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Review

Numerosity coding in the brain: from early visual processing to abstract representations

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Numerosity estimation refers to the ability to perceive and estimate quantities without explicit counting, a skill crucial for both human and animal cognition. Traditionally, this process has been associated with higher-order cortical regions like the intraparietal sulcus (IPS) and prefrontal cortex (PFC), thought to support abstract number representations. However, noninvasive electrophysiological and neuroimaging studies, along with psychophysical investigations, suggest that early visual areas such as V1 and V2 may play a role in processing visual numerosity, similar to the way low-level visual features are encoded. Recent research shows that the early visual cortex encodes information related to numerosity through the spatial frequency content of visual displays. Numerosity-tuned neurons, however, emerge later in the visual processing hierarchy, where more abstract and location-independent representations are formed in association areas such as the IPS and PFC. This is further supported by single-neuron data revealing spatiotopic integration and tuning curves for specific numerosities within these associative cortical regions. A comprehensive understanding of numerosity processing in the brain requires investigating numerosity presentations across time, space, and sensory modalities, all of which engage association cortices rather than sensory-specific regions.

Keywords: number; neuronal code; association cortex; intra-parietal cortex; prefrontal cortex.

Introduction

The ability to estimate numerosity—the number of items in a set—without explicit counting is a fundamental cognitive skill that is deeply ingrained in both humans and animals. This capacity is evident even in individuals who have never been taught formal counting, such as young children (Lipton and Spelke 2003), newborns (Izard et al. 2009), and certain adult groups, including indigenous communities like the Pirahã (Gordon 2004) and the Munduruku (Pica et al. 2004), who lack conventional numerical systems. In addition, the widespread occurrence of this ability across different species suggests that numerosity estimation is a biologically rooted trait, evolved over time and essential to survival (Nieder 2021).

Because the grasp of numerosity is intuitive and largely innate (Lorenzi et al. 2025; Nieder 2025b), it forms the foundation of what is known as "number sense." This term, first coined by Dantzig (1930) and later developed by Dehaene (1997), refers to the natural ability to perceive and understand numerical quantities without formal training. Number sense is crucial not only for basic cognitive functions but also for more complex mathematical reasoning (Nieder 2019, 2025a). This intrinsic skill highlights the early developmental emergence of numerosity recognition and its integral role in human cognition. How and were in the brain is this capability represented?

The neural basis of numerosity: the late processing hypothesis

In the quest to identify brain areas involved in numerical capabilities, studies of patients with brain lesions causing acalculia—an acquired impairment of numerical and calculation abilities—highlighted high-level association cortices as key sites of number representation. These include the prefrontal cortex (PFC) and distinct regions of the posterior parietal cortex (PPC), particularly the intraparietal sulcus (IPS) (Henschen 1925), findings later confirmed by neuropsychological studies (Lemer et al. 2003; Ashkenazi et al. 2008).

Neuroimaging research has repeatedly identified the PPC, particularly the IPS, along with the PFC, as crucial regions for representing numerosity (Piazza et al. 2004; Ansari and Dhital 2006; Cantlon et al. 2006; Jacob and Nieder 2009; Harvey et al. 2013; Kersey and Cantlon 2017; Harvey et al. 2017). Single-neuron recordings from the cerebral cortex of behaving nonhuman primates further revealed the neuronal code for non-symbolic numerosity representations (Nieder et al. 2002, 2006; Sawamura et al. 2002; Okuyama et al. 2015; Nieder 2016). These studies pinpointed numerosity-selective neurons in the IPS of the PPC and the PFC as critical for number representation. Interestingly, even in non-mammalian species lacking a neocortex, but with differently evolved telencep-halic brain structures,

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numerosity-selective neurons have been identified in analogous high-level associative pallial brain regions (Ditz and Nieder 2015, 2020; Kirschhock and Nieder 2022; Kobylkov et al. 2022).

For many years, it was therefore widely accepted that the sense of number arises from higher-order brain processes later in the neural processing hierarchy. This *Late Processing Hypothesis* of numerical information posits that number sense emerges in association cortices, such as the IPS and PFC, which integrate information across sensory modalities and cognitive processes. The visual system processes information hierarchically, starting from early sensory inputs and gradually constructing a detailed representation of the visual environment (Hochstein and Ahissar 2002; Grill-Spector and Malach 2004). The key question is: at what point along this pathway, and through what mechanisms, is numerical information extracted? While the Late Processing Hypothesis, emphasizing the IPS and PFC, was widely accepted for decades, recent research challenges this view, suggesting that number sense may already involve early sensory regions of the brain.

The role of early visual areas in numerosity perception according to the Early Processing Hypothesis

The *Early Processing Hypothesis* suggests that numerosity, more precisely visual numerosity, is extracted through basic visual features such as size, density, and spatial frequency, with early visual areas like V1 and V2 directly contributing to numerosity perception. According to this perspective, numerical perception operates as an automatic, low-level sensory process, akin to the perception of fundamental visual features like brightness or motion.

One of the primary pieces of psychophysical evidence supporting this hypothesis is the phenomenon of number adaptation effects. Number adaptation effects refer to the phenomenon where prolonged exposure to a specific number alters subsequent perception of numerosity, typically resulting in biases or shifts in number judgments. For example, exposure to high-numerosity displays (eg 160 dots) reduces the perceived numerosity of subsequent displays, making 100 dots appear as fewer (eg 80). Conversely, exposure to low-numerosity displays increases the perceived numerosity of subsequent stimuli (Burr and Ross 2008; Ross and Burr 2012; Anobile et al. 2016; Castaldi et al. 2016; Fornaciai et al. 2016). Number adaptation effects persist even when non-numeric attributes that often covary with number, such as size, density, and brightness, are carefully controlled (Burr and Ross 2008; Ross and Burr 2012; Castaldi et al. 2016). These effects suggest that numerical perception is modulated by low-level sensory mechanisms, similar to the processing of basic visual features like motion and orientation in early visual areas. This has led to the hypothesis that numerical estimation may constitute a fundamental or "primary" component of visual processing (Burr and Ross 2008; Anobile et al. 2016; Fornaciai and Park 2018).

In light of these psychophysical findings, human imaging studies have reported that visual number perception can be reliably decoded from early visual regions, independent of the abstract number code in the IPS. For instance, number signals have been decoded from EEG signatures in early visual regions as early as 75 milliseconds after numerosity presentation (Park et al. 2015; Fornaciai et al. 2017). Similarly, fMRI studies have shown that number-specific BOLD signals in response to dot displays can be decoded starting in V2, with some evidence of decoding in V1, while no such evidence was found within the IPS (DeWind et al. 2019). (but see Castaldi et al. (2016, 2019) challenging this view, showing that number adaptation effects are detectable in higher-order multimodal areas like the IPS, but not in early visual regions such as V1).

These EEG and fMRI findings indicate that responses in early visual cortex to numerosity stimuli increase monotonically with numerosity, regardless of variations in item size or spacing. Given that these monotonic responses emerge very quickly after stimulus presentation, they are thought to reflect feedforward processing. Moreover, numerosity adaptation has been shown to suppress early visual responses (Zhang et al. 2024) and changes fMRI numerosity selectivity (Tsouli et al. 2021), suggesting that adaptation effects observed in later numerosity-tuned neural populations may originate in early visual areas that respond to image contrast in the adapting stimulus. Collectively, these results suggest that the encoding of visual numerosity begins at an early stage of visual processing, with basic visual detectors in the brain capable of forming and encoding numerical representations. Whether the visual cortex exhibits monotonic firing of single neurons in response to numerosity remains unknown. Among approximately 30 single-neuron studies across various species that have identified tuned numerosity-selective neurons (eg human: Kutter et al. 2018, 2023, 2024; monkey: Sawamura et al. 2002; Nieder et al. 2002; Okuyama et al. 2015; crow: Ditz and Nieder 2015, 2020; chick: Kobylkov et al. 2022), the only study reporting monotonic responses was conducted in the macaque lateral intraparietal area (LIP) (Roitman et al. 2007).

Modifications to the Early Processing Hypothesis of numerosity

However, as new empirical data emerge, methodological and conceptual modifications to the *Early Processing Hypothesis* have been required. For example, a recent fMRI study by Paul et al. (2022) highlights a close relationship between numerosity and the spatial frequency distribution of visual stimuli. This spatial frequency content appears to carry information that enables the visual system to estimate numerosity. By carefully characterizing and dissociating spatial frequency in visual stimuli from numerical information (Fig. 1A), the study demonstrated that aggregate spatial frequency—a holistic measure of the spatial frequency spectrum of a visual stimulus—provides information that allows numerosity to be estimated in primary visual cortex (V1), particularly at the retinotopic location of the stimulus. Variations in aggregate spatial frequency of numerical stimuli were found to be more reliable predictors of changes in monotonic coding than variations in numerosity itself (Fig. 1B). In line with this observation, untrained neural networks (networks not trained for object discrimination) indeed respond to such simple image statistics (Chapalain et al. 2024). In other words, the early visual system is encoding image contrast in the spatial frequency domain indicative of numerosity (Harvey 2025). While early sensory responses are sensitive to numerosity via numerosity's effects on the spatial frequency distributions, numerosity-tuned responses appear to emerge only later in the visual processing hierarchy, beyond the lateral occipital cortex, where they are no longer tied to retinotopic location (Fig. 1B). These responses typically exhibit bell-shaped tuning curves, peaking at preferred numerosities. This pattern of bell-shaped numerosity tuning curves has been repeatedly observed in single-neuron recordings from humans (Kutter et al. 2018, 2023) and various animal species (Nieder 2016, 2021).

Building on the findings of Paul et al. (2022), the role of spatial frequencies in numerical encoding was further investigated

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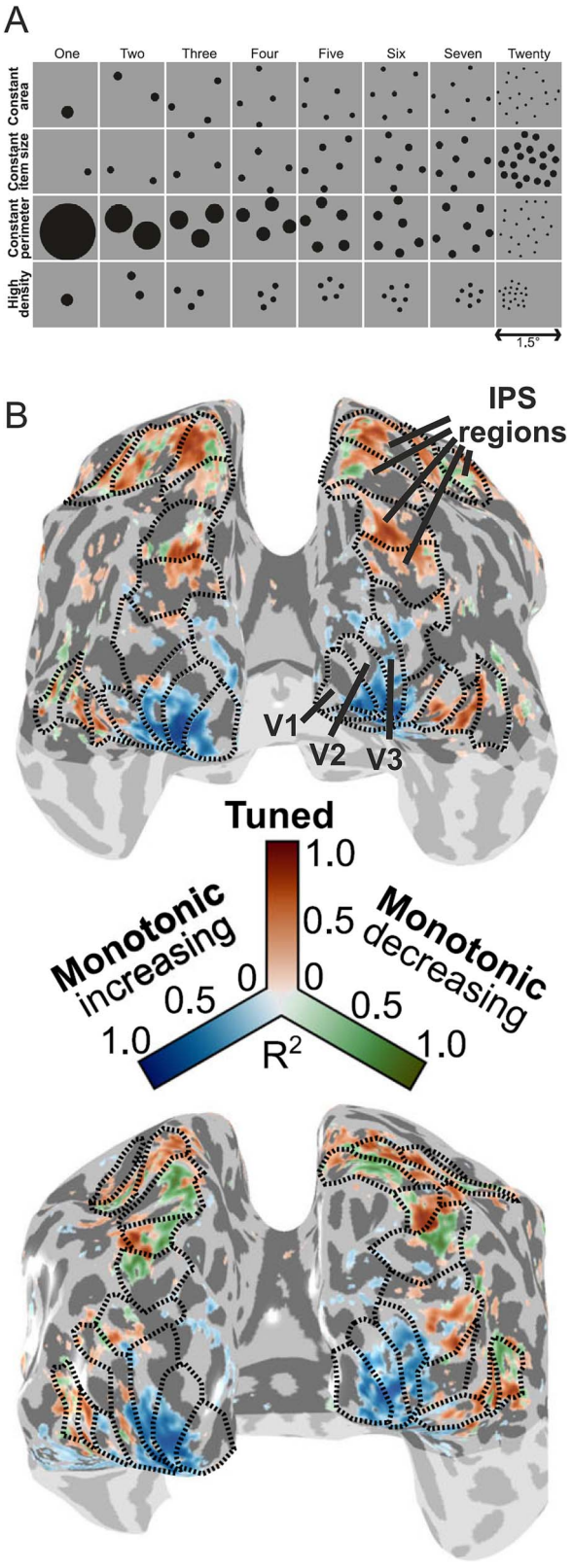

Figure 1. Functional magnetic resonance imaging of numerosity displays in the human brain. A) Example dot numerosity displays. Different displays ensured constant area of all dots (first panel), constant size (second panel), constant perimeter (third panel), and high density (last panel). Numerosities one through seven were shown alternatingly with baseline numerosity twenty. B) Blood flow data to numerosity dot displays obtained with 7 T fMRI. Colored regions show activation in different cortical areas in two representative participants (posterior view of

psychophysically by Bonn and Odic (2024). Using a cross-adaptation paradigm, the authors first exposed participants to sinusoidal spatial-frequency patterns—stimuli devoid of distinct, countable items. They then tested whether this exposure carried over to dot displays and systematically influenced participants' numerical judgments. The results revealed that adaptation to spatial frequency gratings led to a robust number-adaptation effect: participants significantly underestimated the number of dots in subsequent displays after being adapted to the gratings (Bonn and Odic 2024). These findings suggest that spatial frequency alone, even in the absence of explicit numerical information, can shape numerical perception. They further imply that early visual cortex represents the complex spatial frequency content of dot arrays rather than the actual number of items, and this representation subsequently influences number judgments.

In addition to stimulus-related aspects, the scope and limitations of the signals measured by EEG and fMRI in studies supporting the *Early Processing Hypothesis* (Park et al. 2015; Fornaciai et al. 2017; DeWind et al. 2019) have an impact on the interpretation of these brain signals. EEG captures the combined electrical activity of millions of neurons in a spatially imprecise way, while fMRI reflects blood flow, which indirectly correlates with neuronal activity across large populations. In contrast, individual neurons in the early visual cortex, such as those in V1, respond to very specific small regions of the visual field, known as receptive fields (RFs) (Hubel and Wiesel 1962). Within these confined RFs, neurons detect basic visual properties like orientation and spatial frequency. From the point of view of neurons, this creates a conceptual challenge, as the RF of a single neuron in V1 or other early visual areas is spatially restricted and cannot process more than a small portion of the visual field in which items are presented.

For numerosity-selective neurons to arise, they need to integrate information from large portions of the visual field, where the items to be counted are distributed. This spatial integration could occur through two primary mechanisms: First, RFs may expand progressively along the visual processing hierarchy, ultimately encompassing a larger portion of the visual field. This is seen in the inferior-temporal cortex, the endpoint of the temporal "what" visual pathway (Rolls et al. 2003), although this area is not involved in numerosity extraction (Nieder and Miller 2004). Second, neurons, even with relatively small RFs (such as those in the PPC), may integrate information across multiple RFs. This could be achieved through long-range horizontal connections or feedback (top-down) signals from higher-order, spatially-global areas, such as the PFC (Gilbert and Li 2013).

Figure 1. a graphically inflated human cerebral cortex). The activation exhibited distinct relationships between numerosity and stimulus-evoked BOLD response amplitude. These relationships were well described by three response models: monotonically increasing, monotonically decreasing, or tuned responses to the logarithm of numerosity (red). To evaluate these models, it was compared how well they explained response variance in cross-validated data. Monotonically increasing responses were consistently observed only in the central visual field representation of the early visual cortex (V1, V2, V3) (*blue*). In contrast, numerosity-tuned responses were identified beyond the early visual cortex, specifically in regions such as the temporal-occipital, parietal-occipital (IPS), superior parietal, and frontal cortices (*red*). These areas are known to contain topographic numerosity maps. Monotonically decreasing responses were found adjacent to areas exhibiting tuned responses (*green*). Dashed black lines and labels show visual field map borders and cortical names, respectively (from Paul et al. 2022).

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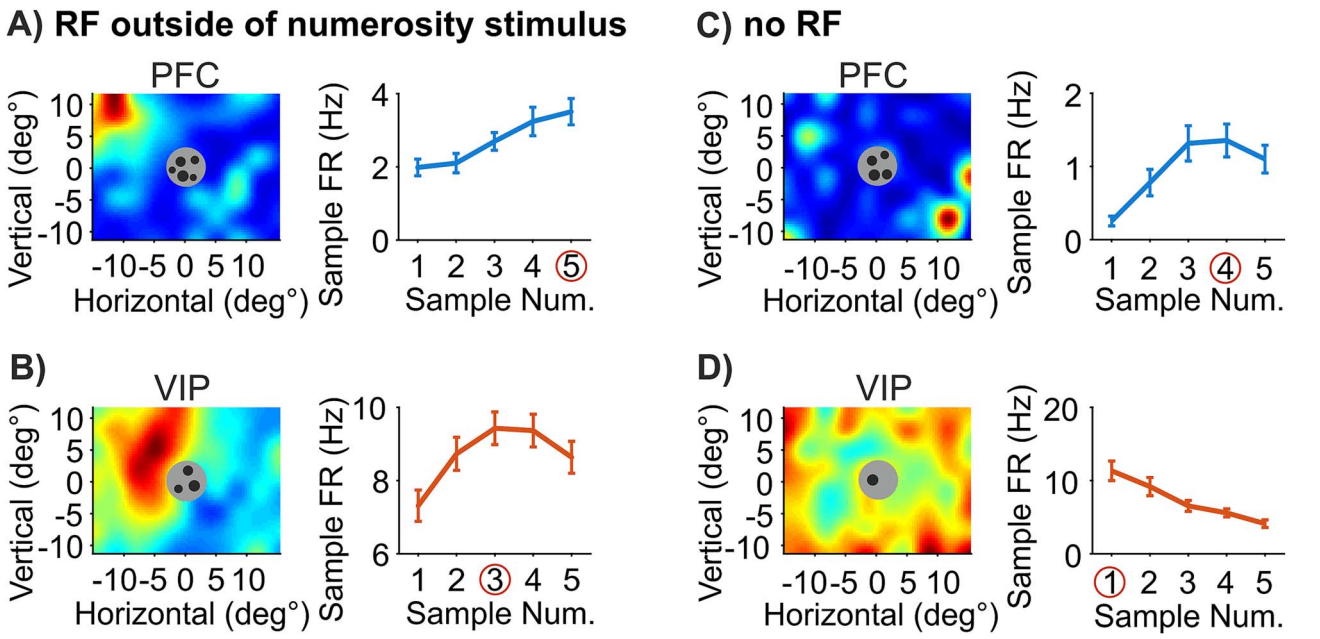

Figure 2. Example numerosity-selective neurons with their RFs outside of the stimulus area, or no RF at all. A) PFC neuron that responds selectively to the numerosity 5 despite having a very eccentric contra-lateral RF. *Left:* The panel shows the dimensions of the stimulus screen with the spatial dimension of the numerosity dot pattern in the center. The color map indicated the normalized firing rate to small mapping stimuli placed across the monitor regions. The excitatory center of this neuron's RF (red) is in the top left corner, far away from the numerosity stimulus. *Right:* Tuning function (average firing rate plotted against sample numerosity) of the same neuron responding selectively to numerosity 5 in the center of the screen during the delayed match-to-numerosity task (ANOVA, $P < 0.01$). Error bars are the standard error of the mean. B) VIP neuron that responds selectively to the numerosity 3 despite having a large para-foveal RF outside of the dot display. Layout as in A. C) PFC neuron that responds statistically indifferent during RF mapping (no RF), but exhibits selectivity for numerosity 4. Layout as in A. D) VIP neuron that responds indifferently to all the mapped locations (no RF) and is selective for numerosity 1. Layout as in A. (from Viswanathan and Nieder 2020).

Spatiotopic and abstract numerosity processing in the IPS and PFC

Indeed, a recent study in monkeys suggests that numerosity-selective neurons in the ventral intraparietal areas (VIPs) of the IPS and PFC are no longer limited by their classical RFs and can integrate information across much larger areas of the visual field. In this study, the RFs of individual neurons in the PFC and VIP of rhesus monkeys were first precisely mapped (Viswanathan and Nieder 2017a, 2017b). Next, the same neurons' responses to numerosities in dot displays were recorded as the monkeys performed a delayed match-to-numerosity task (Viswanathan and Nieder 2020). This allowed to determine whether and how a neuron's numerosity selectivity depended on the location of its visual RF. It was found that PFC and VIP neurons showed numerosity selectivity regardless of whether they had a classic RF (Fig. 2) (Viswanathan and Nieder 2020). Moreover, for neurons with determinable RFs, their numerosity tuning was independent of the RF's specific location, highlighting a remarkable ability to encode numerical information outside of the RF, and beyond spatial constraints (Fig. 2). Additionally, neither the presence nor the location of RFs had an influence on the tuning precision or number coding quality of these numerosity-selective neurons (Viswanathan and Nieder 2020). These findings suggest that neurons in the frontal and parietal cortices integrate abstract visuospatial information to generate global, spatially-independent number representations.

Beyond their role in processing numerical information, neurons in the IPS have also been shown to represent behaviorally relevant categorical information in a globally integrated and spatially independent manner. For example, in a study with monkeys trained to categorize visual motion patterns into two arbitrary groups (eg dots moving up/left versus down/right), researchers recorded the activity of neurons in the LIP of the IPS while the monkeys performed the categorization task (Freedman and Assad 2009). In this experiment, stimuli were presented either inside the neurons' RFs or in the opposite visual field. While most LIP neurons exhibited strong spatial dependence—showing greater responses when stimuli appeared within their RFs—many neurons also encoded the category membership of stimuli even when those stimuli were presented outside their RFs. A similar finding occurred in a task involving saccadic responses toward or away from the RF. LIP neurons continued to maintain selectivity for motion categories even when the stimuli were outside their RFs (Rishel et al. 2013). These results suggest that LIP neurons can represent nonspatial information, such as motion categories, independently of spatial information like saccadic direction. Moreover, when LIP was inactivated, spatial signals were impaired, but the abstract, nonspatial information required for the task was preserved (Balan and Gottlieb 2009). This indicates that nonspatial signals in LIP likely arise from feedback connections with other brain areas involved in processing such information. Together, these findings support the notion that the association cortex plays a crucial role in abstracting information from spatial contexts. This abstraction enables parietal and frontal cortical regions to process global numerical stimuli, resulting in numerosity-tuned neurons (Gottlieb and Snyder 2010; Freedman and Assad 2016; Viswanathan and Nieder 2020).

Recent psychophysical adaptation studies have provided further evidence for spatially abstract numerosity representations by investigating whether numerosity perception is influenced by the spatial location of dot arrays in either retinotopic (relative to eye position) or spatiotopic (relative to head or world position) coordinates. Retinotopic aftereffects, where numerosity adaptation occurs when the adapter and test stimuli are presented in the

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same retinotopic position, are typically explained by the analysis of texture density in early visual processing areas (Durgin 2008). To examine the spatial frame of reference for numerosity adaptation, subjects were shown adapter and test stimuli at specific locations, but with their eyes moving between presentations. The stimuli could either be in the same retinotopic position or the same spatiotopic position. The results revealed that adaptation to numerosity was stronger when the adapter and test stimuli shared the same spatiotopic coordinates, but weaker when presented in the same retinotopic position (Arrighi et al. 2014).

These findings suggest that numerosity adaptation relies on mechanisms that go beyond the retinotopic organization of early visual cortex and involve spatiotopically organized areas, where neuronal RFs are linked to body or head position rather than eye position. Notably, the IPS and PFC are known to be organized in spatiotopic, body-centered coordinates, rather than in eye-centered ones (Duhamel et al. 1992, 1997; Zirnsak et al. 2014). In line with this, visual RFs in primate association areas are not organized topographically, and neighboring neurons do not receive information from adjacent spatial locations (Viswanathan and Nieder 2017b). Note that the picture is different when considering blood-flow signals, as a visuotopic organization of the macaque PPC has been demonstrated using fMRI (Arcaro et al. 2011).

These insights from single-neuron studies are supported by fMRI research, which shows that numerosity-tuned regions in the association cortex often overlap with higher-level visual field maps (Harvey and Dumoulin 2017). However, the spatial population RFs (pRFs) in these areas—representing the regions of the visual field to which groups of neurons within a voxel respond—do not necessarily correspond to the location of the numerosity stimulus (Harvey et al. 2015; Harvey and Dumoulin 2017). Moreover, numerosity preferences in these regions are unrelated to the position or size of their pRFs (Harvey et al. 2015). This greater independence from classical RFs and spatiotopic organization sets fronto-parietal association areas apart from early visual areas and likely contributes to numerosity adaptation effects observed within these fronto-parietal regions.

Despite the insights gained from recent studies on association cortex, such as spatiotopic organization and independence from RFs, current computational models of numerosity estimation fail to capture these crucial characteristics. In these models, whether the stimulus consists of a small number of dots or a dense array, the neural network layers involved have spatial access to the entire stimulus layout (Stoianov and Zorzi 2012; Zorzi and Testolin 2017; Nasr et al. 2019; Nasr and Nieder 2021). However, this approach overlooks the hierarchical structure of the visual system, where spatial independence and abstraction—key features of the higher-order areas involved in numerosity processing—must be developed progressively along the pathway (but see Szinte et al. 2024, for the view that visual locations are encoded in a retinotopic reference frame throughout the visual hierarchy.). Interestingly, an fMRI study by Paul et al. (2022) found that the independence of spatial RFs emerges at the same level of the visual hierarchy as numerosity-tuned responses. However, it remains unclear whether this finding, based on blood flow signals, holds true at the level of single-neuron activity. In addition, Park and Huber (2022) identified key neurocomputational principles—namely, center-surround contrast filters operating at multiple spatial scales and divisive normalization across network units—that account for how early visual responses can be sensitive to numerosity while remaining relatively insensitive to continuous visual dimensions such as size and spacing. Future research should address where in the network hierarchy the observed numerosity-selective neurons first become independent of visual RFs and transition from retinotopic to spatiotopic processing.

Conclusion

Empirical findings challenge the *Early Processing Hypothesis* by highlighting the role of spatial frequency, rather than number, in early visual cortex activation. Numerosity perception develops later in the visual processing hierarchy. In higher-order association areas like the IPS and PFC, abstract, location-independent representations are formed, supported by spatiotopic integration and neuronal tuning curves for specific numerosities.

It is often overlooked that numerosity is an abstract concept that spans across sensory modalities. Therefore, brain regions involved in numerosity coding must integrate information from multiple senses. Evidence for this includes findings that visual number adaptation can influence auditory number perception and vice versa, implicating multimodal regions like the IPS and PFC (Nieder 2012; Arrighi et al. 2014). Additionally, the sensorimotor system plays a role in numerosity judgments: repetitive finger tapping affects visual numerosity estimates, with faster tapping, reducing perceived numbers and slower tapping increasing them (Anobile et al. 2016, 2024). These results suggest that numerosity coding relies on a generalized, multimodal mechanism located in association areas such as the IPS, rather than sensory-specific regions like the primary visual cortex, which cannot process auditory or motor inputs.

This line of research emphasizes that studying the number sense solely through dot patterns is limited and may lead to incorrect conclusions about the brain regions and physiological principles involved in number representation. The number sense operates not only for spatial arrangements like dot arrays but also for sequences of items across time (Nieder et al. 2006). Moreover, to fully understand how the abstract concept of numerosity is represented in the brain, it's essential to test visual numerosity displays alongside presentations in other sensory modalities (Nieder 2012; Hofstetter et al. 2021).

Furthermore, at some point in human development, non-symbolic numerosity must be linked to shapes, which, through symbolic understanding, become number symbols: words and numerals (Nieder 2009). This process, too, relies on the association cortex, as primary sensory areas lack the necessary multi-modal and cognitive representations. A complete understanding of the neurobiology of the number sense can only emerge when different types of stimuli are studied in combination.

Author contributions

Andreas Nieder (Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing—original draft, Writing—review & editing).

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