

REVIEW

Neuroethology of number sense across the animal kingdom

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ABSTRACT

Many species from diverse and often distantly related animal groups (e.g. monkeys, crows, fish and bees) have a sense of number. This means that they can assess the number of items in a set – its ‘numerosity’. The brains of these phylogenetically distant species are markedly diverse. This Review examines the fundamentally different types of brains and neural mechanisms that give rise to numerical competence across the animal tree of life. Neural correlates of the number sense so far exist only for specific vertebrate species: the richest data concerning explicit and abstract number representations have been collected from the cerebral cortex of mammals, most notably human and nonhuman primates, but also from the pallium of corvid songbirds, which evolved independently of the mammalian cortex. In contrast, the neural data relating to implicit and reflexive numerical representations in amphibians and fish is limited. The neural basis of a number sense has not been explored in any protostome so far. However, promising candidate regions in the brains of insects, spiders and cephalopods – all of which are known to have number skills – are identified in this Review. A comparative neuroscientific approach will be indispensable for identifying evolutionarily stable neuronal circuits and deciphering codes that give rise to a sense of number across phylogeny.

KEY WORDS: Brain evolution, Protostomes, Deuterostomes, Vertebrates, Number sense, Numerical competence, Neural coding

Introduction

The ability to assess the number of elements in a set – its numerosity – is a form of abstract categorization and key to intelligent behaviour (Miller et al., 2003; Nieder, 2020c). Numerical competence (see Glossary) provides survival and reproductive advantages for a plethora of species and therefore is of adaptive value (see Glossary) (Nieder, 2020b). Numerical skills enhance an animal’s survival chances in finding food, avoiding predation, hunting prey and persisting in social interactions. In addition, it promotes the chances of fertilizing an egg and increases the viability of offspring (Nieder, 2020b). Consequently, the ability to estimate set size is widespread across the animal kingdom. The most notorious problem in studying the number sense (see Glossary) is in controlling for non-numerical quantity, such as amount or size of stimuli. However, based on several well-controlled investigations, it has been demonstrated that a ‘number sense’ exists in animals and is deeply rooted in evolution (Box 1). Humans and nonhuman animals share an approximate number system (see Glossary) that constitutes a phylogenetic and ontogenetic precursor to the uniquely human symbolic counting and mathematical skills (Pica et al., 2004; Gordon, 2004; Cantlon and Brannon, 2006; Nieder and Dehaene, 2009; Nieder, 2019).

Like any other behavioural and cognitive feat, the ability to represent and process numbers arises from the workings of the brain. The structural requirements and physiological mechanisms which underpin number representation are therefore of major biological interest. The past two decades have seen impressive advances in locating and deciphering numerical representations in the brains of human and nonhuman primates (Nieder and Dehaene, 2009; Nieder, 2016a, 2016b, 2020a). However, behavioural studies have also identified numerical competence in phylogenetically distantly related species with strikingly different brain structures that evolved in parallel for long periods (Fig. 1). This Review examines the fundamentally different types of brains and neural mechanisms from which numerical competence originates across the animal tree of life. Moreover, promising candidate regions are identified in brains of protostomes in which the neural basis of a number sense has not been explored so far.

The parallel evolution of bilaterian brains

In order to appreciate the diversity of animal brains and their association with numerical competence, it is necessary to consider our current understanding of the evolution of animals (Metazoa) and their central nervous systems. This is a fascinating but controversial issue (Holland et al., 2013; Arendt, 2018; Holland, 2020). All animals that have been tested for a sense of number are bilaterians (see Glossary). Although the last common ancestor of bilaterian animals (the ‘urbilaterian’) undoubtedly had neurons, it remains uncertain whether and to what extent those neurons might have been centralized into nerve cords, cerebral ganglia or primitive brains (Fig. 2) (Moroz, 2012; Holland et al., 2013). This question is even more problematic given that the phylogenetic relationships among the different taxa arising from the urbilaterian around 800 million years ago are still disputed.

Reconstructing the evolutionary history of the nervous system from specific traits (or combinations thereof) found in different taxa of known phylogenetic relationships suggests that highly centralized nervous systems evolved separately in the lineages leading to deuterostome chordates and several times within the protostomes (Moroz, 2009; Northcutt, 2012; Dunn et al., 2014; Striedter and Northcutt, 2020). In contrast, similarities in gene expression patterns between the embryonic brains of protostome and deuterostome species (De Robertis and Sasai, 1996; Tomer et al., 2010) seem to suggest that the last common ancestor of all these species must already have possessed a centralized nervous system (Denes et al., 2007; Shubin et al., 2009; Strausfeld and Hirth, 2013a; Wolff and Strausfeld, 2015). A problem of this latter hypothesis is that centralized nervous systems must have been lost repeatedly in diverse lineages during evolution because many extant animal groups lack a condensed brain (Hirth, 2010). In addition, some of the gene expression similarities may reflect the conservation of ancient mechanisms responsible for body patterning, rather than the development of central nerve cords and brains per se (Lowe et al., 2015; Martin-Durán et al., 2018). Therefore, neuroanatomical features that lack phylogenetic continuity and thus show no

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Glossary

Adaptive value

Trait that helps an organism to survive and reproduce, i.e. traits that provide greater fitness in an environment are of adaptive value.

Approximate number system

Cognitive/mental system that supports the estimation of numerical quantity without relying on language or symbols.

Association brain area

Brain areas that integrate multi-modal sensory and memory information and link it to motor output.

Bilaterian

Animals that exhibit bilateral symmetry at least at some point in their development and share a bilaterian last common ancestor.

Fechner's law

Psychophysical law that states that the subjective sensation of magnitudes scales with the logarithm of objective magnitude.

Immediate early genes

Genes that are quickly and transiently expressed when neurons are stimulated and become active; expression of these genes can thus be used as markers of neuronal activity.

Neuropil

Fibrous network of nerve fibres interrupted by numerous synapses and located in concentrations of nervous tissue.

Number neurons

Neurons that increase their firing rate when presented with or memorizing numerical quantities. They are tuned to numerosity and respond maximally to a single presented quantity.

Number sense

Intuitive understanding of numerical quantity (numerosity).

Numerical competence

The ability to represent, discriminate and process numerical quantity information.

Object tracking system

Visual mechanism that is thought to track up to four objects in a relatively precise but implicit way.

Weber's law

Psychophysical law of proportional magnitude discrimination. It states that the just noticeable difference between two magnitudes divided by the reference magnitude is a constant, the Weber fraction.

common ancestor may still share pre-existing developmental modules and arise in parallel over the course of evolution (Tschopp and Tabin, 2017). This supports the hypothesis that many of the similarities between different taxa and species are the result of convergent evolution (Colquitt et al., 2021), and that centralized nervous systems and brains evolved repeatedly among the Bilateria (Schmidt-Rhaesa et al., 2015; Albertin and Ragsdale, 2018; Holland, 2020; Striedter and Northcutt, 2020).

Number sense in vertebrates (deuterostomes)

Members of all vertebrate classes show numerical competence (Nieder, 2020a). The neural mechanisms have been unravelled down to the level of single neurons (Table 1). In the following sections, I discuss the neural foundations in all species that have been explored so far.

Evolution of the vertebrate brain and pallium

Vertebrates show a five-partite brain. At the most anterior pole lie the two hemispheres of the telencephalon (also called the cerebrum or endbrain), followed by the diencephalon, the mesencephalon (the midbrain), the metencephalon (cerebellum and pons) and finally the myelencephalon (Fig. 3). The telencephalon encompasses two principal subdivisions, the pallium (the coating from which the cerebral cortex in mammals emerges) and the subpallium. Of special interest for number representations are the pallium-derived integration centres of the brain (Goffinet, 2017).

Box 1. Varieties of number representations

Numerical quantity, the number of objects in a set, can be represented in different ways. The most fundamental distinction is the one between symbolic and non-symbolic number representations (Nieder, 2019). Symbolic number representations (number word and numerals) are human specific; they are part of a symbol system with a compositional syntax and semantics to allow counting and formal arithmetic.

In contrast, simpler non-symbolic number representations, the focus of this Review, are also found in different animal species. Non-symbolic number representations are primordial, both from a human developmental as well as from an evolutionary point of view. They allow children to count before they have learned symbolic number representations, and they allow innumerate adults to assess numerical quantity. Animals exclusively rely on non-symbolic number representations.

Two separate mental systems allow subjects to represent number without symbols: the approximate number system (ANS) and the object tracking system (OTS) (see Glossary). The ANS allows one to estimate explicitly (consciously) an unlimited number of elements. The ANS represents the number of items approximately and exhibits two important behavioural characteristics: the 'numerical distance effect' refers to the finding that discrimination performance systematically improves the more different two values are; the 'numerical size effect' captures the finding that number discrimination becomes systematically less precise in proportion to increasing numbers (discrimination is ratio dependent). Both effects are captured by the psychophysical Weber law, which characterizes the ANS. Using the ANS, subjects find it also easier to discriminate smaller numbers from a given reference number than larger numbers. More precisely, the subjective sensation of number is proportional to the logarithm of the objective stimulus magnitude, a relationship is known as Fechner's law (see Nieder, 2020b, for detailed explanations).

In contrast to the ANS, the OTS allows representing only small set sizes (from 1 to about 4) in an implicit (unconscious) but rather precise way. This system is thought to be responsible for a 'subitizing' effect, which describes an effortless, fast and accurate process used to judge a small number of items (Feigenson et al., 2004).

Some animals exhibit innate and reflexive mechanisms that implicitly detect the number of very specific types of stimuli to prompt stereotypic responses. Such mechanisms may best be regarded as hard-wired sensory filters rather than genuine numerical representations because they do not apply to abstract numerical quantity.

Mammals

In mammals, pallial neurons with apical dendrites form orderly, stacked layers that run parallel to the brain's surface (Naumann and Laurent, 2017); this is known as a 'cortex' (Nauta and Feirtag, 1986). The six-layered cerebral cortex located in the mammalian pallium is termed the 'neocortex' (Brodmann and Garey, 2006), an evolutionary novelty of mammals (Briscoe and Ragsdale, 2019). The association brain areas (see Glossary) of the cerebral cortex give rise to complex cognition including numerical competence in all mammals investigated, from human and nonhuman primates to carnivores (Table 1). Despite an abundance of classic behavioural studies on numerosity discrimination in rodents (e.g. Mechner, 1958; Fernandes and Church, 1982; Meck and Church, 1983; Davis and Albert, 1986), neural data do not exist in mice and rats.

Human primates

Over the course of evolution, the intensely studied human neocortex (reviewed in Lui et al., 2011; Sousa et al., 2017) has much elaborated and enlarged from an already hypertrophied primate condition, such that it covers the larger part of the remaining brain. The human neocortex is about three times larger than that of the chimpanzee, the closest zoological relative, because human-specific gene expression patterns cause more neurons to be generated during

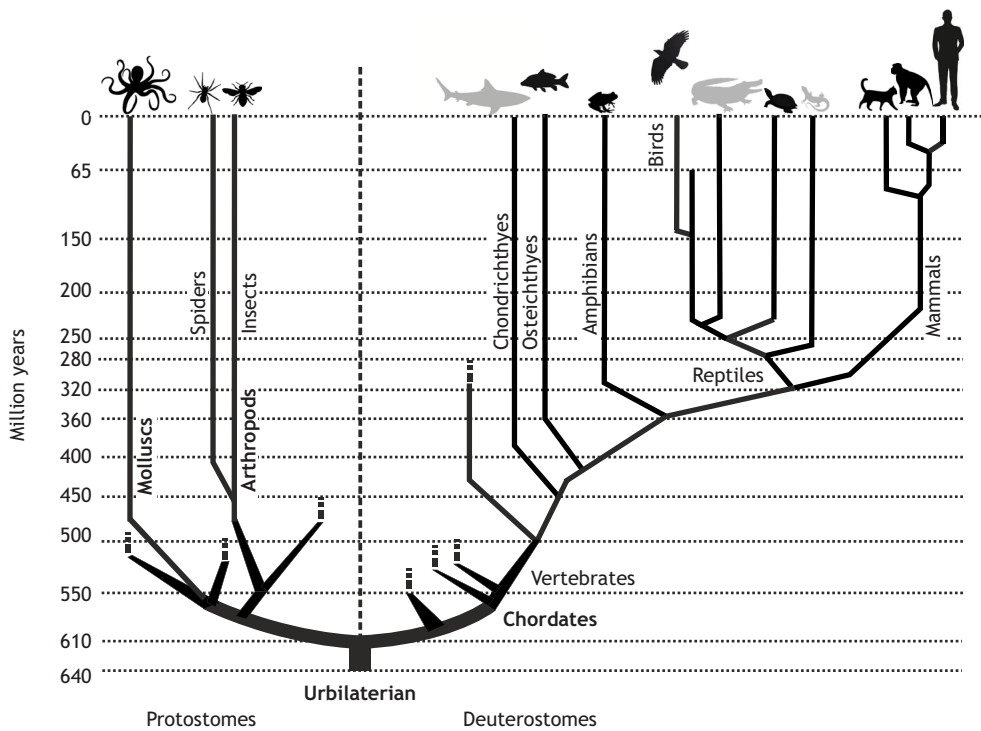


Fig. 1. Simplified tree of animal life displaying major bilaterian animal groups with a 'number sense'. The left side of the tree shows insects and spiders (of the phylum Arthropoda) and cephalopods (of the phylum Mollusca) as representatives of the protostomes that diverged from the deuterostomes on the right side of the tree about 600 million years ago. The right side of the tree depicts the traditional five vertebrate groups: fish (with the major groups Chondrichthyes and Osteichthyes), amphibians, birds, reptiles and mammals. Black silhouettes indicate animal groups for which a number sense has been explored and which are discussed in this Review.

ontogeny (Llinares-Benadero and Borrell, 2019). This increased growth is accompanied by changes in the proportion of cell types allocated to specific sites, the patterning and relative size of the

neocortical areas and connection patterns, as well as other aspects (Briscoe and Ragsdale, 2019). Particularly striking is the relative enlargement of neocortical associative areas in the parietal, temporal and frontal lobes (Van Essen and Dierker, 2007). These areas are associated with 'higher brain functions', such as consciousness, working memory, attention or symbolic competence, and also underlie uniquely human symbolic arithmetic and mathematical skills.

An early review of patients who suffered from 'acalculia', an acquired impairment in performing simple arithmetic, concluded that different types of calculation were represented in the inferior parietal lobule (angular gyrus), the intraparietal sulcus (IPS) and the inferior frontal gyrus (Henschen, 1919; Fig. 4A). The roles of these areas were further confirmed in the years to follow, not only as crucial for symbolic counting and arithmetic (Cipolotti et al., 1991), but also for basic nonsymbolic quantity estimation (Lemer et al., 2003; Ashkenazi et al., 2008).

With the advancement of functional imaging techniques, the cerebral blood flow (hemodynamic response) associated with number processing could be explored non-invasively in healthy subjects (Fig. 4A) (Dehaene et al., 1999; Nieder, 2004). These techniques showed involvement of parts of the posterior parietal cortex (PPC), particularly the IPS, the superior parietal lobe and the prefrontal cortex (PFC) (Piazza et al., 2004; Jacob and Nieder, 2009a; Arsalidou and Taylor, 2011; Harvey et al., 2013). In agreement with findings in acalculic patients, functional imaging implicated the parietal and frontal cortices in performing a variety of symbolic numerical tasks in humans (Dehaene et al., 2003; Piazza et al., 2007; Ansari, 2008; Arsalidou and Taylor, 2011). There is evidence for the involvement of the IPS in the representation of set size, numerals and counting words (Notebaert et al., 2011; Holloway et al., 2013) and even fractions (Jacob and Nieder, 2009b). A meta-analysis comparing activation for the comparison of non-symbolic and symbolic numbers across many studies (Box 1) found significant numerical activation mainly in the PPC, in the superior parietal lobule, IPS and inferior parietal lobule. In

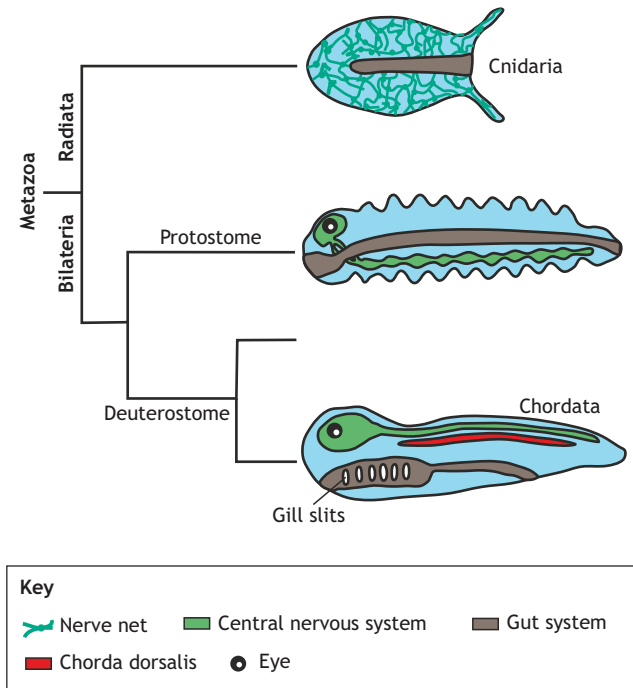


Fig. 2. Comparison of metazoan body plans and nervous systems. The radially symmetrical cnidarians (such as polyps) possess nerve nets lacking centralization. Prototypical protostomes show a centralized nervous system located at the ventral side of the body (with a dorsal gut system), whereas the chordates (a major deuterostome phylum) exhibit a dorsal centralized nervous system (and a ventral gut system). Among the deuterostomes, other phyla exist (indicated by the empty branching point) that show less-centralized nervous systems (after dos Reis et al., 2015; Striedter and Northcutt, 2020).

Table 1. Neural correlates of the number sense in different metazoan species (exemplary references)

Taxon/species	Subject condition	Brain signal	Brain areas	Representation	Reference
Mammals					
Human (<i>Homo sapiens</i>)	Awake-behaving	Hemodynamic responses, electrical stimulation, single-neuron activity, lesions	Association areas of the neocortex, specifically posterior parietal and prefrontal cortex	Symbolic and non-symbolic	Lemer et al., 2003; Piazza et al., 2004, 2007; Roux et al., 2009; Arsalidou and Taylor, 2011; Harvey et al., 2013; Kutter et al., 2018
Rhesus macaque (<i>Macaca mulatta</i>)	Awake-behaving	Single-neuron activity	Posterior parietal and prefrontal cortex	Approximate number system	Nieder et al., 2002, 2006; Nieder and Miller, 2004; Nieder, 2012; Viswanathan and Nieder, 2015
Japanese macaque (<i>Macaca fuscata</i>)	Awake-behaving	Single-neuron activity	Posterior parietal cortex	Approximate number system	Sawamura et al., 2002; Okuyama et al., 2015
Domestic cat (<i>Felis catus</i>)	Anaesthetized	Single-neuron activity	Posterior parietal cortex	Approximate number system	Thompson et al., 1970
Domestic dog (<i>Canis familiaris</i>)	Awake-passive viewing	Haemodynamic responses	Association areas of the neocortex	Approximate number system	Aulet et al., 2019
Birds					
Carion crow (<i>Corvus corone</i>)	Awake-behaving	Single-neuron activity	Nidopallium caudolaterale	Approximate number system	Ditz and Nieder, 2015, 2020; Wagener et al., 2018
Amphibians					
Northern leopard frog (<i>Rana pipiens</i>); Pacific tree frog (<i>Hyla regilla</i>)	Awake-immobilized	Single-neuron activity	Torus semicircularis	Sensory filter	Edwards et al., 2002, 2007
Ray-finned fishes					
Zebrafish (<i>Danio rerio</i>)	Awake-passive viewing	Immediate early gene-expression	Pallium, thalamus	Approximate number system	Messina et al., 2020a,b preprint

addition, the superior, medial and inferior frontal gyri, the precentral gyrus, the cingulate gyrus, the insula and the left fusiform gyrus were activated (Arsalidou and Taylor, 2011).

More direct evidence for the involvement of associative neocortical areas in counting and calculation stems from direct electrical stimulation studies in neurosurgical patients (Roux et al., 2009). When these patients were asked to either speak or perform simple calculations while cortical sites were electrically stimulated, only calculation impairments were registered in almost half of the cortical sites in the left parietal and frontal lobes. Besides corroborating the finding that the posterior parietal and the (pre)frontal lobes are essential in number processing (Della Puppa et al., 2013), this also demonstrates that numbers and language are separately represented in the brain.

The electrical activity of ‘number neurons’ (see Glossary) could be directly recorded in patients undergoing treatment for pharmacologically untreatable epilepsy, who were implanted with electrodes in the medial temporal lobe (MTL) (Kutter et al., 2018). Patients performed addition and subtraction with small numbers that were shown either non-symbolically as dot numerosities, or symbolically as Arabic numerals (Kutter et al., 2018). Many MTL neurons were activated by the number of items in the first set, irrespective of the dot array layout (Fig. 4B). Moreover, a small number of another group of MTL neurons were selectively activated by the numerical values of numerals. Selective neurons were tuned to preferred values, a feature also observed in the numerosity-selective neurons found in the monkey cortex (discussed in more detail below).

Nonhuman primates

Most mammalian species for which numerical cognition has been investigated, either in the laboratory or in the wild, belong to the order ‘Primates’. Nonhuman primates that have been studied so far (from phylogenetically basal to advanced primates) are lemurs,

squirrel monkeys, capuchin monkeys, rhesus macaques, baboons, orangutans, gorillas and chimpanzees (Lewis et al., 2005; Thomas and Chase, 1980; Judge et al., 2005; Beran et al., 2008; Hicks, 1956; Brannon and Terrace, 2000; Beran, 2007, 2001; Merten and Nieder, 2009; Smith et al., 2003; Anderson et al., 2007; Matsuzawa, 1985; Beran and Beran, 2004). The behaviour of these nonhuman primates suggests that they have an approximate number system (Box 1) that obeys Weber’s law (see Glossary): discrimination of set sizes is approximate, shows a numerical magnitude and size effect, and – in accordance with Fechner’s law (see Glossary) – is logarithmically compressed (reviewed in Nieder, 2017b, 2019, 2020b).

A rich set of neural data on numerical abilities exists for macaques. Electrophysiological recordings in the parietal, temporal and frontal association cortices of monkeys trained to discriminate set size show ‘number neurons’ that selectively respond to different numbers of items in dot displays (Fig. 4D) (Nieder et al., 2002; Nieder and Miller, 2003; Nieder, 2016a; Okuyama et al., 2015), auditory and visual sequences (Nieder et al., 2006; Nieder, 2012), and hand movements (Sawamura et al., 2002). Importantly, the activity of numerosity-selective neurons is not affected by changes in the physical appearance of the displays (Nieder et al., 2002). This indicates that the neurons are responding to numerical information rather than non-numerical features that may co-vary with the numbers. Some neurons in the prefrontal cortex (PFC) even represent the same number of both visual and auditory events: they respond to number irrespective of the modality (Nieder, 2012).

Areas of the PPC and the PFC exhibit a substantial proportion of ‘number neurons’; only few neurons are selective in the inferior temporal cortex (as expected by chance) (Fig. 4C) (Nieder and Miller, 2004; Vallentin et al., 2012; Eiselt and Nieder, 2013). In the PPC, the areas in the superior parietal lobule (Sawamura et al., 2002) and particularly in and around the IPS contain many ‘number neurons’ selective to countable sets (Nieder and Miller, 2004;

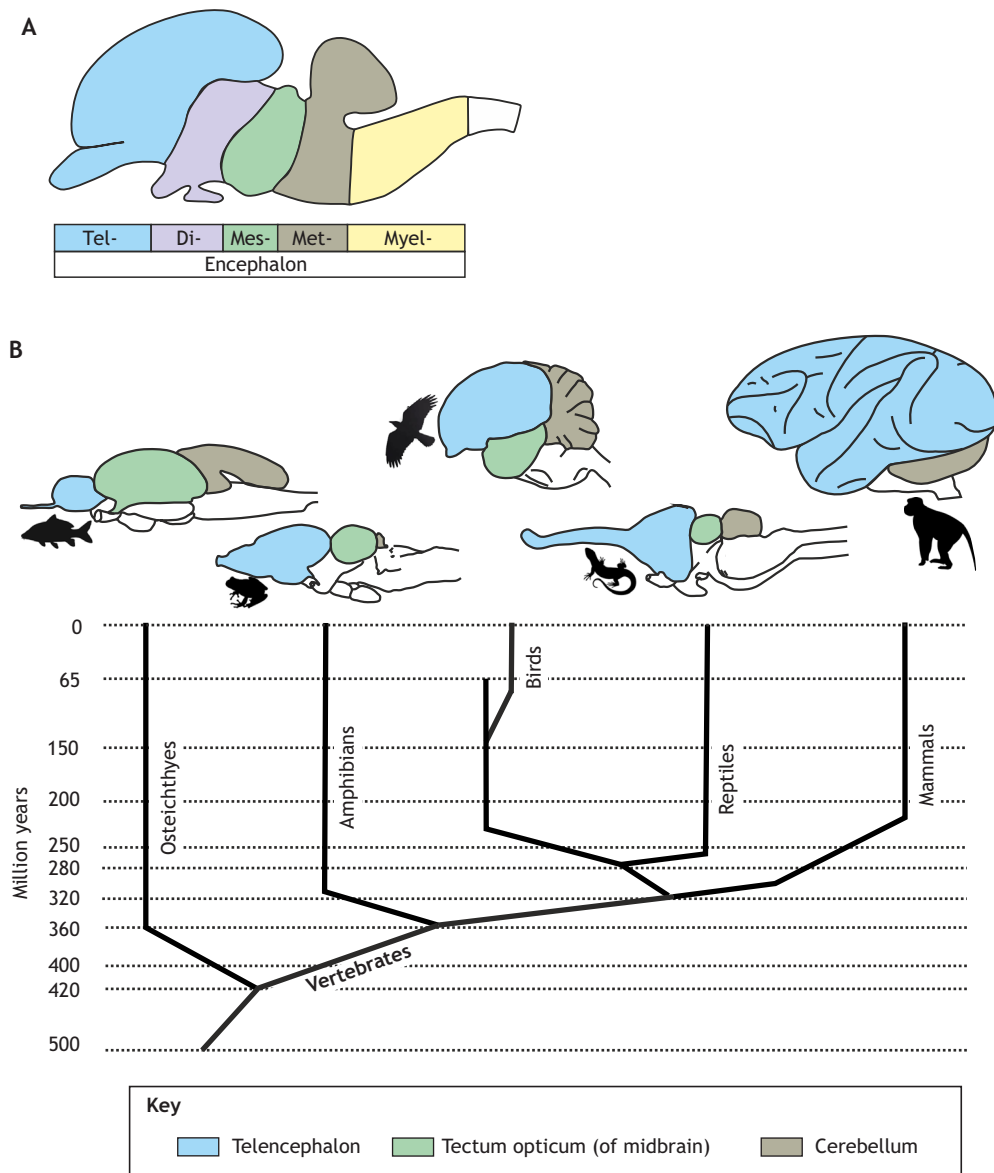


Fig. 3. Vertebrate brains. (A) Schematic lateral view of a generalized vertebrate brain. (B) Lateral views of the brains of extant representative species from the five vertebrate classes (not to scale). The tectum opticum (superior colliculus) is covered by the cerebral cortex in mammals (modified from Northcutt, 2002).

Nieder et al., 2006; Jacob and Nieder, 2014; Viswanathan and Nieder, 2013, 2015, 2020) and even empty sets (Okuyama et al., 2015; Ramirez-Cardenas et al., 2016; Nieder, 2016b). The highest proportion of number neurons in the posterior parietal cortex is found in area VIP (ventral intraparietal area) in the fundus of the IPS; here, around 20% of the recorded neurons are ‘number neurons’ (Nieder and Miller, 2004; Nieder et al., 2006; Tudusciuc and Nieder, 2009; Jacob and Nieder, 2014). About 20–30% of ‘number neurons’ are found in areas around the monkey principal sulcus in the lateral PFC (Nieder et al., 2002, 2006; Nieder and Miller, 2004; Diester and Nieder, 2007, 2008; Nieder and Merten, 2007; Viswanathan and Nieder, 2015). These areas are likely to constitute the monkey homologues of the number-responsive IPS and PFC areas in the human brain (Nieder, 2016a).

The responses of ‘number neurons’ results in a bell-shaped tuning curve with the peak at the respective neuron’s preferred numerosity (Fig. 4B,D). One numerosity-selective neuron can only represent a

small range of the ‘number line’, but the sequentially arranged overlapping tuning curves of a group of number neurons cover the entire range of relevant numerosities (Nieder, 2016a). The coding properties of ‘number neurons’ can explain three pervasive psychophysical effects of set size discrimination (Nieder, 2005, 2016a). First, the overlapping bell-shaped tuning curves of a population of number neurons account for the numerical distance effect, i.e. why animals cannot precisely discriminate similar numerical values (Nieder, 2020b). Second, the numerical size effect (at a given numerical distance the discrimination of larger numerosity becomes more difficult) is explained by the neuronal tuning functions becoming broader with increasing preferred numerosity. Third, and much like the behavioural data (Merten and Nieder, 2009), the tuning curves are mildly asymmetrical when plotted on a linear number scale: only when plotted on a logarithmic scale do they become symmetrical (Nieder and Miller, 2003), an effect also emerging in deep-learning networks (Nasr et al., 2019).

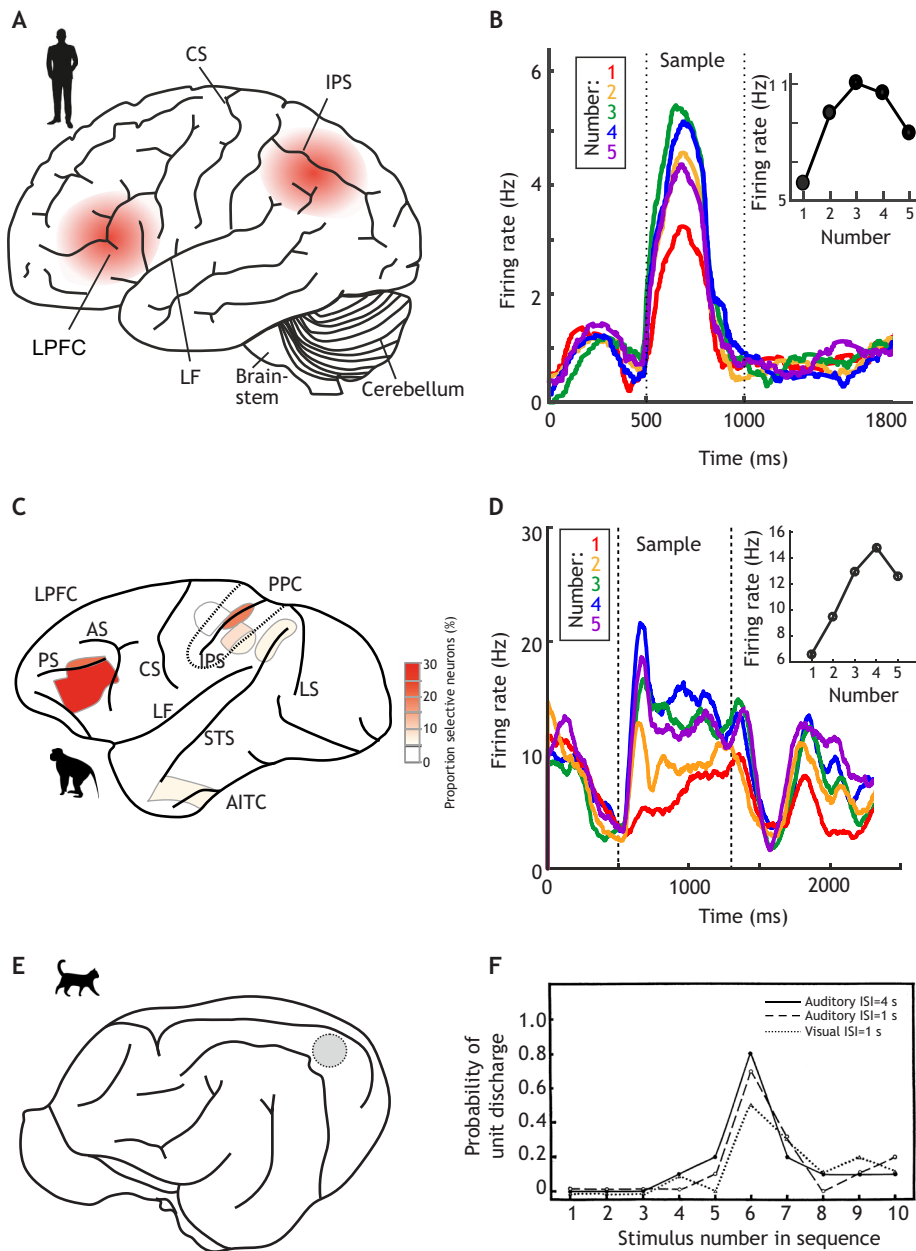


Fig. 4. Representation of number in the mammalian brain. (A) Lateral view of a human brain (left is anterior); red shading shows areas that are consistently activated by numbers in functional imaging studies. (B) A 'number 3' neuron recorded from the medial temporal lobe (MTL) of humans performing a simple arithmetic task with dot numerosities. The spike-density histogram shows the time-resolved average firing rate of a single neuron while the patient sees the number of dots in a sample display (onset at 500 ms, offset at 1000 ms). The firing rate is highest to the preferred numerosity 3, and progressively drops at more remote numerosities. Colours correspond to specific tested numbers from 1 to 5. The inset shows this neuron's numerosity tuning function, i.e. the average firing rate of this neuron as a function of the shown numerosity (after Kutner et al., 2018). (C) Lateral view of a rhesus monkey brain (left is anterior). Recording sites in lateral prefrontal cortex (LPFC), posterior parietal cortex (PPC) and anterior inferior temporal cortex (AITC) are shown. The proportions of numerosity-selective neurons in each area are colour coded according to the colour scale. (D) A 'number 4' neuron recorded from ventral intraparietal (VIP) area of a behaving rhesus monkey during a number discrimination task. The spike-density histogram shows the time-resolved average firing rate of a single neuron while the monkey sees the number of dots in a sample display (onset at 500 ms, offset at 1300 ms). The firing rate is highest to the preferred numerosity 4. The inset shows this neuron's numerosity tuning function (after Viswanathan and Nieder, 2015). (E) Fronto-lateral view of a cat brain (left is anterior). Number neurons were found in the posterior part of middle supra-sylvian gyrus (PMSA) (gray). (F) A 'number 6' neuron recorded from PMSA of the anaesthetized cat. The tuning function shows the probability of discharges as a function of stimulus number in a series of auditory or visual pulses (after Thompson et al., 1970). AS, arcuate sulcus; CS, central sulcus; IPS, intraparietal sulcus; LF, lateral fissure; LS, lunate sulcus; PS, principal sulcus; STS, superior temporal sulcus.

Number neurons are relevant for the monkeys' numerical behaviour. First, when monkeys make judgment errors, the neurons' discharges to the preferred numerosity are noticeably reduced (Nieder et al., 2002; Nieder and Miller, 2004; Nieder and Merten, 2007). Second, transient inactivation of a superior parietal lobule region containing number neurons causes monkeys to make significantly more errors in enumerating their hand movements (Sawamura et al., 2010). The inactivation specifically impairs the number of actions, because the monkeys can perfectly select between different actions and produce hand movements in control tasks (Sawamura et al., 2010). This supports that idea that numerosity-selective neurons underpin the numerical capabilities of primates.

Carnivorans

Carnivorans have been shown to discriminate quantity spontaneously in forced choice tests both in the wild and after training in the laboratory. The species that have been tested include dogs, cats, bears, lions, hyenas, sea lions and raccoons (West and

Young, 2002; Pisa and Agrillo, 2009; Chacha et al., 2020; Vonk and Beran, 2012; McComb et al., 1994; Benson-Amram et al., 2011; Abramson et al., 2011; Davis, 1984).

The first electrophysiological exploration of a neuronal correlate of a number sense was done in 1970 in cats (Thompson et al., 1970). Recordings were obtained from the posterior association cortex (posterior part of middle supra-sylvian gyrus) of the anesthetized cat during passive exposure to sequences of auditory or visual stimuli (Fig. 4E). A few neurons were found that responded mostly to certain numbers of stimuli in the series, regardless of stimulus modality or frequency (Fig. 4F). However, only five of the 500 tested neurons showed such number-selective activity, a number that could be expected by chance alone. Nevertheless, this study was an important first attempt to reveal the neural basis of the number sense. More recently, a functional imaging study in awake dogs passively viewing dot arrays found patchy quantity activations in different cortical regions, and for some dogs also in parietal areas (Aulet et al., 2019). These quantity representations in the carnivoran

parietal association cortex region could potentially constitute an equivalent of the numerosity sensitivity found in primate PPC.

Birds

During the course of evolution, the dorsal part of the telencephalic pallium gave rise to the cerebral cortex (neocortex) in mammals, of which the associative cerebral cortex is the origin of the mammalian sense of number. Outside of mammals, however, other regions of the pallium evolved into drastically different arrangements several times independently in the different vertebrate groups (Briscoe and Ragsdale, 2019).

The pallium in sauropsids (birds and non-avian reptiles), which separated from the mammalian lineage around 320 million years ago, lacks a six-layered neocortex. Instead, non-avian reptiles exhibit a three-layered cerebral cortex (Ulinski, 1983). However, in birds, descendants of archosaur reptiles, a three-layered cerebral cortex is surprisingly absent. Compared with other reptiles, birds have large brains relative to their body sizes (Tsuboi et al., 2018) and have massively increased numbers of neurons (Olkowicz et al., 2016). Neurons in the avian pallium group together in dense clusters (called 'nuclei') (Reiner et al., 2004). Nevertheless, the avian pallium seems to share a conserved set of neuronal cell types and circuitries with other amniotes, including the mammals (Karten, 1969; Dugas-Ford et al., 2012; Jarvis et al., 2013; Briscoe and Ragsdale, 2018). The sauropsid pallial 'dorsal ventricular ridge', which is thought to be homologous with the mammalian claustrum and amygdala rather than with the mammalian neocortex (dorsal pallium) (Tosches et al., 2018; García-Moreno et al., 2018; Cárdenas et al., 2018), developed particularly prominently in birds, and it displays morphological features that are not seen in other reptiles. In a fascinating case of convergent evolution, these pallial specializations endowed some birds with superior cognitive abilities (Nieder, 2017a) that rival those of even phylogenetically advanced nonhuman primates (Clayton and Emery, 2015; Nieder, 2017b).

In the wild, birds use numerical information to forage for food (Hunt et al., 2008; Bogale et al., 2014), to communicate with conspecifics (Templeton et al., 2005) or to counteract nest parasitism (Lyon, 2003; Wang et al., 2020). Unlike non-avian reptiles, birds can be trained to discriminate stimuli based on the controlled number of

objects (Emmerton and Renner, 2006; Scarf et al., 2011). Besides newly hatched chicks (Rugani et al., 2008), gray parrots (Pepperberg and Gordon, 2005) and other birds, members of the corvid family of songbirds (jays, magpies, crows and ravens) are particularly renowned for their flexible behaviour (Emery and Clayton, 2004) and number skills (Koehler, 1941, 1951; Smirnova et al., 2000; Bogale et al., 2011; Ditz and Nieder, 2016b). In fact, the behavioural performance of crows looks almost identical to that of monkeys. Crows show the characteristics of Weber's and Fechner's laws (Ditz and Nieder, 2016b) and understand empty sets as a quantitative category (Kirschhock et al., 2021).

The neuronal signatures of number discrimination in birds have been explored in combined behavioural and neurophysiological experiments analogous to the monkey studies (Table 1). In crows that distinguished the number of visual objects in controlled dot arrays, single-cell activity was recorded from their nidopallium caudolaterale (NCL) (Fig. 5A) (Ditz and Nieder, 2015, 2016a, 2020). The NCL, which arose during evolution from the sauropsid dorsal ventricular ridge in the posterior bird telencephalon, is a high-level pallial integration centre (Veit et al., 2015; Moll and Nieder, 2015; Rinnert et al., 2019; Rinnert and Nieder, 2021; Nieder et al., 2020). As a multimodal pallial area, the avian NCL receives input from all sensory modalities and projects to premotor regions. It is modulated by dopamine, and interacts with limbic, visceral and memory-related structures. The NCL is therefore considered to be a potential functional equivalent of the mammalian PFC (Divac et al., 1985; Güntürkün, 2005), but may also adopt functions of the mammalian posterior parietal cortex, or association cortices in general.

The corvid NCL contains 'number neurons', just like the monkey IPS and PFC, and an analysis of error trials shows that the activity of NCL number neurons is related to the accuracy of the crows' performance (Fig. 5B) (Ditz and Nieder, 2015). Moreover, NCL neurons are approximately tuned to number, and they show a neuronal distance and size effect that follow Weber's law. In addition, and as expected by Fechner's law, the neuronal tuning functions are best described on a logarithmic number line (Ditz and Nieder, 2015, 2016a). NCL neurons also encode the number of sequentially presented dots (Ditz and Nieder, 2020), again equivalent to IPS neurons in monkeys (Nieder et al., 2006).

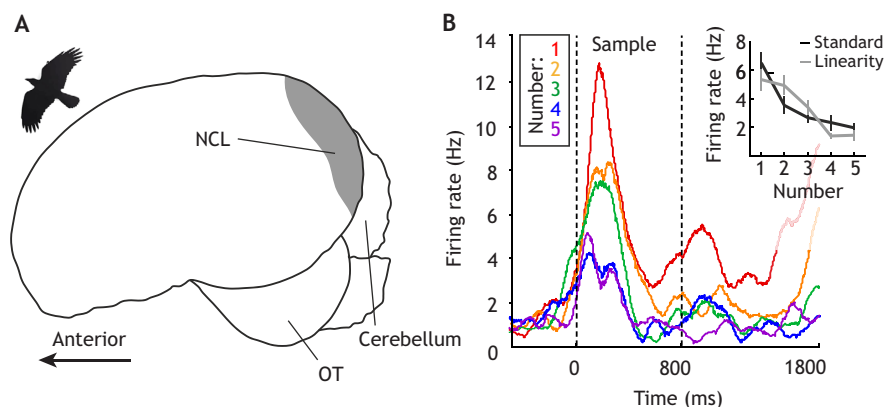


Fig. 5. Representation of number in the crow brain. (A) Lateral view of a crow brain depicting the nidopallium caudolaterale (NCL, shaded) in the telencephalon. OT, optic tectum. (B) A 'number 1' neuron recorded from the NCL of crows performing number discrimination with dot numerosities. The spike-density histogram shows the time-resolved average firing rate of a single neuron while the crow sees the number of dots in a sample display (onset at 0 ms, offset at 800 ms). The firing rate is highest to the preferred numerosity 1, and progressively drops towards more remote numerosities. Colours correspond to specific tested numbers from 1 to 5. The inset shows this neuron's numerosity tuning function to two different arrangements of the dots: in the 'standard' arrangement, black dots of different size were randomly presented on a grey circular background; in the 'linearity' arrangements, all dots were presented along a straight line. Irrespective of the dot arrangement, the neuron showed the same tuning (Ditz and Nieder, 2015).

Interestingly, and in contrast to findings in human hippocampus (Kutter et al., 2018), neurons in the crow hippocampal area are unresponsive to set size (Ditz et al., 2018). This shows that number representations are anatomically confined and not found throughout the bird brain. It also highlights interesting discrepancies in number processing between the primate and avian brain, despite the striking coding similarities found in the mammalian cerebral cortex and the avian NCL.

The numerical skills of the close relative of birds, the (non-avian) reptiles (Dyke and Kaiser, 2011), have rarely been investigated, and neuronal studies are lacking entirely. The first studies in lizards reported a lack of spontaneous discrimination of numerosity (Miletto Petrazzini et al., 2017, 2018). Only one study, in tortoises, reported successful discrimination of both size and numerical quantity, albeit for controlled stimuli only for 1 versus 2 discriminations (Gazzola et al., 2018).

Amphibians

Amphibians (e.g. salamanders and frogs) show a far simpler pallial architecture compared with mammals and sauropsids that lack clear nuclear or layered cell arrangements (Briscoe and Ragsdale, 2019). Although the roles of the amphibian telencephalon are not well understood, the relatively large midbrain with optic tectum and torus semicircularis shows integrative functions (Fig. 3) (Wilczynski, 2009).

Whether amphibians can be trained to respond to complex stimuli such as numerical categories remains to be seen, but they spontaneously respond to rudimentary quantity information (Uller et al., 2003; Krusche et al., 2010; Stancher et al., 2015), even as tadpole larvae (Balestrieri et al., 2019). For example, frogs (*Bombina orientalis*) reliably choose three food items over two, six items over three, and eight items over four (Stancher et al., 2015), and they show 'ratio-dependent' approximate quantity discrimination (Box 1).

Neuronal data related to quantity information have been recorded in the anuran midbrain in the context of acoustic communication (Table 1). Many advertisement calls in frogs consist of a specific temporal patterning in the form of a series of pulses which are required for call recognition by females (Klump and Gerhardt, 1987; Gerhardt, 1988). As a neural substrate for this auditory selectivity, 'pulse-integrating' neurons that show sharp tuning to pulse repetition rate have been recorded in the awake-immobilized frog midbrain, more precisely the torus semicircularis (Alder and Rose, 1998). Such neurons fire in response to constant call sequences that have just one more pulse than the specific threshold number of pulses. It was concluded that these neurons were 'counting' the number of fixed consecutive inter-pulse intervals (Edwards et al., 2002, 2007; Naud et al., 2015; Rose, 2018). However, such neurons are not generalizing across sensory features, as would be expected for abstract number neurons. They only respond to very regular calls with a constant inter-pulse interval (e.g. 10 pulses always separated by 10 ms); they do not respond to calls with mixed intervals, even if the stimulus has the same average pulse rate as the constant-interval stimulus. Such 'interval-counting' neurons may therefore best be characterized as sensory filters for the reflexive recognition of very specific frog calls rather than as number neurons responding to abstract set sizes.

Ray-finned fishes

Numerical abilities in fish have been studied extensively in recent years (reviewed in Agrillo and Bisazza, 2018; Agrillo et al., 2017). For example, individual fish in an unfamiliar environment tend to join the larger of two shoals (Hager and Helfman, 1991; Mehrlis et al., 2015). Fishes show ratio-dependent discrimination (Agrillo

et al., 2008), indicating that performance obeys Weber's law (Potrich et al., 2015). Despite this interest in fish numerical behaviour, the underlying neural mechanisms remain largely unknown (Table 1).

Recent studies in zebrafish aimed to elucidate major brain regions involved in quantity discrimination using not electrophysiology, but the histological verification of the expression of immediate early genes (IEGs; see Glossary) (Gallo et al., 2018). In these studies, a spontaneous habituation/dishabituation protocol was used (Messina et al., 2020a,b preprint). The rationale is that, after repeated presentation of a habituation numerosity, a sudden change to another, dishabituation numerosity will activate neurons tuned to this new quantity. For instance, zebrafish passively viewed repeated presentations of three dots controlled for continuous physical variables (e.g. surface area, position, density) during habituation; then, during the dishabituation phase, the fish saw nine dots. After the fish were killed and their brains processed, IEG expression (c-fos and egr-1) was explored in the major brain regions of the fish brain. The most consistent modulation in IEG expression as a function of numerosity change was observed in the telencephalon and thalamus (Messina et al., 2020a). In the telencephalon, a specific activation of the caudal part of the dorso-central division of the pallium was reported (Messina et al., 2020b). The latter finding suggests a pallial mechanism for approximate numerical quantity that share similarities across vertebrates.

Number sense in protostomes

In contrast to deuterostome chordates (including vertebrates), which have a dorsal central nervous system, protostomes evolved a ventral nerve cord with a circumoesophageal anterior brain (Fig. 2). Despite the fact that many phylogenetically advanced arthropods and molluscs show quantitative or even numerical skills, the neural correlates have not been explored in any protostome so far. Below, I discuss promising candidate regions in the insect, spider and cephalopod brain that – owing to their connectivities and processing characteristics – could contain neurons sensitive to the number of elements in a (visual) stimulus.

Arthropods

Arthropods (including crustaceans, insects and spiders) are defined by their segmented bodies, hard outer skeletons and the name-giving jointed limbs. They are by far the largest and most diverse phylum of animals on the planet. According to current estimates, there are a total of 7 million terrestrial arthropod species; of those, 5.5 million are insects, of which 1.5 million are beetles (Stork, 2018). They all share a common protostome ancestor that lived more than 550 million years ago. In arthropods, the central nervous system consists of a ventral, solid nerve cord and a series of linked ganglia associated with various body segments (Fig. 6A). In the head region, the 'supraoesophageal zone' (the 'brain') and 'suboesophageal zone', respectively, refer to brain tissue above and below the level of the oesophagus (Ito et al., 2014). The brain consists of a protocerebrum, deutocerebrum and tritocerebrum.

Insects

Most of the behavioural evidence for numerical competence among the protostomes comes from insects, and honey bees in particular (reviewed in Pahl et al., 2013; Skorupski et al., 2017; Giurfa, 2019). Bees use numerical information to navigate (Chittka and Geiger, 1995) and to assess the quantity of flowers available in a patch to maximize foraging efficiency (Howard et al., 2020). Importantly, bees can also readily be trained to discriminate number under

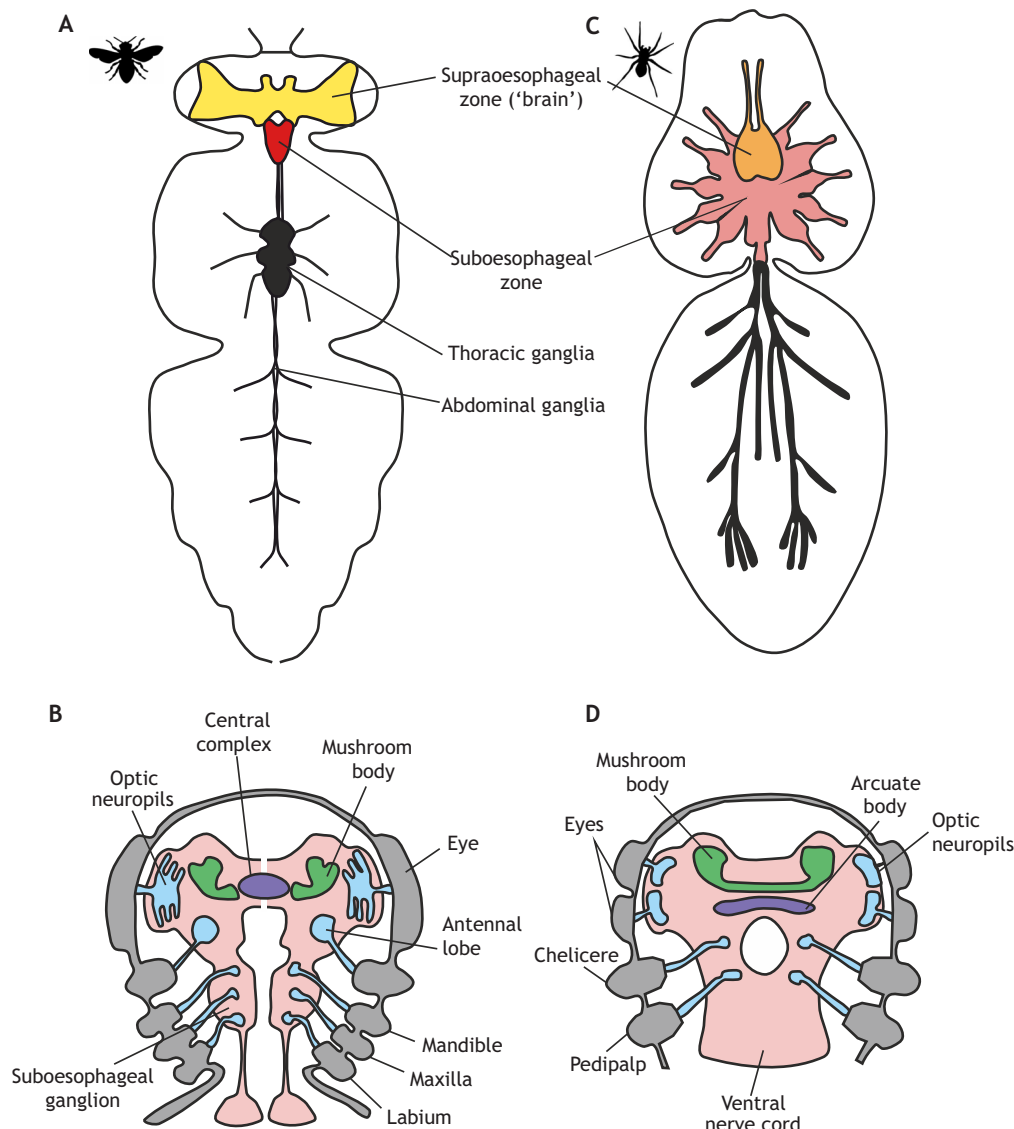


Fig. 6. Arthropod central nervous system. (A) Dorsal view of a simplified insect central nervous system (top is anterior). (B) Closeup of head region with schematic representation of the brain and head sensory organs of insects. Nerve tissue in pink, sensory nerves in blue (colours differ from A). (C) Dorsal view of a simplified spider central nervous system (top is anterior). (D) Closeup of head region with schematic representation of the brain and head sensory organs of spiders. Images in B,D after Hartenstein, 2017.

controlled conditions (Dacke and Srinivasan, 2008; Howard et al., 2018). Training studies show that bees can form abstract numerical concepts about absolute numerosity, the numerosity zero, ordinal rank and the greater than/less than rule (Howard et al., 2018; Bortot et al., 2019). Compared with the 86 billion neurons that make up our human brain (Azevedo et al., 2009), bees perform these tasks with a brain that has a volume of 1 mm³ and less than a million neurons (Menzel and Giurfa, 2001). Where could information about the number of visual items be represented in the bee brain?

A first and preliminary representation of the number of visual items could be realized in the optic lobes. They constitute the primary visual centres of the bee brain and show behaviourally relevant processing (Paulk et al., 2014). Neurons in the optic lobes could extract early visual numerosity information in an automatic way (Skorupski et al., 2017). Modelling approaches, some directly inspired by the behavioural results from bees, suggest that basic numerical competence could be achieved by a very limited number

of neurons (Skorupski et al., 2017). For example, a computational study showed that a network composed of only four neurons could be sufficient to master the discrimination and ordering of small quantities (Vasas and Chittka, 2019). This model relies on the hypothesis that bees scan the elements in a scene sequentially and visit each (flower-like) element once during enumeration, a mechanism that seems to be realized in bumblebees (MaBouDi et al., 2020).

For a simultaneous assessment of numerosity at a single glance or for more complex enumeration, the optic lobes would not suffice because they process basic visual features rather than quantitative categories. Higher-order associative areas in the insect brain, specifically the protocerebrum, would be required to give rise to more abstract, perhaps even cross-modal number representations. One candidate area is the central complex (Fig. 6B), which has been claimed to be homologous to the vertebrate basal ganglia (Strausfeld and Hirth, 2013b; Fiore et al., 2015). Interestingly, the basal ganglia

(as well as a selection of other subcortical areas) are activated in the human brain during number and calculation tasks (Arsalidou and Taylor, 2011). The central complex receives highly processed and topologically ordered visual input via the optic lobes and other visual neuropils (Glossary) (Pfeiffer and Homberg, 2014), and its neurons are involved in visual object recognition and visual memory (Ofstad et al., 2011; Pan et al., 2009), which would be required to represent the number of items in a stimulus. As a hub between sensory input and motor output, the central complex is also involved in action selection, motor coordination, orientation and navigation (Fiore et al., 2015; Plath and Barron, 2015; Barron et al., 2015). Its control of the temporal structure of motor movements could also serve in extracting the sequential number of items or producing sequential numerical output.

Perhaps the most promising candidate region for abstract and cross-modal number representations in arthropods are the bilateral mushroom bodies in the protocerebrum (Fig. 6B). The multimodal associative mushroom bodies are the iconic learning and memory centres of insects; they are known to be responsible for non-elemental learning, that is forms of learning that go beyond simple associations between two stimuli (e.g. Pavlovian conditioning) or between a stimulus and a response (Giurfa, 2003; Devaud et al., 2015; Plath et al., 2017; Li et al., 2017). The anatomy and physiology of the mushroom bodies has been compared to neural architecture of the mammalian cerebellum and pallial structures such as the hippocampus, amygdala and prefrontal cortex (Tomer et al., 2010; Farris, 2011; Menzel, 2014; Oswald and Waddell, 2015; Hige et al., 2015), all of which are implicated in number coding in the human brain (Arsalidou and Taylor, 2011; Kutter et al., 2018). As cognitive brain centres, mushroom bodies integrate highly processed multimodal information (Strube-Bloss and Rössler, 2018), and would thus constitute an ideal candidate for an abstract, cross-modal representation of numbers.

Spiders

Spiders (together with scorpions, mites and ticks) belong to the arthropod subphylum Chelicerata. Spiders seem to be the cognitively most advanced chelicerates, and there is suggestive evidence that spiders spontaneously use numerical cues during foraging. For instance, communal spider-eating spiders (*Portia africana*) base their decision of whether to settle near a prey spider's nest on the number of conspecifics already present; they prefer one conspecific spider over zero, two or three spiders (Nelson and Jackson, 2012). Sit-and-wait spiders also seem to rely on numerical cues. For example, golden orb-web spiders (*Trichonephila clavipes*) accumulate prey pantries on their webs. If they lose their pantries, the spiders search for them, and their search time increases proportionally to the prey counts they lost (but also to the prey mass they lost) (Rodríguez et al., 2015). This behaviour suggests some rudimentary memory of prey numerosity in spiders. Whether spiders can be trained to discriminate numerosity under controlled stimulus conditions has not been tested so far, but it might be possible (De Agrò et al., 2017).

The chelicerate bauplan consists of two tagmata, the prosoma and the opisthosoma. In spiders, the ganglia of the central nervous systems fuse into large masses in the prosoma, giving rise to a rather condensed and centralized brain (also called synganglion) (Fig. 6C) (Barth, 2002; Foelix, 2010). The oesophagus runs through the synganglion and divides it into supraoesophageal ('brain', largely protocerebrum) and suboesophageal parts. The protocerebrum is associated with visual and more cognitive processing (Hartenstein, 2017; Long, 2021), and is therefore a potential candidate for quantity processing.

The protocerebrum encompasses large optic lobes and neuropils that process visual information from the eyes, and a centre with a number of structured neuropils (Strausfeld et al., 2009). One of these prominent structures is a central complex termed the 'arcuate body' (Doeffinger et al., 2010) which comprises several layers of structured neuropil crossing the midline and also receives input from the midbrain (Fig. 6D) (Barth, 2002). The arcuate body is involved in spatial orientation and navigation requiring multimodal integration (reviewed in Strausfeld, 2019; Strausfeld, et al., 2016). Neuronal recordings show that the spider arcuate body processes multimodal information and responds to high-level visual (Menda et al., 2014), auditory and tactile information (Shamble et al., 2016).

Another prominent structure in the protocerebrum are the paired bilateral mushroom bodies (Fig. 6D). The mushroom bodies in spiders are targeted mainly by second order visual interneurons (Strausfeld et al., 1993, 1998), but their function is less well explored compared with those of insects. The mushroom bodies could also be a candidate region for abstract visual number representations.

Molluscs

So far, only one behavioural study suggests rudimentary quantity discrimination in molluscs, specifically in a cephalopod – the cuttlefish *Sepia pharaonis* (Yang and Chiao, 2016). In spontaneous two-alternative choice tests, cuttlefish prefer to capture two over one, three over two, four over three, and five over four live shrimps. In these experiments, their choice of prey number depends on the quality of the prey and on their appetite state. Behavioural experiments under controlled stimulus conditions and in trained cephalopods have so far not been performed.

The prototypic nervous system of molluscs shows tetraureny, with four nerve cords originating from a nerve ring. Cephalopods, however, have a highly compact brain (Moroz, 2009). For example, the cephalopod *Octopus vulgaris* has a very large brain for a mollusc and a protostome in general, with over 30 lobes (Young, 1971). In total, the octopus nervous system contains more than 500 million neurons (Young, 1963), which is probably more than any other invertebrate. However, more than half of these neurons are in the arm ganglia. In the cephalopod nervous system, a large range of quite delicate processes is delegated to peripheral centres. The central masses of the nervous system, comprising a series of ganglia of molluscan origin that form lobes, thus contains less than 200 million nerve cells (and three-quarters of these are in the optic lobes). The remaining ~40 million nerve cells are in the actual brain (central lobe system), divided between two regions: the supraoesophageal mass and the suboesophageal mass (Young, 1963).

Attempts have been made to identify analogies between various lobes of the cephalopod brain and parts of the vertebrate brain (Shigeno et al., 2018), which allows us to speculate about putative quantity representations in cephalopods. Visual quantity could be represented in the optic lobe (which receives information from the simple cephalopod retina and performs some important functions of the vertebrate retina), and its recipient structure, the peduncle lobe, could represent simple types of visual numerosity. More complex, potentially multi-modal, quantity representation might be expected in higher centres, such as the frontal lobe and vertical lobe systems that have been functionally equated with the pallium of the vertebrate endbrain. Moreover, the vertical lobe has been anatomically linked with the arthropod mushroom body (Shomrat et al., 2011). These lobe systems have been shown to be involved in visual and tactile discrimination and memory processing through ablation experiments in combination with behavioural assays

(Boycott and Young, 1957; Wells and Wells, 1958; Wells, 1959; Maldonado, 1963, 1965; Young, 1991). Unfortunately, the neurophysiology of the lobe system is rarely explored (Butler-Struben et al., 2018; Turchetti-Maia et al., 2019), and neuronal recordings in behaving cephalopods seem to be missing.

Conclusions and future directions

Neurophysiological studies in different vertebrate taxa, such as mammals, birds and fishes, have demonstrated that the pallial regions of the endbrain are involved in explicit number representations. Where and how number is represented in the protostomian brain remains so far elusive.

The location and mechanisms of numerical skills are best understood in the human and primate brain, and to some extent in the bird brain. However, to find out whether some of these skills and the underlying brain structures might have been present in the last common ancestor of birds and mammals, reptiles also need to be explored. The best behavioural evidence of numerical competence in reptiles comes from turtles, which are regarded as a sister taxon to archosaurs (Chiari et al., 2012). Turtles would therefore be good candidates to learn about amniote number competence.

From a comparative point of view, the most pressing question is the neural correlate of numerical competence in protostomes. Among the three tested protostome groups – insects, spiders and cephalopods – the behavioural evidence of a sense of number is – with only one study – weakest in cephalopods. Compared with arthropods, the cephalopod brain is barely explored, both from a neuroanatomical and particularly from a neurophysiological point of view. A combination of characteristics, such as a relatively short lifetime, absence of a skeleton, and a marine lifestyle render cephalopod neuroscience extremely challenging. Thus, cephalopods are probably not the ideal candidates in which to explore abstract quantity representations in protostomes; arthropods seem to be more promising.

Compared with insects, spiders are exotic models in neuroscience. Despite some spiders showing spontaneous (but also very rudimentary) numerical skills, it is currently not known whether they could be trained to discriminate controlled numerosity stimuli. Spiders have been trained successfully to discriminate simple stimuli and based on their acute vision, they might be able to discriminate dot displays. Although challenging, recording neuronal activity from the brain of spiders is possible and this could be explored in the number domain.

The most promising candidate for a neuroscientific exploration of a protostome sense of number would be insects. Although flies are frequently studied in neuroscience, it is the honeybee that exhibits sophisticated numerical and other cognitive skills. It would certainly be most rewarding for cognitive neuroscience if it were possible to transfer the methodological tool kit that has been established for flies – from genetic to imaging approaches – to the bee brain. Of course, the bee brain is anything but simple, but it offers the best chance of understanding numerical processing in a brain that is so radically different from a vertebrate brain.

In order to understand how evolution shaped different animal brains to process numerical information, a comparative neuroscientific approach will be indispensable. Studies in both closely and distantly related animal species will be necessary. The first approach will help us to decipher functional divergence of neural structures and operation due to adaptive pressures exerted on brains of common origin. The latter approach will be necessary to allow us to understand functional convergence of neural structures and operation in phylogenetically distinct animal lineages.

Competing interests

The author declares no competing or financial interests.

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