Multisensory Number Representation:

How the Brain Weaves Numbers Across Senses and Formats

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Résumé

La cognition numérique constitue une pierre angulaire de l'intelligence humaine, sous-tendant aussi bien les activités quotidiennes, comme le paiement des factures, que les réalisations complexes telles que l'ingénierie et les découvertes scientifiques. L'information numérique est intrinsèquement multisensorielle : que nous voyions cinq stylos sur une table, entendions cinq coups frappés à une porte ou sentions cinq coups de marteau sur un clou, nous percevons spontanément le concept numérique du chiffre cinq. Cette thèse part de cette nature multisensorielle de la numérosité pour explorer comment le cerveau représente et développe l'information numérique. Dans le premier chapitre, nous avons examiné comment la numérosité intermodale (c'est-à-dire vision vs audition) et inter-format (séquentiel vs simultané) est représentée et converge dans le cerveau. À l'aide de l'imagerie par résonance magnétique fonctionnelle (IRMf) combinée à multivariate pattern analysis (MVPA), nous avons examin é l'organisation fine des représentations neuronales de l'information numérique. Ces analyses révèlent comment les schémas d'activité distribués à travers les régions sensorielles et pariétales codent la numérosité, et comment ces codes peuvent se généraliser – ou rester distincts – selon les modalités sensorielles et les dimensions temporelles. Dans le second chapitre, nous questionnons une hypothèse de longue date dans la littérature: la numérosité serait intrinsèquement liée à la vision. En nous appuyant sur des données comportementales, psychophysiques et en neuroimagerie, je montre que l'expérience visuelle n'est pas une condition préalable au développement de la cognition numérique. Dans son ensemble, cette thèse participe à améliorer notre compréhension de la manière dont le cerveau humain encode l'information numérique, et ce à travers les différentes modalités et formats sensoriels.

Abstract

Numerical cognition is a fundamental skill for human being, underlying everyday activities such as paying bills as well as complex achievements like engineering and scientific discovery. Numerical information is inherently multi-sensory: whether we see five pens on a table, hear five knocks on a door, or feel five taps of a hammer, we are able to estimate their numerosity. This thesis begins from this multi-sensory nature of numerosity to explore how the brain represents and develops numerical information. In the first chapter, we investigated how cross-modal (i.e., vision vs. audition) and cross-format (i.e., sequential vs. simultaneous) numerosity are represented and converge in the brain. Using functional magnetic resonance imaging (fMRI) combined with multivariate pattern analysis (MVPA), we examine the fine-grained organization of neural representations of numerical information. These analyses reveal how distributed activity patterns across sensory and parietal regions encode numerosity and how such codes may generalize, or remain distinct, across sensory and temporal dimensions. In the second chapter, we challenge a long-standing assumption in the literature: that numerosity is inherently tied to vision. Drawing on behavioral, psychophysical, and neuroimaging evidence, we argue that visual experience is not a prerequisite for developing numerical cognition. Together, this thesis advances our understanding of how the human brain encodes numerical information across sensory modalities and formats.

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Chapter 1

General Introduction

1. General Introduction

Numerosity perception constitutes a fundamental ability in humans and animals. For example, when our ancestors had to decide whether to hunt or run away, quickly estimating the number of rivals was essential. A wrong estimation could directly put their survival at risk. Interestingly, our distant amphibian relatives, the túngara frogs of Central America, also demonstrate a form of number sense in the context of reproduction. Male frogs compete by producing advertisement calls, while females attend to these calls, compare their number, and ultimately choose to mate with the male that produces the most (Rose, 2018).

These two simple examples provide a clear illustration of how critical and ubiquitous numerosity perception is. Extensive scientific studies further support this, showing that the ability to process numerical information is present in new-born infants (Coubart et al., 2014; Izard et al., 2009; Turati et al., 2013; Visibelli et al., 2024), in birds such as crow and chicks (Ditz & Nieder, 2020; Kobylkov et al., 2022; Lorenzi et al., 2024; Rugani et al., 2008), in fishes and even in insects (Agrillo et al., 2008; Agrillo & Bisazza, 2018; Andreas Nieder, 2018; Bortot et al., 2019; Luu et al., 2024; Messina et al., 2022), suggesting a common evolutionary origin of this ability. Because of this ubiquitous and deep in evolutionary roots, the ability to perceive numbers is considered to be as a primary perceptual property: we perceive 'threeness' as readily as we perceive 'redness' in color, 'roundness' in shape, or 'frontness' in spatial position (Anobile, Cicchini, et al., 2016; Anobile et al., 2021; Burr & Ross, 2008; Dehaene, 2011).

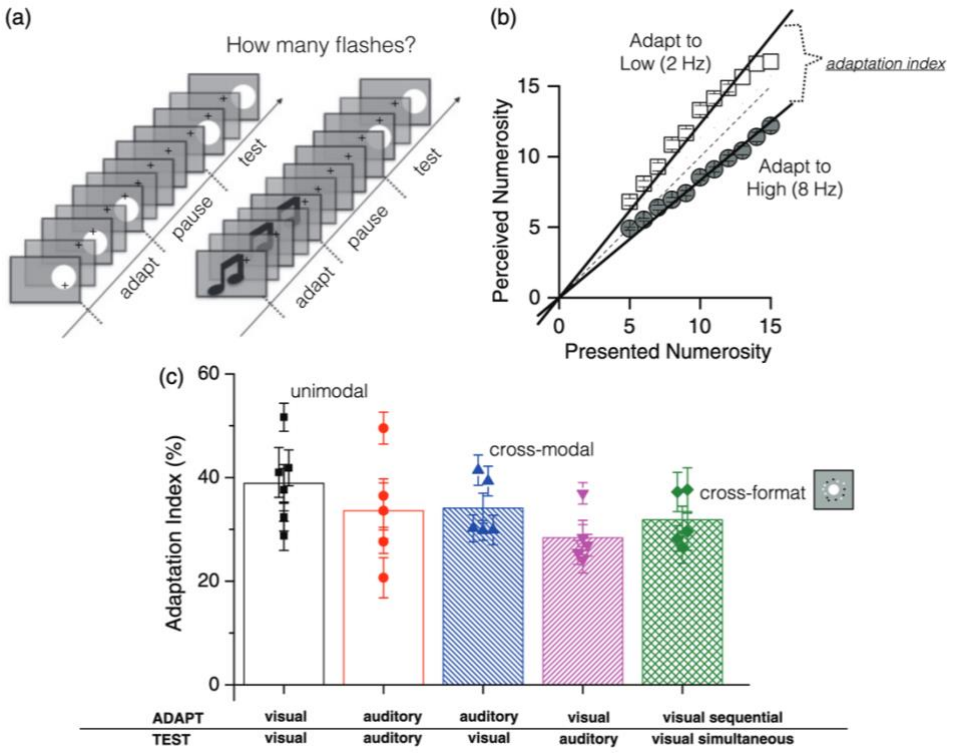
1.1 A generalized number sense

What we can learn from these examples is not only that number sense is ubiquitous across species, but also that it manifests in multiple forms and modalities. Numerosity is an abstract concept: whether we see five pens on a table, hear five knocks on a door, or strike a nail five times with a hammer, we can estimate their numerosity. It is therefore widely believed that numerical information—regardless of modality (vision or audition), format (simultaneous in space or sequential in time), or notation (symbolic[1] or non-symbolic)—converges on a unified, abstract[2] representation in the brain (Dehaene et al., 1998; Nieder & Dehaene, 2009).

[1] 'symbolic' refers to number representations that use culturally invented symbols, such as Arabic digits (e.g., '3') or written/spoken number words ('three'), rather than quantities perceived directly.

[2] 'abstract' numerosity representations are described as format-independent, meaning they arise after sensory processing and encode number in a form that is not tied to vision, audition, or any surface feature of the stimuli.

This view is supported by a wide range of behavioral evidence. At the behavioral level, a unified, abstract numerical representation implies that effects associated with one type of input should generalize across modalities. For instance, the amodal[3] spatial-numerical association of response codes (SNARC effect), where participants respond faster to small numbers with the left hand and to large numbers with the right hand, occurs independently of modality (Dehaene et al., 1993; Fias, 2001; Fias & Fischer, 2005; Nuerk et al., 2005). Similarly, the distance effect confirms this abstract representation: participants' reaction times increase as the numerical distance between two values decreases, and this effect holds regardless of modality or notation (Dehaene, 1996; Dehaene & Akhavein, 1995; Moyer &



Landauer, 1967; Naccache & Dehaene, 2001; Schwarz & Keus, 2004). In line with this, Barth and colleagues (2003) found no measurable cost in reaction times when participants compared numerosities across modalities (vision vs. audition) or formats (simultaneous vs. sequential) compared with within-modality comparisons, further supporting the idea of a modality- and format-independent representation of numerosity.

Figure 1.1. A: Examples of stimuli used in the serial numerosity adaptation experiment. On the left are visual unimodal stimuli, while on the right are auditory–

[3] In the context of the SNARC effect, 'amodal' means that the spatial-numerical association does not depend on the sensory modality through which numbers are presented. Whether numbers are seen, heard, touched, the same spatial pattern reliably emerges.

visual cross-modal stimuli. B: Example results from the visual unimodal adaptation task are illustrated. When participants adapted to low numerosities (2 Hz; open squares), they tended to overestimate numerosity, whereas adaptation to high numerosities (8 Hz; gray circles) led to underestimation. The data were accurately modeled using linear regressions (lines) constrained to pass through the origin. The adaptation strength, or adaptation index, was calculated as the difference between the slopes of the regression lines. C: Average adaptation indices are presented for different experimental conditions: unimodal visual and auditory adaptation, cross-modal auditory–visual and visual–auditory adaptation, and cross-format adaptation (where adaptation occurred with serial presentation and testing with simultaneous presentation). Bars represent group averages, and symbols indicate individual participant data. Adapted from Arrighi et al. (2014).

Adaptation studies provide converging evidence as well. These studies exploit the principle that neurons tuned to a specific stimulus reduce their firing rates when the stimulus is repeatedly presented (Krekelberg et al., 2006). Such neural adaptation gives rise to behavioral aftereffects: following repeatedly exposure to an adaptor stimulus, subsequent stimuli are often misperceived, typically in the opposite direction, producing strong negative aftereffects (Fedorov et al., 2018; Storrs, 2015; P. Thompson & Burr, 2009). Cross-modal adaptation study on numerosity has been demonstrated that adapting to numerical sequences in audition influences the perception of numerical sequences in vision, and vice versa (Arrighi et al., 2014, see Figure 1.1). In their study, Arrighi and colleagues measured how prior exposure to fast or slow sequences (e.g., 2Hz vs. 8Hz) biases the perceived numerosity of a subsequent test sequence. Test numerosity ranged from 2 to 20, but their analyses focused on the subset from 5 to 15 to avoid subitizing and edge effects. To quantify the strength of this adaptation, they subtracted the perceived numerosity after 2 Hz adaptation from that after 8Hz adaptation for the same physical numerosity. They then fit a zero-anchored regression to this difference curve, and the slope of this regression is taken as the adaptation index, an estimate of the magnitude of adaptation. This adaptation index captures the proportional perceptual distortion caused by adaptation and allows direct comparison of adaptation strength across locations, reference frames, modalities, and presentation formats. Interestingly, later studies extended this principle from perception to action. A short period of rapid tapping led participants to underestimate the number of visual stimuli, whereas slow tapping induced overestimation (Anobile, Arrighi, et al., 2016; Anobile et al., 2021).

Although fewer in number, several studies have challenged the notion of a generalized number sense. Tokita and Ishiguchi (2012) compared the precision of approximate numerosity comparison between simultaneous, sequential and cross-format numerical presentations, using standard numerosities of 10 and 20 and comparison values ranging from 8 to 24. They found that discrimination of an auditory sequence was more precise than that of a visual sequence, with performance in cross-modal trials falling in between. These results suggest the involvement of multiple mechanisms in cross-modal and cross-format

numerosity perception. Most recently, Yousif et al. (2025) have even questioned the fundamental view of number adaptation.

Taken together, although evidence against a generalized numerosity system exists, the majority of findings support the view that numerosity is a highly generalized system, capable of integrating numerical information across senses, formats, and domains of action and perception (Anobile, Cicchini, et al., 2016; Togoli et al., 2020; Togoli & Arrighi, 2021).

1.2 Neural basis of numerosity processing

1.2.1 Theoretical models

Numerosity perception is a fundamental cognitive ability, and understanding its underlying neural mechanisms has become one of the most intriguing topics in cognitive neuroscience. Among the leading theoretical frameworks, the Triple Code Model (TCM) is one of the most widely accepted models of numerical cognition (Dehaene, 1992; Dehaene & Cohen, 1997; Nieder, 2016; Figure 1.2). The TCM posits that numerosity is represented through three distinct representational codes: (1) auditory verbal number words (e.g., “three”), (2) visual Arabic numerals (e.g., “3”) and (3) non-symbolic analogue magnitude representations. Each code is supported by functionally distinct neural substrates (Klein et al., 2016).

The verbal number word code is primarily associated with retrieving well-learned arithmetic facts, such as addition and multiplication tables, and is linked to left-hemisphere language areas. For example, Schmithorst and Brown (2004) demonstrated activation of the inferior frontal gyrus (IFG) and broader perisylvian language networks, including the supramarginal gyrus (SMG), middle temporal gyrus (MTG), and superior temporal gyrus (STG). Similarly, Dehaene and colleagues (2003) highlighted the role of the left angular gyrus (AG) in verbal number coding, showing consistent activation in tasks with high verbal demands. The visual Arabic number code, which represents numbers in their symbolic Arabic form, is typically engaged during tasks such as multidigit calculation and parity judgments (Dehaene, 1992). Neuroimaging studies have implicated the right caudal fusiform gyrus and AG in supporting this representation (Grotheer et al., 2016; Pinel et al., 1999; Price & Ansari, 2011; Shum et al., 2013; Yeo et al., 2017). Finally, the non-symbolic analogue magnitude code underlies the estimation and spatial representation of quantity, often conceptualized as a “mental number line” (Dehaene, 1992). This code is strongly associated with the horizontal segment of the intraparietal sulcus (hIPS), which plays a critical role in approximate number processing (Dehaene & Akhavein, 1995; Hubbard et al., 2005; Nieder & Dehaene, 2009; Piazza, 2010; Piazza et al., 2004).

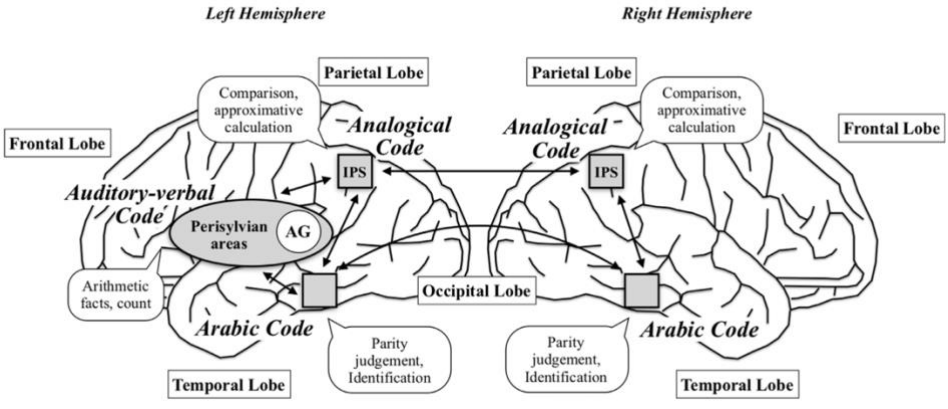


Figure 1.2: The Triple Code Model. This figure, adapted from Dehaene and Cohen (1995), offers an external representation of how the Triple Code Model (TCM) is organized in the brain. The arrows indicate how information flows and is exchanged both between the different numerical codes and across the two hemispheres.

Dehaene et al. (2003) updated the tripartite organization of numerical cognition based on a wide range of neuroimaging and neuropsychological evidence. They propose that the horizontal segment of the intraparietal sulcus functions as a core quantity system. It is systematically activated whenever numbers are manipulated, independently of number notation and modality. It is thought to implement an internal 'number line', a domain-specific representation of quantity. A second region, the left angular gyrus, supports the verbal coding of numbers, for example, arithmetic facts such as multiplication that are stored in a language-specific format. The third component, a bilateral posterior superior parietal system, contributes attentional and spatial processes that allow us to navigate along the 'mental number line' when tasks require shifting attention between quantities.

There have also been more recent updates to the triple-code model. For example, Arsalidou and colleagues (2011) conduct a quantitative fMRI meta-analysis to identify brain regions involved in number processing and calculation. They found that both types of tasks reliably activated parietal regions, particularly the inferior and superior parietal lobules. However, the differences between them were most notable. For example, calculation tasks recruited more prefrontal areas than number tasks, suggesting greater reliance on cognitive resources such as working memory and executive control. This study also revealed distinct neural patterns across arithmetic operations: addition was predominately left-lateralized, subtraction showed bilateral activation and multiplication was primarily right-lateralized. Based on these results, the authors propose an update to the traditional triple-code model, emphasizing including working memory or executive-control systems and reframing numerical processing as supported by multiple interacting networks rather than three isolated codes.

Verguts and colleagues (2005) propose a computational model of how small symbolic numbers are represented. They argue that prior models of the 'mental number line' often assume magnitude coding, compressed scaling and increasing variability with number size. As a results, these models predict asymmetries between small and large numbers and expect the size effect, as a property of representation itself, to appear whenever the number line is used. However, this is inconsistent with empirical findings (Dehaene, 2004, Butterworth, Zorzi, Girelli, & Jonckheere,2001; Reynvoet, Brysbaert, & Fias, 2002). For example, Dehaene's study in 2004 have showed that even when primes are smaller and larger than the target by the same distance, priming effects are equal. Moreover, naming and parity judgment tasks clearly involve access to the number line yet produce no size effect. Verguts and colleagues therefore introduce a model that implements a linear non-compressed place coding with fixed variability across numbers. In this framework, each number activates an equal amount of units along the number line, and linear scaling ensures that the distance between adjacent numbers is constant. Constant variability implies that all numbers share activation curves of identical width, ensuring equal representational

precision rather than increasing noise with number size. This model outperforms prior models by explaining the two empirical findings they cannot: it produces symmetric distance-related priming and predicts that a size effect emerges only in comparison, due to nonlinear mapping from the numbers line to the output system rather than form the representation itself.

Walsh's ATOM (A Theory of Magnitude, 2003) proposes that the brain relies on a single, shared system centered in the parietal cortex, to process different kinds of magnitudes, including time, space, number, size and other quantitative dimensions. Rather than treating these domains as separate cognitive abilities, ATOM argues that they rely on common neural mechanisms because the brain must represent them together to guide movement and interaction with the world. From this perspective, number abilities likely evolved by building upon an older, more general magnitude-processing system originally dedicated to guiding movement and interaction with the environment.

Dehaene & Changeux (1993) define the accumulation process for numerosity from a spatial summation mechanism (Figure 1.3). In their model, visual input is first processed through filters that act like difference-of-Gaussians, creating a spatial map that captures both the location and approximate size of each object. This map then feed into summation units that add up the total activity and fire only when the total activity becomes high enough. These summation signals are then passed on to numerosity-sensitive units tuned to specific ranges of total activity, allowing them to respond selectively to numerosities.

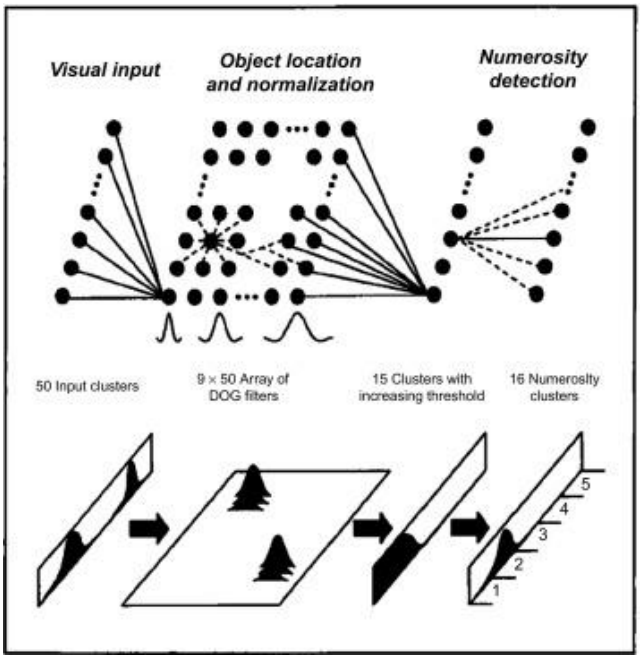


Figure 1.3: Figure illustrated the structure and function of the numerosity detection model proposed by Dehaene & Changeux (1993). Objects of different sizes at the input

are first normalized to a size-independent code. Activations are then summed to yield an estimate of input numerosity.

In addition to the visual stream, the model simulates an auditory route that mirrors the logic of the visual system but operates sequentially rather than spatially. At any given moment, only one of fifteen auditory input clusters can be activated, each representing a single auditory "object" or event. These inputs project to an intermediate layer in which strong recurrent connections allow activity to persist briefly, forming a simple echoic memory that holds onto recent auditory items over time. Because auditory objects typically arrive one after another rather than all at once, this intermediate layer allows accumulate individual object in parallel with visual items. The sustained activity in the echoic layer is then sent to the same set of summation clusters used for visual processing.

1.2.2 Intraparietal sulcus as a numerical central hub

Using methods such as electrophysiology, neuroimaging, and computational modeling, numerous studies have validated these neural substrates (Dormal et al., 2012; Harvey et al., 2013; Nieder, 2016; Rinsveld et al., 2020; Skagenholt et al., 2018; Stripeikyte et al., 2021; Van Rinsveld et al., 2020). Among them, the intraparietal sulcus (IPS) has emerged as particularly crucial for numerosity perception, serving as a central hub for processing numerical magnitude across symbolic and non-symbolic formats (Dehaene et al., 2003; Dormal et al., 2012; Eger et al., 2003; Piazza et al., 2004).

As early as the 1970s, Thompson and colleagues (1970) demonstrated that the posterior parietal cortex of cats contains neurons responsive to numerosity. Subsequent work in macaque monkeys confirmed this finding: Sawamura et al., (2002) showed that neurons in the anterior bank of the IPS respond selectively to numerical information. Another study revealed that IPS neurons remain sensitive to numerical stimuli even after controlling for confounding factors such as object size, density, spacing, and spatial layout. Although numerosity-selective responses have also been observed in the prefrontal cortex (PFC), latency analyses suggest that numerical information is first extracted in parietal neurons and subsequently projected to frontal regions. Importantly, the tuning functions of these neurons follow Weber's law, with tuning curve widths increasing linearly as the encoded numerosity grows.

Consistent findings across non-human primates reinforce this view. Numerosity-selective responses have been reported in both the lateral PFC and the ventral intraparietal area (VIP), the putative macaque homolog of the human IPS (Nieder et al., 2002, 2006). Moreover, similar numerosity-selective neurons have been identified in crows (Ditz & Nieder, 2020; Kirschhock & Nieder, 2022), providing compelling evidence that the neural foundations of numerosity are evolutionarily ancient rather than mere by-products of education and experience.

In human neuroimaging studies, IPS is consistently recruited when adults from diverse cultures perform basic numerical tasks, such as comparing quantities or calculating with

symbolic notations like Arabic numerals or number words (Dehaene et al., 2003). This consistent activation has led researchers to identify the IPS as the core hub for representing numerical magnitude.

Neuroimaging has also taken advantage of the above-mentioned principle of neuronal adaptation: the tendency of neurons to reduce their firing rate when repeatedly exposed to the same stimulus (Krekelberg et al., 2006). In fMRI, this phenomenon is expected to manifest as a decline in blood oxygen level–dependent (BOLD) responses with repeated presentations. Such paradigms provide a way to test whether human neurons are selectively tuned to numerosity (Nieder, 2025). In one fMRI adaptation study (Piazza et al., 2004), participants were repeatedly shown dot arrays of a fixed numerosity to induce neuronal adaptation. Occasionally, deviant numerosities were introduced, ranging from half to double the adapted value. The results revealed that only the left and right horizontal segment of the IPS (hIPS) exhibited sensitivity to these numerical deviations, showing activation that scaled with the ratio between the adapted and deviant numerosities, independent of whether the change reflected an increase or a decrease. Since then, the activation of hIPS to numerosity stimuli has been replicated extensively by using different stimuli such as sequences of sounds, serial presentation of visual stimuli and using different paradigms such as passive viewing versus active computations (Castelli et al., 2006; Piazza et al., 2007, 2006). Moreover, hIPS start to response to numerosity for infants as early as three-month-old, which confirmed again that this brain activation is already functional early in life, and prior to arithmetical education (Izard et al., 2009; Gennari et al., 2023).

Evidence for the causal role of the hIPS in numerosity processing comes from TMS studies showing that disrupting activity in the hIPS, but not unlike in adjacent but distinct regions such as the left and right angular gyrus, impairs numerosity judgments. Importantly, disruption of the hIPS selectively affects numerosity processing while leaving duration judgments intact (Cappelletti et al., 2007; Dormal et al., 2008).

1.2.3 Visual cortex plays a role in numerosity processing

Recently, several studies showed the early visual cortex also plays a role in numerosity processing (Castaldi et al., 2019; DeWind et al., 2019; Fornaciai et al., 2017; Park et al., 2016). In a study by Castaldi et al., (2019), participants viewed arrays of dots while undergoing fMRI scanning and were instructed to attend either to the number of dots or to their size. This design allowed the researchers to disentangle brain activity specific to numerosity from that associated with other visual features. Their findings showed that attending to numerosity enhanced activation as early as area V3AB, suggesting that the human visual system is capable of directly perceiving numerosity. Consistent evidence comes from several human scalp EEG studies. For example, Park et al. (2016) demonstrated event-related potentials (ERPs) specifically sensitive to number very early in visual processing (around 75 ms) over medial occipital regions. This ERP component varied monotonically with numerosity, with scalp voltage increasing as the number of items increased. Further support comes from Fornaciai et al., (2017) who used the connectedness illusion to highlight the role of perceptual segmentation in forming numerical

representations. They asked whether early visual activity reflects perceptual units of numerical magnitude rather than the raw sensory properties of the stimulus. Their results showed that the effect of connectedness emerged in visual area V3 and was traceable from approximately 150ms after stimulus onset. By contrast, earlier neural responses—at or before 100ms in area V2—showed no effect of connectedness and were strictly modulated by numerosity regardless of grouping. This suggests that these early stages encode only the raw sensory representation of the stimulus, which is then further processed to form perceptual units of numerosity. Although further research is needed to clarify what is represented in the early visual cortex and why V3(AB) appears to be the entry point for numerosity encoding, these studies provide strong neural evidence that numerosity is a primary perceptual feature encoded in early sensory brain regions.

1.3 A generalized numerosity representation in the brain: inconsistent evidence

The number sense is thought to enable us to comprehend quantities in an abstract fashion, independent of notation (e.g., symbolic or non-symbolic), presentation format (e.g., simultaneous or sequential), or sensory modality (e.g., visual or audibly). But where in the brain is this abstract concept represented? And how is numerical information from different sensory inputs abstracted into a generalized numerosity representation?

A large body of neuroimaging evidence points to the intraparietal sulcus (IPS) as a critical region supporting such abstract representations (Dormal et al., 2010; Eger et al., 2003, 2009; Piazza et al., 2007). For example, several studies have shown that IPS activation varies as a function of the numerical distance effect, and this modulation is consistent across notations. In other words, the IPS does not show interactions between notation and numerical distance (Eger et al., 2003; Pinel et al., 2001). Adaptation studies further support this view, demonstrating that repeated presentation of the same quantity induces adaptation in the left parietal lobe regardless of notation, consistent with an abstract representation (Piazza et al., 2004). Eger et al. (2003) compared stimuli across different categories—including numbers, letters, and colors—presented in both visual and auditory modalities, using numbers ranging from 1 to 9. They found that only for numerical stimuli did the parietal cortex show similar activation patterns across modalities, suggesting that the IPS supports a generalized numerosity representation. Similarly, Piazza and colleagues (2004) reported right-lateralized IPS activation when participants estimated the number of temporal sequences, whether visual or auditory, using numerosities ranging from 8 to 32. Crucially, this activation was not modulated by the modality in which stimuli were presented. Extending this evidence, Dormal et al. (2010) examined cross-format processing, comparing sequential and simultaneous presentations of small numerosities (6 and 8). They observed overlapping activation in the right IPS and precentral gyrus for both formats. Voxelwise analyses revealed highly similar activation patterns in these regions across stimulus types. Taken together, these studies provide strong neural evidence that the IPS encodes numerosity in a notation-, modality-, and format-independent manner, supporting its role as a core hub for abstract numerical representation.

However, despite the evidence reported in previous studies, the reasoning behind this assumption remains incomplete and is subject to both methodological and theoretical limitations (Cohen Kadosh & Walsh, 2009). First, the claim that numerosities are represented independently relies heavily on null results—specifically, on the absence of differences across notations, modalities, or formats. Yet such null results may equally stem from insufficient statistical power or from the limited sensitivity of the paradigms employed (Button et al., 2013; Cremers et al., 2017). Moreover, while different numerosity stimuli do elicit similar patterns of brain activation, such similarity within a region likely reflects the activity of distinct neuronal subpopulations. Traditional univariate fMRI analyses, which average responses across neural populations within a given region, are therefore unable to disentangle the contributions of individual neurons or voxels (Kriegeskorte et al., 2006, 2008; Norman et al., 2006).

To address this limitation, multivoxel pattern analysis (MVPA) has been introduced as a powerful tool to examine whether distributed neural activity is shared across conditions (Kriegeskorte, 2011; Kriegeskorte et al., 2008; Naselaris & Kay, 2015; Norman et al., 2006). Unlike univariate approaches, MVPA leverages fine-grained voxel-level response patterns, enabling the detection of representational similarities with greater sensitivity by comparing distributed activity rather than averaged signals. Cross-decoding, where a classifier is trained on one condition and tested on another, allows researchers to assess whether information generalizes across conditions (Kaplan et al., 2015). This approach provides positive evidence for shared neural representations, rather than relying on null results as in traditional univariate analyses.

Over the past two decades, researchers have extensively used MVPA to search for generalized representations of numerosity across different dimensions (Bulthé et al., 2015; Cavdaroglu et al., 2015; Cavdaroglu & Knops, 2019a; Damarla et al., 2016; Damarla & Just, 2013; Eger et al., 2009; Lyons et al., 2015). The first dimension to be tested was notation, comparing symbolic and non-symbolic numerosities. In a pioneering study, Eger et al. (2009) demonstrated a generalized representation across Arabic digits and dot arrays with numbers ranging from 2 to 8. They showed that parietal activation patterns for individual numerosities could be reliably discriminated across changes in low-level stimulus parameters. Crucially, they observed an asymmetrical generalization between dots and digits: the numerosity of dot sets could be predicted above chance from brain activation patterns evoked by digits, but not vice versa. This asymmetry was explained by the different neural populations engaged in numerosity processing: populations encoding non-symbolic numerosities are broadly tuned and include neurons that later acquire narrower selectivity for symbolic numbers. Thus, when training on digits, the classifier engages these shared neurons, enabling above-chance generalization to dot patterns. In contrast, when training on dots, the classifier relies on the broader, coarsely tuned population, many of which do not respond to symbolic digits, thus resulting in poor generalization.

However, subsequent studies have reported inconsistent findings. Bulthé et al. (2015) for example, examined numerosities 1, 2, 4, and 8, and found that both dots and Arabic digits could be decoded in parietal regions, with dots yielding broader decoding than digits.

Yet, they did not observe above-chance decoding when testing for cross-notation generalization. Instead, they found that Arabic digits were reliably classified as corresponding to the one-dot pattern, rather than to the dot pattern matching the same numerical magnitude. They explained the results by "object cognition account," suggesting that Arabic digits are classified as similar to the one-dot condition because both stimuli consist of a single visual element. A similar study by Damarla et al. (2013) find no evidence for generalization across pictorial mode (e.g., a picture of 5 hammers) and digit mode. Lyons et al. (2015) using RSA found no evidence of shared symbolic and nonsymbolic number-specific representations as well.

The second dimension to test was modality, referring to numerical information presented through different sensory channels, such as vision or audition. Here, we define cross-modal numerosity as cases where the numerosity differs only in modality, without variation in other dimensions such as format (e.g., simultaneous vs. sequential). For example, a cross-modal numerosity comparison could involve sequential visual dots versus sequential auditory tones. However, the limitations of the human auditory system make it difficult to reliably count simultaneous sounds. The literature suggests that humans can typically discriminate only around 3 to 5 simultaneous sounds under experimental conditions (Abeßer et al., 2023). This constraint makes it challenging to study cross-modal simultaneous numerosity representations between vision and audition.

One study investigated cross-modal simultaneous numerosity across vision and touch using numbers from 1-7 (Hofstetter et al., 2021). Visual stimuli consisted of dot arrays, while tactile stimuli were plastic spheres placed in the participant's right hand. The authors found that responses to visual and haptic numerosities recruited a similar cortical network, but only partially overlapped, suggesting that the underlying neural populations are related yet distinct. Notably, in the tactile condition, participants had to actively explore the spheres to determine their number. As a result, the haptic task likely combined simultaneous and sequential processing, rather than providing a purely simultaneous representation.

Several studies have investigated cross-modal numerosity representations using sequential stimuli across vision and audition (Damarla et al., 2016; Nieder, 2012). An electrophysiological study in macaque monkeys showed that neuronal populations in the prefrontal and parietal cortices encode sequential numerosity across sensory modalities (Nieder, 2012). In humans, Damarla et al. (2006) examined whether small sequential numbers are represented in a modality-independent manner across vision and audition. They reported evidence for cross-modal representations in both frontal and parietal regions. However, their stimulus design did not carefully control for low-level confounds such as overall sequence length or the duration of individual items (Dehaene et al., 2005). When generating object sets as stimuli for numerosity experiments, the nature of the stimuli imposes obligatory correlations between intensive and extensive variables. For example, once numerosity is fixed, individual item length and total energy become linearly related: changing one necessarily alters the other. This creates unavoidable confounds, if individual item length is held constant, total energy covaries with numerosity, and vice versa. As a

result, neural responses attributed to numerosity might actually reflect sensitivity to changes in item length. In addition, because the interstimulus interval was fixed, participants may have relied on rhythmic cues rather than numerosity per se when making their judgments (Dormal et al., 2010).

Cavdaroglu et al., (2015) more carefully controlled for low-level features in their study. They employed four different stimulus sets, each designed to control for specific factors such as single-item duration, total duration, inter-item interval, and frequency. Their experimental design allowed them also to dissociate numerosity estimation from comparison and response-related processes. Interestingly, numerosity could be reliably decoded from parietal brain regions only during the response period. To further test generalization across conditions, they conducted cross-condition analyses and found borderline results. The confusion matrix revealed that these borderline results were primarily driven by the smallest numerosity in the stimuli (number 5), which limits the broader interpretability of the findings. Although the study largely reported null effects, it highlights two important factors for understanding generalized numerical representations: task-related processes and the range of numerosities tested. To make this clearer, I will specify the numerical ranges used in each study throughout the following introduction, and I will return to a more detailed discussion of these issues later in the text.

The last dimension I would like to discuss is format, which refers to the way numerosity is embedded—either simultaneously in space or sequentially in time. Different formats of presentation rely on distinct cognitive mechanisms. Simultaneous numerosity depends on spatial processing and is extracted in parallel through location maps, whereas sequential numerosity unfolds over time, requiring serial accumulation and engaging temporal processing. Since vision is considered the dominant modality for developing spatial representations and abilities, most research on simultaneous numerosity has focused on the visual domain (Castronovo, 2014). A few studies have explored tactile simultaneous numerosity perception, but these remain at an exploratory and behavioral level (Gallace et al., 2007; Hochman et al., 2020; Krause et al., 2013; Riggs et al., 2006). For example, Gallace et al., (2007) presented participants with 1–7 vibrotactile stimuli delivered simultaneously via tactors placed on different parts of the body fig. The findings showed that error rates increased sharply once more than two tactors were activated, providing no evidence for a subitizing effect in simultaneous tactile numerosity judgments. Neuroimaging studies on simultaneous numerosity perception in both humans and macaque monkeys highlight the critical role of the posterior parietal cortex (Dehaene et al., 2004). However, a persistent challenge in visual numerosity research is disentangling numerosity from low-level visual features of the stimuli (Gebuis et al., 2014, 2016; Gebuis & Reynvoet, 2012a, 2012b; Leibovich et al., 2017). For instance, Gebuis and colleagues (2012a, 2012b) demonstrated that performance in numerical comparison tasks is influenced by the congruency between numerosity and non-numerical features such as object size, convex hull, and total occupied area. While many studies attempt to control for these confounds by using multiple stimulus sets that balance out different features (Dehaene et al., 2005; Rinsveld et al., 2020; Santens et al., 2010), it remains extremely difficult, if not

impossible, to fully decorrelate numerosity from all other sensory attributes. In this context, cross-format numerosity offers a powerful approach for investigating true numerosity perception. Because simultaneous and sequential formats share no common sensory features, cross-format paradigms provide a means to probe numerical processing independently of low-level stimulus properties.

Nieder et al.'s study (2006) investigated how neurons in the macaque brain respond to both spatial and temporal numerosity. Monkeys were first trained on simultaneous and sequential numerosity discrimination. They then performed a delayed match-to-quantity task: in each trial, two numerosities were presented, one during the sample period and one during the test period. The monkeys were required to grasp a lever and release it if the two numerosities matched. Neural activity was recorded from randomly selected neurons in the intraparietal sulcus (IPS). The results showed that distinct neuronal populations were engaged in spatial versus temporal enumeration processes. However, once the enumeration was completed, a separate neuronal population encoded the cardinality of the set in an abstract, format-independent manner. Comparable findings were reported in crows. In a study by Ditz and Nieder (2020) trained crows performed a similar match-to-quantity task. During the sensory encoding stage, format-dependent representations were observed, with distinct groups of neurons selectively tuned to spatial or temporal input. Yet, once the encoding stage was completed and the numerosities had to be memorized, an abstract, format-independent numerosity code emerged.

Of note, because of the difficulty of training animals, both studies focused on small numerosities within the subitizing range: 2, 3, and 4 in the first study, and 1 to 4 in the second. It remains unknown whether the specific range of numbers influences the formation of a generalized numerosity representation. Piazza et al. (2006) conducted an fMRI study comparing exact and approximate judgments of cross-modal numerosity. They found that the two types of judgment engaged distinct brain networks, yet both were independent of stimulus modality. However, the limitation of the above-mentioned univariate analysis constrains the interpretation of these results. It is generally assumed that representational precision decreases as numerosities increase, since internal noise accumulates with magnitude (Dehaene et al., 2003; Izard et al., 2009). Intuitively, aligning two representations becomes more difficult if each is inherently noisy. Moreover, evidence shows differences in precision and accuracy between modalities: visual stimuli are often overestimated relative to auditory ones (Tokita et al., 2013). This asymmetry would likely lead to greater misalignment between modalities when larger numerosities are involved.

Another potential factor influencing the formation of a generalized number representation is the role of task-related processes. In both studies, animals were required to compare numerosities and produce task-related responses. Cavdaroglu et al. (2015) demonstrated that in the absence of such processes, numerosity could not be decoded in the parietal cortex. This aligns with the suggestion that intraparietal sulcus (IPS) activity during numerical tasks may reflect response-selection mechanisms rather than the direct mapping of numerosity onto a parietal “number module” (Göbel et al., 2022). Moreover, these tasks demand a substantial degree of attentional engagement. Evidence indicates that attention is

necessary to elicit numerosity-selective responses: for instance, when participants viewed dot arrays composed of black and white subsets, neural activity corresponded specifically to the subset of dots they were instructed to attend to (Cai et al., 2022). Further research is needed to determine the prerequisites for the emergence of a generalized parietal representation of number.

One study investigated how spatial and temporal numerosity are represented in the human brain (Cavdaroglu & Knops, 2019a). They found that spatial numerosity, but not temporal numerosity, is processed in posterior parietal regions. Another study on temporal numerosity confirmed these findings by showing no activation in the posterior parietal cortex; instead, they found temporal numerosity represented in the prefrontal cortex (PFC)(Uluç et al., 2020). This pattern makes sense, as the posterior parietal cortex, being part of the dorsal stream, plays a key role in processing spatial information (Kravitz et al., 2011; Trés & Brucki, 2014). Several studies have shown that BOLD signals in the posterior parietal cortex increase with the number of objects presented across space (Shafritz et al., 2002; Xu & Chun, 2006). In contrast, when different numbers of items are shown at a single location, activity remains unchanged (Shafritz et al., 2002; Xu & Chun, 2006), indicating that the posterior parietal cortex encodes numerical information across space rather than over time. On the other hand, sequential numerosities are assumed to involve an accumulator mechanism, where activity increases with numerosity, possibly aided by processes that keep track of the serial position of items in a sequence (Nieder et al., 2006). Studies in macaque monkeys have found that neurons in the lateral intraparietal area (LIP) are closely linked to evidence accumulation over time (Hanks et al., 2015; Shadlen & Newsome, 2001). Whether sequential and simultaneous numerosity engage the same neural processes in the human brain remains an open question.

An interesting trend regarding generalized numerosity representation is that most univariate studies support its existence (Eger et al., 2003; Piazza et al., 2007), whereas MVPA studies often do not provide evidence for it (Cavdaroglu et al., 2015; Cavdaroglu & Knops, 2019b). One possible explanation, as mentioned earlier, is that similar activation within a region could reflect the activity of distinct neuronal subpopulations (Ojemann et al., 2010). Because traditional univariate fMRI analyses average responses across neural populations, they cannot disentangle the contributions of individual neurons or voxels. However, it is also important to note that the evidence from univariate studies comes in the form of null results, which means they show no differences between conditions, whereas the absence of evidence in MVPA studies likewise represents a null result rather than definitive evidence against a generalized representation. Another possibility is that the current resolution of fMRI is insufficient to detect reliable brain signals for such a representation (Cai et al., 2021). Consequently, both approaches may produce null findings: univariate analyses may appear to support generalized numerosity representation, while MVPA tends not to reveal it. In this context, conclusions based on null results should be treated with caution, and greater weight should be given to positive evidence (Stein et al., 2024).

As early as 2009, a widely discussed opinion paper and its accompanying commentaries debated whether numerical representations in the parietal lobes are abstract or not (Cohen Kadosh & Walsh, 2009). The author challenged the dominant view that numbers are represented abstractly in the brain, drawing on behavioral, neuroimaging, and neurophysiological evidence to argue that numerical representations are often non-abstract—that is, format-, modality-, or notation-dependent. According to this view, the intraparietal sulcus (IPS) supports multiple distinct numerical codes rather than a single abstract one. The commentaries revealed a divided field: some supported the non-abstract position, while others defended the abstract view. Interestingly, several contributors suggested a third possibility, namely that abstract and non-abstract representations may co-exist or lie on a continuum. For instance, Vallar & Girelli (2009) argued that the abstract/non-abstract dichotomy is too coarse to capture the diversity of potential supramodal numerosity representations. Similarly, Pesenti & Andres (2009) questioned the usefulness of the distinction itself, noting that researchers have applied loose and inconsistent criteria, leading to contradictory claims such as the idea of an "abstract number line" and undermining the theoretical framework. As this debate highlights, the question of whether numerical representation is "abstract or non-abstract" may oversimplify the computational principles underlying numerical processing in the human brain. A more nuanced characterization is needed to capture the continuum of representational formats.

Developmental evidence further complicates the picture. Although limited evidence of generalized numerical representation has been found in the adult human brain, studies in infants and children suggest that such representations may exist early in life (Gennari et al., 2023; Nakai et al., 2023). For example, Nakai et al. (2023) used multivariate fMRI adaptation to examine brain responses to Arabic numerals and dot arrays in children aged 5 to 8, spanning the onset and progression of formal schooling. They found that format-independent neural representations of quantity were present in 5-year-olds but no longer detectable by age 8. The authors proposed that non-symbolic representations may scaffold the acquisition of symbolic numerical skills in early childhood, but with formal education and increasing experience with numerical symbols, these representations become differentiated. In line with this developmental perspective, Gennari et al. (2023) conducted a tentative study with 3-month-old infants and found evidence for a neural representation of number as early as 400 ms after stimulus onset. This representation was able to decode auditory sequences with varying quantities and, importantly, generalized to visual arrays with matching numerosities. These findings suggest that numerical representation may begin as generalized and modality-independent but gradually evolve into format- and modality-specific systems as we grow older (Gennari et al., 2023).

An open question that remains largely unexplored is how different dimensions interact in numerosity processing. By dimensions, we refer to modality (e.g., auditory vs. visual), format (e.g., sequential vs. simultaneous), and notation (e.g., symbolic vs. non-symbolic). When the brain abstracts numerical information, it is still unclear whether these dimensions are integrated into a unified representation or whether they compete along the processing pathway. What is the brain's priority in this process? Does it first align information across

modalities and only later resolve differences in format, or is the reverse true? Understanding how these dimensions dynamically interact is crucial for uncovering the computational principles of numerosity processing and, ultimately, for deepening our knowledge of how the brain constructs numerical representations. Yet, studies using different analytical approaches such as multivariate pattern analysis (MVPA) have primarily focused on pairwise comparisons of different numerical representations (Cavdaroglu et al., 2015; Cavdaroglu & Knops, 2019b; Eger et al., 2009), limiting their scope to only one dimension at a time (e.g, cross-modal, cross-format or cross-notation), preventing a broader understanding of how numerical representations are organized in the brain.

Moreover, there is also a technique limitation to be considered. Although multivariate "cross-classification" decoding approaches (i.e., using multivariate analyses across different types of numerical representations) may serve as a more stringent approach to address the existence of a shared representation, it can only answer the binary 'shared versus non-shared' question. However, the absence of significant cross-classification for other pairs does not necessarily indicate equivalent levels of dissimilarity in their neural representations. Representational similarity analysis (RSA) should thus complement cross-classification decoding by moving beyond a simple dichotomy of shared versus non-shared information to a more comprehensive exploration of the geometry of numerical representations.

1.4 How visual is number sense?

Even though number sense is ubiquitous across multiple forms and modalities, vision is more efficient compared with the other senses in assessing numerical information (Thinus-Blanc & Gaunet, 1997). Vision permits hundreds of items to be estimated simultaneously within just seconds, which cannot be done through auditory or tactile channels since they are limited in the rate of discrimination and the amount of information that can be apprehended (Miller, 1956; Sperling, 1960). In spatial cognition, vision is often the dominant modality for building large-scale spatial maps given that distant or spatially distributed stimuli are readily apprehended visually, whereas touch is restricted to proximal contact and audition often provided only coarse localization cues (Dakin et al., 2011; Pasqualotto & Proulx, 2012).

Because vision offers unique affordances, it has become the dominant modality in numerosity research, with far fewer studies probing auditory or tactile representations of number. Consequently, much of the literature links numerical cognition to visual perception. Number sense has been argued as a primary perceptual dimension, similar to color or motion, capable of adaptation (Burr & Ross, 2008; Castaldi et al., 2021). Computational models further support this view: hierarchical generative architectures, trained on visual sets, spontaneously develop internal representations of numerosity over time (Kondapaneni & Perona, 2024; Testolin et al., 2020). Neuroscience studies are consistent with a vision of number. Neural tuning to numerosity has been localized in the intraparietal sulcus (IPS) along the dorsal visual pathway, raising the possibility that vision

plays a foundational role in the early development of the Approximate Number System (ANS) (Paul et al., 2022).

Congenital blindness provides a unique window into the role of vision in the development of numerical processing (Crollen & Collignon, 2020). If vision were truly critical for this development, congenitally blind individuals should exhibit atypical numerosity processing. However, findings from numerous studies with congenitally blind participants do not support the idea that vision is compulsory for numerical cognition. For example, Szucs and Csépe (2005) tested congenitally blind participants and sighted but blindfolded participants on a comparison task with the number 5 in the auditory modality. They found that congenitally blind participants showed similar distance and size effects as their sighted peers. Castronovo & Seron (2007) replicated and extended these results by demonstrating a SNARC effect in both groups. Likewise, another study asked participants to perform a numerical bisection task. Sighted individuals typically bisect numerical intervals to the left of their true midpoint, and interestingly, blind participants exhibited the same leftward bias (Cattaneo et al., 2011). In a finer-grained scale, a study showed that congenitally blind and sighted individuals demonstrated equal precision when estimating the numerosity of auditory tone sequences (Castronovo & Seron, 2007a). For both groups, performance was well described by the same psychophysical function. These results suggest that vision is not required for typical ANS development. Some studies even report superior numerical processing in blind individuals. For instance, Castronovo et al. (2007a) asked both blind and sighted participants to complete a numerical estimation task, where they had to actively and approximately generate numerosities corresponding to target numbers by pressing a key at a rapid pace to prevent counting. Blind participants outperformed the sighted group, presenting less variability in their estimates (smaller coefficients of variation) and significantly greater accuracy. Similarly, Collignon et al. (2009) found that congenitally blind individuals exhibit enhanced spatial attention in both tactile and auditory selective attention tasks, as well as in bimodal divided attention tasks. The authors concluded that early visual deprivation fosters compensatory mechanisms, engaging higher cognitive resources such as attention, to effectively interact with the environment. Converging evidence from neuroimaging studies leads to a similar conclusion: visual experience is not required to establish approximate number representations in the human brain—specifically in the intraparietal sulcus (IPS). Using multivoxel pattern analysis (MVPA), one study revealed ratio-dependent IPS responses in both blind and sighted participants (Kanjlia et al., 2021).

The above-mentioned studies challenge the hypothesis that vision plays a foundational role in the early development of numerical cognition, making such an assumption less plausible. Taking vision as the default entry point is risky, as it may obscure a deeper understanding of how number sense truly develops. Yet, both the literature review by Lorenzi (2025) and the commentary by Ben Harvey (2025) implicitly assume that the number sense is primarily visual in nature. Even though the empirical finding do not support this claim. For example, single-cell recordings in visually naïve young chicks reveal that a substantial proportion of neurons in the nidopallium are selectively tuned to specific numerosities, showing canonical features such as tuning curvesm ratio dependence, and decreased responses to non-prefered numbers (Kobylkov et al. 2022). These results

demonstrate that numerosity-selective coding arises independently of visual experience. Lorenzi (2024) also reports behavioral findings from fully dark-reared chicks, showing that even without any visual experience, newborn chicks can spontaneously discriminate changing versus fixed numerosities, and this discrimination reliably activates a distributed set of brain regions including the visual Wulst, hippocampus, mesopallium, and NCL. Together, these findings suggest that vision is not the developmental foundation of number sense. As we will argue in Chapter 2, vision should be understood as one convenient access point among several—not the sole or primary gateway to numerical cognition.

Although broadly similar, congenital blindness reveals subtle differences in numerical processing compared to sighted individuals (Crollen et al., 2013). These nuances provide important clues about how different scaffolds shape the representation of numerosity. For instance, while blind participants exhibit a SNARC effect comparable to sighted individuals, researchers have used hand-posture manipulations to test the role of spatial reference frames. Strikingly, early blind participants showed a reversed SNARC effect when their hands were crossed, a pattern not observed in late blind or sighted participants (Crollen et al., 2013). This finding suggests that early visual experience plays a critical role in establishing an external coordinate system for mapping numbers onto physical space. In its absence, the brain may instead rely on a body-centered reference frame, leading to the reversed SNARC pattern under crossed-hand conditions. Further evidence comes from EEG studies examining how numerical–spatial associations manifest at the neural level (Salillas et al., 2009). In these experiments, participants were presented with number cues that were either congruent or incongruent with the position of a target. Behaviorally, both blind and sighted groups exhibited similar performance, showing the typical "congruency effect." However, the ERP results revealed notable differences. In the sighted group, congruency modulated the early N100 component, reflecting a top-down amplification of sensory processing. In contrast, in the blind group, congruency effects emerged only at the later P300 component, associated with higher-level processes such as working memory updating, stimulus categorization, and the maintenance of representations in memory. Based on these results, the authors suggest that numerical processing in blind individuals may be more controlled and more dependent on working memory resources compared to sighted individuals.

1.5 Methodology

1.5.1 Multivariate pattern analyses

Multi-voxel pattern analysis (MVPA) is a method in fMRI research that shifts the focus from individual brain voxels to the distributed patterns of activity across many voxels (Kriegeskorte et al., 2006). Traditional fMRI analyses often search for single regions that show stronger activation in one condition than another, but this approach can overlook subtle or distributed forms of representation. Multivariate Pattern Analysis has become an increasingly popular approach in functional magnetic resonance imaging research over the past decade. This rise is unsurprising, given the advantages MVPA offers over traditional

univariate methods. Unlike univariate analyses, MVPA takes into account distributed patterns of voxel activities, making it more sensitive for distinguishing between experimental conditions, even when individual voxels show only subtle but consistent differences. Researchers utilized machine learning algorithms that can detect and classify patterns of voxel responses to extract meaningful information. A variety of classifier have been used, ranging from relatively simple correlation-based methods and linear discriminant analysis to more powerful techniques such as support vector machine (SVM). SVM is one of the most popular classifiers in neuroimaging, particularly within multivoxel pattern analysis (MVPA), owing to their capacity to address the high-dimensional and small-sample characteristics of brain imaging data (Orru et al., 2012). Unlike more complex nonlinear models, which often risk overfitting under these conditions, linear SVMs achieve reliable generalization by identifying separating hyperplanes that effectively discriminate between experimental conditions. This balance of sensitivity and robustness has made SVMs especially valuable for decoding cognitive states from fMRI data.

1.5.2 Feature selection

Another common strategy to address the imbalance between the very large number of features and the relatively small number of observations in neuroimaging studies is feature selection (Mwangi et al., 2014). This process mitigates the curse of dimensionality by removing noisy or redundant voxels and retaining only those that contribute meaningfully to distinguishing between experimental groups or conditions. A widely used supervised feature selection approach relies on statistical tests such as Analysis of Variance (ANOVA). In this approach, voxel-wise activity is compared across more than two groups to determine whether mean differences are statistically significant. Voxels that pass a predefined threshold are retained as informative features, while the rest are discarded. This univariate filter method is computationally efficient and straightforward to implement, making it particularly attractive for high-dimensional fMRI datasets. Although ANOVA does not account for multivariate interactions among voxels, it provides a practical first step to reduce dimensionality and improve the performance and interpretability of subsequent machine learning models.

1.5.3 Cross-validation

Cross-validation is a method to assess how well a classifier generalizes beyond its training data. One commonly used approach is leave-one-run-out cross-validation (LORO-CV). In this procedure, each fMRI run is treated as an independent unit: the classifier is trained on all runs except one and then tested on the held-out run. This process is repeated across all runs, and performance metrics (e.g., accuracy) are averaged across folds. This method respects the natural temporal and experimental structure of fMRI data, ensuring that training and testing sets are independent in terms of run-specific fluctuations (e.g. scanner drift, session effects). Importantly, because trials within a run often share correlated noise and other motion parameters, excluding an entire run from training helps to prevent

"leakage" of these confounds into both training and test sets, which would otherwise artificially inflate decoding performance.

1.5.4 Representational Similarity Analysis

Representational Similarity Analysis (RSA) is a multivariate technique used to investigate how information is encoded in brain activity beyond mere activation magnitude (Kriegeskorte et al., 2008). Rather than asking whether a region shows stronger activity under one condition than another, RSA characterizes the geometry of neural representations by comparing the pattern similarity structure across conditions. To do this, one computes, for each region (or ROI or searchlight), a representational dissimilarity matrix (RDM) or similarity matrix: each cell compares the neural response patterns for a pair of experimental conditions (e.g. via 1 – correlation, Euclidean distance, Mahalanobis distance). Because these matrices abstract away from individual voxel-level correspondence, they allow direct comparisons between modalities (e.g. fMRI and models), across participants, and even between brain and computational models. In practice, RSA proceeds by first estimating the pattern of neural activation for each stimulus or experimental condition (e.g. beta weights in fMRI). Then pairwise similarity (or dissimilarity) is computed across all stimulus pairs, yielding the RDM. This neural RDM can then be compared to one or more model RDMs (derived from behavioral data, stimulus features, or computational models) by correlating their off-diagonal entries. Regions who's neural RDM correlates significantly with a model RDM are inferred to encode the hypothesized representational structure. Crucially, RSA can test representational hypotheses about continuous structure rather than just categorical differences, making it especially suited for questions about how fine-grained distinctions are encoded in the brain.

1.6 Research Goals

Numbers can be perceived in many ways: we can see dots on a screen, hear a series of beeps, or read a symbolic digit. Despite these differences, humans and other animals can estimate the numerosity in a wide range of contexts. The aim of this thesis is to explore how the brain represents numerical information across senses and formats, and more critically, how it abstracts numerical information from various sensory inputs. While many theories assume that the brain converges these inputs into a single abstract code, I take a more skeptical stance. By examining numerosity across multiple dimensions, I investigate whether the brain may instead rely on alternative organizational principles.

This thesis investigates numerosity in both vision and audition, in sequential and simultaneous formats, and in symbolic and non-symbolic systems. To do so, I employ methods such as multivariate decoding and representational similarity analysis. Multivariate pattern analysis (MVPA) enables me to ask whether numerical representations generalize into a unified code, while representational similarity analysis (RSA) allows me to probe the geometry and organization of these representations across the cortical hierarchy. Particular attention is given to the intraparietal sulcus, a region long proposed as the hub of numerical abstraction. By dividing it into subregions based on an atlas, I also

investigate whether its subdivisions support more fine-grained roles in numerical processing.

In chapter two, I turn to the assumption is deeply embedded in much of the numerical literature: numerosity is inherently tied to vision. I challenge this view by arguing that vision is not the necessary foundation of numerical cognition. Drawing on behavioral and neural evidence, I propose that the number sense is better understood as a supramodal faculty: one that can be accessed through whichever sensory and cognitive channels are available. From this perspective, blindness is not a limitation but rather a powerful test case, demonstrating that numerical thinking can emerge and flourish independently of visual experience.

1.7 References

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Chapter 2

Brain representation of numerosity across the senses and presentation formats

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Reference

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2. Brain representation of numerosity across the senses and presentation formats

2.1 Abstract

Humans can extract numerosity from different senses and a variety of context. How and where the brain abstract numerical information from low-level sensory inputs remains debated. Using multivariate pattern decoding and representational similarity analysis applied to fMRI data, we comprehensively investigate how the brain represents numerical information (range 2-5) across different modalities (auditory, visual), presentation formats (sequential, simultaneous) and notations (symbolic, non-symbolic). We identify a set of brain regions along the dorsal pathway -from early visual cortex to the intraparietal and frontal regions- that encode specific non-symbolic numerical information across formats and modalities. The numerical distance effect, a hallmark of magnitude encoding, was observed in most of these regions. We found aligned representation of numerical information across visual and auditory modalities in intraparietal and frontal regions, but only when they shared a sequential presentation format. Maintaining a distinction between spatial and temporal numerical representations may thus be a fundamental aspect of numerical processing. RSA further revealed a posterior-to-anterior gradient in the intraparietal sulcus (IPS) showing that the dominant factors influencing distributed numerical representations shifted from sensory modality in the posterior parietal regions to presentation format in the anterior parietal areas. Our study reveals a multifaceted brain representation of numerosity across the senses and presentation formats.

2.2 Introduction

Whether we encounter five pens on the table, hear five knocks on the door, or hit five strikes of a hammer on a nail, we are able to estimate their numerosity. Such ability to seamlessly encode numerical information across the senses and presentation formats has led to the hypothesis of an abstract numerical code in our minds, wherein different types of numerical information are abstracted into a unified representation by discarding irrelevant physical properties (Dehaene & Changeux, 1993; Wiese, 2003). The intraparietal sulcus (IPS) has often been proposed as the neural hub supporting this abstraction (Dehaene et al., 1998, 2004; Eger et al., 2003, 2009; Nieder, 2012; Piazza et al., 2004, 2006).

However, inconsistent findings across studies have made this argument controversial. Behavioral support for an abstract numerical mental code comes from studies showing no additional cost when comparing numerical quantities across spatial versus temporal formats (Barth et al., 2003) or from cross-modal adaptation effect (Arrighi et al., 2014). In contrast, other studies show format-dependent differences in the precision of numerical estimates

(Tokita et al., 2013), suggesting modality-dependent representations. Consistent evidence for the existence of such abstract representations in the human brain remains elusive. While most studies suggesting the presence of an abstract numerical code in the human brain relied on invariant mean BOLD signals in parietal regions (mostly Intraparietal sulcus, or IPS) across sensory modalities and presentation formats (Dormal et al., 2010; Eger et al., 2003; Piazza et al., 2006), these results are not conclusive of abstraction since similar BOLD intensity could result from distinct neural activation within the same region. Indeed, experiments employing multivoxel pattern analysis (MVPA) to investigate whether numerical representations are supported by shared distributed neural patterns have produced inconsistent results, with some studies supporting shared representations (Damarla et al., 2016; Eger et al., 2009; Gennari et al., 2023; Nakai et al., 2023; Wilkey et al., 2020) and others failing to find evidence of abstraction (Bulthé et al., 2015; Cavdaroglu et al., 2015a; Cavdaroglu & Knops, 2019a; Czarnecka et al., 2023; Lyons et al., 2015).

These inconsistencies emerging from previous research suggest that the 'abstract vs. non-abstract' dichotomy may oversimplify the computational principles underlying numerical processing in the human brain. The process of abstraction may be more nuanced than generally thought. An important property of numerosity perception is that numerical quantities span multiple dimensions. It can be perceived through various sensory modalities, such as vision and audition; represented in distinct formats, including spatial (simultaneous) and temporal (sequential) arrangements; and encoded in different systems, like non-symbolic or symbolic forms. Numerical information within each format is often linked in our daily experience of the world. For example, when clapping after a show, the sequence of clapping is both seen and heard. However, co-occurrences or interactions across formats are relatively rare, as simultaneous presentations rarely have sequential counterparts across modalities. This raises the possibility that the brain may align numerical information along distinct dimensions rather than converge them into a fully unified abstract system. Results from a prior behavioral study from Arrighi and colleagues (2014) support this idea by showing cross-modal adaptation effect for temporal numerosity, which is adapting to auditory temporal numerosity effect the perception of visual temporal numerosity, and vice versa. In contrast, cross-format adaptation (e.g., adapting to temporal numerosity and testing spatial numerosity, or the reverse) have been found to be unidirectional. These findings suggest a shared representation for temporal numerosity across modalities but an asymmetry in the processing of spatial versus temporal numerosities. At the neural level, studies done in primate such as macaques and crows presented by numerosities presented either temporally or spatially found that format-independent representations emerged only after the encoding stage is finished and numerosities need to be memorized, while format-dependent representations dominated the numerosity encoding phase (Ditz & Nieder, 2020; Nieder et al., 2006; Nieder (2012)). The observation that temporal numerosity abstraction occurs during encoding, while cross-format numerosity abstraction arises only afterward, suggests different neural encoding mechanisms for temporal versus spatial numerical information. Yet in the human brain the processing of temporal and spatial numerosity, as well as their interaction, remain largely unexplored. Studies exploring whether abstracted numerical representation exist across the

senses did not find evidence for an abstract multisensory representation code (Hofstetter et al. (2012); Cavdaroglu et al. (2015,2019), but those studies did not comprehensively investigate how numerical representation may align across the sense if sharing similar vs different presentation format (e.g., spatial vs temporal).

The intraparietal sulcus (IPS) plays a key role in representing numerosity. Neuroanatomical studies have shown that the IPS consists of distinct subdivisions, each with unique connectivity patterns and functional roles (Foster et al., 2022; Nelson et al., 2010; Sheng et al., 2025). Regarding numerosity, the discrete portion of the IPS seem to support specific functions (Castaldi et al., 2020; Chiou et al., 2023; Harvey et al., 2017a): the posterior parietal region is involved in presenting numerosity in space (Cavdaroglu & Knops, 2019b; Hubbard et al., 2009; Knops et al., 2009), while the anterior IPS is associated with finger counting (Andres et al., 2007). How the distinct subdivisions of the IPS contribute to the abstraction of numerical information presented in different sensory modalities or presentation formats has never been systematically tested.

In the current study, we aim to investigate numerical representation across multiple dimensions within a unified framework by using numerosity stimuli presented across modalities (vision and audition), formats (sequential and simultaneous) and notations (symbolic and non-symbolic). This approach allows us not only to investigate the effect of each dimension individually but also gain a broader perspective on the relationships between different types of representations. To minimize the intrinsic noise associated with representing large numerosities and avoid their representational overlap (e.g., Nieder & Miller, 2003; see Tsouli et al., 2021 for a review), which may limit the ability to separate distinct numerosities using fMRI and their alignment across different formats and modalities, we purposedly decided to rely on a small numerical range (2 to 5). A multivariate pattern analytical approach (MVPA) was used to determine (1) whether and where the brain encodes numerical information across the senses and presentation format or notation, (2) whether those regions implement an invariant neural representation across different dimensions and sensory input and (3) elucidate the neural organization of numerical representation across dimensions using representational similarity analyses (RSA) combined with theoretical models.

2.3 Methods

2.3.1 participants

A total of twenty-three individuals participated in the experiment, completing two 90 minutes fMRI scanning sessions on two different days. The mean age of the participants was 23.69 years (SD = 3.46), with an age range of 19 to 35 years. All participants were right-handed and had normal or corrected-to-normal vision. Participants reported no history of neurological conditions. Two subjects were excluded from data analysis due to either lack of response during fMRI acquisition, suggesting no attention to the task, or incorrect acquisition parameters. The protocol was approved by the research ethics committee in Saint-Luc University Hospital (protocol number 45.327.621). Written consent was acquired

from all participants before participation. Participants were monetarily compensated for their participation. The sample size of the experiment was determined a priori based on similar fMRI MVPA study on numerosity representations (Cavdaroglu et al., 2015a; Cavdaroglu & Knops, 2019a; Czarnecka et al., 2023).

2.3.2 Numerosity decoding experiment and stimuli

Participants engaged in a numerosity one-back task in which four numerosities from five different stimulus conditions (see below) were presented in a pseudo-randomize order. The sequence was designed so that the same stimulus condition could not be presented in consecutive trials. Participants were asked to compare the current numerosity with the previous one, regardless of the condition formats or modalities, and to press a button with their right index finger when the stimulus in the current trial had the same numerosity as the previous trial (target stimuli, 10% of the trials). Participants were instructed to avoid active counting during the task.

Numerosities 2, 3, 4, 5 using visual sequential, auditory sequential, visual simultaneous, visual symbolic (Arabic), auditory symbolic (verbal number words) conditions. Visual simultaneous and visual sequential numerosities were presented on a black background using white dots. Visual symbolic numerosities were presented as white Arabic numerals on a black background.

To minimise the possibility that participants encode numerosity based on low-level stimuli features, the non-numerical sensory features of non-symbolic stimuli were balanced using two types of stimuli. For visual simultaneous stimuli (arrays of dots), intensive parameters (individual item size and density) are controlled for one set while extensive parameters (total area and convex hull) are controlled for the other set (Dehaene et al., 2005). Stimuli were generated using GeNEsIS, a software platform designed for creating visual numerical arrays with precise control over continuous variables (Zanon et al., 2022). The average individual dot size, convex hull, total area and density for each set and numerosity can be found in supplementary materials (Table S2.1). Stimuli were displayed on an area of approximately 4.8 × 4.8 visual degree. The low-level features of auditory sequential stimuli (sequential beeps) were similarly controlled by 2 sets. For one set the total sequence duration is fixed while for the other set the individual beep duration is fixed. Individual beep durations and inter-beep intervals were jittered to avoid any regular patterns that might predict numerosity and interfere with any counting strategy (Kanjlia et al., 2021). The audio frequency of each individual beep was 440 Hz. The auditory stimuli were prepared using custom MATLAB scripts (R2019b; MathWorks). The duration of individual beeps was designed to be less than 270 ms to prevent counting (Cavdaroglu et al., 2015a; Piazza et al., 2006; Tokita & Ishiguchi, 2011). However, for the set that the total sequence duration is fixed, it is impossible to keep individual beeps shorter than 270 ms especially for small numerals such as 2 and 3. Therefore we use beeps longer than 270ms for them. The single beep durations and total stimulus duration are provided in supplementary materials (Table S2.2). The visual sequential stimuli were generated based on the same logic applied to auditory sequential stimuli. However, during piloting, we

observed that visual sequential stimuli were more challenging to discriminate compared to auditory ones. To ensure comparable difficulty levels across conditions, we increased the total duration to 1.2 times longer than auditory stimuli while maintaining the internal structure unchanged. Visual sequential stimuli are presented on a black background using white dots, spanning about 0.73 visual degrees. The single dot durations and total stimulus duration are provided in supplementary materials as well (Table S2.2). In visual symbolic conditions, the position and size of digits on the screen varied across trials to prevent adaptation to low-level features, with the position varying within a range of 1.21 visual degrees. In auditory symbolic conditions, number words for each numerosity were presented using two different voices—one male and one female—to avoid adaptation effects.

The experiment comprised 20 runs, containing 40 trials (5 conditions × 4 numerosity × 2 sets of condition controlled for low-level features) and four additional target trials (44 trials in each run). The inter-stimulus interval between each stimulus ranged from 3.5s to 4.5s. Auditory stimulation was delivered through in-ear MRI-compatible earphones (Sensimetric S14, SensiMetrics, USA) at a loud but comfortable volume, defined with each participant before the start of the MRI acquisition. Visual stimuli were presented on a screen through a mirror at a distance of 170 cm and with a resolution of 1920x1200 pixels. To ensure fixation and to minimize eye movements, a fixation cross was shown in the center of the screen throughout each run, except during the presentation of the visual sequential stimuli, where flashing dots were presented at the center of the screen. Visual simultaneous stimuli were presented for 1.25s. Auditory sequential stimuli had a total duration between 0.55s and 1.6s. Visual sequential stimuli had a total duration between 0.59 to 1.74s. Visual symbolic stimuli were presented for 1s, and auditory symbolic stimuli were played for 500ms. The stimulus delivery was controlled using the Psychophysics toolbox implemented in Matlab R2019b (The MathWorks).

2.3.3 Behavioral Data Analysis

In order to characterize the behavioral performance, we used the d' measure (Snodgrass & Corwin, 1988) instead of the simple accuracy rate. This is because accuracy rate only accounts for hit or miss target trials (10%), making it one-sided. Instead, the d' not only considers the hit rate of target trials but also penalizing for responses following non-target trials (false alarm). The d′ is calculated from hit rate and false-alarm (FA) rate using the formula d′ = ZHit – ZFA.

2.3.4 fMRI data Acquisition and preprocessing

Functional images were acquired at the Saint-Luc University Hospital, Brussels, Belgium with 3T GE scanner (Signa™ Premier, General Electric Company, USA) with a 48-channel head coil. Before the experiment, a T1-weighted image (MPRAGE) was collected as high-resolution anatomical reference (voxel size = $1\times1\times1mm^3$, repetition time (TR) = 2189.12ms, echo time (TE) = 2.96ms, flip angle = 8°, field of view (FoV) 256 mm, 156 slices). T2*-weighted gradient-echo echo-planar images were collected for the localizer

experiment (TR = 1750ms, TE = 30ms, flip angle = 75°, FoV = 220 × 220mm^2, resolution = 2.6 × 2.6 mm^3, 58 interleaved ascending slices, slice thickness = 2.6mm) and the decoding experiment (TR = 1750ms, TE = 35ms, flip angle = 75°, FoV = 220 × 220mm^2, resolution = 2.3 × 2.3 mm^3, 52 interleaved ascending slices, slice thickness = 2.3mm) respectively.

MRI data were converted and organized into 'Brain Imaging Data Structure' (BIDS) format using dcm2bids (Boré et al., 2023) to ensure standardization and anonymization of data (Gorgolewski et al., 2016). Data were preprocessed with the preprocessing pipeline fMRIPrep 23.1.4 (Esteban et al., 2019) with the default processing steps incorporating the software packages: FSL, Freesurfer, ANTs and AFNI. First, each T1-weighted volume was corrected for intensity nonuniformity and skull-stripped to reconstruct brain surfaces. Brain-extracted T1-weighted images were then spatially normalized to the MNI152Lin2009cAsym standard space. Brain tissue segmentation of CSF, white matter, and gray matter was performed on the brain-extracted T1- weighted image. Functional data were slice time-corrected, motion-corrected and coregistered to the normalized T1-weighted template (for further details, including software packages for each preprocessing step in FMRIPrep, see the online documentation under https://fmriprep.org/en/ stable/). Finally, we applied spatial smoothing using a 3D Gaussian kernel (univariate analysis, FWHM= 6 mm; MVPA analysis, FWHM = 2mm) using SPM 12 (Wellcome Department of Imaging Neuroscience, London, United Kingdom).

Numerosity processing has been shown to interact with spontanenous eye movement (Knops et al., 2009). To minimize the potential confounds of eye movement on brain activation, we computed eye displacement and included it in the Generalized Linear Model (GLM) as a nuisance regressor. Eye movement data were acquired using BIDSMReye (Gau et al., 2024), which is bidsified based on DeepMReye to decode eye motion from fMRI time series data, in particular from the MR signal of the eyeballs (Frey et al., 2021). Each run, the following values were computed: variance for the X gaze position, variance for the Y gaze position, framewise gaze displacement, number of X gaze position outliers, number of Y gaze position outliers, and number of gaze displacement outliers. Outliers were robustly estimated using an implementation of the median rule (Carling, 2000).

2.3.5 Univariate analysis

The univariate fMRI analysis was conducted using bidspm (v3.0.0 by Gau et al.,) and SPM12 (version 7771) on MATLAB (R2019b). The pre-processed images for each participant were analyzed using a general linear model (GLM). Motion parameters (three translational motion, three rotational motion parameters), eye displacement (extracted from DeepMReye; Gau et al., 2024) and button presses were modelled as regressors of no interests. The contrast images for each condition against baseline were computed for each subject individually. The individual contrasts were further smoothed with a 6-mm FWHM kernel and entered into a random effects model for the second-level analysis. P-values were set at $p < 0.05$ FWE corrected, with probabilistic approach for threshold-free cluster enhancement (pTFCE).

2.3.6 Multivariate pattern analysis

For the numerosity decoding task, a general linear model was implemented for each subject to estimate beta maps associated with each numerosity (2,3,4,5) separately for the five stimulus conditions. For each level of numerosity within each condition, two subsets with different low-level features were modelled together as one beta to control for the low-level features of the stimuli. Motion parameters (three translational motion, three rotational motion parameters), eye displacement and button presses were modelled as regressors of no interests. For each run, one beta estimate is extracted for each 20 regressors of interest for further MVPA.

The MVPA analysis was performed in CoSMoMVPA (Oosterhof et al., 2016, http://www.cosmomvpa.org/), implemented in MATLAB. Classification analyses were performed using a multiclasses linear support vector machine (SVM) classifiers as implemented in LIBSVM (Chang & Lin, 2011). To explore the brain regions that can decode numerosity within each stimulus condition, we implemented a whole-brain searchlight approach to investigate which regions across the entire cortex could decode numerosity. A sphere of 3-voxels radius moved across the whole brain, where in each step, each voxel became the center of the searchlight sphere. Within each sphere, cross-modal decoding was implemented in the same manner described in the regions of interests (ROI) analysis. The searchlight analysis results in a whole brain cross-modal decoding accuracy map for each subject. The individual accuracy maps were smoothed with 8 mm FWHM smoothing kernel and entered in a second-level model. A one-sample t test was performed to test if the cross-modal decoding accuracy was above the chance level (25%). P values were set at $p < 0.001$ for cluster-level correction corrected for multiple comparisons using pTFCE (probabilistic approach for threshold-free cluster enhancement). For the numerosity condition that could be decoded, a conjunction analysis was conducted on the accuracy maps from the different conditions, using a threshold of $p< 0.001$ (uncorrected), to identify regions in which numerosity could be decoded across all conditions. The peak coordinates from conjunction analysis were then used along with activation map to create ROIs for further the multivariate analysis. To define each region of interest (ROI), a 10 mm-radius sphere was first centered on each of the peak coordinate. This sphere was then progressively expanded and intersected with the activation map until the ROI reached approximately 300 voxels. When a sufficient number of voxels was not available, the intersection step was omitted, and a simple sphere around 300 voxels was drawn instead. The label of our ROIs were defined using the Jülich Brain Atlas in the JuBrain Anatomy Toolbox (Eickhoff et al., 2005).

To ensure that successful decoding was not driven by low-level features specific to one subset of stimuli, we conducted a control analysis in which a classifier was trained on data from both subsets but tested only on one subset. If decoding relied on discriminative low-level features from one subset, it should fail when tested on the other subset. We reported classifier performance as the average across the two subsets used as the testing set. This analysis was performed for all three non-symbolic conditions.

To assess the existence of the distance effect in regions that identified through conjunction analysis (Dehaene et al., 1990; Nieder et al., 2002), we performed pairwise decoding between different numerosities within each condition, then averaged the decoding accuracy based on numerical distance, resulting in three groups. The first group corresponds to a numerical difference of one, the second group to a difference of two, and the third group to a difference of three. A linear regression model was then applied to the decoding accuracy across these groups. A linear increase in the decoding accuracy across groups would indicate the presence of a distance effect. To minimize multiple comparisons; ROIs were grouped into three cortical regions: occipital, parietal and frontal ROI regions. False discovery rate (FDR) was applied to P values across regions.

Cross-classification was performed in the ROIs that allowed to successfully decode numerosities to further test whether a shared numerosity representation existed across different conditions in these regions. Before the cross-classification, the pattern of each numerosity within each condition was demeaned individually to ensure the mean activity across conditions was mathematically equated. For each pair of conditions, a multiclass linear SVM classifier (C parameter = 1) was trained on one condition and tested on the other condition to classify four numerosities for each subject individually, and vice versa. The classifier was trained using a cross-validation leave-one-out procedure, with n-1 runs used for training and the remaining one run used for testing. We implemented an ANOVA-based feature selection on the training data within each cross-validation fold to use the most informative 150 voxels in each subject and each ROI. The normalization parameters from the training data were applied to the test data, and the performance of the SVM classifier was evaluated on the test data (1 run). The previous step was repeated 20 times (N-fold cross-validation) where in each fold the classifier was tested on a different run. A single classification accuracy value was obtained by averaging the classification accuracies for all the cross-validation folds. Successful performance above the chance level (25%) would indicate that specific ROIs are capable of decoding numerosities within the condition.

2.3.7 Statistical significance

Statistical significance in the multivariate classification analyses was assessed using nonparametric tests permuting condition labels and bootstrapping (Stelzer et al., 2013). Each permutation step included shuffling of the condition labels and rerunning the classification 100 times on the single-subject level. Next, we applied a bootstrapping procedure to obtain a group-level null distribution that is representative of the whole group. From each individual's null distribution, one value was randomly chosen and averaged across all of the participants. This step was repeated 10,000 times, resulting in a group-level null distribution of 10,000 values. The statistical significance of the MVPA results was estimated by comparing the observed result to the group-level null distribution. This was done by calculating the proportion of observations in the null distribution that had a classification accuracy higher than the one obtained in the real test. To account for the multiple comparisons, all p values were corrected using FDR correction method.

2.3.8 Representational similarity analysis (RSA)

To further explore the differences in the representational formats used to encode numerosities, we relied on RSA. RSA allow capturing the (dis)similarity structure of numerosities across different representational formats and sensory modalities by testing which theoretical model best explains the observed data. To remove spatially correlated noise and yields generally more reliable dissimilarity estimates, multivariate noise normalization (Walther et al., 2016) was applied to the beta coefficients obtained for each stimulus by using The Decoding Toolbox (Hebart et al., 2015). For each ROIs that allowed to successfully decode numerosities, individual neural representational dissimilarity matrices (RDMs) were constructed using 1- Pearson correlation, characterized as 1 minus the Pearson correlation of the β-weight patterns across all pairwise conditions.

We built three theoretical models that we thought could represent how brain regions encode our different numerosities (see Figure 2.1C). First, the Condition-Numerosity (CondNum) model assumes that numerosities are more similar within than across each condition. The dissimilarity between numerosity from different conditions was arbitrarily set to 1 (maximum dissimilarity), while within condition dissimilarity is based on numerical distance. For example, the dissimilarity of numerosity 2 compared to numerosities 3, 4, and 5 increases progressively, with values of 0.16, 0.33, and 0.5 respectively. Second, the Modality-Numerosity model (ModalNum) assumes that numerosities from the same modality (e.g. vision) are more similar than those from different modalities even across format. The dissimilarity between numerosities from different modalities is set to 1, while within the same condition, dissimilarity is determined by their numerical distance following the same logic as the CondNum model. Third, the Format-Numersity model (FormatNum) follows a similar principle with the previous model, but focuses on presentation formats (e.g., sequential vs. simultaneous). Numerosities in the same format are more similar than those from different formats, with dissimilarities between formats set to 1. Within a format, numerical distance determines the dissimilarity, with values of 0.16, 0.33, and 0.5 for numerosities 2, 3, 4, and 5; respectively.

To assess the between-subjects reliability of the neural data, we computed the noise ceiling of the data for each fROI. The bottom half of RDMs was first converted into a vector and z-transformed. A lower bound was computed by the following approach: the vector of one subject was left out and those of remaining subjects were averaged and correlated with the left-out subject's vector. The same process was repeated for all subjects, and the resulting correlation coefficients were averaged. An upper bound was computed by correlating between each participant's individual RDM and the group-average RDM (Nili et al., 2014).

We correlated the individual neural RDM with each theoretical model to assess which model best describes the neural data. The median correlations across subjects were tested for significance with Wilcoxon signed-rank tests. Results were corrected for multiple comparisons using FDR correction.

2.3.9 Partial correlations and variance partitioning

To determine the contribution of each individual model when considered in conjunction with the other models, we performed two additional analyses: partial correlations, in which each model was correlated (Pearson r) while partialling out the other two models, and variance partitioning based on multiple linear regression (see Groen et al., 2018; Ritchie et al., 2021 for similar approach). In the present analysis, CondNum (a), ModalNum (b) and FormatNum (c) models were converted into vectors and included as predictors in a set of multiple linear regression analyses. Each model was tested individually, as well as in all possible pairwise and three-way combinations, to predict individual participants' RDMs. Subsequently, seven R2 values were obtained: R2y•a, R2y•b, R2y•c, R2y•ab, R2y•ac, R2y•bc, R2y•abc. The first six R2 were based on either individual models or combinations of pairwise model, while the last R2 indicated the full model. By comparing the explained variance (R2) of full model to the R2 obtained when each model is left out one at a time, we can infer the amount of variance uniquely explained by the excluded model. The results were visualized in a Euler diagram using EulerAPE software (Micallef & Rodgers, 2014).

Partial correlations were calculated for each individual participant separately. The median correlations across subjects were tested for significance with Wilcoxon signed-rank tests. Results were corrected for multiple comparisons using FDR correction.

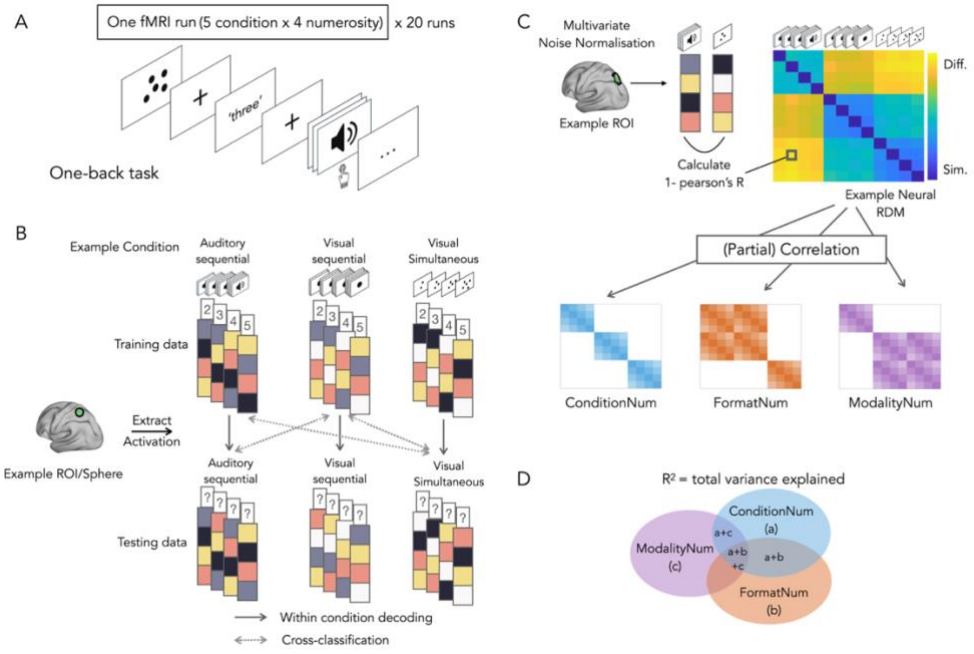


Figure 2.1. Experimental design and data analysis scheme. A. experiment task. During the fMRI session, Participants were instructed to press a button whenever the quantity of

the current numerosity matched that of the previous one, regardless of format or modality. B. For decoding analysis, voxel-wise neural activation patterns were extracted for each region of interest (ROI) in the ROI-based analysis, or for each searchlight sphere in the searchlight analysis. Pattern vectors were divided into training and testing sets. For within-condition decoding, both sets were taken from the same condition. For cross-classification, training and testing sets were from different conditions. C. For RSA analysis, multivariate noise normalization was first applied to the beta coefficients obtained for each stimulus. Then for each ROI, a neural representational dissimilarity matrix (RDM) was constructed by computing pairwise dissimilarities between condition vectors (1 – Pearson correlation). Three theoretical model RDMs were generated based on specific hypotheses. Correlations and partial correlations were computed between each model RDM and the neural RDM. D. The Euler diagram illustrates the results of the variance partitioning analysis. The total explained variance of the full model is indicated by R2. Each region of the diagram represents the proportion of variance uniquely or jointly explained by the individual model components.

2.4 Results

2.4.1 Behavioral performance:

We assessed the response accuracy in the localizer task and the main numerosity task, to confirm that participants were attending and processing the stimuli. The behavioral results showed overall good performance (localizer task: mean accuracy = 83%, ranging from 68% to 91%; decoding task: d-prime score = 3.2102 on average, ranging from 1.0683 to 4.9301), suggesting that participants were actively attending to the experiment.

2.4.2 fMRI results

Univariate results

The contrast images for each condition versus baseline revealed the brain regions involved in processing each modality. As expected, the visual condition primarily activated the occipital cortex, while the auditory condition engaged the temporal cortex. In addition to these low-level sensory areas, activation was also observed in parietal and frontal regions, which are typically associated with numerosity processing (Figure 2.2).

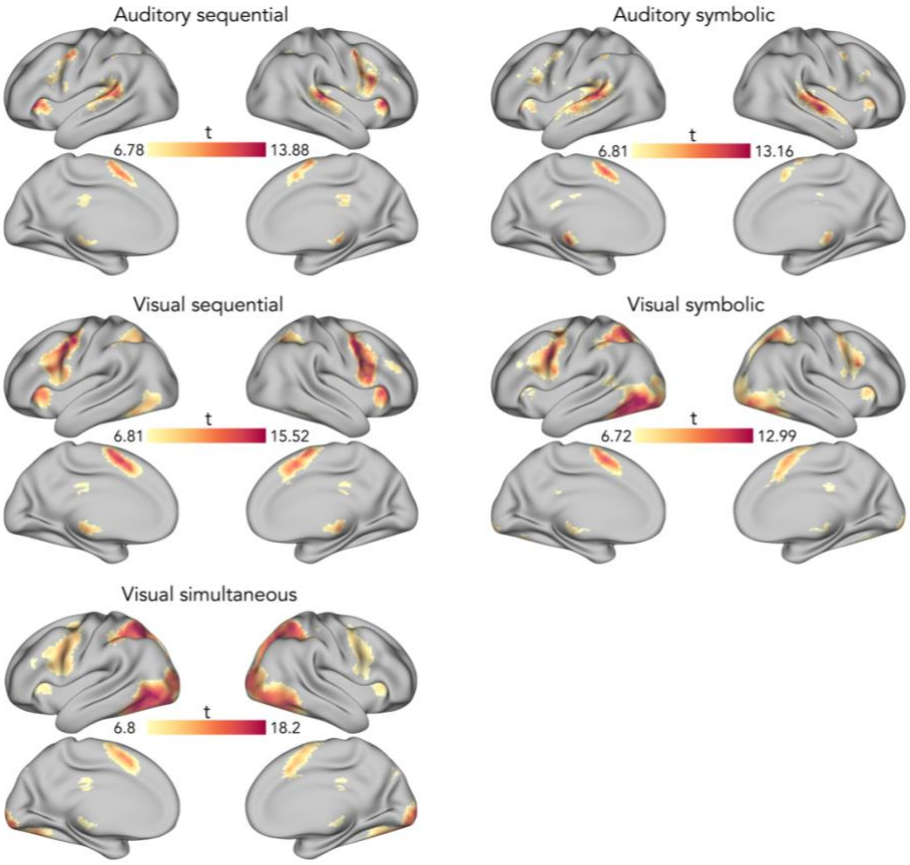


Figure 2.2 The univariate results of the contrast each stimuli condition against baseline. P-values were set at $p < 0.05$ for cluster-level correction controlling family-wise error (FWE) with probabilistic threshold-free cluster enhancement (pTFCE). Results are displayed on an inflated brain (Marcus et al., 2013).

Whole brain searchlight decoding analysis

To get an overview of brain regions involved in representing numerosities across conditions, we conducted a whole-brain searchlight analysis for each condition. The resulting maps corresponding to all stimulus conditions are shown in Figure 2.3. The auditory sequential and visual sequential conditions exhibited similar patterns, with significant decoding observed across a widespread network that includes the frontal, parietal, occipital and temporal areas. For the visual simultaneous condition, significant decoding was observed in the occipital, parietal and frontal cortices. In contrast, the two symbolic conditions exhibited much less, if any, significant decoding. In the auditory symbolic condition, numerosity decoding could only be found in small cluster of right superior temporal cortex. No significant voxels were identified in the searchlight results for

the visual symbolic condition, and thus, no results map was presented for this condition. We examined the beta estimates for each ROI and condition to assess whether the absence of decoding could be attributed to a lack of activation (Tong et al., 2012). However, this explanation is unlikely, as the univariate beta estimates did not show significant differences between the symbolic and non-symbolic conditions (see Text S2.3, Figure S2.2, Tables S2.3 and S2.4). Therefore, due to the limited or absent decoding observed in the symbolic conditions, we excluded them from further analysis.

To localize brain regions consistently engaged in decoding numerosity across all non-symbolic conditions, we conducted conjunction analyses (Nichols et al., 2005) of the searchlight maps for the auditory sequential, visual sequential and visual simultaneous conditions. The results revealed overlapping regions along the dorsal stream, extending from lower-level occipital areas to the parietal and frontal regions, which were engaged in decoding numerosity across all non-symbolic conditions (Figure 2.3B). Among these regions, a total number of seven clusters showed significant decoding with FWE-correction (.05) at cluster level and were thus identified as regions of interest (ROIs) for further analysis (Table 2.1). One ROI was in the visual cortex, five in the parietal cortex, and one in the frontal cortex (Figure 2.5A). The control analysis showed above-chance level decoding accuracy when a classifier was tested on data from only one subset for all three non-symbolic conditions. This suggests that the successful decoding was not fully driven by low-level features. (Figure S2.3).

Region	Cluster-level p (FWE-corr)	Peak_level t	x	y	z (mm)
Left hIP8	0.002	5.90	-22	-72	48
		4.93	-19	-74	34
		4.76	-24	-65	39
Left V3A	<0.001	5.46	-19	-88	13
Left V1		5.36	2	-79	25
Left hIP4		5.31	-33	-79	20
Right hIP2	0.002	5.44	53	-32	41
		4.90	44	-41	53
Right hIP3	<0.001	5.40	35	-58	50
Right hIP4		5.18	35	-76	27
Right hIP7		5.04	30	-81	23
Precentral	0.012	5.31	49	10	27
		4.18	44	6	39

Table 2.1. Clusters identified in conjunction analysis of three non-symbolic searchlight accuracy map. Results are corrected for multiple comparison using FWE correction at the cluster level. Coordinates are reported in MNI space.

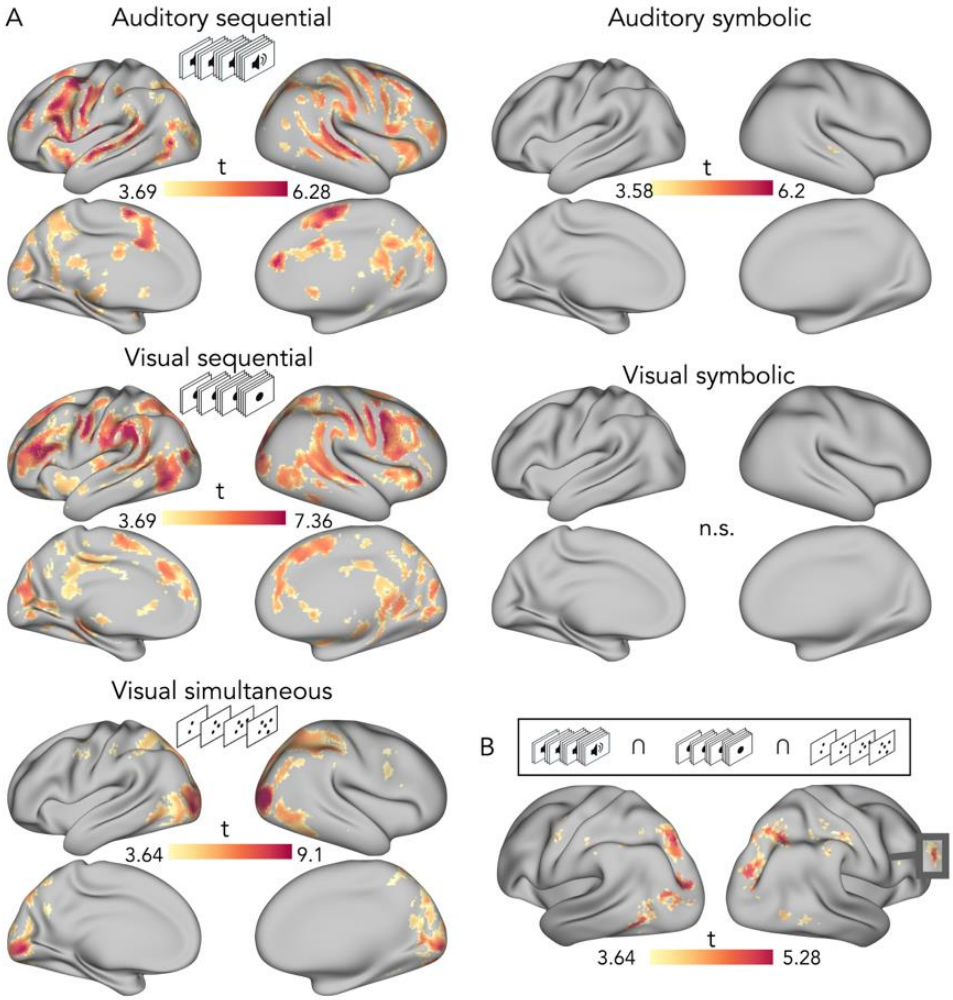


Figure 2.3. A: With-in condition Searchlight numerosity decoding from different conditions. P values were set at $p < 0.001$ for cluster-level correction with probabilistic threshold-free cluster enhancement (pTFCE). B: The results map for the conjunctions of the searchlight maps for three non-symbolic conditions (i.e., auditory sequential, visual sequential, visual simultaneous conditions) with a threshold of $p< 0.05$ FWE corrected at cluster level.

2.4.3 ROIs Analyses

Distance effect

ROIs were grouped into three cortical regions: occipital, parietal and frontal ROI regions and the numerical distance effect, a hallmark of magnitude encoding, was examined for each condition in each group. The numerical distance effect was observed across all conditions in the parietal region and in most conditions in the frontal region (Figure 2.4). Specifically, in the parietal region, decoding accuracy increased linearly with numerical distance across all conditions (auditory sequential: $t(61) = 3.90$, $p_{corr} < 0.001$, Cohens'd = 0.60; visual sequential: $t(61) = 4.47$, $p_{corr} < 0.001$, Cohens'd = 0.60; visual simultaneous: $t(61) = 4.06$, $p_{corr} < 0.001$, Cohens'd = 0.62). In frontal region, significant linear increases in decoding accuracy were observed for the auditory sequential and visual simultaneous conditions (auditory sequential: $t(61) = 2.72$, $p_{corr} = 0.025$, Cohens'd = 0.42; visual simultaneous: $t(61) = 3.42$, $p_{corr} = 0.003$, Cohens'd = 0.53), but not for the visual sequential condition. No significant linear increase in decoding accuracy was observed in the visual region.

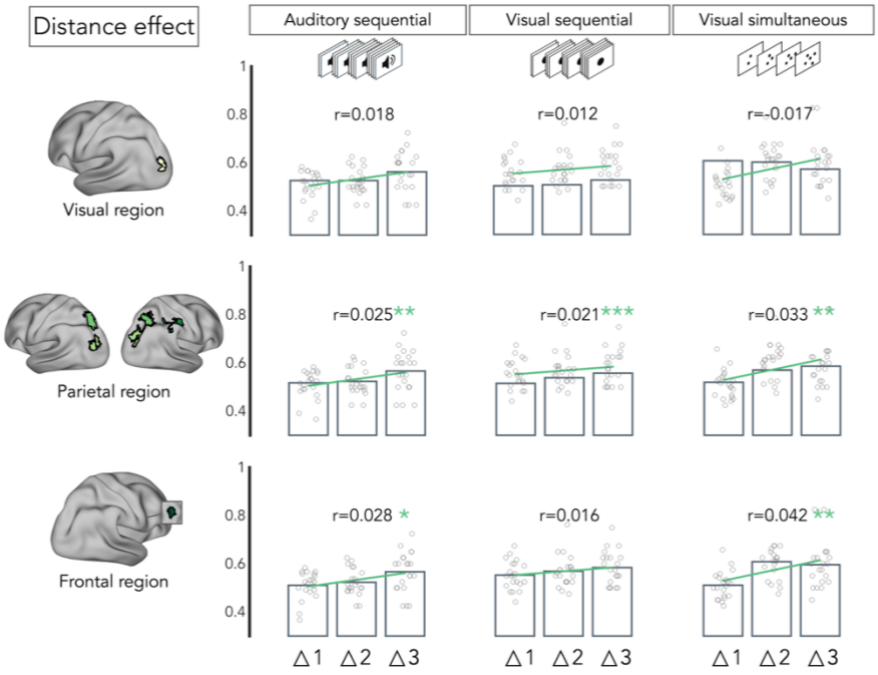


Figure 2.4. Distance effect for ROIs in each cortical region. Results are FDR corrected for three conditions for each region (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

2.4.4 Cross-classification Analysis

To identity whether ROIs that can decode numerosity across all non-symbolic conditions (i.e., ROIs identified through conjunction analysis) exhibit invariant representation patterns for numerosities, we conducted cross-classification analyses where the classifier was trained on numerosities from one condition and tested on numerosities from another condition and reversely (e.g., training on visual sequential condition and testing on the auditory sequential condition, and vice versa; FDR-corrected). The decoding accuracy reported here represents the average across both directions of training and testing. For visual sequential versus auditory sequential pairs, significant cross-classification results were observed in all the parietal ROIs (LhIP4, $p = 0.0124$, LhIP8, $p = 0.0104$, RhIP2, $p < 0.001$, RhIP3, $p = 0.0019$, RhIP4, $p = 0.0099$) and frontal ROIs (Precentral, $p < 0.001$) but not in the visual cortex (LV3A, $p = 0.2423$) (Figure 2.5B). Decoding accuracy for each individual direction is provided in the supplementary material (Figure S2.1).

For both auditory sequential versus visual simultaneous pairs and visual sequential versus visual simultaneous pairs, no significant cross-classification was observed across any of ROIs, either in the average of the two directions or in each direction separately (Figure 2.5B, Figure S2.1).

2.4.5 Representational similarity analysis

RSA analyses complement cross-classification decoding by moving beyond a simple dichotomy of shared versus no-shared information to a more comprehensive exploration of the geometry of numerical representation. By using RSA and theoretical models, we were able to further quantify the similarities and differences in numerical representations across conditions and modalities.

First, we observed a numerically high and similar upper-bound level of the noise ceiling across fROIs regions showing high inter-subjects consistency in how these regions react to our stimuli space. Interestingly, some models were close to this noise ceiling level according to the region tested, supporting their validity.

We tested the correlation between the neural dissimilarity matrix (DSM) of each ROI in each subject with three theoretical models (Figure 2.6 A, B). All three models are significantly correlated with neural DSM across all ROIs [all: $W(21) \leq 21$, $rbc \leq 0.0909$, $p \leq 0.001$]. However, the relative contributions of the models varied across ROIs. A gradual shift was observed from posterior to anterior areas: the contribution of the modality numerosity model decreased while that of the format numerosity model increased. More precisely, in the early visual cortex and several posterior parietal subregions, the modality numerosity model exhibited the strongest correlation with neural patterns while in RhIP2, the most anterior parietal subregion examined, the format numerosity model showed the highest correlation. Detailed statistical results are provided in the Supplementary Material (Text S1).

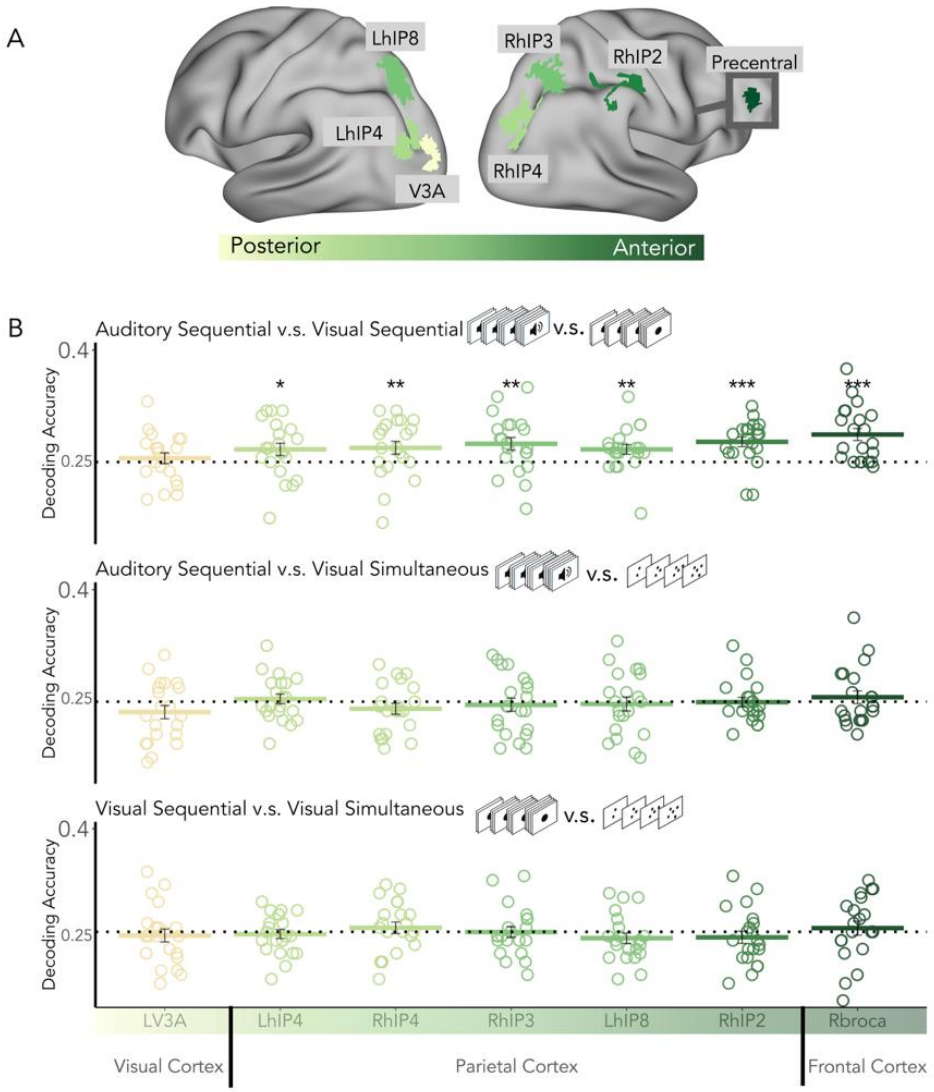


Figure 2.5. A: ROI that were identified from conjunction map. ROIs are illustrated as colored patches, with color progressing from light green to dark green along the cortical surface from posterior to anterior. B: Cross-classification results in ROIs illustrated in Figure 2.5A. Chance level (dotted line) is 25%. Individual points reflect individual subjects' results. Results are FDR corrected (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Error bars represent standard error of mean.

2.4.6 Partial correlation and variance partitioning

To explore independent contribution of each model to the neural activity, we computed partial correlations between the models and neural activities (Figure 2.6C). In general, although the condition numerosity model was significant in most fROIs, its contribution was consistently lower than that of the modality and the format models, suggesting that these two features of stimuli presentation were crucial in representing how numbers are encoded in these regions. The modality numerosity model and format numerosity model were both significantly correlated with neural DSM across all ROIs [all: $W(21) \leq 31$, $rbc \leq 0.1342$, $p \leq 0.002$]. Importantly, we observed a dissociation across ROIs regarding the relative contributions of the modality and format models. A gradual shift was observed from posterior to anterior areas: the contribution of the modality numerosity model decreased while that of the format numerosity model increased. Specifically, in the early visual cortex V3A and posterior parietal subregions left hIP4 and right hIP4, the modality model contributed the most to the neural activity, with significantly stronger effects than the format model [all: $W(21) \leq 46$, $rbc \leq 0.1991$, $p \leq 0.005$]. In the lateral parietal subregions left hIP8 and right hIP3, the contributions of the modality and format models were not significantly different [left hIP8: $W(21) = 115$, $rbc = 0.4978$, $p = 0.2305$; right hIP3: $W(21) = 62$, $rbc = 0.2684$, $p = 0.0537$]. In contrast, in the anterior parietal subregion left hIP2, the format model contributed the most, showing a significantly greater influence than the modality model [$W(21) = 25$, $rbc = 0.1082$, $p \leq 0.001$]. Finally, in the frontal Precentral region, the contribution of modality model and format models did not differ significantly [left hIP8: $W(21) = 99$, $rbc = 0.4286$, $p = 0.0735$]. Detailed statistical results are provided in the Supplementary Material (Text S2).

When all three predictors were regressed on the neural dissimilarity matrix, the full model explained significant portion of the variance in the group neural RDMs (all: $R2 > 0.338$, $p<0.001$). However, the distribution of explained variance varied across ROIs (Figure 2.6D). In the early visual cortex and posterior parietal subregions (LhIP4 and RhIP4), the modality model uniquely explained large portions of the variance. The MDS plot reveals a clear separation of modality across conditions (Figure 2.6E). In the lateral parietal subregions (LhIP8 and RhIP3), both modality and format models contribute substantively to the explained variance. In contrast to the posterior parietal subregions, the format model was the primary contributor to explain variance in the anterior parietal subregions. The MDS plot show a clear division between format across conditions. In frontal regions, the format models remained the stronger contributor, though its advantage over the modality model was less pronounced compared to the anterior parietal subregions. Overall, these variance partitioning results corroborate those observed with RSA.

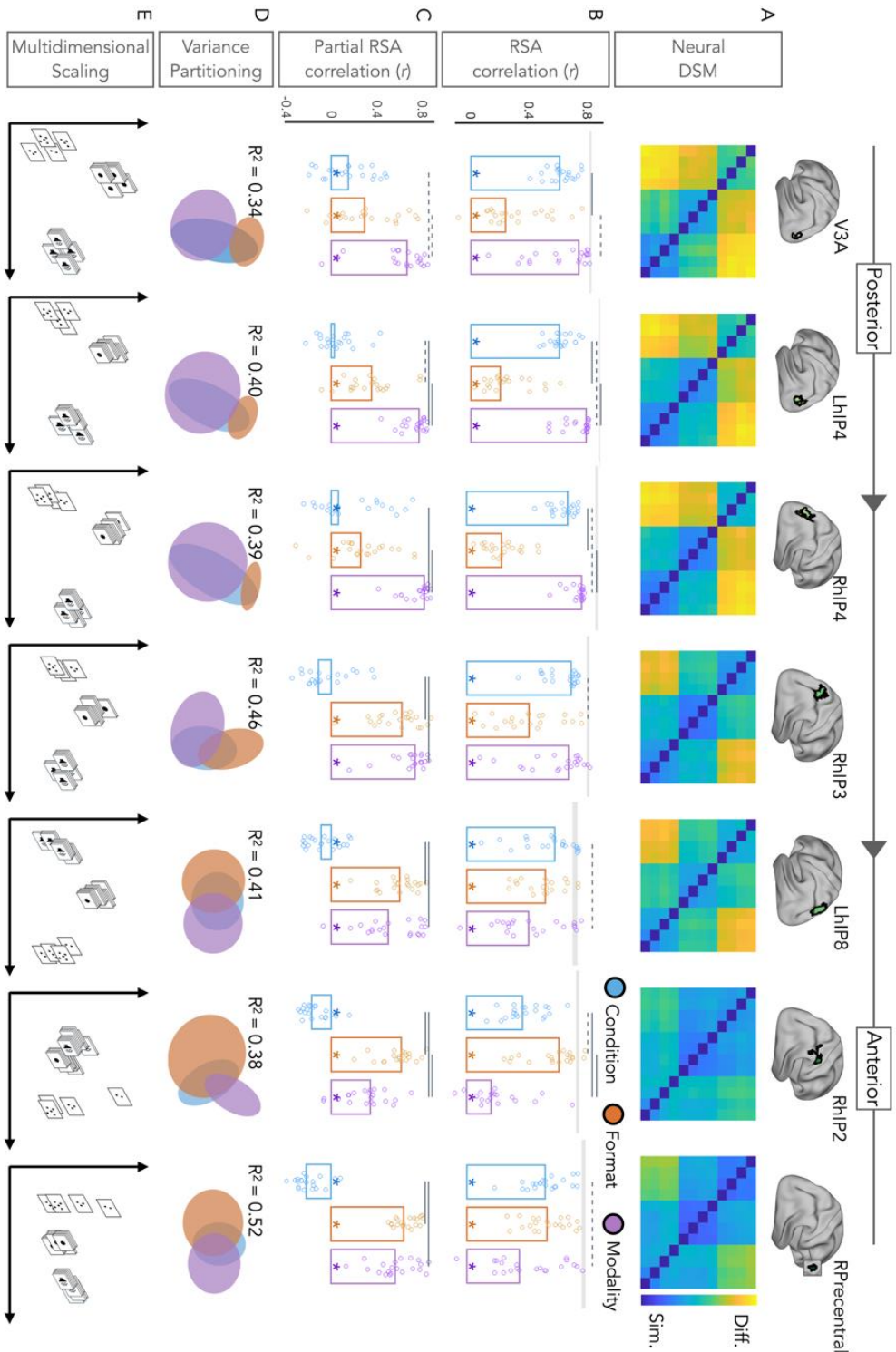

A
B
C
D
E
Neural DSM
RSA correlation (r)
Partial RSA correlation (r)
Variance Partitioning
Multidimensional Scaling
Posterior
Anterior
V3A
LhIP4
RhIP4
RhIP3
LhIP8
RhIP2
RPrecentral
Sim.
Diff.
Condition
Format
Modality
R² = 0.34
R² = 0.40
R² = 0.39
R² = 0.46
R² = 0.41
R² = 0.38
R² = 0.52

Figure 2.6. A: Group-averaged neural RDMs. B: Bar charts indicating the median Spearman's r rank-order correlations between neural RDMs for individual subjects (dots) and model RDMs. Gray blocks indicate the noise ceiling; Stars mark models whose correlations differ significantly from zero (one-sided Wilcoxon signed-rank test, $p < 0.05$). Connecting bars show two-sided pairwise comparisons between model correlations: solid bars indicate $p < 0.001$, dashed bars indicate $p < 0.05$. C: partial correlation for each model RDM. Stars mark models whose correlations differ significantly from zero (one-sided Wilcoxon signed-rank test, $p < 0.05$). Connecting bars show two-sided pairwise comparisons between model correlations: solid bars indicate $p < 0.001$, dashed bars indicate $p < 0.05$. D: Euler diagram depicting results of variance partitioning the individual dissimilarity in each ROI between models. E: Two-dimensional multidimensional scaling applied to the dissimilarity matrices. Stimulus modality and presentation format are indicated by shape: circles represent auditory sequential numerical stimuli, crosses represent visual sequential stimuli, and triangles represent visual simultaneous stimuli. The size of each shape scales with numerosity.

2.5 Discussion

Humans and other animals seamlessly extract numerosity from a countless variety of situation. Whether the human mind and brain implement an abstract numerical code has been debated for the last two decades (Cohen Kadosh & Walsh, 2009). In this study, we examined how numerical representations are organized across different sensory modalities and representation formats. Relying on multivariate decoding we first aimed to identify regions that encodes numerical information in their distributed activity patterns across the senses and presentation format. We first reveal a set of overlapping brain regions, spanning from V3A to multiple IPS subregions and precentral area in prefrontal cortex that successfully encode numerical information in all three non-symbolic conditions. These results confirm the crucial role of a dorsal occipito-parieto-frontal network in numerical processing (Castaldi et al., 2019; Dehaene et al., 2003; Harvey et al., 2017b; Knops, 2017; Kido et al., 2025), extending its role to reliable encoding of numerosities across senses and formats. Cross-classification analysis further revealed a shared numerosity code across vision and audition when numerosities are presented using a similar temporal code. Finally, using representational similarity analyses, we identified a posterior-to-anterior gradient in the IPS with numbers being encoded in posterior regions primarily relying on the senses while anterior region coding more for the format of numerosity presentation.

Numerosity is inherently embedded within both spatial and temporal domains, each engaging distinct cognitive mechanism. While simultaneous numerosity relies on visuospatial processing and are parallelly extracted through location maps (Anobile et al., 2018; Dehaene & Changeux, 1993), sequential numerosity unfolds over time, requiring serial accumulation and engaging temporal processing. Previous studies have suggested that parietal and frontal cortices perform a 'normalization' process in which numerosity representations are abstracted into a unified representation by discarding irrelevant physical properties (Croteau et al., 2024; Dehaene & Changeux, 1993; Park & Huber, 2022). However, our findings suggests that this normalization process does not entirely eliminate

physical information but instead maintains a distinction between spatial and temporal numerosity representations. Indeed, our cross-classification analysis showed that in parietal and frontal cortex, there is an invariant neural pattern for numerosity representation across visual and auditory modalities but only when sharing a sequential representation format. This shared representation does not extend across different presentation formats: neural patterns for numerosity in sequential (visual/auditory) formats do not align with those from simultaneous (visual) presentations. In other words, even in regions that both code for spatial and temporal numerical information, no alignment is found across those two formats of numerical displays, even if presented within the same modality (here, vision). This result can be understood by daily statistics since numerosities within each presentation format – and especially the sequential format – tend to be closely linked to each other and often co-occur. In contrast, co-occurrence or interactions across different presentation formats is rare. The brain may internalize these statistical patterns from everyday experience (Qu et al., 2024; Zhao & Yu, 2016), classifying numerosities from the same presentation formats more closely to one another even if coming from different senses. From an efficiency perspective, generalizing numerical representations within the temporal domain while preserving a distinction between spatial and temporal representations may serve to optimize processing efficiency and reduce inter-domain interference (Czajko et al., 2024).

We carefully controlled low-level features for numerosities from each condition by using two sets of stimuli. We further restrict our cross-classification analysis on brain regions that successfully decode all non-symbolic numerosities to exclude brain regions sensitive to specific low-level features. However, since the cross-classification only succeeds when numerosity shared a similar temporal code, one may still question whether this cross-classification could be driven by low-level temporal features. This is unlikely for several reasons. First, total sequence duration, individual beep/dot duration and inter-beep/dot intervals were varied across the two stimulus subsets, making it difficult to rely on any of these features to discriminate numerosity (Cavdaroglu et al., 2015b; Dehaene et al., 2005). Second, both the individual beep/dot durations and inter-beep/dot intervals were jittered to prevent any regular patterns and participants relying on the frequency of stimuli as a cue to discriminate numerosity. A prior study where participants maintained a 6-second tactile vibration or visual flicker with embedded frequency information did not identify a distributed supramodal frequency representation in parietal regions (Dakin et al., 2011). Our cross-classification results in a set of parietal subregions suggest that it may be the extraction of numerosities, rather than frequency, that facilitates the alignment of sequentially presented numerosities across the senses.

Our findings align with a previous study showing that number-selective neurons in the prefrontal and parietal cortices of non-human primate encodes sequential numerosity across sensory modalities (Nieder, 2012). To our knowledge, the current study is the first to reveal such an alignment in the human brain. While Cavdaroglu et al., (2015a) previously attempted to examine cross-modal alignment of sequential numerosity in the human brain using similar cross-classification approach, their results did not support the existence of an alignment. In contrast, our results provide unequivocal evidence of cross-modal alignment

for sequential numerosity. Compared to Cavdaroglu et al.'s study, which used a broad range of numerical stimuli ranging from 5 to 16, we intentionally relied on a small number range in order to trigger a salient representation of specific numerosities, something unlikely with larger numbers since their internal representations become noisier, less precise and less accurate (Tokita et al., 2013). This in turn may reduce the brain's capacity to create a unified representation of larger numerosities across different stimulus types or modalities. Furthermore, our study shows that an active response is unnecessary for detecting numerosity representations or their alignment (Cavdaroglu et al., (2015a)). Our experiment relied on a one-back task requiring participants to memorize previous quantity and discriminate if the ongoing quantity is the same as the previous one. Response was not needed for most of the trials. One may argue that the activation of a verbal code during the comparison phase might be necessary for aligning numerosity representations. However, our results argue against this interpretation since alignment occurred only when numerosity shared a representation format. Furthermore, the structure of the task was identical for symbolic numerosities for which we did not observe reliable decoding. Altogether these results suggest that the activation of a verbal code does not underly our observation of a shared temporal numeral code across the senses, but rather the presence of a shared representation format that ultimately determines alignment.

In the current study, we did not find any invariant neural patterns across presentation formats, that is, across the sequential and simultaneous presentation formats. Nieder's study examined number-selective neurons for visual numerosity across these formats in the non-human primate brain and found that when the enumeration process was completed and animals needed to maintain the quantity in mind for an upcoming quantity-matching task, a subset of neurons (19 % of recorded neurons) encoded the quantity irrespective of the presentation format (simultaneous, sequential). Although our participants also need to retain the quantity in memory, we did not observe an invariant neural activity pattern across presentation formats. One potential explanation for this discrepancy is that only a small group of neurons exhibit such shared representation, potentially impeding the ability of classic fMRI to detect such restricted signal in space. Alternatively, the limited temporal resolution of fMRI makes it challenging to capture fast and transient changes in neural activity in a timely manner as was done by Nieder and colleagues' study who could see that across format alignment does not express during the encoding but only during the maintaining phase (Ditz & Nieder, 2020; Nieder et al., 2006). Such abstraction process might thus require a finer level of spatial and temporal resolution to be successfully assessed, not easily accessible with classic fMRI. Future research using ultra high-field fMRI combined with techniques having temporal sensitivity (e.g., i/M/EEG) could provide deeper insights into the presence of an abstract representation across presentation formats in the human brain.

A notable finding in the present study is the successful decoding of non-symbolic numerosity, including auditory sequential numerosity, in V3A. The extent to which early visual cortex supports numerosity processing remains debated. People supporting this idea argue that numerosity is a primary perceptual property, which can be perceived directly

(Castaldi et al., 2019, 2021; Cicchini et al., 2016; DeWind et al., 2019; Fornaciai & Park, 2018; Park et al., 2016; Testolin et al., 2020) and animals (Lorenzi et al., 2024; or even before, see: Luu et al., 2024; Messina et al., 2022), while others suggest that numerosity can only be perceived indirectly through other visual cues (Dakin et al., 2011; Durgin, 2008; Gebuis et al., 2014; Paul et al., 2022). Our results contribute to this debate by showing that, beginning in V3A, the early visual cortex is able to extract numerical information from a variety of sensory inputs (Fornaciai & Park, 2018). Moreover, the successful decoding of auditory sequential numerosity in V3A indicates that its function extends beyond the processing of spatial visual features. However, the numerosity representation in V3A appear to remain tied to their sensory origin rather than being abstracted.

Surprisingly, we did not observe any reliable decoding for visual or auditory symbolic numerosity across the whole brain. The very strong decoding in other conditions refute the idea this null result relates to the sensitivity of our paradigm, fMRI acquisition parameters or analytical scheme. A prior study compared visual symbolic numerosity, dot arrays and braille numerosities and neither did find representations of visual symbolic numerosity (Czarnecka et al., 2023). They hypothesized that symbolic numerosity, due to overtraining, evoked lower activation and therefore lower "decodability". In the current study, univariate analyses for the symbolic conditions evoked comparable univariate activation level when compared to the non-symbolic conditions ruling out such interpretation (see Figure 2.2). Another possibility would be that symbolic numerosity representations may require higher spatio-temporal sensitivity to be detected. This idea is consistent with the hypothesis that non-symbolic numerosity, as the evolutionarily older one, is probably represented by a larger neuronal population (Ansari, 2008; Eger et al., 2009) that is potentially innate (Lorenzi et al., 2025).

By constructing theoretical models and correlating them with distributed neural activity patterns using RSA, we further unravelled a posterior-to-anterior organization gradient along the dorsal pathway. In the most posterior part of the IPS and V3A, numerical representations are mainly encoded in terms of sensory inputs while the most anterior IPS is primarily encoding numbers in terms of their presentation format. Intermediate regions, including the lateral IPS, exhibit a comparable influence of both model and may function as a transition hub from modality to format processing. Unlike the cross-classification results, which served as a more stringent approach to address the presence of partially abstracted numerical representation in a region, RSA provides a finer-grained measurement of a progressive transition from primarily modality-based to primarily format-based processing along the parietal cortex. The posterior IPS regions are highly connected with extrastriate visual areas (Bray et al., 2013). In contrast, hIP2, the most anterior IPS subdivision, situated next to premotor cortex, exhibits a close link with the ventral premotor cortex (Uddin et al., 2010). This differential connectivity profile suggests that visual sensory inputs processed in posterior IPS regions are transformed into motor actions through connections from the anterior IPS to the prefrontal cortex. Indeed, studies in non-human primates have found that posterior IPS had the strongest functional connectivity to regions involved in motion

processing and eye movements, while anterior IPS was functionally connected to regions associated with motor, tactile, and proprioceptive processing, as well as regions involved in reaching, grasping, and processing peripersonal space (Knops et al., 2009; Sheng et al., 2025). In numerosity studies, the anterior IPS also show a linkage between numerical perception and motor functions, exemplified by its role in encoding finger counting (Kaufmann et al., 2008; Krinzinger et al., 2011). We therefore speculate that the temporally structured organization in the anterior IPS region hIP2, given its anterior position and link to the premotor cortex, may serve for supporting motor actions (Anobile et al., 2016; Kirschhock & Nieder, 2022; Sawamura et al., 2020; Togoli et al., 2020). Recently, researchers have proposed a sensorimotor theory of numerosity processing, indicating a more generalized system in the brain that integrates action with the processing of other quantitative magnitudes such as space and time (Anobile et al., 2021; Sixtus et al., 2023). Our results may reflect this sensorimotor organization of numerosity, suggesting that the brain automatically aligns numerosity information based on its temporal structure. Such an organization may facilitate motor actions, as action unfold over time, making their numbers embedded in their sequential nature. The anterior IPS region hIP2, where we found stronger format-based coding, may therefore serve as a key locus in this sensorimotor organization. Although we focused on dorsal regions, recent work shows ventral areas may also encode visual numerosity (Karami et al., 2025), raising questions for future studies about the role of ventral area in cross-format/cross-modal numerosity representation.

In conclusion, our study investigated how numerical representations from various sensory modalities and formats converge into a higher-level numerical representation in the brain, revealing a multifaceted organization of numerosity across modalities and formats. We observed a posterior-to-anterior gradient organization along the dorsal pathway, beginning with numbers encoded mostly based on their sensory attributes in early visual cortex, progressing with a mixture of processing of sensory and format information in the posterior parietal cortex and ending to a primarily format-based processing in anterior parietal cortex. This distributed gradient encoding offers critical insights into the brain's mechanisms dedicated to numerical processing from various sensory inputs and format of presentation. Our study suggests that numerosity might not converge into a single, generalized representation abstracted from all physical properties. Instead, it appears to preserve a distinction between spatial and temporal numerosity representations, possibly reflecting statistical regularities in daily experience and putatively contributing to more efficient neural processing. This temporal organization of numerosity becomes most salient in anterior parietal, maybe playing a role in transferring numerosities into a corresponding action effectively.

2.6 References

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2.7 Supplementary materials

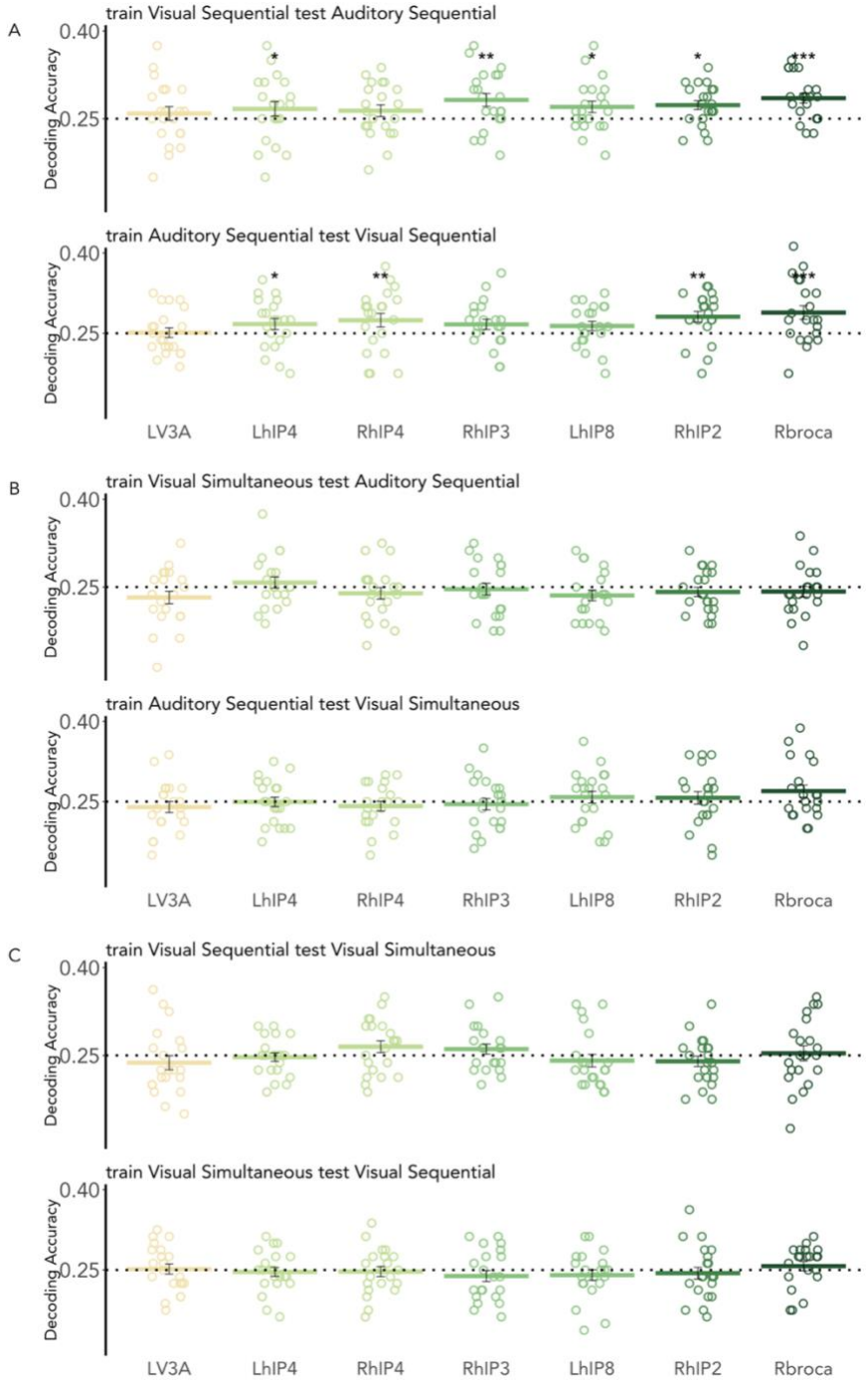


Figure S2.1. Cross-classification results for each classification direction within every pair of non-symbolic numerosity conditions. Chance level (dotted line) is 25%. Cross-bar colors encode the ROIs, shifting from light to dark green as the regions move along the cortical surface from posterior to anterior. Individual points reflect individual subjects' results. Results are FDR corrected (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Error bars represent standard error of mean. **A.** Visual sequential v.s. auditory sequential numerosities. **B.** Auditory sequential v.s. Visual simultaneous numerosities. **C.** Visual sequential v.s. Visual simultaneous numerosities.

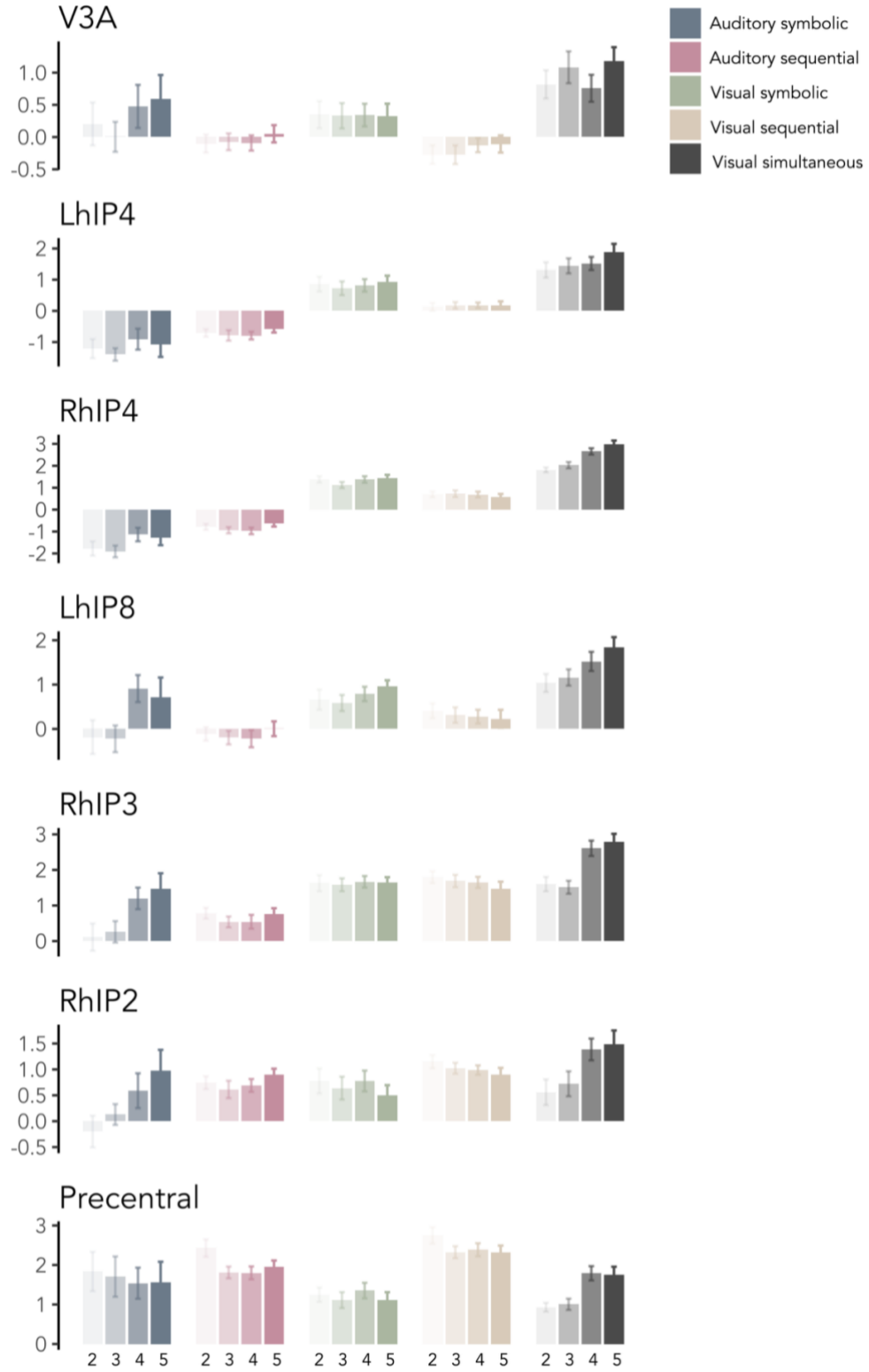

V3A
LhIP4
RhIP4
LhIP8
RhIP3
RhIP2
Precentral
Auditory symbolic
Auditory sequential
Visual symbolic
Visual sequential
Visual simultaneous
2 3 4 5

Figure S2.2. Beta parameter estimates extracted from the ROIs defined by conjunction map. Error bars represent the standard error of the mean. Increasing bar alpha levels represent increasing numerosity.

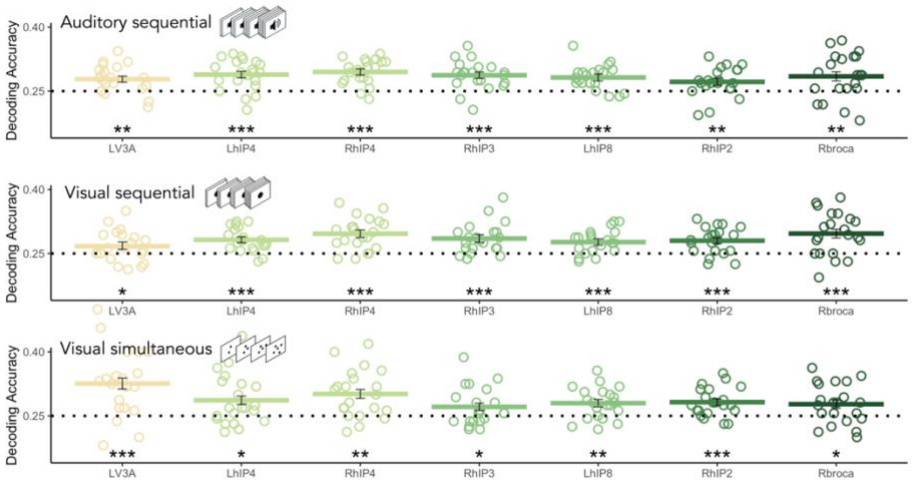


Figure S2.3. Decoding accuracy when the classifier was trained on data from both stimulus subsets but tested on only one subset. Classifier performance reported here is the average across the two subsets used as the testing set. Results are FDR corrected (*p < 0.05, **p < 0.01, ***p < 0.001). Error bars represent standard error of mean.

		convex hull	density(N/convex hull)	inter-distance	total area	total perimeter	radius
2	subset1	90,0019947	0,02222173	13,8721102	40	31,7066184	2,52313252
		90,0012929	0,0222219	13,8719721	40	31,7066184	2,52313252
3	subset1	90,0002661	0,03333323	8,3532217	40	38,8325183	2,06012908
		90,0000771	0,0333333	8,254024	40	38,8325183	2,06012908
4	subset1	90,0018426	0,04444354	6,92706994	40	44,8399297	1,78412412
		90,0032252	0,04444285	7,82048802	40	44,8399297	1,78412412
5	subset1	90,0008139	0,05555505	7,23772541	40	50,1325655	1,59576912
		90,0021445	0,05555423	6,62875581	40	50,1325655	1,59576912
		convex hull	density(N/convex hull)	inter-distance	total area	total perimeter	radius
2	subset2	42,5794864	0,04697098	7,99940581	23,404237	24,2530953	1,93
		42,5673277	0,04698439	7,99625244	23,404237	24,2530953	1,93
3	subset2	67,8586757	0,04420953	7,9988023	35,1063554	36,3796429	1,93
		78,941948	0,03800261	7,99661894	35,1063554	36,3796429	1,93
4	subset2	108,840337	0,03675108	8,00278454	46,8084739	48,5061906	1,93
		110,96689	0,03604679	7,99735734	46,8084739	48,5061906	1,93
5	subset2	136,016481	0,03676025	7,99581817	58,5105924	60,6327382	1,93
		124,809709	0,04006099	8,00062427	58,5105924	60,6327382	1,93

Table S2.1. Detailed information for dots arrays for each subsets of each numerosity. Convex hull: the area of the smallest convex polygon containing all the elements. Inter-distance: the average of the distances between all the possible pairs of elements. Density: the number of elements (n) divided by the total occupied area (D = n/CH). Radius: the specific dimension of a single dot. Total perimeter: the sum of the perimeters (contours) of all elements. Total area: the sum of the areas (surfaces) of all elements (Zanon et al., 2022). For each numerosity in each condition, two dots arrays are generated within each set and are randomly assigned across participants.

visual sequential	Dots Duration		Inter Dot Interval		Total Sound Duration		Total Length	
numerosity	set1	set2	set1	set2	set1	set2	set1	set2
2	0.634(0.254)	0.240(0.035)	0.653(0)	0.180(0)	1.267	0.48	1.92	0.66
3	0.422(0.121)	0.240(0.027)	0.326(0.524)	0.180(0.088)	1.267	0.720	1.92	1.08
4	0.317(0.067)	0.240(0.036)	0.217(0.045)	0.180(0.089)	1.267	0.960	1.92	1.5
5	0.240(0.020)	0.240(0.020)	0.180(0.095)	0.180(0.095)	1.200	1.200	1.92	1.92
auditory sequential	Beeps Duration		Inter Dot Interval		Total Sound Duration		Total Length	
numerosity	set1	set2	set1	set2	set1	set2	set1	set2
2	0.528(0.168)	0.187(0.032)	0.544(0)	0.175(0.035)	1.056	0.375	1.6	0.55
3	0.352(0.079)	0.200(0.032)	0.272(0.009)	0.150(0.058)	1.056	0.6	1.6	0.9
4	0.264(0.041)	0.200(0.019)	0.181(0.072)	0.150(0.071)	1.056	0.8	1.6	1.25
5	0.211(0.058)	0.200(0.020)	0.136(0.044)	0.150(0.080)	1.056	1	1.6	1.6

Table S2.2. Timing information (mean (SD)) for visual and auditory sequential numerosity conditions. Dots/Beeps duration represents the duration of individual dots/beeps within a sequence. Inter dot/beep interval represents the duration between individual dots/beeps. Total sound/beep duration represents the summed duration of dots/beeps in a sequence, excluding the intervals. Total length is the combined duration of the total dot/beep duration and the total inter-dot/beep intervals. For each numerosity in each condition, two sequences are generated within each set and are randomly assigned across participant.

Brain region	effect	F value	Pperm value
LV3A	condition	F(4,80) = 5.84	P = 0.002 *
	numerosity	F(3,60) = 8.42	P < 0.001 *
	Condition*numerosity	F(12,240) = 3.26	P = 0.007 *
LhIP4	condition	F(4,80) = 8.29	P < 0.001 *
	numerosity	F(3,60) = 8.50	P < 0.001 *
	Condition*numerosity	F(12,240) = 3.20	P = 0.01 *
LhIP8	condition	F(4,80) = 61.19	P < 0.001 *
	numerosity	F(3,60) = 2.98	P = 0.021 *
	Condition*numerosity	F(12,240) = 0.75	P > 0.05
RhIP2	condition	F(4,80) = 6.37	P < 0.001 *
	numerosity	F(3,60) = 7.00	P < 0.001 *
	Condition*numerosity	F(12,240) = 3.27	P = 0.013 *
RhIP3	condition	F(4,80) = 14.04	P < 0.001 *
	numerosity	F(3,60) = 7.56	P < 0.001 *
	Condition*numerosity	F(12,240) = 2.86	P = 0.016 *
RhIP4	condition	F(4,80) = 103.57	P < 0.001 *
	numerosity	F(3,60) = 8.17	P < 0.001 *
	Condition*numerosity	F(12,240) = 2.37	P = 0.048 *
Rprecentral	condition	F(4,80) = 7.75	P = 0.1092
	numerosity	F(3,60) = 1.82	P <0.001 *
	Condition*numerosity	F(12,240) = 2.16	P = 0.0664

Table S2.3. Statistical results of the non-parametric ANOVA for beta estimates parameters.

Brain region	Sig. effect	Pairwise condition	Stats
LV3A	interaction	Vis-sim: 2 vs 4	W = 16, p<0.001
		Vis-sim: 2 vs 5	W = 16, p<0.001
		Vis-sim: 3 vs 4	W = 22, p<0.001
		Vis-sim: 3 vs 5	W = 31. P=0.002
LhIP4	interaction	Aud-num: 3 vs 4	W = 39, p=0.038
		Vis-sim: 2 vs 4	W = 16, p<0.001
		Vis-sim: 2 vs 5	W = 16, p<0.001
		Vis-sim: 3 vs 4	W = 25, P=0.002
		Vis-sim: 3 vs 5	W = 27, P=0.002
LhIP8	numerosity	3 vs 5	W = 1913, p=.033
	condition	Aud-num vs aud-seq	W = 1160, p=0.005
		Aud-num vs vis-num	W = 135, p<0.001
		Aud-num vs vis-seq	W = 369, p<0.001
		Aud-num vs vis-sim	W = 36, p<0.001
		Aud-seq vs vis-num	W = 34, p<0.001
		Aud-seq vs vis-seq	W = 103, p<0.001
		Aud-seq vs vis-sim	W = 0, p<0.001
		Vis-num vs vis-seq	W = 3264, p<0.001
		Vis-num vs vis-sim	W = 169, p<0.001
		Vis-seq vs vis-sim	W = 10, p<0.001
RhIP2	interaction	Vis-sim: 2 vs 4	W = 6, p<0.001
		Vis-sim: 2 vs 5	W = 8, p<0.001
		Vis-sim: 3 vs 4	W = 24, P=0.001
		Vis-sim: 3 vs 5	W = 28, P=0.002
RhIP3	interaction	Vis-sim: 2 vs 4	W = 10, p<0.001
		Vis-sim: 2 vs 5	W = 18, p<0.001
		Vis-sim: 3 vs 4	W = 3, p<0.001
		Vis-sim: 3 vs 5	W = 19, p<0.001
RhIP4	interaction	Vis-sim: 2 vs 4	W = 5, p<0.001
		Vis-sim: 2 vs 5	W = 8, p<0.001
		Vis-sim: 3 vs 4	W = 6, p<0.001

		Vis-sim: 3 vs 5	W = 13, P<0.001
Rprecentral	condition	aud_sym v.s. vis_seq	W = 2376 P <0.001
		aud_seq v.s. vis_sym	W = 5248, P<0.001
		Aud_seq v.s. vis_seq	W = 2343, P<0.001
		Aud_seq v.s. vis_sim	W = 5024, P<0.001
		Vis_sym v.s. vis_seq	W = 1048, P<0.001
		Vis_seq v.s. vis_sim	W = 5817, P<0.001

Table S2.4. Post hoc Wilcoxon pairwise comparisons following significant main effects or interactions in beta estimates parameters.

Text S2.1. Statistical results of correlation between neural dissimilarity matrix and theoretical models.

We tested the correlation between the neural dissimilarity matrix (DSM) of each ROI in each subject with three theoretical models (Figure 2.6A, 2.6B). In the early visual cortex, the median correlations of the three model RDMs were all significant [all: $W(21) < 7$, $rbc < 0.0303$, $p \leq 0.001$]. Additionally, we also observed significant differences between the condition numerosity model (CondNum) versus the format numerosity model (FmtNum), and the format numerosity model versus the modality numerosity model (ModalNum) [$W(21) < 56$, $rbc < 0.2424$, $p \leq 0.003$]. In the posterior parietal subregion left hIP4, the median correlations of the three model RDMs were all significant [all: $W(21) = 0$, $rbc = 0$, $p \leq 0.001$]. The differences between every two models were also significant [all: $W(21) \leq 64$, $rbc \leq 0.2771$, $p \leq 0.0117$]. In the posterior parietal subregions right hIP4, the median correlations of the three model RDMs were all significant [all: $W(21) = 0$, $rbc = 0$, $p \leq 0.001$]. The differences between every two models were also significant [all: $W(21) \leq 59$, $rbc \leq 0.2554$, $p \leq 0.0015$]. In the lateral parietal left hIP8 region, all three models showed significant partial correlations [all: $W(21) \leq 4$, $rbc \leq 0.0173$, $p \leq 0.001$]. Additionally, there was a significant difference between the condition numerosity model versus the modality numerosity model [$W(21) = 65$, $rbc = 0.2814$, $p = 0.0078$]. In the lateral parietal right hIP3 region, all three models showed significant partial correlations [all: $W(21) = 0$, $rbc = 0$, $p \leq 0.001$]. In the anterior parietal subregions left hIP2, all three models showed significant partial correlations [all: $W(21) \leq 6$, $rbc \leq 0.026$, $p \leq 0.001$]. There was also a significant difference between condition numerosity model versus format numerosity model [$W(21) = 8$, $rbc = 0.0346$, $p = 0.0012$]. In the frontal Precentral region, all three models showed significant partial correlations [all: $W(21) \leq 21$, $rbc \leq 0.0909$, $p \leq 0.001$]. There are significant difference between condition numerosity model versus modality numerosity model [$W(21) = 49$, $rbc = 0.2121$, $p = 0.0057$].

Text S2.2. Statistical results of partial correlation between neural dissimilarity matrix and theoretical models.

To assess the independent contribution of each model to the neural activity, we computed partial correlations between the models and neural activities (Figure 2.6C). In the early visual cortex area V3A, significant partial correlations were found for all three models [all: $W(21) \leq 64$, $rbc \leq 0.2771$, $p \leq 0.012$]. In the posterior parietal subregions left hIP4, significant partial correlations were observed for both the modality and format models [$W(21) \leq 11$, $rbc \leq 0.0476$, $p \leq 0.001$]. In the posterior parietal subregions right hIP4, significant partial correlations were found for all three models [all: $W(21) \leq 49$, $rbc \leq 0.2121$, $p \leq 0.019$]. In the lateral parietal left hIP8 region, all three models showed significant partial correlations [all: $W(21) \leq 71$, $rbc \leq 0.3074$, $p \leq 0.0032$]. In the lateral parietal right hIP3 region, significant partial correlations were obtained for the modality and format model [both: $W(21) = 0$, $rbc = 0$, $p \leq 0.001$]. In the anterior parietal subregions left hIP2, significant partial correlations were obtained for all three models [all: $W(21) \leq 9$, $rbc \leq 0.0390$, $p \leq 0.001$]. Likewise, in the frontal Precentral region, all three models showed significant partial correlations [all: $W(21) \leq 51$, $rbc \leq 0.2208$, $p \leq 0.001$].

Text S2.3. Beta parameter estimates

To examine the activity levels associated with different conditions and numerosities, and to determine whether specific conditions or numerosities consistently evoked higher or lower brain activity, we extracted univariate beta parameter estimates in each fROI where we observed successful numerosity decoding. We conducted non-parametric ANOVAs. In case of significant main effect or interaction effect, post hoc tests were conducted using a series of Wilcoxon tests, and were adjusted for multiple comparisons using the false discovery rate (FDR) methods (Benjamini & Yekutieli, 2001).

Six out of seven ROIs demonstrated significant main effects of numerosity, condition, as well as a significant numerosity × condition interaction (Figure S2.2). Post hoc pairwise comparisons revealed that the interaction effect was mostly driven by the significant beta difference in the visual simultaneous condition. Detailed results of the non-parametric ANOVA and post hoc Wilcoxon pairwise tests are provided in Table S2.3-S2.4.

The number sense: Likely innate, surely not visual

Reference

Yang, Y., & Collignon, O. (2025). The number sense: likely innate, surely not visual. A commentary on “Is there an innate sense of number in the brain?”. Cerebral Cortex, 35(7), bhaf207

3. The number sense : Likely innate, surely not visual

3.1 Abstract

Lorenzi et al. (2025) convincingly support the idea of an innate number sense. However, in their paper, and in most of the commentaries it triggered, authors assume that the number sense is visually grounded. We challenge this view based on two key arguments: the number sense is supramodal and can develop in congenitally blind people. Together, these points suggest that the number sense is a modality-independent faculty, accessible through any sensory and cognitive channels, with vision being just one convenient gateway among others.

3.2 Commentary

Lorenzi et al. (2025) offer compelling evidence that the number sense is innate. They support this claim with converging behavioral and neural findings from newborn animals suggesting a sensitivity for numerical information since birth, in the absence of specific training or experience. They for instance demonstrate that newly hatched chicks display a number sense immediately after birth when tested on visual display. However, the paper and most of the ensuing commentaries it triggered implicitly assume that the number sense is primarily visual in nature. This view is most explicitly expressed in Harvey's comment, in which it is suggested that the innate number sense is "an innate property of vision, derived from the spatial frequency-based representation of images in the visual systems" (Harvey, 2025). According to this view, numerical representations emerge from the visual system's extraction of spatial frequency information in the environment. The early visual system is hard-wired to encode image contrast in the spatial frequency domain, and because the total frequency energy of an image correlates very closely with numerosity, numerosity can be straightforwardly derived by subsequent stages of processing (Harvey, 2025; Paul et al., 2022).

While this visual-centric perspective offers a compelling low-level explanation of how the brain might extract numerical information from visual input, it raises an important question: is vision truly a mandatory building block for the emergence of the number sense?

Vision indeed provides clear advantages in processing numerical information. It can simultaneously handle a large amount of information, while audition and touch are more limited to how much information they can process simultaneously (Anobile et al., 2016). Perhaps one of the most striking (but debated; see Yousif et al., 2024) demonstration of a visual number sense (as explicitly mentioned in the title of the original paper) relies on the observation that perceived numerosity is susceptible to adaptation, like any primary visual properties (Burr & Ross, 2008). Visuospatial coding of numerosity is also supported by the

SNARC effect, where participants respond faster when smaller numbers are associated with the left hand and larger numbers with the right (Dehaene et al., 1993; Gevers et al., 2006). Additionally, subitizing, the rapid and accurate enumeration of small sets, is commonly believed to rely on the visual system's capacity to index multiple objects in parallel (Dehaene & Cohen, 1994; Kaufman et al., 1949).

However, we challenge the notion that the number sense is inherently based on vision relying on two key arguments: first, the supramodal nature of the number sense; and second, its development in individuals who have never had visual experience.

First, extensive evidence supports that the number sense relies on mechanisms that are not exclusive to the visual system. Numerical abilities have been well documented across auditory and tactile modalities (Arrighi et al., 2014; Tokita & Ishiguchi, 2011; Yang et al., 2025). Individuals can estimate and compare numerical quantities as sequences of sounds or tactile stimuli. One might wonder whether numerical representations arising across different senses derive from similar mechanisms or instead arise independently—such that the representational format of the visual numerosity might be different from the one in audition and touch. Several lines of evidence suggest that this is unlikely. First, numerical estimation and discrimination in touch and audition follow the same governing principles observed in vision, such as the distance effect (where numbers that are numerically closer are harder to discriminate) and the size effect (where larger numbers are harder to process) (Krause et al., 2013; Piazza et al., 2006; Szűcs & Csépe, 2005). Second, the magnitude of the SNARC effect does not significantly differ across modalities, suggesting a shared underlying representational format (Crollen et al., 2013). Third, and maybe more convincingly, cross-modal adaptation studies show that adapting to numerical information in one sense has a repulsive perceptual effect on numerical estimation in another sense (Anobile et al., 2016; Togoli & Arrighi, 2021).

These observations immediately complicate explanations of numerosity that posit a direct link between visual experience and numerosity. The fact that numerosity arises in - and generalize across- audition, touch as well as vision points to more fundamental origins than learned mapping from visual input.

One may however still argue that numerical estimation based on non-visual information might depend on projecting non-visual information onto a visual scaffold; vision would represent the developmental foundation on which other senses build on to develop a mature sense of number. However, the strongest argument against this idea comes from the studies of individuals who never had visual experience. If vision was essential for developing a number sense, congenitally blind individuals would show severely impaired numerical abilities (Crollen & Collignon, 2020). Yet, numerous studies have shown that blind individuals perform similarly to, or even sometimes better than, sighted individuals in numerical tasks, including numerical estimation and arithmetic operations (Castronovo & Seron, 2007; Kanjlia et al., 2018, Dormal et al., 2016). Blind individuals also exhibit the typical distance and size effects when perceiving numerosity through non-visual modalities, suggesting that an analog number line can develop without visual calibration (Castronovo

& Seron, 2007; Szűcs & Csépe, 2005). Similarly, they display a SNARC effect, indicating that spatial coding of number can emerge independently of vision (Crollen et al., 2013). Remarkably, subitizing - long thought to rely on the visual system's capacity for parallel item processing- has also been observed in blind individuals, suggesting that subitizing is a general mechanism rather than a vision-specific computation (Ferrand et al., 2010). Neuroimaging studies further support these behavioral observations by revealing that similar brain regions, particularly the intraparietal sulcus, are involved in numerical thinking in both congenitally blind and sighted individuals (Crollen et al., 2019; Kanjlia et al., 2016); with the additional engagement of dorsal occipital regions in blind people).

Actually, Lorenzi et al. mention that newly hatched chicks are exposed to proprioceptive sounds or tactile simulation before hatching, raising the intriguing possibility that non-visual sensory input may support the early development of the number sense. This idea converges with our proposition that vision might not be a prerequisite for the emergence of the number sense. Taken together, these arguments undermine the notion that the number sense develops based on visual experience. Instead, the number sense appears to be a modality-independent faculty that the brain can access through whichever sensory and cognitive channels are available, with vision merely one convenient gateway among many. By moving beyond a vision-centric perspective, the field of numerical cognition can gain deeper insights into the fundamental principles governing the (innate) emergence of the number sense.

3.3 references

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General Discussion

4. General Discussion

4.1 discussion

The ability to make sense of number is critical for human-being. Importantly, we can seamlessly extract numerosity from a countless variety of situation, which lead to a dominant view that diverse numerical inputs converge into a unified representation in the brain. Specifically, IPS stores an abstract representation of numerosity which is independently of presentation notation (i.e., symbolic vs. non-symbolic), format (i.e., simultaneous or sequential) and sensory modality. In chapter one, I explored this question by systematically examine numerosity representation across multiple dimensions. We not only use MVPA to examine the existence of a generalized number representation but also use RSA to capture the geometry of number representation in the brain. We found a set of overlapping brain regions, spanning from V3A to multiple IPS subregions and precentral area in prefrontal cortex that successfully encode numerical information in all three non-symbolic conditions. Cross-classification analysis further revealed a shared numerosity code across vision and audition when numerosities are presented using a similar temporal code. Using RSA, we further found an interesting posterior-to-anterior gradient in the IPS with numbers being encoded in posterior regions primarily relying on the senses while anterior region coding more for the format of numerosity presentation.

Previous studies also show that numerosity is processed in a hierarchical way in the brain, with attention progressively enhancing its representation along the dorsal visual stream (Castaldi et al., 2019). Moreover, a hierarchical organization was observed in the fronto-parietal regions from absolute to relative encoding of numerosity (Kido et al., 2025). Our results, in line with these studies, show a hierarchical organization within the parietal region, transitioning from a low-level sensory coding to a higher-level coding based on the temporal structure.

Our results revealed a shared numerosity code across vision and audition for sequential numerosity. Cavdaroglu et al. (2015) also examined sequential numerosity representations across these two modalities. Interestingly, they reported significant cross-modal generalization only in one direction: when the classifier was trained on auditory numerosities and tested on visual numerosities. Moreover, inspection of their confusion matrix showed that this effect was primarily driven by numerosity 5, which was the smallest numerosity in their stimulus set. Cavdaroglu et al.'s study is important for interpreting and contextualizing our results. Although we found significant cross-classification for all numerosities tested, it is noteworthy that our study used a very small number range (2–5). As a result, the smallest numerosity in Cavdaroglu et al.'s study, 5, corresponds to the largest numerosity in ours. While we cannot test this directly, and the experimental designs differ across the two studies, it remains possible that generalized number representations emerge more robustly for small numerosities. A plausible explanation is that small-number representations are less susceptible to internal noise,

making it easier to align representations across modalities. This interpretation fits with broader findings in the literature on the distinction between subitizing and estimation. For instance, single-neuron recordings from the human medial temporal lobe have shown different neuron activities for small versus large numbers: neurons exhibited superior tuning selectivity and surround inhibition effects (suggestive of a mechanism to increase selectivity) for small numerosities, whereas tuning selectivity decreased beyond four items, consistent with a ratio-dependent estimation system (Kutter et al., 2023). Future research should therefore investigate how the number range influences the emergence of generalized numerosity representations across modalities.

While we acknowledge the importance of number range in shaping a generalized number representation, we do not intend to suggest that our findings are limited to small number ranges. Although our study focuses on relatively precise numerosity processing and involves very low quantities, the network that we identified for the three types of non-symbolic numerosity seems to largely overlap with other results obtained with larger numerosity ranges (Castaldi et al., 2019; Fornaciai et al., 2017; Harvey et al., 2017). In our design, we also minimized the influence of counting using specific stimuli and experimental instructions. Our results indeed did not show the left-lateralized activation that is usually observed in exact numeral counting tasks (Dehaene et al., 1999; Piazza et al., 2006). Therefore, we believe that it is unlikely that our results are limited to precise numerosity processing (i.e., subitizing), but are likely to generalize to higher numerosity ranges. However, future studies are needed to better understand whether the organization of numerosity that we observed in the current study exist in both estimation and precise processing stage.

One recurring issue in MVPA and cross-classification studies is that cross-classification often works only in one direction. For example, the first study to use MVPA to compare neural representations of symbolic Arabic digits and non-symbolic dot arrays found that generalization occurred only from digits to dots (Eger et al., 2009, see figure S4.1). The authors explained this asymmetry by suggesting that non-symbolic numerosity, as an evolutionarily older representation, is encoded by a larger population of neurons. Within this population, only a subset gradually learns to represent symbolic numerosity, while the rest remain unresponsive to symbolic numbers. Consequently, generalization is possible from symbolic to non-symbolic representations (a smaller neuronal group to a larger one), but not the other way around. Similar one-directional generalization has been reported in Cavdaroglu's study and in the present work (Cavdaroglu et al., 2015). In both cases, generalization was observed when classifiers were trained on auditory numerosities and tested on visual numerosities, but not vice versa. In the current study, some brain regions showed this pattern, while others exhibited the reverse direction. However, unlike the case of symbolic versus non-symbolic numerosity, it is difficult to explain these findings using the same evolutionary argument, since auditory and visual numerosities do not have a clear "older" versus "newer" distinction. A detailed analysis by Van Den Hurk and Op De Beeck (2019) demonstrated that asymmetry does not necessarily imply that the brain encodes one stimulus type differently or "prefers" one direction of generalization. Instead, their

simulations show that purely data-driven factors are sufficient to produce asymmetry, without the need to invoke evolutionary or neurocognitive explanations. For example, differences in signal-to-noise ratio (SNR) play a key role: generalization works best when training on the noisier dataset and testing on the cleaner dataset, but not the reverse. Further research is therefore needed to disentangle whether cross-classification asymmetry reflects genuine high-level cognitive mechanisms or is primarily driven by such data-related factors.

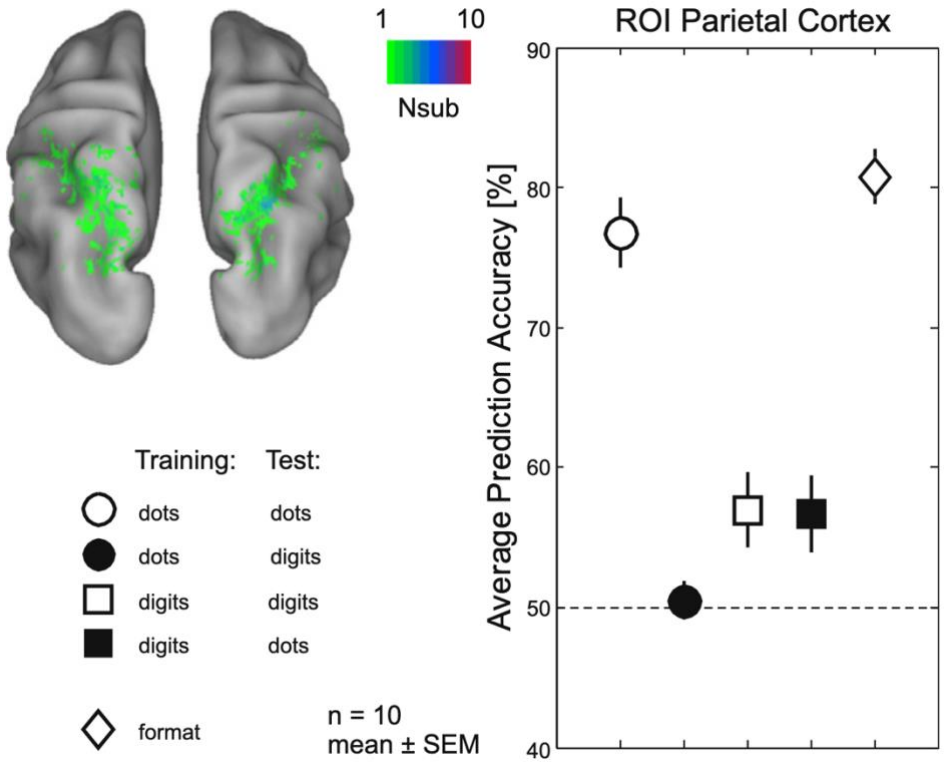


Figure 4.1. Cross-classification between dot and digit stimuli revealed successful decoding only in one direction, which is when the classifier was trained on digits and tested on dots (from Eger et al., 2009). The surface mapping gives an illustration of the regions included and the across-subject overlap of voxels (color coding indicating the number of subjects activating the corresponding voxel).

We found a generalized representation for numbers across sensory modalities, but only when they shared a common temporal code. In contrast, no generalization was observed across different presentation formats, even when they originated from the same sensory

modality. Although this pattern has not been explicitly reported before, previous studies offer indirect hints. For example, Nieder (2012) demonstrated that single neurons in the primate brain encode numerosity independently of sensory modality, revealing a supramodal neuronal code for number. In their work, rhesus monkeys discriminated auditory (sound pulses) and visual (dot sequences) numerosities in a delayed match-to-sample task while neuronal activity was recorded in the lateral prefrontal cortex (PFC) and ventral intraparietal sulcus (VIP). Neurons in both regions were tuned to specific numerosities, with subsets responding to both visual and auditory quantities, indicating modality-independent coding. In contrast, Ditz & Nieder (2020) examined how crows represent numerosity across different presentation formats and found a two-stage process: during sensory encoding, neurons responded in a format-dependent manner, whereas a format-independent, abstract numerical code emerged only during the memory delay period. This suggests that cross-format generalization requires an additional normalization stage. Given that their task involved active comparison across formats, it is also possible that such normalization only occurs when explicitly required by the task demands. However, no previous work has directly compared both cross-modal and cross-format numerosity within a single experiment. The present study is the first to do so, showing generalized cross-modal but not cross-format representation. This finding, combining with previous studies, might suggests that cross-modal numerosity generalization arises naturally, while cross-format generalization might rely on higher-level normalization processes that were not engaged in the present study. It is important to note, however, that the absence of cross-format generalization represents a null result and may reflect methodological limitations rather than a true lack of neural generalization. Further research will be needed to clarify this issue.

The specific localization of the hierarchical transition, particularly the primarily format-based processing in the anterior parietal subregion hIP2, is intriguing. A previous study investigated the interaction between numerosity and time perception in parietal cortex (Hayashi et al., 2013). A key region identified as critical for modulating the influence of numerosity on time perception is the right intraparietal cortex (IPC), which is anatomically close to the hIP2 region identified in the current study. Notably, disruption of the right IPC has been shown to disrupt the interaction between numerosity and time by amplifying the effect of numerosity. Given that hIP2 plays a critical role in aligning temporal numerical representations in the current study, one possibility is that this aligned organization of temporal numerosities may further influence the integration of magnitudes when considering both numerosity and time (Harvey et al., 2020).

The non-symbolic stimuli used in the present experiment were carefully controlled for low-level visual features. As a result, for sequential presentations, the timing of individual stimuli varied across numerosities and conditions. Due to these complex stimulus durations, it was difficult to compute reliable reaction times for participants' responses. In addition, only about 10% of the trials required an explicit behavioral response, making it challenging to obtain a sufficient number of trials for robust behavioral analyses. The relationship between decodable activity patterns in the brain and behavioral numerical proficiency has

been explored in several studies (Lasne et al., (2019); Wilkey et al., 2020; Pennock et al., 2021). For instance, Lasne et al. (2019) examined how the precision of behavioral numerosity discrimination relates to neural activity patterns. Participants first completed a delayed numerosity comparison task outside the scanner, and then performed a similar task during fMRI acquisition. Their results showed that decoding accuracy in the parietal cortex, but not in the early visual cortex, was correlated with behavioral numerosity discrimination. These findings suggest that the parietal, rather than early sensory, cortex supports numerical representations that can be explicitly accessed for numerical judgments and behavior. In the current study, we observed an interesting dissociation within the parietal cortex: posterior regions were more sensitive to sensory modality, whereas anterior regions were more responsive to presentation format. A promising direction for future work would be to determine which of these neural patterns contribute most directly to behavioral numerosity discrimination.

While our study revealed an intriguing organization of numerosity in the temporal domain, it left the organization of numerosity processing in the spatial domain less clear. Spatial numerosity engages distinct processing, such as visuospatial processing, which differ from those involved in temporal numerosity (Anobile et al., 2018). Specific brain regions, including the PSPL, known for encoding visuospatial representations (Fink et al., 2000; Szczepanski et al., 2010), are more closely associated with spatial rather than temporal numerosity (Cavdaroglu & Knops, 2019). Furthermore, a cross-modal adaptation study demonstrated that the numerosity adaptation effect works in one direction for spatial and temporal numerosity but not in the reverse, suggesting an asymmetric in their neural organization (Arrighi et al., 2014). However, spatial numerosity appears to be represented exclusively in vision rather than audition, due to the strong limitation of auditory spatial source localization (Zhong & Yost, 2017). Consequently, our study was unable to exhaustively examine the organization of spatial numerosity across different sensory modalities. Future study could consider other modalities, such as tactile modality, that could represent numerosity in both the spatial and temporal domain (Gallace et al., 2007). This would allow to investigate whether the brain organizes spatial numerosity similarly to temporal numerosity, as well as the relationship between them.

Numerosity is an evolutionary ancient ability deeply rooted in biology (Harvey et al., 2017; Lorenzi et al., 2025). However, numerosity perception is also highly influenced by culture and education due to the intensive numerical learning and experiences in human societies (Ansari, 2008). Research including neonates, indigenous people and species ranging from insects to primates to aim to investigate the role of those influences (Andreas Nieder, 2018; Bortot et al., 2019; Brannon & Terrace, 1998; Butterworth et al., 2008; Izard et al., 2009; Kobylkov et al., 2022; Lorenzi et al., 2024; O'Shaughnessy et al., 2023; Pitt et al., 2021). Nevertheless, the variability in stimuli, tasks and methods used to study numerosity in different species complicates the comparison of findings (Harvey et al., 2017). A unified method across different groups and species is crucial for enabling comparisons and increasing our understanding of how numerosity is processed independently of cultural and educational factors. We propose that the RSA approach used

in the current study could represent a promising tool to reach this goal. RSA does not focus on direct activity patterns but instead build a structure that capture the relative (dis)similarity among conditions (Kriegeskorte & Kievit, 2013). This structure is abstracted from the actual neural activity signals, allowing the comparisons of brain activity across models, imaging techniques, demographic group and even species (Kriegeskorte et al., 2008; Nili et al., 2014). Despite its potential, RSA has only rarely been applied to numerosity research. For example, a recent study combined ultra–high-field (7T) fMRI with RSA to investigate how the brain encodes internally generated numerical outcomes during approximate calculation (Czajko et al., 2024). Participants viewed a dot array, performed a mental arithmetic operation (multiplication or division by 2 or 4), and held the result in memory. By designing separate theoretical models focusing on the sample numerosity, operation, operand, and result, the authors were able to disentangle neural codes associated with each task component. They found that stimulus-evoked numerosities were represented along the dorsal visual and intraparietal pathways, whereas internally generated results were encoded in higher-level areas such as the angular gyrus and lateral prefrontal cortex. This innovative combination of task design and RSA modeling illustrates the method's potential for advancing numerosity research. However, no study to date has used RSA to directly compare numerosity representations across different human groups. Future studies could thus employ RSA to compare brain activities from different groups collected by different imaging techniques with different models to investigate how the organization of numerosity processing is shaped by educational, evolutional and cultural factors.

One limitation of this study is that although we made substantial efforts to control low-level features and performed cross-decoding analyses on different subsets of stimuli, the fact that successful cross-decoding was observed only across temporal numerosity does not fully rule out the possibility that low-level features may still be contributing to the effect. This reflects a broader challenge in the numerosity field, where completely disentangling numerosity from its correlated visual or temporal features is inherently difficult. A second concern is that the observed activity may reflect an early stage of the accumulation process rather than genuine numerosity encoding. The accumulation stage produces a monotonic signal in which more items simply generate more activity, whereas true numerosity coding emerges only later, when this signal is transformed into a selectively tuned representation. Our univariate analyses did not show increasing activation with numerosity in the two sequential conditions, which is inconsistent with a straightforward monotonic accumulation process. However, we cannot fully exclude the possibility that some form of accumulation contributed to the observed effects. Future work could utilize computational modeling to characterize neural response profiles more precisely and clarify which stage of processing is being captured. Additionally, numerosity illusions such as the connectedness effect may help disentangle numerosity from confounding perceptual features.

4.2 General Conclusion

In conclusion, this thesis studies multi-sensory numerosity representation in the brain and, based on this multi-sensory nature, challenges the assumption deeply embedded in much of the numerical literature that numerosity is inherently tied to vision. In the first chapter, we investigated how numerosity representations from various sensory modalities and formats converge into a higher-level numerical representation in the brain, and revealing for the first time a hierarchical organization of numerosity across them. We observed a posterior-to-anterior gradient organization along the dorsal pathway, beginning with pure sensory processing in the early visual cortex, progressing with a mixture of processing of sensory and format information in the posterior parietal cortex and culminating to a primarily format-based processing in anterior parietal cortex. This hierarchical organization offers critical insights into the brain mechanisms dedicated to numerosity processing from various sensory inputs. Our study suggests that numerosity might not be abstracted into a unified, generalized representation by discarding all irrelevant physical properties, but instead maintains a distinction between spatial and temporal numerosity representations, potentially to gain more efficiency. This temporal organization of numerosity becomes most salient in anterior parietal, and it might play a role in transferring numerosity into action effectively. In the second chapter, we argue that, based on the multi-sensory nature of numerosity and its development in individuals without any visual experience, the number sense is a fundamental, modality-independent faculty of the brain. Vision, though often the most convenient channel, is not its necessary foundation.

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