

Trends in Cognitive Sciences

Volume 21 Number 6
June 2017
ISSN 1364-6613



Is There an Evolved Capacity for Number?

CellPress

June 2017
Volume 21, Issue 6

In this issue of *Trends in Cognitive Sciences*, Núñez critically evaluates the idea that humans have an evolved capacity to represent number and perform arithmetic. He marshals evidence from non-industrialized nations and calls for a clearer distinction in the field between quantal and numerical cognition. Nieder and Núñez exchange letters further debating these ideas. Cover image from iStockphoto/Mike_Kiev. Cover design by Rebecca Schwarzlose.

Opinion

Is There Really an Evolved Capacity for Number?

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Humans and other species have biologically endowed abilities for discriminating quantities. A widely accepted view sees such abilities as an evolved capacity specific for number and arithmetic. This view, however, is based on an implicit teleological rationale, builds on inaccurate conceptions of biological evolution, downplays human data from non-industrialized cultures, overinterprets results from trained animals, and is enabled by loose terminology that facilitates teleological argumentation. A distinction between quantal (e.g., quantity discrimination) and numerical (exact, symbolic) cognition is needed: quantal cognition provides biologically evolved preconditions for numerical cognition but it does not scale up to number and arithmetic, which require cultural mediation. The argument has implications for debates about the origins of other special capacities – geometry, music, art, and language.

An Evolved Capacity Specific for Number and Arithmetic?

Where do **numbers** (see [Glossary](#)) come from? Some say they are God-given [1], exist in Plato's heaven [2], or are formal meaningless entities [3]. To scientists, who endorse views consistent with a naturalistic understanding of the world, these proposals are far from satisfactory. Although the empirical study of discrete quantity (or **numerousness**) discrimination is not new ([Box 1](#)), these naturalistic constraints have given the question of the origin of numbers a new impetus. Understanding the origin of the 'number sense' – a term made prominent in the 1930s by the mathematician Tobias Dantzig [4] – is today at the core of the dynamic and growing field of 'numerical cognition'. The field has made considerable progress in investigating the abilities of human and nonhuman animals to perceive, estimate, and process quantities [5,6]. Furthermore, the observation that our intuition of 'one, two, three, . . . ' is sharp, pristine, and immediate has, under the banner of evolution, paved the way for a view that there must be something about 'pure numbers' that we are born with – a grasp of certainty that serves as a rock-solid foundation for the edifice of mathematics.

Inspired by this view, a significant amount of behavioral and neural data – from humans and nonhuman animals – has led many within the field of numerical cognition to endorse as unproblematic claims that there is a specific 'evolved capacity for number' [7], 'evolutionary foundations for number' [8], 'numerical abilities and arithmetic in infancy' [9], 'monkey mathematical abilities' [10], and that there are 'numerical and arithmetic abilities in non-primate species' [11], and so on. Similarly, in cognitive neuroscience, authors have argued that 'every brain is hardwired for math' [12], and that there is 'single-neuron arithmetic' in the brain of cats, monkeys, and humans [13]. Countless contemporary scholarly publications also display similar claims prominently in their titles, thus consolidating the current conventional wisdom.

In a nutshell, this view posits that there is an essential 'mathematical core' – formed around fundamental 'numerical abilities' – which humans seem to share with many other animal species. This 'mathematical core' would be the result of natural selection, which gave selective

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There is a widely accepted view in cognitive neuroscience, child psychology, and animal cognition that there is a biologically evolved capacity specific for number and arithmetic that humans share with other species.

However, data from various sources – humans from non-industrialized cultures, trained nonhuman animals in captivity, and the neuroscience of symbol processing in schooled participants – do not support this view.

The use of loose and misleading technical terminology in 'numerical cognition' has facilitated the elaboration of teleological claims which underlie the above view.

Biologically evolved preconditions for quantification do exist, but the emergence of number and arithmetic proper – absent in nonhuman animals – has materialized via cultural pre-occupations and practices that are supported by language and symbolic reference – crucial dimensions that lie largely outside natural selection.

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Box 1. Quantity: The Gain and Loss of Conceptual Rigor

The empirical study of quantity discrimination began at the dawn of scientific psychology, in the 19th century. Already in 1871 a report in *Nature* observed that people grasp a small amount of items by ‘an instantaneous and apparently single act of mental attention’ ([112] p. 281). Experimental psychologists in the 1940s would later conclude that, when discriminating and estimating ‘numerousness’, people operate with two fundamentally distinct processes: one quick and reliable for very small quantities, later coined ‘subitizing’ [113], and one for large quantity discrimination (LQD) [114] that worked in a fuzzy, imprecise way. The search for an understanding of these phenomena led experimental psychologists and psychophysicists of the mid-20th century to develop a rigorous terminology [75,76,115] (e.g., ‘numerousness’, ‘numerosity’, ‘number’) for making fine distinctions to properly evaluate and measure stimuli – especially when studying rats, pigeons, and infants – without having to necessarily assume the presence of conceptual understanding such as that involved in the notion of number (Table I). Unfortunately, this rigorous quantity-related terminology was overshadowed a few decades later by the consolidation of the ‘cognitive revolution’ in the 1980s [116]. By rejecting the behavioristic tenet – that when studying the mind all that researchers can do is to observe the relationship between stimuli and behavior – the cognitive revolution called for the investigation of, and theorizing about, what’s inside the ‘black box’ – the mind and its ‘mental representations’ [116], which eventually in neuroscience led to the search for the ‘representation of number in the brain’ (e.g., [50]). This inviting but hazardous step seemed to have licensed quantity-related researchers to loosen the use of terminology resulting in the attribution of ‘number’ – or the ‘mental representation’ of it – to the mind of the cognizing agent, be it an infant, a monkey, or a fish. This is routinely reflected in the titles of articles in infant and comparative psychology, in which ‘number’ is rarely exact or symbolic – for example ‘Spontaneous number representation in mosquitofish’ [117], ‘Chicks with a number sense’ [118] ([23,119–123] for other examples). Thus, with respect to quantity-related concepts, the rejection of behavioral psychology appears to have come at the price of weakening conceptual rigor.

The two aforementioned abilities for discriminating small and large quantities continue to intrigue scientists today [124]. Nonetheless, it is now well established that many nonhuman animals exhibit basic quantity-related behaviors similar to those of humans [43–45], and the investigation of such behaviors has therefore been put, and properly so, in an evolutionary context. Unlike the cautious and rigorous psychophysicists of the mid-20th century, however, the field of ‘numerical cognition’ has now, teleologically, built the term ‘number’ into the working theoretical constructs themselves, as in the case of the postulated approximate number system (ANS) discussed in the text.

Table I. Prototypical Properties of ‘Number’

Prototypical properties of number (as in the familiar sequence ‘one, two, three, . . .’)	Example: the number ‘seven’
(i) It quantifies in an exact and discrete manner	It designates exactly a specific discrete quantity that is not merely most of the time different from ‘six’ or ‘eight’, but it is absolutely and categorically distinct from them
(ii) It is abstract in the sense that it transcends the quantification of specific items or commodities, or specific types of stimuli	‘Seven’ is abstract, transcending what psychologists call ‘sensory modalities’ [44]
(iii) It has a cardinal sense (produced by counting)	The exact quantification of collections with numerosity 7 can be assured by counting, which gives its cardinal sense
(iv) It has an ordinal sense (required for enumerating and counting)	It has an ordinal sense, as when the seventh element in a row is designated
(v) It is relational	The properties of ‘seven’ are defined in relation to other numbers (e.g., smaller than ‘ten’, successor of ‘six’)
(vi) It is combinative, operable	‘Seven’ can be combined to produce other numbers via specific operations, such as adding ‘three’ to it, to yield exactly ‘ten’
(vii) It is referred to symbolically	It is referred to symbolically via specific signs (numerals) such as the word ‘seven’, the digit ‘7’, the Roman ‘VII’, or ‘111 ₂ ’ (base 2)
Non-prototypical properties	‘Seven’ is a prime number; it is the positive square root of 49; it is the base-ten logarithm of 10 000 000, etc.

advantages to individuals who, while foraging, for instance, were able to discriminate food sources that had more items from those that had fewer.

This nativist view of the origins of number and arithmetic seems sensible, attractive, and convenient. It appears to straightforwardly link the quintessential abstraction, exactness, and

Glossary

Approximate number system (ANS): a hypothesized neural system which, following the Weber–Fechner law, handles the processing of quantities above the subitizing range. It is claimed to be an evolutionarily ancient innate system for ‘approximate number’.

Biologically evolved preconditions (BEPs): necessary conditions for the manifestation of a behavioral or cognitive ability which, although having evolved via natural selection, do not constitute precursors of such abilities (e.g., human balance mechanisms are BEPs for learning how to snowboard, but they are not precursors or proto-forms of it).

Distance effect: the fact that it is harder to discriminate between collections of items that differ by a small amount than between collections that differ by a large amount.

Enculturation: the gradual acquisition of cultural traits (the characteristics and norms of a culture or group) by an individual or another culture.

Large quantity discrimination (LQD): the rough discrimination of collections of discrete items above the subitizing range, whose numerosities usually differ by a substantial amount.

Number: exact symbolic quantifier that designates the cardinality of a collection of objects. It is abstract, relational, and operable. In its most prototypical case it is associated with the familiar counting sequence ‘1, 2, 3, . . .’

Numeral: a sign for a number, such as the Hindu-Arabic digit ‘5’, the Roman ‘V’, or the French word ‘cinq’, that signify the number five.

Numerosity: a scale of measurement for evaluating the numerousness of stimuli (e.g., a collection of discriminable objects) utilized especially by psychophysicists in the mid-20th century, and by means of which an experimenter establishes the cardinal attribute of physical collections of objects.

Numerousness: a property or attribute of a stimulus (discrete quantities) which can be measured by an investigator in units of numerosity.

usefulness of numbers and arithmetic with genes, brains, and evolution, portraying mathematics as the inevitable result of the evolutionary process that brought *Homo sapiens* to being.

Nonetheless, is the underlying theoretical account of the view sound? Do the data support it? I will argue here that this is not the case, and offer an alternative naturalistic account of the existing data and of the nature of numbers and arithmetic. The argument has implications for debates about the origins of many other special capacities, such as geometrical and musical cognition, naïve (or folk) physics, art, and language.

Why Is the Nativist View of Number and Arithmetic Attractive?

Attempts to provide a nativist account of number and numerical competences are not new. Already in the 1960s scholars proposed nativist arguments [14,15] against Jean Piaget's constructivist account of number in the mind of a child [16,17]. The new data-gathering methods of the 1980s then brought the debate to another level, providing compelling reasons for believing that the capacity for number has been endowed via natural selection. Already by 3 or 4 days of age, a human baby can visually discriminate between collections of two and three items [18], and, acoustically, between the sounds of two or three syllables [19]. Ten- to 12-month-old infants can, under some conditions, visually distinguish three items from four [20,21]. Moreover, by four and a half months, babies exhibit behaviors that appear to indicate a degree of sensitivity to elementary 'arithmetic operations' akin to 'one plus one is two' and 'two minus one is one' [22]. In addition, as early as 6 months infants discriminate between large collections of objects provided that their quantities differ by a large amount (for example, 8 items vs 16 items, but not 8 vs 12) [23]. These capacities appear to be in place early in ontogeny before any clear influence of culture or language. Moreover, studies with children have shown that quantity discrimination acuity may be stable over the first year of life [24] and that it correlates with achievement in school mathematics [25,26].

Importantly, nonhuman animals also seem to exhibit impressive abilities dealing with quantity. Nonhuman primates can compare collections of items (usually pieces of food) and choose the ones with more (or less) items [27–29], as can many other mammals including bottle-nose dolphins [30], horses [31], black bears [32], and dogs [33]. Some birds [34–36], amphibians [37,38], and fish [39–42] have been reported to do so as well.

Furthermore, the abilities for handling quantities seem to have specific properties shared by human and nonhuman animals [43–45]. The perception and discrimination of quantities appear to be supported by two distinct processes. One, **subitizing**, is exact, fast, and error-free, and in humans operates in the range of one to about four items. The other, **large quantity discrimination** (LQD), works in a rough, imprecise manner and exhibits a behavior that follows the non-linear **Weber–Fechner Law**, which underlies well-established **distance**, **size**, and **ratio effects**. Neural correlates of this psychophysical law have been found in the primate prefrontal cortex where individual neurons – 'number neurons' [46,47] – have been reported to exhibit a logarithmic coding of **numerosity** [48]. Furthermore, neural correlates of distance effects have been reported in the human intraparietal sulcus (IPS) – known for its involvement in various number-processing tasks – for both non-symbolic and symbolic stimuli [49]. In general, human and nonhuman primate neural data, gathered through a variety of methods, have provided substantial evidence that quantity-related information is processed by regions of the prefrontal and posterior parietal lobes, with the IPS playing a crucial role in the treatment of the semantic aspect of quantity [50].

Further strengthening the nativist case, studies with trained animals have produced impressive results. For instance, after long and intensive training a grey parrot named Alex was taught to

Quantical: pertaining to quantity-related cognition (e.g., subitizing) that is shared by many species and which provides BEPs for numerical cognition and arithmetic, but is itself not about number or arithmetic. Quantical processing seems to be about many sensorial dimensions other than number, and does not, by itself, scale up to produce number and arithmetic.

Quantifier (natural): determiners or pronouns which occur in all natural languages and indicate the magnitude of quantities, such as the English 'few' or 'many'.

Quantitative: relating to, measuring, or measured by the quantity of something rather than its quality.

Ratio effect: the fact that to compare collections of items that differ by the same amount it is more difficult to do it if they are large collections than if they are small.

Size effect: the fact that it is harder to discriminate collections of large amounts than of small amounts.

Subitizing: the quick, reliable, and accurate discrimination of small quantities (usually within numerosities 1–4).

Teleology: the explanation of phenomena by the purpose they serve rather than by postulated causes. It is particularly problematic in evolutionary accounts because it mistakenly *ex post facto* considers phenomena to be goals targeted by natural selection (e.g., assuming numbers and arithmetic as given in view of their ubiquity and usefulness in the industrialized world).

Weber–Fechner law: a general psychophysics law which states that the perceived subjective intensity of a stimulus is proportional to the logarithm of the stimulus intensity. It holds for a variety of perceptual domains such as brightness, loudness, and numerosity.

identify small arrays of visually perceivable objects, and could vocally respond to questions about the shape, color, or number of items in a given collection [51]. A female chimpanzee named Ai was taught to use arbitrary visual signs for objects and shapes, as well as digits, which she could use to report the type of object, color, and quantity of items in various arrays [52]. Remarkably, Sheba, another chimpanzee, was able to perform, after many years of training, some basic ‘arithmetic operations’ at a symbolic level with the digits ‘1’, ‘2’, and ‘3’ [53], the closest an animal has come to human symbolic calculation abilities [54].

Together, these findings seem to support the claim that ‘mathematical objects may find their ultimate origin in basic intuitions of space, time, and number that have been internalized through millions of years of evolution in a structured environment and that emerge early in ontogeny, independently of education’ ([55] p. 1217). In particular, these findings suggest that some specific ‘numerical’ capacities have evolved, biologically, in countless unrelated species, including humans. However, the interpretation of these results and the corresponding theoretical conclusions with respect to biological evolution have serious problems.

Biological Evolution and Teleology

Perhaps the biggest problem for the nativist claim that there is a biologically evolved capacity specific for number and arithmetic is that it is implicitly **teleological**. It takes numbers, and to some extent arithmetic, as given, and *ex post facto* considers them – by virtue of their power and entrenchment in industrialized societies – to be goals targeted by natural selection. It takes basic quantity-related capacities that may have evolved biologically via natural selection as primitive precursors on the inevitable path towards number. These capacities, however, appear to be **biologically evolved preconditions** (BEPs) that when scaffolded by certain cultural practices and products eventually materialize in number and arithmetic. Essentially, it is equivalent to take say, snowboarding, as given and claim that there is an evolved capacity for it because this activity today is crucial for the snow-sports and tourism industries. With respect to biological support, learned competences, and the development of human activities, snowboarding shares many properties with exact symbolic quantification and arithmetic. For instance, the manifestation in the ontogeny of infants of crawling and of the mastery of balance and limb coordination necessary for bipedal locomotion may be part of a biologically endowed developmental program. Crawling may be a precursor of bipedal locomotion in humans, and both may constitute necessary BEPs for snowboarding. Crucially, however, in themselves these BEPs do not have anything to do with snowboarding. Thus, referring to crawling or bipedal locomotion as ‘precursors’ of snowboarding, or as proto-snowboarding, early-snowboarding, or approximate snowboarding would be obviously misguided on teleological grounds. Nevertheless, as the analogy makes clear, the same applies to number and arithmetic (Box 2). As biologists warn [56], teleology is particularly problematic in accounts of evolution because natural selection does not operate by aiming at specific pre-given goals.

Granted, vaguely teleological expressions do appear periodically in titles of books and articles, often driven by authors seeking a flashy effect even when not endorsing – word by word – the full extent of what a title might state (e.g., *The God Gene* [57]). I myself have done so. In *Where Mathematics Comes From*, when analyzing the remarkable abilities for quantity that human infants and many nonhuman animals exhibit, George Lakoff and I titled our first chapter ‘The brain’s innate arithmetic’ [58]. Although we did not defend a nativist position therein, I now realize that the wording of the title imparts misleading conceptions of natural selection. When such titles are read with a dose of teleology, the result is a fallacious understanding of the role innateness and biological evolution play in shaping mental capacities and concepts.

Box 2. An Evolved Capacity for Snowboarding? An Analogy

The teleological rationale underlying the claim that there is an evolved capacity specific for number and arithmetic might be better appreciated via an analogy: snowboarding. With respect to the learning of specialized competences, the underlying biological support, and the development of human activities, snowboarding shares several properties with exact symbolic quantification and arithmetic (Table I). In particular, both cases require biologically evolved preconditions (BEPs) – namely, motor-balance regulation and optic flow navigation in the case of snowboarding; subitizing and large quantity discrimination (LQD) in the case of number and arithmetic.

Importantly, although these BEPs for snowboarding emerged via natural selection, they (1) are not ‘precursors’ of snowboarding, (2) are not about snowboarding, and (3) cannot scale up to explain its emergence. In addition to specific BEPs, and to ecological niches foreign to most of human evolution (e.g., mountain slopes with snow), snowboarding requires cultural gestation and mediation: snowboarders do not learn to snowboard as isolated organisms. They must be members of a culture that has already solved problems of thermal insulation for avoiding lethal hypothermia, that has invented sophisticated materials for optimal board-sliding, and that has invented ski-lifts that make the optimization of energy consumption and positive learning curves possible. That technology, reflecting specific cultural traits (pre-occupations and practices), enables fast and efficient improvement of snowboarding techniques which develop in the ontogeny of the learners, ultimately leading to a very peculiar competence: fast downhill locomotion with highly restricted lower-limb movement taking place in freezing conditions.

Similarly, humans may indeed have quantal BEPs shared with other animals, for example subitizing and Weberian LQD, which support the learning of numerical and arithmetical abilities. These basic quantal capacities are (1) not precursors of exact symbolic quantification and arithmetic, (2) are not about them, and (3) do not scale up to explain their emergence. For the establishment of number and arithmetic, as in snowboarding, considerable cultural factors need to be present – such as language, symbolic reference, material artifacts (eventually, writing technology), education, and, importantly, specific preoccupations (e.g., bookkeeping of commodities), all of which occur outside natural selection. Snowboarding might be entrenched in the lives of the residents of a small Alpine village – as are numbers and arithmetic for citizens of the industrialized world – but for them to claim that there is an evolved capacity specific for snowboarding by virtue of its ubiquity and usefulness in their world would lead them, perhaps unwittingly, to a fallacious teleological argument.

Table I. A Number–Snowboarding Analogy

Properties	Capacities, abilities	
	Snowboarding	Exact symbolic quantification and arithmetic
It is only observed in humans (it has never been observed in non-human animals in the wild)	✓	✓
It is not practiced by all humans, but only by those who have been immersed in a specific set of practices and training	✓	✓
It involves the mediation of human-invented materials and technology	✓ (snow gear, ski lifts)	✓ (numeral systems, material artifacts, writing technology for arithmetic)
It manifests behaviorally in individuals, but its practice requires considerable cultural scaffolding	✓ (parental involvement, snowboarding lessons)	✓ (parental involvement, schools)
It necessitates years of dedicated practice for the necessary skills to be developed over ontogenetic time	✓	✓
It makes active use of biologically evolved preconditions (BEPs).	✓ (optic flow navigation, balance-keeping mechanisms)	✓ (subitizing and large quantity discrimination, LQD)
The underlying BEPs are not precursors of the corresponding capacity or activity, and by themselves cannot scale up to generate it. Instead, they are preconditions that need considerable cultural scaffolding for the capacity to emerge, and these occur outside natural selection	✓ (optic flow navigation and balance-keeping mechanisms are not precursors of snowboarding, and by themselves cannot scale up to generate it)	✓ (subitizing and LQD are not precursors of number and arithmetic, and by themselves cannot scale up to generate them)

Downplaying Human Data from Non-Industrialized Cultures

Another problem is that the investigation of how humans perceive, discriminate, and treat quantity has been conducted mostly with populations from the industrialized world. This provides a biased view of humanity [59]. Observations focused exclusively on industrialized populations are often over-generalized, as seen in statements such as: ‘Humans know that the number 109 is as different from 111 as the number 2 is different from the number 4 Nonhuman animals, however, could not discriminate between those two large quantities as easily as the two small ones’ ([60] p. 185). Such statements only hold if what is meant by ‘humans’ is individuals who grow up in cultures that have writing traditions, organized educational systems, measuring and notational conventions, and so on, or that, at the very least, have a language that can exactly symbolize those numbers and their relations. In the context of biological evolution, holding this assumption is unwarranted. The fact is that healthy humans from many relatively isolated cultures without scholastic traditions speak languages that have very limited **numeral** systems [61–63] (i.e., they have a number lexicon and expressions that can only designate quantities within or around the subitizing range) and do not entertain exact and categorically distinct number concepts such as our familiar ‘seven’ or ‘nine’. Contrary to reports that these cases are uncommon [64], a recent survey of 189 Aboriginal Australian languages representing 13 families reported that 139 (74%) have an upper numeral limit of only ‘three’ or ‘four’, and an additional 21 languages (11%) have a limit of ‘five’ [63]. Another survey, analyzing 193 hunter-gatherer languages from different continents, found that most of these languages have an upper limit of ‘five’ or below (61% in South America, 92% in Australia, and 41% in Africa) [65] (some languages, such as the Amazonian Pirahã [66,67] and some Yanomami languages [65], as well as some Australian languages [65], have been reported to have a limit of only ‘two’). Importantly, beyond this low limiting numeral range, all these languages designate quantities with natural **quantifiers** – such as the English ‘several’ and ‘many’ (Box 3). In the case of the Mundurukú of the Amazon, these numeral properties have also been studied experimentally (Figure 1) [62].

Box 3. Languages, Quantifiers, Numbers, and Enculturation

Many groups around the world speak languages with a very limited numeral system, most having relatively specific terms or expressions only for numerosities within the subitizing range (one to four), and using quantifiers such as ‘some’ and ‘many’ above that [61,62,63,65]. Natural quantifiers exist in all languages, usually operating beyond the subitizing range and labeling quantities in an inexact manner. Although imprecise in their handling of quantity, quantifiers have very specific meanings and provide an extremely useful network of inferences. For example, if a boy is said to have a ‘few’ oranges and a girl ‘many’ oranges, a safe inference – without the need of exact calculations – is that the girl has more oranges than the boy. Moreover, the precision of quantifiers can be enhanced via the use of grammatical intensifiers (‘really a lot’), term repetition (‘many, many, more’), prosodic intensifiers (‘maaaaaany more’), or combinations of these. Indeed, speakers of languages with limited numeral systems have shown some good quantity-related performances. When Amazonian Mundurukú children and adults were asked to estimate relative quantities, their performance was similar to that of other cultures with elaborate number lexicon [62]. Although the standard interpretation is that this is so because they possess an approximate number system (ANS), an alternative explanation is that their good performance is due to their efficiency in operating with quantifiers which, being part of their natural language, do not require any specifically dedicated training. Similarly, the good small quantity-related performance observed in children speakers of Aboriginal Australian Warlpiri and Anindilyakwa [125] could be explained (other than by the use of spatial heuristics and perhaps distinctions based on borrowed English numerals) by an efficient use of natural quantifiers.

What appears to be universal in human languages is not that they have exact terms for a large range of numbers, but instead that they have (1) specific terms for at least numbers roughly within the subitizing range, and (2) terms that reflect the imprecise discrimination of large quantities (i.e., quantifiers such as ‘some’ vs ‘many’) [105]. Importantly, the learning of how to use the lexicon of exact subitizing-range numbers and of quantifiers in natural language does not require explicit training or schooling, hence their universal presence.

What does require extensive training and cultural scaffolding is the learning of exact numbers and arithmetic, as occurs in the industrialized world. Importantly, this enculturation process affects even the most fundamental aspects of neural processing of number. A fMRI study compared the brain activation of educated native speakers of Chinese and English while they performed simple addition and made relative magnitude judgments. Although both groups were presented with the same symbols – Hindu-Arabic numerals – different brain activation and functional connectivity between brain

regions were found [111] (Figure I). These findings support the idea that the neural circuits and brain regions that are recruited to sustain exact symbolic number processing are crucially mediated by cultural factors.

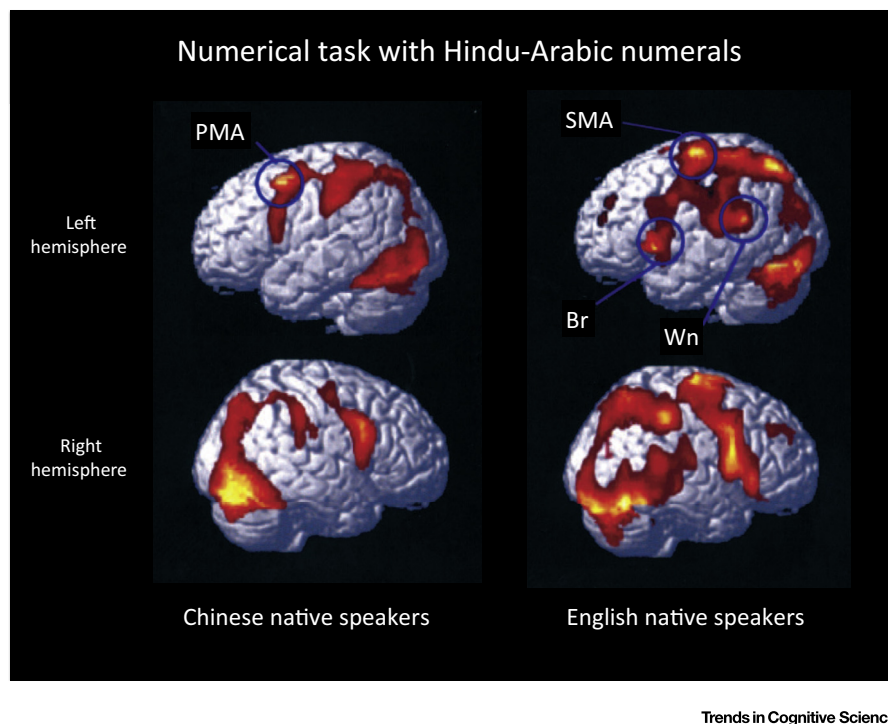
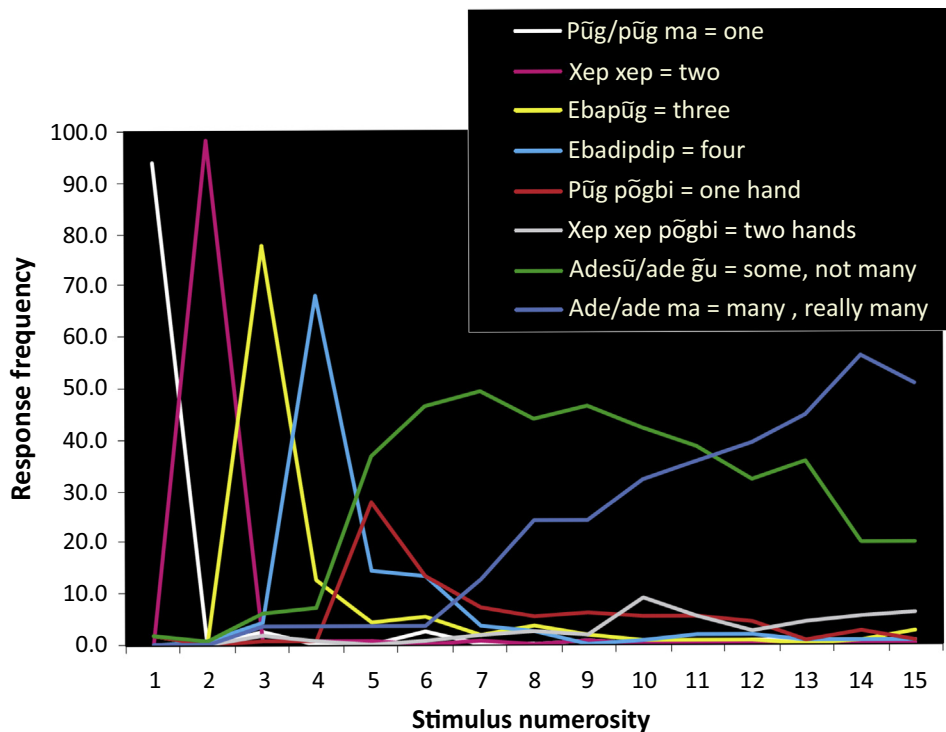


Figure I. Quantity, Language, and the Enculturated Brain. Results from a fMRI study that compared the brain activation of educated native Chinese and English speakers while performing simple mental arithmetic and making relative magnitude judgments. Although the symbolic stimuli – Hindu-Arabic numerals – were the same for both groups, different activation and functional connectivity between brain regions were found. Native Chinese speakers showed more activation in premotor regions (PMA, top left), whereas native English speakers showed more activation in the left supplementary motor (SMA) and perisylvian regions, including Broca's (Br) and Wernicke's (Wn) areas (top right), which are usually associated with language production and comprehension. These findings support the claim that the neural circuits and brain regions that are recruited to sustain even the most fundamental aspects of exact symbolic number processing are crucially mediated by cultural factors, such as writing systems, educational organization, and enculturation. Adapted, with permission, from [111]. Tang, Y. *et al.* (2006) Arithmetic processing in the brain shaped by cultures. *Proc. Natl. Acad. Sci. U. S. A.* 103,10775–10780. Copyright (2006) National Academy of Sciences, U.S.A.

Healthy humans from cultures who speak these languages do not traditionally have writing practices and do not carry out exact calculations. They live lives with imprecise quantities, and essentially without exact numbers and arithmetic, presumably as humans without explicit training have done successfully for tens of thousands of years. The study of small-scale hunter-gatherer or subsistence-farming groups reveals that the development of numerical notions (when they exist) is, contrary to claims focused exclusively on individual psychology (e. g., [16]), inherently cultural [68,69] – a cultural trait. An industrial-centric view of humanity downplays, or even neglects, the crucial implications of this fact: humans do not innately (i.e., without cultural mediation) manifest a specific capacity for generalized exact quantification, namely number.

Overinterpretation of Animal Data

Another problem with the nativist view is the overinterpretation of animal data. Although research with trained animals has produced some impressive results, they do not straightforwardly support evolutionary arguments.



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Figure 1. Limited Numeral System in an Amazonian Culture. The Mundurukú language from the Amazon is one of many languages with a very limited numeral system [61,62]. In a quantity-naming task, Mundurukú speakers were shown random collections of one to fifteen dots and were asked to name the quantity. Only stimuli with numerosities between one and four had preferred words or phrases that were picked more than 60% of the time when the corresponding numerosities were presented (only 'one' and 'two' were picked more than 90% of the time). Beyond that range the quantifier equivalent to the English 'some' began to be picked, and beyond 'twelve' a quantifier equivalent to 'many' was preferred. Importantly, with the exception of 'two', no other numerosity was designated close to 100% of the cases with an unambiguous categorically distinct numeral. From [62]. Pica, P. *et al.* (2004) Exact and approximate arithmetic in an Amazonian indigene group. *Science* 306, 499–503. Reprinted with permission from AAAS.

First, most quantity-related feats by nonhuman animals in the laboratory result from training that is 'often arduous and requires considerable environmental support' ([44] p. 602). By this the authors mean environments that have been intentionally and carefully designed and controlled by humans. These human-concocted and -selected environments have not existed in the ecological niches and evolutionary paths of these animals; they have occurred outside biological evolution and natural selection.

Second, the learning process usually follows extensive and dedicated painstaking training, which sometimes takes years to complete. Training a monkey on a simple quantity match-to-sample task, for instance, can take over 4 months and 20 000 trials, only to achieve discrimination of collections at a 3:4 ratio with a 75% accuracy [70]. Such long and extremely frequent exposure to narrowly targeted stimulation simply did not occur in the ecosystems of these animals' lineages.

Third, unsuccessful training of nonhuman animals in 'numerical competence' is understated and rarely reported. Demonstrations of numerical competence do not come easily. As animal psychologist H. Davis put it: 'They are no mean feat, and for each of the successes you have heard about, there are untold failures. Although the nondissemination of negative evidence is

the way science normally progresses, it is particularly unfortunate in the case of numerical competence in animals because it clouds the question of how general or easily established this ability truly is' ([71] p. 110).

Fourth, even when nonhuman animals get to the point of doing (more or less) what experimenters want them to do, the outcome with respect to 'number' is usually guided by associative learning and is rarely exact. Often the researcher criteria for 'success' are relatively weak; sometimes even 'above-chance' performance is considered a success. When trying to establish competence with the exactness of number and arithmetic, this lacks validity. A basic competence involving, say, the number 'eight', should require that the quantity is treated as being categorically different from 'seven', and not merely treated as often – or highly likely to be – different from it. This essential exactness is criterial of number but is rarely obtained with nonhuman animal responses, even after intensive training.

For these reasons animal results cannot support the claim that there is an evolved capacity specific for 'number' and 'arithmetic'. The behaviors and abilities resulting from human training should not be used as evidence to support evolutionary arguments. Training a dog to snowboard (Box 2), or to skateboard to see if it transfers the capacity to snowboarding, may provide valuable data for particular purposes, but not for supporting the conclusion that canines have an evolved capacity for snowboarding.

Loose Terminology in the Service of Teleology

Contemporary 'numerical cognition' routinely uses technical terms such as number, numeral, numerousness, and numerosity in a loose manner, and this facilitates teleological argumentation (Box 1). Researchers in the evolution of language are promptly corrected when loosely referring to the 'grammar' of gorillas or the 'language' of bees [72]. The use of 'number' and 'numerical' should demand nothing less. Questions of terminology are not 'just about words': they often convey profound theoretical implications. One must therefore ask: are the biologically endowed quantity-related capacities inherently about number at all? – and can we label them as numerical, let alone arithmetical?

The first difficulty for addressing these questions is that the term 'number' is highly polysemous, not only in everyday language ('a number of things'; 'passport number') but also in technical language ('ordinal number'; 'infinitesimal number'). Second, the field of numerical cognition has been notorious for not employing precise terminology when dealing with the concept of number. Already three decades ago scholars investigating 'numerical competence' in nonhuman animals and children spoke of the 'terminological chaos' ([44] p. 562), the lack of 'clarification of terms' ([73] p. 601), and the unnecessary suffering 'from the misapplication of terms' ([74] p. 580) that existed in the field. The situation is no better today because relatively precise definitions of various number-related terms – some of which were carefully coined by the psychophysicists of the mid-20th century [75,76] – are routinely blurred (Box 1). Sometimes 'number' is used to mean 'numeral' (e.g., [77]), or sometimes 'numerousness' (e.g., [78]), despite warnings that 'numerousness discrimination . . . represents a simple perceptual ability that bears no obvious relation to number' ([79] p. 1222). More importantly, 'number' is often loosely used in place of 'numerosity'. Articles in developmental (e.g., [80] p. B15) and comparative (e.g., [45] p. 86) psychology while properly discussing 'numerosity' when describing stimuli, leap to 'number' in conclusions. Similar loose inter-changeability can be found in neuroscience publications (e.g., [81] p. 177). Occasionally one finds reminders pointing to this loose and misleading use of terminology (e.g., [54] p. 35; [60] p. 176). However, such recommendations are rare, and in practice they are not adopted, which reifies teleological claims about evolved capacities for number and arithmetic.

Towards an Alternative Proposal

How are we to understand the well-established human and nonhuman animal data? To begin, leaving everyday language and teleology behind, we must not assume that 'number' is a 'natural domain of competence' ([18] p. 695) or 'a natural perceptual category' ([47] p. 370). And, importantly, we must be precise about the use of the term 'number' and of the associated adjective 'numerical.'

Minimal Criteria for Number

Beyond the natural polysemy of the term, a reasonable step is to begin with the most prototypical and fundamental properties ascribed to 'number' when evoking the familiar counting sequence 'one, two, three, . . . ' – the meat of 'numerical cognition'. Accordingly, number:

- (i) quantifies in an exact and discrete manner
- (ii) is abstract in the sense that it transcends the quantification of specific commodities or specific types of stimuli
- (iii) has a cardinal sense (produced by counting)
- (iv) has an ordinal sense (required for enumerating and counting)
- (v) is relational
- (vi) is combinative, operable
- (vii) is referred to symbolically.

This minimal – non-exhaustive – collection of properties does not cover all instances of 'number', but it covers the most prototypical and fundamental cases (Table I in Box 1 for details). For example, the number 'seven' (i) quantifies in an exact manner collections with numerosity 7, and (ii) it is abstract in the sense that it transcends what psychologists call 'sensory modalities' [44]. 'Seven' also has a cardinal (iii) and an ordinal sense (iv) which are involved in counting, and (v) it is specified relationally, as, for instance, the successor of 'six'. The cardinal and relational properties, although apparently simple, should not be taken for granted. The learning of the 'cardinality principle' by children is more than merely learning 'words' and it is far from trivial [82], and the generalization of the successor function is achieved only years after learning to count [83]. Finally, (vii) 'seven' is referred to symbolically via specific signs (numerals) such as the word 'seven', the digit '7', or the Roman 'VII', which support precise combinativity, operability (vi), and the generation of other numbers.

Crucially, property (vii) – being referred to symbolically – is by nature a conventional cultural feature, a signature of *Homo sapiens* [84]. Developing sociohistorically, symbolic reference puts 'number' in a qualitatively separate realm from the quantity-related phenomena observed in nonhuman animals (and in humans from many non-industrialized cultures). As biological anthropologist T. Deacon puts it: 'symbolic reference must be acquired by learning, and lacks both the natural associations and trans-generational reproductive consequences that would make such references biologically evolvable' [85]. Symbolic reference is not only observed in the familiar '0–9' Hindu-Arabic numerals (digits) or in the number words we use today – it was already present among trained individuals in societies that developed writing practices and basic accounting techniques in Mesopotamia [86,87]. In addition, in the absence of writing technology, it manifests, for instance, in the use of body parts as numerals common in native groups in Papua New Guinea [88,89], in the use of knot-based artifacts such as the *kipu* of the Incas in the Andes [90], in the development of sophisticated linguistic constructions to support complex arithmetic, such as the binary calculating system in the Polynesian Mangarevan [91,92], and possibly even in those meticulously human-trained chimpanzees Ai [52] and Sheba [53], and grey parrot Alex [51]. Written or not, symbolic reference places 'number' outside the reach of biological evolution via natural selection. If the quantity-related phenomena observed in non-human animals and infants do not exhibit these prototypical properties of

'number', labeling them as 'numerical' is not only inappropriate and misleading but also paves the way for teleological arguments.

Quantal and Numerical Phenomena: A Crucial Distinction

The above characterization of number entails that the quantity-related capacities observed in infants and nonhuman animals are not about numbers, but are about quantity, and therefore should not qualify as numerical. The adjective 'numerical' in 'numerical cognition', however, is crucially over-inclusive: any cognition or behavior relating to quantity in babies, monkeys, rats, or fish – whether exact or inexact, symbolic or non-symbolic, operational or not – is labeled as being 'numerical'. This loose over-inclusiveness licenses stating – teleologically – that thousands of species, from fish to humans, by virtue of being able to discriminate quantities, *de facto* have 'number representations' as a result of biological evolution.

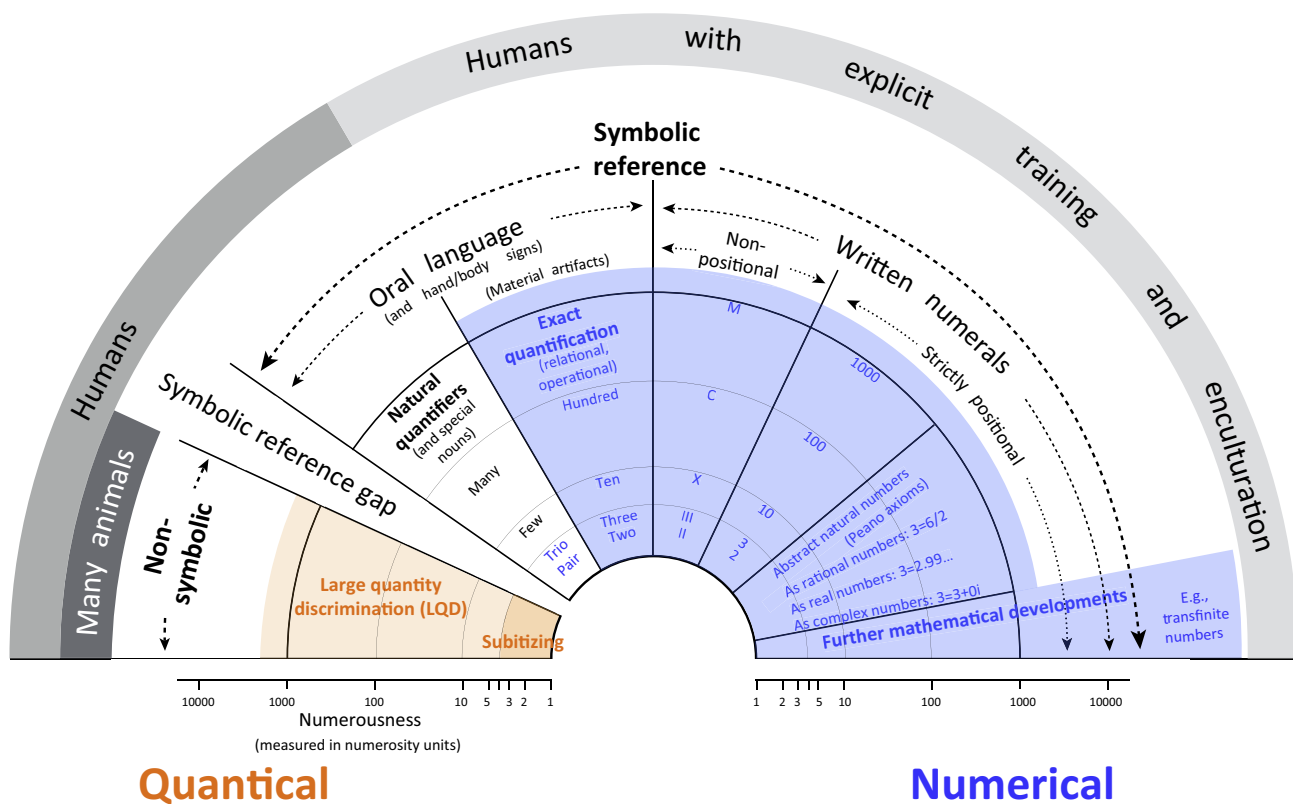
To avoid confusion and fallacious reasoning the adjective 'numerical' should be reserved for those phenomena that exhibit the prototypical properties listed above. It should not be used to label cognition, abilities, or behaviors that refer to phenomena such as subitizing and LQD. What then should we call these biologically endowed phenomena? The English language (like others) does not have an adjective to label phenomena that are quantity-related but lack the properties listed above. One possibility would be to call them **quantitative** capacities [60], but this term – usually contrasted with 'qualitative' – relates to measurements and their numerical and mathematical treatment. I propose to refer to these biologically endowed capacities as **quantal** – in contrast to 'numerical' (Figure 2, Key Figure).

The quantal–numerical distinction reveals how misleading certain theoretical constructs in the field of 'numerical cognition' are. For example, the so-called **approximate number system** (ANS) – which, following the Weber–Fechner law, is claimed to be an 'evolutionarily ancient innate system for approximate number' [25,93] – is believed (not without criticisms [94–97]) to neurally handle quantities above the subitizing range. Observed similarities of ratio effects obtained with non-symbolic and symbolic stimuli are often taken as evidence for the ANS account [54,93]. However, these similarities can be explained by different underlying mechanisms for quantal (non-symbolic) and numerical (symbolic) processing [98,99], and this supports the idea that quantal and numerical cognition are not only fundamentally distinct but they also relate to each other in non-obvious ways. Thus, the claim that 'when we learn number symbols, we simply learn to attach their arbitrary shapes to the relevant non-symbolic quantity representations' ([100] p. 552) is questionable. Furthermore, the term ANS implicitly takes 'numbers' as pre-existing primitives to which noisy mental representations are 'approximate' to. The term 'ANS' is thus a teleologically driven oxymoron, which puts 'number' – with its richness and complexities – directly in the category of what is biologically endowed. To capture the discontinuity brought by exact symbolic quantification, the quantal–numerical distinction is crucial. The adjective 'quantal' does not take pre-existing numbers as primitives with representations being approximate to them. Instead, it labels LQD, for instance – upon which quantifications such as 'few' and 'many' build – without being 'approximate' to anything.

In sum, quantal cognition is biologically endowed, but numerical cognition is not. Quantal cognition may be the manifestation of BEPs for numerical cognition and arithmetic, but is itself not about number or arithmetic. Indeed, quantal processing seems to be about many sensorial phenomena and dimensions other than number *per se* [95,96,101,102]. Crucially, quantal cognition does not, by itself, scale up to produce number and arithmetic. Quantal capacities are not 'precursors' of numerical capacities, but rather biologically evolved pre-conditions (BEPs) for them (Box 2).

Key Figure

The Handling of Discrete Quantity



Trends in Cognitive Sciences

Figure 2. The study of quantity discrimination and conceptualization requires important distinctions, some of which are schematized here. Increasing levels of numerosity are represented radially on a logarithmic scale measured in numerosity units. Subitizing and large quantity discrimination (LQD) are biologically endowed quantal capacities (orange sector) which manifest spontaneously in humans and many nonhuman animals. These capacities are non-symbolic and imprecise beyond the subitizing range (numerosities 1~4). Clockwise from there, human language allows for quantification via symbolic reference: natural quantifiers (e.g., 'many'; white sector). However, as observed in many non-industrialized cultures [61–63,65–67], language in itself does not lead to number – exact symbolic quantification that is relational and operable with precision – or to numerical capacities proper (blue sectors). For this to occur, specific cultural traits (practices and preoccupations, e.g., bookkeeping of commodities) – supported by language, symbolic reference, material artifacts, and eventually writing technology – are required. Blue sectors ordered clockwise represent increasingly more elaborate numerical entities leading to arithmetic and more sophisticated mathematics, which necessitate progressively longer and more-complex explicit training and enculturation. Importantly, quantal phenomena, being the product of natural selection alone, cannot scale up to numerical phenomena (i.e., exact, relational, operational) across the symbolic reference gap (left). Symbolic reference must be acquired by learning and is not biologically evolvable [85]. Quantal capacities are biologically evolved preconditions (BEPs) for number, but they are not themselves numerical. The realization of numerical capacities demand extra crucial ingredients – symbolic reference, language, and cultural practices and preoccupations – which unfold via cultural evolution, and largely outside natural selection.

Not Only Language and Symbols, But Also Evolving Cultural Preoccupations

Language and symbols are often taken to be sufficient conditions for an account of the observed discontinuity between human and non-human animal quantity-related capacities [96,103,104]. However, the often neglected study of small-scale non-industrialized human cultures reveals that language and symbolization may be necessary conditions for the formation of number, but alone do not produce numbers and arithmetic. All human cultures and societies have developed and employ spoken (or signed) language, but not all have developed a system of exact numbers beyond the subitizing range (Box 3). Instead, they have developed

quantifiers which appear to symbolize seemingly universal quantity-related experiences brought by biologically endowed quantal cognition. Crucially, although very functional in dealing with quantities in everyday life, quantifiers in natural language – like quantal competences in animals – cannot scale up to build an exact number system and arithmetic [105]. To yield exact results for specific operations, the concept of number is needed. This seems to require the crucial contribution of particular cultural traits (preoccupations and practices [86,87,106]) which, in the case of numbers, have been well documented for groups in Papua New Guinea [68,88] and Polynesia [91,92], for instance. Sustained by language [91,92], symbolic reference [88,92,107] (e.g., body count systems [68,88,89]), and imagination and metaphor [58,108,109], these preoccupations and practices are not brought forth via biological evolution proper but via cultural evolution and the **enculturation** of the human brain [110] (Box 3).

Concluding Remarks and Future Perspectives

Humans and many nonhuman species do have biologically endowed abilities for perceiving and discriminating quantities, at least in an imprecise manner and in particular formats (e.g., food items). Although robust, these observations do not support claims that there is an evolved capacity specific for number and arithmetic.

Such claims are based on an implicit teleological rationale supported by loose and misleading terminology. They build on an inaccurate conception of biological evolution that takes ‘number’ and ‘arithmetic’ as targets in natural selection, on the grounds of their utility and entrenchment in the modern industrialized world. Through this lens, influential views in developmental psychology, animal cognition, and cognitive neuroscience have downplayed human data from non-industrialized cultures and overinterpreted results with trained animals in captivity, resulting in an overstated role for biological evolution in the origins of numbers.

‘Number’ is a complex and polysemous concept which must be specified in detail, especially when evaluating claims about evolution. Accordingly, the behaviors, capacities, and cognition that are to be labeled as ‘numerical’ must be treated with care. To understand the existing data in light of evolution, we must disentangle biologically endowed quantal capacities – which are imprecise and non-symbolic – from strictly speaking numerical capacities that exhibit exact symbolic quantification. The distinction makes clear that quantal capacities do not scale up to numerical capacities via natural selection alone.

In humans, exact, systematic, and symbolic quantification beyond the subitizing range has materialized via cultural preoccupations and practices involving language and symbolic reference, crucial dimensions that lie outside natural selection. Questions about how this took place abound (see Outstanding Questions). What does it take to move from quantal cognition to numerical cognition, and how do these two forms relate to each other? One promising direction is to study the neural underpinnings of the enculturation underlying exact numerical symbols and arithmetic [110,111]. A complementary research path is to investigate whether natural quantifiers, moving from symbolic imprecise quantification to exact symbolic quantification [105], might play a role in consolidating the ‘number sense’.

Although ubiquitous today in the industrialized world, numerical cognition should not be taken at face value. The answer to the question of what it takes to move from quantal to numerical cognition is not trivial. Indeed, only some humans – in the right sociohistoric contexts, and after tens of thousands of years – have made that leap.

Acknowledgments

I am grateful to Josephine Relaford-Doyle, Kensy Cooperrider, Daniel Ansari, Federico Rossano, Tyler Marghetis, Marta Kutas, Jeff Elman, Pascal Gagneux, Rebecca Schwarzlose, and three anonymous reviewers for valuable comments on earlier drafts.

Outstanding Questions

What exactly does it take to move from quantal cognition to numerical cognition, and how do the two forms relate to each other?

What selective pressures may have given rise to quantal cognition?

Quantal processing seems to be about many sensorial dimensions other than number proper. What aspects of quantity processing then makes it numerical?

Exactly what aspects of quantal/numerical cognition can be attributed to biological evolution, what aspects to cultural evolution?

With respect to exact symbolic quantification, how do biological phenomena constrain cultural evolution and enculturation?

What are the necessary conditions for a culture to develop exact quantification and number systems? Why have not all human cultures developed them?

What is the role of natural quantifiers in the consolidation of the number sense in children?

Building on quantal cognition, how does exact symbolic quantification get grounded and neurally instantiated?

What are the neurological underpinnings of the learning of quantifiers in natural language?

What can we learn from cultures that have achieved sophisticated number and arithmetic concepts without writing technology, but instead with complex material artifacts (e.g., the *kipu* from the Andes – a device based on strings and knots) or sophisticated linguistic constructions (e.g., the Mangarevan binary calculating system)?

How can archaeological evidence improve our understanding of the origins of numbers?

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