

Review

The Evolutionary History of Brains for Numbers

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Humans and other animals share a number sense', an intuitive understanding of countable quantities. Having evolved independent from one another for hundreds of millions of years, the brains of these diverse species, including monkeys, crows, zebrafishes, bees, and squids, differ radically. However, in all vertebrates investigated, the pallium of the telencephalon has been implicated in number processing. This suggests that properties of the telencephalon make it ideally suited to host number representations that evolved by convergent evolution as a result of common selection pressures. In addition, promising candidate regions in the brains of invertebrates, such as insects, spiders, and cephalopods, can be identified, opening the possibility of even deeper commonalities for number sense.

A Sense of Number Emerging from Phylogenetically Diverse Brains

Humans and nonhuman animals across the animal kingdom share an intuitive understanding of countable quantities, or **numerical quantity** (see [Glossary](#)) (henceforth 'number') [1]. Distinct zoological groups arising from a common ancestral **bilaterian** ([Box 1](#)) – from vertebrates like fishes, birds, and mammals to invertebrates such as insects, spiders, and cephalopods – all possess the ability to discriminate numerical quantity. Numerical quantity refers to the number of elements in a set ('numerosity') and needs to be differentiated from a representation of **continuous quantity** ([Box 2](#)). This '**sense of number**' provides survival and reproductive advantages in various animal **taxa** that can be traced through evolutionary history [2].

However, these diverse species have evolved in parallel and independent from one another for hundreds of millions of years. As a consequence, the brains of these distantly related species differ radically in their complexity, mechanisms, and organization. So, how is it that all of these diverse brains can give rise to a similar sense of number?

One explanation would be that a sense of number was present already in the last common ancestors of vertebrates, or even bilaterians. If this is true, it can be expected that all descendants share the conserved brain structures from which numerical competence emerged. According to this scenario, numerical competence would be a homologous trait that reaches back hundreds of millions of years to the last common ancestor of the basal animal taxa.

Alternatively, a sense of number could have evolved independently in several lineages and without a numerically competent common ancestor via **convergent evolution**. The brains supporting numerical competence may have been shaped by similar **selection pressures** that diverse animal populations faced in the struggle for survival. For instance, choosing the larger of two dissimilar numbers of food items assures greater energy intake and possessing a numerical advantage in social interactions could determine the outcome of potentially lethal fights across and within species [3]. If diverse animals benefit from numerical competence, independent brain changes endowing them with a sense of number would arise and be maintained in these populations.

Highlights

Diverse species from across the animal tree of life share an intuitive understanding of countable quantities.

In vertebrates such as fishes, birds, and mammals, the telencephalic pallium emerges independently as a key brain area for numerical representations. This suggests that the pallium is an ideal candidate brain region for number representations in convergently evolved brains.

The neural basis of the number sense has not been studied in invertebrate species so far, but promising candidate regions in the brains of insects, spiders, and cephalopods can be identified.

Number representations seem to have evolved by convergent evolution as a result of common selection pressures in different vertebrate taxa.

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Box 1. Phylogeny of Bilateral Animals: Protostomes and Deuterostomes

All advanced animals we see on the planet today are 'bilaterians'; they have a bilaterally symmetrical body with a front and a rear end. Around 600 million years ago, the large bilaterian trunk of the animal tree of life split into two major branches.

One branch constitutes the protostomes – animals that maintain the primordial mouth that forms early in ontogeny into the adult stage. Protostomes evolved a central nervous system (nerve cord) on the ventral side of the body.

The other branch constitutes the deuterostomes – animals that do not maintain the primordial mouth formed early in ontogeny but instead develop a new mouth opening to the gut system. The vertebrates (as members of the phylum Chordata) belong to the deuterostomes. They have evolved a central nervous system (neural tube) on the dorsal side of the body.

Some bilaterian taxa, such as the protostome arthropods and the deuterostome vertebrates, have evolved brains as neuron concentrations at the anterior pole of the body, but not all have. This finding and different gene expression patterns in diverse taxa suggest that the last common ancestor of bilateral animals, the hypothetical 'urbilaterian', most likely did not possess a brain [136]. From this it is generally inferred that the brains of major bilateral taxa must have evolved independent from one another (unless one maintains the unlikely scenario that brains that had already existed in common ancestors vanished several times over in evolution). However, despite this parallel evolution of brains, the genes that become expressed to build brains across phylogeny, as well as the neuronal circuitries seen in remotely related animal taxa, are surprisingly similar. This points to evolution facing harsh constraints when reinventing brains over the course of evolution. Evolution thus seems to resort to strikingly similar principles when building brains based on convergent evolution, including brains for number processing.

Independent evolutionary innovations often capitalize on pre-existing favorable properties that originally served other functions before further modification [4]. This also applies to the brain, in which specific areas appear more malleable in the development and support of elaborate

Box 2. Demonstrating Numerical Representations in Animals

Animal studies on numerical cognition differ widely with respect to the testing procedures, the stimuli, and the complexity of numerical representations. These differences need to be considered when evaluating claims of numerical competence [137].

In the wild and in untrained animals, mainly free-choice experiments are performed. Here, subjects spontaneously choose between two alternatives (e.g., sets of food items) according to preference. A systematic preference of one choice over the other indicates that sets can be discriminated. Because choice items need to be inherently relevant to the focal animals, numerical quantity is usually confounded by continuous quantity. Moreover, the motivational status of wild animals (whether they want to choose between quantities) is typically unknown in free-choice approaches. These studies can also only probe simple abilities, such as relative numerosity judgments that only require 'more than' versus 'less than' decisions. Therefore, spontaneous choice tests provide only suggestive evidence for numerical competence.

These problems are bypassed when training animals in a controlled environment. Here, performance can be tested in motivated animals and with meticulously designed stimuli that control for non-numerical factors. Training studies can also test more advanced numerical capabilities, such as flexible discrimination of precise numerosities and numerical processing based on rules. Last but not least, they can be combined with brain research.

A notorious problem in numerical cognition is the control for non-numerical, continuous quantity. Without specific adjustments, non-numerical quantity (e.g., the total area of items in an array, the presentation duration of items shown sequentially) co-varies with changes in number, and animals could learn to respond to such factors. For instance, four bananas occupy twice as much visual area as two and an animal may discriminate the total amount of yellow area rather than the number of bananas. Control over non-numerical factors can be achieved only by equating such factors in computer-controlled stimuli and/or using test protocols in which several co-varying magnitudes are shown in the same session and unbeknown to the focal animal [55,61]. Representation based on the number of items can be ensured if the animal continues to discriminate stimuli irrespective of the controlled appearance of the stimuli.

To demonstrate an abstract sense of number, animals are required to represent number across time (i.e., items presented sequentially one-by-one) and space (items presented in arrays) and across sensory modalities (e.g., visual and auditory items). Because of methodological constraints, this list of requirements cannot be fulfilled in a single experiment. However, several studies with different combinations of controlled stimuli clearly show that at least some animal species, most notably monkeys [66,138] and crows [42], discriminated specific numbers in a flexible way and irrespective of spatiotemporal changes and sensory modalities. This flexibility has not yet been demonstrated in fishes or bees, which usually are trained to discriminate one specific numerosity from others or different numerosities based on a fixed rule.

Glossary

Approximate number system: cognitive/mental system that supports the estimation of numerical quantity without relying on language or symbols.

Bilaterians: advanced animals (e.g., arthropods, mollusks, vertebrates) that exhibit bilateral symmetry at least at some point in their development and share a bilaterian last common ancestor.

Cerebral cortex ('neocortex'): neural aggregate in the dorsal telencephalon that comprises six layers of different neuronal populations and their associated fibers; found only in mammals (and in a reduced form in reptiles).

Continuous quantity: uncountable and continuous quantity.

Convergent evolution: the process through which phenotypically similar traits evolve independently (i.e., not from a common ancestor) in two species.

Delayed match-to-sample task: behavioral protocol in which a sample stimulus needs to be matched to a temporally delayed choice stimulus; classic task to test discrimination and working memory performance.

Deuterostomes: bilateral animals, such as vertebrates, whose mouth develops from a new and secondary embryonic opening; sister group of the protostomes.

Endothermy: 'warm-blooded' animals that metabolically produce heat and maintain a high, stable body temperature.

Expectancy-violation protocol: tests spontaneous stimulus discrimination. Differences in behavior when the outcome of a stimulus transformation matches or violates a subject's supposed expectation are taken as evidence of discriminability.

Habituation-dishabituation protocol: test of the spontaneous ability of a subject to discriminate two stimuli. After habituation to a repeatedly presented stimulus, a dishabituation response to a novel stimulus signifies discrimination by the subject between the two stimuli.

Immediate early genes (IEGs): genes that are activated transiently and rapidly in response to stimuli. The products that result from the activation regulate neuronal function.

Numerical quantity: countable quantity; the number of objects/events; set size, cardinality, or numerosity.

cognitive functioning than others. This review uses a comparative, evolutionary approach to explore the anatomy and physiology of diverse vertebrate brains from which numerical capabilities emerge. I argue that the anatomical and physiological properties of various parts of the telencephalic **pallium** of vertebrates (members of the ‘**deuterostomes**’) were ideally suited to independently give rise to a sense of number that was not yet present in the last common ancestor of vertebrates. Neural data for the even more distantly related invertebrates (more precisely, ‘**protostomes**’) are currently lacking, but promising high-level brain regions in arthropods and cephalopods can be identified for future research into the phylogenetic roots of a sense of number.

Number Sense Emerges from Pallial Endbrain Areas in Vertebrates

Fishes

The most basal but also extremely diverse group of aquatic vertebrates are the jawless cyclostomes (hagfish, lampreys), the cartilaginous fishes (sharks, rays), and the bony fishes (coelacanth, lungfishes, and ray-finned fishes). Ray-finned fishes, most of them belonging to the teleosts, are extremely diverse and exhibit many evolutionary innovations, partly as a result of several whole-genome duplications [5].

Some fishes have been reported to possess basic numerical skills in the visual domain, but these reports all involve teleosts (henceforth ‘fishes’) [6–9]; by contrast, data on cyclostomes and cartilaginous fishes are lacking. For instance, fish ‘go for more’ by picking the larger quantity when presented with two quantities of hedonic stimuli (e.g., food items) in alternative choice tasks. Fish discriminate larger numbers of items in an approximate fashion by showing more precision for small as opposed to large sets, as expected for discriminations based on an **approximate number system**.

Recent studies explored the neural correlates of number representations and these studies have implicated the pallium of the fish **telencephalon** (Box 3). The pallium of fishes is relatively underdeveloped in both size and differentiation [10] (Figure 1, Key Figure). In bony fishes (teleosts), the pallium is generally subdivided into five parts: a medial (Dm), dorsal (Dd), central (Dc), lateral (Dl), and posterior (Dp) subdivision [11,12]. Despite its relative simplicity, these subdivisions of the pallium and their homologies to regions in other vertebrate groups have not been resolved and remain controversial, especially since the telencephala of bony fishes develop through a unique process of outward folding [13].

Neurons that have specific responses to numbers have recently been identified in the zebrafish pallium via histological methods [14]. The fish were behaviorally tested in a passive **habituation–dishabituation protocol** with the stimuli comprising arrays containing different numbers of dots. This paradigm builds on how repeated presentation of the same stimulus causes a reduction in the activity of specific neurons responsive to that stimulus (habituation). After this process, a sudden switch to a new stimulus will engage neurons sensitive to this new stimulus (dishabituation). So, for example, the fish would be repeatedly presented with three-dot arrays (controlled for continuous physical variables) during the habituation phase; after a while, the fish would suddenly be presented with a nine-dot stimulus during the dishabituation phase. The changes in numbers in the dishabituation phase can be associated with changes in neuronal activation that were identified postmortem using the expression of **immediate early genes (IEGs)** as an activity marker. As a key finding, IEG expression increased in the fishes’ pallium (and the thalamus) with changes in numerosity [14]. Selectivity to shape and surface areas was largely absent, demonstrating that the changes in activity were specifically related to changes in number. These numerosity activity changes were specific to the central division (Dc) of the zebrafish pallium (Figure 1) [15]. Since

Pallium: Latin *mantle*; dorsal portion of the telencephalon. The embryonic vertebrate pallium is traditionally subdivided mediolaterally into four regions (medial, dorsal, lateral, and ventral). Different parts of the pallium give rise to the cerebral cortex (‘neocortex’) in mammals and the pallial regions of the avian endbrain.

Protostomes: bilateral animals, such as arthropods and mollusks, whose mouth develops from a primary embryonic opening; sister group of the deuterostomes.

Selection pressure: conditions that cause a selection of traits over generations that support survival and reproduction.

Sense of number: intuitive understanding of numerical quantity (number of items).

Subpallium: ventral portion of the telencephalon forming the basal ganglia.

Taxon (pl. ‘taxa’): a scientifically classified and ranked group of life forms (e.g., phylum, order, family).

Telencephalon, or endbrain: Greek *telos*, end, *egkephalos*, brain; the most anterior division of the vertebrate brain comprising the pallium and the subpallium.

Viviparity: live birth; development of the embryo inside the body of the parent.

Weber–Fechner law: psychophysical law of proportional magnitude discrimination. It also states that the subjective sensation of magnitudes scales with the logarithm of objective magnitude.

Box 3. Evolution of the Vertebrate Telencephalon (Endbrain)

All vertebrates possess a brain with five principal divisions, with the telencephalon, or **endbrain**, at the most anterior pole. The telencephalon comprises two parts: the pallium (Latin *mantle*) and the subpallium; the latter includes the striatum and septum. The telencephalon is a vertebrate innovation and is often regarded as a crowning achievement of vertebrate brain evolution [10]. Originally associated with the evolution of an expanded olfactory system in early vertebrates, the endbrain began in evolution as a relatively small, simple, and undifferentiated brain part. This condition is still visible in fishes. With the rise of the early tetrapods that conquered the land (amphibians), the telencephalon changed only a little.

However, dramatic changes and large expansions in endbrain organization accompanied the evolution of amniotes (mammals and sauropsids; i.e., reptiles and birds). Independently over time, the endbrain, and the pallium in particular, became the dominant and largest neural integration center in mammals and birds. The expanded pallium comprises four parts: medial, dorsal, lateral, and ventral. The destinies of these pallial regions differ drastically between mammals and birds: while the dorsal pallium expanded in the lineage leading to mammals, the ventral pallium expanded dramatically in the lineage leading to modern birds.

Mammals transformed the dorsal pallium into a unique six-layered 'neocortex' that runs parallel to the brain surface as the prime neural integration center from which advanced cognition emerges. The dorsal cortex in reptiles and birds instead evolved into a simple, small dorsal cortex in reptiles and the so-called 'Wulst' (German for 'bulge') in birds. Both the reptilian dorsal cortex and the avian Wulst receive only unimodal sensory input from the thalamus [139]. The mammalian neocortex is far more complex than the reptilian dorsal cortex. In addition, the neocortex is structurally rather dissimilar to the avian Wulst.

Different from the situation in mammals, the ventral pallium became the dominating pallial structure in sauropsids, forming a large, elongated ridge that protrudes into the ventricle and is therefore called 'dorsal ventricular ridge' (DVR). In birds, the anterior DVR develops into a number of nuclear subdivisions termed the hyperpallium, entopallium, mesopallium, nidopallium, and arcopallium, which comprise most of the avian telencephalon [140]. Aspects of these pallial regions in birds assume the functions of associative neocortical regions in mammals. By contrast, the ventral pallium in mammals develops into the claustrum-amygdala complex.

Both groups retained their medial pallium, which is the hippocampus in birds and mammals. Similarly, the lateral pallium became the olfactory endbrain in these groups.

different derivatives of the pallium are also involved in number representations in birds and mammals (as I will show in the following), this finding indicates that the properties of the telencephalon invite the realization of a sense of number.

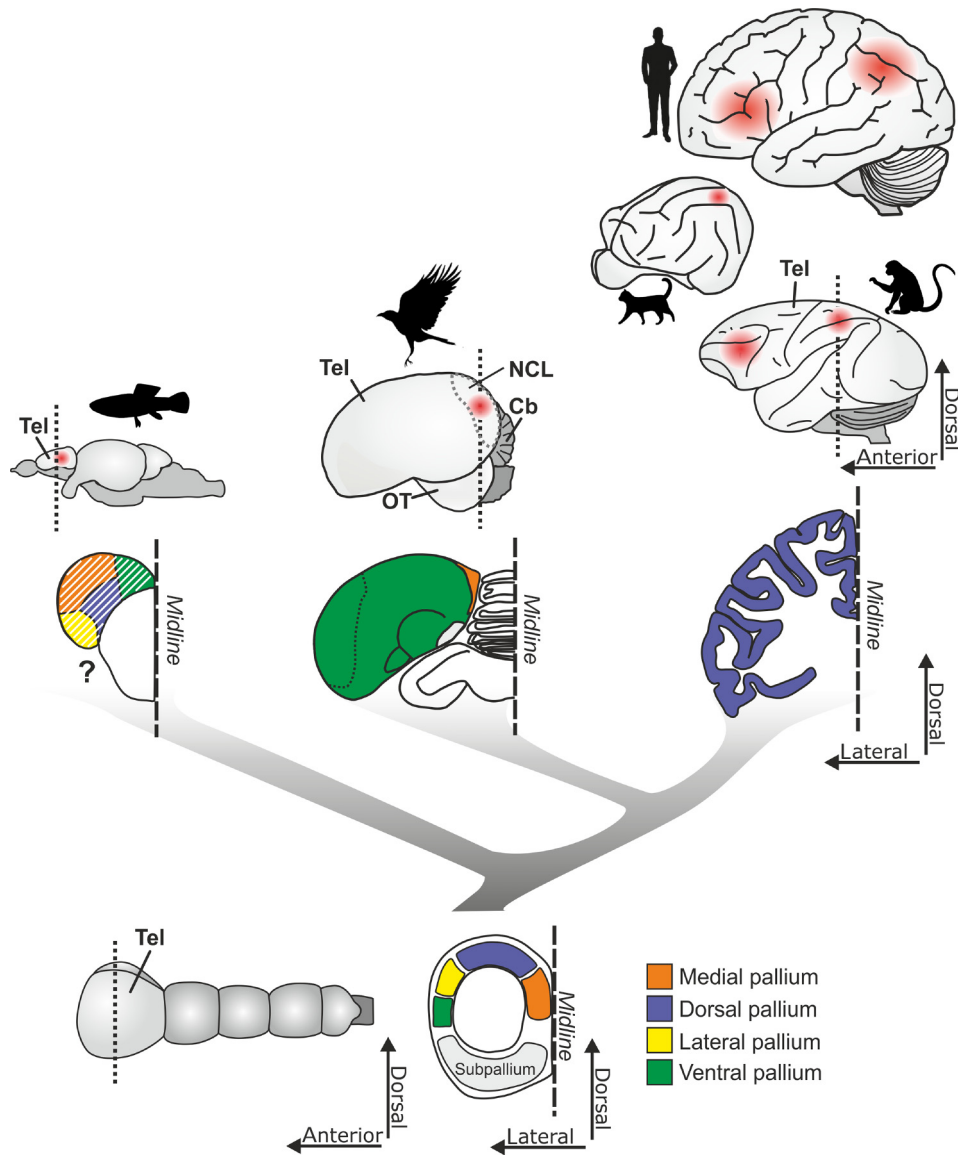
With the rise of the amphibians (e.g., newts, frogs), early tetrapods conquered the land. When discriminating sets in free choice tasks, amphibians tend to rely on continuous quantities [16]. Controlled numerical discriminations are observed for only very small numerosities in frogs (one versus two) [17]. So, in the absence of training studies with controlled stimuli, differences in continuous quantity best explain the rudimentary discrimination behavior of amphibians (Box 2). Interestingly, neurons that constitute sensory filters and detect the number of acoustically distinct call intervals have been described in the frog brains as potential precursors of number neurons [18]. If and how abstract numerical quantity is represented in amphibian brains is currently unknown, suggesting a phylogenetic discontinuity in numerical competence with the advent of the first tetrapods.

Birds

Despite a parallel, independent evolution from a last common ancestor with mammals 320 million years ago, birds join mammals in belonging to the most advanced classes of vertebrates. Numerical competence in birds has been studied for almost a century [19]. Numerical skills have been demonstrated (at least in the visual domain) in phylogenetically diverse orders of birds, such as pigeons [20], parrots [21], chickens [22], and songbirds [23], suggesting that the number sense is broadly distributed among modern birds. In the wild, birds use numerical information when reproducing [24], foraging [25], and socially interacting [26]. When tested with stimuli closely controlled for non-numerical cues, the birds' behavioral discrimination precision is on a par with that of primates [27].

Key Figure

Divergent Evolution of the Vertebrate Pallial Brain Areas for Number Representations



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Figure 1. Bottom (left): Lateral view of early embryonic formation of the five brain vesicles with the telencephalon (two hemispheres) at the anterior pole. Coronal sections through the telencephalon (at the level of the broken line) showing the embryonic layout of the telencephalon representing the hypothetical ancestral vertebrate condition with the four pallial regions forming the roof of the telencephalon. Middle (left to right): Coronal sections of the fish, corvid, and monkey brains showing the number-representing pallial regions in each of the three vertebrate classes. While the pallial derivatives in the fish pallium are speculative, the nidopallium [nidopallium caudolaterale (NCL)] originating from the ventral pallium represents numbers in crows, whereas the cerebral cortex emerging from the dorsal pallium encodes numbers in

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

Birds show the signatures of the approximate number system when tested with a broad range of numbers: discrimination performance is systematically enhanced when the two numbers are more different (the ‘numerical distance effect’) and performance worsens with increasing magnitudes (the ‘numerical size effect’) [20,23]. Moreover, subjective sensation of number is proportional to the logarithm of the objective stimulus magnitude [23], a relationship known as Fechner’s law [2].

Accompanying their advanced cognitive skills [28,29], birds have large brains relative to their body size [30] and vastly increased numbers of neurons compared with brains of non-primate mammals of equal volume [31]. In stark contrast to mammals, the evolution of avian brains is accompanied by a massive expansion of the ventral telencephalic pallium, which became the dominant neural integration center of avian brains (Box 3).

One of the prominent territories emerging from the ventral pallium is the nidopallium, an enigmatic structure that evolved most distinctly in birds and that resists comparison with the mammalian neocortex (Figure 1) [32]. Within the nidopallium lies the high-level association area, the nidopallium caudolaterale (NCL). The NCL is involved in many cognitive functions [29,33–37] and multimodal processing [38] and has been identified as neural correlate of number representations. Neurons selectively responsive to specific numbers (‘number neurons’) were found in the NCL of crows (*Corvus corone*) trained to discriminate the quantity of visual items controlled for non-numerical cues in **delayed match-to-sample tasks** [39–41]. Both the number of dots shown simultaneously in arrays and those sequentially presented are encoded [42]. The neurons’ bell-shaped tuning curves show a peak firing rate at the neurons’ respective preferred quantities (Figure 2A). The coding properties of number neurons can explain why the crows’ performance is imprecise (numerical distance effect), why it loses precision with increasing quantities (numerical size effect), and why it shows logarithmic scaling according to the **Weber–Fechner law** [39]. Corresponding to the behavior, number neurons respond less when the crows err in the task compared with when they perform accurately [39,42]. Number neurons in the NCL are also spontaneously present in crows even without specific number training [43], a finding suggesting that the neuronal mechanisms for number extraction are inherent to NCL circuits [44,45]. In contrast to NCL neurons, neurons in the crow hippocampus are unresponsive to numbers [46]. This shows that number neurons are anatomically confined and not found in all association areas of avian brains.

Birds descended from the original group of reptiles and, from a phylogenetic perspective, are dinosaurs. They are therefore more closely related to recent reptiles (crocodiles, turtles, lizards, and snakes), with which they form the ‘sauropsids’. The few available studies show that (non-avian) reptiles predominantly use continuous quantity to spontaneously discriminate sets [47,48]. Turtles spontaneously choosing between tomato slices of equal size discriminate between one and four slices with a precision of 69%, but all other set size discriminations (two versus four, two versus three, and three versus four) are close to chance (59% and lower) [49]. Even with equal-size slices, the tortoises’ discrimination could have been based on continuous physical variables that covary with numerosity (Box 2). These data in recent reptiles together with findings in amphibians (from which the reptilian-like stem amniotes evolved) argue that the last common ancestor of tetrapods and most likely vertebrates did not possess a sense of number. Numerical competence seems to have emerged independently in bony fishes, birds, and mammals.

monkeys (and mammals in general). Top (left to right): Lateral views of the brains of a zebrafish (representing fishes), a crow (representing birds), and a rhesus macaque, a cat, and a human (representing mammals). Red spots depict key brain areas for number representations in the respective species. Abbreviations: Dc, central subdivision; Dd, dorsal subdivision; Dl, lateral subdivision; Dm, medial subdivision; Dp, posterior subdivision; Tel, telencephalon.

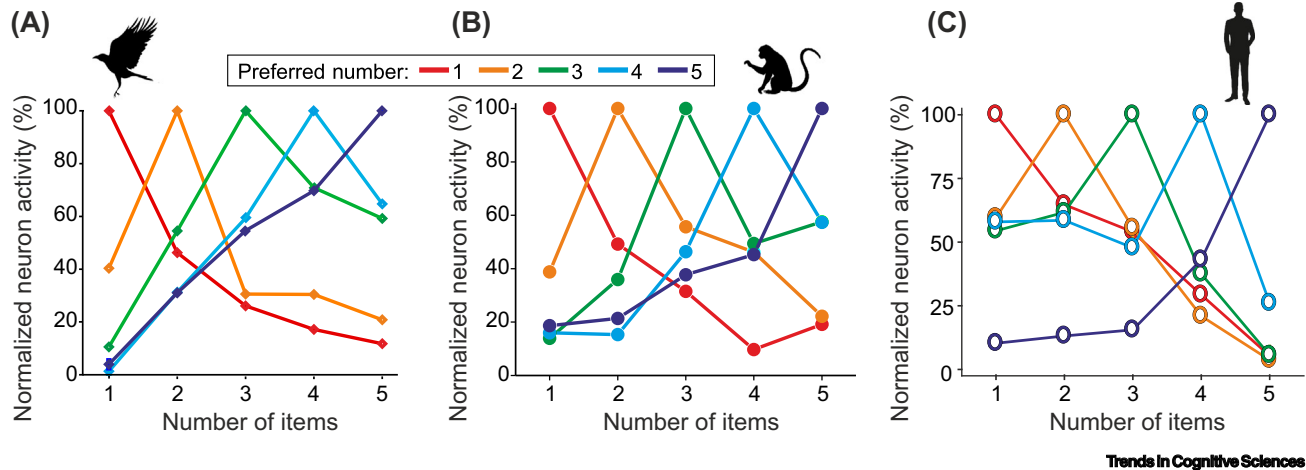


Figure 2. Number-Selective Neurons in Vertebrate Brains. (A) Number neurons in the nidopallium caudolaterale of the crow (*Corvus corone*). Shown are the normalized tuning functions averaged for neurons preferring the same numerosity (indicated by same color) [39]. (B) Number neurons in the intraparietal sulcus of the rhesus macaque (*Macaca mulatta*) [62]. (C) Number neurons in the medial temporal lobe of the human [83].

Mammals

In contrast to birds, a six-layered **cerebral cortex ('neocortex')** evolved from the dorsal pallium as the highest integration center in mammals (Box 3) [10,50]. Particularly in the primate lineage, expanded associative cortical territories – along with sensory input and motor output cortices – give rise to complex cognition.

Numerical cognition has been found in several mammalian orders investigated, both in the wild and in the laboratory. This includes rats (rodents) [51], whales and dolphins (cetaceans) [52], hyenas (carnivores) [53], elephants (proboscideans) [54], and primates (e.g., monkeys, apes, humans) [55–57]. As in birds, mammals represent nonsymbolic numbers via an approximate number system that obeys the Weber–Fechner law [55,57].

Brain studies in carnivores, nonhuman primates, and humans have repeatedly implicated the association areas of the cerebral cortex, in particular the parietal and frontal cortices, in number processing (Figure 1). The first electrophysiological investigation of a neuronal correlate of number representations was conducted in 1970 in anesthetized cats [58]. During passive presentation of sequences of auditory or visual stimuli, a very small proportion of neurons in the feline posterior association cortex (posterior part of the middle supra-sylvian gyrus) responded to the specific numbers of items. More recently, functional imaging has revealed patchy quantity activations in various cortical regions, including parietal areas, in awake dogs passively viewing dot arrays [59].

A rich set of neural data on number representations, in combination with numerical behavior, exists for awake-behaving nonhuman primates (specifically macaques) [60]. A significant proportion of number neurons tuned to the specific numbers of visual items (presented simultaneously or in sequence) [61–65], multimodal visual–auditory events [66], or hand movements [67] were recorded from the posterior parietal and frontal cortices. Even tuned responses to empty sets as a precursor to the number zero were found [64,68]. As in crows, monkey number neurons exist spontaneously without specific training in neocortical circuitries [69]. The number neurons' activity is linked to the monkeys' numerical skills [61–63,65,66,70]. Moreover, the tuning characteristics of these number neurons show the signatures of the approximate number system (Figure 2B) [60]. Far from representing only the perception of numerical categories, number

neurons are engaged in processing numerical information in agreement with conceptual decisions during working memory periods [71–75].

The human neocortex has additionally elaborated and enlarged during evolution from an already hypertrophied primate condition. Human-specific gene expression patterns drive the generation of more neurons during ontogeny [76]. This increased growth is accompanied by various structural changes in the cerebral cortex [50], such as a relative enlargement of neocortical associative areas in the parietal, temporal, and frontal lobes [77]. These enlarged association cortices could enable uniquely human symbolic competence, including formal arithmetic and mathematical skills.

In agreement with traditional findings that lesions in the frontal and posterior parietal cortices can leave patients impaired in number processing ('acalculic') [78,79], many functional imaging studies implicate the posterior parietal and frontal cortices in representing a variety of nonsymbolic and symbolic numerical tasks in children and adults (reviewed in [80–82]). Additionally, number neurons have been recorded in the hippocampal pallium of patients that show the same characteristics as those in the cerebral cortex of nonhuman primates and the NCL of corvids (Figure 2C) [83]. This finding of number neurons in the human hippocampus also highlights an interesting discrepancy in number processing between primates and birds, because the avian hippocampus does not contain number neurons [46].

Putative Neural Basis of Number Sense in Invertebrates (Protostomes)

In contrast to vertebrates, there has been a dearth of studies into the neural basis of the number sense in invertebrate species so far. Although bees, spiders, and squids are all known to be able to discriminate between sets, technical difficulties in establishing protocols with immobilized invertebrates impeded neuroscientific explorations. In the following, promising candidate regions for representation of numbers in the brains of insects, arachnids, and cephalopods for future neuroscientific exploration are identified.

Insects and Spiders (Arthropods)

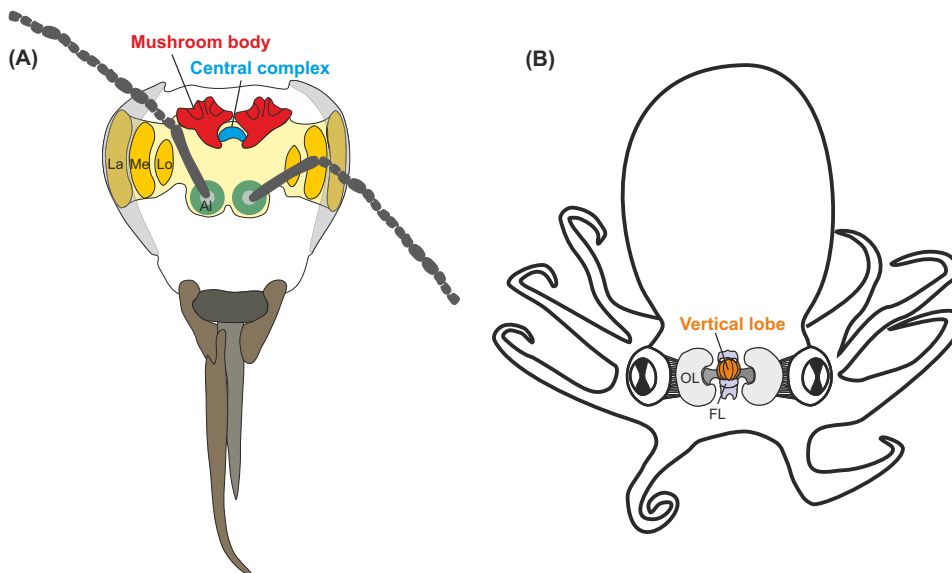
Arthropods (including insects and spiders) with an estimated 7 million species (compared with roughly 70 000 vertebrate species [84]), are by far the largest and most diverse phylum of animals on the planet [85]. Using an **expectancy-violation protocol**, the spider-eating spider (*Portia africana*) can represent the number of prey items that are visible only at the beginning and the end of a chase [86]. When there is a number mismatch, the spider is more reluctant to approach after the chase. This response is maintained even if prey size and arrangement are controlled for. So, this provides evidence that spiders represent small numbers to guide their behaviors [87,88].

More direct evidence for number representation is reported from insects. Several controlled studies in honey bees (*Apis mellifera*) trained to discriminate the quantity of landmarks [89,90] or visual elements in controlled arrays revealed the workings of the approximate number system with numerical distance and size effects similar to vertebrates [91–93]. Bees can even order numbers according to rules and understand that the empty set is a quantity smaller than one [91,94].

The central nervous system of arthropods comprises a ventral nerve cord with linked ganglia and a centralization in the head region reaching around the anterior digestive tract to form the 'subesophageal zone' and the 'supra-esophageal zone' [95]. In spiders, the centralization in the head region is even more pronounced and called the 'synganglion' [96]. The supra-esophageal zone is considered the brain in arthropods; it comprises (from anterior to posterior) a protocerebrum, deutocerebrum, and tritocerebrum.

Where might neurons representing numerical information reside in the brains of insects and spiders? Arthropods possess a conspicuous integration center that crosses the midline of the protocerebrum. This central structure is the ‘central complex’ in insects and the ‘arcuate body’ in spiders (Figure 3A). Despite major differences, these two structures may originate from a common ancestral midline structure in arthropods [97] and act as high-order associative structures in arthropod brains [98,99]. Receiving highly processed visual input, particularly in spiders, neurons in these areas are involved in visual object recognition and visual memory [100,101] and could thus represent quantity categories [102]. Neuronal recordings in spiders show that the arcuate body processes multimodal information and responds to high-level visual [103], auditory, and tactile information [104]. In insects, the central complex constitutes a sensory-motor hub and plays a role in orientation and navigation [105], action selection [106], and motor coordination [107,108]. The central complex’s role in the temporal structure of movements could be exploited to encode the number of successively presented items. Its motor functions could also support the production of specific numbers of movements.

Possibly the most promising candidate regions for abstract and cross-modal number representations are the bilateral mushroom bodies in the protocerebrum of insects and spiders [102] (Figure 3A). Although underexplored in spiders, the mushroom body of insects integrates highly processed multimodal information [109] and constitutes the iconic associative learning and memory center [109–111]. An insect-inspired neural network model suggested that a recurrent short-term memory circuit could be potentially implemented in either the central complex or the mushroom body to act as a counter of sequentially presented elements in insects [112]. Based on gene expression patterns and circuit motifs, the mushroom body has been compared with the mammalian pallium in structure and function, including the hippocampus, amygdala, and



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Figure 3. Candidate Structures for Number Representations in Arthropod and Molluskan Brains. (A) Schematic drawing of a honeybee brain (*Apis mellifera*). The visual lobes (VL) comprise the lamina (La), the medulla (Me), and the lobula (Lo) and receive visual inputs from the compound eyes. The antennal lobes (AL) receive the inputs from the olfactory neurons of the antennae. The mushroom bodies and the central complex process multimodal information and participate in learning and memory. (B) Cephalopod nervous system anatomy (*Octopus*). Two large optic lobes (OL) flank the supra- and subesophageal masses that constitute the brain (colored). Abbreviation: FL, frontal lobe.

prefrontal cortex [113,114]. Interestingly, all of these pallial regions are implicated in number processing in humans [80,83]. In sum, the mushroom body would constitute an ideal candidate for an abstract, cross-modal representation of numbers in arthropods.

Cephalopods (Mollusks)

Coleoid cephalopods, such as octopuses, cuttlefish, and squids (henceforth cephalopods), are large-brained mollusks. Some studies suggest that they exhibit interesting cognitive attributes, such as elaborate perception, skilled motor capabilities, and learning and memory [115,116]. A single study tested number discrimination in cephalopods. Juvenile cuttlefish (*Sepia pharaonis*) choosing between one to five live shrimps showed a preference for the larger numbers [117]. Studies with trained cephalopods and more controlled stimuli would help to better reveal their number-crunching capabilities and contrast them with continuous quantity discrimination (Box 2).

The cephalopods' central nervous system, in terms of gene expression [118], brain network organization [119], and gross anatomy [120], is the most distinct compared with all other animal phyla (including arthropods). The central nervous system is divided into three parts (Figure 3B): a central lobe system (the brain) encompassing tens of brain lobes comprising the supra- and subesophageal brain masses that surround the esophagus; large paired optic lobes that receive visual information directly from the eyes' photoreceptors; and massive ganglia and nerve cords in the arms to independently control each of the arms. Their neuron count is unusually high; for instance, the common octopus (*Octopus vulgaris*) possesses around 40 million neurons in the central lobe system, 130 million neurons in the optic lobes, and roughly 300 million neurons in peripheral centers such as the arms [121].

Of the many lobes in the brains of cephalopods, the vertical lobe (VL), is considered the highest integration center (Figure 3B). The VL appears to not be involved in direct motor or sensory functions [122,123]. Instead, lesions in the VL cause deficits in associative learning and long-term memory related to prey capture and navigation [124,125]. The VL has therefore been suggested to have a function similar to that of the insect mushroom bodies and the mammalian hippocampus memory system [126], although its genealogy and circuitry differ vastly compared with these structures. Due to its integrative and learning-related role, the VL would be a prime candidate region to search for numerical representations in cephalopods.

Concluding Remarks and Future Directions

In all vertebrates studied so far, various aspects of the telencephalic pallium have emerged as key brain areas for numerical representations. Neurons in the pallium of fish signal numerical changes and number neurons in the massively expanded and independently evolved nidopallium of birds and the pallial cerebral cortex (the 'neocortex') of mammals explicitly represent numerical quantities.

Although numerical representations capitalize on the telencephalic pallium, this does not necessarily mean that the last common ancestor of vertebrates (or even sauropsids) possessed a sense of number as an inherited trait (see Outstanding Questions). On the contrary, because teleost fishes, birds, and mammals independently (and convergently) increased their relative brain sizes during phylogeny, it is likely that they also underwent convergent evolution of multiple behavioral traits. Such convergent evolutionary trajectories can be seen on many levels. For instances, different types of **viviparity** evolved independently in diverse vertebrate taxa, as well as **endothermy** in birds and mammals. The same is likely to be true for number representations.

A closer look at the pallium confirms major differences across taxa that argue for independent evolution. Already within the same ancestral subdivision of the pallium, such as the dorsal pallium in

Outstanding Questions

What are the minimum evolutionary criteria in terms of connectivity and physiology that a brain region must fulfil to be suited as a potential site for a sense of number? Solving this question would also help to address the emergence of general cognitive processing abilities (i.e., intelligence) across animal taxa.

What are the evolutionary origins of number competence in advanced vertebrates? The examination of a greater variety of species, especially from basal lineages, would allow stronger inferences about the condition in the hypothetical ancestral vertebrates.

Where is numerical information represented in the brains of protostomes? Transferring the methodological tool kit that has been established for investigations of the fly brain to the brains of numerically competent bees would help to understand the functional convergence of neural structures and operation in phylogenetically distinct animal lineages.

How is the representation of numbers, a type of abstract conceptual understanding, related to the processing of other advanced cognitive functions in the pallium?

reptiles and mammals, one-to-one homologies (in gene expression) between the two taxa are absent for specific cell and layer types [127–129]. Adding to these differences, dissimilar pallial territories – the dorsal pallium (neocortex) in mammals and the ventral pallium (containing the nidopallium) in birds – represent the same functions (e.g., number processing, working memory, other cognitive functions). Interestingly, the sensory aspects of the avian pallium, but not the higher-level association territories such as the NCL, show a cortex-like organization with iteratively repeated canonical circuits arranged into stacked, horizontal neural lamina and orthogonally located vertical columns [130]. However, these circuits (originating from the ventral pallium) in birds seem to engage entirely separate classes of excitatory and inhibitory pallial neurons that have no counterpart in the mammalian neocortex (dorsal pallium) [131]. These findings argue for a distinct and independent origin of major pallial integration centers in birds and mammals as a clear signature of convergent evolution.

Irrespective of which territory evolves into the highest integration center (the ventral pallium in birds versus the dorsal pallium in mammals), something about the circuit properties of the pallium invites the representation of abstract categories and concepts [44,45]. Among the strategic benefits of the pallium is its role as an intermediary between (thalamic) sensory input and (volitional) motor output. This enables it to respond to perceived numerical information in an explicit and goal-directed way. It also allows for the synthesis of information across sensory modalities. Because numbers are abstract categories that operate beyond specific modalities (three sounds and three pictures are both instances of the number three), numerical representations rely on such a merging of the senses, which is found in associative pallial areas [66]. Pallial circuitries enable recurrent processing (cascades of feedforward and feedback projections between hierarchical processing levels) where information re-enters previous processing units to exert top-down influences and activity can be maintained in associative networks. Cognitive functioning – of which numerical processing is one instantiation – relies on temporal buffering of information via reciprocal and reentrant connections [132,133]. Finally, the pallium in different vertebrates exhibits conserved wiring motifs giving rise to densely connected locally operating modules embedded in overarching processing modules. Despite independent evolution, the avian and mammalian pallial connectomes are very similar [134,135]. This is likely to enable equivalent processing dynamics required for number representations and other cognitive functions. Broad comparative analyses based on genetically identified cell types as well as microcircuit analyses, ideally in behaving vertebrates, will help to resolve the structural and functional attributes that seem to have made the pallium an ideal candidate brain region for number representations in convergently evolved brains.

In contrast to vertebrates, studies on the neural basis of the number sense are lacking in any invertebrate species so far. By analyzing and synthesizing current molecular, structural, and physiological knowledge about invertebrate brains, promising candidate regions in the brains of insects, spiders, and cephalopods can be identified for future neuroscientific exploration. Because physiological investigations in cephalopods are hampered by arduous methodological challenges, insects – and bees in particular – might be the most promising candidate for a neuroscientific exploration into the sense of number in any protostome. Transferring the methodological toolkit that has been established for flies, from genetic to imaging approaches, to bees may open a new avenue to explore the evolutionary foundations of number representations. Of course, such a transfer of methods from flies to bees will be challenging, but perhaps this would reveal that the neural constituents of the number sense exploit even more fundamental similarities in the brains of protostomes and deuterostomes.

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Declaration of Interests

No interests are declared.

References

- Nieder, A. (2019) *A Brain for Numbers: The Biology of the Number Instinct*, MIT Press
- Nieder, A. (2020) The adaptive value of numerical competence. *Trends Ecol. Evol.* 35, 605–617
- Benson-Amram, S. et al. (2017) Numerical assessment in the wild: insights from social carnivores. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373, 20160508
- Jacob, F. (1977) Evolution and tinkering. *Science* 196, 1161–1166
- Pasquier, J. et al. (2016) Gene evolution and gene expression after whole genome duplication in fish: the PhyloFish database. *BMC Genomics* 17, 368
- Agrillo, C. et al. (2010) Large number discrimination by mosquitofish. *PLoS One* 5, e15232
- Agrillo, C. et al. (2014) Numerical acuity of fish is improved in the presence of moving targets, but only in the subitizing range. *Anim. Cogn.* 17, 307–316
- Miletto Petrazzini, M.E. et al. (2015) Relative versus absolute numerical representation in fish: can guppies represent “fourness”? *Anim. Cogn.* 18, 1007–1017
- DeLong, C.M. et al. (2017) Small and large number discrimination in goldfish (*Carassius auratus*) with extensive training. *Behav. Process.* 141, 172–183
- Striedter, G.F. and Northcutt, R.G. (2020) *Brains Through Time: A Natural History of Vertebrates*, Oxford University Press
- Nieuwenhuys, R. (2009) The forebrain of actinopterygians revisited. *Brain Behav. Evol.* 73, 229–252
- Ganz, J. et al. (2014) Subdivisions of the adult zebrafish pallium based on molecular marker analysis. *J. Comp. Neurol.* 3, 308
- Mueller, T. et al. (2011) The dorsal pallium in zebrafish, *Danio rerio* (Cyprinidae, Teleostei). *Brain Res.* 1381, 95–105
- Messina, A. et al. (2020) Response to change in the number of visual stimuli in zebrafish: a behavioural and molecular study. *Sci. Rep.* 10, 5769
- Messina, A. et al. (2020) Neurons in the dorso-central division of zebrafish pallium respond to change in visual numerosity. *bioRxiv* Published online November 11, 2020. <https://doi.org/10.1101/2020.11.11.377804>
- Krusche, P. et al. (2010) Quantity discrimination in salamanders. *J. Exp. Biol.* 213, 1822–1828
- Stancher, G. et al. (2015) Numerical discrimination by frogs (*Bombina orientalis*). *Anim. Cogn.* 18, 219–229
- Rose, G.J. (2017) The numerical abilities of anurans and their neural correlates: insights from neuroethological studies of acoustic communication. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373, 20160512
- Koehler, O. (1941) Vom Erlernen unbenannter Anzahlen bei Vögeln. *Naturwissenschaften* 29, 201–218 (in German)
- Scarf, D. et al. (2011) Pigeons on par with primates in numerical competence. *Science* 334, 1664
- Pepperberg, I.M. (2006) Grey parrot numerical competence: a review. *Anim. Cogn.* 9, 377–391
- Rugani, R. et al. (2013) One, two, three, four, or is there something more? Numerical discrimination in day-old domestic chicks. *Anim. Cogn.* 16, 557–564
- Ditz, H.M. and Nieder, A. (2016) Numerosity representations in crows obey the Weber–Fechner law. *Proc. Biol. Sci.* 283, 20160083
- Wang, L. et al. (2020) Cuckoos use host egg number to choose host nests for parasitism. *Proc. Biol. Sci.* 287, 20200343
- Hunt, S. et al. (2008) Adaptive numerical competency in a food-hoarding songbird. *Proc. Biol. Sci.* 275, 2373–2379
- Templeton, C.N. et al. (2005) Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science* 308, 1934–1937
- Nieder, A. (2017) Evolution of cognitive and neural solutions enabling numerosity judgements: lessons from primates and corvids. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373, 20160514
- Clayton, N.S. and Emery, N.J. (2015) Avian models for human cognitive neuroscience: a proposal. *Neuron* 86, 1330–1342
- Güntürkün, O. and Bugnyar, T. (2016) Cognition without cortex. *Trends Cogn. Sci.* 20, 291–303
- Tsuboi, M. et al. (2018) Breakdown of brain–body allometry and the encephalization of birds and mammals. *Nat. Ecol. Evol.* 2, 1492–1500
- Olkowicz, S. et al. (2016) Birds have primate-like numbers of neurons in the forebrain. *Proc. Natl. Acad. Sci. U. S. A.* 113, 7255–7260
- Briscoe, S.D. et al. (2018) Neocortical association cell types in the forebrain of birds and alligators. *Curr. Biol.* 28, 686–696.e6
- Veit, L. et al. (2015) Associative learning rapidly establishes neuronal representations of upcoming behavioral choices in crows. *Proc. Natl. Acad. Sci. U. S. A.* 112, 15208–15213
- Nieder, A. (2017) Inside the corvid brain – probing the physiology of cognition in crows. *Curr. Opin. Behav. Sci.* 16, 8–14
- Rinnert, P. et al. (2019) Neuronal correlates of spatial working memory in the endbrain of crows. *Curr. Biol.* 29, 2616–2624.e4
- Nieder, A. et al. (2020) A neural correlate of sensory consciousness in a corvid bird. *Science* 369, 1626–1629
- Rinnert, P. and Nieder, A. (2021) Neural code of motor planning and execution during goal-directed movements in crows. *J. Neurosci.* Published online February 19, 2021. <https://doi.org/10.1523/JNEUROSCI.0739-20.2021>
- Moll, F.W. and Nieder, A. (2015) Cross-modal associative mnemonic signals in crow endbrain neurons. *Curr. Biol.* 25, 2196–2201
- Ditz, H.M. and Nieder, A. (2015) Neurons selective to the number of visual items in the corvid songbird endbrain. *Proc. Natl. Acad. Sci. U. S. A.* 112, 7827–7832
- Ditz, H.M. and Nieder, A. (2016) Sensory and working memory representations of small and large numerosities in the crow endbrain. *J. Neurosci.* 36, 12044–12052
- Kirschhock, M.E. et al. (2021) Behavioral and neuronal representation of numerosity zero in the crow. *J. Neurosci.* <https://doi.org/10.1523/JNEUROSCI.0090-21.2021>
- Ditz, H.M. and Nieder, A. (2020) Format-dependent and format-independent representation of sequential and simultaneous numerosity in the crow endbrain. *Nat. Commun.* 11, 686
- Wagener, L. et al. (2018) Neurons in the endbrain of numerically naive crows spontaneously encode visual numerosity. *Curr. Biol.* 28, 1090–1094.e4
- Nasr, K. et al. (2019) Number detectors spontaneously emerge in a deep neural network designed for visual object recognition. *Sci. Adv.* 5, eaav7903
- Kim, G. et al. (2021) Visual number sense in untrained deep neural networks. *Sci. Adv.* 7, eabd6127
- Ditz, H.M. et al. (2018) Neurons in the hippocampus of crows lack responses to non-spatial abstract categories. *Front. Syst. Neurosci.* 12, 33
- Miletto Petrazzini, M.E. et al. (2017) Quantitative abilities in a reptile (*Podarcis sicula*). *Biol. Lett.* 13, 20160899
- Miletto Petrazzini, M.E. et al. (2018) Quantity discrimination in trained lizards (*Podarcis sicula*). *Front. Psychol.* 9, 274
- Gazzola, A. et al. (2018) Continuous and discrete quantity discrimination in tortoises. *Biol. Lett.* 14, 20180649
- Briscoe, S.D. and Ragsdale, C.W. (2019) Evolution of the chordate telencephalon. *Curr. Biol.* 29, R647–R662
- Fernandes, D.M. and Church, R.M. (1982) Discrimination of the number of sequential events. *Anim. Learn. Behav.* 10, 171–176
- Abramson, J.Z. et al. (2013) Relative quantity judgments in the beluga whale (*Delphinapterus leucas*) and the bottlenose dolphin (*Tursiops truncatus*). *Behav. Process.* 96, 11–19
- Benson-Amram, S. et al. (2011) Numerical assessment and individual call discrimination by wild spotted hyaenas, *Crocuta*. *Anim. Behav.* 82, 743–752
- Perdue, B.M. et al. (2012) Putting the elephant back in the herd: elephant relative quantity judgments match those of other species. *Anim. Cogn.* 15, 955–961

55. Brannon, E.M. and Terrace, H.S. (1998) Ordering of the numerosities 1 to 9 by monkeys. *Science* 282, 746–749
56. Beran, M.J. (2007) Rhesus monkeys (*Macaca mulatta*) enumerate large and small sequentially presented sets of items using analog numerical representations. *J. Exp. Psychol. Anim. Behav. Process.* 33, 42–54
57. Merten, K. and Nieder, A. (2009) Compressed scaling of abstract numerosity representations in adult humans and monkeys. *J. Cogn. Neurosci.* 21, 333–346
58. Thompson, R.F. *et al.* (1970) Number coding in association cortex of the cat. *Science* 168, 271–273
59. Aulet, L.S. *et al.* (2019) Canine sense of quantity: evidence for numerical ratio-dependent activation in parietotemporal cortex. *Biol. Lett.* 15, 20190666
60. Nieder, A. (2016) The neuronal code for number. *Nat. Rev. Neurosci.* 17, 366–382
61. Nieder, A. *et al.* (2002) Representation of the quantity of visual items in the primate prefrontal cortex. *Science* 297, 1708–1711
62. Nieder, A. and Miller, E.K. (2004) A parieto-frontal network for visual numerical information in the monkey. *Proc. Natl. Acad. Sci. U. S. A.* 101, 7457–7462
63. Nieder, A. *et al.* (2006) Temporal and spatial enumeration processes in the primate parietal cortex. *Science* 313, 1431–1435
64. Okuyama, S. *et al.* (2015) Representation of the numerosity 'zero' in the parietal cortex of the monkey. *Sci. Rep.* 5, 10059
65. Viswanathan, P. and Nieder, A. (2015) Differential impact of behavioral relevance on quantity coding in primate frontal and parietal neurons. *Curr. Biol.* 25, 1259–1269
66. Nieder, A. (2012) Supramodal numerosity selectivity of neurons in primate prefrontal and posterior parietal cortices. *Proc. Natl. Acad. Sci. U. S. A.* 109, 11860–11865
67. Sawamura, H. *et al.* (2002) Numerical representation for action in the parietal cortex of the monkey. *Nature* 415, 918–922
68. Ramirez-Cardenas, A. *et al.* (2016) Neuronal representation of numerosity zero in the primate parieto-frontal number network. *Curr. Biol.* 26, 1285–1294
69. Viswanathan, P. and Nieder, A. (2013) Neuronal correlates of a visual "sense of number" in primate parietal and prefrontal cortices. *Proc. Natl. Acad. Sci. U. S. A.* 110, 11187–11192
70. Sawamura, H. *et al.* (2010) Deficits in action selection based on numerical information after inactivation of the posterior parietal cortex in monkeys. *J. Neurophysiol.* 104, 902–910
71. Bongard, S. and Nieder, A. (2010) Basic mathematical rules are encoded by primate prefrontal cortex neurons. *Proc. Natl. Acad. Sci. U. S. A.* 107, 2277–2282
72. Vallentin, D. *et al.* (2012) Numerical rule coding in the prefrontal, premotor, and posterior parietal cortices of macaques. *J. Neurosci.* 32, 6621–6630
73. Eisele, A.K. and Nieder, A. (2013) Representation of abstract quantitative rules applied to spatial and numerical magnitudes in primate prefrontal cortex. *J. Neurosci.* 33, 7526–7534
74. Jacob, S.N. and Nieder, A. (2014) Complementary roles for primate frontal and parietal cortex in guarding working memory for distractor stimuli. *Neuron* 83, 226–237
75. Jacob, S.N. *et al.* (2018) Structuring of abstract working memory content by fronto-parietal synchrony in primate cortex. *Neuron* 99, 588–597.e5
76. Linares-Benadero, C. and Borrell, V. (2019) Deconstructing cortical folding: genetic, cellular and mechanical determinants. *Nat. Rev. Neurosci.* 20, 161–176
77. Van Essen, D.C. and Dierker, D.L. (2007) Surface-based and probabilistic atlases of primate cerebral cortex. *Neuron* 56, 209–225
78. Lemer, C. *et al.* (2003) Approximate quantities and exact number words: dissociable systems. *Neuropsychologia* 41, 1942–1958
79. Ashkenazi, S. *et al.* (2008) Basic numerical processing in left intraparietal sulcus (IPS) acalculia. *Cortex* 44, 439–448
80. Arsalidou, M. and Taylor, M.J. (2011) Is 2+2=4? Meta-analyses of brain areas needed for numbers and calculations. *Neuroimage* 54, 2382–2393
81. Arsalidou, M. *et al.* (2018) Brain areas associated with numbers and calculations in children: meta-analyses of fMRI studies. *Dev. Cogn. Neurosci.* 30, 239–250
82. Anobile, G. *et al.* (2021) A sensorimotor numerosity system. *Trends Cogn. Sci.* 25, 24–36
83. Kutter, E.F. *et al.* (2018) Single neurons in the human brain encode numbers. *Neuron* 100, 753–761 e4
84. IUCN (2021) IUCN Red List Version 2020–3. Table 1a. IUCN
85. Stork, N.E. (2018) How many species of insects and other terrestrial arthropods are there on earth? *Annu. Rev. Entomol.* 63, 31–45
86. Cross, F.R. and Jackson, R.R. (2017) Representation of different exact numbers of prey by a spider-eating predator. *Interface Focus* 7, 20160035
87. Nelson, X.J. and Jackson, R.R. (2012) The role of numerical competence in a specialized predatory strategy of an araneophagous spider. *Anim. Cogn.* 15, 699–710
88. Rodríguez, R.L. *et al.* (2015) *Nephila clavipes* spiders (Araneae: Nephilidae) keep track of captured prey counts: testing for a sense of numerosity in an orb-weaver. *Anim. Cogn.* 18, 307–314
89. Chittka, L. and Geiger, K. (1995) Can honey bees count landmarks? *Anim. Behav.* 49, 159–164
90. Dacke, M. and Srinivasan, M.V. (2008) Evidence for counting in insects. *Anim. Cogn.* 11, 683–689
91. Howard, S.R. *et al.* (2018) Numerical ordering of zero in honey bees. *Science* 360, 1124–1126
92. Bortot, M. *et al.* (2019) Honeybees use absolute rather than relative numerosity in number discrimination. *Biol. Lett.* 15, 20190138
93. Howard, S.R. *et al.* (2019) Surpassing the subitizing threshold: appetitive-aversive conditioning improves discrimination of numerosities in honeybees. *J. Exp. Biol.* 222, jeb205658
94. Nieder, A. (2016) Representing something out of nothing: the dawning of zero. *Trends Cogn. Sci.* 20, 830–842
95. Ito, K. *et al.* (2014) A systematic nomenclature for the insect brain. *Neuron* 81, 755–765
96. Foelix, R. (2010) *Biology of Spiders* (3rd edn), Oxford University Press
97. Homberg, U. (2008) Evolution of the central complex in the arthropod brain with respect to the visual system. *Arthropod. Struct. Dev.* 37, 347–362
98. Pfeiffer, K. and Homberg, U. (2014) Organization and functional roles of the central complex in the insect brain. *Annu. Rev. Entomol.* 59, 165–184
99. Honkanen, A. *et al.* (2019) The insect central complex and the neural basis of navigational strategies. *J. Exp. Biol.* 222, jeb188854
100. Liu, G. *et al.* (2006) Distinct memory traces for two visual features in the *Drosophila* brain. *Nature* 439, 551–556
101. Ostad, T.A. *et al.* (2011) Visual place learning in *Drosophila melanogaster*. *Nature* 474, 204–207
102. Giurfa, M. (2019) An insect's sense of number. *Trends Cogn. Sci.* 23, 720–722
103. Menda, G. *et al.* (2014) Visual perception in the brain of a jumping spider. *Curr. Biol.* 24, 2580–2585
104. Shamble, P.S. *et al.* (2016) Airborne acoustic perception by a jumping spider. *Curr. Biol.* 26, 2913–2920
105. el Jundi, B. *et al.* (2015) Neural coding underlying the cue preference for celestial orientation. *Proc. Natl. Acad. Sci. U. S. A.* 112, 11395–11400
106. Hulse, B.K. *et al.* (2020) A connectome of the *Drosophila* central complex reveals network motifs suitable for flexible navigation and context-dependent action selection. *bioRxiv* Published online December 9, 2020. <https://doi.org/10.1101/2020.12.08.413955>
107. Martin, J.P. *et al.* (2015) Central-complex control of movement in the freely walking cockroach. *Curr. Biol.* 25, 2795–2803
108. Fiore, V.G. *et al.* (2015) Evolutionarily conserved mechanisms for the selection and maintenance of behavioural activity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 370, 20150053
109. Menzel, R. (2014) The insect mushroom body, an experience-dependent recording device. *J. Physiol. Paris* 108, 84–95
110. Heisenberg, M. (2003) Mushroom body memoir: from maps to models. *Nat. Rev. Neurosci.* 4, 266–275
111. Cognigni, P. *et al.* (2018) Do the right thing: neural network mechanisms of memory formation, expression and update in *Drosophila*. *Curr. Opin. Neurobiol.* 49, 51–58
112. Vasas, V. and Chittka, L. (2019) Insect-inspired sequential inspection strategy enables an artificial network of four neurons to estimate numerosity. *iScience* 11, 85–92

113. Tomer, R. *et al.* (2010) Profiling by image registration reveals common origin of annelid mushroom bodies and vertebrate pallium. *Cell* 142, 800–809
114. Oswald, D. and Waddell, S. (2015) Olfactory learning skews mushroom body output pathways to steer behavioral choice in *Drosophila*. *Curr. Opin. Neurobiol.* 35, 178–184
115. Schnell, A.K. and Vallortigara, G. (2019) 'Mind' is an ill-defined concept: considerations for future cephalopod research. a reply to Mather, Octopus Mind. *Anim. Sentience* 26, 16
116. Schnell, A.K. *et al.* (2020) How intelligent is a cephalopod? Lessons from comparative cognition. *Biol. Rev. Camb. Philos. Soc.* 96, 162–178
117. Yang, T.I. and Chiao, C.C. (2016) Number sense and state-dependent valuation in cuttlefish. *Proc. Biol. Sci.* 283, 20161379
118. Albertin, C. *et al.* (2015) The octopus genome and the evolution of cephalopod neural and morphological novelties. *Nature* 524, 220–224
119. Shigeno, S. and Ragsdale, C.W. (2015) The gyri of the octopus vertical lobe have distinct neurochemical identities. *J. Comp. Neurol.* 523, 1297–1317
120. Moroz, L.L. (2009) On the independent origins of complex brains and neurons. *Brain Behav. Evol.* 74, 177–190
121. Young, J.Z. (1963) The number and sizes of nerve cells in *Octopus*. *Proc. Zool. Soc. Lond.* 140, 229–254
122. Zullo, L. *et al.* (2009) Nonsomatotopic organization of the higher motor centers in octopus. *Curr. Biol.* 19, 1632–1636
123. Hochner, B. and Shomrat, T. (2014) The neurophysiological basis of learning and memory in an advanced invertebrate: the octopus. In *Cephalopod Cognition* (Darmaillacq, A. *et al.*, eds), pp. 72–93, Cambridge University Press
124. Florito, G. and Chichery, R. (1995) Lesions of the vertical lobe impair visual discrimination learning by observation in *Octopus vulgaris*. *Neurosci. Lett.* 192, 117
125. Graindorge, N. *et al.* (2006) Effects of dorsal and ventral vertical lobe electrolytic lesions on spatial learning and locomotor activity in *Sepia officinalis*. *Behav. Neurosci.* 120, 1151–1158
126. Shomrat, T. *et al.* (2015) The vertical lobe of cephalopods: an attractive brain structure for understanding the evolution of advanced learning and memory systems. *J. Comp. Physiol. A.* 201, 947–956
127. Tosches, M.A. *et al.* (2018) Evolution of pallium, hippocampus, and cortical cell types revealed by single-cell transcriptomics in reptiles. *Science* 360, 881–888
128. Nomura, T. *et al.* (2018) Species-specific mechanisms of neuron subtype specification reveal evolutionary plasticity of amniote brain development. *Cell Rep.* 22, 3142–3151
129. Nomura, T. *et al.* (2020) Changes in Wnt-dependent neuronal morphology underlie the anatomical diversification of neocortical homologs in amniotes. *Cell Rep.* 31, 107592
130. Stacho, M. *et al.* (2020) A cortex-like canonical circuit in the avian forebrain. *Science* 369, eabc5534
131. Colquitt, B.M. *et al.* (2021) Cellular transcriptomics reveals evolutionary identities of songbird vocal circuits. *Science* 371, eabd9704
132. Goldman-Rakic, P.S. (1995) Cellular basis of working memory. *Neuron* 14, 477–485
133. Eriksson, J. (2015) Neurocognitive architecture of working memory. *Neuron* 88, 33–46
134. Shanahan, M. *et al.* (2013) Large-scale network organization in the avian forebrain: a connectivity matrix and theoretical analysis. *Front. Comput. Neurosci.* 7, 89
135. van den Heuvel, M.P. *et al.* (2016) Comparative connectomics. *Trends Cogn. Sci.* 20, 345–361
136. Martín-Durán, J.M. *et al.* (2018) Convergent evolution of bilaterian nerve cords. *Nature* 553, 45–50
137. Leibovich, T. *et al.* (2017) From "sense of number" to "sense of magnitude": the role of continuous magnitudes in numerical cognition. *Behav. Brain Sci.* 40, e164
138. Jordan, K.E. *et al.* (2008) Monkeys match and tally quantities across senses. *Cognition* 108, 617–625
139. Medina, L. (2007) Do birds and reptiles possess homologues of mammalian visual, somatosensory, and motor cortices? In *Evolution of Nervous Systems* (Vol. 2) (Kaas, J.H. and Bullock, T.H., eds), pp. 163–194, Elsevier
140. Jarvis, E.D. *et al.* (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nat. Rev. Neurosci.* 6, 151–159