended working memory contents may require a static code. Following this rationale, the parahippocampal cortex may encode the short-term memory of arithmetic rules, while downstream in the hippocampus numerical processing according to the arithmetic rule occurs. This insight helps explain why perceiving a "+" sign alone led to increased BOLD activity in the right hippocampus in 12-yr-old children, correlating with their proficiency with the "+" sign (364). Furthermore, this finding supports the hypothesis of hippocampal involvement in calculation operations.

Despite these insights concerning the representation of arithmetic rules, the relationship between perceived number and internally calculated number remains largely unknown. A recent high-field neuroimaging study aimed to disentangle activity patterns reflecting the result of a nonsymbolic calculation (multiplication or division with numbers of dots) from those representing the perceived operands, i.e., the visual numerosities constituting the operands (365). It was found that perceived sample numerosities were distinguished in activity patterns along the dorsal visual pathway and within frontal and occipito-temporal regions, whereas a representation of the internally generated result was detected in higher-order regions such as AG and lateral PFC. The neuronal mechanisms of such number transformations during calculation are yet to be explored.

6.3. Arithmetic Strategies and Knowledges

Proficiency in elementary arithmetic, encompassing basic operations such as addition, multiplication, subtraction, and division, serves as a fundamental tool for addressing diverse numerical problems and lays the groundwork for advanced mathematical skills (366, 367). Drawing on a combination of methodological approaches, arithmetic is thought to rely on three categories of interrelated knowledges and strategies that engage at least partially separate neuronal networks (347, 368–371) (**FIGURE 10**).

The first category is arithmetic fact knowledge. Arithmetic fact knowledge involves the automatic retrieval of basic arithmetic facts from long-term memory without the need for counting or calculation. This strategy is commonly applied to simple and common arithmetic problems with one-digit operands, like $5 + 2 = 7$. Memorizing multiplication tables is a classic example of this, where individuals can recall facts such as $6 \times 6 = 36$ without having to calculate it each time. The acquisition of arithmetic facts shows advantages, as fact retrieval proves more efficient and needs less working memory compared to the cognitively demanding and error-prone arithmetic procedures, such as counting (372).

The second category is procedural knowledge by applying procedural (or derivation) strategies. It relates to understanding and executing of the step-by-step procedures or algorithms for transforming numerical magnitudes and carrying out mathematical operations. Substrategies include counting (incrementing/decrementing numbers), carrying out addition and subtraction by regrouping numbers (carrying and borrowing), and algorithmic procedures (following rules), (e.g., $6 + 7 = 6 + 6 + 1$) (312, 373).

The third and final category is conceptual knowledge. In arithmetic, it involves the comprehension and articulation of fundamental principles, the laws that form the basis of mathematical operations. This encompasses understanding of concepts such as place value within a number system and fundamental properties inherent in mathematics. For instance, the commutative law (including the "inversion strategy") asserts that the order of operands does not alter the result of addition or multiplication, illustrated by examples like $3 \times 5 = 5 \times 3$ or $3 + 5 = 5 + 3$. The distributive law reveals the interaction between multiplication and addition (or subtraction), demonstrated in equations like $[(5 + 3) \times 2] = [(5 \times 2) + (3 \times 2)]$ and including an understanding that multiplication can be viewed as a form of repeated addition, exemplified by $6 \times 4 = 6 + 6 + 6 + 6 = 24$. Finally, the associative law states that the order in which numbers are grouped does not matter during addition or multiplication, as seen in $(2 \times 3) \times 4 = 2 \times (3 \times 4) = 24$.

Of these three categories, the retrieval of arithmetic fact knowledge has been investigated most extensively, whereas procedural knowledge has received more limited attention and conceptual knowledge has only recently been more thoroughly addressed. The ordering below therefore reflects this study bias, not the arithmetic significance or developmental trajectory.

6.3.1. Arithmetic fact knowledge based on memory retrieval.

It is widely accepted that adults retrieve single-digit multiplication operations but also addition problems as stored facts from long-term memory (366, 370) (**FIGURE 10**). Such arithmetic facts are thought to be stored as verbal associations and are retrieved by engaging a verbal circuit in the left hemisphere (374). In children, the application of fact knowledge and memory retrieval strategies therefore depends on children's mastery of

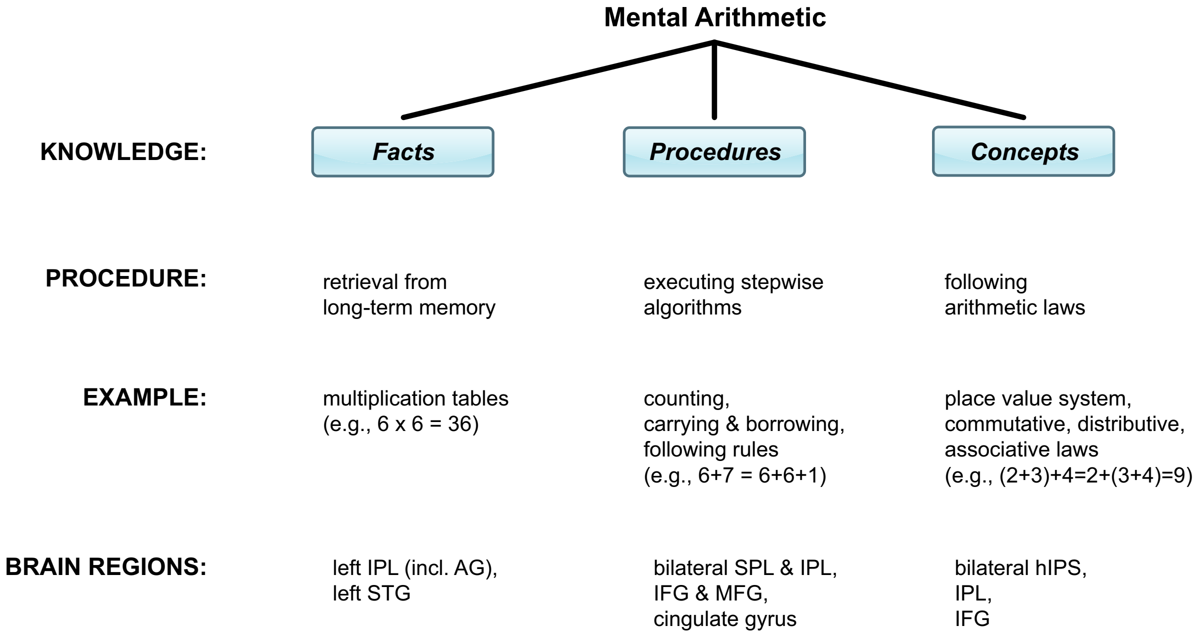


FIGURE 10. Taxonomy of arithmetic operations. AG, angular gyrus; hISP, horizontal segment of the IPS; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; MFG, middle frontal gyrus; SPL, superior parietal lobule; STG, superior temporal gyrus.

symbolic number (306). It should be noted that although the development of simple arithmetic skills typically progresses from reliance on procedures to dependence on retrieval (calculations first need to be calculated before they can be rote-learned), achieving exclusive dependence on direct retrieval may be a rare occurrence (375). The presence of hidden mixtures of strategies within and across subjects naturally complicates investigations into their neural correlates.

A recent meta-analysis in functional neuroimaging (376) compared fMRI activation patterns for arithmetic problems typically solved through a retrieval strategy (simple calculations with 1-digit operands, e.g., $2 + 3$) with those for problems usually solved using a procedural strategy (i.e., more complex calculations involving >2 operands or 2-digit operands, such as $4 + 3 - 7$ or $43 - 27$). In both the retrieval and procedural activation maps, a common activation of the bilateral inferior parietal lobule (IPL), with a larger cluster on the left that includes the SPL, was found (**FIGURE 11*A***). Since the bilateral parietal lobules are known to process number (68, 377, 378), the overlapping activation for both retrieval and procedural problems instantiated in the bilateral parietal lobules likely reflects the general processing of magnitude. Specific activations for arithmetic procedural strategies are associated with bilateral superior and inferior parietal lobule, inferior and middle frontal gyrus, cingulate gyrus, and insula (**FIGURE 11*B***). The only region activated more by retrieval compared to procedural problems was a single cluster in the left hemisphere spanning the AG, superior temporal gyrus (STG), and middle temporal gyrus (MTG) (378) (**FIGURE 11C**).

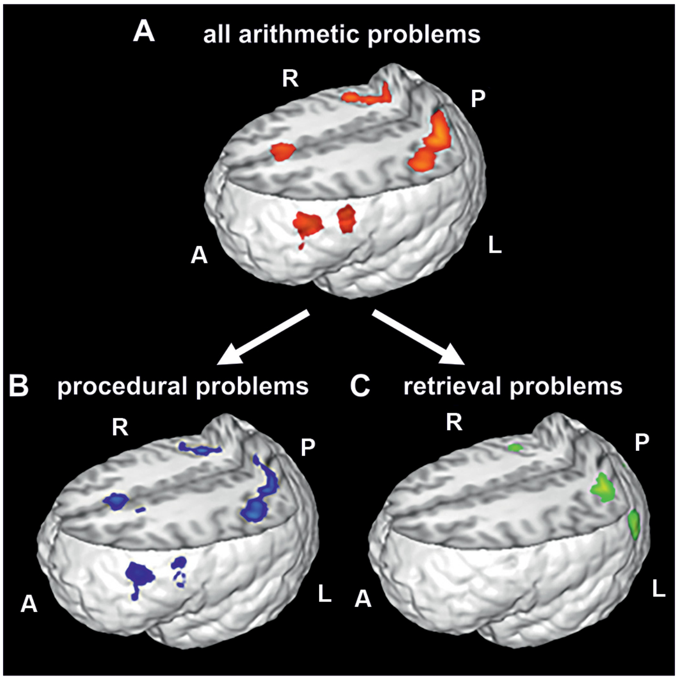


FIGURE 11. Consistent functional MRI (fMRI) activation of brain areas during mental arithmetic. *A*: activation map for all types of arithmetic problems together. *B*: specific activations for arithmetic procedural strategies. *C*: specific activations for arithmetic retrieval strategies. Coordinate planes are $Y = -60$; $Z = 40$ in Talairach space. L, left; R, right; A, anterior; P, posterior. Image from Ref. 376 and used with permission from *Human Brain Mapping*.

Whereas parietal areas such as the left AG and the IPS are consistently found in neuroimaging studies of arithmetic fact retrieval, sometimes subcortical regions like the thalamus and the basal ganglia were additionally activated (379). This is noteworthy given that neuropsychological case studies have found that the thalamus and the basal ganglia are essential for arithmetic fact retrieval (349, 374, 380, 381). In such patients, a disruption of cortico-subcortical loops involving the basal ganglia may lead to specific deficits in fact retrieval even in the absence of verbal deficits.

Since the groundbreaking neuropsychological research of the early twentieth century (382), and with continued support from neuroimaging studies (68, 328, 377, 383–385), the AG is considered crucial for the retrieval of arithmetic facts. The influential triple-code model thus posits that activation in the left AG during simple arithmetic reflects the retrieval of arithmetic facts stored in verbal memory (386). However, recent experimental data challenge a direct involvement of the AG in arithmetic fact retrieval (reviewed in Refs. 387, 388). For instance, no enhancement of fMRI activity in the AG was found with training multiplication problems compared to a pretraining stage (389); instead, a central role for hippocampal, parahippocampal, and retrosplenial structures in arithmetic fact retrieval was proposed. Similarly, there is a general lack of evidence of specific AG involvement in multiplication processing in children (390, 391). Additionally, inhibition of the left AG via transcranial magnetic stimulation (TMS) during adults' solving of multiplications and subtractions revealed a disruptive effect on both retrieval and procedural calculation strategies, challenging the assumption of a specific role of the AG in retrieval (392). The controversy has been fueled by a recent study utilizing intracranial local field potential (LFP) recordings that provide direct and precise anatomical information in human patients (393). Surprisingly, this study found that the AG was deactivated, not activated, during arithmetic tasks, and no significant differences emerged when comparing multiplications and additions. The limited AG recording sites showing activation were near other parietal areas, such as the SMG and IPS, suggesting that neuroimaging results may have been erroneously interpreted or, alternatively, may have blurred the anatomical boundaries of the AG (393).

One hypothesis concerning the role of the AG in arithmetic therefore is that arithmetic fact retrieval is not represented within or across the AG but in adjacent brain areas (393, 394). Another hypothesis suggests that not the AG directly but its connectivity with other relevant brain regions via white matter is relevant; in stroke patients, disconnections between parietal areas (including the AG) and language-related areas (such as the STG and MTG) specifically impede arithmetic fact retrieval during multiplication (395). Yet another hypothesis, the symbol-referent hypothesis, suggests that the AG might support symbol-referent mapping in general and also beyond the number domain (396). Finally, the AG may serve as a broad attentional resource, as it is a component of the default mode network that supports bottom-up attentional processes during memory retrieval (397).

6.3.2. Procedural knowledge applying a procedural (or derivation) strategy.

Ontogenetically, procedural strategies necessarily precede retrieval strategies, as arithmetic fact knowledge learned by heart is based on initially calculated results (**FIGURE 10**). When young children learn formal arithmetic, the prevailing perspective therefore is that they mainly employ procedural strategies, such as counting (398). With age and proficiency, children switch strategies and arithmetic facts evolve from conceptual and procedural knowledge (399, 400). However, different strategies remain available over development, even in adulthood (401).

Not only behavioral but also neuropsychological studies suggest a dissociation of arithmetic procedural from fact knowledge. Just as selective impairments with arithmetic fact retrieval have been observed, selective deficits with procedural arithmetic have also been described (402). For instance, a patient with dementia demonstrated well-preserved abilities in addition, multiplication, and subtraction facts. Nevertheless, the individual exhibited a selective impairment of arithmetical procedures, experiencing severe difficulties with various tasks, including multidigit sums, decimals, and fractions (403).

With neuroimaging, procedural calculation strategies have commonly been linked to widespread activation in the frontoparietal network (404, 405). In the aforementioned meta-analysis contrasting fMRI activation patterns for fact and procedural arithmetic problem solving, the frontal cortex was implicated in procedural problems (376). In contrast to retrieval problems, procedural problems triggered activation in the frontal cortex, specifically involving the cingulate gyrus and left inferior frontal gyrus (IFG) (376). Frontal lobes exhibit increased activation when participants compute arithmetic problems for which they lack training or practice (406, 407) or when they self-report the use of a procedural calculation strategy (408). This suggests that the brain regions responsible for procedural calculation strategies are involved in attention, working memory, and mental manipulation.

Study designs in which participants become more fluent with arithmetic after training reveal that such training leads to a shift from frontoparietal and putative procedural activation to greater activation in the left AG during assumed more fact-based arithmetic problem solving (385, 406, 409). This fronto-to-parietal shift has also been reported in children as they become more proficient in arithmetic (329). Thus, whereas the frontoparietal network for procedural numerical magnitude manipulation appears to be the ontogenetic starting point of arithmetic, the posterior parietal cortex, situated at the junction to the temporal lobes, assumes dominant functions later in life in fact-based arithmetic.

6.3.3. Knowledge of concepts and principles.

Understanding of arithmetic principles, as indicated in behavior by faster arithmetic problem solving compared to standard problems, can already be found in preschoolers (**FIGURE 10**) (410, 411). However, older children are more likely than younger children to apply arithmetic principles, such as inversion strategies, when solving arithmetic problems (412). The observed behavioral dissociations suggest that the understanding of arithmetic principles is a related but largely independent component compared to procedural and retrieval arithmetic abilities (411, 412).

Support for the existence of conceptual arithmetic knowledge as an independent component in arithmetic comes from neuropsychology. Patient studies have consistently reported a preservation of conceptual arithmetic principles despite impairments in simple retrieval- or procedural-based calculation after damage to various brain areas, including the left temporal lobe (371, 413), bilateral temporoparietal areas (279), or the left basal ganglia (380). For instance, a patient exhibited impaired performance in simple computations (e.g., $18 \div 6$, 4×9) but demonstrated the ability to apply arithmetic principles to derive correct answers (e.g., $4 \times 9 = 9 \times 2 + 9 \times 2 = 36$) (380). Additionally, reverse dissociations have been reported, wherein arithmetic principles were selectively impaired while arithmetic calculation remained relatively intact (278, 414). For example, after the surgical removal of a left parietal tumor, a patient experienced a loss of arithmetic conceptual knowledge including understanding of basic concepts of the four calculation operations (414): the patient exhibited an inability to answer questions such as “If $13 + 9$ is 22, what is $9 + 13$?” However, despite this conceptual deficit, there was preservation of some ability to solve simple arithmetic problems, specifically in multiplications and certain additions and subtractions. Importantly, conceptual knowledge of arithmetic can be relatively preserved despite severe impairment of nonarithmetic conceptual knowledge (415–417). This adds to the argument that conceptual knowledge is a distinct component in arithmetic processing.

Neuroimaging studies focusing on arithmetic concepts are scarce. One of the earliest fMRI studies delving into arithmetic principles investigated the production of multiplication problems involving zero (e.g., 3 × 0) and compared activity patterns to those of multiplications with small operands (e.g., 2 × 4) or large operands (e.g., 8 × 7) (379). Zero-problems serve as instances of applying arithmetic principles, as they can be solved by applying the zero rule (i.e., $n \times 0 = 0$) (401). In contrast to nonzero multiplications, zero-problems are either uniformly impaired or spared in neuropsychological patients (278, 418). Compared to multiplications with small numbers (fact retrieval), multiplications involving zero (concepts) elicited a stronger BOLD signal in the head of the left caudate nucleus, the left AG adjacent to the left middle temporal gyrus, and the right inferior frontal gyrus (379).

More recently, fMRI patterns were compared when subjects judged the correctness of three categories of statements (419): arithmetic principles (e.g., "when a number is multiplied by several numbers continuously, exchanging the position of the numbers does not change the result"), arithmetic calculations/computations (e.g., "when the number 8 is divided by the number 4, then multiplied by the number 3, the result is the number 6"), or linguistic sentences (e.g., "Nowadays electronic banking is getting more and more popular, so people seldom pay their bills with cash"). It was found that arithmetic principles elicited stronger activation in the bilateral horizontal IPS and right supramarginal gyrus than did language processing. Additionally, arithmetic principles triggered stronger activation in the left middle temporal lobe and the left IFG than did calculations/computations (419). The results suggest that arithmetic principles engage a neural network that overlaps but is distinct from the networks involved in calculation/computation and language processing.

6.3.4. Dissociations between arithmetic operations.

The discussion above on various forms of arithmetic knowledge (facts, procedures, and concepts) suggests that the distinct basic arithmetic operations (addition, subtraction, multiplication, and division) capitalize to different degrees on these arithmetic strategies, thereby characterizing them to some extent within the brain (**FIGURE 10**).

It is widely accepted that single-digit multiplications (e.g., 2 × 3) are almost exclusively solved through memory retrieval of arithmetic facts (420, 421). Multiplication, unlike any other basic arithmetic operation, is taught systematically in school (e.g., in the form of multiplication tables) and therefore depends heavily on rote memory. Behavioral studies support this notion by finding that adults solve single-digit multiplication problems quickly (398) and usually report the use of fact retrieval when inquired (375). Consistent with the notion of verbal encoding of arithmetic facts, neuroimaging studies of multiplication reveal brain activation patterns related to language processing (422).

Another operation typically solved through fact retrieval from long-term memory, albeit to a slightly lesser degree than multiplication, is simple single-digit additions (e.g., 4 + 6) that are solved in ∼70–90% based on retrieval strategies. This is supported by both self-reports and the finding that addition problems are solved equally fast as multiplication (375). However, there is a debate about whether very small addition problems (operands from 1 to 4) may be solved by procedural strategies via quantity manipulation (423, 424). Multiplication and addition are not only heavily trained in school but also share fundamental conceptual properties (or laws, as mentioned above), unlike division and subtraction. These commonalities could contribute to the establishment of problem-answer associations in long-term memory, making multiplication and addition more conducive to fact retrieval (372). Shared characteristics for simple multiplication and addition that indicate arithmetic fact retrieval strategies include the problem size effect, where problems involving large-value operands generally yield longer reaction times and higher error rates than problems involving small numbers. Additionally, the problem distance effect is observed, indicating that retrieval tends to be faster and more accurate for problems with smaller numerical differences compared to those with larger differences. Addition and multiplication facts are therefore thought to be stored in an interrelated semantic network (314, 420).

In contrast to fact retrieval-based multiplication and addition, subtractions and even more divisions rely considerably more on a combination of procedural strategies and reasoning skills (sometimes called "backup strategies") (375). This is evidenced by longer response times to solve subtraction and division problems and by self-reports according to which simple subtraction is solved in 30–40% by procedural strategies, and even more for larger subtraction problems (425, 426). This is likely influenced by the fact that there are more subtraction and division facts to be remembered compared to addition and multiplication facts, which may contribute to the emphasis on procedural strategies and reasoning skills in these operations (427). Furthermore, the typical sequence of learning, where addition precedes subtraction and multiplication precedes division, may contribute to less proficiency in acquiring subtraction and division facts. Importantly, however, fact retrieval strategies are far from absent for simple subtraction and division problems and can be dissociated based on characteristic eye moments (426).

Among the four basic arithmetic operations, division, the last operation that children learn in school, has been studied the least by far. Whereas adults may rely primarily on retrieval to solve simple division problems (427), children in grades 4 through 7 initially use laborious backup strategies, such as addition (adding the divisor until the dividend is reached) and later multiplication (reorganizing the division problem as a multiplication problem), to solve simple division problems (428). Surprisingly, the frequency of direct retrieval did not increase across grades and never became the dominant strategy of choice. Based on these findings it has been argued that division may be special among the four basic arithmetic operations (428).

Operation-specific deficits in patients have been reported several times in the neuropsychology literature. In one group of acalculic patients, performance was consistently worse for multiplication than for addition and subtraction (418). Other case studies have also demonstrated that addition and/or subtraction can be preserved while multiplication tables are severely impaired (380, 429). A patient with semantic dementia from predominantly left temporal hypometabolism was more impaired in multiplication than in subtraction, as predicted by a verbal deficit (350). The inverse dissociation, preserved multiplication but deficient addition and/or subtraction, has also been reported (374, 429, 430). A patient with a focal lesion of the left parietal lobe resulting in Gerstmann's syndrome was more impaired in subtraction than in multiplication (350). Sometimes, subtraction has been observed to be better preserved than multiplication and addition (431–433). However, the inverse dissociation with selectively impaired subtraction is also known (429). Often, though not universally, the dissociated deficits align with selective impairments in retrieval-versus-procedural strategies for mathematical operations.

Neuroimaging identified several brain regions showing activation when participants solve different types of arithmetic problems (387). Multiplication and reading activate the left STG and MTG more compared to subtraction, indicating verbal strategies for both processes. In contrast, subtraction activated the IPS together with the supramarginal gyri and IFG more than multiplication (422, 434). The hippocampus is more strongly activated for addition relative to subtraction (76, 406, 434), indicating that addition, but not subtraction, may require increased retrieval resources.

In agreement with the notion that multiplication depends on symbolically memorized facts, a school grade-related increase of activity for multiplication, but not for subtraction, was observed in a language-related region of the left MTG (435). Conversely, a grade-related increase of activity for subtraction, but not for multiplication, was detected in a region of the right PSPL. Thus, fluency in simple arithmetic in children may be achieved both by increasing reliance on symbolic retrieval for multiplication and by greater use of efficient quantity-based procedures for subtraction. Interestingly, a positron emission tomography (PET) study in adults found that retrieval of simple arithmetic multiplication facts was not mediated by perisylvian language areas [i.e., left IFG (Broca's area) and posterior part of the STG and MTG (Wernicke's area)], suggesting a dissociation of calculation and language (133).

For more complex 2-digit addition and subtraction problems, a similar picture emerged. Addition is more likely to engage retrieval-based circuits including temporo-parietal and subcortical-limbic areas in the left hemisphere, whereas subtraction activates more (magnitude) processing circuits including specific frontoparietal brain areas and especially again the right IPS (436). This processing distinction between multiplication and subtraction extends to signed numbers in deaf American Sign Language signers, not just hearing adults (437). This suggests the recruitment of quantity-related processes for subtractions, but not for multiplications, in both signing and hearing groups.

Because of the undisputed importance of the IPS in magnitude processing, the study of brain activity during arithmetic has inappropriately often been narrowed down to this key brain area. However, arithmetic tasks typically recruit a large set of bilateral regions (372). They include the ventral occipito-temporal cortex [including fusiform gyrus (FG)], the medial temporal lobe, temporoparietal cortex (AG) and supramarginal gyrus (SMG) but also frontal cortices such as the dorsolateral PFC, ventrolateral PFC, and anterior cingulate cortex (ACC) (68, 79). Activity in this network is modulated by the type of arithmetic operation (438), strategy (404, 439), expertise (408), and training (385). Thus, in addition to domain-specific factors thought to primarily reside in the IPS, more domain-general processes are also involved in arithmetic. Executive functions and working memory (440–442), retrieval from long-term memory (372, 443), and phonological processing (444, 445) are significantly related to individual differences in arithmetic performance. Restrictions to the parietal cortex would, therefore, overlook important factors contributing to arithmetic performance.

Several transcranial magnetic stimulation (TMS) studies investigating arithmetic operations by inducing temporary disruption effects targeted at certain anatomical localization have concentrated on the posterior parietal cortex and the temporoparietal junction (**TABLE 1**) (446). These studies revealed that inactivation of the left and right IPS disrupted multiplication and subtraction processes (447, 448). Inactivation of the left AG impaired the retrieval of multiplication and subtraction problems (392), whereas inactivation of the left SMG slowed down the calculation of price discounts, but not adding prices (449).

A rather extensive TMS study systematically tested the contributions of 52 cortical locations over the two cortical hemispheres in simple arithmetic operations (450). Highest calculation error rates during disruption were observed for multiplication in the left AG (30%), for addition in the left anterior STG (35%), for subtraction in the in the right AG (40%), and for division in the left MFG (45%). Notably, none of these cortical sites exclusively induced operation-specific errors in more than half of the cases, and for all operations additional high error rate sites surfaced. As participants were required to verbalize their answers and controls for language functions were not included in the study, it remains uncertain whether the observed deficits were specific to calculation or rather related to disturbances in language. Nevertheless, these results underscore the existence of cortical circuits for individual arithmetic operations rather than a singular site exclusively representing the operation (450).

6.4. The Spatial Connotation of Calculation

A peculiar feature of quantity is its interaction with another abstract domain, namely space (451, 452). The prevailing spatial-numerical framework is the “mental number line,” suggesting that humans conceptualize numbers in ascending order on an oriented line, typically from left to right. Three key empirical effects support this notion: first, the SNARC effect (“spatial-numerical association of response codes”) (453): in parity judgment tasks, participants respond faster to small numbers with the left hand and faster to large numbers with the right hand; second, the line bisection task, where participants marking the midpoint of numeral strings show automatic biases, favoring the left for small numbers and the right for large numbers (454); and third, the operation momentum effect, where opposite shifts of spatial attention along the mental number line are observed during addition versus subtraction: When adding two numbers, spatial attention is shifted to the right along the mental number line, moving participants “too far” on the representation to the right, which in turn leads to an overestimation of the addition result with respect to the correct outcome; the opposite effect, an underestimation, is observed for subtraction (455–457) (**FIGURE 12*A***). Number-space mappings seem to be rooted in evolution, as already infants (459, 460) and remotely related animal taxa such as monkeys (461), birds (462), and insects (463) show space-number associations. However, in humans the directionality of space-number association is shaped by cultural experiences, usually following the culturally dominant reading direction (464).

A coupling of space and number is also evident at the neural level (465). Lesions to the parietal lobe have long been recognized as leading to combined impairments in numerical and spatial processing (382, 466–468). Moreover, TMS over the IPL impairs the mental number line or spatial representation of numbers (469–471). Finally, number processing, mental arithmetic, and spatial mental rotations all activate the IPS along with nearby areas in the IPL and SPL, as has been shown across 83 neuroimaging studies (377).

The interaction between calculation operations and movement in physical space as indicated by eye movements is seen in the brain. In a remarkable study (458), fMRI activation was first measured when participants moved their eyes rightward and leftward in physical space. It was found that BOLD activity from the posterior SPL was strongly related to such eye movements (**FIGURE 12*B***). In a second step, brain activation during calculation was measured. Here, the participants saw two successive operands and had to add or subtract them according to the instruction. The SPL, known to be critical for the manipulation of information in working memory (472), was part of the activated brain calculation network. When a statistical classifier was trained with fMRI data from the posterior SPL when the participants made leftward and rightward eye movements, the classifier could predict better than chance correct addition and subtraction operations based on the fMRI data from the posterior SPL measured during the participants’ performing only calculations (458) (**FIGURE 12*C***). This important result established a neural relationship between calculation operations and mental movements along a directed spatial line. Moreover, a classifier trained on activity patterns obtained during calculation with numerals (symbolic format) transferred to calculations with sets of dots (nonsymbolic format). This cross-format transfer suggests that the posterior SPL region is comparably involved in solving mental arithmetic problems in both symbolic and nonsymbolic formats (458).

Addition and subtraction operations, in contrast to multiplication or division, elicit systematic spatial shifts of attention (473–475). Once established, these associations occur automatically and implicitly, so that the mere presence of operators like “+” and “−” influence left-right spatial biases (474, 476). An accompanying fMRI

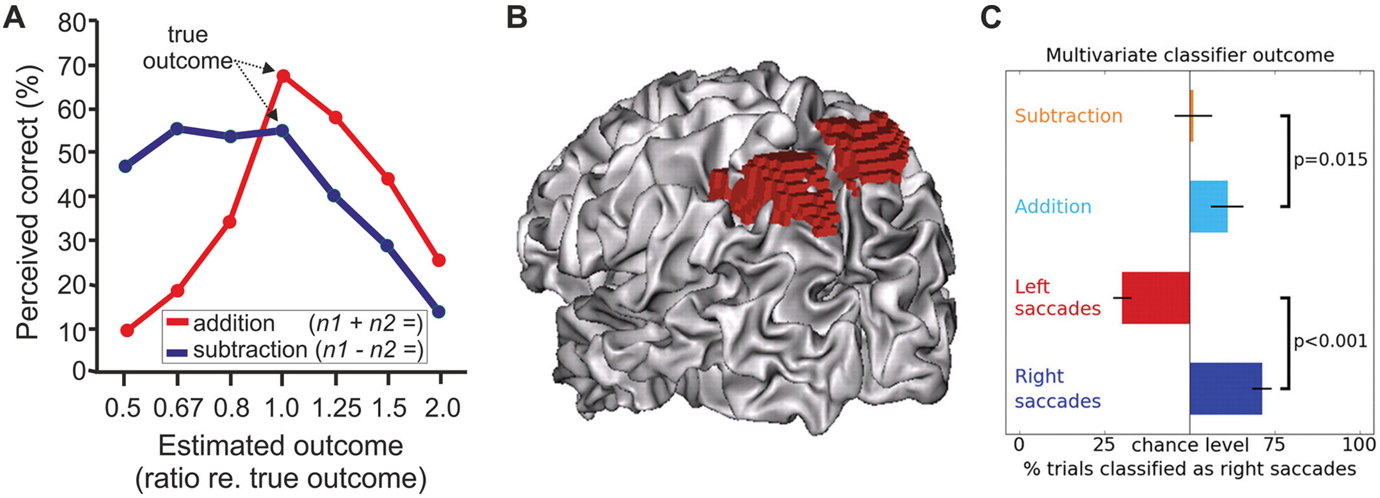


FIGURE 12. Calculation and space. *A*: behavioral operational momentum effect during calculation with dot arrays. The participants viewed videos of sets of dots being added or subtracted from one another behind an occluder and judged whether the final numerosity was correct or incorrect. The 2 functions show the average performance curves for addition and subtraction problems. The percentage of estimated outcomes is plotted as a function of the ratios of the true outcome, which is a measure of the numerical distance from the estimated outcome to the true outcome. For instance, if the true outcome of a calculation is 16, a ratio of ×0.5 refers to 8, whereas a ratio of ×2 corresponds to 32. The momentum effect is evident by the participants being more likely to overestimate the outcome of addition problems and underestimating the results of subtraction problems. *B*: in a posterior-lateral view of a human brain, regions in the left and right posterior superior parietal lobule (PSPL) are highlighted in red. These regions are identified as areas from which the direction of eye movements could be derived. Activity patterns observed during eye movements within these regions were utilized to train a classifier. Subsequently, this classifier was tested to predict addition and subtraction operations. *C*: when a classifier was trained on blood oxygen level-dependent (BOLD) activity patterns in the PSPL during rightward saccade trials, it significantly predicted both rightward (blue) and leftward (orange) saccades. Upon testing this classifier, which was initially trained on rightward saccades, with addition trials, it classified them as rightward saccades 61% of the time (violet). For subtraction trials, only 49% of them were classified as leftward saccades (red). Despite a small effect size, overall the functional MRI (fMRI) patterns associated with rightward saccades allowed a classifier to significantly predict addition trials. Image in *A* is from Ref. 455 and used with permission from *Perception & Psychophysics*; images in *B* and *C* are from Ref. 458 and used with permission from *Science*.

study (477) showed that the mere perception of a "+" sign (compared with a "×" sign) triggers activity in several brain regions, such as the right PSPL, the right frontal eye field (FEF), and the right middle occipital gyrus (MOG), areas that also underlie the orienting of spatial attention (478). Collectively, these findings suggest that subtraction and addition, in contrast to multiplications and divisions, are more influenced by processes associated with spatial-numerical associations.

6.5. Lateralization of Arithmetic Functions

The idea that calculation functions may be lateralized and preferentially represented in one endbrain hemisphere over the other is a recurring theme in numerical cognition. Traditionally, calculation is considered a left hemisphere function in right-handers, with a crucial role for the parietal lobe (479). This is because acalculia, an acquired disorder in calculation abilities (see sect. 6.2.1), typically is reported after left PPC damage (for acalculia after left frontal lesion, see Refs. 480–482). With time, however, more calculation disorders after right hemisphere lesions were reported (483–485).

Based on the extensive meta-analyses across many imaging studies, systematic differences between the two parietal hemispheres were reported (68). On average, addition was left-lateralized, whereas subtraction led to mainly bilateral activations with only a mild left-lateralization. In contrast, multiplication was mainly right-lateralized (390). However, functional imaging based on blood flow may not be the most reliable method for determining brain lateralization. For instance, functional imaging studies often show bilateral activation of language-related brain regions (486), despite language being highly lateralized, usually to the left hemisphere. Therefore, for the determination of cerebral dominance, intraoperative brain mapping (487, 488) remains the golden standard.

Direct electrical stimulation studies in which applied currents transiently inactivate brain regions (**TABLE 1**) have traditionally focused on the left parietal lobe because of the need to map language functions, which are typically left-lateralized. This bias has led to the premature conclusion that only the left parietal lobe is involved in number processing, a conclusion challenged by newer results. One study observed that electrical stimulation of either parietal hemisphere in patients impaired simple subtraction problems, with multiplication remaining unaffected in the right parietal lobe (489). Another study found that electrical stimulation of the parietal hemispheres, specifically the area around the IPS, consistently impaired multiplication and addition in each patient (490). Hemispheric differences were nuanced, with the left AG and SMG exclusively being associated with multiplication while the same structures in the right hemisphere were involved in both operations. The SPL inconsistently contributed to calculation processing (40% on the left and 75% on the right side). The involvement of both parietal lobes in both addition and multiplication was confirmed in a further electrical stimulation study (491); in this study, the analysis of calculation errors after stimulating (and thus inhibiting) either the left or right hemisphere confirmed the role of the left hemisphere in retrieval-based operations versus the right hemisphere in approximation mechanisms. It was concluded that exact calculation is not solely attributed to an isolated symbolic left hemisphere network but requires the bilateral orchestration of posterior parietal areas, with each hemisphere making specific contributions (491).

Disruption of the posterior parietal areas (PPC) via TMS (**TABLE 1**) found some effect on the processing of numerical values; however, there is no agreement about the respective contributions of the left and right sides. The results concerning left versus right hemispheres in calculation are equally inconsistent, and sometimes diverge from neuroimaging findings. One study found left hemisphere predominance, particularly in the angular gyrus, for exact addition (492). In contrast, two other TMS studies reported the involvement of the bilateral IPS during addition, subtraction, and multiplication (447, 448). A rather extensive study used TMS systematically on 52 cortical locations distributed over the two cortical hemispheres and anatomically identified for every subject (450). It was found that, across all four types of arithmetic problems (addition, subtraction, multiplication, and division), both left and right hemispheric disruption sites in MFG, STG, and AG caused high error rates.

7. ADVANCED MATHEMATICS DISSOCIATED FROM LANGUAGE

Given that number processing and mathematics utilize symbols and apply syntactic routines, some researchers have posited that mathematical thought might leverage the syntactical machinery inherent in language (493). Under this conceptualization, mathematical reasoning could be construed as a derivative or abstraction of language processes (494). However, several neuropsychological and neuroimaging studies offer contrasting evidence and show largely independent brain networks for mathematics and language. Because algebra, as an advanced branch of mathematics, does not directly engage number representations, it is particularly suited to investigate the neural relationship between linguistic and mathematical syntax.

Neuropsychological experiments in brain-lesioned patients indicate a dissociation of arithmetical and algebraic abilities from the language faculty. For instance, patients with deficits in mathematical skills can demonstrate preserved language skills (374). Conversely, patients with severe aphasia may exhibit preserved syntactical skills for mathematics (495, 496). Despite extensive left hemispheric lesions leading to severe linguistic impairments, some patients were able to judge the equivalence of algebraic notation and to transform and simplify mathematical expressions. These patients showed proficiency in solving expressions containing numeric or abstract algebraic symbols [e.g., $8 - (3 - 5) + 3$ vs. $b - (a - c) + a$] (496). Moreover, some patients with severe global aphasia or semantic dementia may remain capable of performing nested arithmetic computations (413, 497–499).

In a direct electrical stimulation study in 16 neurosurgical patients, language and calculation arrests were compared (**TABLE 1**) (500). To test language functions, the participants were asked to name objects or read words while electrical stimulation was applied to different cortical areas. If the patients could not name objects or read during the stimulation, the respective cortical site was necessary for language. The tests for calculation comprised the addition of two-digit numbers that were presented on a paper sheet during electrical stimulation. If the patients could not give an answer or gave the wrong answer, the respective site was marked as relevant for calculation. Stimulation in about half of the cortical sites in the left parietal (AG and around the IPS) and about one-fifth of the sites in the frontal (MFG, F2) lobes resulted only in calculation impairments, while language remained intact (500) (**FIGURE 13**). These findings highlight the retention of elementary mathematics despite severe aphasia and provide evidence for the preservation of symbolic capacities in the number faculty independent of language.

Several brain-imaging studies indicate the involvement of separate neural substrates in mathematical versus linguistic manipulations. During mental complex calculation tasks, such as 32 × 24, PET imaging has revealed activation in two specific functional brain networks: a left parieto-frontal network and bilateral ITG (133). Conversely, cerebral blood flow decreased in perisylvian language areas during both simple and complex calculations, suggesting a relative independence of language and arithmetic processing (133). In an fMRI study,

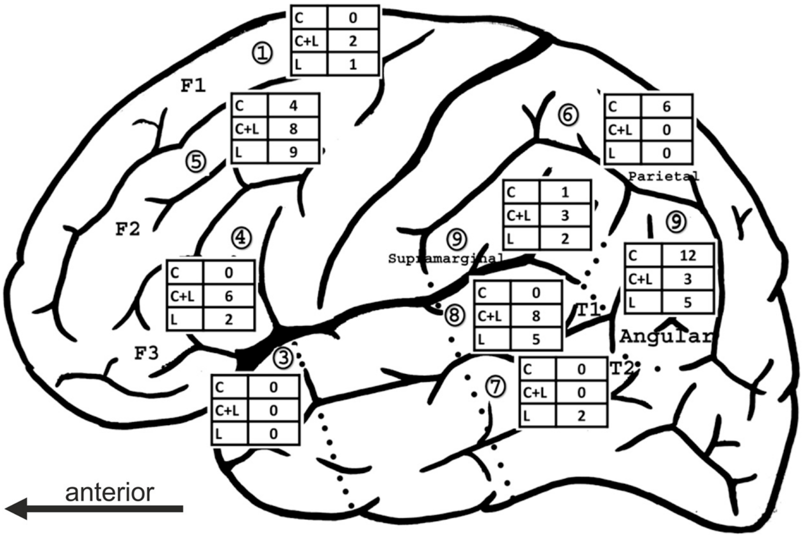


FIGURE 13. Dissociation of calculation and language using electrical stimulation during neurosurgery. The lateral view of a human brain shows the localization of calculation interference sites found in the left hemisphere. Circles with numbers indicate the number of times a cortical region was studied (>16 brain mappings). C = number of specific calculation interferences found in the region tested; C + L = number of common calculation and language (naming and/or reading) interferences found; L = number of specific naming or reading interferences found. Image is from Ref. 500 and used with permission from *Journal of Neurosurgery*.

participants were asked to evaluate whether pairs of linguistic or algebraic propositions were algebraically equivalent or grammatically well formed. It was found that algebraic equivalence recruited bilateral intraparietal sulci, while linguistic equivalence recruited left fronto-temporal perisylvian regions (501). Additionally, classical language areas were not recruited when students were asked to process the syntax of nested mathematical expressions, such as “(((3 + 4) − 2) + 5) − 1” (502).

When professional mathematicians and control subjects with comparable academic qualifications judged whether mathematical (e.g., “A square matrix with coefficients in a principal ideal domain is invertible if and only if its determinant is invertible.”) or nonmathematical (e.g., “The concept of robots and avatars was already present in Greek mythology.”) statements were true, false, or meaningless, a special brain network for advanced mathematics was identified with fMRI, but only in expert mathematicians (503, 504). Only professional mathematicians activated a set of bilateral frontal, intraparietal, and ventrolateral temporal regions in response to mathematical statements (**FIGURE 14**). The math network was closely linked to and overlapped with the brain’s core number network, consisting of the bilateral PFC, IPS, and inferior temporal (IT) regions. Moreover, these areas of the math network were distinct from the classical language areas and coincided with sites showing increased gray matter in mathematicians relative to control subjects of equal academic standing (505). The connectivity between those regions, mediated by the superior longitudinal fasciculus, also increases during normal numerical and mathematical education and in mathematically gifted students relative to others (506–508).

The areas of the math network appear to contribute to other forms of intelligence as well. Similar fronto-parietal activations have been observed in mathematically gifted subjects performing classical executive function tasks such as the Tower of London task (509). Interindividual variations in this network predict corresponding variations in fluid intelligence (510, 511), and fluid intelligence is a predictor of mathematical skills independently of other language skills.

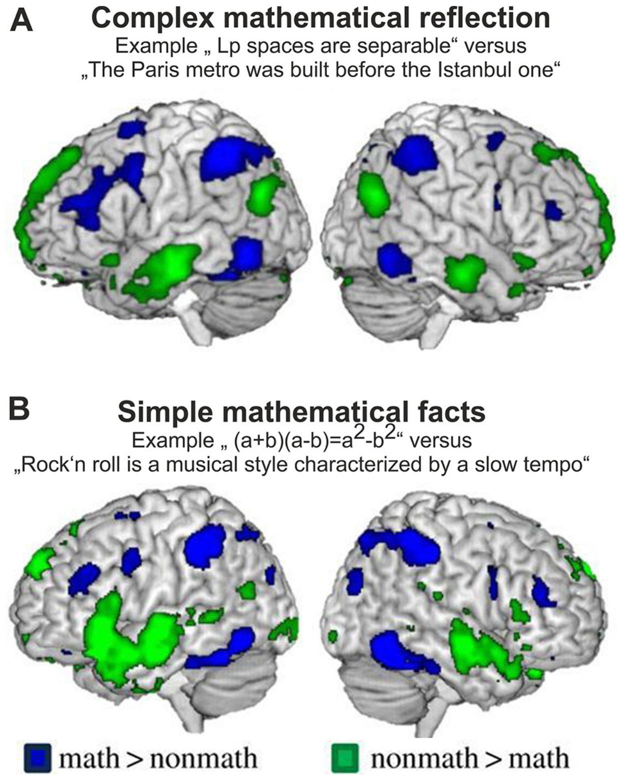


FIGURE 14. Functional MRI (fMRI) in professional mathematicians shows a reproducible dissociation between mathematical and general semantic knowledge. *A*: whole brain view of areas more strongly activated during reflection on complex mathematical statements (blue) vs. general knowledge (green). *B*: brain activity evoked by simpler mathematical facts asking for an immediate response (blue) vs. nonmathematical facts (green). Image is from Ref. 503 and used with permission from *Proceedings of the National Academy of Sciences USA*.

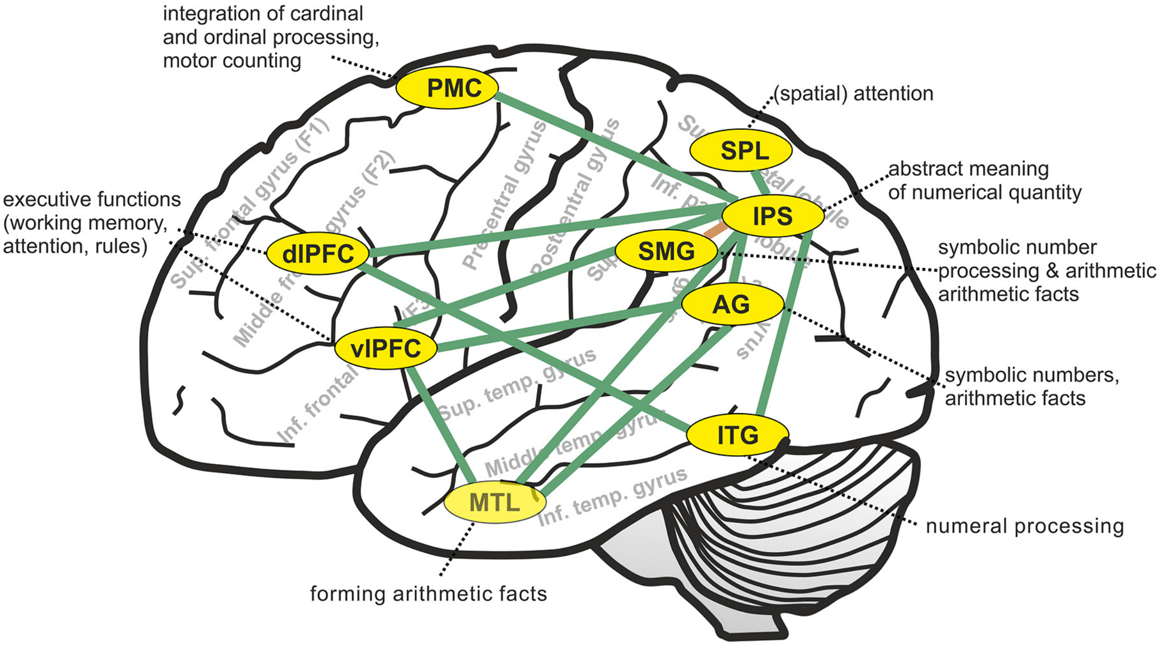


FIGURE 15. Schematic diagram of brain areas involved in arithmetic cognition. Lateral view of a human brain (*left* is anterior). All connections are reciprocal. The core functions of individual areas is referenced by dotted lines. AG, angular gyrus; dlPFC, dorsolateral prefrontal cortex; IPS, intraparietal sulcus; ITG, inferior temporal gyri; MTL, medial temporal lobe; PMC, premotor cortex; SMG, supramarginal gyrus; SPL, superior parietal lobule; vlPFC, ventrolateral prefrontal cortex.

8. CONCLUSIONS

Our understanding of the calculating brain has advanced significantly since early researchers examined the brain of Carl Friedrich Gauss to find the basis for mathematical genius. Initially, these approaches aimed to understand advanced mathematical abilities directly. However, it is now clear that studying simpler, nonsymbolic quantity capabilities provides a better foundation. This perspective is driven by two main insights: first, human-specific symbolic calculation relies partly on a nonsymbolic number sense; second, complex numerical tasks involve various cognitive functions, not all specific to numbers, requiring the identification of core numerical brain areas.

Research over the past decades has shown that number processes have dedicated regions in the brain, particularly within the prefrontal, temporal, and posterior parietal cortex (**FIGURE 15**). This network is distinct from but partially overlaps with language faculties, emphasizing the unique nature of mathematical reasoning as a cognitive domain. The observed dissociation between mathematics and language, such as the ability of individuals with global aphasia to perform mathematical tasks, underscores that certain cognitive aspects are independent of linguistic abilities (512).

Studies on innumerate indigenous people, preverbal infants, toddlers, and diverse animal species have been instrumental in advancing our understanding of numeracy. Research on animals has been particularly valuable because it allows for experimental investigation of the cellular foundations of number sense, such as neurons selectively tuned to numerosities. These findings have inspired human studies using both invasive and noninvasive methods to explore numerically responsive brain areas and maplike organizations of cortical sheets.

A major challenge in numeracy research is the "symbol grounding problem," which involves understanding how abstract numerical symbols (like numerals and number words) acquire meaning by connecting to basic, nonsymbolic representations of quantity. Studies on children learning numerical symbols and undergoing formal mathematical education reveal significant reorganization of the brain with age and increasing numerical proficiency. These changes, both anatomical and physiological, appear to stem from nonsymbolic numerical processes and brain areas.

Understanding the neural mechanisms behind calculation abilities is even more complex than grasping basic number representations. Calculation operations rely on the core number system to transform numerical values, but depending on the strategies used for basic arithmetic, additional brain networks and physiological mechanisms are involved. These include working memory for procedural strategies and long-term memory for rote-learned arithmetic facts.

Higher-order questions about individual arithmetic capabilities, such as the genetic, developmental, and environmental factors influencing numerical abilities, are only beginning to be explored. One goal of this research is to develop intervention strategies for people with acquired or developmental calculation problems. Often, deficits in calculation can be traced back to a lack of understanding of basic quantitative concepts, highlighting the importance of a strong nonsymbolic number sense. Understanding the interplay between nonsymbolic and symbolic numerical processing is key to developing educational tools and therapeutic approaches that foster robust numerical abilities from a young age.

Ongoing research into the neurobiological underpinnings of mathematical cognition promises to enhance our understanding of how the brain processes abstract concepts and engages in complex reasoning tasks. These insights have practical implications for education, cognitive rehabilitation, and our broader understanding of human intellectual capacities.

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AUTHOR CONTRIBUTIONS

A.N. conceived and designed research; analyzed data; interpreted results of experiments; prepared figures; drafted manuscript; edited and revised manuscript; and approved final version of manuscript.

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