

Neural coding of numerosness

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ABSTRACT

Perception of numerosness, i.e. number of items in a set, is an important cognitive ability, which is present in several animal taxa. In spite of obvious differences in neuroanatomy, insects, fishes, reptiles, birds, and mammals all possess a “number sense”. Furthermore, information regarding numbers can belong to different sensory modalities: animals can estimate a number of visual items, a number of tones, or a number of their own movements. Given both the heterogeneity of stimuli and of the brains processing these stimuli, it is hard to imagine that number cognition can be traced back to the same evolutionary conserved neural pathway. However, neurons that selectively respond to the number of stimuli have been described in higher-order integration brain centres both in primates and in birds, two evolutionary distant groups. Although most probably not of the same evolutionary origin, these number neurons share remarkable similarities in their response properties. Instead of homology, this similarity might result from computational advantages of the underlying coding mechanism. This means that one might expect numerosness information to undergo similar steps of neural processing even in evolutionary distant neural pathways. Following this logic, in this review we summarize our current knowledge of how numerosness is processed in the brain from sensory input to coding of abstract information in the higher-order integration centres. We also propose a list of key open questions that might promote future research on number cognition.

1. Introduction

In everyday life animals are continuously facing different stimuli and need to evaluate different options; the meaning they attribute to them strongly depends on the context. For example, when selecting between two food sources (e.g. fruit trees) we would need to compare the amount of food provided by these sources (how many fruits are on the trees). When returning home facing different streets, we would try to take the shortest route possible. This need to compare different amounts or entities makes quantity discrimination very important for all animal species.

It is possible to differentiate between continuous and discrete quantities. Continuous quantities - like the length of a route or the total weight of fruits - are extensive and can be infinitely subdivided in several continua. On the contrary, discrete quantities - like a number of steps or a number of fruits - are of a specific cardinality (i.e. how many elements are in a set) and can be divided up to indivisibles.

We can use numbers to measure continuous quantities by dividing these into a finite number of units, thus reducing them to a cardinal set - e.g. the book weighs 400 units of gram - or more directly to measure

discrete quantities - e.g. there are 3 windows in this house. In general, numbers are abstract concepts (Frege, 1953) and there are both cardinal and ordinal numbers. They are different from *numerals* - signs that refer to specific numbers/quantities and we use to make mathematics - as well from *numerosness* and *numerosity*. Stevens (2006) introduced the term *numerosness* referring to the concrete items that we *directly* perceive and *approximately* estimate, e.g. the number of fruits on our table when we enter the room. On the other side, *numerosity* is the property of a set - simply cardinality - that can be assessed through counting or one-to-one correspondence, e.g., if we want to be sure to have enough fruits for each diner at our table we can progressively associate each fruit to a numeral or to each person.

Despite being used without distinctions in the literature, the difference between numerosness and numerosity is meaningful because these terms refer to separate phenomena (Dos Santos, 2022). When animals discriminate two different groups of food items, they are dealing with a direct perception of *numerosness* and its approximate quantity estimation. It is a direct perception supported by our sensory system (see below for discussions on sensory adaptation etc.). Instead, in order to be assessed, numbers (*numerosity*) require a procedure (counting or

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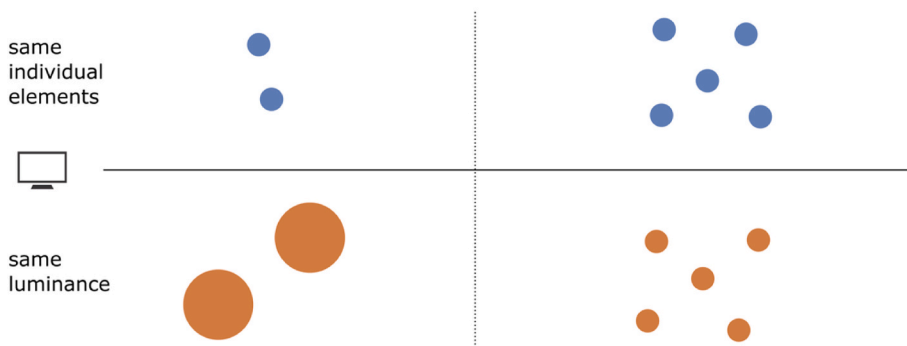
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one-to-one correspondence) and the use of some tools (e.g. numerals, names or items) as we learn to do at school. Therefore, this process involves different cognitive abilities and should be distinct from the first process. Indeed, few animal species seem able to perform some form of counting or use of symbolic tools if trained (e.g. [Kirschhock and Nieder, 2022](#)) while most of them can approximately perceive and discriminate different quantities of food or mates. Another important distinction regards most experiments on quantity estimation: while the experimenter has a precise measure of the number of stimuli presented (numerosity), the tested animal approximately estimates them (numerousness).

Numerousness can refer to simultaneous-spatial or sequential-temporal quantities, for example the number of fish in a pond or the number of calls of a bird. Also, it can be perceived by very different sensory modalities. For example, the number of conspecifics in a group can be perceived through the visual system (e.g. [Stancher et al., 2013](#)) while the number of warning calls can be detected by the auditory system ([Templeton et al., 2005](#)); Even from these overly simplified examples, it is apparent that numerousness is usually correlated with continuous variables: the more fruits the more the weight, the more calls the longer the duration. Animals facing a set of elements could be driven by these continuous variables rather than by numerosness while evaluating the stimulus (for a detailed discussion see [Leibovich et al., 2017](#)). This creates a major problem for scientists who want to study the mechanisms of numerosness perception: when dealing with (non-linguistic) animals, the experimental design needs to control for confounding continuous magnitudes. In the case of visual discrimination, these controls usually include the total area and perimeter of elements in a set, as well as their disposition and density. However, when presenting two stimuli for comparing their numerosness, it is impossible to control for all the involved magnitudes simultaneously, given the geometrical constraints ([Fig. 1](#)). For example, if we want to control for the overall area in a 2 vs 5 comparison, such that an animal could not be biased by the total stimulus dimension or luminance, we end up with smaller stimuli in the larger set, a different possible confounding factor (for a more detailed discussion and a software to create controlled stimuli see [Zanon et al., 2022](#)).

It's of major importance to consider these technical challenges not only when studying the behavior, but also when investigating the brain

a. 2 vs. 5 spatial/parallel representation



b. 2 vs. 5 temporal/sequential representation

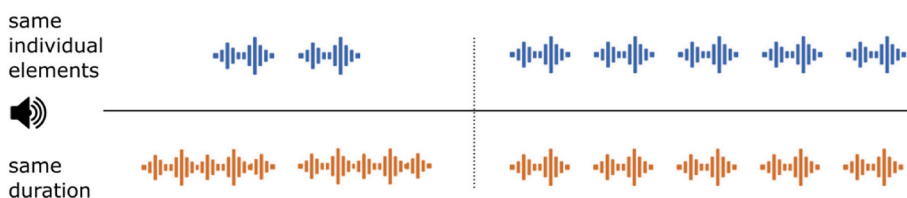


Fig. 1. Examples of stimuli in a 2 vs. 5 comparison. a. Visual arrays with a different number of dots are a classical example of stimuli used in experiments investigating parallel (i.e. simultaneous in space) numerosness discrimination in the visual domain. b. Sequences with a certain number of tones or sounds could be used to investigate temporal (i.e. with a sequential presentation) discrimination in the auditory domain. Generally, specific attention should be given to other possible confounding physical variables different from numerosness. For example, maintaining all the individual elements identical across all the stimuli (blue examples), when comparing two different amounts not only the number of items will vary but also other quantities (e.g. luminance and sound duration, respectively for visual and auditory presentation). A possible solution is to alternate the previous stimuli with others in which these confounding quantities are equalized between different numerosness (orange examples).

level, trying to unravel the neural coding of these stimuli.

The term “neural code” usually refers to the way in which a given property of the world is transformed into the activity of single neurons or neural populations. This idea relies on a communication metaphor: some neurons communicate with other neurons, sending and interpreting messages.

The concept of a neural code derives from Shannon’s coding theory ([Gallistel, 2018](#)), which defines the code more generally as a mapping between a set of symbols (concepts or objects with meaning) and a set of signals (physical entities) - e.g. the symbols A, B, and C can be encoded into binary signals 101, 010, and 111 respectively. The code is used to encode information (symbols) into signals in a way that can be transmitted over a communication channel, such as a telephone line or a wireless network. Information theory assumes a receiver or interpreter who can understand both signals and symbols, as well as their relationship; a noise source is contemplated as well ([Nizami, 2019](#)). See [Fig. 2](#) for a schematic.

Applying this definition to the process of numerousness perception, we could hypothesize that: (i) the information source is the external stimulus (e.g. an array with a certain number of dots, which we perceive visually; see [Fig. 1a](#)); (ii) the transmitter is represented by the sensory system, which translates the external input into a signal suitable for transmission; (iii) the transmission channel is the neuronal network connecting the sensory areas to upstream brain regions which act as (iv) receiver, i.e. reconstruct the message (e.g. the so-called “number neurons” reconstructing the tuning curves to provide an estimation, see later); (v) the destination is represented by the motor areas and body elements the message is intended for and which are supposed to drive action accordingly; (vi) the noise source is contemplated at the level of signal propagation and is apparent in the uncertainty in numerousness estimation (as described by Weber’s law, see later).

In particular neural processing can be affected by multiple noise sources: for example, sensory noise due to physical limitations of sensory perception can limit the ability to perceive external stimuli. Additionally, cellular noise at the level of single neural activity comes from stochasticity of many cellular mechanisms and results in the variability of neural response ([Faisal et al., 2008](#)).

However, some scholars do point out to the fact that the term “neural code” might be misleading and the framework not appropriate when

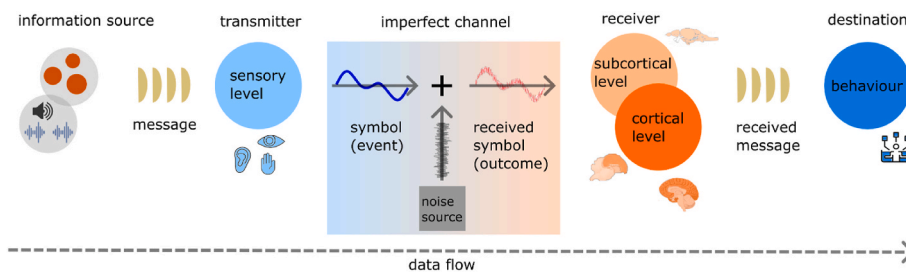


Fig. 2. Schematic of different steps in numerosity estimation according to Shannon's theory. A possible interpretation of the neural code for numerosity estimation could be described in terms of Shannon's theory: in this case (i) the information source is given by the number of elements in stimuli, (ii) the transmitter is the sensory system, (iii) the channel is the nervous system, (iv) the receiver are neural ensembles at the subcortical level and in the cortex (e.g. number neurons) (v) the destination is the behavioral output, (vi) the noise source is provided by the noisy neural transduction but could also be dictated by biological elaboration needs (e.g. logarithmic scale

representation; in this case, we can see the noise source as the ANS itself, i.e. a lossy compression of numerosity). (Adapted from [Nizami, 2019](#)).

speaking about information for organisms (e.g., [Bickhard, 2009](#); [Brette, 2019](#)). While it is often used technically for correlations between two experimental measures (neural activity and properties of stimuli such as location, orientation, numerosity etc.), the claim of neural codes is to explain how a certain property is *represented* in the brain, i.e. how it can be represented independently from other properties and thus be transmittable to other neurons.

For example, when we measure the activity of a bunch of neurons in a specific time window while an animal is looking at a screen with some dots, we can find that the firing rate changes when also the number of dots is changing. However, it is not clear how neurons can associate a change in firing rate to a specific property of the stimuli (e.g. number of dots) unambiguously. In the same way, I listen to a word but unless I know that language I cannot understand the object it refers to and distinguish its meaning from other words. Also, it is not clear how neurons could distinguish a good signal and a bad signal for something, i.e. how can they verify the information. If I do not know a language, I cannot know whether the word 'cat' in the sentence 'my cat always barks' is wrong or not.

In this review, we aim to give a short overview of the experimental evidence behind number cognition. There are two major disclaimers here: first, when speaking about a neural code we will use the term in the technical correlational sense. The existence itself of a neural code in the Shannon sense is a metaphor and still a hypothesis. Most of the literature we are going to discuss tells us about interesting correlations for an involvement of specific brain areas or neurons in the perception of numerosity.

Second, most probably no general coding mechanism for numerosity exists in the evolutionary sense. The scope of number cognition combines the diversity of both the stimuli (in terms of their different physical modalities) and of the phylogenetically diverse nervous systems dealing with these stimuli. At the same time, the evidence suggests that numerosity perception is based on some common principles shared among different animals both at the level of behavior (see chapter "Behavior") and at the level of neural responses (see chapter "Cortical processing"). Hence, we suggested that these common principles might be not because of the shared evolutionary origin, but merely a reflection of strong computational advantages and, hence, of parallel evolutionary processes.

2. Behavior

There is large evidence of abilities in discriminating numerosity across animal species ([Butterworth et al., 2020](#)). Ranging from invertebrates (see [Bortot et al., 2021](#) for a review) to vertebrates (see [Lorenzi et al., 2021](#); [Nieder, 2020a,b](#) for reviews), different animal species can solve tasks involving comparison of numbers of animals or items: among others, insects ([Giurfa, 2019](#); [Bortot et al., 2019](#); [d'Ettorre et al., 2021](#); [Bengochea et al., 2022](#)), reptiles ([Gazzola et al., 2018](#)), amphibians ([Stancher et al., 2015](#)), fish ([Stancher et al., 2013](#); [Potrich et al., 2015, 2022](#)), birds ([Ditz and Nieder, 2016](#); [Rugani et al., 2008](#)), monkeys ([Nieder and Miller, 2004](#)), newborn humans ([Izard et al., 2009](#);

[Coubart et al., 2014](#)) and infants ([Feigenson, 2011](#); [Benavides-Varela and Reoyo-Serrano, 2021](#)).

Several studies showed that animals can be trained to discriminate between two artificial stimuli differing in the number of elements (e.g. dot arrays, tones). For example, [Bortot et al. \(2021\)](#) reported how bees can discriminate between 2 vs. 3 and 3 vs. 4 dots and if trained to always choose the 3 dots in one of these specific comparisons they learn it as an absolute cue (i.e., during a generalization test bees maintain their choice for 3 dots). [Potrich et al. \(2022\)](#) showed how archerfish can discriminate 2 vs. 3, 3 vs. 4, 3 vs. 6, 5 vs. 8 and 6 vs. 9 dots spontaneously adopting a relative rule during generalization tests. Young chicks can be trained to discriminate between sets of different numerosities ([Rugani et al., 2008, 2013, 2014](#)), while adult corvids can be trained on a delayed match-to-sample task with stimuli representing up to 30 dots ([Ditz and Nieder, 2016](#)).

Moreover, many animals show spontaneous abilities to discriminate different number of elements, thus suggesting that these abilities might be an inborn feature of the brain. For example, female frogs show an innate preference for complex male calls, i.e. vocal sequences with a greater amount of chunks ([Rand and Ryan, 1981](#)); males can reproduce the number of calls in a sequence emitted by a conspecific and increase the number of chunks up to 8 notes to result in more attractiveness for females ([Rose, 2018](#)). Another example comes from the study on carpenter ants. When presented with two groups of dummy cocoons, a nurse ant would spontaneously select the larger one using both chemical and visuotactile cues ([d'Ettorre et al., 2021](#)). Humans also show these abilities even before they start speaking. 6-Month-old infants can match a certain number of sounds with the number of elements in an image, showing more surprise (longer fixation time) for bigger mismatches ([Feigenson, 2011](#)).

All these examples show how widespread these abilities are around the animal kingdom, both as spontaneous or acquired by training. Moreover, they highlight their multimodal character: animals can perceive numerosity with different sensory modalities.

All these capacities can effectively be described by similar psychophysical rules, namely Weber's law ([Weber, 1850](#); [Dehaene, 2011](#)). This law is a general principle originally developed to explain the human perception of a change in a continuous physical quantity (e.g. weight, length, light intensity etc.). According to Weber's law, the just-noticeable difference between two stimuli depends on their magnitudes. Thus, the discrimination threshold between two stimuli does not depend on their absolute difference, but on their ratio.

Similar to continuous physical stimuli, Weber's law perfectly describes the perception of discrete quantities ([Ditz and Nieder, 2016](#)) both at the level of animal behavior and at the level of selective neurons (see Cortical paragraph; [Ditz and Nieder, 2015](#); [Kobylkov et al., 2022](#)). First of all, we are better at discriminating quantities the more apart from each other they are ("distance effect"). Second, we commit more estimation errors with increasing size or number of elements ("size effect"). Often, the Weber law is coupled with Fechner's reformulation of it ([Fechner, 1948](#); [Dehaene, 2003](#)), namely that perception could be better described on a logarithmic scale. See [Fig. 3](#).

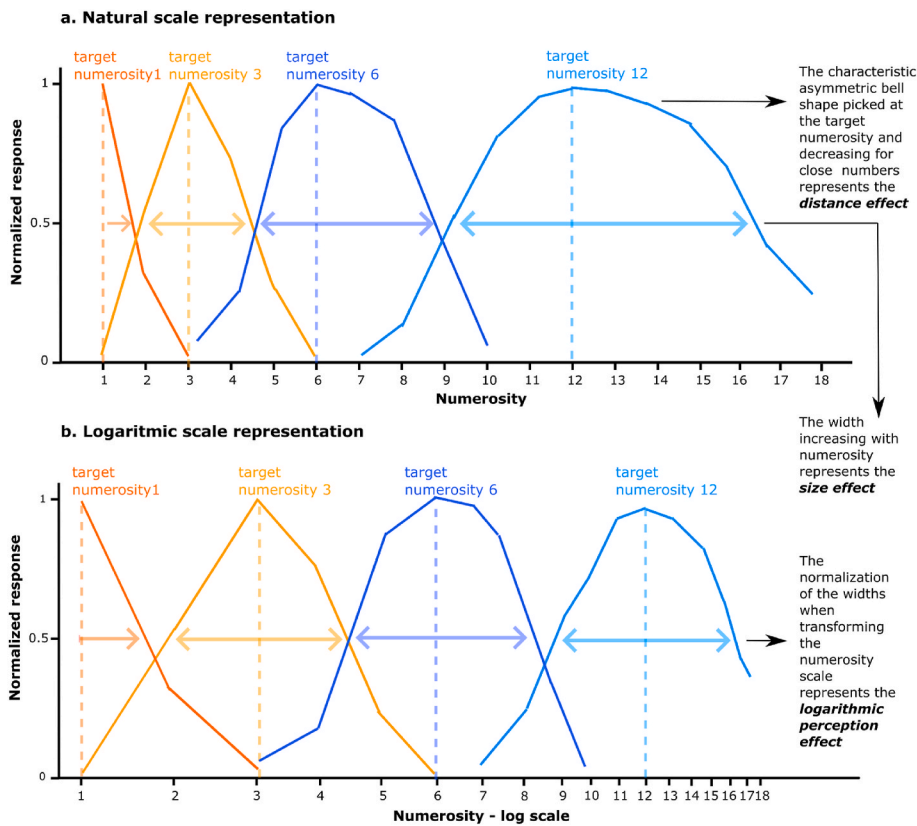


Fig. 3. Schematic of tuning curves. Similar response, following Weber's law, can be found both at a behavioral level (in experiments on numerosity discrimination) and at the brain level (with number neurons preferentially responding to a specific presented quantity). The characteristic bell shape, peaked at the target numerosity (i.e. numerosity to be evaluated) and skewed towards higher numbers with respect to the target, represents the increasing error for comparisons of closer quantities ('distance effect'). The error is more relevant for higher numbers ('size effect'). **a.** Representing the numerical axis in natural scale the width of the tuning curves naturally increases with numbers (describing our imprecise estimation). **b.** If reporting the data with numbers in a logarithmic scale the width of the tuning curves becomes constant across quantities, representing our logarithmic compression in the perception of numerosity (Fechner's observation).

When referring to numerosity estimation, which follow Weber's law, neuroscientists often speak about the so-called approximate number system (see for example Brannon and Merritt, 2011), which provides animals with an imprecise but effective estimation. It is worth mentioning that other mechanisms have been considered, though not of

a quantitative nature but as a by-product of working memory, which would allow an exact representation for up to 4 entities (the so-called subitizing range) and it is usually referred to as object file or object tracking system (Kahneman et al., 1992; Xu, 2003; Chesney and Haladjian, 2011).

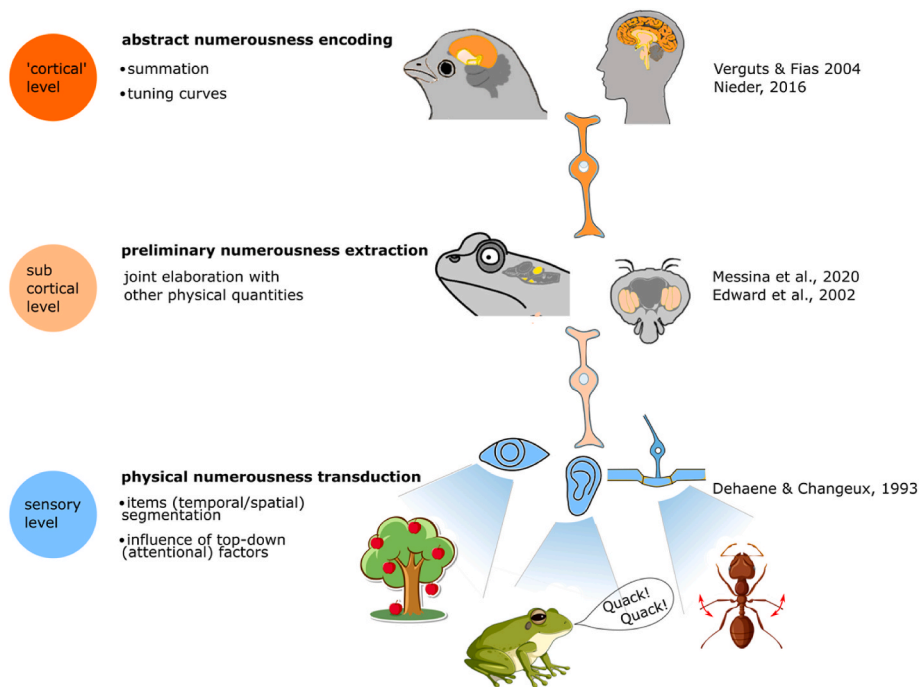


Fig. 4. Scheme of different levels in the codification of numerosity. We structured this review trying to provide different cross-species examples of elaboration of this type of information at different levels of the neuronal pathway. A general summary of the different code levels presented in this work is depicted, with some representative references.

In the following we will try to illustrate the current knowledge about the neural mechanisms underlying cognitive abilities of animals (see Fig. 4).

3. Sensory processing

Numerosity, as an abstract property, can refer to very different sensory modalities. Number of conspecifics in a group is perceived through the visual system (e.g. Stancher et al., 2013); number of warning calls is detected by the auditory system (Templeton et al., 2005); number of steps can be detected by proprioceptors (Wittlinger et al., 2006). Therefore, it is difficult to figure out common principles for coding of numerosity at the first stage of sensory processing, when physical stimuli are transformed into neural responses. However, we would argue that there are shared aspects of sensory processing that might influence or limit the perception of numerosity, which can be generalized across different sensory modalities. These limitations are dictated by a combination of physiological properties of sensory organs (sensory threshold) and by physical properties of stimuli (signal-to-noise ratio).

A first important prerequisite for numerosity perception is the ability of a given sensory organ to detect individual items in a set. In the case of an auditory system, which can sequentially “count” sensory events, this would imply that the stimuli should be temporally segregated from each other and also distinguished from the surrounding noise. An example of a very specialized numerosity discrimination system in the auditory domain comes from acoustic communication behavior of some anurans. For example, for the Pacific tree frog, not only the number but also the frequency of calls distinguishes “advertisement” from aggressive behavior (Rose, 2018).

The somatosensory system can also be involved in the perception of sequential numerosity, based for example on proprioception. *Cataglyphis* ants, living in a desert environment without any landmarks, are able to measure travel distances by estimating the amount of leg movements (Wittlinger et al., 2006). In this case, what is relevant is the sequential segmentation of self-induced movements.

While temporal resolution is highly important for the perception of sequential quantities, simultaneous numerosity, usually in the visual domain, require segregation of individual items (i.e., figure—ground segregation) and strongly depend on the visual acuity. According to the leading hypothesis, visual numerosity is directly extracted from the retinal input by simple segmentation and normalization algorithms (Dehaene and Changeux, 1993). This would enable a rapid extraction of information regarding the number of elements already at the earliest stages of sensory processing, independent of the size and position of single elements (but see e.g. Morgan et al., 2014). However, whether this filtering process happens already in the retina or at the later stages of sensory processing remains unknown.

One of the aspects of numerosity perception that has not yet been widely investigated at the neural level is the effect of directed attention on sensory perception. For example, visual detection of single individual objects would depend both on the position of the object in the visual field and on our attention. Recent psychophysical experiments performed by Li et al. (2021) suggest that numerosity perception in humans depends on this spatial context. The estimation of numerosity presented in the central/peripheral visual field was affected by distracting contextual stimuli. This suggests that numerosity perception is affected by both bottom-up (sensory) and top-down (directing attention) factors. For evidence of these kinds of effects in comparative perspective see e.g. (Bertamini et al., 2018).

Another aspect of numerosity perception, which makes “number sense” comparable to perception of continuous variables, is the fact that numerosity judgment is susceptible to sensory adaptation. In psychophysical experiments involving various sensory modalities, apparent numerosity is decreased by adaptation to large numbers of elements and increased by adaptation to small numbers (Burr and Ross, 2008;

Togoli and Arrighi, 2021). Usually sensory adaptation is assumed to originate directly in the sensory organ. In the visual system, for example, contrast adaptation happens through multiple mechanisms within the retina: e.g., the depression of bipolar cell output or synaptic inhibition of bipolar cell terminals and ganglion cell dendrites (Demb, 2008). Whether this is the case for numerosity remains elusive.

4. Subcortical processing

Apart from simply detecting numerosity as a part of a complex sensory input, it is rather unlikely that abstract information, i.e. separated from confounding physical variables, can be extracted from the sensory stream at this level. On the contrary, several lines of evidence suggest that abstract numerosity might be decoded at the subsequent processing stage.

In vertebrates, the majority of sensory inputs pass via the midbrain and thalamus before reaching higher cognitive areas in the forebrain. These structures play an important role in innate cognitive functions that do not require any learning or experience. Multiple behavioral studies in young animals suggest that numerosity perception also belongs to this core knowledge system and is present from birth (Val- lortigara, 2012, 2021). Therefore, it is quite likely that numerosity might be also extracted already at this early stage of processing.

Recent studies in zebrafish showed that the thalamus might indeed be involved in perception of discrete quantities irrespective of low-level continuous variables (Messina et al., 2020, 2022). Zebrafish were first habituated to stimuli with same number of elements that varied in position and size and subsequently presented with stimuli different in number, size, or shape. Authors observed changes in neural activity (based on the expression of immediate-early genes) in the thalamus and the most caudal part of the dorso-central (Dc) pallium, which was linked to changes in number of elements.

In humans, some indirect evidence also suggests that information regarding the number of elements could be extracted already at the subcortical level. A functional imaging study by Kovas et al. (2009) reported that thalamic nuclei are involved in numerosity approximation, while results from a more recent psychophysical experiment by Collins et al. (2017) support this hypothesis.

However, it is important to note that all of the abovementioned studies only demonstrate that subcortical structures are involved in numerosity perception. They do not show how it is encoded at the neural level, i.e. how it is represented in the activity of single neurons.

The evolutionary diversity of the animal groups that show number cognition makes it very unlikely that the numerosity-processing network is a fully homologous structure shared among vertebrates, not to mention insects. At the same time, behavioral studies clearly show that invertebrates including insects possess the ability to discriminate between different numbers of elements (see the chapter “Behavior”). A recent study by Bengochea et al. (2022) reports that even fruit flies can do so. In the same study authors showed that LC11 neurons of the optic lobe are crucial for this behavior. Among other functions, these neurons respond to the movement of small objects (Keleş and Frye, 2017). While it is particularly difficult to draw any homologies between vertebrate and insect brain structures, LC11 neurons might functionally resemble neurons in the tectum of a zebrafish responsible for prey detection (Förster et al., 2020). Surprisingly, silencing the mushroom bodies or the central complex (higher cognitive brain structures) of fruit flies did not seem to affect their numerosity perception. This suggests that in fruit flies this process does not require higher cognitive processing. However, it is important to note that the neural mechanism at the level of single-cell responses underlying these abilities in insects remains to be uncovered.

Apparently, the only direct evidence of a neural mechanism at the subcortical level, which encodes numerosity, comes from single-cell recordings from the midbrain of Pacific treefrogs (Edwards et al., 2002). Here, single neurons start responding only after a series of

inter-pulse intervals, which corresponds to the number of calls required for conspecific recognition. In this case, the neurons are selective not only to the number of calls, but also to the frequency of the stimulus. Only the optimal inter-pulse rate will elicit the neural response after a specific number of pulses.

Strictly speaking, interval-counting neurons in the midbrain of treefrogs (Edwards et al., 2002) differ substantially from number-selective neurons (described in the next chapter), which do not respond to low-level features of stimuli. However, this case illustrates that sometimes numerosness information becomes biologically relevant only in combination with other physical parameters. Another example of a biologically relevant contextual stimulus involving numerosness that might be encoded at the subcortical level is a prototypic face-like configuration. Nguyen et al. (2014) recorded neural responses from the monkey superior colliculus to a face-like pattern (three dark dots on a bright oval), representing eyes and the mouth. The neural response to this triangular configuration was different to scrambled images. Therefore, in this case three dots become meaningful only when presented in a face-like configuration.

5. “Cortical” processing

While information on the number of elements might be extracted from the sensory input, generally together with other physical parameters already at the subcortical level (see the chapter “Subcortical Processing”), estimation of abstract quantity information across sensory modalities requires sensory integration in higher-order brain areas.

In primates and humans, the fronto-parietal cortical network plays a major role in numerosness perception. Functional magnetic resonance imaging (fMRI) studies have shown that the intraparietal sulcus (IPS) of the posterior parietal cortex and the lateral prefrontal cortex (LPFC) become activated during numerosness processing (Piazza et al., 2006, 2007; Castelli et al., 2006; Jacob and Nieder, 2009).

Moreover, single-cell recordings in these brain areas have shown how the information of number of stimuli is processed at the level of single neurons and neural ensembles.

5.1. Monotonic and labeled-line code

According to the currently prevailing hypothesis, neural coding of numerosness in the forebrain is a two-step process (Verguts and Fias, 2004). First, accumulator neurons extract numerosness by monotonically decreasing/increasing their firing rate with the number of items. Such neurons were found in the lateral intraparietal area of macaque monkeys (Roitman et al., 2007). Some neurons were responding stronger to lower numbers, and some were increasing their response rate with increasing numbers. In this way, these two neural populations provided a low-pass and a high-pass filter. Subsequently, numerosness detectors encoding single quantities would result from the overall activity of the monotonically responsive neurons. These numerosness detectors, in the literature also referred to as “number neurons”, preferentially respond to a given numerosness, and the response decays with the numerical distance (labeled-line code, see Fig. 3). Number neurons have been described in monkey prefrontal (Nieder and Merten, 2007) and parietal cortices (Sawamura et al., 2002; Nieder, 2012). The tuning properties of number neurons follow Weber’s law (see “Introduction”).

While mammalian cortical structure does not exist in other vertebrates, number neurons are not an exclusive feature of the mammalian brain. For example, birds are evolutionary very distant from mammals (ca. 300 million years apart). Nevertheless, number neurons with tuning properties very similar to the primate ones have been described in the caudolateral nidopallium (NCL) of carrion crows (Ditz and Nieder, 2015) and domestic chicks (Kobylkov et al., 2022). The NCL is a functional analogue of the mammalian PFC, which is involved in a variety of higher cognitive functions: memory and executive control (Rose and

Colombo, 2005), abstract rule learning (Veit and Nieder, 2013), and categorical representation (Wagener and Nieder, 2023).

5.2. Number neurons specificity

The key component of the experimental design on numerosness perception is to exclude the effect of confounding variables (e.g. area and perimeter) that are normally associated with numerosness (see “Introduction”). Number neurons are statistically defined as those, which firing rate significantly depends on numerosness, but not on other physical variables. Of course, in an in vivo electrophysiological experiment it would be virtually impossible to control for all possible variables. By this approach, we select neurons, whose response rate reflects significantly stronger the number of items rather than the other physical properties of these items (e.g. size). At the same time, it does not automatically mean that these neurons are only there to encode numerosness. When crows were trained to discriminate between dot arrays of different combinations of numbers and colors based only on the color itself, Wagener et al. (2018) found neurons that were encoding the number of dots irrespective of their size. However, almost 40% of these neurons still showed an additional significant color-specific response.

5.3. Number neurons supramodal coding

A subsequent step in the neural processing of numerosness is supramodal enumeration. Stimuli with different number of elements could be presented simultaneously or sequentially and in various sensory modalities (e.g. auditory or visual). Supramodal numerosness detection would require neurons that are insensitive to these different stimuli formats. Such neurons have been found in the prefrontal and posterior parietal cortices of rhesus monkeys (Nieder, 2012). In this study, animals were trained to discriminate between both the number of auditory sounds and visual items presented in the same session. The majority of number neurons both in the PFC and in the IPS responded only to auditory (sequential) or to visual (simultaneous) stimuli. However, a smaller subpopulation of neurons (11% of all recorded neurons in the PFC and 3% in the IPS) encoded information of number of elements irrespective of the stimuli format. Interestingly, in the IPS the authors found only supramodal number neurons tuned to one, which might be related to the fact that neurons responding to one item is the most abundant category of number neurons.

Number neurons that show supramodal response to abstract quantities might be an important evolutionary prerequisite for a semantic association between numerosness, numerosity and an arbitrary sign (e.g. a digit). The PFC seems to play a major role in this process. In monkeys trained to associate number of dots with digits, many number neurons in the PFC, but not in the IPS, responded similarly to the numerosness and to the associated digit (Diester and Nieder, 2007).

Abstract representation of numerosities might be a crucial step for other cognitive functions like arithmetic operations. To perform addition and subtraction it is necessary to maintain values in the working memory and to apply abstract arithmetic rules to these values. While behavioral data suggest that several animal species can do at least simple arithmetic operations (domestic chicken (Rugani et al., 2009); fish (Schluessel et al., 2022)), its underlying neural mechanism has been mainly studied in humans. Recent data on single-cell recordings in the medial temporal lobe (MTL) of human patients revealed encoding of abstract arithmetic rules in this area (Kutter et al., 2022).

The corresponding neural mechanism for arithmetics in other species still remains unknown. One might, however, hypothesize that this mechanism might be similar to more basic mathematical rules, such as comparisons, i.e. “greater than” and “less than”. These rule-selective neurons have been described in the PFC of monkeys (Eiselt and Nieder 2013).

5.4. The executive function of number neurons

To act as a receiver of the information according to Shannon's theory (see "Introduction"), number neurons need to carry out executive function, i.e. send motor commands to elicit a behavioral response. Most of the electrophysiological studies provide correlative evidence for this: in a match-to-sample behavioral task, error trials are usually correlated with the reduced neural response of the corresponding number neurons. Another way to show that number neurons can drive behavioral output is to train an animal to perform a number of actions corresponding to the numerosness of the stimulus. For example, in a recent study, [Kirschhock and Nieder \(2022\)](#) trained crows to observe a series of sequentially appearing dots (or a sign corresponding to a specific numerosness); then crows had to translate the numerosness of the stimulus into the number of pecks on the screen. 24% of all recorded neurons in the NCL were modulating their activity with respect to the target number. Hence, these sensorimotor neurons were representing the number of planned motor responses.

5.5. Sparsely distributed code

Despite the fact that the frontoparietal network plays a crucial role in number cognition, number neurons do not seem to reside within specific morphologically defined areas. Instead, both in primates and in birds, number neurons seem to be sparsely distributed within this network (but see an fMRI study by [Harvey et al., 2013](#) suggesting a topographic organization of numerosness representations). Moreover, analyses of response features of selective neurons both in the PFC of primates ([Diestler and Nieder, 2008](#)) and in the NCL of crows ([Ditz et al., 2022](#)) have shown that two different cell types (pyramidal cells and interneurons) contribute to the abstract quantity categorization. These cell types create neural microcircuits that further shape the response of single neurons to a specific number of elements.

If to extract information one needs only sparsely distributed neural microcircuits, we can expect to find similar numerosness selective neurons in other forebrain areas. Indeed, single-cell recordings in the human medial temporal lobe (MTL) revealed that 16% of randomly selected neurons in this area were numerosness-selective ([Kutter et al., 2018](#)). MTL is not a part of the frontoparietal network, but it is a higher associative brain area involved in the representation of abstract categories ([Quiroga et al., 2005](#)). Furthermore, direct cell recordings ([Kutter et al., 2022](#)) show that the human hippocampus is also involved in number cognition, specifically in arithmetical operations. However, extracellular recordings in the hippocampus of crows did not reveal any numerosness-selective responses ([Ditz et al., 2018](#)).

5.6. Population level code

Importantly, the mechanism of numerical cognition should not be reduced to the activity of single number neurons. Neurons respond to stimuli in a semi-stochastic fashion, and the characteristic tuning curves observed during neural recordings are the result of averaging over multiple trials. At the same time, the brain needs to compute a behavioral response on a trial-by-trial basis. Therefore, it is suggested that the final estimate of numerosness is coded at the populational level. Every presented number of elements, e.g. 3, will elicit not only the response of the number neurons that "prefer" that 3, but also, to a lesser extent, the response of neurons preferring adjacent quantities 2 and 4. At the same time, the neurons tuned to numerosness 1 and 7 (equidistant from 3 on a log-scale) would not respond to 3. In this way, every quantity creates an activation pattern over the whole population of number neurons that can be used as a read-out for creating a complementary behavioral output.

6. Conclusions

Number cognition is a sophisticated process involving many sensory modalities and widespread throughout the whole evolutionary diverse animal kingdom. Therefore, every attempt to reduce this process to a single common neural coding mechanism is an a priori simplification. Being aware of that, in this review we tried to disengage ourselves from an evolutionary point of view. Instead, we aimed to represent numerosness perception as a multi-step process happening in the brain. During this process the information has to be first encoded by a sensory system. Then, it is preprocessed at the subcortical level. Here numerosness can already be extracted together with other physical features in the form of innately relevant stimuli (e.g. frog calls or faces). At the level of cortical (or equivalent pallial structure) processing, abstract quantity information, separated from confounding physical parameters of stimuli, can be extracted. Numerosness processed within subcortical structures and in the associative cortical areas can elicit behavioral responses. Moreover, top-down processes like directed attention could actively affect numerosness perception at the sensory level. Thus, in our view, the neural code for numerosness is not limited to the activity of number neurons in higher-order associative brain areas, but encompasses the whole brain. Still the exact mechanism of how all the involved brain areas interact remains unknown.

Following the widely accepted concept of a "neural code" and information theory, we have put numerosness perception into the framework of Shannon's coding theory, where the sensory system translates quantity information from stimuli into the neural signal, and the neural network transmits this signal to a receiver (e.g. number neurons). However, as already mentioned some neuroscientists point to the fact that the term "neural code" might be misleading since it's often meant to explain how certain properties are *represented* in the brain ([Brette, 2019](#)).

One of the main problems is indeed representational instances of neural codes. According to Shannon theory, a property should be encoded independently from others, e.g. binary signals to encode the symbols A, B, and C must be different (101, 010, and 111) in order to distinguish between different letters. However, when speaking of neurons independent selectivity is a strong requirement and few scientists would likely endorse it. Neurons might encode many different properties depending on the stimuli, modulating their activity accordingly. The assumption is that these properties should be then inferred from the activity of neurons by other neurons in the pathway. However, it is not clear how neurons could retrieve the "meaning" of this code (i.e. the property) from the pattern of activity, given that this meaning is external to the domain of spikes and their relationship is not univocal. This is usually called *symbol grounding problem*.

Patterns of activity at the single-cell level appears almost identical even in evolutionary distant groups, e.g. number neurons in the PFC of monkeys and in the NCL of birds. Parallel evolution driven by similar selection pressure resulted in the functionally analogous and, apparently, computationally advantageous, neural mechanism.

One could hypothesize that number neurons could emerge as a byproduct of sensory perception and categorization. Then, numerosness detectors at the neural level could spontaneously emerge from basic network structural connectivity.

For example, considering the organization of the visual system one could define a common network structure shared among different nervous systems. This network consists of an alternation of neural layers which perform convolutional operations, filtering small image locations, with layers performing pooling operations, extracting the maximum activation from the previous layer ([Hubel and Wiesel, 1962](#)). This computation principle is the basis of modern convolutional neural networks (CNN) for image classification and computer vision applications ([Rawat and Wang, 2017](#)).

Several computational studies have shown that units selective to number of elements can emerge in the last layers of these CNNs. In

particular, Nasr et al. (2019) spotted number-tuned units reminiscent of biological number neurons spontaneously emerging (i.e. without training on the stimuli explicitly varying in number of elements) in the last layer of the feature extraction network. Moreover, Zorzi and Tesolin (2018) showed that units monotonically responding to number of elements can also be found in the CNNs. This shows how extraction of information could emerge from a process of categorization provided by specific network connectivity.

The results obtained from the analysis of CNNs, however, cannot be directly extrapolated to the biological brain network. CNNs, even if inspired by the biological system, are not an analogue of the biological brain. One possibility is that the very structure of the CNNs, i.e. convolutional and pooling layers, is a necessary prerequisite for the number selectivity.

Summing up, the topic of number cognition has gained significant progress over the last decades. Multiple behavioral studies have shown that animals from different taxa can estimate numerosness. Imaging studies have revealed some key brain structures involved in this process. Finally, single-cell neural recordings have demonstrated how this information might be encoded at the level of single neurons and neural populations.

Nevertheless, the neural code for numerosness is far from being cracked. At the end of this review we would like to highlight what we believe are the most intriguing open questions in the field of number cognition.

1. Do number neurons exist in invertebrates or is their computational scheme completely different from vertebrates?
2. What direct neural input do number neurons require to be able to extract abstract quantity information?
3. Can information from number of elements be directly extracted from the neural network activity without number neurons tuned to specific quantities?
4. Do number neurons with similar response properties, but found in different brain areas (e.g. PFC and IPS) have different functions?
5. Can we find number detectors in artificial networks with structures different from CNN and/or in other deeper layers?
6. Is the neural code for numerosness (e.g. the emergence of tuning curves at higher brain areas) refining with development and experience?
7. How does the processing of numerosness work at the sensory level? Can we better disentangle the early information, trying to connect the gaps between the different steps in data flow from sensory to cortical brain areas?
8. Would number neurons activity be different in a more naturalistic experimental design involving a broader variability and higher complexity of the stimuli?
9. Which mechanism links the activity of number neurons to perception and consequent behaviours?

This list of questions is not exhaustive but aims to promote a fruitful discussion among scientists from different disciplines, which would hopefully result in new insights about the coding mechanisms exploited by our nervous system to elaborate numerosness.

Authors Contribution

D.K., M.P., G.V., M.Z. conceived the manuscript. D.K., M.P., M.Z. wrote the original draft (M.P. Introduction, M.Z. Behavior, D.K. Sensory processing, Subcortical processing, Cortical Processing, D.K., M.P., M.Z. Conclusions). D.K., M.Z. created the images. D.K., M.P., G.V., M.Z. reviewed the manuscript. All authors edited and then approved the submitted version.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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