Trends in Cognitive Sciences

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Review

Representing Something Out of Nothing: The Dawning of Zero

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Zero stands for emptiness, for nothing, and yet it is considered to be one of the greatest achievements of humankind. This review first recapitulates the discovery of the number zero in human history, then follows its progression in human development, traces its evolution in the animal kingdom, and finally elucidates how the brain transforms 'nothing' into an abstract zero category. It is argued that the emergence of zero passes through four corresponding representations in all of these interrelated realms: first, sensory 'nothing'; then categorical 'something'; then quantitative empty sets; and finally the number zero. The concept of zero shows how the brain, originally evolved to represent stimuli ('something'), detaches from empirical properties to achieve ultimate abstract thinking.

Trends

Recent studies in human history, developmental psychology, animal cognition, and neurophysiology provide evidence that the emergence of zero passes through four stages.

In the first and most primitive stage, the absence of a stimulus ('nothing') corresponds to a (mental/neural) resting state lacking a specific signature.

In the second stage, stimulus absence is grasped as a meaningful behavioral category but its representation is still devoid of quantitative relevance.

In the third stage, nothing acquires a quantitative meaning and is represented as an empty set at the low end of a numerical continuum or number line.

Finally, the empty-set representation is extended to become the number zero.

These different stages of zero-like concepts reflect progressing levels of mental abstraction and pave the way for a full-blown number theory.

> The point about zero is that we do not need to use it in the operations of daily life. No one goes out to buy zero fish. It is in a way the most civilized of all the cardinals, and its use is only forced on us by the needs of cultivated modes of thought. (Alfred North Whitehead)

> In the history of culture the discovery of zero will always stand out as one of the greatest single achievements of the human race. (Tobias Dantzig)

Special Status of Zero among the Natural Numbers

Any number is an abstraction, a recognition that collections may have something in common even if the elements of the collections are very different [1,2]. The number 2 is the common property of all sets containing a pair, the number 3 of all sets that contain a triple, and so on [3]. However, although they are abstract and demanding, positive integers correspond to real 'things' that can be enumerated [4]. Therefore, we first learn to count small numbers of items and later use this counting procedure to comprehend infinite positive numbers [1].

Zero, however, does not fit into this routine (Box 1). While the counting procedure is based on the assumption that there is something to be counted, a set with no elements cannot be assessed via counting. Understanding that zero is still a collection (even if empty) and a numerical concept requires abstract thinking that is detached from empirical experience [5]. The problem is that 'nothing' needs to become 'something'. The absence of elements needs to become a mental category – a mathematical object [1,6].

As a reflection of this mental challenge, it took a long stretch of human history for zero to be recognized and appreciated [7,8]. This cultural hesitation is mirrored in a protracted ontogenetic understanding of numerosity zero in children [9]. Unsurprisingly, only advanced nonhuman animals with which we share a nonverbal quantification system exhibit rudiments of a grasp of

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Box 1. Zero and the Empty Set

Definition and Features of Zero [3,73]

- Zero is a number to describe 'no quantity' or 'null quantity'.
- Zero is the only natural number (by most definitions) that is not positive.
- Zero is neither positive nor negative.
- Zero is the integer immediately preceding 1.
- Zero is an even number because it is divisible by 2.
- Zero is the only number that can be divided by every other number.
- Zero is the only number that can divide no other number.
- Zero is a prerequisite to understanding negative numbers.
- Beyond denoting null quantity, zero has a second and discrete function as a placeholder sign (or digit) in other numbers (e.g., 30, 103).

Empty Set in Set Theory

- Set theory is the mathematical theory of well-determined collections, called *sets*, of objects that are called *members*, or *elements*, of the set. The size of a set (its number of elements) is called its *cardinality*.
- A set that contains no elements is called an empty set or a null set and is denoted by $\varnothing$ or {} (null-set axiom of Zermelo–Fraenkel set theory); for instance, if set $A = \{2, 3, 4\}$ and $B = \{5, 6, 7\}$, then $A \cap B = \{\}$.
- The empty set is not the number 0.
- The empty set is not nothing, because a set containing no element still is a set [74].

zero numerosity [10]. For a brain that has evolved to process sensory stimuli (something), conceiving of empty sets (nothing) as a meaningful category requires high-level abstraction. It requires the ability to represent a concept beyond what is perceived.

The Four Stages of Zero-Like Concepts

Until recently, the biological origins of the understanding of zero were unknown. Recent studies from human history, developmental psychology, animal cognition, and neurophysiology provide evidence that the emergence of zero passes through four stages. These four stages are used to structure this review (Figure 1, Key Figure). In the first and most primitive stage, the absence of a stimulus (nothing) corresponds to a (mental/neural) resting state lacking a specific signature. In the second stage, stimulus absence is grasped as a meaningful behavioral category but its representation is still devoid of quantitative relevance. In the third stage, nothing acquires a quantitative meaning and is represented as an empty set at the low end of a numerical continuum or number line. Finally, the empty set representation is extended to become the number zero, thus becoming part of a combinatorial number symbols system used for calculation and mathematics. As outlined in the following, these different stages of zero-like concepts reflect progressing levels of mental abstraction.

Zero in Human History

The number zero is a surprisingly recent development in human history [7]. Zero was first used as a simple sign to indicate an empty place for integers in a so-called **positional notation system** (see Glossary) (**place-value system**). In a positional notation system, a numeral has different numerical values according to its position in a record: units, tens, hundreds, and so on. For instance, the 3 in the number 302 stands for three hundreds, whereas in the number 203 it denotes three. Without a sign for an empty space, any place-value number record is highly ambiguous. This can be seen, for instance, when in China around 500 BC [11] rod numerals were placed on the columns of a counting board to represent digits in a base-ten decimal system and perform calculations (Figure 2A). Zeroes were represented by an empty space [8]. The problem with this notation is that an entry such as ||| | may represent any one of several numbers: 31, 301, or 310 among others.

Zero as a sign for an empty column in positional notation appears to have first been used around 400 BC in ancient Mesopotamia by the Babylonians, who used two slanted wedges as a place holder (Figure 2B) [7,11–13]. Slightly later, the Greeks used a circle as a placeholder, probably

Glossary

Numerical-distance effect: psychophysical phenomenon of magnitude discriminations; the greater the magnitude difference between two numerosities, the more easily they can be discriminated.

Place-value systems: numerals adopt different numerical values according to their position in a record. Each position is related to the next by a constant multiplier; for example, units, tens, hundreds, and so on.

Positional notation system: see place-value systems.

Prefrontal cortex (PFC): associative cortical region in the anterior frontal lobe of mammals central to cognitive control (executive) functions and high-level cognition.

Single-cell recordings: measurement of the electrical action potentials of single neurons as physical carriers of information in the brain.

Ventral intraparietal area (VIP): associative cortical area in the fundus of the intraparietal sulcus of the parietal lobe of primates.

Key Figure

Four Stages of Zero-Like Concepts Appearing in Human Culture, Ontogeny, Phylogeny, and Neurophysiology

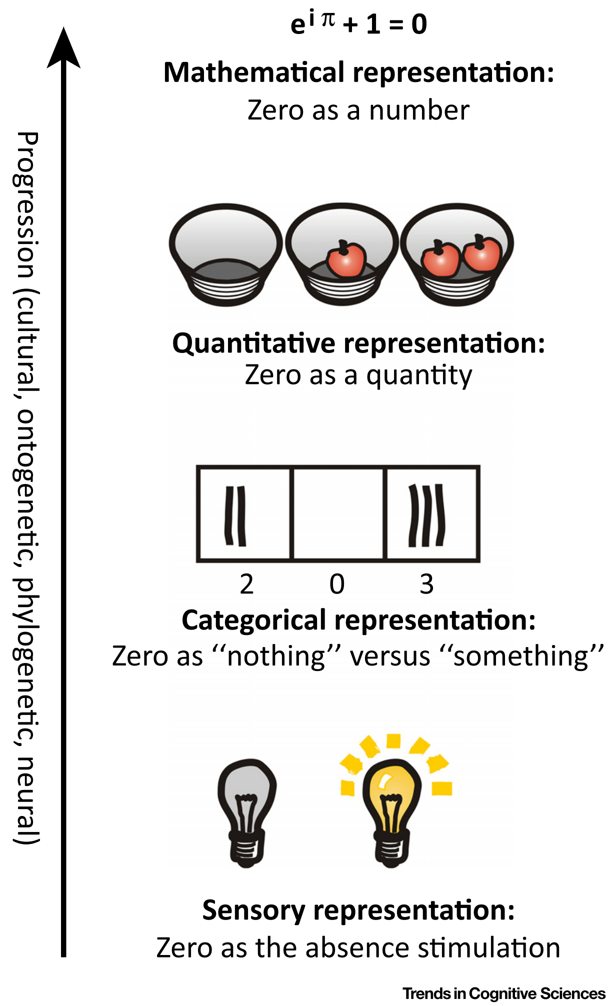

Figure 1. At the most primitive, sensory representation stage (bottom), sense organs register the presence of stimuli such as light. In the absence of stimulation, sense organs are in an inactive resting state. At the next-higher level, 'nothing' is conceived as a behaviorally relevant category, as exemplified by the blank (empty space) used for 0 in Chinese counting-rod systems to depict the number 203. With the advent of quantitative representations, a set containing no elements is realized as an empty set or a null set. Finally, zero becomes the number 0 used in number theory and mathematics. For instance, 0 is the additive identity in Euler's identity, often judged as the most beautiful equation in mathematics (e, Euler's number; i, imaginary unit; π, pi). The equation combines five of the most important numbers in mathematics, including zero. Each higher stage encompasses the previous lower one: the conception of zero as a number requires a quantitative understanding of empty sets, which in turn necessitates a grasp of nothing as an abstract category.

based on Babylonian influence [7]. Independently from the Babylonians, the ancient Mayan civilization introduced a shell-like sign as zero around the beginning of the Christian era [14] (Figure 2C). Nothing – the absence of a numeral in a positional notation system – was now first realized to be a meaningful category and denoted by a sign.

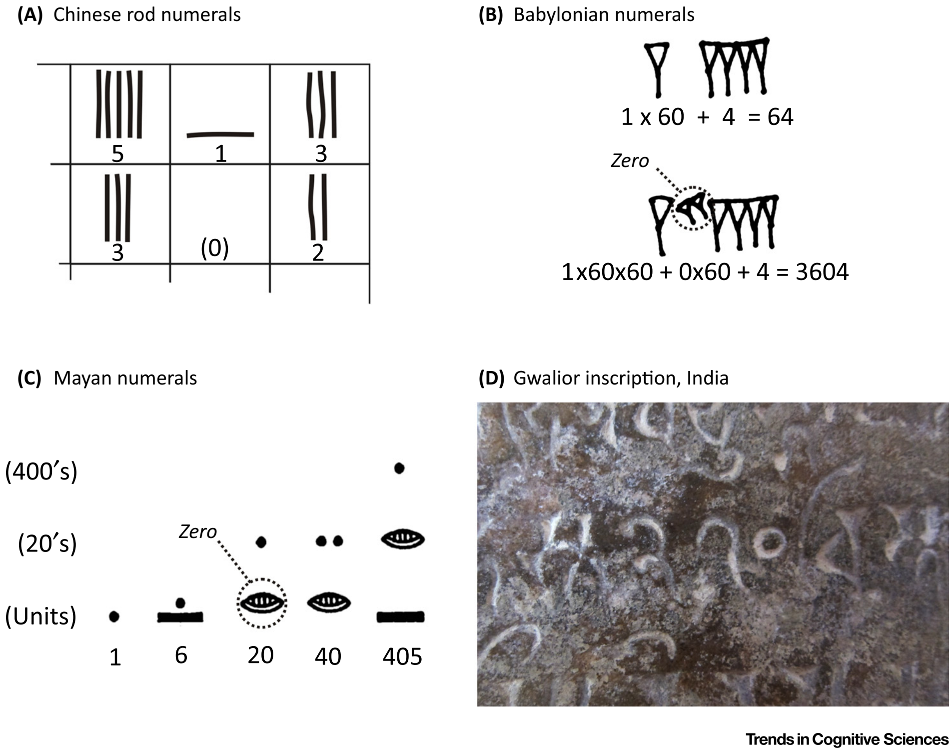

Figure 2. Signs of Zero. (A) In China, bamboo rods were placed on a counting board to represent numbers in a decimal system and perform arithmetic operations. From right to left, each column represents a decimal order: the first column is for units, the second for tens, the third for hundreds, and so on. Zeroes were represented by an empty space. (B) Babylonian base-60 (sexagesimal) number system, read from left to right. The Babylonians wrote in cuneiform, a writing system optimized for writing in damp clay tablets. Because they used a sexagesimal positional notation number system, a new place value begins at 60. The number 64 (top) would be written with one wedge to the left (1 sixty) and four to the right (4 ones). The Babylonians used an oblique and superscript double wedge as sign for the empty place. In the second number (bottom), the second place is empty, so this sexagesimal number in decimal writing is 3604. (C) Mayan base-20 (vigesimal) positional numeral system, read from bottom to top. After the number 19, larger numbers were written in a vertical place-value format using powers of 20. (D) Ninth century inscription from Gwalior, India. The number 270 is in the middle of the image. Photograph by courtesy of Alex Bellos.

Importantly, however, these signs for zero had no numerical value and therefore cannot be interpreted as representations of the number zero [7]. None of these zero signs appeared in isolation or independently of other digits in positional notation. The realization that zero has its own quantitative (null) value marks a cognitive turning point because it requires the insight that even if a set is empty, it still is a quantitative set.

Zero first became associated with an elementary concept of number in India around the 7th century AD. Now zero was a number that became part of a complex number theory. The first written record of the use of zero as a number in its own right comes from the Indian mathematician Brahmagupta [7,11,12]. In his book *Brahmasphutasiddhanta* (AD 628), written in Sanskrit and completely in verse, *Brahmagupta* was the first to provide rules to compute with zero, which is a clear sign of zero as a number. For instance, he writes ‘When zero is added to a number or subtracted from a number, the number remains unchanged; and a number multiplied by zero becomes zero’.

The numeral for zero as we know it today (0) first appeared in an Indian inscription on the wall of a temple in Gwalior (central India) dated AD 876 [11,15] (Figure 2D). Zero was called *sunya* (‘empty’) in Sanskrit. When the Arabs became acquainted with zero in the 9th century, they

Box 2. The Poet and Nothingness: William Shakespeare

The concepts of nothingness and zero play prominent roles in Shakespeare's work (Figure I). For instance, in his tragedy *King Lear* he used the term 'nothing' approximately 40 times in different contexts. When King Lear decides to divide his kingdom among his three daughters and his youngest daughter Cordelia, who loves him most, cannot find the words to articulate this love, the tragedy unfolds from her nothing [75].

> Lear: What can you say to draw
> A third more opulent than your sisters? Speak.
> Cordelia: Nothing, my lord.
> Lear: Nothing?
> Cordelia: Nothing.
> Lear: Nothing will come of nothing. Speak again.

Shakespeare's contemporaries were, of course, familiar with the idea of nothingness, but nothingness as a number, something that they could count and manipulate, was a rather new idea [76]. In the second half of the 16th century, William Shakespeare belonged to the first generation of children in England to have learned about zero [77], based on Robert Recorde's *The Ground of Artes* (1543) [78]. From this standard arithmetic textbook of the time, he also knew the arithmetic meaning of a number's 'place' in a place-value system [79]. Shakespeare uses this place-value idea of zero in his plays; for instance, when Polixenes in *The Winter's Tale* explains:

> And therefore, like a cipher [zero]
> (Yet standing in rich place), I multiply
> With one 'We thank you' many thousands more
> That go before it

Shakespeare seems to be the first poet to use 0, the symbol for the Arabic zero, metaphorically. He does so with zero not only as a place holder but also as a sign to denote 'a mere nothing' in an almost quantity-like meaning: Shakespeare used zero as a signifier of utter abandonment and annihilation when the Fool speaks.

> Now thou art an 0 without a figure. I am better than thou art now. I am a fool, thou art nothing. (*King Lear*, Act 2, Scene 4)

Here, Lear is compared to an isolated zero that does not increase the value of other numerals ('without a figure') but indicates empty quantity. Just like zero adopts different values as a function of its position in a number, so is human identity determined by one's commensuration with others [79].

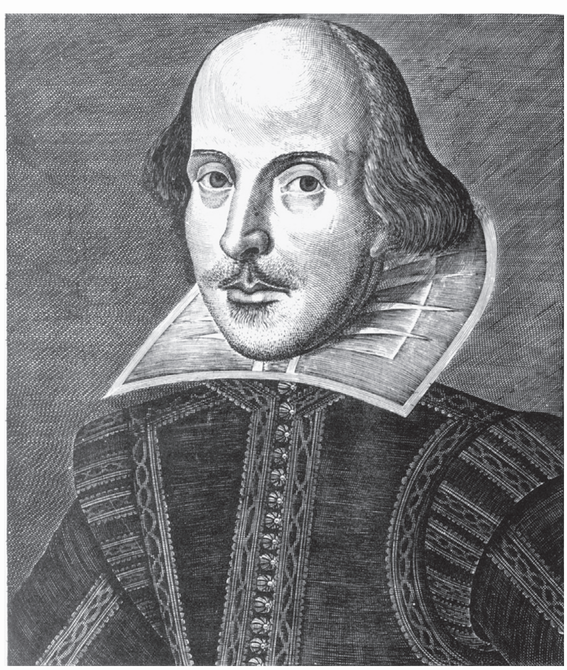

Figure I. William Shakespeare.

translated the Indian name *sunya* literally into the Arabic *as-sifr* ('the empty'). In the West, zero arrived circa AD 1200 when the Italian mathematician Fibonacci (a.k.a. Leonardo of Pisa) brought it back from his travels to North Africa along with the rest of the Arabic numerals and a base-ten positional numeral system. In the 13th century, the Arabic *as-sifr* was transformed in the West into the Latin forms *cifra* and *cephirum* [15]. The Indian numerals, the place-value principle, and the zero in particular faced considerable resistance during the early Middle Ages [15]. As a reflection of the uncertainty about zero, the word *cifra* was used as a secret sign soon after its introduction in Europe. The English verb 'decipher' remains as a monument to these early days [8]. Mathematicians, philosophers, and poets have been fascinated by zero and by the magic that it can create, although in itself it is nothing (Box 2).

Development of Zero-Like Concepts in Children

The cultural hesitation to appreciate zero as a quantity and later a number is mirrored in a protracted ontogenetic development of zero relative to positive integers in children. Five-month-old infants already have the capacity to represent the number of items in a set [16–18]. Moreover, they solve basic addition and subtraction operations in puppet shows that demonstrate the appearance or disappearance of objects [19]. Infants look for longer when the numerical outcome of the play is inconsistent with the operation (for example, if $2 - 1 = 2$ instead of 1), which is interpreted as an indication of a violation of their expectation [19]. Surprisingly, however, 8-month-old infants do not differentiate operations of $1 - 1 = 1$ versus $0 + 1 = 1$ [20]. This has been interpreted as the inability of infants to conceive of a null quantity, although they can already represent small numbers of items [20].

Even many years later, 3.5–6.5-year-old preschoolers master the numerical (cardinal and ordinal) properties of small numbers before incorporating zero in a proposed three-phase progression that different children may pass at different ages [9]. In a backward-counting task, children at age 3–4 years first comprehend that the condition arrived at by taking away the last cube is 'none' or 'nothing' or can be called the special name 'zero' [9]. Thus, zero becomes an index for absence. However, zero is not yet integrated with their quantitative knowledge of other small integers. For example, when asked 'Which is smaller, zero or one?' children often insist that one is smaller [9]. That children around age 3–4 years represent zero as nothing but not yet as a null quantity has also been reported in a study in which children were asked to distribute cookies, note the quantity of cookies on a Post-It Note, and read their notation later [6]. Interestingly, the most common way of denoting zero was to leave the Post-It Note blank. When asked about leaving the paper blank, children frequently said 'It means none cookies' or 'Because there is no cookies' [6]. The empty Post-It paper serves as an iconic representation of absence or nothing, much like the empty column denoting an empty position in a positional notation system.

The next developmental stage for children is understanding zero as a quantity and placing it on a numerical continuum along with other integers. When faced with symbolic notations of zero and integers (i.e., number words and numerals), children realize that zero is the smallest number in the series of (non-negative) integers by about age 6 years [9]. To avoid the burden of transcoding magnitudes into symbolic representations and to investigate a more direct, nonverbal access to the representation of zero, 4-year-old children (and adults) were tested with numerosities, represented by the number of dots in displays [21]. In this numerical ordering task, children were required to select the quantitatively smaller of two numerosities (Figure 3A,B). Confirming an earlier grasp of countable items, children were more accurate at ordering countable numerosities than ordering pairs that contained an empty set. To determine whether children treat empty sets as quantitative stimuli (analog magnitudes) rather than a category that has nothing to do with numbers, the **numerical-distance effect** was exploited: the greater the magnitude difference between two numerosities, the more easily they can be discriminated. Thus, if empty

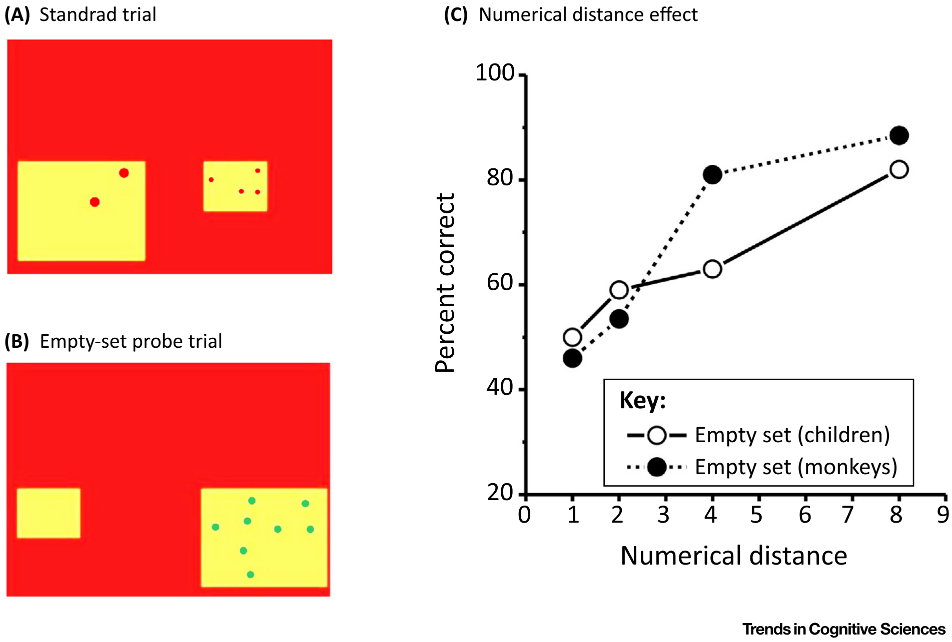

Figure 3. Behavioral Empty-Set Representations in Children and Monkeys. (A) Children and monkeys learned in standard trials to order numerosities (dot collections on yellow background) in ascending order by selecting them on a touch-sensitive screen. In this example image, they had to first select numerosity 2 (left) and then numerosity 4 (right). (B) In intermingled empty-set probe trials, one of the sets contained no item. Again, the two sets had to be touched in ascending order. (C) Performance accuracy of 4-year-old children and two rhesus monkeys for empty sets as a function of numerical distances of 1, 2, 4, and 8. For instance, accuracy at distance 1 represents performance for empty sets and numerosity 1, accuracy at distance 2 represents performance for empty sets and numerosity 2, and so on. Images in (A,B) and child data in (C) after [21]. Monkey data in (C) from [10].

sets are represented with a quantitative meaning in relation to countable numerosities, it should be most difficult to discriminate empty sets from the smallest numerosity, 1. At age 4 years, childrens' performance with empty sets was variable; children exhibiting poor numerosity performance were at chance on empty-set comparisons and showed no distance effect [21]. However, children who were more proficient with comparisons of countable numerosities also showed higher accuracy levels and distance effects with empty sets (Figure 3C). This suggests that around 4 years of age children begin to include a non-quantitative representation of nothing as an empty set into their mental number line [21].

Understanding zero as quantity later in life seems to function as a bridge to a true concept of zero as a number and an early algebraic understanding [9]. Children aged 6–9 years are increasingly able to correctly affirm and deny simple algebraic rules, particularly if they involve zero (such as, 'If you add 0 to a number it will be that number'). From age 7 years on, children typically understand three general rules, namely: $0 < n$, $n + 0 = n$, and $n - 0 = n$. Their ability to justify and reason about such rules, again with zero, also develops dramatically. It was concluded that young elementary-school children possess some understanding of simple algebraic rules and that zero holds a special status in fostering their reasoning about such rules [9].

Zero remains a special number even in adults. Psychophysical experiments indicate that the representation of zero is based on principles other than those used for integers. For instance, while adult humans' reading time for numbers from 1 to 99 grows logarithmically with the number magnitude, zero takes consistently more time to read than expected based on the logarithmic function [22]. In parity-judgment tasks, zero is not judged as a typical even number and is suggested not to be investigated as part of the mental number line [23,24] (but see [25] for a different opinion). Not only spontaneous but also explicit processing of zero remains intricate. When elementary-school teachers were tested on their knowledge about zero, they were reluctant to accept zero as an attribute for classification, exhibited confusion about whether zero is a number, and showed stable patterns of calculation errors using zero [26].

Zero stands out among other integers. Still, it shows a close recapitulation of the cultural history in ontogeny and progresses from a representation of nothing to a grasp of empty sets as quantity. Finally, zero was conceived as number zero.

Zero-Like Concepts in Animals

Research over the past decades has shown that humans and animals share an analog magnitude system for processing the numerical quantity of countable items [4,27–35]. Could it be that nonhuman animals also show the different representational stages indicative of precursors to a concept of zero? As a first requirement, animals can be trained to report not only the presence but also the absence of stimuli (nothing) [36,37]. Rhesus monkeys, for instance, can be taught to press one of two buttons to indicate the presence or absence of a light touch [38] or to respond depending on rule contingencies to the presence or absence of a faint visual stimulus [39]. This indicates that animals are able to represent nothing not just as the absence of a stimulus but also as a behaviorally relevant category.

Can animals ascribe a quantitative meaning to nothing? In an attempt to mimic ‘symbolic’ number processing, animals have been trained to associate set sizes with visual or vocal labels, including a sign for ‘no item’. An African grey parrot used human speech sounds to report the absence or presence of same/different relationships between objects [40]. For instance, when asked ‘What's different?’ when faced with two identical objects, he correctly responded with ‘None’ [41]. However, he failed to utter none when asked how many items were hidden under two empty cups in a follow-up study [42]. Maybe the parrot used none to signify the absence of object attributes rather than the absence of the objects themselves [42]. Alternatively, none may have simply indicated a failed search [10]. Thus, attributing a quantitative meaning to the parrot's utterance ‘none’ would be premature, especially in the absence of reports of numerical-distance effects.

Similar interpretational limitations arise for studies with nonhuman primates that were trained to associate sets with specific visual signs (Arabic numerals). A female chimpanzee learned to match a 0 sign with an empty tray [43]. Moreover, when she was shown a pair of numeral signs, she was able to select the sign that indicated the arithmetic sum of the two signs (e.g., 0 + 2, select 2). However, a quantitative interpretation of the 0 sign is not required since only addition problems for which the chimpanzee would have succeeded if she had simply ignored the 0 sign that denoted nothing were investigated. In another study, squirrel monkeys were trained to choose between all possible pairs of the numerals 0, 1, 3, 5, 7, and 9 to receive that many peanuts [44]. The monkeys always chose the larger sum between two sets of numeral signs (e.g., 1 + 3 versus 0 + 5). However, even if the monkeys performed numerical operations in this task, which was confounded by hedonic value (i.e. amount of reward), the 0 sign is likely to have meant ‘nothing’ to the squirrel monkeys rather than the null quantity. Finally, a female chimpanzee was trained to match certain numbers of dots to signs using a computer-controlled setup [45]. She learned to match blank squares containing no dots to the sign for zero. However, when tested later on her ability to order the signs in ascending order, she failed to transfer the zero sign from the matching task (cardinal domain) to the ordinal task without further training [45,46]. The aforementioned studies allow only limited conclusions about zero-like concepts in animals. First, it cannot be excluded that the animals associate the 0 sign with nothing instead of null quantity. Second, although animals learn to associate the absence of items with arbitrary shapes, transfer to novel contexts (e.g., from cardinal to ordinal tasks) is severely limited.

Evidence of a distance effect is essential to demonstrate that animals represent empty sets quantitatively with other numerosities along a 'mental number line'. Empty sets should be more often confused with numerosity 1 than with any other numerosity. This was shown in monkeys that were proficient at matching and ordering dot numerosities [10]. In arbitrarily reinforced transfer trials that prevented learning, the monkeys were immediately able to numerically match or order empty-set stimuli of variable appearance, thus indicating conceptual understanding of null quantity (Figure 3C). Importantly, the monkeys showed distance effects in both matching and ordering tasks [10]. A numerical-distance effect for empty sets was recently also reported in rhesus monkeys performing a visual delayed match-to-numerosity task for numerosities 0 to 4 [47]. Both monkeys mistakenly matched empty sets to numerosity 1 more frequently than to larger numerosities. Distance effects for the empty set were also observed in rhesus monkeys trained to perform numerical operations on visual dot displays (by adding or subtracting items through manipulation of a hand device to match a target numerosity) [48].

For animals to transcend the empty set representation to arrive at number zero representations that satisfy number theory, they would need to comprehend a symbol system. However, a true understanding of numbers as part of a symbol system, including a grasp of relationships between numbers [1,49] and application of (algebraic) rules (i.e., syntax) for combining them in a meaningful way [50], is beyond their reach [51]. Because of this lack, the highest stage of understanding zero as a number is also out of reach of animals.

Neuronal Representations of Nothing and Empty Sets

For the brain, representing nothing, empty sets, or the number zero is a challenge. This is because sensory neurons have evolved to represent 'something' (i.e., the energy of stimuli that constitute a collection). In the absence of stimulus energy, neurons are inactive and generate spontaneous action potentials as the signature of a default or resting stage. Without light, a visual neuron does not signal optical information; without sound, an auditory neuron conveys no acoustic information. For simple animals with a humble behavioral repertoire, an active representation of nothing is out of reach.

For cognitively advanced animals, the absence of stimulation can become behaviorally relevant so that nothing is no longer merely a lack of a sensory stimulus but a behavioral category and as such would need to be actively encoded by neurons. This active encoding of nothing was tested in a rule-based detection task in which monkeys subjectively judged whether they had or had not seen a barely visible stimulus. After a delay phase, a cue informed the monkey if and how to respond to its judgment to dissociate the decision about stimulus absence or presence from motor-preparation processes. Subsequent **single-cell recordings** from the **prefrontal cortex (PFC)** of these behaving monkeys showed neurons that increased discharge rates whenever the monkeys later reported to have seen the stimulus (Figure 4A) [39,52]. Such a response might be expected for a neuron that integrates energy from a present stimulus and similar responses have also been reported for touch in the frontal lobe [38,53]. Interestingly, a second class of neurons increased their discharge whenever the monkeys decided that they had not seen a stimulus (Figure 4B). Analyses of error trials showed that the activity of these neurons predicted the monkeys' present/absent judgments even before a response could be planned. Notably, the active coding of the 'stimulus-absence' decision was not a visual response but emerged during the delay phase when the monkey needed to decide whether it had seen the stimulus. This indicates that the categorical stimulus-absence signal arises during a post-sensory cognitive processing stage. Thus, behaviorally relevant stimulus-absence decisions are not encoded by default (baseline) neuronal responses but rather by internally generated signals. The brain seems to translate the lack of a stimulus into a categorical and active stimulus-absence representation.

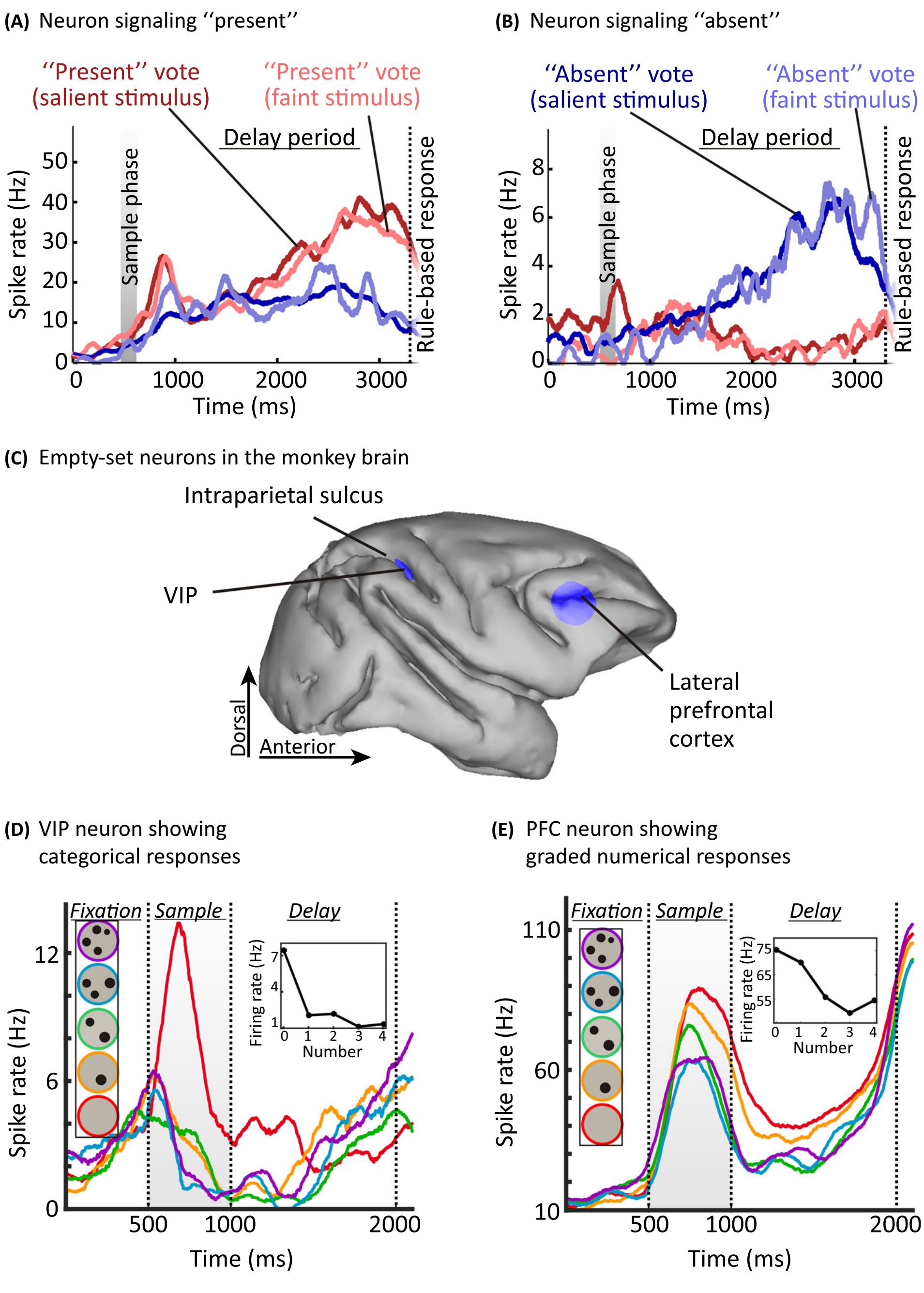

Figure 4. Neuronal Representations of Nothing and Empty Sets. (A) Prefrontal cortex (PFC) neurons signal the monkey's decision that a visual stimulus (onset at 500 ms, gray-shaded time interval) was present. This neuron showed elevated firing rates during a delay period before the monkey reported a stimulus. Activity reflected the monkey's judgment rather than stimulus intensity, because discharges were indistinguishable for high-intensity (red) and low-intensity (pink) stimuli. Spike-density histograms of the neuronal responses are shown. The vertical dotted bar indicates onset of the response rule. (B) Some PFC neurons actively represented the monkey's decision that a visual stimulus was absent. This neuron increased its spike rate whenever the monkey was about to report the absence of a stimulus. Even if a faint stimulus was presented, the neuron signaled the monkey's 'stimulus-absence' decision (light blue) just as it did when no stimulus was presented (dark blue). Same layout as in (A). (C) A lateral view of a monkey brain shows the recording sites in the ventral intraparietal area (VIP) and PFC from which empty-set representations were recorded. (D) VIP neurons encoded empty sets as categorically distinct stimuli. This example VIP neuron was tuned to empty sets but showed no progressive decrease of

(Figure legend continued on the bottom of the next page.)

As a signature for a quantitative representation, neurons are expected not only to represent the absence of stimulus but also to place empty sets at the lower end of a numerical continuum. Again, numerical-distance effects are instrumental to demonstrating systematic ordering of magnitudes. Number neurons found in the parietofrontal number network of primates (Figure 4C) are tuned to preferred numerosities by maximum activity and show such a distance effect by a progressive decline of activity relative to the preferred numerosity [54–58]. A recent study in monkeys performing a numerical matching task including empty sets and countable numerosities found that single neurons and neuronal populations represent empty sets as conveying a quantitative null value, albeit to different degrees [47]. At the input to the number network, neurons in the **ventral intraparietal area (VIP)** did not exhibit a strong distance effect and encoded empty sets as a category distinct from all other numerosities (Figure 4D). A similar finding for VIP neurons has been reported in one monkey trained to perform numerical operations on visual dots [59]. Thus, VIP neurons still signal the more primitive presence versus absence of items. Higher up the cortical hierarchy, however, PFC neurons represented empty sets more similarly to numerosity 1 than to larger numerosities, exhibiting numerical-distance effects (Figure 4E) [47]. Moreover, prefrontal neurons represented empty sets abstractly and irrespective of stimulus variations. Compared with the VIP, the activity of numerosity neurons in the PFC also predicted better the successful or erroneous behavioral outcome of empty-set trials [47]. These results suggest a hierarchy in processing from the VIP to the PFC along which empty sets are gradually detached from visual properties and gradually positioned in a numerical continuum. This brain-internal sequential process mirrors the timeline of the cultural and ontogenetic advances described above. The brain transforms the absence of countable items (nothing) represented in brain areas lower in the hierarchy, like the VIP, into an abstract quantitative category (zero) in areas higher in the hierarchy such as the PFC. Because the PFC is also engaged in representing basic quantitative rules [60–63], it could provide the basis for symbolic reasoning about numbers in children [9].

Both stimulus-absence and empty-set representations require transformation from a sensory none event to an internally generated categorical activity. Understanding the physiological mechanism behind this process will be challenging. In contrast to countable numerosities, which are represented spontaneously [64–67], coding the absence of stimuli and null quantity requires explicit training. As a behaviorally relevant category, zero-like representations need to develop over time as the result of trial-and-error reinforcement learning. If behavioral feedback is provided, reward prediction-error signals arising from the dopamine system [68,69] could modulate reward-dependent plasticity. Reinforcement learning could refine functional connectivity between parietal and frontal neurons or recurrent connections within associative cortical areas to support neuronal selectivity and sustained working memory coding [70,71]. A recent cortical-circuit model showed how category selectivity could arise from reinforcement learning. According to this model [72], weak but systematic correlations between trial-to-trial fluctuations of the firing rates and the accompanying reward after appropriate behavioral choices lead neurons to gradually become category selective. An interesting property of this model is that it does not require initial tuning of the neurons for successful learning; even nonselective neurons developed categorical tuning as long as they carried neuronal fluctuations that correlated with behavioral choices. Therefore, when a subject learns to respond appropriately to absent stimuli or empty sets to receive a reward, such a mechanism might suffice to produce empty-set-tuned neurons from originally untuned neurons.

activity towards 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. (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 towards larger numerosities. Layout as in (C). Data in (A,B) from [39]; data in (D,E) from [47].

Concluding Remarks

The neuronal scenario pictured above indicates an effortful cognitive process to arrive at representations of empty sets, not to mention a concept of the number zero. Since cognitive capabilities originate from the workings of neurons, the historical and ontogenetic struggle of humankind to arrive at a concept of zero may at least partly, and in addition to sociocultural factors, be a reflection of this neurobiological challenge. With the advent of the number zero, however, abstract thinking and mathematics rose to a new level. Now, negative numbers were also conceivable by extending the number line towards numbers smaller than zero, leaving the realm of empirical quantities behind and enabling a full-blown number theory. Fundamental calculations would not be possible without zero. No wonder the discovery of zero as a number was celebrated as a true revelation [8].

Outstanding Questions

Where are empty sets and the number zero represented in the human brain and would they be part of a 'number map'?

How can zero be represented as a meaningful category in computational models of numbers that have so far dealt only with positive numbers?

Are animals in taxa only remotely related to humans, such as fish or even insects, able to represent empty sets as a quantitative category?

How are zero-like concepts neurophysiologically encoded in animals that did not evolve a layered neocortex (cerebral cortex), such as birds?

Are empty sets represented in an abstract, supramodal format and what is the mechanism behind it?

How are zero-like representations maintained and transformed in working memory to process numerical information in a goal-directed way?

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