Università degli Studi di Padova

Head Office: Università degli Studi di Padova
Department of Developmental Psychology and Socialization (DPSS)

Ph.D. COURSE IN: Psychological Sciences
SERIES XXXV

The role of continuous quantities in non-symbolic number processing: theoretical implications and methodological challenges

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Abstract

In recent years, the interaction between numerosity and continuous quantities has grown from a methodological nuisance to a theoretically relevant issue to understand the mechanisms of numerosity perception and representation, as well as to clarify the connection between basic numerical abilities and formal mathematical skills. This thesis explores the interplay between numerosity and continuous magnitude processing by investigating the role of spatial and temporal features in numerosity judgments. After a first overview of the relevant literature, we describe two studies where we introduce an innovative stimulus space inspired by a recently developed method to assess the influence of temporal information during sequential numerosity judgments. Based on this method, we present a study demonstrating that individuals do not rely uniquely on non-numerical information in temporal numerosity discrimination, but they can be significantly biased by temporal cues both in the visual and auditory modalities. Moreover, a second study shows that temporal biases emerge even in absence of an explicit conflict between magnitudes at the response-selection level, such as in numerosity estimation tasks, in support of theoretical accounts that assume a partial representational overlap between magnitudes, specifically for the temporal and numerical domains. A third study focuses on the investigation of non-numerical interference effects in developmental dyscalculia, to understand the specificity of the numerical difficulties displayed in this learning disability compared to domain-general deficits. We compared children with dyscalculia and children with average mathematical skills but similar visuospatial memory abilities in an explicit numerosity comparison task and a spontaneous categorization task assessing the saliency of numerosity and total surface area of the elements. We found in children with dyscalculia evidence of a reduced precision in discrimination without increased reliance on continuous features, suggesting a deficit in numerosity representation not necessarily linked with reduced filtering abilities. Finally, the last work introduces a new tool for generating non-symbolic numerical stimuli with precise manipulation of spatial visual features of the images. Specifically, through a user-friendly interface, the presented program aims at helping researchers with different levels of expertise to generate experimental sets with flexible and personalized characteristics, based on the specific experimental questions. Taken together, the original empirical studies and methodological innovation described in this work provide a multi-faceted contribution to understand the mechanisms of numerosity perception and the refinement of basic numerical skills.

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Synopsis

The current thesis presents three contributions related to the investigation of the relationship between numerosity and continuous magnitude processing, specifically exploring the interference of non-numerical temporal and spatial features on numerosity judgments.

The first part of the thesis will introduce the general framework where the current work originates. **Chapter 1** will offer a broad overview of numerical cognition, with a particular focus on numerosity representation, in the context of the Number Sense theory (Dehaene, 1997). The ability to rapidly assess and manipulate the numerical information present in the environment, shown by human and non-human animals, will be presented as an expression of the Approximate Number System, a specialized system characterized by an abstract code of numerical magnitude (Feigenson et al., 2004). A brief introduction to the most common methods used in the field will also anticipate the methods used in the experimental work of the following section. **Chapter 2** will then introduce the debate regarding the interplay between numerosity representation and continuous quantity processing, presenting the evidence demonstrating that numerosity judgments can be modulated by non-numerical quantities covarying with numerosity (Clayton et al., 2015; Gebuis & Reynvoet, 2012). The chapter will then focus on the competing theoretical proposals that have been offered to describe the interaction between numerical, spatial, and temporal processing, with alternative proposals claiming that interference between numerical and non-numerical magnitudes arises from a conflict at the response-selection level or suggesting a more prominent role of continuous magnitudes at the sensory extraction level or a commonality in representation (Gebuis et al., 2016; Leibovich et al., 2017; Walsh, 2003). The second part of the thesis stems from this unresolved debate, offering three different contributions to increase our understanding of the interplay between numerosity and continuous magnitudes from three different points of view.

In the first work, we tried to better characterize the effect of temporal magnitudes on different numerosity judgments in the healthy adult population. While spatial biases in visual parallel numerosity processing have been extensively studied, the impact of temporal features of the stimuli on numerosity judgments is still largely unknown. Specifically, current studies provide contradictory evidence on the existence and direction of interference effects from temporal quantities (e.g., duration, rate) on sequential numerosity perception (Dormal et al., 2008; Tokita & Ishiguchi, 2011). **Chapter 3** will then describe an online study in which we explored the impact of several temporal quantities in a non-symbolic sequential numerosity comparison task in either visual or auditory modality. To this aim, we introduce a novel stimulus space based on the adaptation of a recently developed methodological framework (DeWind et al., 2015) that allows to vary the temporal properties of sequences to assess their contribution to response and individuate potential non-numerical biases and strategies. Results suggest an interaction between temporal and numerical magnitude in shaping participants' numerical judgments, with a similar pattern in the two sensory modalities. **Chapter 4** presents a similar online investigation in which we assessed the impact of temporal quantities in a numerosity estimation task with either visual or auditory sequences. Using a similar method to the previous study we varied sequences of events in numerosity, Duration, and Temporal Spacing, aiming to better assess the direction of non-numerical biases using an unrestricted response. Results replicated the findings obtained with the numerosity comparison task in both sensory modalities, confirming a significant interaction between numerical and temporal information even in the absence of an explicit conflict in response selection. A discussion on the possible locus of interaction between magnitudes is then presented.

The second contribution focused on investigating the link between interference effects and mathematical learning deficits. Since numerosity representation has been linked to symbolic numerical skills (Chen & Li, 2014), the study of interference effects in numerosity perception can be useful to understand the role of basic number processing in the acquisition of formal mathematical abilities, both in typical and atypical development (Gilmore et al., 2013; Piazza et al., 2018). In particular, impaired numerosity perception in developmental dyscalculia has been interpreted as evidence of reduced representational precision in the neurocognitive system supporting non-symbolic number sense (Mazzocco et al., 2011). However, recent studies suggest that poor numerosity judgments might stem from stronger interference from non-numerical visual information, in line with alternative accounts that highlight domain-general impairments in executive functions and visuospatial abilities in the etiology of dyscalculia (Bugden & Ansari, 2016). In **Chapter 5** we present a study investigating the specificity of numerosity impairments, assessing the contribution of numerical and non-numerical features in an explicit numerosity comparison task and the relative saliency of number and total surface area in a spontaneous categorization task. Children with dyscalculia were compared to control children with average mathematical skills but matched for age, IQ, and visuospatial memory. In both tasks, children with dyscalculia presented weaker number-based responses compared to matched controls, with no evidence of a stronger influence of non-numerical information. Results are discussed in terms of a weaker number encoding in dyscalculia not necessarily related to reduced filtering abilities.

Finally, the third work focused on practical methodological aspects related to the generation of non-symbolic visual collections of elements. In particular, the growing awareness of the research community towards the interplay between numerical and non-numerical quantities has increased the necessity in many different sub-fields of numerical cognition for careful consideration of the continuous magnitudes of visual arrays. **Chapter 6** introduces CUSTOM GUIde, a MATLAB application for creating visual arrays of elements with precise and flexible control of several visual magnitudes of the arrays (e.g., the surface of the elements, convex hull) that we developed to help researchers in the generation of experimental sets. The chapter offers a description of the new program, based on the CUSTOM algorithms (De Marco & Cutini, 2020) but improved and equipped with a user-friendly interface to allow researchers with different backgrounds the creation of sets of single arrays or pairs of arrays and the generation of stimuli suited for a large range of empirical studies. An overview of the versatile applications of the program is offered through examples of how to easily replicate common methods from literature or generate personalized datasets to address novel research questions.

Last, **Chapter 7** will provide a more general discussion, drawing conclusions on the theoretical implications of the results of the experimental studies and the potential applications of the methodological work.

SECTION I

Theoretical Background

1 CHAPTER 1

Numerical Cognition

Numbers are abstract mathematical objects associated with symbolic numerals such as Arabic digits or number words. As such, they are cultural concepts learned through language and formal education, at the basis of sophisticated human inventions such as algebra and calculus. However, the word number is also used to describe discrete quantities, such as the cardinality of a set of individual objects. In this sense, number, also called numerosity, is a property of the environment.

1.1 An approximate sense of number

As first introduced by the mathematician Tobias Dantzig in 1930, humans and even some non-human animals are endowed with the ability to appraise the numerosity of sets quickly and effortlessly, an ability he called “number sense”. Originally, the author was referring to the exact enumeration of elements in small sets, similar to the process defined by the current term of “subitizing” (Kaufman et al., 1949). Nowadays, number sense is more generally used to describe the ability to intuitively attend, perceive, discriminate and manipulate numerical information (Dehaene, 1997).

In fact, when prevented from counting, individuals show to estimate the cardinality of a set in an approximate and imprecise manner (Dehaene, 1992) and the variability in the estimates increases with the numerosity to be estimated (Whalen et al., 1999; Jevons, 1871). More specifically, when asked to discriminate which between two sets contains more elements, individuals become faster and more accurate as the numerical distance between collections increases (numerical distance effect), while their response times and error rates worsen when, for equal numerical distances, the absolute numerical magnitude of the sets increases (size effect) (Moyer & Landauer, 1967). In other words, it appears that the discriminability between numerosities does not depend on their absolute distance, but rather on their relative distance (i.e., their ratio). This is in accordance with Weber’s law, stating that the minimum change in stimulus intensity that an individual can perceive (just noticeable difference or discrimination threshold) is a constant proportion of stimulus intensity (but see Testolin & McClelland, 2020).

According to the most credited theory in numerical cognition, the ability to discriminate and estimate numerosity without counting is thought to rely on a nonverbal mechanism, called the Approximate number system (ANS), consisting of an analog representation of numerical magnitude (Feigenson et al., 2004). This representation is conceptualized as distributions of activation mapped on an internal continuum, often referred to as a "number line", with two competing mathematical formulations. The first one models numerosity distributions as linearly spaced and defined by a variability proportional to numerical magnitude (Scalar variability model), so that large numerosity distributions are characterized by a progressively larger overlap that increases the likelihood of confounding nearby numerosities (Gallistel & Gelman, 1992). In the second model (Logarithmic model), numerosity curves are characterized by equal noise, but they are compressed in a logarithmic scale, resulting in a similarly larger overlap between the distributions of larger numerosities (Dehaene & Changeux, 1993).

Despite the different mathematical definitions, these two formal models make similar psychological predictions compatible with the described signatures of numerosity processing, and they have therefore been often used interchangeably in the literature to model response accuracy in psychophysical tasks. However, it must be noted that neurobiological evidence in human and non-human animals favors the idea of a compressive scaling of numerosity representation (Dehaene, 2003; Nieder & Miller, 2004; Piazza et al., 2004).

More generally, numerosity perception is believed to rely on an accumulator process that, after object identification, sums the input items normalizing their physical properties, resulting in an approximate estimate of numerosity irrespective of their position and dimension (Dehaene & Changeux, 1993; Nieder, 2016).

1.1.1 Measuring number processing

As previously described, in both conceptualizations of the ANS, the discriminability between two numerical magnitudes depends on the overlap between their distributions. More specifically, we can take the width of the Gaussian curves (or a scaling factor of the width, in the linear model of the mental number line) as the noise in the approximate representation (Dehaene, 2007). This is referred to as the internal Weber fraction (w) and it is taken as a measure of number acuity, an indirect index of the quality of the underlying numerosity representation (Halberda & Odic, 2015).

Behaviorally, the Weber fraction can be estimated from performance in basic numerosity judgments. One of the most common tasks used in this field is the numerosity discrimination (or comparison) task, which consists in presenting participants with pairs of sets of items, varying in their numerical ratios, and asking them to indicate which set contains more. Variants of this task include the comparison of single sets with an internal reference or reporting if two sets contain the same number of items, also called match-to-sample task.

An alternative method relies on asking participants to estimate the number of elements in sets by providing verbal labels (numerosity estimation task or numerosity-labeling task). As previously introduced, in this type of tasks participants' estimates become progressively more variable as the target numerosity increases, with variability increasing proportionally to mean estimates (i.e., scalar variability). Following the linear model of the ANS, the precision of the response is then represented by the Coefficient of Variation (CoV), the standard deviation of the estimates divided by the mean estimate, which is expected to be constant across target numerosities (Izard & Dehaene, 2008).

Another characteristic of numerosity estimation is the tendency of participants to largely underestimate the number of items in the sets, which increases for larger sets following a power-law function. However, it is assumed that this phenomenon is related to a mismatch in the translation from the internal activation of the number line to number words, due to a different scaling of the response criteria used by participants (Izard & Dehaene, 2008). In this line, estimation tasks that do not require verbal labels, like tasks where participants are asked to reproduce the number of elements, can elicit different patterns of responses (Crollen et al., 2011).

1.1.2 Subitizing, estimation, and texture ranges

In contrast with the described approximate and ratio-dependent performance, when individuals are asked to estimate or compare collections with a few items, up to four or six, they provide fast and errorless responses, an ability called "subitizing" (Kaufman et al., 1949). In this range, performance in numerosity comparison tasks usually violates Weber's law, and participants display similar accuracy and speed for different numerosities and ratios (Choo & Franconeri, 2014). Although in one view this phenomenon would be just a by-product of the scalar variability of the numerical representation, which predicts almost perfect discriminability for small numerosities (Cheyette & Piantadosi, 2020; Gallistel & Gelman, 1992; Sengupta et al., 2017), it has been proposed that "subitizing" might reflect an ability to precisely identify, localize and keep track of objects, related to a domain-general system called the Object Tracking System (OTS) (Feigenson et al., 2004; Trick & Pylyshyn, 1994). In support of this view, it has been shown that it is easier to compare two numerosities in the subitizing range compared to two sets with a similar ratio but higher magnitude (Revkin et al., 2008). In addition to this discontinuity in performance, several studies report that subitizing and estimation are differently affected by attentional load, with a major disruption of subitizing abilities due to an increase in attentional load (Burr et al., 2010), while larger numerosity processing appears less dependent on attentional mechanisms (Piazza et al., 2011). More specifically, the number of items that individuals can immediately appraise (i.e., their subitizing limit) seems connected to working memory capacity (Green & Bavelier, 2003).

A deviation from the typical patterns associated with numerosity estimation and discrimination has been identified also for high numerosities (hundreds of items). When sets of visual items are densely packed and the individual elements are difficult to perceptually segregate, participants appear to base their numerosity judgments on other aspects of the sets related to their density (Anobile et al., 2014). The switch between different mechanisms is suggested by changes in numerosity discrimination thresholds, proportional to numerosity for sparse arrays and increasing with the square root of numerosity after certain increments in the number of items or their density (Anobile et al., 2015). Moreover, a discontinuity between mechanisms is supported also by different patterns in reaction times (Pomè, Anobile, Cicchini, & Burr, 2019) and different susceptibility to attentional costs in sparse sets and texture-like arrays (Pomè, Anobile, Cicchini, Scabia, et al., 2019). Additional support for distinct mechanisms involved in different numerosity ranges comes from neuropsychological evidence. A recent case study reported that a patient with a brain injury leading to deficits in object-tracking presented not only increased thresholds in discriminating small numerosities below ten but also large numerosities above sixty, with a concurrent impairment in discriminating inter-item distance (i.e., density). Instead, they displayed a relatively spared performance for intermediate numerosities, further suggesting a partial independence of numerosity perception from attentional control (Anobile, Tomaiuolo, et al., 2020).

Altogether, these distinct characteristics suggest the implication of separate mechanisms differently or additionally involved in small number processing and in texture perception compared to numerosity estimation.

1.2 Origin and development of basic numerical abilities

The ability to attend to the numerical information in the environment is not uniquely human, but it is displayed by various animal species. Several non-human animals show spontaneous numerical assessments supporting adaptive behaviors such as joining a larger group of conspecifics as a defensive strategy (Ledesma & McRobert, 2008), maximizing foraging decisions (Giurfa, 2019), or evaluating whether to engage in fights (Benson-Amram et al., 2011). For example, Hauser and colleagues (2000) report that rhesus monkeys spontaneously discriminate small numbers of apple slices with discrimination ability up to 3 vs. 4 and 3 vs. 5. Similarly, mosquitofish tend to select the larger shoal if different groups present a large enough ratio (Agrillo et al., 2008).

As for humans, numerosity performance displayed spontaneously or by trained animals follows Weber's law. For example, rhesus monkeys tested in numerosity ordering judgment, with different ranges from 1 to 30 items, show response times and accuracy modulated by the numerical ratio (Cantlon & Brannon, 2007). Ratio dependency in numerosity-related responses is also displayed by other vertebrates and invertebrates (Agrillo et al., 2012; Ward & Smuts, 2007). Moreover, a dissociation in discrimination performance related to small and large numerosity has been individuated even in distant taxa like fish and primates or monkeys, suggesting their reliance on different systems for small and large quantities (Bisazza et al., 2010; Hauser et al., 2000). Taken together, these results indicate that basic numerical abilities in humans could be subserved by evolutionarily ancient mechanisms common to different animal species.

This view is further supported by studies on the numerical abilities of infants, which report that humans are sensitive to numerosity shortly after birth. Izard and colleagues (2009) showed that infants within one week from birth, after being familiarized with a stream of auditory syllables, presented a preference (longer looking times) for visual-spatial arrays with the same number of elements, discriminating large numerosity differing by a 1:3 ratio. This result was replicated in a later study, where newborns showed to differentiate a 1:3 ratio with large numerosities (4 vs. 12 or 3 vs. 9), although they failed when the comparison pair involved numerosity equal to 2 (Coubart et al., 2014). Altogether, these results from human infant studies and comparative cognition research have been interpreted as evidence that the mechanisms supporting numerical abilities could be innate. However, it must be noted that computational studies have revealed that numerosity representation can also emerge from simple architectural constraints and domain-general learning processes (Zorzi & Testolin, 2018).

Nonetheless, converging evidence suggests that numerical competence is present or emerges in early development and that it undergoes a rapid progressive improvement over the first years of life. Rudimentary discrimination of sets differing by a 1:3 ratio has been reported not only in newborns but also in 4-month-old infants, through habituation paradigms with redundant visual and auditory numerical inputs (Wang & Feigenson, 2021). Discrimination precision improves over development, with 6-month-olds successfully discriminating 1:2 ratios and 9-month-olds being able to distinguish sequences of tones differing by a 2:3 ratio (Lipton & Spelke, 2003; Xu & Spelke, 2000). Similar attention to the numerical information has been reported also using violation-of-expectation paradigms, in which 9-month-old infants show to look preferentially at unexpected results of additions and subtractions (McCrink & Wynn, 2004). This increase in numerical acuity has been reported to continue throughout childhood and adolescence (Halberda & Feigenson, 2008; Piazza et al., 2010; Sella, Berteletti, et al., 2016) with adult participants being able to discriminate numerosities up to 9:10 or 10:11 ratios (Barth et al., 2003; Halberda & Feigenson, 2008; Pica et al., 2004). Despite the methodological differences between studies in paradigms, stimulus modality, and manipulation of visual properties, which decrease the comparability of the presented results, the overall picture emerging from developmental studies suggests a progressive increase in the ability to discriminate numerosity during the lifespan.

1.3 Supramodal numerosity processing

Although prevalently investigated through the presentation of visual arrays of items, numerosity perception is not limited to dot arrays, but it concerns also other modes of presentations (time-variant or time-invariant, such as spatial arrays or temporal sequences of events) and other sensory modalities (visual, auditory or tactile).

We have already mentioned that even newborns and infants respond to numerosity integrating information converging from different modalities, for example showing, after familiarization with sequences of auditory stimuli, a preference for visual arrays with the same number of items (Izard et al., 2009; Jordan & Brannon, 2006). Recently, it has also been shown that infants can benefit from redundant information from different modalities, which increases discrimination precision (Wang & Feigenson, 2021). This ability to generalize or match numerical information across sensory modalities has also been reported in non-human animals such as rats (Church & Meck, 1984) and monkeys (Jordan et al., 2005, 2008).

Moreover, similarities in response to numerosity conveyed through different sensory modalities have been identified from infancy to adulthood. Lipton and Spelke (2003) report that 6-month-old infants can discriminate auditory sequences differing by a 2:1 ratio, similar to the threshold described in another study for a group of infants with the same age in response to visual arrays (Xu & Spelke, 2000). Other studies highlighted similar precision in the estimation of numerosity from visual or auditory sequences as well as for parallel visual arrays, both in children and adults (Anobile et al., 2018), and individuated in adult participants similar thresholds in the numerosity discrimination of auditory or tactile streams of events (Tokita & Ishiguchi, 2016). Moreover, both children and adults seem able to compare numerosity across different sensory modalities or modes of presentation without additional cost in performance or speed (Barth et al., 2005; Barth et al., 2003).

Additional support for the abstractness of numerosity representation, independent from modality and mode of presentation, comes from a line of research reporting adaptation effects to numerosity. Specifically, it has been demonstrated that individuals judge as more numerous visual arrays of elements preceded by arrays with small numerosities and perceive as less numerous arrays preceded by a large number of elements (Burr & Ross, 2008). This effect has been reported not only with visual arrays of items but also using sequences of flashes or tones, thereby suggesting that it is not modality specific. More importantly, it has been shown that adaptation occurs also across sensory modalities and generalizes across modes of presentation, so that repeated exposition to auditory sequences with high numerosity leads to underestimation of visual sequences, and adaptation to time-variant numerosity affects estimates of time-invariant stimuli (Arrighi et al., 2014). Interestingly, a similar distortion of perceived numerosity has been found also when numerosity judgments were performed after motor adaptation to a sequence of self-generated motor routines (i.e., finger tapping in mid-air), with fast tapping decreasing estimates of large numerosities and slow tapping leading to overestimation, with similar results in either simultaneous or sequential mode and both in the visual and auditory modality (Anobile, Arrighi, et al., 2016; Maldonado Moscoso et al., 2020; Togoli et al., 2020). This interaction between motor actions and numerosity perception further suggests a supramodal encoding of numerical magnitude constituting a link between perception and action (Anobile et al., 2021).

However, it must be noted that differences between sensory modalities and presentation modes have also been reported. For example, Tokita and colleagues (2013) found that adults are more precise in discriminating sequential numerosity in the auditory modality compared to the visual one, with an in-between performance for cross-modal comparisons. Differences between presentation modes have also been reported by the same authors, with higher precision in discriminating simultaneous arrays compared to visual sequences of events (Tokita & Ishiguchi, 2012).

In conclusion, although research with infants and adaptation studies point to a generalized mechanism to represent and process numerosity irrespective of modality and presentation mode, some discrepancies across sensory modalities suggest a distinct processing.

1.4 From numerosity to mathematics

Given the possible hereditary origin of the number sense, and more in general its non-verbal nature, it has been proposed that the approximate number system could play a scaffolding role in the acquisition of symbolic number representation and the construction of more advanced mathematical abilities (Piazza, 2010, for a review).

The idea that symbolic numerals might be grounded in approximate magnitude representations arises from evidence showing that ANS signatures such as size and distance effects are present also in tasks that involve exclusively symbolic numbers (Dehaene et al., 1990). This effect has been interpreted as direct access to the analog magnitude representation of quantity independently from format, as postulated by the Triple Code Model (Dehaene, 1992), or more specifically as a semantic mapping between numerals and approximate numerosity representation that individuals would form during the acquisition of counting (Gallistel & Gelman, 1992). However, the general underestimation shown by individuals in perceptual estimation tasks, when they are asked to assign a symbolic label to a non-symbolic quantity, suggests a more complex mapping between the two formats. Moreover, other authors have failed in finding psychophysical similarities between symbolic and non-symbolic processing (Sasanguie et al., 2017) and observed that individuals are slower and less precise when they have to integrate numerical information in symbolic and non-symbolic formats (Lyons et al., 2012; Marinova et al., 2020), suggesting a less immediate cross-format access (Leibovich & Ansari, 2016).

A more general supporting role of the ANS in the development of numerical competence is proposed by studies that relate inter-individual differences in numerical acuity and mathematical achievement, especially during development (Gilmore et al., 2010; Halberda et al., 2008; Libertus et al., 2011, 2013). The correlational nature of most studies leaves open the interpretation of this relationship. In fact, a bidirectional influence has been proposed, so that the acquisition of formal mathematical abilities and symbolic labels for number shows an impact on the performance in approximate tasks (Elliott et al., 2019; Piazza et al., 2013; Pica et al., 2004). Nonetheless, several longitudinal studies have more precisely identified numerical acuity in infancy as a predictor of later mathematical abilities during childhood, irrespective of other general skills such as IQ and verbal competence (Mazzocco et al., 2011b; Starr et al., 2013; van Marle et al., 2014). However, different studies suggest that such a relationship could be mediated by other performance predictors such as executive functions (Gilmore et al., 2013), which have been also related to the acquisition of mathematical skills (Cragg & Gilmore, 2014, for a review). Studies on the adult population also led to mixed results. While some found a significant relationship between numerical acuity and concurrent mathematical abilities (Castronovo & Göbel, 2012; Halberda et al., 2012), others report no relationship between the two (Anobile et al., 2018; Inglis et al., 2011; Starr et al., 2017). Recent meta-analyses report stable, although moderate associations between numerical acuity and mathematical abilities only during childhood, while the predictive role of basic symbolic judgments seems more stable also in adulthood (Chen & Li, 2014; De Smedt et al., 2013; Fazio et al., 2014; Schneider et al., 2017).

This open question extends further in the discussion regarding the etiology of the specific learning disorder with impairment in mathematics. This neurodevelopmental disorder, also known as Developmental Dyscalculia (DD), is characterized by persistent difficulties in the acquisition of mathematical and numerical skills that cannot be explained by a lack of adequate education and learning experience, intellectual disability, or sensory deficits (American Psychiatric Association, 2013). One view proposes that mathematical difficulties in DD could be related to a deficit in numerosity representation. Specifically, children and adolescents with DD have shown increased numerical distance effects (Mussolin, Mejias, et al., 2010; Price et al., 2007), higher thresholds in discriminating two numerosities (Decarli et al., 2020; Mazzocco et al., 2011a; Piazza et al., 2010), and a reduced precision in estimating non-symbolic numerical quantities (Mejias, Mussolin, et al., 2012) suggesting a noisier representation of numerical magnitude. On the other hand, other studies have failed to find differences between younger children with DD and their peers in non-symbolic magnitude judgments, reporting instead a reduced precision in the discrimination and manipulation of symbolic numbers (Iuculano et al., 2008; Rousselle & Noël, 2007). These results led to the proposal that difficulties in DD would emerge from a deficit in connecting numerical symbols with their semantic meaning (De Smedt & Gilmore, 2011; Vanbinst et al., 2014). Moreover, given the bidirectional influence between ANS and formal mathematical education (Piazza et al., 2013), in DD an initial deficit in linking exact symbols with approximate magnitude could prevent the refinement of the non-symbolic representation during development (De Smedt et al., 2013). Alternatively, different accounts relate mathematical and arithmetic difficulties to impairments in domain-general cognitive abilities such as working memory, visuospatial skills, or inhibition (Mammarella et al., 2018; Passolunghi & Siegel, 2004; Szucs et al., 2013), relating the low mathematical performance of DD on a continuum with the typical population (Mammarella et al., 2021; Peters & Ansari, 2019).

Reports on the association between basic non-symbolic numerical processing and mathematical skills have also inspired intervention studies that aimed at training the former in order to improve the latter. However, evidence on the efficacy of a training in non-symbolic numerical abilities to potentiate mathematical abilities is mixed. On one hand, computerized games with a partial focus on non-symbolic numbers have proved to be effective in enhancing symbolic numerical abilities in preschool children (Sella, Tressoldi, et al., 2016) and improving the overall number skills in children with DD and Down Syndrome (Sella et al., 2021; Wilson et al., 2006). Moreover, similar protocols based on practicing approximate calculation have led children with widely different cultural origins to improve their arithmetic skills (Hyde et al., 2014; Khanum et al., 2016). On the other hand, other studies on adults failed to find improvements in symbolic numerical abilities after training in approximate addition and subtraction (Szkudlarek et al., 2021), suggesting that training in approximate arithmetic might be more effective during development.

Taken together, results suggest that the approximate numerical representation could play a more important role during the initial acquisition of symbolic numerical concepts, with decreasing importance following formal education. However, the inconsistent results across studies on DD and regarding the relationship between non-symbolic and symbolic numerical processing in the general population are inconclusive regarding the foundational role of the ANS in the development of mathematical abilities.

1.5 Neural bases of number representation

Converging neuroscientific evidence has associated numerical processing with frontoparietal cortical networks (Nieder, 2005; Nieder & Dehaene, 2009). Piazza and colleagues (2004), using a functional magnetic resonance imaging (fMRI) adaptation paradigm, revealed a rebound effect in the hemodynamic response in the left and right intraparietal sulcus (IPS) selective to change in the numerosity of non-symbolic arrays of items, with a response proportional to numerical ratio, in line with the behavioral signatures of ANS. Similar regions had previously shown consistent activation in response to numerical information with modulations from numerical magnitude or distance, which led to the proposal that the IPS could be an important neural substrate supporting numerosity representation (see Dehaene et al., 2003, for a review). Indeed, recent studies using multi-voxel pattern analysis (MVPA) report successful decoding of numerical magnitude from visually presented non-symbolic numerical stimuli in parietal cortices (Bulthé et al., 2014; Cavdaroglu & Knops, 2019; Eger et al., 2015). Moreover, other studies using population receptive field (pRF) models describing population activity with Gaussian functions, showed tuned responses to passively observed numerosity in bilateral human posterior parietal cortex, with tuning width increasing with preferred numerosity (Harvey et al., 2013). Additional numerosity-selective neural populations with a topographic organization were identified in the association cortex, such as at the lateral temporo-occipital junction, at the superior end of the parieto-occipital sulcus, around the postcentral sulcus and in between the precentral and superior frontal sulci, suggesting a role of quantity information in several perceptual, cognitive and motor processes (Harvey & Dumoulin, 2017a). Furthermore, several studies report the involvement of the parietal cortex in numerical magnitude processing during different tasks such as approximate computations (Bugden et al., 2019; Castaldi et al., 2020).

Neurophysiological studies on animals further support the involvement of the parietal cortex in numerosity representation. Nieder and Miller (2004) report a parietal-frontal cortical circuit in the macaque with an initial response to numerosity in the posterior parietal cortex (PPC) and subsequent propagation in the lateral prefrontal cortex (PFC). The same group individuated, during a delayed match to sample task, numerosity selective neurons in the ventral portion of the parietal cortex (VIP), with an approximate response tuned to a preferred numerosity. Furthermore, numerosity-selective neurons were found also in the PPC and PFC of monkeys in the absence of an explicit numerical task

(Viswanathan & Nieder, 2013). Taken together, these neural parallelisms with humans support the idea of a primitive shared mechanism for numerosity representation (Nieder, 2016). However, it must be noted that both animal studies and some human studies found numerosity selectivity for a limited numerical range, usually not beyond the subitizing range (Harvey & Dumoulin, 2017a; Nieder & Miller, 2004). Moreover, IPS response to numerosity has sometimes been associated with response-related processes more than numerosity processing itself (Göbel et al., 2004; Cavdaroglu et al., 2015).

While decoding of non-symbolic numerosity has been successful in response to visual arrays of items, results are mixed regarding the existence of an abstract representation of numerosity, irrespective of presentation mode (temporal or spatial) and sensory modality. Some studies report similar modulation in human frontoparietal cortical networks from visual and auditory stimuli in simultaneous or sequential presentation mode (Castelli et al., 2006; Dormal et al., 2010; Piazza et al., 2006). Moreover, a neuronal population responding to numerical magnitude irrespective of mode of presentation has been reported in monkeys, alongside separate ones with selective responses for time-variant or time-invariant presentations of numerical stimuli (Nieder et al., 2006). Additionally, in the neural activity of crows between visual numerosity perception and reproduction, Kirschhock and Nieder (2022) individuated, in neural areas implicated in number processing and movement planning, a neuronal population whose activity was not only preferentially tuned to input numerosity but also predicting the number of pecks in the subsequent self-generated sequence, thereby reinforcing the hypothesis that numerosity perception could be tightly linked to action preparation. However, in humans, recent studies using support-vector classification (SVC) were able to significantly decode from parietal sites large numerical magnitude only for time-invariant arrays but not for temporal sequences. In addition, they failed in finding common neural substrates in response to visual arrays of elements and visual streams of events (Cavdaroglu & Knops, 2019). The same authors also failed in decoding numerosity-selective activation in response to sequential numerosity in both visual and auditory modality in the absence of an active task (Cavdaroglu et al., 2015). Instead, other authors individuated neural populations responding to haptic numerosity, showing a partial overlap with those individuated in response to visual stimuli. However, the different topographic organization of numerosity-selective responses in the two modalities suggests modality-specific populations as part of a supramodal functional network rather than a common representation (Hofstetter et al., 2021).

Mixed evidence also characterizes the debate on a shared semantic representation of numerosity for different formats (symbolic vs non-symbolic) and specific symbolic notations (Arabic digits and number words). A meta-analysis from Sokolowski and colleagues (2017) reports several regions, including bilateral inferior parietal lobules, left superior parietal lobule, and right superior frontal gyrus, showing overlapping activation from symbolic and non-symbolic numerical processing during explicit or implicit tasks. More specifically, several studies have reported that IPS shows adaptation to numerical information irrespective of presentation mode or format, and that adaptation effects occur also in cross-format conditions (Cohen Kadosh et al., 2007; Piazza et al., 2007). However, while overlapping activation in response to the two format is robust, a similarity at a more fine-grained scale is still debated. Eger and colleagues (2009) report an overall less accurate SVC decoding of small numerical magnitudes from activation in response to Arabic digits compared to visual arrays but found that pattern classification generalized from symbolic to non-symbolic format (although not vice-versa), suggesting a similarity in the neural patterns evoked by the two formats. Instead, Bulthé and colleagues (2014) did not find a generalization across formats in the classification of neural patterns in response to visual arrays and digits, neither in IPS nor in smaller regions individuated through searchlight analysis. Similarly, Lyons and colleagues (2015) could not detect, using representational similarity analysis (RSA), a significant relationship between the neural dissimilarity matrices derived from activation in response to symbolic and non-symbolic stimuli.

In sum, while parietal cortical regions have been consistently implicated in numerical processing, possibly as part of the neural substrates involved in approximate magnitude representation, neuroimaging studies are inconclusive regarding the existence of a common representation of numerical magnitude irrespective of its source and modality and regarding similarities in the processing of non-symbolic and symbolic numerical information, leaving open the debate on the existence of an abstract numerosity representation as postulated by the Number Sense theory.

2 CHAPTER 2

Number in Time and Space

Whether we are studying infants or adults' behavior, monkey electrophysiology, human neuroimaging, or computational models, one of the most pervasive challenges in studying the response to numerosity is the intrinsic correlation between the number of items and other perceptual features of the stimuli, namely continuous spatial magnitudes in case of visual (or tactile) arrays of items, and temporal features in case of sequences of visual, auditory or tactile events. More generally, it is believed that associations between the number of elements and other features occur with statistical regularity in the natural environment, so that in daily life the need to rely on numerical information independently from other quantities is rare (Gebuis et al., 2016). Critically, even in experimental setups, with carefully controlled stimuli, it has been demonstrated that it is mathematically impossible to vary the number of items of sets without changing other temporal or spatial features of the sets and that equating one feature inevitably causes others to vary proportionally to the number of elements (DeWind et al., 2015; Leibovich et al., 2017; Salti et al., 2017; Starr et al., 2017). Researchers in the numerical cognition field have always tried to develop elaborated manipulations and clever experimental designs to disentangle the effect of numerical information from other perceptual cues, but the natural and intrinsic relationship between magnitudes has also fueled theoretical accounts of magnitude processing alternative or complementary to the theory presented in the previous chapter, that try to explain and incorporate the intrinsic covariance between spatial, temporal and numerical domains.

2.1 Quantity interference in number processing

It is now widely accepted that in performing a numerosity discrimination task, individuals can be influenced by other characteristics of the sets to be compared. For example, when comparing which of two visual arrays is more numerous, children and adults are faster and more accurate when the numerically larger set is distributed in a larger convex hull (i.e., the smallest envelope that contains all the elements of the set), than if the most numerous array is displayed in a smaller area (Clayton et al., 2015; Gebuis & Reynvoet, 2012a; Gilmore et al., 2016). Other studies have also reported a significant influence of the dimension of the items, although the direction of the effect is not consistent (Clayton & Gilmore, 2015; Dakin et al., 2011; Gebuis & Reynvoet, 2012b; Leibovich & Henik, 2014; Starr et al., 2017; Yousif & Keil, 2020) and some studies have failed in finding a significant influence from item size (DeWind et al., 2015; Odic, 2018).

Less clear is the effect of time cues, such as duration, on numerical judgments. Some have reported a positive influence of the duration of the stimuli on the numerosity estimation of visual arrays (Javadi & Aichelburg, 2012). Experiments using dynamic arrays with time-variant presentation have shown an opposite effect of overestimation of shorter events (Lambrechts et al., 2013; Martin et al., 2017) or null results (Dormal & Pesenti, 2013). Although some inconsistencies can be related to differences in the nature of the stimuli, results are also mixed from investigations using a fully sequential presentation of events. Some studies did not report any interference on numerosity from the overall duration of the sequences (Agrillo et al., 2010; Dormal et al., 2006; Droit-Volet et al., 2003) while others reported that variation in duration and rate in the sequences leads to a decrease in discrimination performance and influences the estimation of the number of events in the sequences (Philippi et al., 2008; Tokita & Ishiguchi, 2011). In sum, further investigations are required to better clarify under which conditions numerical and temporal quantities interact, while interference across discrete and continuous magnitude processing is more evident between numerosity and spatial extent.

As previously introduced, the significant interference of continuous magnitudes during numerosity-related paradigms is relevant in the investigation of numerical magnitude processing and representation from a methodological point of view. Researchers in the field have always tried to control the non-numerical aspects of their stimuli, for example by varying continuous cues across trials or in different subsets to disrupt their correlation with numerosity (Piazza et al., 2004). However, this control method has been heavily criticized, since it assumes that individuals are not switching between different criteria attending to different features in different trials (Gebuis et al., 2016). It has been shown that spatial features can bias numerical decisions even when single features are not an informative cue, that is, when they do not correlate with numerosity in the entire set, and that congruency effects can arise from combinations of different cues (Gebuis & Reynvoet, 2012a). Moreover, it was reported that during numerosity decisions, individuals can be aware of alternative strategies and use them in a flexible way (Roquet & Lemaire, 2019). This concern was further supported by evidence showing that measures obtained with separate protocols are affected by the specific manipulation of the continuous features of the stimuli used, casting doubts on the reliability of past results based on numerical acuity measures and numerosity-related performance (Clayton et al., 2015; DeWind & Brannon, 2016). Most importantly, the growing body of evidence on the interaction between numerosity and continuous magnitudes revealed the necessity to better characterize this relationship to understand the neurocognitive mechanisms of number and quantity processing.

2.2 From sensory extraction to response conflict

The nature of interference effects in numerosity judgments is the subject of an open and passionate debate in the field, with separate proposals differing on the processing level at which interaction between quantities might occur.

A seminal model based on a neural network designed to explain numerosity perception is the Numerosity Detection System proposed by Dehaene & Changeux (1993). In this model, visual objects elicit activation in an input retina, projecting to a layer coding for object location that normalizes input size through lateral inhibition mechanisms. Normalized inputs would then elicit the activation of summation clusters, estimating the input numerosity in a threshold-like manner. Last, numerosity detectors, tuned to specific numerosity, would be activated based on the activity pattern of summation clusters. Later computational studies, revealing the emergence of numerosity representation in deep generative models of visual arrays of items, identified signatures of a normalization signal in inhibitory connections from units responding to the cumulative size of the items to numerosity detectors (Stoianov & Zorzi, 2012). This led to the idea that numerosity can be coded independently from other continuous properties of the sets. Moreover, they showed that degradation in the inhibitory connections worsened the numerosity discrimination abilities of the model on arrays where the cumulative area was equated (Cappelletti et al., 2014). In this vein, interference from the physical properties of the sets can occur due to inefficient mechanisms of normalization in the extraction of numerosity from the environment. However, it must be noted that this impaired mechanism was used to explain atypical performances in numerosity decisions, such as decreased discrimination in elderly individuals, rather than the typical numerosity response of healthy adults. Alternative models have been recently proposed for the extraction of numerical information from basic visual properties of the environment, such as aggregate Fourier power, that could explain modulation in numerosity perception due to variations in density (Paul et al., 2022). However, a fundamental issue in placing non-numerical biases at the sensory extraction level of visual numerosity is the flexibility that seems to characterize interference between numerical and non-numerical magnitudes, both in strength and direction. Moreover, biases in other sensory modalities or presentation formats remain unaddressed.

To account for all the interactions between magnitudes during quantity judgments, one credited theory proposes that separate magnitude representations could compete at response selection if they provide contrasting information, such as in incongruent trials (Dramkin et al., 2022; Gilmore et al., 2013; Nys & Content, 2012; Rousselle & Noël, 2008). This effect has been often compared to a Stroop-like conflict, in which the automatic reading of a word interferes with naming the word color, although the semantic meaning of the word is irrelevant to the task (Odic & Starr, 2018). At the neural level, it was recently reported that during a comparison task, congruent and incongruent trials elicit similar ratio-dependent responses at the parietal level, while differences between trials emerge as a difference in overall activation in task-related regions such as the inferior frontal gyrus, suggesting that congruency conditions would not differ in the underlying mechanism of numerosity extraction but in the recruitment of additional resources due to attentional and inhibitory control demands (Wilkey et al., 2017). At the behavioral level, DeWind & Brannon (2012) showed that trial-by-trial feedback during a numerosity comparison task diminished the influence of total surface area, in support of a malleable process subject to top-down control. Moreover, other research highlighted how biases from task-irrelevant cues or congruency effects between different magnitudes might emerge more prominently during comparison tasks than other tasks with a less explicit response conflict, such as estimation tasks or match-to-sample tasks (numerosity and size: Dramkin et al., 2022; Smets et al., 2015; duration and size: Yates et al., 2012). However, this theory is severely undermined by other studies that have reported a significant influence of spatial cues on numerosity estimation tasks, where a symbolic numerical response was required (Abalo-Rodríguez et al., 2022; Gebuis & Reynvoet, 2012b; Picon et al., 2019).

2.3 Indirect numerosity perception

Other theoretical frameworks interpret the malleable interaction between quantities as evidence that numerosity is not spontaneously and automatically extracted from the environment through a dedicated and specialized neurocognitive system, in direct contrast with the ANS account. Instead, they posit that numerical information is inferred from the combination of other continuous magnitudes. In one view, numerosity representation could emerge during development and language acquisition, through statistical learning of the correlation between non-numerical features (Leibovich et al., 2017). According to other perspectives, humans would not possess a numerosity representation at all, at least in the abstract sense proposed by the ANS, and numerosity judgments would entirely depend on the dynamic integration of non-numerical quantities (Gebuis et al., 2016; Gevers et al., 2016). More specifically, the *Sensory Integration Theory* (Gebuis et al., 2016) proposes that numerosity estimates are based on the simultaneous evaluation and integration of the sensory features present in the sets, which would contribute to the final estimate with a weight proportional to their saliency. According to the authors, this mechanism would explain the flexible pattern of non-numerical biases emerging across studies and in particular inverse congruency effects, following several reports of overestimation of sets of items with small item sizes (Gebuis & Reynvoet, 2012a; Pekár & Kinder, 2020). Moreover, a complete reliance on non-numerical features could also be related to the inaccurate performance of individuals in numerosity estimation tasks, due to the absence of an immediate reference (Gebuis & Reynvoet, 2012b; Izard & Dehaene, 2008).

In contrast to this view, several studies suggest that performance in numerosity comparison tasks cannot be reduced to a simple combination of the features characterizing the dimension or dispersion of the items in space (DeWind et al., 2015; Starr et al., 2017). Further evidence against an indirect extraction of numerosity comes from the effect of connectedness, so that visual arrays where items are connected by segments or clustered by enclosed shapes are systematically underestimated, compared to arrays of unconnected objects, even if the arrays present identical item size or density (Franconeri et al., 2009; He et al., 2009, 2015). Notably, this effect has been replicated also by studies that used open collinear inducers eliciting illusory connections between items, in which participants reported different numerosity estimates based on the alignment of the illusory contours in otherwise identical visual configurations (Adriano et al., 2021; Kirjakovski & Matsumoto, 2016). More importantly, different studies investigating the spontaneous saliency of numerical information in the categorization or reproduction of visual sets revealed that the performance of children, adults, and even non-human animals is better explained by their reliance on numerical magnitude than other visual features (Cicchini et al., 2019; Ferrigno et al., 2017; Roitman et al., 2007). Finally, in contrast with estimates entirely based on visual features, it was recently shown that in numerosity estimation individuals are minimally influenced by the physical properties of the array used to calibrate their numerical response (Abalo-Rodríguez et al., 2022).

Additional evidence for a direct and separate extraction of numerical information derives from electrophysiological and neuroimaging studies. Using a stringent manipulation of visual magnitudes and evaluating their contribution to neural activity during passing viewing of visual non-symbolic arrays, several EEG studies found visual evoked potentials modulated by numerosity as early as 75 ms in early visual areas (Fornaciai et al., 2017; Park et al., 2016), suggesting that numerosity processing occurs at early stages of the dorsal visual stream. Numerosity-related responses in the low-level visual cortex were also revealed by an event-related fMRI paradigm (DeWind et al., 2018) and were detected, independently from other visual features, with MVPA techniques (Castaldi et al., 2019). Furthermore, other studies implementing frequency-tagging EEG paradigms revealed occipital responses to changes in numerosity, rather than other visual magnitudes in adults (van Rinsveld et al., 2020), although this response seems to emerge in children between 3 and 10 years of age (Park, 2018).

Another result unexplained by the Sensory Integration theory is the bidirectional influence that characterizes quantities. Specifically, while there is evidence showing spatial and temporal interference during numerosity judgments, several studies highlighted the opposite interference of numerical magnitude during spatial or temporal decisions. For example, numerical information showed to bias participants' response in cumulative area discrimination, hindering performance in case of incongruent trials (Nys & Content, 2012) with a stronger bias in children, negatively influenced by the number of items in reporting which between two sets had more area (Tomlinson et al., 2020). Similarly, Dormal and colleagues (2006) report that participants make more errors and are slower in reporting which of two sequences lasts longer when the number of events is incongruent with the duration of the sequence. Overall, the presence of these reverse biases is not accounted for by the proposal of an indirect extraction of numerical information from other magnitudes.

2.4 A common magnitude system

In addition to the bidirectional interference between different quantities, a large body of evidence shows that there are strong similarities in the way we track numbers, space, and time. There is consensus that when individuals perform quantity judgments on either one of these domains, they display a performance that adheres to Weber's law, with scalar variability in estimates or ratio-dependent thresholds in comparing numerosities, spatial extents, or temporal durations.

This similarity is at the basis of a different framework proposing a common magnitude system involved in quantity processing of discrete and continuous spatial and temporal magnitudes. Walsh (2003) coined the term *A theory of magnitude* (ATOM), proposing that numerical, spatial, and temporal processing would be subserved by common parietal circuits and would share similar representational co-ordinates, due to the human need to integrate space, time, and quantity to produce action response. In the original conceptualization, the author specifically proposed that the inferior parietal cortex could be the neural substrate of a common magnitude system, operating from birth and progressively creating "apparent specializations" for each domain. Notably, this interpretation not only relates numerosity with spatial and temporal extent processing but also hypothesizes a common mapping of spatial, numerical, and temporal order and position, linked to the existence of spatial-numerical and spatio-temporal behavioral associations (e.g., SNARC and STARC effects) (Bueti & Walsh, 2009).

2.4.1 Generalized magnitude behavior

In support of a common magnitude system, comparable precision in the discrimination of number, duration, and surface area has been reported in infancy (Brannon et al., 2006; VanMarle &

Wynn, 2006; Xu & Spelke, 2000). Similar sensitivity across the different magnitudes has been reported also in children and adults, although with mixed results. Droit-Volet and colleagues (2008) report that in comparison tasks of numerosity, duration, and line length, all quantity discrimination tasks for both children and adults were characterized by similar and superimposed psychophysical functions, at least when all three domains were presented sequentially. However, several studies report differences between magnitude processing, with higher precision for area discrimination than for numerosity comparison (Leibovich & Henik, 2014) or the opposite (Tomlinson et al., 2020). Mixed results were obtained also by studies investigating the correlation of discrimination precision within individuals, with reports of similarities between the threshold of numerical, length or density discrimination (DeWind & Brannon, 2012; Tibber et al., 2012) while others failed to replicate such results (Nys & Content, 2012). A progressive differentiation of magnitude domains is suggested also by cross-sectional studies focusing on children from 3 to 11 years of age and adults that revealed different developmental trajectories of discrimination acuity across different domains, with a fast improvement in area and length discrimination and a slower growth in the comparison of temporal duration or density, with numerosity discrimination showing an intermediate trajectory (Odic et al., 2013; Odic & Starr, 2018).

As previously stated, a common metric in the representation of different magnitudes could also account for the bidirectional cross-domain interaction observed during quantity judgments. In this vein, congruency effects have been found since infancy. Newborns and infants show congruency effects between numerical, spatial, and temporal quantities that lead them to attend to changes in length, compared to familiarization, only when they are congruent with changes in the number of concurrent auditory streams of syllables or changes in the duration of a continuous tone, but show no preference for discordant changes (De Hevia et al., 2014; Lourenco & Longo, 2010). Moreover, it was shown that the strength of the size-to-numerosity congruity effect in infancy predicts later interference in numerosity discrimination tasks in preschool age, even controlling for domain-general predictors such as inhibition skills (Lourenco & Aulet, 2019). Additional support for a cross-magnitude interaction preceding response selection derives from evidence that adaptation effects generalize across domains. Several studies report that adaptation to long temporal durations (Togoli, Fedele, et al., 2021; Tsouli, Dumoulin, et al., 2019; Tsouli, van der Smagt, et al., 2019) or large areas (Zimmermann & Fink, 2016) leads to underestimation of a subsequent array of elements.

Other studies have highlighted a connection between magnitude processing and action, as proposed by the ATOM theory. As introduced in the previous chapter, some studies show that adaptation to numerical information can occur also when adaptors are self-generated actions, suggesting a common processing of numerosity deriving from external events in the environment or internal events (Anobile, Arrighi, et al., 2016). Crucially, similar cross-modal distortions were reported also in temporal and spatial domains. In separate studies, adaptation with fast (or slow) mid-air finger tapping led to an underestimation (or overestimation) of the temporal duration of subsequent visual stimuli and the length of the distance between two elements (Anobile, Domenici, et al., 2020; Petrizzo et al., 2020). A link between magnitude representations subserving action is further supported by studies reporting a bidirectional influence between number processing and hand-grasping movements. Some studies report a priming effect of Arabic digits on grasp hand shaping, with numerical magnitude influencing the speed and the extent of grip aperture (Andres et al., 2004; Namdar et al., 2014). Others showed a reverse priming effect of grasp movement on random number generation, with a spontaneous production of numeral congruent with the observed grip aperture (Badets et al., 2012). While these studies used symbolic numbers, a similar connection was recently revealed also in infants of 7-9 months, who showed to spontaneously associate large grip apertures to large non-symbolic numerical magnitudes during a habituation paradigm (Decarli, Veggiotti, et al., 2022).

Overall, all these results contribute to suggesting the existence of a generalized system involved in sensorimotor transformations of numerical, spatial, and temporal magnitudes to enable effective action planning and execution (Anobile et al., 2021). However, the flexible direction of cross-magnitude biases, sometimes causing reverse congruency effects, remains unexplained in the context of a common magnitude representation (Gebuis & Reynvoet, 2012a).

2.4.2 Shared neural circuits

In parallel to the behavioral evidence, a common ground between magnitudes is suggested also at the neural level. Several neuroimaging studies implicate partially overlapping neural circuits in parietal regions, including the intraparietal sulcus, in numerosity, spatial and temporal processing (Cohen Kadosh et al., 2005; Dormal et al., 2012; Fias et al., 2003; Hubbard et al., 2005; Pinel et al., 2004). Moreover, transcranial magnetic stimulation (TMS) on IPS has been associated with a disruption in the comparison of the numerosity of sets, the discrimination of length, and judgments of duration (Dormal et al. 2012; Hayashi et al., 2013; but see Dormal et al., 2008). Recently, a meta-analysis identified a frontoparietal network implicated in discrete and continuous magnitude processing, involving bilateral parietal lobules and the right medial frontal gyrus. However, additional regions showed independent activation for numerosity processing (Sokolowski, Fias, Bosah Ononye, et al., 2017). Moreover, it remains discussed if the spatial overlap between domains at a larger scale could still be the expression of distinct neural populations.

Evidence of a more fine-grained overlap in the mechanisms of magnitude processing has instead been reported in non-human animals. Single units recording in macaque monkeys revealed in their PFC and PPC neurons simultaneously encoding numerosity and length with a tuned response for both, but also distinct populations, although anatomically interleaved, separately encoding discrete and continuous magnitude information (Tudusciuc & Nieder, 2007; Tudusciuc & Nieder, 2009). Recently, topographic maps of tuned responses to object size have been reported also in humans (Harvey & Dumoulin, 2017a), in similar and partially overlapping locations to numerosity ones. In favor of a similar magnitude system and potentially explaining cross-magnitude interferences, significant correlations were identified between numerosity and size preferences in the overlapping areas. However, differences in the qualitative organization of the maps and partial independence between sites also suggest that while numerosity and size representation might share the same topographic organization, they could be the expression of different mechanisms. Moreover, a recent computational study showed that the interaction between numerical and non-numerical information might emerge from a partially shared representational space, and that cross-magnitude interference can decrease, through experience, due to a progressive disentangling in the encoding of numerical and non-numerical features (Testolin et al., 2020).

In sum, current behavioral and neuroscientific data show general similarities in the processing mechanisms of different magnitudes and cross-magnitude interferences unrelated to conflicts in response selection and potentially linked to sensorimotor integration. However, partially independent neural substrates implicated in the three domains and differences in the developmental trajectory of discrimination abilities do not support the literal predictions of the original ATOM proposal. To account for these discrepancies, more liberal interpretations of this theory are being forwarded, for example by hypothesizing a developmental differentiation of discrete and continuous magnitude processing from an innate generalized magnitude system (developmental divergence model of quantity representation; Hamamouche & Cordes, 2019).

2.5 The role of inhibitory control

Irrespective of the specific interpretation of the underlying mechanism responsible for the interaction between discrete and continuous magnitude processing, converging evidence suggests that, although interactions commonly occur also in adulthood, the strength of congruency effects decrease during development (Gilmore et al., 2013; Starr et al., 2017; Tomlinson et al., 2020). This result led all the different accounts presented in the previous paragraphs to consider a role of inhibitory and filtering processes in the development of basic numerical abilities. In particular, theories assuming an indirect perception of numerosity propose a fundamental role of cognitive control to increase the ability to integrate multiple continuous features to solve numerical tasks, instead of responding to single salient cues (Gebuis et al., 2016). Similarly, domain-general abilities such as inhibition and executive functions are likely to affect numerosity judgments even if we assume a late-stage interaction between separate magnitude representations.

This phenomenon is particularly relevant in the discussion regarding the connection between basic numerosity processing and more formal mathematical skills (see paragraph 1.4) since several studies suggested that correlations between numerical acuity and mathematical abilities would be an artifact mediated by the inhibitory control demands of numerosity-related tasks. In particular, some studies highlighted that the significant relationship between numerosity discrimination precision and formal math achievements holds only considering incongruent trials and becomes irrelevant when controlled for inhibitory skills (Fuhs & Mcneil, 2013; Gilmore et al., 2013). The involvement of inhibitory control in measuring, if not shaping, numerosity-related task performance, extends to research with clinical populations, such as developmental dyscalculia. Some studies claim that reduced numerical acuity in this population emerges only when numerical information conflicts with other magnitudes and that it would be a by-product of impaired executive functions or inhibitory skills (Bugden & Ansari, 2016; Szucs et al., 2013). However, contrasting data failed in finding a significant relationship between cross-magnitude interference and inhibition abilities in infancy and childhood (Lourenco & Aulet, 2019; Starr et al., 2017) and highlighted developmental improvements in numerical acuity irrespective of congruency (Wilkey et al., 2021). Notably, different filtering mechanisms have also been proposed in the refinement of numerical representation, not as domain-general abilities, but as a specific mechanism of quantity magnitude processing during development, supported by formal learning (Piazza et al., 2018). However, the specific mechanism responsible for this phenomenon is still being investigated.

Crucially, this unresolved discussion unveils the critical implications of cross-magnitude interference not only in the theoretical debate regarding the extraction and representation of numerical information, but also in the practical effort of outlining the typical and atypical development of basic numerical abilities. In this vein, understanding the mechanisms of numerical and non-numerical quantity processing becomes fundamental for the development of effective educational programs and interventions to enable or facilitate an effective acquisition of numerical and mathematical concepts.

SECTION II

Experiments and Works

3 CHAPTER 3

Measuring temporal bias on sequential numerosity comparison[1]

3.1 Introduction

To summarize what introduced in the previous section, humans are able to quickly appraise the number of elements in collections of items without counting, although in an imprecise manner. Response to the numerical information of the environment is displayed even by young infants (Xu & Spelke, 2000) and shared also with several non-human species (Agrillo et al., 2008; Bortot et al., 2019; Cantlon & Brannon, 2007) indicating an ancient evolutionary and ontogenetic origin of nonverbal number abilities. According to an influential theory, this intuitive number sense is supported by a specialized cognitive system called the Approximate number system (ANS), consisting of a noisy representation of numerical magnitude (Feigenson et al., 2004). The ANS is often modeled as a logarithmically compressed number line where numerosities are defined by partially overlapping Gaussian curves (Dehaene, 2003). This conceptualization originates from the evidence that behavioral and neural response to numerosity is dependent on the relative difference between numerosities (Weber's law) (Piazza et al., 2004). Notably, the precision of numerosity discrimination increases during development and it has been identified as a predictor of symbolic numerical abilities, suggesting a pivotal role of the ANS in the acquisition of formal mathematical skills (see Chen & Li, 2014, for a meta-analysis).

Non-symbolic number processing is also thought to be independent of presentation mode (time-variant or invariant; e.g., spatial arrays vs. sequences of flashes) or sensory modality (e.g., visual or auditory). Individuals show similar precision in discriminating or estimating visual collections of elements as well as sequences of visual, auditory, or tactile events, and they can compare numerosity across modality or presentation mode with little or no cost in performance (Anobile et al., 2018; Barth et al., 2003; Tokita & Ishiguchi, 2016). However, inconsistencies between different sensory modalities and modes of presentation have also been reported (Droit-Volet et al.,

[1] In collaboration with Simone Cutini, Alberto Testolin and Marco Zorzi

2008; Tokita et al., 2013). Nonetheless, the ability to integrate numerical information across sensory modalities seems to appear early in life, as infants and newborns match the number of visual collections of elements with the number of sounds in auditory sequences (Izard et al., 2009; Jordan & Brannon, 2006). A supra-modal encoding of numerical information is supported also by studies reporting effects of adaptation to numerosity that generalize across modality and presentation mode (Arrighi et al., 2014). Yet, neuroimaging studies are still inconclusive regarding a possible overlapping neural circuitry involved in numerosity perception across modality and presentation mode, especially in the absence of an explicit task (Cavdaroglu & Knops, 2019; Eger et al., 2003; Cohen Kadosh & Walsh, 2009; Piazza et al., 2006).

Another open question regarding numerosity perception concerns the relationship between discrete and continuous quantity processing. Converging evidence shows that visual numerosity judgments are influenced by spatial non-numerical quantities covarying with numerosity, such as total surface area, convex hull, or density, with a general overestimation of sparse arrays (Clayton et al., 2015; Dakin et al., 2011; Gebuis & Reynvoet, 2012a). According to one hypothesis, these interactions can be explained by a partially overlapping representation of numerical and non-numerical quantities (Walsh, 2003), subserved by shared neural resources (Sokolowski et al., 2017, for a meta-analysis). Alternatively, another possibility is interference between competing representations at response selection level after an initial parallel processing (Nys & Content, 2012), as suggested by the variability of interference effects in different contexts (Dramkin et al., 2022). Crucially, some authors explain this dynamic effect of visual cues as evidence that numerical information would be indirectly extracted by weighting non-numerical quantitative information, proposing that numerosity responses could be entirely driven by non-numerical features (Gebuis et al., 2016; Gevers et al., 2016).

Despite the lack of consensus on the underlying mechanism, the interplay between spatial extent and numerosity is well documented. On the other hand, the relationship between numerical magnitude and time is less clear. While few studies report significant interference from temporal duration during parallel numerosity comparison, with an overall overestimation of arrays displayed for longer intervals of time (Javadi & Aichelburg, 2012), the specific effect of time on static numerosity is difficult to disentangle from the possible role of exposure duration on performance (Inglis & Gilmore, 2013). However, studies using dynamic visual stimuli indicate that interference also emerges when duration and numerical information similarly accumulate over time (Togoli, Fornaciai, et al., 2021). For example, in numerosity discrimination tasks with arrays of appearing and disappearing dots, participants report a general underestimation of numerosity associated with longer stimuli duration (Lambrechts et al., 2013; Martin et al., 2017; but see Dormal & Pesenti, 2003).

Investigations based on a sequential presentation of events similarly suggest that duration can influence numerosity processing, but with inconsistent results on the direction of its effect. In a comparison task, Tokita and Ishiguchi (2011) found that participants perceive visual stimuli presented at shorter intervals as more numerous, while Philippi and colleagues (2008) found that faster presentation rates lead to the underestimation of visual, auditory, and tactile sequences. Moreover, a large portion of studies on developmental or adult populations failed altogether to find any interference from the duration of the stimuli on numerical judgments of sequences of visual or auditory events (Agrillo et al., 2010; Dormal et al., 2006; Droit-Volet et al., 2003). Finally, almost all studies limited their focus to the effect of the duration of the overall sequence or intervals between events, ignoring other potential interferences related to the duration of individual events.

From current evidence it is thus still largely unclear if temporal duration influences numerosity judgments and what could be the nature of such interference. The goal of the current study is then to investigate the interplay between numerical and non-numerical magnitude processing as well as to individuate potential relevant temporal cues in numerosity perception. To this aim, we adopted and translated to the temporal domain a recent framework (DeWind et al., 2015; Park, 2021) that proposes to systematically vary several features of the stimuli to quantify their separate contribution to response. Specifically, we performed two comparison tasks where participants were presented with sequences of either flashing dots or tones varying in number, duration, and distance in time, to shed light on how temporal cues impact numerical judgments. We conducted the experiments in both visual and auditory modalities in order to identify potential differences in strategy or in the extent of non-numerical bias, as well as numerical precision.

3.2 Materials and method

3.2.1 Participants

One hundred forty individuals took part in the study, with 69 participants completing the comparison task in the visual modality and 71 in the auditory modality. Due to the internet-based data collection procedure (see below), we first excluded 13 participants for which we could detect technical issues in the presentation of the stimuli and 28 participants who showed poor comprehension of task instructions (accuracy below 50% in practice trials), or low attention during the task, indicated by low accuracy in the easiest trials or a high number of outlier response times. Finally, 13 additional participants were excluded during the analyses (see Analysis section). The final sample was then composed of 41 participants (28 females) with a mean age of 24.12 (range: 20 – 36) for the visual modality and 45 participants (34 females) with a mean age of 22.47 (range: 20 – 31) for the auditory modality. This sample size provides 80% power to detect a 0.44 effect size with a 0.05 significance level in a one-sample t-test (R *pwr* package). Participants were students from the University of Padova that received course credits for their participation and volunteers recruited through social media. All participants gave their written informed consent. Research procedures were approved by the Psychological Science Ethics Committee of the University of Padova.

3.2.2 Stimuli

The stimulus dataset was built following the framework originally developed in the seminal work of DeWind and colleagues (2015), later described by Park (2021). As noted by the same authors, a sequence of events is characterized not only by the number of events, but also by other intrinsic (related to the individual events) and extrinsic (related to the entire sequence) temporal features (see Fig. 3.1). Specifically, we define mean event duration as the average duration of the individual events (MED) and total event duration as the sum of the length of all pulses (TED). Similarly, we refer to total stimulus duration as the time from the beginning of the first pulse to the end of the last pulse, intervals included (TSD), and mean event period as the total stimulus duration divided by the number of events (MEP). Based on the relationship between intrinsic and extrinsic features, on a logarithmic scale, we derived two dimensions orthogonal to numerosity, named *Duration* and *Temporal Spacing* (see Fig. 3.2). Mathematically, these two dimensions can be defined as:

$$log_2(Duration) = log_2(TED) + log_2(MED) \tag{3.1}$$

$$log_2(Temporal\ Spacing) = log_2(TSD) + log_2(MEP) \tag{3.2}$$

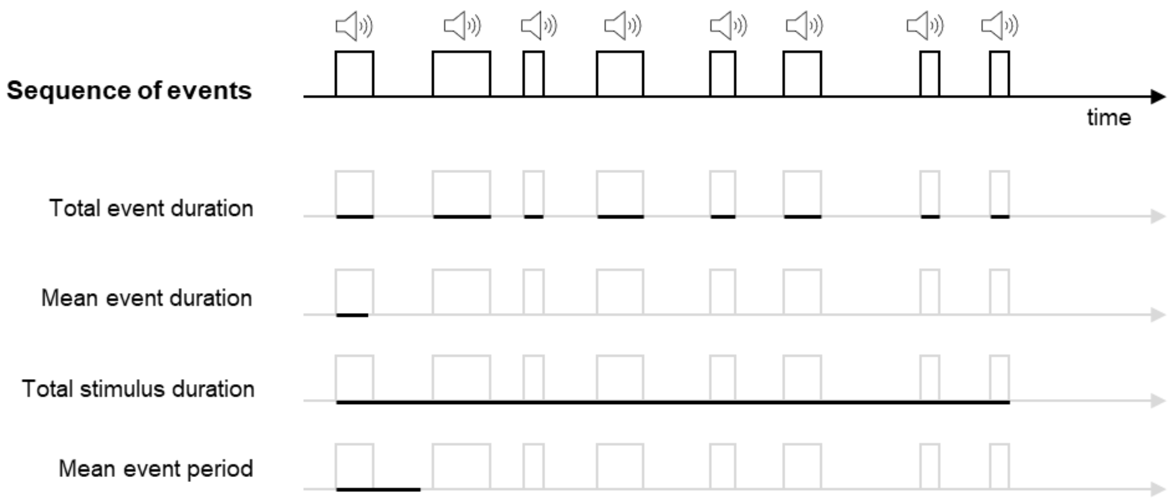

Figure 3.1. Temporal magnitudes in sequential non-numerical stimuli. Schematic representation of an example of an auditory sequence of events. Black sections of the sequence timeline highlight on separate rows the temporal features considered in the present study.

In this sense, Duration is the dimension that varies simultaneously TED and MED, keeping numerosity constant, while Temporal Spacing is the dimension that changes both TSD and MEP holding numerosity constant. For a fixed number of events, a change in Duration is associated with a change in the average temporal length of the events spread in a fixed interval, while a change in Temporal Spacing can be imagined as a change in their temporal distance, keeping a fixed average duration.

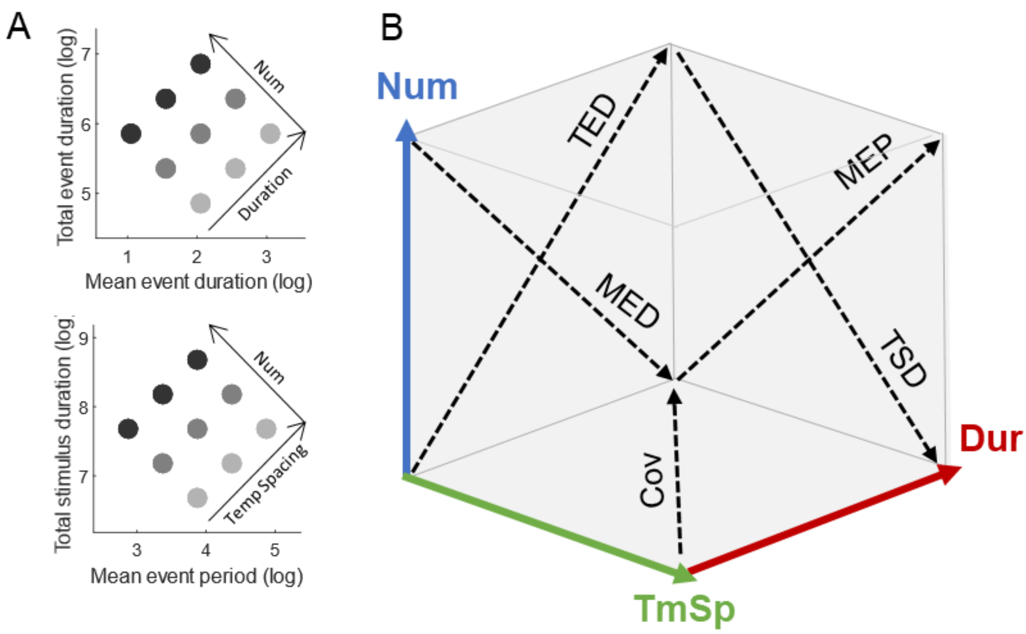

Figure 3.2 Relationship between extrinsic and intrinsic temporal features. (A) Depiction of the relationship between the considered intrinsic and extrinsic temporal magnitudes and numerosity. Duration is the axis orthogonal to numerosity representing a change in total event duration (TED) and mean event duration (MED). Similarly, Temporal Spacing is the axis representing a change in both total stimulus duration (TSD) and mean event period (MEP). (B) Schematic representation of the three-dimensional parameter space defined by taking numerosity, Duration, and Temporal Spacing as cardinal axes, inspired by Park et al. (2021).

We then varied independently Numerosity, Duration, and Temporal Spacing across 13 levels equally distant on a logarithmic space. Numerosity varied between 7 and 28. A similar maximum range of 1:4 was used for Duration and Temporal Spacing. Sequences were not homogeneous, so the individual duration of an event and the single interval between one pulse and the next were variable within the same stimulus, with events lasting between 2 and 16 frames (33 ms – 270 ms at 60 Hz) and empty intervals between 3 and 30 frames (50 ms – 500 ms).

An initial dataset of 500 pairs was created: to build each pair, we selected a ratio between 1:1.12 and 1:2 independently for Numerosity, Duration, and Temporal Spacing. Then, sequences were created from the combination of appropriate pairs of Numerosity, Duration, and Temporal

Spacing randomly selected from the 13 levels. For each participant, at the beginning of the experiment, a subsample of 120 pairs, randomly drawn from the initial dataset to obtain an equal range for the three orthogonal dimensions and a balanced distribution of the ratios in the entire dataset, was presented in a randomized order.

Stimuli were created in MATLAB (R2020a) (The Mathworks Inc., Natick, MA) as sequences of timestamps and instantiated online directly in PsychoPy/PsychoJS (Peirce et al., 2019) as sequences of visual or auditory events. Visual stimuli were sequences of flashes (white discs on a grey background) presented centrally on the screen. The dimension of the dot scaled with the resolution of the participants' screen. Auditory stimuli were sequences of sounds (pure tones at 400 Hz). At the beginning of the experiment, participants were allowed to adjust the volume as they preferred. Independently from modality, all durations were controlled in frames.

3.2.3 Task

All participants performed a computerized numerosity comparison task with either visual or auditory sequences of events (see Fig. 3.3). They were presented with pairs of sequences of rapid flashes or tones and were instructed to indicate which one contained more events by pressing the left and right arrow keys to select respectively the first or the second sequence. Each trial began with a fixation cross lasting 1 s, after which the two sequences were presented, one after the other, with a fixed interval of 2 s between the first and the second one. The duration of the sequences changed depending on the stimulus, ranging from 1.70 to 6.83 s. During the interval between the two sequences, a green fixation cross appeared in the center of the screen to indicate the end of the first sequence, to prevent participants from consistently overestimating the duration of the first stimulus. After the second sequence, a blank screen was presented until the participant response, followed by a pseudorandom blank inter-trial interval between 500 and 1500 ms. Participants did not receive any feedback based on their responses. Both tasks consisted of 120 test trials (around 40 minutes), divided into four blocks; participants could take a short break between blocks. Before the test phase, each participant completed five easy practice trials with a numerical ratio equal to 1:4, identical to the test block: in this phase, participants received feedback indicating if their response was correct or incorrect.

3.2.4 General procedure

The experiment was conducted online through Pavlovia, a hosting platform for running online PsychoPy tasks. Stimuli were generated and presented using PsychoJS, which allows online experiments to run with high timing precision (Bridges et al., 2020). Participants were instructed to perform the task in a single session, on a laptop or computer, in a quiet environment without distractions, and sitting approximately one arm from the screen. Differences in screen refresh rate between participants were accounted for *a posteriori*, and all participants with a refresh rate different from 60 Hz were discarded, independently from modality. In the case of the auditory comparison task, participants were free to use the speakers or headphones connected via cable to the computer. In the final sample, 18 participants performed the task using a headset or earphones, while the remaining ones used computer speakers.

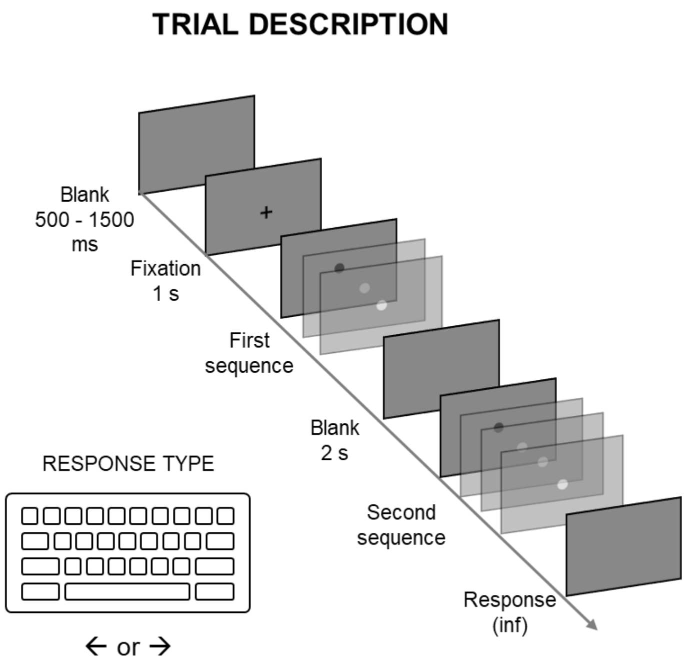

Figure 3.3 Comparison task. Schematic depiction of one trial of the sequential numerosity comparison task.

3.2.5 Data analysis

Before the analyses, we excluded participants that were not appropriately engaged in the task. Due to the reduced number of trials, we planned to consider the largest numerical ratio (1:2) as catch trials, discarding participants with an accuracy below 75% in the easiest condition. As previously reported, with this procedure we excluded 12 participants in each sensory modality. To exclude unattended trials, in both modalities we discarded responses recorded before 200 ms (anticipations) or later than 4 s (Halberda et al., 2012), planning to exclude participants if more than 20% of their total trials were discarded. Based on this cut-off, we excluded one additional participant in the auditory task.

We then modeled individual participant choice data (selection of the first sequence) with a generalized linear model (GLM) with binomial error distribution and probit link function, with regressors for the log ratios of Numerosity, Duration, and Spacing of the first and second sequences (see DeWind & Brannon, 2016, and Tomlinson et al., 2020, for examples of the same analysis method applied to parallel numerosity comparison). As previously mentioned, we excluded from subsequent analyses 8 participants for the visual task and 5 participants for the auditory task whose performance was not well described by the GLM, indicated by an R^2_{adj} below 0.2.

The combination of the estimated coefficients of the regressors (β_{Num}, β_{Dur}, and β_{TempSp}) is informative regarding the influence of numerical and non-numerical quantity on participant selections. If the response is entirely based on numerical ratios and is unaffected by non-numerical temporal features, it will lead to a positive coefficient for Numerosity, and coefficients for Duration and Temporal Spacing equal to zero. In this context, β_{Num} can also be considered an indication of numerical acuity, with larger values of the numerosity coefficients corresponding to a better performance in discriminating more difficult ratios. Instead, β_{Dur} and β_{TempSp} quantify the influence of temporal features (the duration of the events and their spread in time) on participant responses. A positive β_{Dur} is associated with an overestimation of long events, while a negative coefficient for Duration indicates that shorter events are perceived as more numerous. Similarly, a positive coefficient for Temporal Spacing indicates that events separated by longer intervals are perceived as more numerous, while negative β_{TempSp} is related to an overestimation of higher rates of events. We tested the significance of coefficients at the group level with one sample Student t-tests against zero.

Following the method from DeWind and colleagues (2015), the three coefficients can also be thought of as defining a discrimination vector in the parameter space. The vector norm depends on overall discrimination acuity, while its orientation is informative about the relevant features determining performance. In the case of a response unbiased by temporal magnitudes, the discrimination vector is perfectly aligned with the numerosity axis; significant non-numerical biases, instead, cause the vector to deviate from the numerosity dimension. Thus, irrespective of the orientation of the discrimination vector, its angle from the numerosity axis can be used to quantify non-numerical bias. Moreover, thanks to the linear relationship between the three orthogonal axes and the individual features (see the equations in Appendix I), the contribution of each temporal feature to participant choice can be estimated considering the proximity of the discrimination vector to the individual feature dimensions. If the point defined by the three coefficients is closer to a specific feature rather than the numerosity dimension, we can assume that the participant selection is based on that feature. For example, a participant consistently selecting the sequence with a longer total duration of the events would be characterized by a positive and equal coefficient for Numerosity and Duration (i.e., the vector would be aligned with the total event duration dimension).

From individual coefficient estimates, we thus estimated the non-directional angle, and we computed the vector projections onto the dimensions of the temporal features. We determined the closest to the discrimination vector at the group level with a series of paired t-tests. Non-parametric tests (Wilcoxon signed rank) were performed in case of violation of the normality assumption, and Bonferroni's method was used to correct multiple comparisons whenever necessary. We also assessed differences in acuity and bias between modalities with frequentist and Bayesian t-tests. In the latter case, we report the Bayes factor BF_{10}, expressing the probability of current data under H1 relative to H0 (Kass & Raftery, 1995). Values larger than one are in favor of H1 and values smaller than one are in support of H0. A BF between 1 and 3 (or between 1 and 0.33) can be considered anecdotal evidence, a BF between 3 and 10 (0.33-0.10) can be considered moderate evidence and a BF larger than ten (< 0.03) can be considered as strong evidence (van Doorn et al., 2020). Bayesian analyses were conducted using Jasp (ver. 0.12.1 2020), with default priors. Analyses were otherwise performed with MATLAB.

3.3 Results

Overall, accuracy (as the proportion of correct responses over the total number of trials) was above chance in both the visual (M = 0.80, range 0.68-0.88) and auditory modality (M = 0.81, range 0.65-0.93). Mean response times ranged between 457 and 1498 ms (M = 878 ms) in the visual modality and between 454 and 1506 ms (M = 1010 ms) in the auditory modality.

We then estimated the contribution of Numerosity, Duration, and Temporal spacing on individual participant responses. The GLM fit was significantly better than a constant model for all participants in the final sample of the visual comparison task (mean $R^2_{adj} = 0.44$, all $\chi^2 > 29.82$, all *p*s < .001) and the auditory comparison task (mean $R^2_{adj} = 0.46$, all $\chi^2 > 27.71$, all *p*s < .001). The individual coefficient estimates are presented in Fig. 3.4, with the lines representing non-orthogonal temporal features. At the group level, the model coefficients were significantly different from zero for Numerosity (M (SD) = 1.89 (0.53), $t(40) = 22.96$, $p < .001$, $d = 3.59$), Duration (M (SD) = -0.16 (0.32), $t(40) = -3.21$, $p = .002$, $d = -0.50$) and Temporal Spacing (M (SD) = 0.24 (0.40), $t(40) = 3.85$, $p < .001$, $d = 0.60$) in the visual modality. For the auditory task, β_{Num} (M (SD) = 1.95 (0.77), $t(44) = 16.90$, $p < .001$, $d = 2.52$) and β_{TmSp} (M (SD) = 0.31 (0.52), $t(44) = 4.07$, $p < .001$, $d = 0.61$) were significantly different from zero at group level, while the coefficient magnitude of Duration was not significantly different from zero (M (SD) = -0.05 (0.31), $t(44) = -1.16$, $p = .25$, $d = -0.17$) (see Fig. 3.5a).

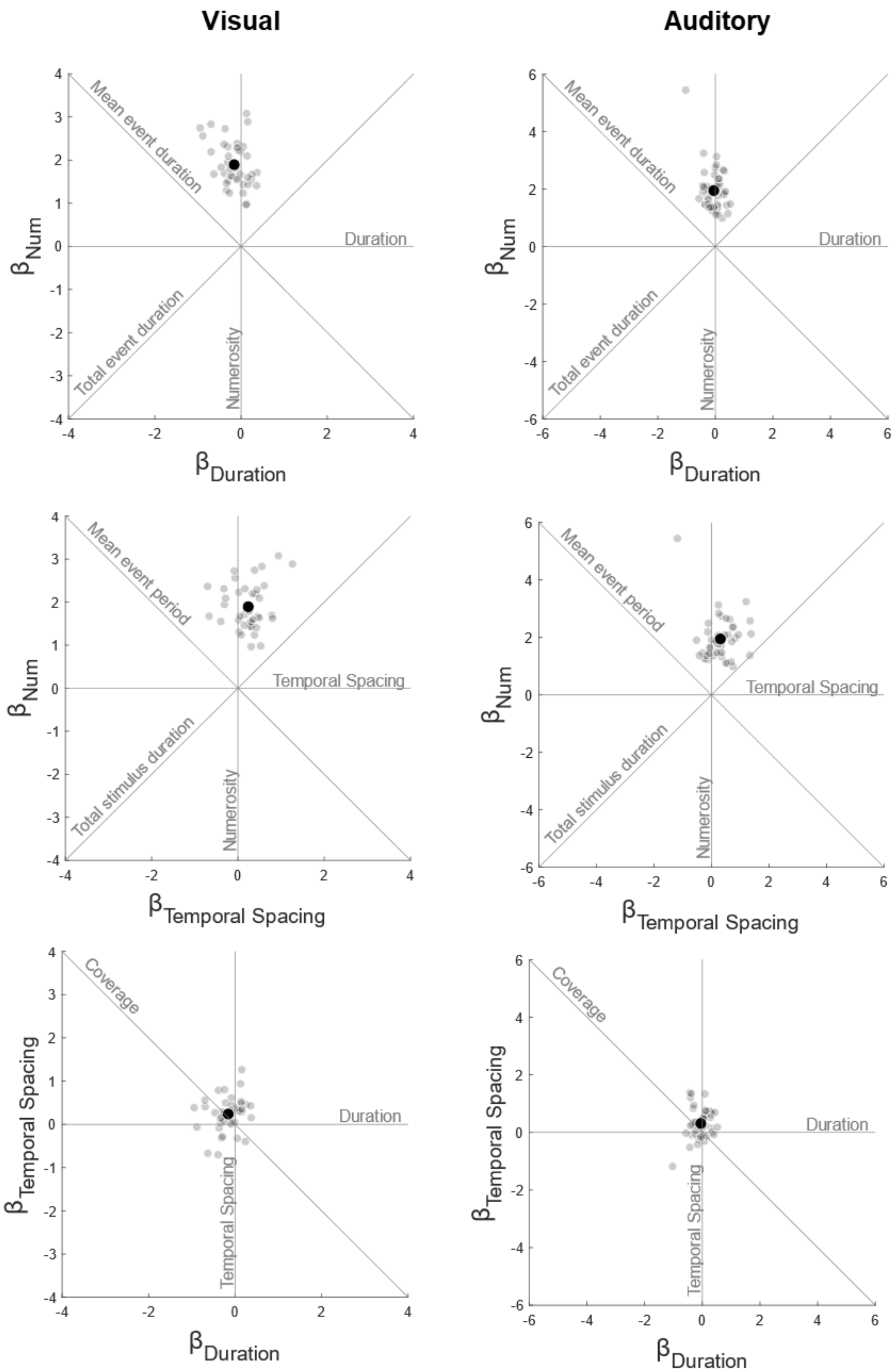

Figure 3.4 Results from GLM analysis of visual and auditory comparison tasks. Individual coefficient estimates are plotted in the three orthogonal planes defined by the cardinal axes, with visual modality in the left column and auditory modality in the right column. Grey dots indicate individual participants, while the black dots indicate the group means. Grey lines represent the temporal features.

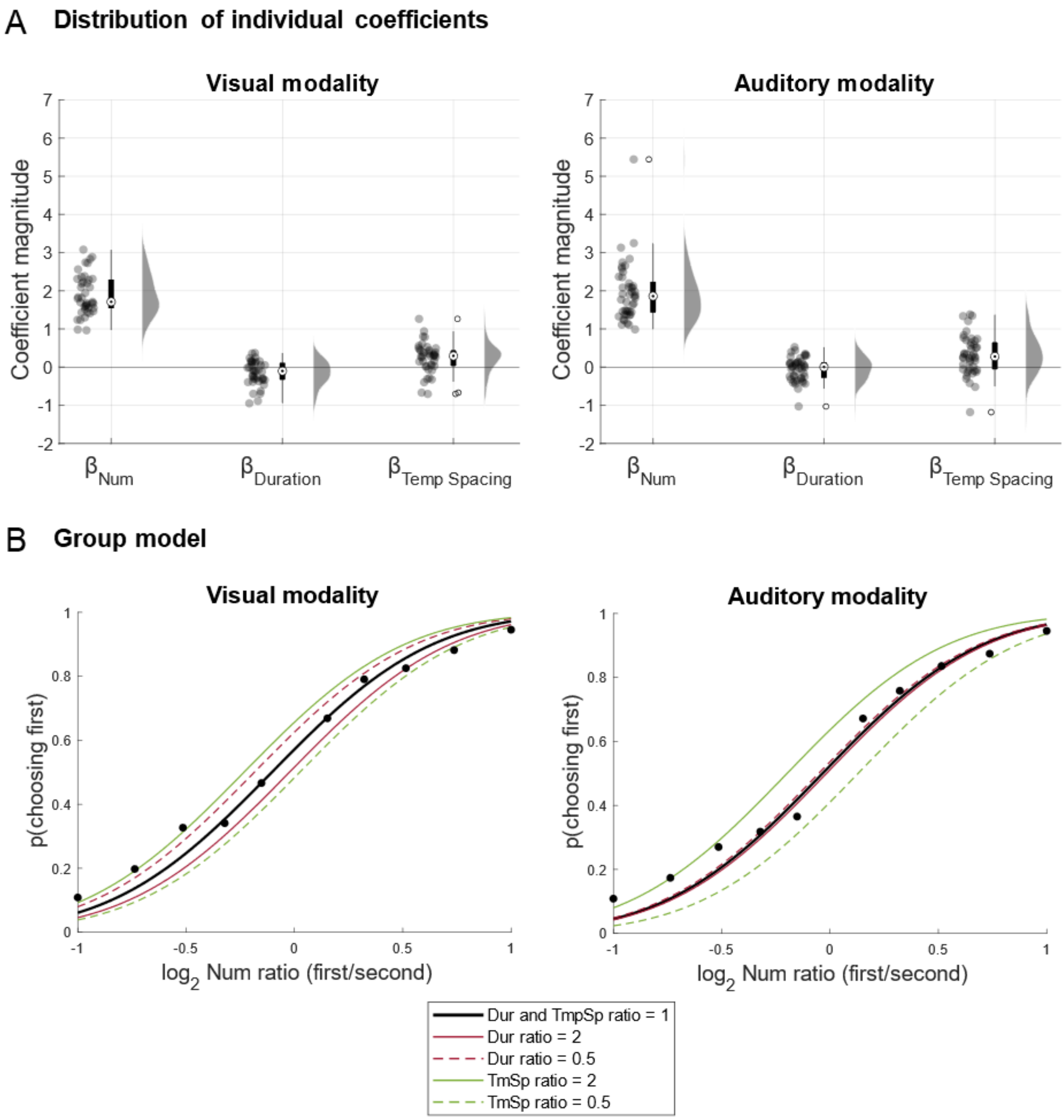

Figure 3.5 Group results of visual and auditory comparison tasks. (A) Distributions of individual coefficient estimates for Numerosity, Duration, and Temporal Spacing in the visual (left) and auditory modality (right). (B) Psychometric curves derived from the coefficients estimated at the group level. Black lines represent the predicted probability of choosing the first sequence as a function of the logarithm of the first to second numerical ratios when the ratios of Duration and Temporal Spacing are equal to 1. Red lines represent the same probability in trials with large ratios of Duration, with Temporal Spacing ratio equal to 1, while green lines are predicted curves for trials with large Temporal Spacing ratios, with Duration ratio equal to 1. In both cases, full lines represent trials where the first sequence has a larger Duration or Temporal Spacing than the second, and dashed lines indicate the opposite.

To confirm the results, we also fit a mixed-effect model on all data, separately for the two modalities, with similar fixed effects but including random intercepts and slopes for each participant. In the visual task, we found a significant β_{Num} (M (SE) = 1.73 (0.06), $t(4699) = 26.82$, $p < .001$), β_{Dur} (M (SE) = -0.14 (0.04), $t(4699) = -3.20$, $p = .001$), and β_{TmSp} (M (SE) = 0.22 (0.05), $t(4699) = 4.18$,

$p < .001$). In the auditory task, we found a significant effect of numerosity ratio (M (SE) = 1.75 (0.07), $t(5094) = 22.92$, $p < .001$) and Temporal Spacing ratio (M (SE) = 0.29 (0.06), $t(5094) = 4.45$, $p < .001$), while the effect of Duration was not significant (M (SE) = -0.03 (0.04), $t = -0.80$, $p = .42$). Psychometric curves obtained by the estimated fixed effect from these two group models are presented in Fig. 3.5b.

To assess the relevant dimensions in participants' selection, we then computed at the individual level the vector projections onto the non-orthogonal dimensions and tested if any other magnitude projection was higher than the numerosity coefficient. Differences between the numerosity coefficient and the feature magnitude projections are shown in Fig. 3.6. β_{Num} was higher than the projection on the Mean event duration, Total event duration, Total stimulus duration, Mean event period, and Coverage lines in the visual modality (Paired t-tests with Bonferroni correction: all ts(40) > 8.16, ps < .01, ds > 1.28) as well as auditory modality (Wilcoxon signed-rank tests with Bonferroni correction: all $W > 930.00$, ps < .01, $r > 0.79$).

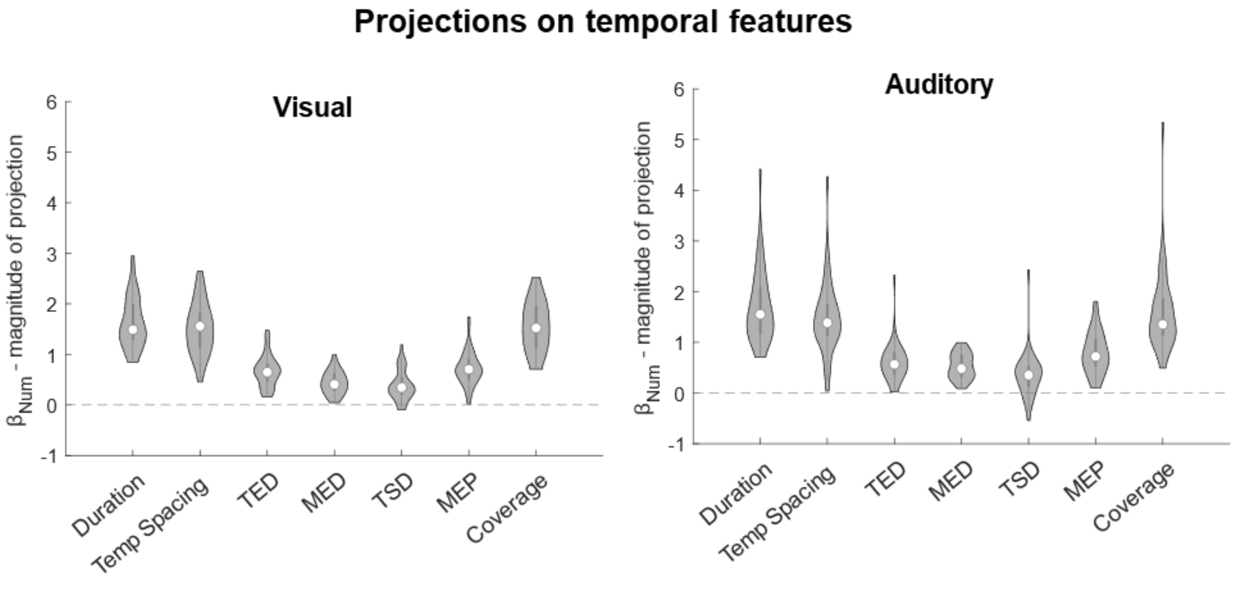

Figure 3.6 Results from projection analysis in visual and auditory tasks. Distribution of differences between the numerosity coefficient and the projection of the individual discrimination vector onto each temporal feature line for the visual (left) and auditory modality (right). Positive values indicate discrimination vectors closer to the numerosity dimension compared to the considered feature, while negative values indicate closer proximity to the specific feature.

We then compared the numerosity coefficient, as a numerical acuity indicator, in visual and auditory modality. The magnitude of the numerosity coefficient was not significantly different between sensory modalities ($t(84) = 0.38$, $p = .70$, $d = 0.08$, $BF_{10} = 0.24$ (0.03), moderate evidence). As for bias, we estimated the angle between the numerosity dimension and individual discrimination vectors as a non-directional measure of non-numerical bias (see Fig. 3.7). No difference emerged in the vector-line angle estimated in visual (M (SD) = 15.15° (6.59)) and auditory (M (SD) = 16.50° (9.40)) modality ($U = 941$, $p = .88$, $r = 0.02$, $BF_{10} = 0.29$ (0.03), moderate evidence).

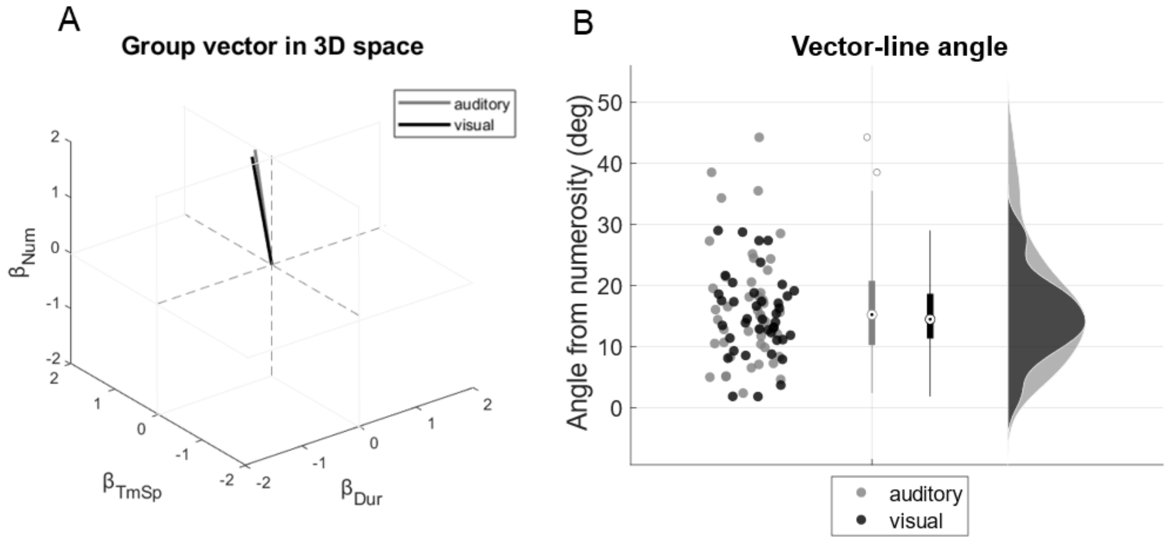

Figure 3.7 Comparison of vector-line angle between modalities. (A) Group discrimination vector in the three-dimensional parameter space (visual: black; auditory: grey). (B) Distribution of the angles (in degrees) between the individual discrimination vectors and the numerosity dimension in the two modalities (visual: black; auditory: grey).

3.4 Discussion

The present study aimed to assess the role of temporal information in numerosity perception and to individuate potentially relevant cues for sequential numerosity judgments in different sensory modalities. To this aim, we measured the contribution of numerosity and several temporal features on the discrimination of the number of visual and auditory events presented sequentially in time.

Specifically, we adopted the framework proposed by DeWind and colleagues (2015), which allows a quantitative estimation of how much participants rely on numerical and non-numerical information and to identify biases or entirely non-numerical strategies. This work extends the use of this method to the sequential mode of presentation of non-symbolic number stimuli and the investigation of numerosity perception in time.

Our results show that in both visual and auditory comparison tasks, adults are significantly influenced by both numerical and non-numerical information in their decision. The pattern of coefficients and the projection analysis indicate that, at the group level, our participants discriminated sequences prevalently based on the number of flashes and tones and were only marginally affected by temporal cues present in the sequences. The prominent numerical strategy adopted by our participants adds to a growing body of evidence suggesting that performance in numerosity tasks cannot be uniquely explained by the effect of non-numerical magnitudes (Abalo-Rodríguez et al., 2022; Cicchini et al., 2019; DeWind et al., 2015). More specifically, current results rule out that participants relied consistently on any single time cue considered. However, we note that the used method is not apt to individuate a more complex and dynamic integration of non-numerical magnitudes, proposed by some (informal) accounts as the basis of numerosity perception (Gebuis & Reynvoet, 2012a). To better address this issue, the illustrated model could be applied to electrophysiological and neuroimaging investigations. Previous studies suggest that early visual areas show specific sensitivity to numerosity (DeWind et al., 2018; Fornaciai et al., 2017; but see Park, 2018), but further evidence is needed to corroborate a direct and independent extraction of numerical information with other senses.

As mentioned before, our results also suggest that numerical discrimination is affected, to some extent, by task-irrelevant temporal characteristics of the stimuli. We found that in both modalities participants were particularly influenced by the temporal spread of the events, associated with an overestimation of the number of events in longer sequences with longer blank intervals. Additionally, in the visual modality, we could detect a small bias associated with an overestimation of the number of shorter flashes. These results are inconsistent with those of Dormal and colleagues (2006) or Droit-Volet et al. (2003), who failed to find a temporal bias in numerosity discrimination. However, one possible explanation of this discrepancy could be the different numerical range considered in the cited studies, below the dozen and sometimes extending to possibly subitizable numerosities. Tokita & Ishiguchi (2011), who considered lager set sizes, identified instead a decrease in discrimination performance when visual sequences differed from reference ones in event duration or interval duration, compared to a control condition where event duration was fixed, and interval duration was incongruent with numerosity. Moreover, they report that events separated by longer intervals were overestimated. Similarly, an overestimation of the events occurring in shorter time intervals has been highlighted also in the perception of dynamically appearing spatial arrays (Lambrechts et al., 2013; Martin et al., 2017). However, the authors do not attribute this result to an interference of duration *per se*, but rather to its indirect effect on estimation through the rate of accumulation of evidence, which would affect the noisiness of magnitude representations.

While our study is in agreement with a significant temporal bias, contrary to previous reports we found a tendency to underestimate the numerosity of shorter visual sequences (i.e., faster presentation rates), which contrast with the hypothesis of Martin et al. (2017). At least one study reports underestimation of sequences where events were separated by shorter intervals in visual, auditory and tactile modality, with a larger underestimation of visual events, compared to other modalities, for shorter intervals (Philippi et al., 2008). The same authors suggest that this interaction could have emerged from a flicker-fusion illusion for visual sequences, due to the high presentation rates of their stimuli (up to 33Hz) (Levinson, 1978). Even though our stimuli were slower and with irregular durations of events and intervals, we cannot completely exclude that underestimation of faster sequences could have emerged from a perceptual fusion of extremely close pulses, despite our efforts to keep the minimum interval between pulses above 50 ms. However, the parallel result in the auditory modality, where the temporal resolution is largely below the used average frequency of presentation, is a strong indicator that our results cannot be entirely explained by a possible fusion of close events.

Indeed, we found a similar pattern in the two sensory modalities, both in overall discrimination precision and in the effect of temporal magnitudes. This result is in line with previous reports of similar numerical acuity across auditory or tactile modalities and correlations in the estimation precision of sequences of flashes and sounds (Anobile, Cicchini, et al., 2016; Tokita & Ishiguchi, 2016). Collectively, these results suggest that basic numerosity judgments in different senses could rely on a common mechanism, although evidence for the contrary has also been reported (Tokita et al., 2013). However, in the current results, the moderate statistical evidence and the absence of within-subject measures do not allow us to draw strong conclusions on similarities between sensory modalities. Further investigations could benefit from the introduced methodological framework in exploring the role of temporal cues in visual, auditory, and tactile numerosity, as well as cross-modal or multi-modal presentation.

The significant interference from perceptual features during numerosity judgments is generally interpreted as evidence of an overlap in the representation of numerical and non-numerical magnitude, as proposed by theories that posit the existence of a shared parietal network implicated in processing space, time, and number (Bueti & Walsh, 2009). While our results are among the firsts to demonstrate an influence of temporal cues on sequential numerosity processing, further support for this account derives from studies reporting that adaptation to duration affects numerosity perception (Togoli, Fedele, et al., 2021; Tsouli, van der Smagt, et al., 2019). However, discrepancies in the developmental trajectory of numerical and non-numerical acuities and in neural responses associated to numerical, spatial and temporal processing leave open the possibility that different domains could be associated with different specialized systems (see Hamamouche & Cordes, 2019, for a review). Critically, the current design does not allow us to determine if the non-numerical bias originates from a shared representation of magnitude or a non-perceptual competition at the response-selection level. To elucidate this crucial point, future investigations could adopt a similar manipulation of features to assess the spontaneous saliency of different numerical and temporal magnitudes (Roitman et al., 2007) or test the existence of cross-dimensional adaptation effects on temporal numerosity.

In conclusion, the presented findings reveal a significant interaction between numerical and temporal information in shaping individuals' numerosity judgments, with potential similarities in the visual and auditory modalities. Collectively, these results pave the way for future cross-modal investigations adopting a similar framework and feature manipulation, which could help shed light on the specific nature of the interplay between number and time and obtain a more comprehensive knowledge of human quantitative reasoning.

4 CHAPTER 4

Temporal bias in sequential numerosity estimation[2]

4.1 Introduction

The experiment reported in the previous chapter indicates that the temporal properties of sequences can affect the discrimination of the number of events. In particular, we showed that individuals tend to select a sequence as more numerous when the events are separated by longer intervals. As previously highlighted, the presence of interferences from sensory cues in numerosity tasks has important implications for our knowledge of the neurocognitive mechanisms at the basis of numerical processing, particularly concerning how numerical information is extracted from the environment and how it is mentally and neurally represented.

Although our investigation focused on the unidirectional interference of duration on numerosity perception, several studies report the opposite direction, with numerosity affecting the processing of temporal information (Cappelletti et al., 2009; Dormal et al., 2006; Droit-Volet et al., 2003). Along with behavioral similarities in their perception, the symmetric interference between the two domains has been largely interpreted in favor of a shared magnitude system, as proposed in the Theory of Magnitude (ATOM, Bueti & Walsh, 2009; Walsh, 2003). The ATOM theory has received large support from neuroimaging studies showing that common areas of the parietal cortex are involved in spatial, numerical, and temporal processing (Dormal et al., 2012; Hayashi et al., 2013; Hubbard et al., 2005). Moreover, both distinct and overlapping processing of numerical and continuous quantities has been reported also by electrophysiological studies on non-human animals (Tudusciuc & Nieder, 2007).

However, as mentioned in the previous chapter, the current body of research in the field provides a contradictory picture of the influence of temporal cues in numerosity judgments, with inconsistencies in the overall presence of interaction (Agrillo et al., 2010; Dormal & Pesenti, 2013; Droit-Volet et al., 2003) as well as the potential direction of the effect (Lambrechts et al., 2013;

[2] In collaboration with Simone Cutini, Alberto Testolin and Marco Zorzi

Philippi et al., 2008; Tokita & Ishiguchi, 2011). Notably, variations in the pattern of the interaction between continuous magnitudes and numerosity are a common finding also considering the effect of spatial cues such as size, area, and length. Specifically, while some studies show that large visual features such as dot size and convex hull (i.e., the smallest envelope encompassing all items in a set) lead to an overestimation of the number of items, others report a negative relationship between item size and numerosity, with an overestimation induced by smaller elements, especially for fixed densities (DeWind et al., 2015; Gebuis & Reynvoet, 2012b, 2012a; Guillaume et al., 2013). From the dynamic interaction between numerical and continuous quantities stem alternative proposals on its source, with the main hypothesis proposing that behavioral interference between magnitudes could be related to response-selection conflicts (Yates et al., 2012). Notably, even in the case of a non-perceptual and non-representational bias, a significant effect of continuous magnitudes during numerosity-related paradigms still represents a methodological issue in the investigation of numerical representation, due to the necessity to partial out the contribution of non-numerical magnitudes from behavioral or neural responses and find standardized methods that allow the comparability of measures obtained by using different stimuli and tasks.

The use of different tasks and paradigms could also contribute to the reported inconsistencies on interference effects and their direction. First, different stimulus sets can lead to different non-numerical biases, since their strength and direction can be related to the respective saliency of different numerical and continuous quantities in the presented stimuli (DeWind & Brannon, 2016; Park, 2021; Salti et al., 2017). Additionally, different paradigms could specifically involve additional non-numerical processing. As an example, some studies show that perceptual visual cues have a lower impact on numerosity estimation than numerosity comparison (Smets et al., 2015), in line with the idea that non-numerical biases emerge from a competition in magnitude representation that requires active inhibition (Clayton & Gilmore, 2015). In this vein, several studies found no evidence that the duration of the stimuli impacted on numerosity estimation of sequences of events or dynamic spatial arrays (Agrillo et al., 2010; Dormal & Pesenti, 2013). On the other hand, some studies report that spatial information in the stimuli still affects numerical estimates, possibly due to an implicit inter-trial comparison and integration of visual information on the running average of feature range (Abalo-Rodríguez et al., 2022; Gebuis & Reynvoet, 2012b). Indeed, some research found that individuals tend to overestimate the number of dots presented dynamically when stimulus duration is shorter both in an estimation task and a comparison task (Lambrechts et al., 2013; Martin et al., 2017). However, the direction of the bias in these tasks suggests that the source of such interference could be unrelated to the temporal magnitudes themselves and connected with how temporal numerosity is encoded.

In continuity with the previous study, the goal of the current research is then to verify if an interference of temporal information on numerosity processing also emerges when individuals have to estimate the number of sequentially presented events, to investigate if the influence of temporal cues could be task specific. Moreover, differently from a dichotomous response, the direct estimation of magnitude allows a more direct assessment of the direction of temporal biases, thereby shedding light on the contradictory evidence in the literature. In this work, we present two experiments that address this issue. In the first experiment, we asked participants to estimate the number of rapidly presented dots in a visual sequence. We manipulated the temporal properties of our sequences according to the method developed in the previous chapter and based on the framework introduced by DeWind and colleagues (2015), varying independently the numerosity, Duration, and Temporal Spacing of the sequences to assess their contribution to response and individuate potential non-numerical biases and strategies. In a second experiment, we used an auditory presentation of the sequences to assess the stability of our results in different modalities.

4.2 Experiment 1: numerosity estimation on visual sequences

4.2.1 Materials and method

Participants

The initial sample included 221 participants. Twenty-two were excluded due to a screen refresh rate different from 60 Hz or technical issues in the presentation of the stimuli. Moreover, 25 additional participants who showed low attention during the task and responded incorrectly in more than half the catch trials (see task description) were discarded from further analyses. The final sample was then composed of 174 participants, mean age of 22.80 (range: 19 – 45), with 128 females. The sample size provides 80% power to detect a 0.21 effect size with a 0.05 significance level in a one-sample t-test (R *pwr* package). Participants were students from the University of Padova that received course credits for their participation. All participants gave their written informed consent to take part in the study.

Stimuli

The stimulus dataset was based on the method presented in the previous chapter and inspired by the general framework originally proposed by DeWind and colleagues (2015) (see Fig 3.1). Across sequences of visual events, we varied mean event duration (MED), total event duration (TED), total stimulus duration (TSD), and mean event period (MEP), to manipulate two latent variables orthogonal to numerosity: Duration, and Temporal Spacing (see Equations 3.1 and 3.2 and Appendix I).

We varied independently Numerosity, Duration, and Temporal Spacing using 13 levels equally spaced in logarithmic space. Numerosity varied between 7 and 28. A similar maximum range of 1:4 was used for Duration, varying between 120 and 480, and Temporal Spacing, varying between 1500 and 6000 (see Table 4.1). We used aperiodic irregular sequences, built so that the duration of single events and the interval between two events could vary within the same stimulus, with single pulses lasting between 2 and 16 frames (33 ms – 270 ms at 60 Hz) and blank intervals between 3 and 30 frames (50 ms – 500 ms). An initial dataset of 2197 stimuli was generated by the combination of the different levels of Numerosity, Duration, and Temporal Spacing. For each participant, at the beginning of the experiment, a subset of 91 stimuli was randomly drawn from this dataset to sample from the full range of values and to avoid correlations between the cardinal features. Stimuli were created in MATLAB (R2020a) as sequences of timestamps and instantiated online directly in PsychoJS as sequences of white discs on a grey background, presented at the center of the screen. The size of the disc was scaled depending on the resolution of the participant's screen.

Table 4.1 Cardinal feature values. Values of Numerosity, Duration and Temporal Spacing in the entire dataset (rounded)

Num	7	8	9	10	11	12	14	16	18	20	22	25	28
Dur	120	135	151	170	190	214	240	269	302	339	381	428	480
TempSp	1500	1684	1890	2121	2381	2673	3000	3367	3780	4243	4762	5345	6000

Task

Participants completed a numerosity estimation task where they had to report the number of events of sequences of rapid flashes (see Fig. 4.1). Each trial began with a fixation cross lasting 1 s, followed by the visual sequence. The duration of the sequence changed depending on the stimulus, ranging from 800 ms to 6.83 s. After the sequence, a blank screen was presented for 500 ms, followed by a response cue. The response was unrestricted in range and could be inserted by participants in Arabic format with the keyboard. After the response, a blank inter-trial interval was displayed, varying pseudo-randomly from 500 to 1500 ms.

The task consisted of 98 trials (7 trials for each target numerosity and random combination of Duration and Temporal Spacing, and 7 catch trials with numerosity equal to 3) in randomized order, divided into three blocks of 33, 33, and 34 trials, for a duration of around 30 minutes. Participants were instructed to take a short break between blocks. Before the test phase, each participant performed a calibration phase: four sequences of 13 elements and variable temporal features were presented, with an explicit indication of the number of events contained in the sequence. Numerosity 13 was selected because it was close to the geometric mean of the numerical range, but it was not later displayed in the test phase. During the test phase, participants did not receive any feedback on their responses.

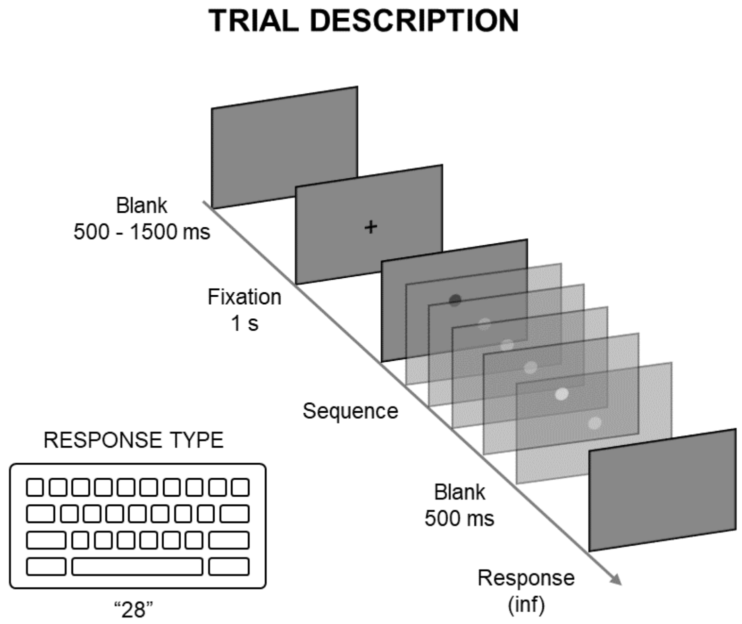

Figure 4.1 Numerosity estimation task. Schematic depiction of one trial of the numerosity estimation task of visual sequences of events.

General procedure

The experiment was conducted online, on Pavlovia, based on PsychoJS. Participants completed the experiment in a single session on their laptops or computers. Due to the use of different devices, individual screen refresh rate was checked *a posteriori*, and all participants with a refresh rate different from 60 Hz were discarded. Participants were asked to perform the task in a quiet environment without distractions, sitting approximately one arm away from the screen. All research procedures were approved by the Psychological Science Ethics Committee of the University of Padova.

Data analysis

To check participant engagement, we inserted 7 catch sequences of 3 events, interleaved with the test trials. Before the analyses, we excluded 25 participants with less than 4 correct responses in these catch trials, which indicates low attention during the task. Moreover, to exclude responses in unattended trials, in both modalities we discarded responses recorded later than 10 s. Before the analysis, for each participant, we also excluded outlier responses above or below four standard deviations from individual mean estimates and estimates below one, assumed to be typing mistakes. With these procedures, we discarded 160 trials, around 0.01% of the total.

For each participant, we then characterized the performance by computing the coefficient of variation (CoV = standard deviation of mean response/mean response) and mean absolute error score (AES = absolute distance between the estimate and target numerosity) by target numerosity. To estimate the contribution of numerosity and temporal magnitudes on estimates, we then fit a linear regression at the individual level modeling the log of the estimate as a function of the log of numerosity, Duration, and Temporal Spacing, expanding the model of numerosity estimation proposed by Izard and colleagues (2008). Both response and predictors were standardized into z-scores.

The resulting combination of coefficients (β_{Num}, β_{Dur}, and β_{TempSp}) is informative regarding the influence of numerical and non-numerical quantity on participant estimates. A response pattern that depends only on the number of events in the sequences without being influenced by temporal magnitudes would be characterized by a positive coefficient for numerosity and null coefficients for Duration and Temporal Spacing. Note that, due to the standardization of the estimates at the individual level, differently from Izard and colleagues (2008) the coefficient of numerosity cannot be easily taken as an indicator of the non-linearity of the response (i.e., a β_{Num} of one does not indicate a linear relationship between target numerosity and estimates). Significant β_{Dur} and β_{TempSp} quantify instead the influence of temporal features on the estimated values, indicating an overestimation or underestimation of longer events caused by variations in the length of the events or their rate of presentation. The group significance of coefficients was tested with one sample Student t-tests against zero. To confirm the results, we also fit a mixed-effect linear regression model at the group level, with identical fixed effects but including random intercepts and slopes for each participant.

Moreover, the linear relationship between the three cardinal features and each temporal magnitude (see the equations in Appendix I) allows the estimation of the contribution of each temporal feature to participant estimates. To do so, we considered the three coefficients as a vector in the parameter space and evaluated its deviation from the numerical axis and its proximity to other individual feature dimensions. When the point defined by the three coefficients is closer to a specific feature rather than the numerosity dimension, we can infer that the participant estimates are based on that feature. For example, a participant who uses the total duration of the sequences as a proxy for estimation would be characterized by a positive and equal coefficient for Numerosity and Temporal Spacing, as their vector would lie on the total stimulus duration dimension.

From the coefficients estimated at the individual level, we then computed vector projections onto the dimensions of the different temporal features and individuated the closest to the vector at the group level with a series of paired t-tests. Non-parametric tests (Wilcoxon signed rank) were performed when the normality assumption was violated, and the Bonferroni method was used to correct multiple comparisons in the projection analysis. Analyses were performed with MATLAB and Jasp (ver. 0.12.1 2020).

4.2.2 Results

Despite the calibration phase, the group showed to greatly underestimate the number of events, especially for the highest numerosities (see Fig. 4.2a). Overall, for all participants mean estimates and their standard deviation increased with target numerosity. The mean coefficient of variation across target numerosity was 0.19 (SD = 0.04), while the mean absolute error score was 4.27 (SD = 1.23). CoV and AES by target numerosity are reported in Fig. 4.2b.

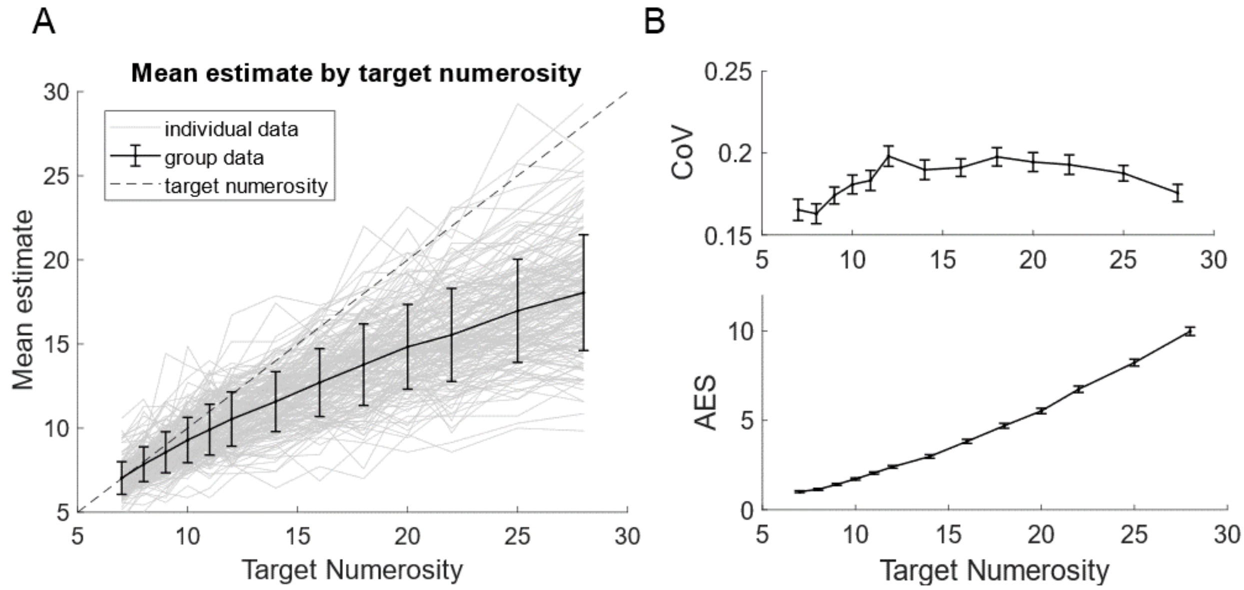

Figure 4.2 Overall performance in visual estimation task. (A) Mean estimate by target numerosity for the visual estimation task. The black solid line represents the group mean, with error bars indicating the standard deviation. Grey lines represent individual participant means. The diagonal dashed line represents the perfect correspondence between target numerosity and estimate. (B) Mean group coefficient of variation (on the top row), and mean group absolute error score (bottom row) by target numerosity. Error bars represent standard errors of the mean.

We then estimated the contribution of numerosity, Duration, and Temporal Spacing on individual participant estimates. The individual fit of the linear regression modeling log estimate as a function of the logarithm of numerosity and the two non-numerical latent variables was significant for all participants (all *F*s > 12.69, *p*s < .001) with a mean R^2 of 0.72 (range 0.28 – 0.94). The individual coefficient estimates are presented in Fig. 4.3, together with the lines representing non-orthogonal temporal features. The group significance of coefficients was tested with one sample Student t-tests against zero. We found a significant effect of Numerosity (M (SD) = 0.80 (0.09), $t(173) = 114.38$, $p < .001$, $d = 8.67$), as well as a significant influence of Duration (M (SD) = - 0.05 (0.06), $t(173) = -10.83$, $p < .001$, $d = -0.82$) and Temporal Spacing (M (SD) = 0.25 (0.10), $t(173) = 32.87$, $p < .001$, $d = 2.49$).

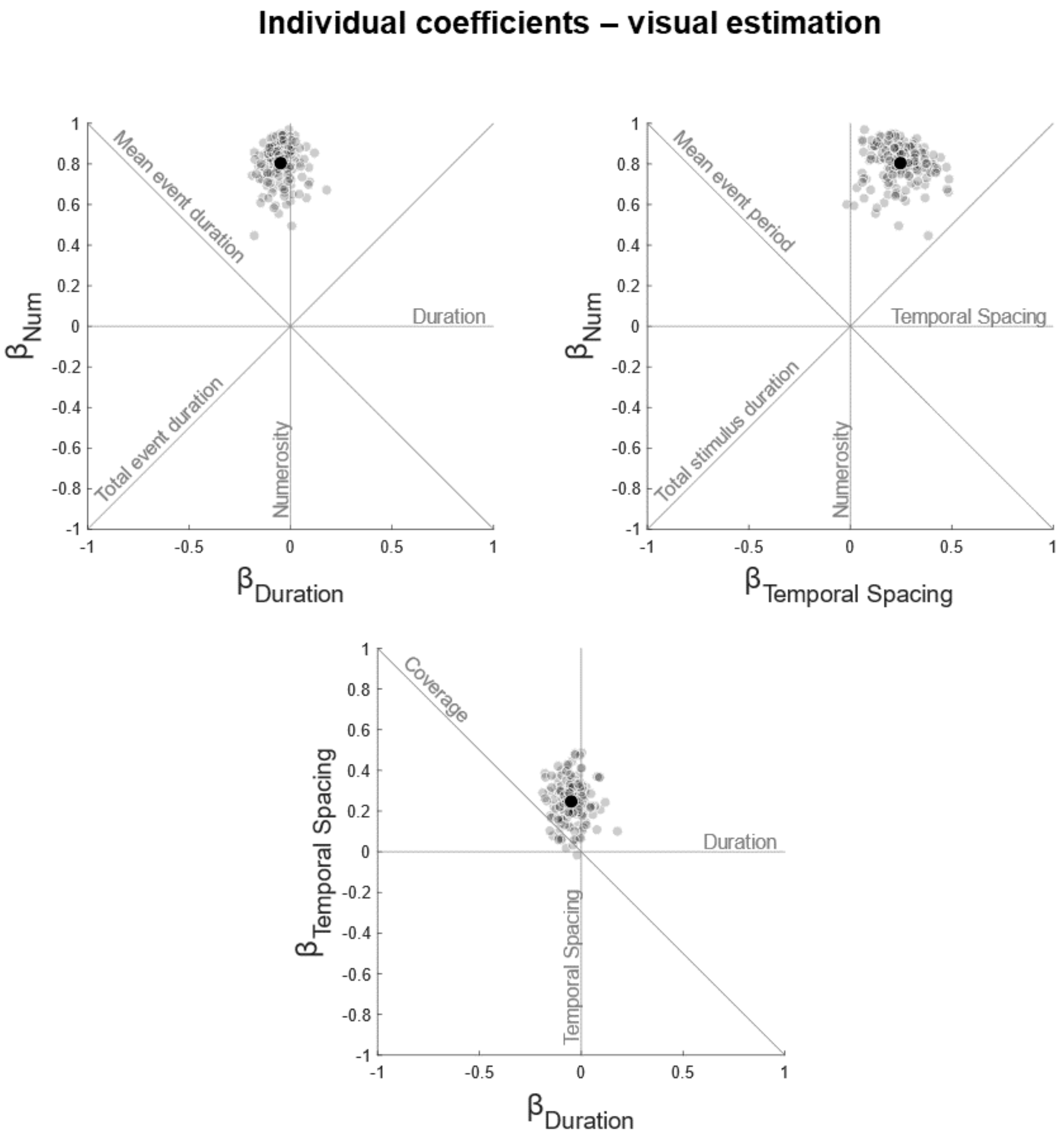

Figure 4.3 Results from regression model analysis of visual estimation task. Individual coefficient estimates plotted in the three orthogonal planes defined by the cardinal axes. Grey dots indicate individual participants, while the black dot indicates the group mean. Grey lines represent the temporal features.

To confirm the results, we also fit a mixed-effect model on all data, with similar fixed effects but including random intercepts and slopes for each participant. The group model indicated a significant β_{Num} (M (SE) = 0.74 (0.009), $t(15698) = 84.60$, $p < .001$), β_{Dur} (M (SE) = -0.05 (0.005), $t(15698) = -9.98$, $p = .001$), and β_{TmSp} (M (SE) = 0.22 (0.006), $t(15698) = 36.42$, $p < .001$). Regression lines plotting the fixed effect of the group model are plotted in Fig. 4.4a.

To assess the relevant dimensions in participants' selection, we then computed at the individual level the vector projections onto the non-orthogonal dimensions and tested if any other magnitude projection was higher than the numerosity coefficient (see Fig. 4.4b). β_{Num} was higher than the projection on the Mean event duration, Total event duration, Total stimulus duration, Mean event period, and Coverage lines (Paired t-tests with Bonferroni correction: all $ts(143) > 10.48$, $ps < .01$, $ds > 0.79$).

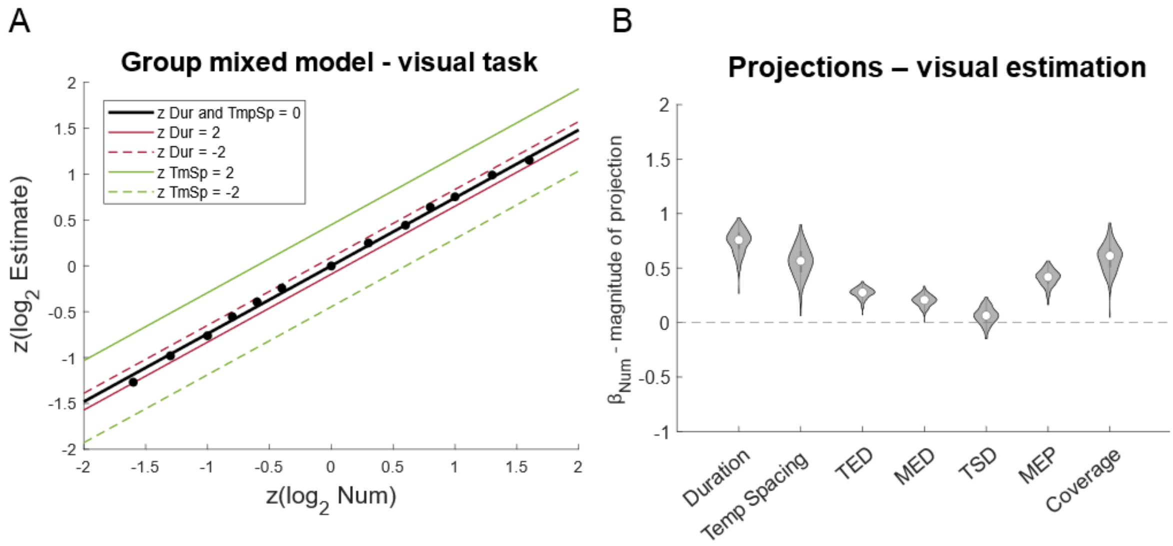

Figure 4.4 Group model and projection analysis for visual estimation task. (A) Regression lines depicting the fixed effects estimated by the group mixed model. Black lines represent the predicted estimate as a function of the log target Numerosity, with mean Duration and Temporal Spacing. Red lines represent the variation in estimates caused by extreme values of Duration (full line indicating the minimum value and dashed line indicating the maximum value) and mean Temporal Spacing, while green lines are predicted estimates for trials with extreme values of Temporal Spacing (full line = minimum value, dashed line = maximum value), and intermediate Duration. All values are standardized into z-scores. (B) Distribution of differences between numerosity coefficient and the projection of the individual vector point, onto each temporal feature line.

4.3 Experiment 2: numerosity estimation on auditory sequences

4.3.1 Materials and method

Participants

Sixty-five participants completed the auditory estimation task. From this sample, we excluded 8 participants due to a screen refresh rate different from 60 Hz or technical issues in the presentation of the stimuli. Moreover, we excluded 3 additional participants who responded incorrectly in more than half the catch trials, indicating poor attention during the task. Finally, 2 participants were excluded during the analyses. The final sample was then composed of 53 participants, mean age of 23.26 (range: 20 – 45), with 43 females. This sample size provides 80% power to detect a 0.39 effect size with a 0.05 significance level in a one-sample t-test (R *pwr* package). Participants were students from the University of Padova that received course credits for their participation.

Stimuli

Stimuli were identical to the one used in the visual estimation task, described in Paragraph 4.2.1. They were created in MATLAB as sequences of timestamps and instantiated online directly in PsychoJS as sequences of sounds (pure tones at 400 Hz). At the beginning of the experiment, participants were allowed to adjust the volume as they preferred.

Procedure and task

The paradigm and procedure used were identical to the visual estimation task described in the previous experiment, except for the auditory nature of the sequences. During the online task, participants were free to use the speakers or headphones connected via cable to the computer. In the final sample, 24 participants performed the task using a headset or earphones, while the remaining ones used computer speakers.

Data analysis

Before the analyses, we excluded participants that showed low attention during the task as indicated by more than 3 errors in catch trials. Based on this criterion, we excluded 3 participants. For each participant, we also discarded outlier trials where a response was inserted later than 10 s after the response cue and responses above or below four standard deviations from individual mean estimates, as well as estimates below one. Based on these criteria, we discarded 49 trials, less than 0.01% of the total. We then performed an analysis parallel to the visual estimation task. Analyses were performed with MATLAB and Jasp (ver. 0.12.1 2020).

4.3.2 Results

For all participants, mean response and the variability of estimates increased a function of target numerosity, but with an overall underestimation of the number of events. In this task, group CoV across target numerosity was 0.17 (SD = 0.05), while the mean AES was 4.11 (SD = 1.33). Mean estimates, CoV, and AES by target numerosity are reported in Fig. 4.5.

We then estimated the effect of numerosity, Duration, and Temporal Spacing on participants' estimates. The individual fit of the linear regression model was significant for all participants (all *F*s > 15.14, *p*s < .001) with a mean R^2 of 0.72 (range 0.32 – 0.94).

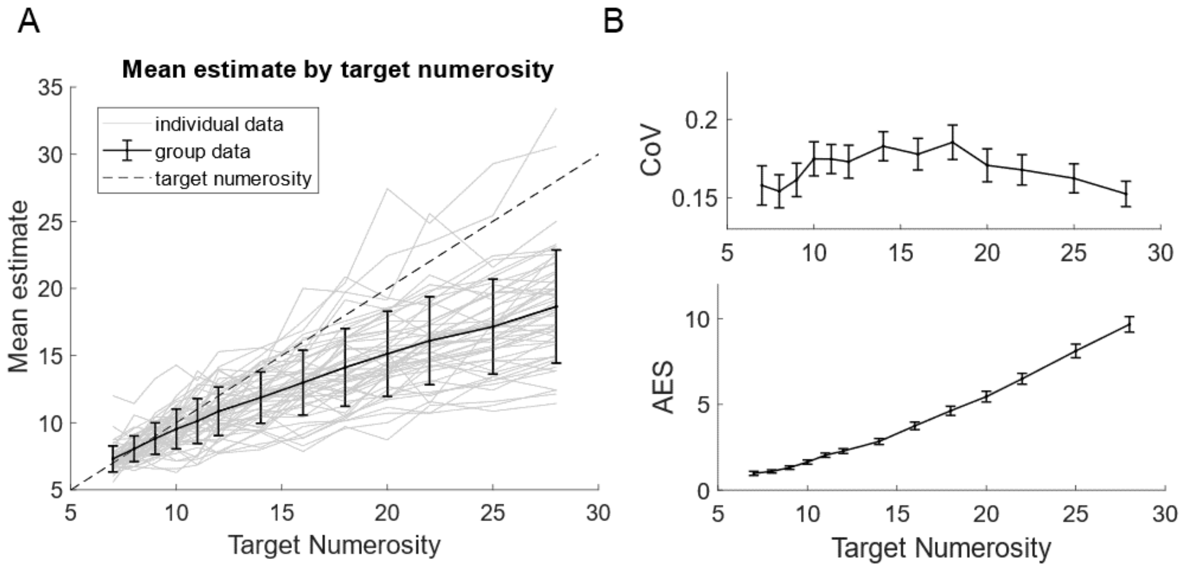

Figure 4.5 Overall performance in auditory estimation task. (A) Mean estimate by target numerosity for the auditory estimation task. The black solid line represents the group mean, with error bars indicating the standard deviation. Grey lines represent individual participant means. The diagonal dashed line represents an ideal perfect response. (B) Mean group coefficient of variation (on the top row), and mean group absolute error score (bottom row) by target numerosity. Error bars represent standard errors of the mean.

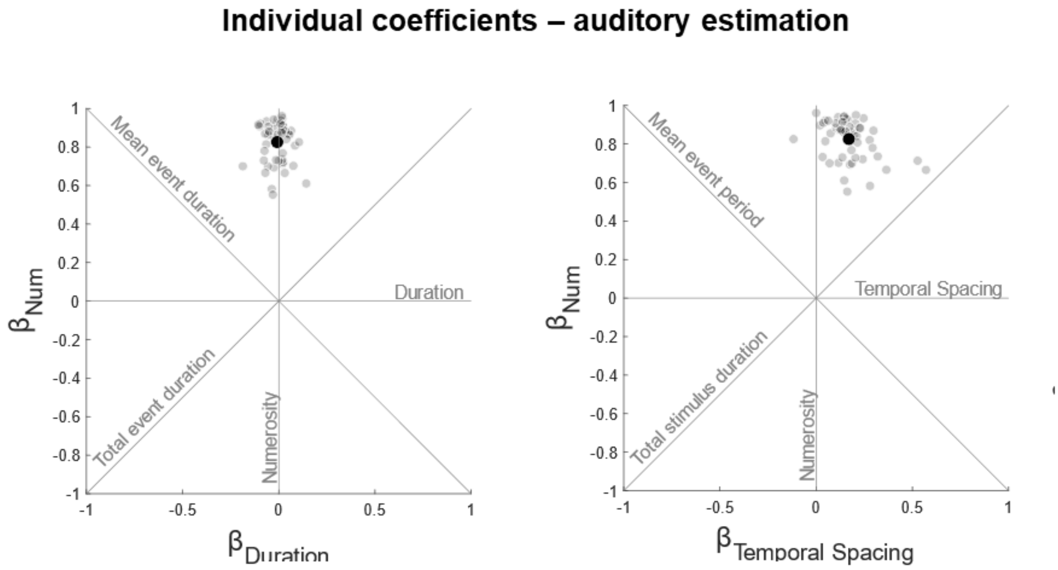

Figure 4.6 Results from regression model analysis of auditory estimation tasks. A) Individual coefficient estimates (grey dots) plotted in the 3D parameter space. Grey lines represent the temporal features.

The individual coefficient estimates of Numerosity, Duration, and Temporal Spacing are presented in Fig. 4.6 in two orthogonal planes of the parameter space. Coefficients were tested with one sample Student t-tests against zero. We found a significant effect of Numerosity (M (SD) = 0.83 (0.10), $t(52) = 57.94$, $p < .001$, $d = 7.96$), and Temporal Spacing (M (SD) = 0.17 (0.12), $t(52) = 10.72$, $p < .001$, $d = 1.47$). The coefficient of Duration was instead not significantly different from zero (M (SD) = - 0.008 (0.06), $t(52) = -1.04$, $p < .001$, $d = -0.14$). The mixed-effect model confirmed these results, highlighting a significant effect of numerosity (M (SE) = 0.75 (0.02), $t(4789) = 35.84$, $p < .001$) and Temporal Spacing (M (SE) = 0.15 (0.01), $t(4789) = 12.03$, $p < .001$), while the effect of Duration was not significant (M (SE) = -0.01 (0.007), $t(4789) = -1.38$, $p = .17$). The predicted estimates derived from the group model are plotted in Fig. 4.7a.

We then computed at the individual level the vector projections onto the non-orthogonal dimensions to test if any other magnitude projection was higher than the numerosity coefficient. Also in this task, the projections of the individual vectors onto each temporal dimension were significantly smaller than the numerosity coefficient (Paired t-tests with Bonferroni correction: all $ts(52) > 9.13$, $ps < .01$, $ds > 1.25$) (see Fig. 4.7b).

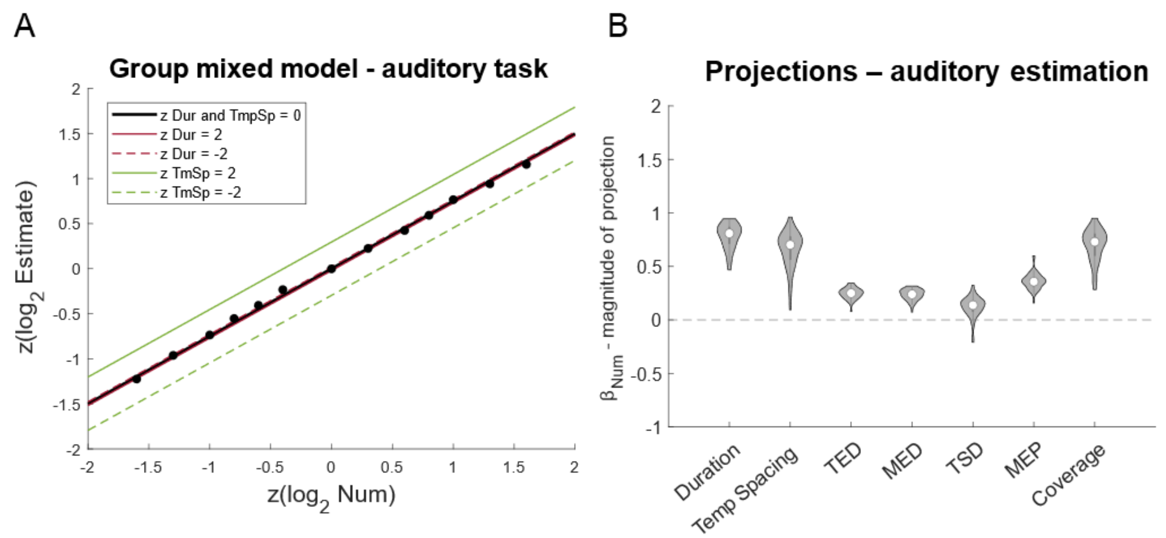

Figure 4.7 Group model and projection analysis for auditory estimation task. (A) Regression lines depicting the predicted values as a function of numerosity for different values of Duration and Temporal Spacing (in different colors). (B) Distribution of differences between numerosity coefficient and the projection of the individual vector point onto each temporal feature line.

4.4 Discussion

The aim of the current study was to assess the influence of temporal features on sequential numerosity estimation. Using the same method as our previous experiment, we sought to verify the stability of our results and increase comparability with previous investigations. In the first experiment, we measured the contribution of numerosity and multiple temporal magnitudes on the estimation of sequences of flashes, varying independently in Numerosity, Duration, and Temporal Spacing. The same stimuli were then presented as auditory sequences in the second experiment to detect potential differences in the overall strategy.

Surprisingly, despite the initial calibration to an explicitly labeled numerosity, both groups of participants showed to largely underestimate the number of events in the sequences during the test phase, especially in case of larger numerosities, in close resemblance to the typical pattern of estimation without calibration in perceptual tasks (Crollen et al., 2011). This result is puzzling compared to the powerful effect of calibration reported in the literature. Izard and Dehaene (2008) showed that not only do individuals become more accurate in their estimates after an exact inducer, but also that providing a misleading calibrator leads to a systematic over- or underestimation of subsequent sets. One possibility could be that the number of example trials used in our paradigm was insufficient to produce an accurate mapping between numeral labels and numerical magnitudes. Indeed, other studies found estimates closer to target numerosities by implementing practice blocks with feedback (Mejias, Mussolin, et al., 2012; Mejias & Schiltz, 2013), or repeating the calibration stimulus periodically (Izard & Dehaene, 2008). However, there is evidence of a recalibration from underestimation to more accurate performance or overestimation even after one single example trial (Abalo-Rodríguez et al., 2022). Critically, in the present research, the absence of pre-calibration measures does not allow us to further clarify the specific effect of the used inducers. Nonetheless, despite the absolute values of the estimates, the overall performance in both experiments matched the typical signatures of numerical estimation tasks. In particular, mean estimates and their standard deviation increased in proportion to target numerosity, resulting in a stable coefficient of variation, with an average precision coherent with previous research using static visual stimuli (Anobile et al., 2018).

In both experiments, participants presented a significant influence of both numerical and non-numerical quantities. The combination of Numerosity, Duration, and Temporal Spacing coefficients from the regression model indicate that participants were primarily basing their estimates on the number of flashes or tones in the sequences. However, in the first experiment, the estimated number of flashes was significantly influenced by the duration of the pulses and by the dispersion of events in time, with an overestimation of shorter and sparser events. Similarly, in the second experiment participants produced larger estimates for slower auditory sequences. Overall, this outcome perfectly replicates the pattern of non-numerical bias found in the numerosity comparison task presented in the previous chapter, both for the visual and the auditory modalities. As in the previous experiment, results reveal that individuals did not use any other single feature as a proxy of numerosity, even though the current task cannot rule out a more complex interaction between temporal features (Gebuis & Reynvoet, 2012b). However, the significant influence of temporal cues on numerical estimates suggest that cross-magnitude interference can arise even in numerosity judgments with a less explicit decisional conflict in response-selection than comparative tasks (Yates et al., 2012).

The specific pattern of bias presented by our participants is once again in contrast with previous reports of an opposite overestimation of arrays of dots dynamically appearing in time, in case of shorter sequences (Lambrechts et al., 2013). In particular, the same authors proposed that the effect of duration on numerosity estimation could be related to the rate of accumulation of sensory evidence, rather than the duration magnitude, which was further supported by a similar underestimation of the surface area of the elements at lower rates of presentation, and an overall resilience of time estimation to numerical and spatial manipulations. While our results are compatible with an influence of the rate of evidence accumulation, they point to the opposite direction, suggesting an underestimation of events in case of faster regimes. However, an exclusive influence of sensory accumulation rate is not consistent with studies showing that static arrays of items, where magnitude information is immediately and simultaneously available, are overestimated when presented for longer time periods (Javadi & Aichelburg, 2012; Togoli et al., 2021; but see Inglis & Gilmore, 2013 for a different interpretation of this phenomenon). Nonetheless, our results are not in contrast with their revision of the ATOM theory in which different magnitudes might be combined at sensory level under Bayesian rules, so that magnitude representation would result from an integration of all quantities (Martin et al., 2017). The inconsistent pattern of results across studies could however be an indicator that interaction between magnitudes can occur at multiple levels, from the encoding of magnitudes through sensory integration to a memory interference between magnitudes (Cai et al., 2018) or competition at response-selection, and that diverse modes of presentation might differently reveal such processes.

The comparison between contradictory results in different studies is further complicated by the use of either static array or dynamic visual arrays, and temporal sequences of events. Indeed, even if in both dynamic arrays and sequences the numerical information is unfolded progressively, dynamic arrays are characterized by a spatial configuration changing over time, while the train of flashes and tones presented in the current study originated from a single source, to exclude additional potential interference from spatial information. Furthermore, differently from trains of flashes or tones, both in Martin et al. (2017) and Lambrecht et al. (2013), a subset of elements of the array was always visible on screen. Additional illusory phenomena related to the perception of filled and empty temporal intervals (Thomas & Brown, 1974) or intervals defined by markers of different durations

(Hasuo et al., 2012) could then modulate the interaction between temporal cues and numerosity perception in case of temporal sequences more than dynamic arrays. While these effects are seldom considered when studying the interaction between time and number, studies focusing on the effect of spatial cues in numerosity estimation suggest that it could be a promising avenue. For example, Dormal and colleagues (2018) have shown that numerosity estimation can be influenced by spatial length even when variations in length are illusory. Moreover, an interesting future direction could be to investigate the estimation of stimuli where a fully sequential presentation of events is combined with a spatial configuration of the flashes, to assess a potential interaction between spatial and temporal cues on numerosity perception.

In conclusion, this second study further confirmed stable interactions between numerical and temporal information even in the absence of an explicit conflict in response-selection, both in visual and auditory modality. Additional investigations are required to clarify inconsistent results in the extent and direction of such biases, to better understand the source of the interaction between different magnitudes.

5 CHAPTER 5

Interference effects in developmental dyscalculia[3]

5.1 Introduction

As outlined in the previous chapters, the ability to compare large numerical sets is believed to rely on a non-verbal system, the Approximate Number System (ANS), where numerical magnitude would be represented as Gaussian distributions of activation on a logarithmically compresses number line (Dehaene et al., 1998). The accuracy in comparing numerical quantities follows the Weber-Fechner law, with error rates increasing when the ratio between the to-be-compared numerical sets approaches one. The precision in numerosity comparison improves over development, allowing discrimination of large 1:3 numerical ratios at birth and up to 9:10 in adulthood (Halberda & Feigenson, 2008; Izard et al., 2009; Libertus & Brannon, 2010; Xu & Spelke, 2002; but see Wang & Feigenson 2021 in support of the malleability of numerical acuity in infants). Moreover, some studies have shown that numerical acuity can predict later mathematical achievements (Chen & Li, 2014; Halberda et al., 2008; Schneider et al., 2017; Starr et al., 2013).

In this vein, a reduced precision of non-symbolic numerical representation has been proposed at the basis of developmental dyscalculia (DD), a learning disability characterized by persistent mathematical impairments that cannot be explained by inadequate education, intellectual disability, or sensory deficits (DSM-5, American Psychiatric Association, 2013). Individuals with dyscalculia present difficulties with arithmetic and number-related concepts that can significantly impact on arithmetic achievements, with negative outcomes, within our technological society, on career success and income (Ritchie & Bates, 2013). In support of the idea of a deficit in numerosity processing, children with DD between 9 and 15 y.o. have shown increased numerical distance effects (Mussolin, Mejias, et al., 2010; Price et al., 2007) or reduced precision in discriminating two numerosities (Decarli et al., 2020; Mazzocco et al., 2011a; Piazza et al., 2010). Similarly, individuals with DD

[3] In collaboration with Gisella Decarli, Maristella Lunardon, Alberto Testolin, Michele De Filippo De Grazia, Francesco Sella, Giuseppe Cossu, Silvia Lanfranchi and Marco Zorzi.

seem less precise compared to their peers in estimating non-symbolic numerical quantities (Mejias, Mussolin, et al., 2012), a difficulty that has been reported to persist into adulthood (Mejias, Grégoire, et al., 2012).

However, the possibility of a deficit in numerosity representation in DD is challenged by several studies demonstrating that performance in non-symbolic comparison tasks can be influenced by other perceptual magnitudes co-varying with numerosity, such as the size of the elements or their position in space (Gebuis & Reynvoet, 2012a; Leibovich & Henik, 2014). As an example, children and adults commit more errors when choosing the larger between two sets of dots when the numerically larger set is enclosed in a smaller space (Clayton et al., 2015; Clayton & Gilmore, 2015; Nys & Content, 2012). In particular, young children struggle to disregard misleading non-numerical features, but the ability to ignore irrelevant characteristics co-varying with numerosity improves during development (Ferrigno et al., 2017; Starr et al., 2017). Crucially, individuals with DD seem more influenced by non-numerical information. Several studies report that children with DD display increased congruency effects from total surface area and density compared to their peers during a discrimination task (Mussolin, Mejias, et al., 2010) or produce more reliable number estimates when cumulative area is congruent with numerosity (Mejias, Mussolin, et al., 2012). Moreover, recent evidence suggests that individuals with DD would exhibit difficulties in numerosity judgments uniquely when the numerical information is competing with these other visual magnitudes. In particular, Bugden & Ansari (2016) found a difference in discrimination acuity between elementary school children with DD and a control group, only in trials where the number of elements and the total area of the items were incongruent, while no difference emerged when the more numerous arrays contained also larger elements. Similarly, another study showed how previous reports of higher numerosity discrimination threshold in DD (Piazza et al., 2010) could be explained by an increased interference effects from non-numerical cues (Piazza et al., 2018).

The mechanism underlying the developmental decrease in non-numerical biases, as well as the higher interference in DD, is still debated. Some studies have highlighted a link between DD error rates in incongruent numerosity comparison and their visuospatial working memory abilities (Bugden & Ansari, 2016), in line with a domain-general account of dyscalculia, which associates cognitive impairments in working memory, visuospatial skills, or executive functions to a reduced arithmetic proficiency (Ashkenazi et al., 2013; Cirino et al., 2015; Peng et al., 2018). Accordingly, one research showed that, in DD, increased congruency effects in non-symbolic comparison were accompanied by stronger bidirectional interferences in symbolic Stroop-like tasks both from physical size during number judgment and from number on size judgment, suggesting a common underlying difficulty in inhibition of task-irrelevant information (Szucs et al., 2013). Importantly, similar executive functions have been related to the acquisition of mathematical abilities in typical development, and inhibition abilities have been proposed to mediate the relationship between basic number processing and mathematical skills (Cragg & Gilmore, 2014; Gilmore et al., 2013). In support of this account, several studies failed in finding impairments in basic number processing in children with dyscalculia while reporting working memory and inhibition deficits (Mammarella et al., 2021; Passolunghi & Siegel, 2004).

However, another view suggests that filtering mechanisms, and therefore filtering deficits, could be specific to magnitude processing and quantity judgments, with learning about symbolic numbers possibly supporting children's ability to focus on numerosity (Piazza et al., 2018). According to this view, higher non-numerical biases in children with DD could be related to a reduced benefit from formal education. In line with this interpretation, some authors did not find a significant relationship between measures of non-numerical bias in a comparison task and inhibitory control abilities in typically developing children of 4 and 6 years of age (Starr et al., 2017). Accordingly, recent evidence shows that adults with DD display higher biases from item size than a control group when discriminating numerosities, but similar influence from numerosity when comparing item size (Castaldi et al., 2018), suggesting that higher interference effects are not necessarily related to domain-general deficits.

In support of this view, several neuroimaging studies report a weaker modulation from numerical distance in the activity of the intraparietal sulcus (IPS) in children with DD (Mussolin, De Volder, et al., 2010; Price et al., 2007). Furthermore, a recent study based on multivariate pattern analysis has found that adults with DD presented less distinct activation in response to different numerosities in parietal and frontal lobes compared to controls, suggesting a noisier numerical representation (Bulthé et al., 2019). However, since inhibition and working memory have been related to similar frontoparietal networks, it has also been underlined how IPS dysfunctions in DD could also be linked to domain-general cognitive functions (Dumontheil & Klingberg, 2012; Rotzer et al., 2008; Szucs et al., 2013). Nonetheless, computational models of numerosity perception based on deep neural networks show that a reduction of bias from non-numerical cues can emerge from experience-dependent refinement in the encoding of numerical and non-numerical information, rather than domain-general processes such as those involved in response selection (Testolin et al., 2020).

To summarize, it is currently unclear whether lower accuracy in incongruent trials in DD might emerge from domain-general difficulties in inhibiting non-numerical features leading to higher interference effects in numerosity comparison, or if it arises from deficient numerical magnitude processing. In the present work, we address this question by assessing the influence of several continuous non-numerical features in 8-to-14-year-old children with severe dyscalculia (< 2 SDs below the normative mean) and controls matched for age, IQ, and visuospatial memory skills. We measured their performance in a numerosity comparison task where we varied pairs of dot arrays independently in numerosity, Size (related to item and total surface area) and Spacing ratios (related to the field area and density of the collections), to estimate the relative contribution of numerical and non-numerical information on participants' response (DeWind et al., 2015). We also administered a spontaneous categorization task, where children spontaneously decided whether to divide small or large sets based on numerosity or area, thereby revealing the saliency of these dimensions when pitted against each other (Ferrigno et al., 2017).

5.2 Materials and method

5.2.1 Participants

One-hundred and ninety-five children between 8 and 14 y.o. (between grade four of primary school and grade three of middle school, in Italy) underwent a full assessment to evaluate the presence of learning and/or cognitive disabilities. From this sample, we first excluded children with an incomplete cognitive assessment, neuropsychological disorders, sensory deficits, ADHD or motor disorders, and children with an IQ below the normal range (WISC score < 85; Wechsler, 2003). In the remaining sample, we classified as children with DD 53 individuals presenting a performance in the clinical range on a standardized battery of mathematical and numerical abilities (BDE-2; Biancardi et al., 2016). Children were included in the DD group when their total score was 2 SDs below the expected mean (< 70) or, in the case of younger children (7-8 years old), if they performed below the 5th percentile in half or more subtests from the battery. We also individuated a control sample of 75 children with average cognitive skills and without difficulties in the numeracy battery, presenting a total score within the normal range (> 85) or with a performance below the 5^{th} percentile in maximum one subtest. We then selected a group from the control sample matching all children from the DD group with the closest individual based on chronological age, visuospatial memory, and IQ. Since the two groups differed in IQ scores, we then iteratively excluded from the control group the individuals with the highest IQ scores until the two groups had similar scores (i.e., Bayes factors < 1 for all matching variables). Due to missing data and additional exclusion of participants during the analyses, the number of participants considered for the two tasks differ (see Table 5.1).

The numerosity comparison task was completed by all children. Before matching DD and control participants, we additionally discarded 10 children from the DD group and 11 children from the control sample due to the exclusion of a large number of trials or to a non-satisfactory fit of the general linear model. The final sample was composed of 43 children in the DD group (17 males) and

34 children in the Control group (29 males). The two groups did not differ for IQ (BF_{10} = 0.84), chronological age (BF_{10} = 0.24), and visuospatial memory (BF_{10} = 0.24). Twenty-nine children in the DD group and 7 in the Control group presented a diagnosis of dyslexia ($\chi^2(1) = 16.74$, $p < .001$). The sample size provides 80% power to detect a 0.65 effect size with a 0.05 significance level in a two-tailed t-test (R *pwr* package). The spontaneous categorization task was completed by 50 children (22 males) of the DD group. A control group (n = 48, 35 males) was selected with the previously described matching procedure and iterative exclusion. The two groups did not differ for IQ (BF_{10} = 0.87), chronological age (BF_{10} = 0.22), and visuospatial memory (BF_{10} = 0.23). Thirty-two children in the DD group and 12 in the Control group presented a diagnosis of dyslexia ($\chi^2(1) = 15.06$, $p < .001$).

Table 5.1 Age, IQ and NEPSY-M3a in the two samples. Mean and standard deviations of age, intelligence, and visuo-spatial working memory scores in the two samples, separately for each task.

M (SD)	Numerosity comparison		Spontaneous categorization	
	DD (n = 43)	Controls (n = 34)	DD (n = 50)	Controls (n = 47)
Age in months	129.51 (18.28)	130.00 (19.11)	129.52 (17.86)	130.17 (19.35)
IQ	97.21 (8.87)	100.26 (6.01)	98.76 (9.68)	101.87 (7.32)
NEPSY-M3a	118.86 (22.12)	118.86 (22.12)	115.60 (22.58)	117.75 (23.25)

5.2.2 Procedure

Assessment and testing were conducted in two different sessions at the child neuropsychiatric unit in Padova, Italy. During the first session, children completed the cognitive and mathematical assessment, while in the second session, they performed a visuospatial memory test, the categorization task, and the comparison task, as well as other computerized tasks not relevant for the current investigation (in random order), presented on a laptop using the E-Prime 2.0 software (Psychology Software Tools). Parents provided their written informed consent for their children to participate in the study. The research protocol was approved by the Psychological Science Ethics Committee of the University of Padova.

5.2.3 Cognitive assessment

Intelligence

Children's intelligence was measured with the *Wechsler Scale of Intelligence* (WISC-IV; Wechsler, 2003) from which a measure of full IQ (M = 100, SD = 15) was extracted for every child, based on chronological age.

Visuospatial memory

This ability was assessed with the *Memory for designs (Immediate)* subtest from the NEPSY-II (Korkman, Kirk & Kemp, 2011). In this test, children were presented with 6-10 pictures placed on a grid for 10 seconds, and they had to memorize and reproduce the pictures and their location. A total score was computed by the combination of correctly remembered pictures and locations.

Numeracy

Children's numerical competence was assessed with the *Batteria per la discalculia evolutiva* (BDE-2) (Biancardi et al., 2016), a standardized battery used in Italy for the clinical assessment of dyscalculia including different subtests related to general number knowledge, calculation abilities, number sense, and arithmetic problems. The raw score of each subtest can be transformed into a normative score, the sum of which corresponds to a total score (M = 100, SD = 15).

5.2.4 Experimental tasks

Numerosity comparison task and stimuli

Children performed a numerosity comparison task that required them to indicate which of two dot arrays contained more elements. In each trial (see Fig. 5.1a), after a readiness cue of 500 ms, two arrays of white dots on a black background were presented simultaneously on the two sides of the screen for 500 ms, followed by a blank screen until response and by an inter-trial interval between 1250 and 1750 ms. Children were instructed to indicate which arrays contained more dots as fast and as accurately as possible by pressing the trackpad buttons corresponding to the side of appearance of the selected array. Before the test phase, the task began with two practice phases of 4 trials each. The first was a slower version with a longer readiness cue and stimulus presentation (1000 ms) and a fixed numerical ratio of 1:2 in all pairs. In these trials, participants received trial-by-trial feedback regarding the correct response. In case of an incorrect response, the experimenter repeated the instructions, and the same trial was presented until a correct response was provided. The second practice block consisted of 4 trials with a similar speed to the test phase and a fixed ratio of 1:2. The transition from practice to test phase was based on an accuracy criterion of 3 out of 4 correct responses in the second practice block. If participants failed to achieve the required accuracy threshold, the practice block was repeated until the criterion was met. In the test phase, children completed 200 trials split in three blocks.

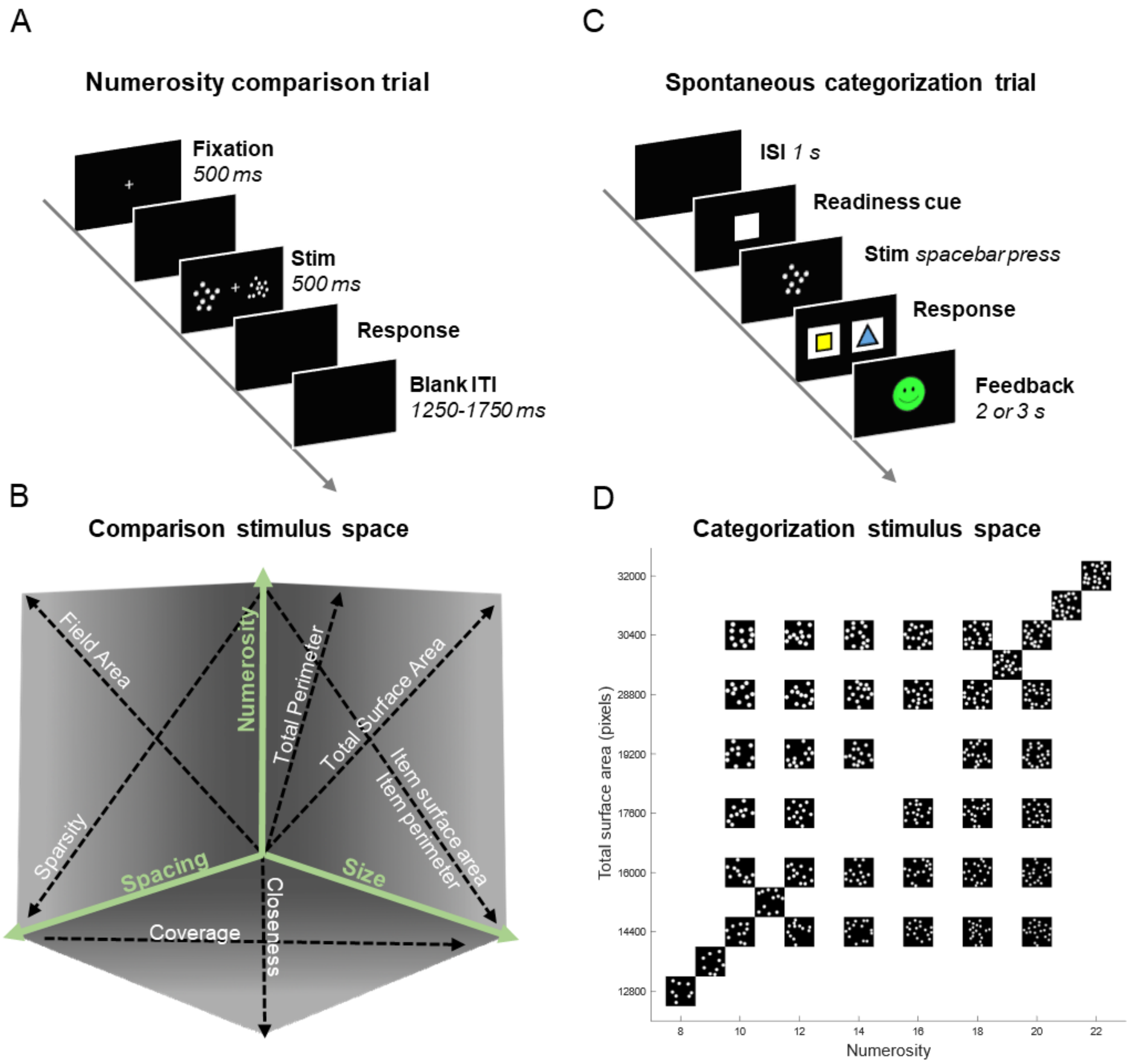

Figure 5.1 Description of the two experimental tasks (A) Schematic description of one trial in the numerosity discrimination task. (B) The three-dimensional stimulus and coefficient space defined by the orthogonal manipulation of Numerosity, Size, and Spacing in the numerosity comparison task. Dashed arrows represent continuous magnitudes. (C) Depiction of one trial from the spontaneous categorization task. (D) Stimuli used in the spontaneous categorization task. On the diagonal, stimuli with a positive correlation between numerosity and total surface area (standard stimuli). In the rest of the images, numerosity and total surface area were independently varied (probe stimuli).

Stimuli were 400 unique images (200x200 pixels) representing white dot arrays on a black background. A dataset inspired by the stimulus set introduced by DeWind and colleagues (2015) was created, with 13 levels of Numerosity (range 7-28), 13 for Size, and 13 for Spacing, evenly spaced on a logarithmic scale. *Size* and *Spacing* are mathematical constructs summarizing information related to the dimension of the dots (Size = Item surface area x Total surface area) and the spread of the elements in space (Spacing = Field Area x Sparsity) (see Fig. 5.1b and Appendix II). Each combination of the three features had 10 different instantiations, resulting in an initial stimulus space of 21970 images. Stimuli were created with a custom program in MATLAB (R2017a). We then selected 200 pairs with a numerical ratio (smaller/larger) between 0.5 and 0.9 and Size and Spacing ratios ranging between 0.25 and 1 (17% with a numerical ratio between 0.5 and 0.6; 33% with a ratio between 0.6 and 0.7; 33% with a ratio between 0.7 and 0.8; 17% with a ratio between 0.8 and 0.9). The combination of Numerosity, Size and Spacing created different congruency conditions: in approximately one quarter of the trials (N = 40) the array containing more dots also presented larger Size and Spacing (fully congruent), while in a similar number of trials (N = 49) the more numerous dot cloud presented smaller Size and Spacing (fully incongruent). In the remaining trials numerosity was congruent with either Size (Size congruent, N = 59) or Spacing (Spacing congruent, N = 52). All participants were presented the same set of pairs and the order of presentation was kept constant to avoid fluctuations due to the sequence order.

Spontaneous categorization task and stimuli

The spontaneous categorization task was inspired by the one used in Ferrigno et al. (2017). In this task, children were presented with individual arrays of dots, and they had to divide dot arrays into two categories (small and large quantity) based on a criterion learned by rote practice. In a first training block, participants learned from trial-by-trial visual feedback to divide non-numerical arrays into the two categories. In this phase, images were built so that the arrays presented a total surface area proportional to the number of stimuli (standard trials), so participants could successfully solve the task by attending to either numerosity or the total surface area of the elements. In the test phase, to disclose the categorization criterion, standard trials were alternated with probe trials where numerosity and total surface area were systematically uncorrelated.

To avoid any influence on the selected criterion, children were given only basic instructions on the nature of the task, through a practical example. They were presented with two examples of standard stimuli, one for each category, with the corresponding category symbol. In the training and test phases, each trial began with a readiness cue, followed by centrally presented arrays of dots (see Fig. 5.1c). After a keyboard press, two category symbols (yellow square and blue triangle) were presented on the two sides of the screen, counterbalanced across participants. Children answered by pressing the trackpad button corresponding to the side of the selected category. After a correct response, positive visual feedback (green smiley face) appeared for 3 s. In case of an incorrect response, a blank screen would appear for 2 s, as mild negative feedback. The feedback was followed by an inter-trial interval of 1 s. The training phase lasted a minimum of 30 trials, in which an equal number of "small/less" and "large/more" stimuli were presented. After 30 trials, participants would proceed to the test phase if they reached an accuracy of at least 60%, otherwise, training continued and performance was re-evaluated after each extra trial, to conclude the training phase after the minimum number of trials necessary for the individual participant to reach the accuracy threshold. After reaching 60% accuracy, children moved to two test blocks of 41 and 43 trials: between blocks, participants were encouraged to take a 2-to-5-minute break. In the test phase standard trials (N = 54) were randomly intermixed with probe trials (N = 30). All responses to probe trials were considered correct and received positive feedback.

Stimuli were black-and-white images (350 by 350 pixels) of dot arrays (see Fig. 5.1d). Training and standard images presented from 8 to 12 dots for category "small/less" and 18 to 22 dots for category "large/more", and they were built so that the arrays presented a total surface area proportional to the number of stimuli. This was achieved by equating the individual dot size to 1600 pixels. For probe stimuli, number (10, 12, 14, 16, 18, 20) and area were systematically uncorrelated, with an average number of 15 dots and an average total surface area of 24000 pixels, ranging from 12800 to 32000. A dataset was created with 100 instances for each combination of numerosity and area. Field area was constant in all stimulus types. During testing and training, for each participant standard stimuli were drawn from the entire dataset with a normal distribution such that each category had approximately a 15% chance at 8 or 18, 21% at 9 or 19, 27% at 10 or 20, 21% at 11 or 21 and 15% at 12 or 22. Probe trials were instead selected from the dataset to sample all the combinations of numerosity and total surface area in the dataset. Stimuli were created with a custom program in MATLAB.

5.2.5 Statistical analysis

For the numerosity comparison task, we estimated the contribution of numerical and non-numerical cues by modeling participants' choice (selection of right stimulus) as a function of the logarithm of the Numerosity, Size, and Spacing right/left ratios with a general linear model with binomial distribution and probit link function, fit at the individual level (Tomlinson et al., 2020). The resulting coefficients provide both an indication of numerical acuity (β_{Num}) and non-numerical bias (β_{Size} and $\beta_{Spacing}$). The discrimination vector was defined by the three individual coefficient estimates and the contribution of each feature was computed by projecting the discrimination vector onto the dimensions of individual features (see the equations in Appendix II) to determine the closest to the discrimination vector. The angle (in degrees) of the discrimination vector from the numerosity dimension (*vector-line angle*) was used as a measure of the non-directional non-numerical bias. Coefficients, projections of the discrimination vectors, and their angles from numerosity were estimated at the individual level. Differences in acuity and bias between groups were then assessed with frequentist and Bayesian t-tests (R *BayesFactor* package with default priors). Multiple comparison tests were corrected using the Bonferroni method. Before the analysis, we excluded trials where the response was provided in less than 250 ms (anticipation) or later than 2 s (possible distraction) from stimulus appearance. With this procedure, we excluded from the initial sample 5 participants from the DD group and 7 from the Control group for which we eliminated more than 15% of the total trials. We also excluded 5 children from the DD group and 4 from the Control group whose performance was not well described by the general linear model ($R^2_{adj} < 0.20$). The GLM fit at the individual level was significant for all participants included in the final sample (mean $R^2_{adj} = 0.53$, all $\chi^2 > 55.97$, all *p*s < .001). As an additional analysis, differences in accuracy in separate congruency conditions between Numerosity, Size and Spacing were assessed with a mixed-effect logistic model of trial-by-trial accuracy with congruency condition (fully congruent, Size congruent, Spacing congruent, fully incongruent) and group (DD or Controls) as fixed effects and including a random intercept of participant to account for individual variability.

For the spontaneous categorization task, the influence of numerosity and total surface area was assessed by fitting for each group a mixed-effect logistic model of category choice in probe trials with numerosity and total surface area as fixed effect predictors. We included a random effect of the participant and a random slope for numerosity and total surface area, to account for individual variability (Ferrigno et al., 2017). The appropriateness of the random effect structure was determined by sequentially inserting random intercepts and slopes in a null model and assessing the fit with likelihood ratio tests (Blini et al., 2016). We then compared coefficients between groups with a z-test (Ferrigno et al., 2017). A complementary analysis of accuracy in the different congruency conditions between numerosity and total surface area was carried out with a mixed-effect logistic model of trial-by-trial accuracy in test trials with group and congruency condition (i.e., congruent, incongruent) as fixed effect predictors and including a random intercept of participant to account for individual variability.

5.3 Results

5.3.1 Numerosity comparison

In the numerosity comparison task, accuracy was well above chance in both groups (DD group: M = 0.82, SD = 0.05; Control group: M = 0.86, SD = 0.05). However, children with DD had lower accuracy compared to their peers ($t(75) = 3.18$, $p = .002$, $d = 0.74$, $BF_{10} = 17.99$). We then estimated at the individual level the relative contribution of Numerosity, Size, and Spacing on trial-by-trial choice. Individual coefficient estimates from the GLM and their relation to the orthogonal and individual features are presented in Fig. 5.2a. In the case of a numerosity-based response, the numerosity coefficient can be interpreted as a measure of numerical acuity: a large numerosity coefficient reflects the ability to discriminate difficult numerical ratios (i.e., closer to 1). Significant coefficients for Size and Spacing, instead, reflect the presence of non-numerical biases.

At the group level, the magnitude of the numerosity coefficient was significantly different from zero in both the DD group (M = 2.12, SD = 0.52, $t(42) = 26.81$, $p < .001$, $d = 4.09$) and the Control group (M = 2.69, SD = 0.98, $t(33) = 16.07$, $p < .001$, $d = 2.76$). Moreover, in both groups the coefficient weights were significantly different from zero for both Size (DD group: M = 0.19, SD = 0.26, $t(42) = 4.93$, $p < .001$, $d = 0.75$; Control group: M = 0.22, SD = 0.26, $t(33) = 5.03$, $p < .001$, $d = 0.86$) and Spacing (DD group: M = 0.30, SD = 0.19, $t(42) = 10.26$, $p < .001$, $d = 1.57$; Control group: M = 0.34, SD = 0.23, $t(33) = 8.62$, $p < .001$, $d = 1.48$), indicating a significant influence from non-numerical cues. However, we found moderate evidence for similar coefficient estimates of Size ($t(71.05) = 0.47$, $p = .64$, $d = 0.11$, $BF_{10} = 0.26$) and Spacing ($t(64.44) = 0.75$, $p = .45$, $d = 0.17$, $BF_{10} = 0.31$) between the two groups. On the contrary, the weight of numerosity was significantly smaller in the DD group ($t(47.42) = 3.12$, $p = .003$, $d = 0.74$, $BF_{10} = 23.77$; strong evidence), indicating that children with DD were, on average, less able to discriminate difficult numerical ratios (see Fig. 5.2b).

We then estimated individual discrimination vectors and computed the projections onto the different feature dimensions. Paired-sample t-tests revealed that, at the group level, the weight of numerosity was significantly larger than any other projection in both the DD (all ts(42) > 3.49, all ps < .05, $d > 0.53$) and Control group (all ts(34) > 4.27, all ps < .001, $d > 0.73$). However, the vector-line-angle was significantly different from zero for both the DD group (M = 11.55, SD = 5.28, $t(42) = 14.34$, $p < .001$, $d = 2.19$) and the Control group (M = 10.14, SD = 3.25, $t(33) = 18.21$, $p < .001$, $d = 3.12$), but it was not significantly different between the two groups ($t(71.08) = -1.44$, $p = .15$, $d = -0.32$, $BF_{10} = 0.53$) (see Fig. 5.2c).

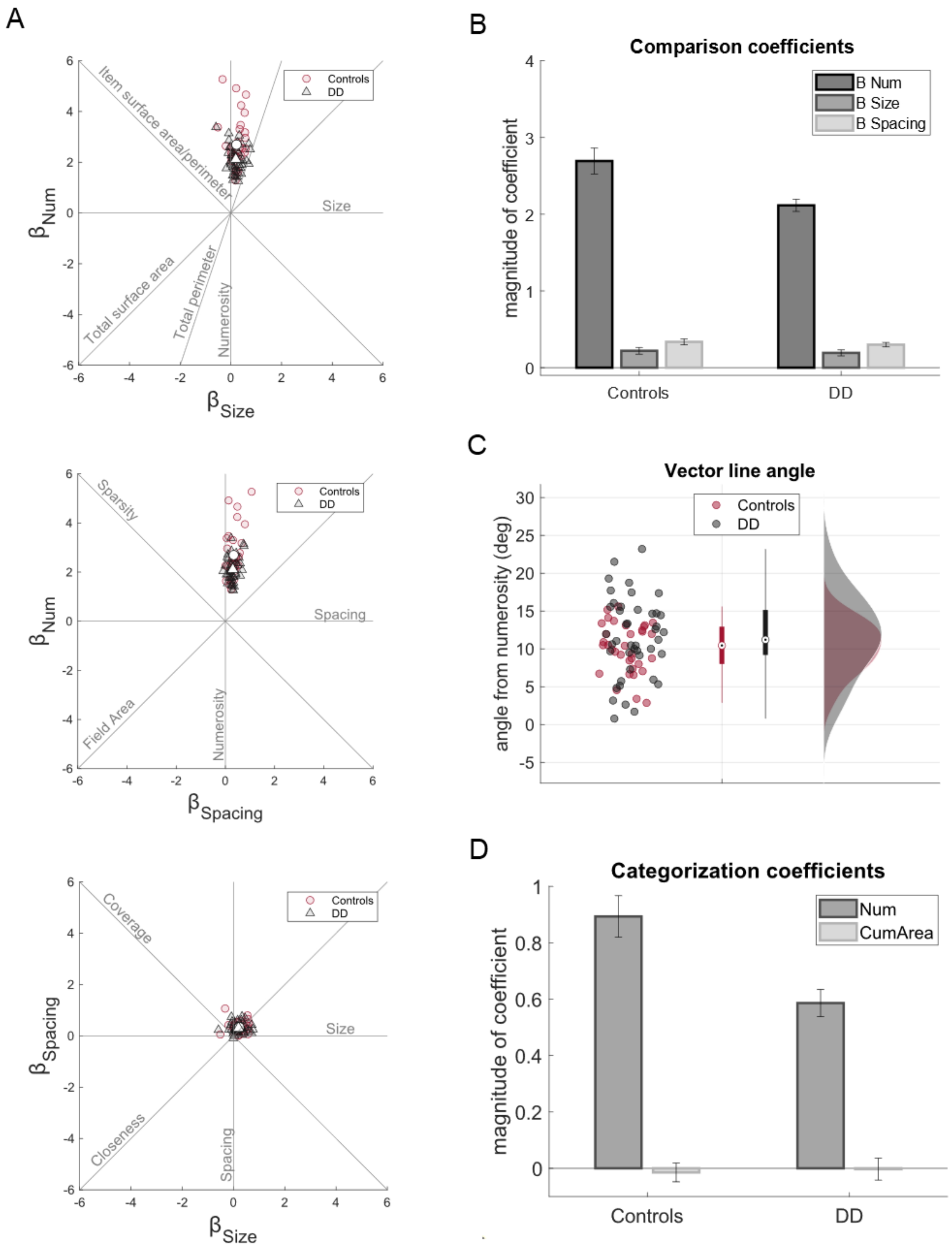

Figure 5.2 Results from experimental tasks. (A) Scatter plots of the coefficients for Numerosity, Size and Spacing, plotted pairwise. Colored shapes (red dots: control group; black triangles: DD group) represent individual participants, white shapes represent group average. Grey lines represent non-numerical visual magnitudes. (B) Mean GLM coefficient estimates (and standard error) in the two groups. (C) Distribution of the angles between individual discrimination vectors and the numerosity dimension in the two groups. (D) Group coefficients (and standard error) for numerosity and cumulative area in the spontaneous categorization task.

The mixed effect logistic model of trial-by-trial accuracy with congruency condition (fully congruent, Size congruent, Spacing congruent, fully incongruent) and group (DD or Controls) as fixed effects and including a random intercept of participant revealed a significant effect of group, with higher accuracy in the Control group compared to the DD group ($\chi^2(1) = 10.84$, $p < .001$), as well as a significant effect of congruency condition ($\chi^2(1) = 441.21$, $p < .001$). The interaction between group and congruency was instead not significant ($\chi^2(1) = 0.51$, $p < .92$). Post hoc tests revealed that the entire sample (both DD and Controls) presented an overall higher accuracy in fully congruent trials (M = 0.92, SD = 0.05) compared to all other conditions, higher accuracy in Spacing congruent trials (M = 0.87, SD = 0.07) compared to Size congruent ones (M = 0.83, SD = 0.06), and a lower performance in fully incongruent trials (M = 0.73, SD = 0.10) compared to all others (all $z > 4.50$, all *p*s < .001).

5.3.2 Spontaneous categorization

The analysis of the categorization task focused on probe trials, where numerosity and total surface area were independently varied. We estimated the relative contribution of numerosity and total surface area on the category selection at the group level with a mixed-effects logistic regression model with numerosity and total surface area as predictors of trial-by-trial category choice. In the DD group, Wald tests of fixed effects revealed a significant effect of numerosity (β (SE) = 0.59 (0.05), $\chi^2(1) = 149.53$, $p < .001$), while the effect of cumulative surface area was not significant (β (SE) = -0.003 (0.03), $\chi^2(1) = 0.006$, $p = .94$). Similarly, in the control group it emerged a significant effect for numerosity (β (SE) = 0.89 (0.07), $\chi^2(1) = 147.30$, $p < .001$) but not for area (β (SE) = - 0.01 (0.03), $\chi^2(1) = 0.19$, $p = .66$). The coefficient estimate of numerosity was smaller for the DD group compared to the Control group ($z = 3.50$, $p < .001$), while no difference emerged in the estimate of cumulative surface area ($z = -0.23$, $p = .82$) (see Fig. 5.2d).

Additionally, the effect of congruency on the proportion of numerically categorized probe trials was investigated with a mixed-effect logistic model with congruency condition (congruent or incongruent) and group (DD or Controls) as fixed effects, and participant as random intercept. A significant effect of the group was individuated, with a higher performance in the Control group compared to DD ($\chi^2(1) = 8.84$, $p = .002$). Instead, the effect of congruency and the interaction between congruency and group were not statistically significant.

5.4 Discussion

The current study aimed to investigate non-numerical biases in developmental dyscalculia during explicit and implicit quantity judgments to evaluate numerical and non-numerical deficits in

DD. To this aim, we compared the performance of children with and without dyscalculia in a numerosity comparison task designed to evaluate the influence of non-numerical cues and in a spontaneous categorization task assessing the relative saliency of numerosity and total surface area.

We found that, in both tasks, typically developing children and children with DD based their responses primarily on the numerical information present in the images. However, in the explicit numerosity comparison task, both groups showed a significant interference from non-numerical features, with an overall positive bias from the size of the elements and their spreading in space. This result adds to the large body of evidence showing how numerosity judgments are modulated by continuous magnitudes of the dot arrays (Abalo-Rodríguez et al., 2022; Clayton et al., 2015; Dakin et al., 2011; DeWind et al., 2015; Gebuis & Reynvoet, 2012b; Salti et al., 2017). However, while the numerical overestimation of sparser arrays seems a strong effect, the direction of the size bias is still debated, with evidence for an over-and underestimation of large items or failure in detecting any bias (Gebuis & Reynvoet, 2012b; Nys & Content, 2012; Starr et al., 2017). This inconsistency emerged also in the present categorization task, where, differently from the explicit task, both DD and controls showed negligible influence from the cumulative area of the elements. However, the discrepancy between the two tasks could be explained by differences in non-numerical feature manipulations. While, in the categorization task, numerosity and total surface area varied in similar ranges, in the comparison task, we used a larger range of size ratios compared to numerical ones, which could have contributed to increasing the saliency and thus reliance on the corresponding perceptual cues (DeWind & Brannon, 2016; Salti et al., 2017). Previous studies that equated perceptual saliency of numerical and non-numerical changes failed to find biases due to item size in the general population (Castaldi et al., 2018).

Crucially, in both computerized tasks, children with DD showed lower performance than their peers, resulting in a reduced numerical acuity in the comparison task and a weaker number-based focus in the spontaneous categorization task. Nevertheless, in both tasks, we did not detect a concurrent increase in non-numerical bias. This pattern of results is therefore not consistent with domain-general accounts of dyscalculia that link poor numerosity judgments to higher interference from task-irrelevant information due to deficits in executive functions (Bugden & Ansari, 2016; Szucs et al., 2013). Moreover, these results are also difficult to reconcile with the proposal that children with dyscalculia would present a delay in domain-specific filtering mechanisms that, through education and symbolic numerical learning, would help differentiate numerical and non-numerical quantities (Piazza et al., 2018). In particular, this interpretation is not supported by the consistent selection of numerosity as the task-relevant dimension in the spontaneous categorization task, despite the learning phase equally encouraging children to rely on non-numerical information. Last, it has also been suggested that increased non-numerical biases could emerge if individuals with dyscalculia used non-numerical cues as a compensatory strategy for an imprecise numerical representation (Castaldi et al., 2018). In line with this interpretation, individuals in the current DD sample presented a reduced precision in discrimination and a weaker numerosity-based categorization consistent with a deficit in numerical representation. However, the lack of an increased non-numerical bias suggests that participants with DD did not additionally exploit other perceptual characteristics of the images to solve the tasks.

Overall, the lack of evidence for increased non-numerical bias is difficult to reconcile with previous studies that consistently showed enhanced congruency effects in DD across comparison and estimation tasks, both in children and adults (Bugden & Ansari, 2016; Mejias, Mussolin, et al., 2012; Mussolin, Mejias, et al., 2010; Piazza et al., 2018). Such inconsistency might be related to the different criteria in the sample selection (Peters & Ansari, 2019). In the present study, we tried to match children with dyscalculia and control children with similar visuospatial memory abilities, which could have resulted in similar non-numerical biases. A previous investigation using a similar matching procedure (Decarli, Sella, et al., 2022) similarly did not find increased congruency effects in DD in performing the Panamath numerosity comparison task (Halberda et al., 2008). Although in that task they did not find any difference in performance between DD and controls, they identified a lower performance in DD in a non-symbolic match-to-sample task. Previous evidence also suggests that DD can be a heterogeneous disorder (Fias et al., 2013), including subtypes characterized by different numerical deficits (Skagerlund & Träff, 2016) or by the co-occurrence of domain-general and domain-specific impairments (Bartelet et al., 2014; Kaufmann et al., 2013; Peng et al., 2018). Moreover, it must be noted that our result is in line with previous evidence that showed, in a similar spontaneous categorization task, a positive relation between mathematical skills and the perceptual salience of numerosity, but not of area (Ferrigno et al., 2017).

In conclusion, the current results show that children with developmental dyscalculia present impairments in numerosity judgments that cannot be ascribed to increased interference effects from task-irrelevant magnitudes. While we do not claim that visuospatial working memory or inhibition skills are not important predictors of mathematical abilities, the current result suggests that the deficits shown by DD in numerosity judgments cannot be entirely ascribed to enhanced interference from non-numerical cues due to domain-general deficits, suggesting the presence of a domain-specific deficit related to a noisier numerical representation.

6 Chapter 6

CUSTOM GUIde: a program to generate visual arrays[4]

6.1 Introduction

The studies presented in the previous chapters add to the large amount of evidence in the numerical cognition literature showing that, during numerical decisions, both children and adults can be influenced by other spatial and temporal magnitudes. However, as previously stated, further investigation is needed to understand the locus of the interplay between numerosity and continuous quantities, from sensory extraction (Gebuis et al., 2016), representation (Walsh, 2003) or response-selection (Nys & Content, 2012). Importantly, differentiating between these alternative hypotheses is crucial for understanding the mechanisms of numerosity perception and the development of basic numerical skills. For example, studies investigating the mechanisms of extraction of numerical information have manipulated visual cues to disentangle numerosity related and unrelated neural response in the visual stream (Castaldi et al., 2019; Fornaciai et al., 2017; Harvey & Dumoulin, 2017b; van Rinsveld et al., 2020). Similarly, the investigation of non-numerical interference revealed a developmental improvement in the ability to focus on numerical information during numerical tasks, highlighting the importance of filtering mechanisms in the maturation of number perception (Piazza et al., 2018; Starr et al., 2017). Moreover, a better understanding of the relation between interference effects and executive functions might be informative also in determining the role of basic number processing in the development of later mathematical abilities (Cragg & Gilmore, 2014). In sum, the interaction between numerosity and continuous visual cues has grown from a nuisance factor to a theoretically relevant aspect to understand the mechanisms of numerosity processing. Therefore, a precise manipulation of continuous magnitudes has become a necessity in a wide range of empirical studies in the field of numerical cognition.

[4] In collaboration with Damiano De Marco and Simone Cutini. We also thank A.D., G.D., E.D., R.S. and M.S. for helping in the beta testing of the program.

As previously underlined, numerosity processing is commonly assessed through the presentation of non-symbolic visual stimuli such as arrays of dots, asking individuals to estimate the numerosity of a group of elements or to report the most numerous between two groups of objects. Several methods have been developed to dissociate numerosity from continuous visual features in this type of experiments. Some of them rely on measuring differences in response related to congruency between numerical and non-numerical information (Gebuis & Reynvoet, 2012a; Salti et al., 2017), while another common approach is based on an independent and parametric variation in numerosity and other visual cues to estimate their separate contribution to behavioral or neural responses (DeWind et al., 2015, 2018). In both cases, useful algorithms to replicate such designs with similar visual stimuli have been made publicly available (Gebuis & Reynvoet, 2012a; Park, 2021; Salti et al., 2017). However, the stimuli produced by those algorithms are inevitably tied to the underlying theoretical background and experimental paradigm (although they can be adapted to novel studies). Moreover, it is worth noting that some manipulations might introduce an imbalance in saliency between numerosity and non-numerical cues (Salti et al., 2017); similarly, specific stimulus designs and protocols might consistently yield different biases originating from non-numerical cues (Clayton et al., 2015; DeWind & Brannon, 2016). Thus, methodological differences in stimulus design can also result in subtle biases in favor of the theoretical frameworks in which they are developed (De Marco & Cutini, 2020). Therefore, researchers need to carefully consider the implications related to the use of a particular algorithm developed to adopt a specific method.

To overcome this issue, more general-purpose instruments to help researchers in generating non-symbolic numerical stimuli have been developed in the latest years (De Marco & Cutini, 2020; Guillaume et al., 2020; Zanon et al., 2022). These programs allow the creation of single arrays or pairs of collections with control over the physical appearance of the images, without being necessarily tied to a specific method. However, they present important differences in the precision of the creation, the features that they take into account, as well as the options available to users (for a detailed comparison, see Zanon et al., 2022). For example, GeNEsIS (Zanon et al., 2022) is a multi-step app that offers high flexibility and precision over features manipulation and has the option to display the stimuli for several experimental designs, but it requires the manual definition of all the characteristics for subsets of single arrays. NASCO (Guillaume et al., 2020), provides the option to directly manipulate the features of pairs of collections or to define multiple sets of images, but with reduced flexibility in the manipulation of the size of the elements. Finally, CUSTOM (De Marco & Cutini, 2020) is constituted by multiple algorithms for a flexible and precise generation of single arrays or pairs of arrays but its usability is severely hindered by the absence of a graphic user interface.

To overcome such limitation, we developed CUSTOM GUIde, a new tool based on a graphical user interface, to facilitate the generation of non-symbolic numerical stimuli with high precision in the control of several visual magnitudes. The program is implemented as a MATLAB app based on the algorithms available in CUSTOM (De Marco & Cutini, 2020), updated and expanded to meet the necessity of researchers with different scientific backgrounds on number processing and programming expertise. To this aim, the program was equipped with a graphical user interface divided in different modules for each of the original functionalities of CUSTOM, so that users can generate datasets of single arrays or pair of arrays varying independently the number, dimension, and position of the elements in the arrays. The interface makes immediately and clearly available to the user the different options for the manipulation of visual features, as well as new customization options (e.g., change in shape of the elements of the arrays, change in shape of the field area) that were previously internal parameters of the functions. Moreover, additional modules were developed to allow a more automatic definition of subsets based on the desired relationship between numerosity and visual features and to facilitate the replication of pre-existing datasets. Crucially, CUSTOM GUIde is a tool meant to rapidly generate stimuli tailored to the preferred design of the experimenter, since it is not tied to any specific method of feature control or manipulation.

6.2 Method

CUSTOM GUIde is a program implemented in MATLAB (MATLAB R2020a, The MathWorks Inc., Natick, Massachusetts, USA) through MATLAB App Designer. With this program, users can easily create stimulus sets of visual arrays of elements with a precise control over the physical qualities of the images. The underlying code to create the stimuli is based on the CUSTOM toolbox described in a previous work (De Marco & Cutini, 2020). The unpackaged app code will be shared to be freely downloaded, together with tutorials, examples and additional detailed documentation. To use it, MATLAB R2020a or more recent versions are required, without any additional toolbox. The program has been tested on Windows (Windows 10 Intel® Core™ i7-1065G7 - CPU: 1.30 GHz- RAM: 16 GB, Intel® Core™ i5-7400 - CPU: 3.00 GHz - RAM: 12 GB, AMD Ryzen 7 3700U - CPU: 2.30 GHz- RAM: 8 GB) and macOS (macOS Catalina on a MacBook Pro Intel® Core™ i5 - CPU: 2.6 GHz - RAM: 8 GB).

6.2.1 Structure of the program

CUSTOM GUIde is organized in independent modules that allow the generation of non-symbolic numerical datasets for several experimental designs, based on the necessities of the user. A *Single stimulus* module can be used to generate single images with arrays of objects or pairs of arrays.

With a *Manual set generation* section, it is possible to create stimulus sets of single arrays or pairs of arrays by manually defining numerosity and several features related to their size and position. The *Guided set generation* module allows to create sets of single arrays by specifying a correlation between number and non-numerical magnitudes or sets of pairs by defining the ratio between numerical and non-numerical properties. Finally, the *Load and generate* section can be used to create different sets of arrays or pairs with features defined in pre-specified CSV files. Last, additional parameters affecting the stimuli appearance and their creation can be specified in a *Setting* page. The different modules are described in the following paragraphs, and an overview of the program organization is depicted in Fig. 6.1. Moreover, a thorough explanation of each component of the app is present in the extensive documentation that can be downloaded with the program.

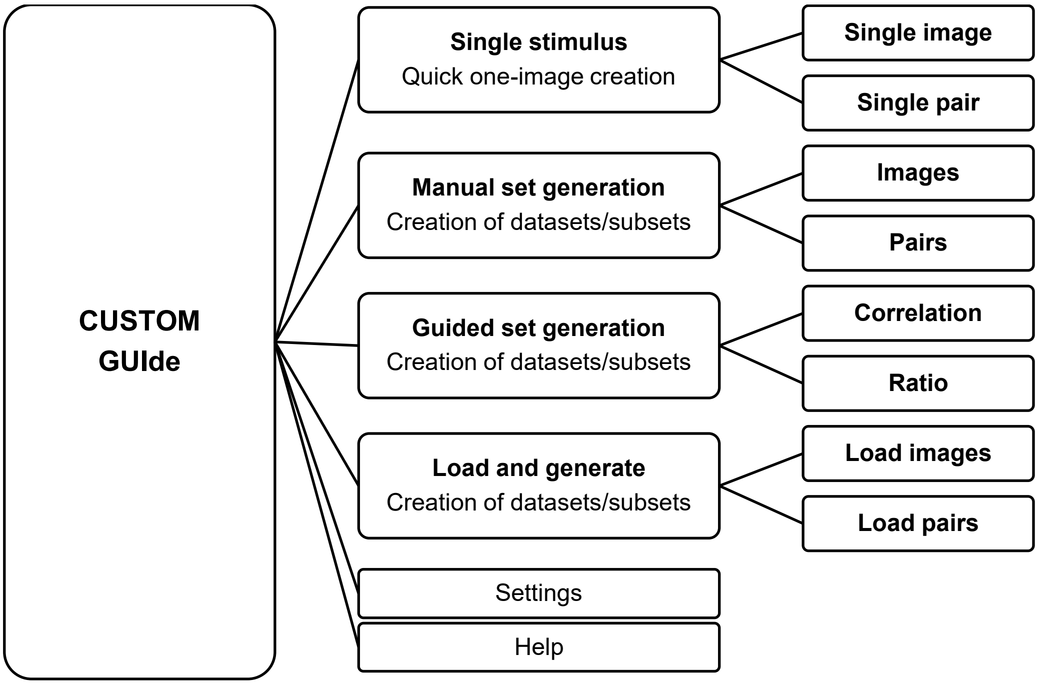

Figure 6.1. Organization of CUSTOM GUIde: different modules allow the creation of single stimuli or entire datasets, offering different methods to specify the visual properties of the arrays. Separate tabs can be used to create single arrays or pairs of arrays.

6.2.2 General parameters of images

CUSTOM GUIde can be used to create a single array of objects or pairs of arrays by specifying parameters related to the number of elements, their dimension, and their placement in the image. In all the different modules, users can manipulate the dimension of the elements, specifying the size of individual objects by selectively defining their *Radius* (or side length, in case of shapes other than circles) or *Individual item area*. Alternatively, users can control the total size of the array by specifying a *Total surface area* or *Total perimeter*. Moreover, it is possible to create arrays that are homogeneous in size or to include variability in the radii/sides of the individual items. Independently from the selected control for the size of the objects, users can manipulate their placement in space, by specifying a general *Field area* in which elements can fall or, more specifically, a *Convex hull* area (i.e., the area of the smallest polygon that will contain all the elements). When creating pairs of arrays, users can specify different values for the two groups of elements. Moreover, the distance between the center of mass of the two collections can be varied in order to generate pairs as arrays of dots separate in space or as color-based pairs with overlapping field areas, similar to the Panamath algorithm (Halberda et al., 2008). In the latter case, it is also possible to directly control the area of appearance of all the elements in the image. Along with the size and positioning control, other general characteristics of the stimuli can be specified, such as the dimension (in pixels) of the image or the RGB color of the background and of the elements.

6.2.3 Generation process

The creation of the images is instantiated with the CUSTOM algorithms (De Marco & Cutini, 2020). The general workflow consists in a Sizing phase to generate objects with a specified dimension and a second Placing phase to achieve a placing compatible with users' requests.

In the initial Sizing phase objects are generated based on the specified dimension and requested variability in element size. It must be noted that, due to geometrical constraints, the size of the elements can be defined by a single feature at a time. This has important implications for the characteristics of the final datasets, since equating one feature will result in a variation in another non-numerical feature, in proportion to the number of elements of the array. For example, while total surface area is kept constant, increasing the number of elements will lead to a negative correlation between numerosity and item size; on the contrary, equating item surface area in arrays with different numerosity leads to a positive relationship between numerosity and total surface area. Similarly, in a pair of arrays with different numbers of objects, equating item surface area automatically leads to congruency between total surface area and numerosity, while equating total surface area leads numerosity to be incongruent with item surface area. As presented in previous chapters, the same relationship also characterizes other extensive/intensive features related to the position of the elements, such as field area/convex hull and density.

In the Placing phase the elements are arranged in the image to achieve the control intended by the user. In particular, precise control over the convex hull area is achieved through an initial placement of the elements and progressive adjustments proportional to the distance between each element and the center of mass, until the expected convex hull value is reached. In this case, a

Tolerance value allowing a certain degree of error in the placement can be specified by the user, to increase the speed of the creation. Finally, iterative discard is used if images do not respect the required feature definition.

Users can create collections of different shapes such as dots, squares and triangles. The Sizing and Positioning phases are always based on circular shapes, but an internal conversion of the features offers a precise manipulation of the dimension and position of the elements (although, in case of shapes other than dots, convex hull measures will be approximated to the circles in which the squares or triangles are inscribed). Finally, users can customize the format in which they prefer to save the specified images and associated database with summary information regarding the physical characteristics of the arrays. In all modules of the program, output images can be saved as PNG files and a table with their characteristics can be generated as a CSV file. Moreover, both the table and the images can be directly saved in a MATLAB file. Notably, in addition to the specified characteristics that can be used for generation, for each image the program provides additional measures of density (total surface area/convex hull), an alternative measure of average distance between dots and a measure of average distance from the center of mass.

6.3 CUSTOM GUIde overview

6.3.1 Single stimulus

In the *Single image* and *Single pair* tabs, users can generate a single array of objects or a pair of arrays and immediately visualize the generated images and the corresponding output table of features directly in the interface (see Fig. 6.2). Each array is defined by the number of elements, a control method for the Sizing and Placing and the corresponding value (in pixels) of the selected variables. In case of pairs, users can create separate arrays or reduce the central spacing between the arrays to create color-based pairs with overlapping field areas (see Fig. 6.3a-b). In case of overlapping arrays, by default the program generates distinct sets of completely visible elements; however, additional options allow to include partial occlusion between arrays.

The *Single stimulus* module is meant to let users familiarize with the program environment and options, as well as with the visual parameters. To this aim, in this section the user is guided by default values that change dynamically with numerosity, image size, size control and position control. Notably, default values are intended as a starting point for the user to individuate an appropriate range of features for the selected numerosity and image size and to emphasize the relation between numerical and non-numerical magnitudes. In addition, users can also visualize the physical properties by graphically highlighting in the output image continuous magnitudes such as Total surface area, Total perimeter and Convex hull (see Fig. 6.3c).

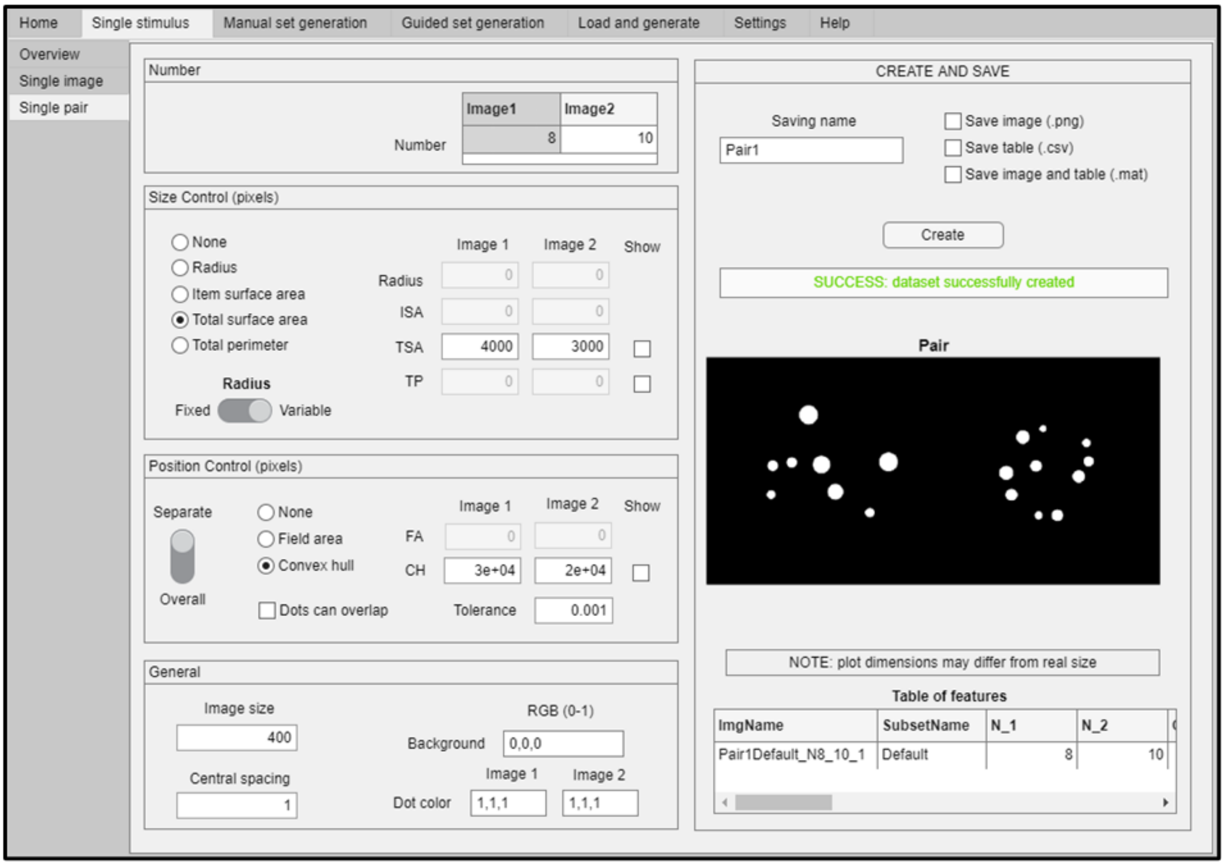

Figure 6.2. Graphic interface for the Single pair tab: In this section, users can generate pairs of arrays by separately defining their numerosity and non-numerical features determining their Sizing and Positioning. Generated images are directly shown in the interface, together with a table of their relevant visual characteristics.

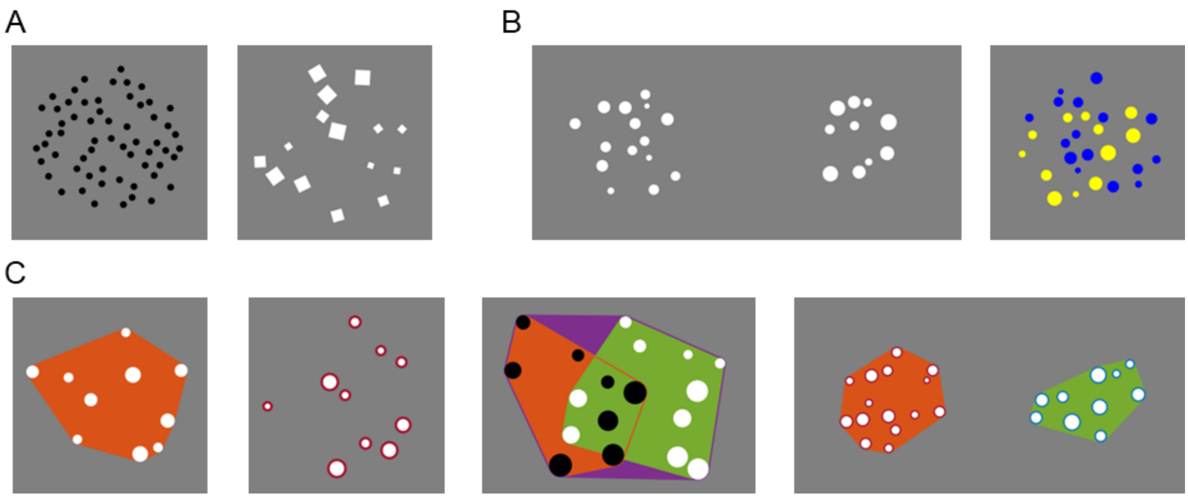

Figure 6.3. Examples of generated images: (A) Examples of single arrays with homogeneous and heterogeneous item size. (B) Examples of pairs, separated in space or defined by different colors. (C) Users can graphically highlight several properties of the arrays, such as the Convex hull area or the Total perimeter.

6.3.2 Manual set generation

The *Manual set generation* module offers the possibility to create sets of multiple single arrays or pairs of arrays (see Fig. 6.4). Differently from the creation of single stimuli, the Images and Pairs tabs allow to specify more numerosities, in order to create one or more stimuli with different numerosities or multiple instantiations of the same numerosity, characterized by the same manipulation of visual properties.

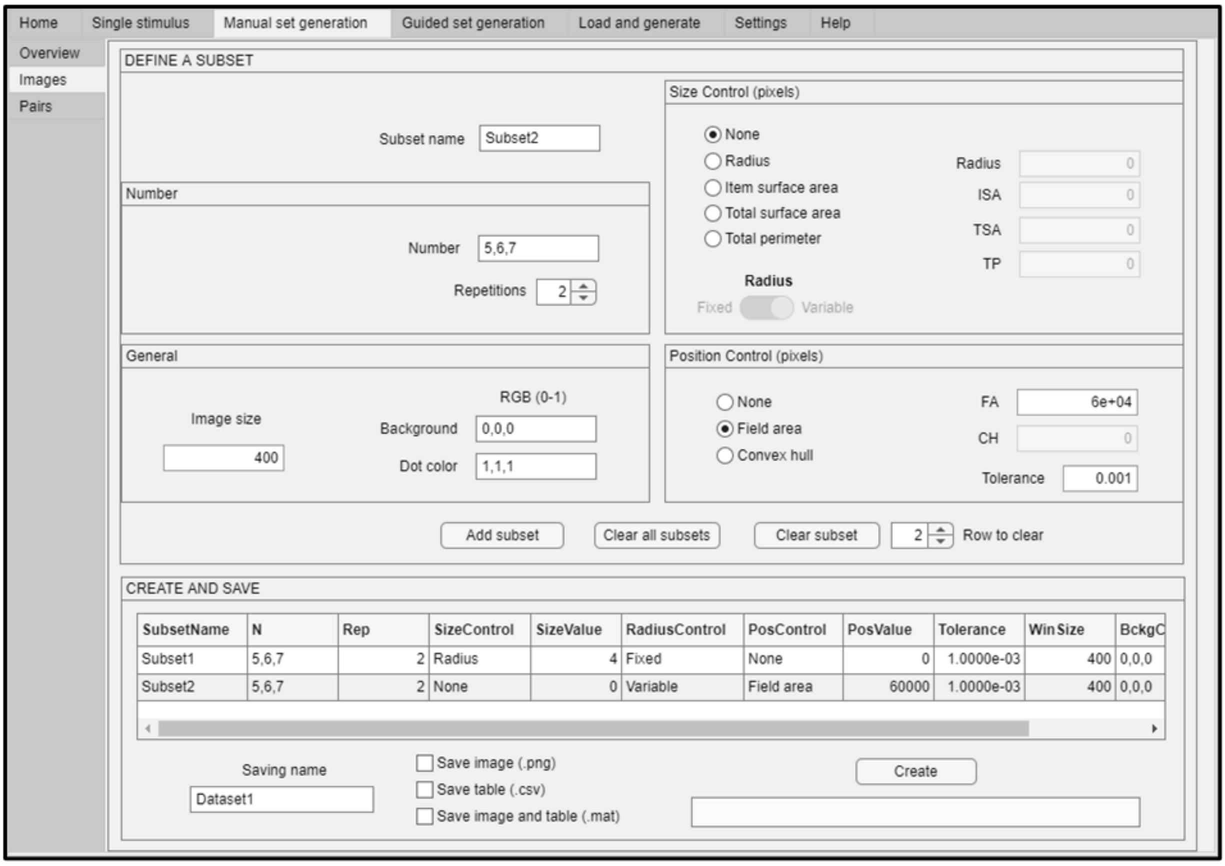

Figure 6.4. Graphic interface for the Images tab in the Manual set generation module. In this section, users can generate subsets of arrays defined by different combinations of numerosity and non-numerical features. Multiple subsets can be specified and reviewed in the corresponding table before generation.

The goal of the *Manual set generation* section is to define multiple subsets of arrays with different combinations of numerosity, Sizing and Positioning control. Subsets of single arrays can be used to incorporate variability in the visual features present in the dataset or to create different correlations between numerosity and visual magnitudes. In addition, in this module users can use multiple subsets to create datasets of stimuli varying independently in numerosity and other visual quantities (see Fig. 6.5). When generating pairs, subsets can be used to create different congruency conditions between numerosity and size or positioning variables or to counterbalance the side or color of the largest array.

The characteristics defining a subset can be temporarily stored in the interface and can be reviewed in the corresponding table before generation, which allows to define multiple subsets at the same time maintaining an overview of the characteristics of previous subsets. Different names can be specified for different subsets and datasets, and they will be reported in the output table and image files based on the selected saving options. Although in this section images and feature tables are not directly shown in the app by default, modifying the additional *Settings* (see Section 6.3.5) it is possible to periodically visualize the stimuli (e.g., one image every five times) during the generation process.

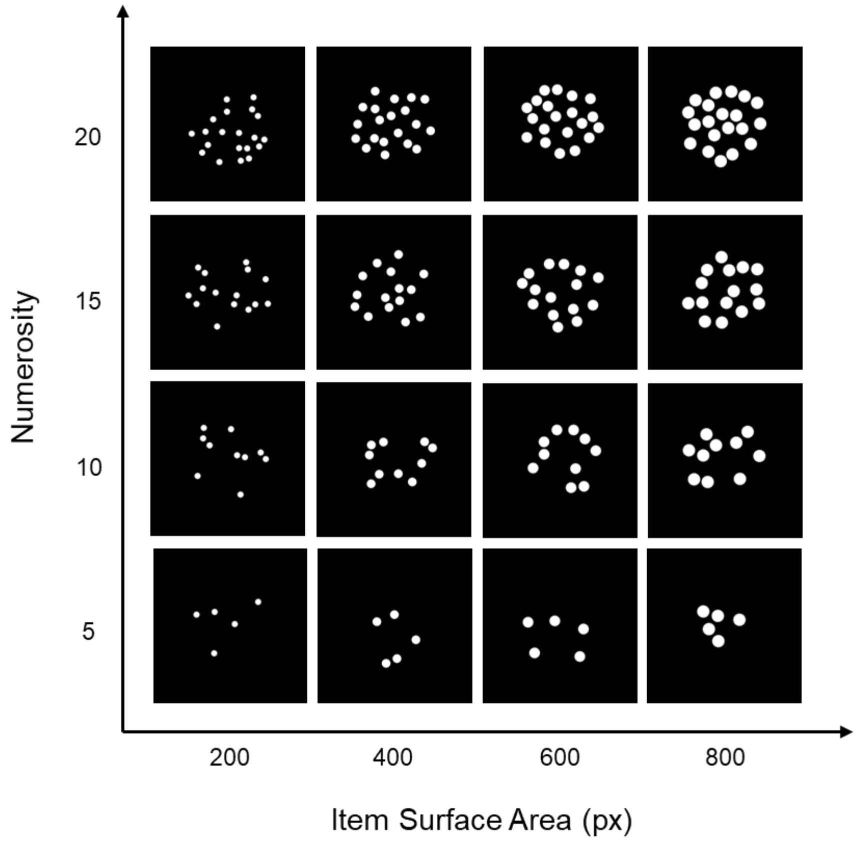

Figure 6.5. Example of images created with Manual set generation: images with orthogonal manipulation between numerosity and Item surface area, created using four different subsets (one for each ISA value) in the Manual set generation module.

6.3.3 Guided set generation

In the *Guided set generation* section, users can generate datasets by specifying in broader terms the relationship between numerosity and non-numerical features. In the *Correlation* tab (see Fig. 6.6a) users can generate sets of single arrays. After defining the desired number of elements, users can select the visual properties to manipulate and define a range of values (in pixels), specifying a positive (+) or negative (-) correlation between numerosity and the selected features. The program will then generate arrays with feature values in the entire specified range between the minimum and maximum value provided by the user, directly or inversely proportional to numerosity (see Fig. 6.6b). Multiple repetitions for the same numerosity can be specified: in this case, all instances will be generated from the same combination of numerosity and visual properties.

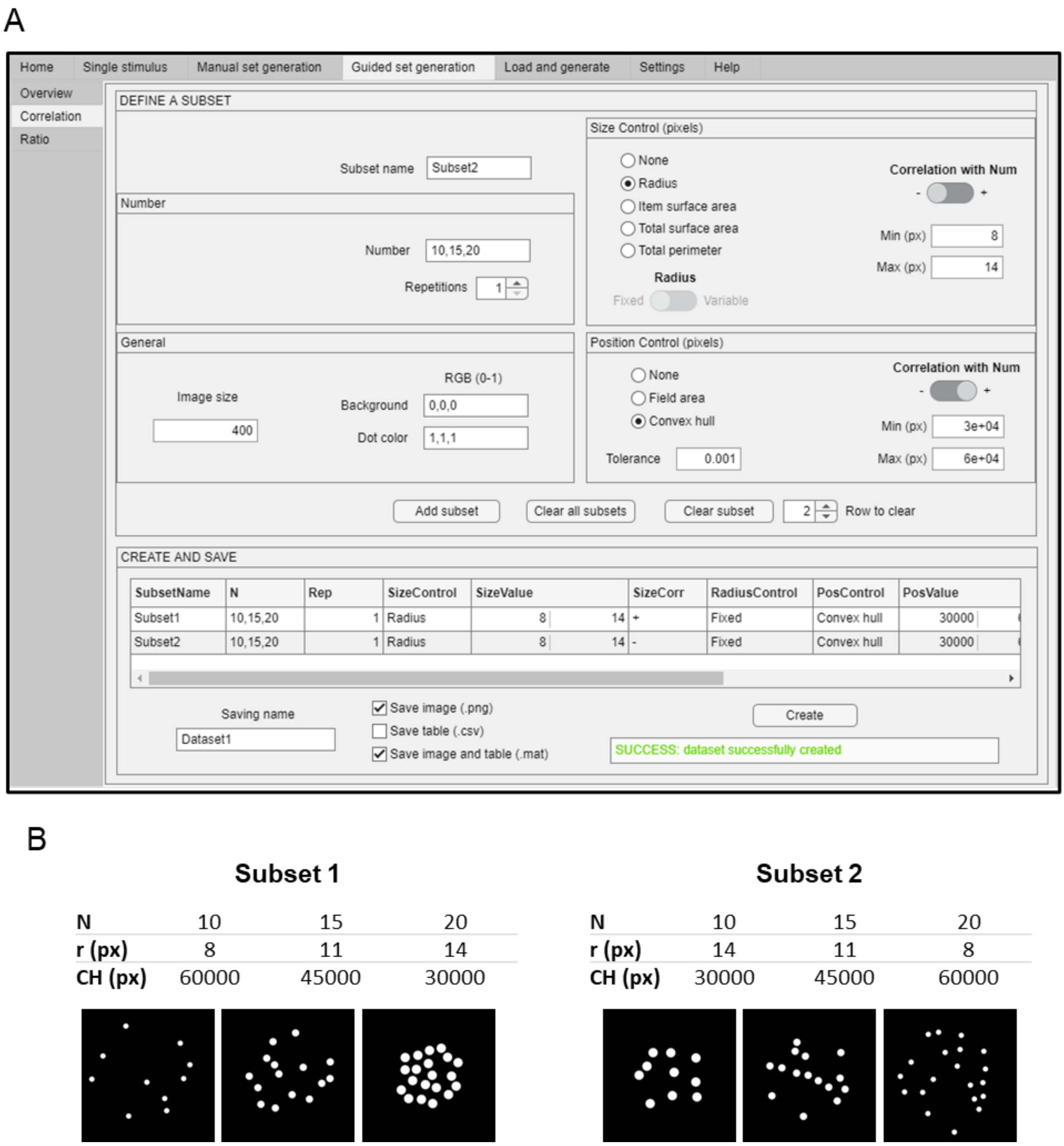

Figure 6.6 Graphic interface and images from the Correlation tab in the Guided set generation module. (A) In this section, users can generate subsets of arrays defined by different correlations between numerosity and non-numerical features. (B) On the left, an example of a subset of single arrays with a positive correlation between numerosity and item size and a negative correlation between numerosity and convex hull; on the right, a subset with a negative correlation between numerosity and item size and a positive correlation between numerosity and convex hull.

In the *Ratio* tab (see Fig. 6.7) sets of pairs can be defined by manipulating the ratio of numerical and non-numerical features between the two arrays. Users are required to define a reference numerosity and select the visual properties to control, by indicating a corresponding range of values (in pixels). Then, pairs of arrays can be generated by specifying independently: i) the ratio between the two arrays in numerosity and ii) the ratio of the selected non-numerical parameters. Each pair will then be generated by randomly selecting both the feature reference values and paired arrays in the defined range, through an iterative process discarding inappropriate combinations based on the desired ratios. In case of large datasets, users can decide to create more instances of the same pairs; in case of multiple repetitions, the precise values of the selected sizing and positioning variables are randomly selected in the specified range for each instantiation.

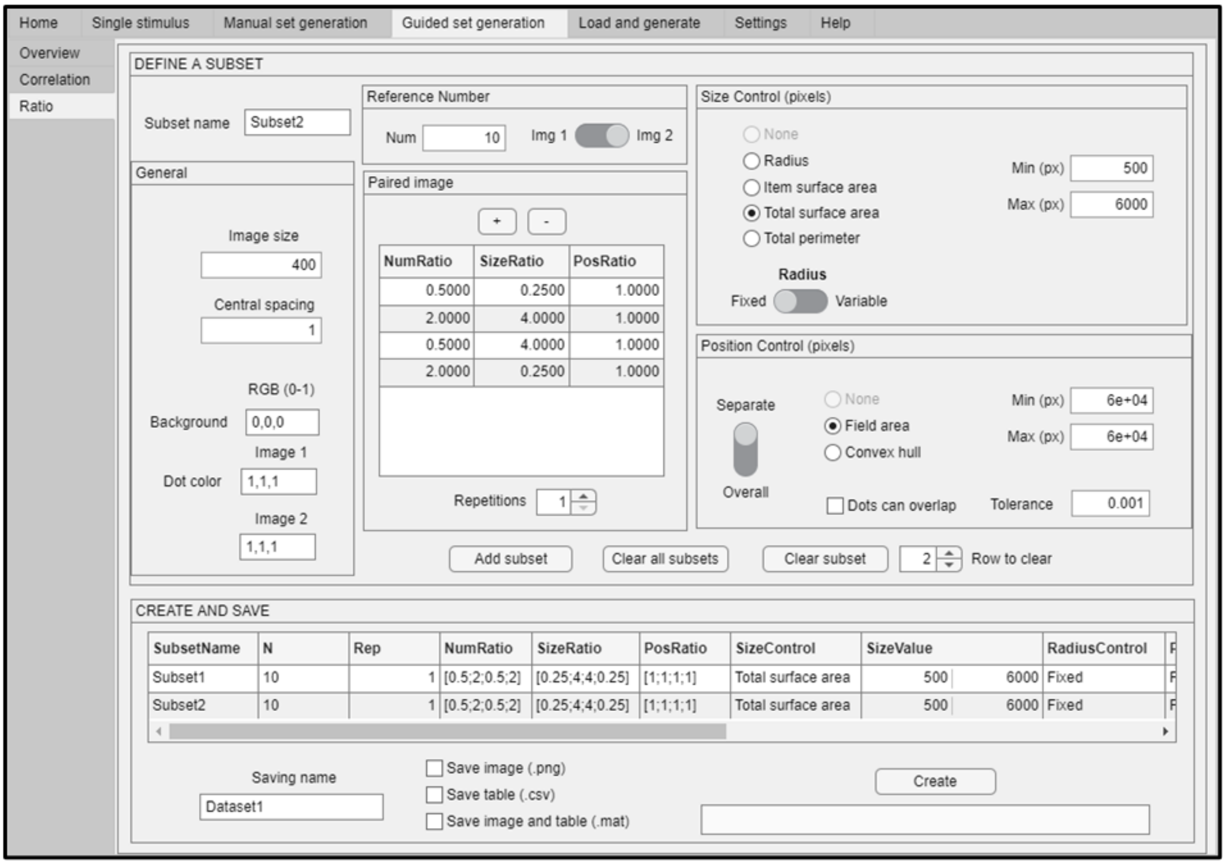

Figure 6.7 Graphic interface of the Ratio tab in the Guided set generation module. In this section, users can generate subsets of pairs defined by different ratios in numerosity and selected non-numerical variables between the two arrays.

The objective of the *Guided set generation* modules is to offer an alternative method to generate datasets based on explicit relations between numerosity and non-numerical properties. Although similar manipulations can be achieved also in the *Manual set generation* module, in this section the explicit definition of the relationship between numerosity and continuous visual properties and the automatized selection of appropriate feature values leads to an easier and faster generation of the required datasets. For example, users can define subsets of pairs with different congruency conditions. Even in this case, by defining multiple subsets it is possible to create datasets with different correlations or congruency conditions between numerosity and size or positioning features (see Fig. 6.8).

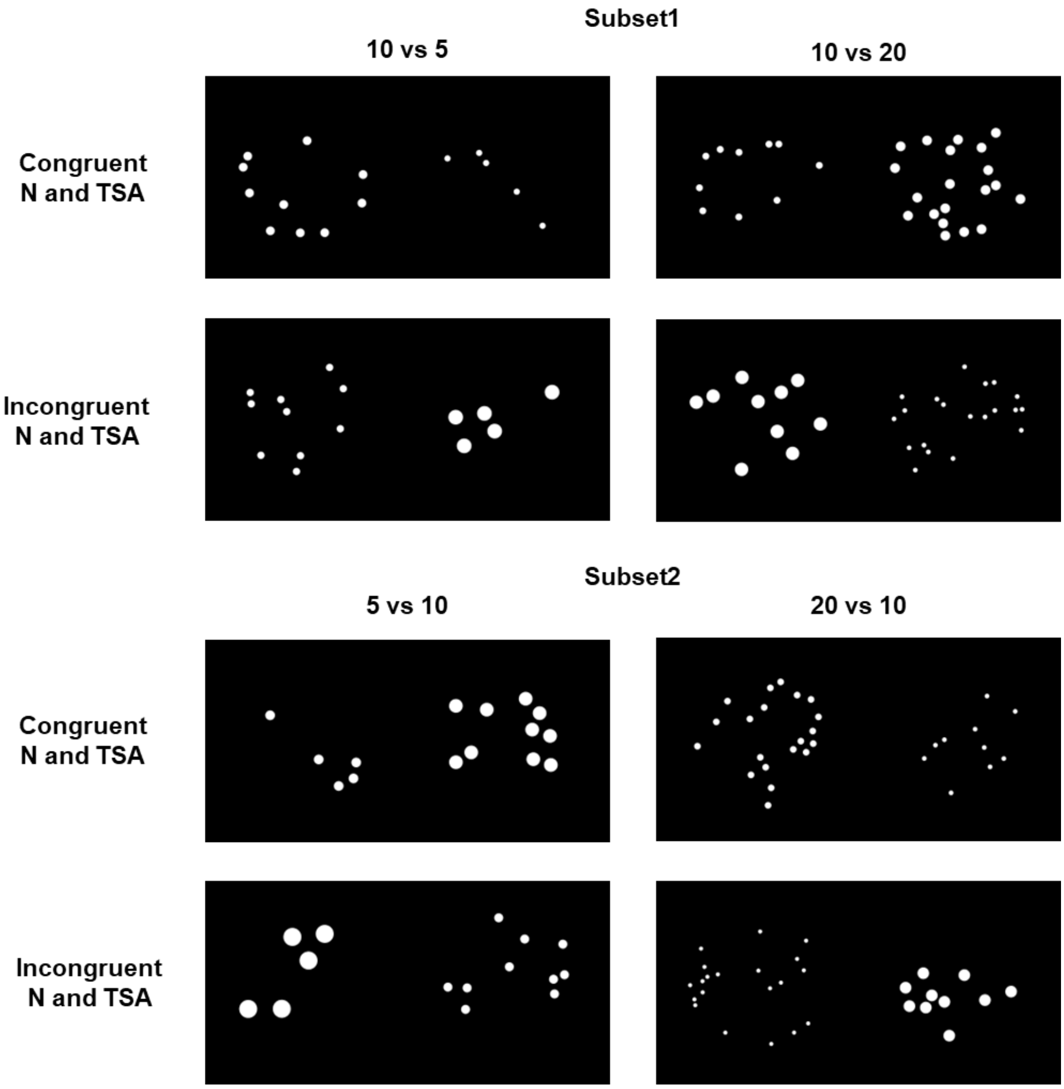

Figure 6.8. Example of images created with the Ratio tab. Images generated from the two subsets shown in Figure 6.7, where numerosity is either congruent or incongruent with total surface area and with counterbalancing of the side of appearance of the array with larger numerosity and larger total surface area.

6.3.4 Load and generate

In the *Load and generate* module, users can create datasets from features defined in pre-specified files. Lists of stimuli and corresponding features can be imported in the app from a CSV file, to generate them with the CUSTOM algorithms. The imported lists can be reviewed in the app before generation. Appropriate variable names and feature control definition are explained in detail in the *Help* page of the program as well as in the additional software documentation. Moreover, a dialog box will display errors if incompatible combinations of features are detected in the specified dataset. Users need to provide specific feature values for each stimulus, but they can set some general characteristic, like the color of the dots, directly from the interface. This section enables experienced users to generate images for complex stimulus designs for which the manual definition of subsets could be time-consuming. In addition, this module is a useful tool to replicate existing datasets and enhance comparability between studies adopting similar methods.

6.3.5 Additional settings

The *Settings* tab contains additional functionalities that were previously defined by internal parameters in the CUSTOM package, to offer a more direct control over advanced properties of the stimuli or the process of image generation, affecting all modules.

Advanced stimulus settings can be used to define the shape of the elements to place in the arrays (dots, squares, or equilateral triangles), with homogeneous or random orientation. Moreover, users can modify the shape of the field area (circular or square) as well as its placement in the image (centered or randomly placed). Last, users can personalize the minimum distance between the objects and the default size range of individual elements when no control is specified for the Size control.

Regarding control over the creation process, users have the option to check the progress in creation during the generation of datasets, through a periodic visualization of the output images directly in the interface. A personalization of the creation algorithm is offered by control over the number of iterations to use in the separate phases of generation and specifically in the adjustment of each feature or the number of resets of stimulus creation in case of failure. Moreover, when creating pairs defined by ratio, users can specify the number of attempts of the iterative process that selects values within the defined feature range to obtain the specified ratio, before reporting an error. Finally, through the Applied tolerance settings affecting Convex hull control, users can specify whether to create overall smaller than specified values, overall higher than specified values, or (default option) allow both smaller and larger values within the tolerance range to be accepted.

6.4 Design decisions and limitations

The main goal of CUSTOM GUIde is to help researchers to generate arrays of elements with precise control over the visual properties of the collections. As such, it is beyond its scope to include the possibility to directly implement experimental paradigms presenting images and recording participant responses. Although this option is present in some tools, it is necessarily limited to a small range of experimental task settings such as numerosity discrimination or habituation (Guillaume et al., 2020; Halberda et al., 2008; Zanon et al., 2022), which would not cover the large variability in experimental applications that stimuli created with this program can achieve.

CUSTOM GUIde is based on separate modules related to the different functionalities of the program. However, stimulus definition is not based on a step-by-step process. Instead of having a serial workflow reflecting the internal processes of generation, we believe that a simultaneous definition of all the numerical and non-numerical parameters of the arrays is helpful for taking into full consideration the interplay between different continuous magnitudes, beside the mere relationship between numerosity and other visual properties. Therefore, in each section we privileged a more comprehensive design that offers a general overview of all the different parameters affecting generation. Instead, separate modules aim at guiding users toward the easiest and fastest method to generate datasets based on experimental needs, required level of control over the physical appearance of the images, and user expertise. Furthermore, a modular design was selected to accommodate future development, to easily incorporate additional sections.

Last, two main limitations of the current program need to be addressed. First, the program does not currently support the creation of elements with other shapes than dots, squares, and equilateral triangles. Second, the current program does not allow a direct manipulation of the density of the arrays, although information regarding density and inter-dot spacing is reported a posteriori among the stimuli characteristics. This choice was motivated by a lack in consensus in the field over the geometrical definition of density, which is alternatively computed as the number of elements, or the area of the elements divided by space occupied (Dakin et al., 2011; Gebuis & Reynvoet, 2012a; Salti et al., 2017). However, it must be noted that an indirect control of density based on the preferred definition can be achieved by the manipulation of the corresponding features (e.g., a combination of Total surface area and Convex hull).

6.5 Discussion

The increasing awareness of how continuous quantities impact numerical judgments requires researchers to take into account the physical appearance of non-symbolic numerical stimuli used in empirical studies. We developed CUSTOM GUIde to propose a flexible and multi-purpose tool that eases the manipulation of continuous magnitudes when generating visual arrays in a user-friendly environment. With the program, users can create arrays of elements that may differ in number, dimension, and position. In addition, images are highly customizable in the shape and color of the elements of the arrays and in the position and shape of the field area, and it is possible to vary the center of mass of paired arrays enabling the creation of pairs separate in space or color-based pairs.

The high flexibility of CUSTOM GUIde allows users to create images suitable for all common paradigms used to investigate numerical cognition in human and comparative research, such as estimation, discrimination or habituation tasks, more complex tasks such approximate calculation, or passive viewing paradigms in electrophysiological or neuroimaging studies. The manipulation of the physical properties of the images is not tied to any underlying theoretical background and can be performed independently of a specific experimental task, allowing users to tailor image parameters to the specific research question under investigation.

Among the different manipulations that can be performed, CUSTOM GUIde enables the creation of different subsets that differs in the relation between numerosity and other non-numerical features, useful for designs based on reference and deviant stimuli (e.g., Guillaume et al., 2020; Piazza et al., 2004) or for the comparison of congruency conditions (e.g., Gebuis & Reynvoet, 2012a; Salti et al., 2017). Moreover, users can define parametric variations in non-numerical features of single images (Abalo-Rodríguez et al., 2022; Aulet & Lourenco, 2021; Castaldi et al., 2019; Ferrigno et al., 2017), or precisely manipulate the ratios of numerical and non-numerical features in pairs of arrays (Castaldi et al., 2018; Tomlinson et al., 2020). Examples and tutorials on how to replicate some of these stimulus designs using the interface are included in the documentation of the program.

Notably, the creation process is carried out in a user-friendly graphical interface that guides the user in the customization through an intuitive display of the different options and informative feedback such as warnings and errors. Several modules help the user with an automatic generation of stimuli based on a requested relationship between numerosity and visual features. Furthermore, during the creation of complex datasets, users can access detailed help pages directly in the interface and additional documentation and tutorials. Similarly, the Single stimulus section and the dynamic default values provided are intended not only for an initial familiarization with the parameters, but as a reference to obtain immediate feedback during the definition of complex stimuli (e.g., to test extreme combinations of parameter values).

Last, CUSTOM GUIde aims at increasing openness and reproducibility. In this regard, the possibility to create stimuli from predefined files allows to easily replicate virtually any existing datasets with known non-numerical features. At the same time, the program code is accessible and modifiable by experimenters based on their necessities, to enable full customization of more advanced settings and to encourage the development of new functionalities.

The presented aspects make CUSTOM GUIde a versatile tool to precisely generate non-symbolic numerical stimuli in a user-friendly environment designed for a wide range of expertise levels. This flexible program can facilitate the manipulation of visual properties of non-symbolic numerical stimuli for all the most popular experimental applications under different theoretical frameworks. In this regard, we believe that this program can represent a useful asset not only in numerical cognition, but also ensemble perception.

7 CHAPTER 7

Conclusive remarks

The common thread of the different contributions presented in this thesis was investigating the role of continuous magnitudes in numerosity processing and their impact on numerosity judgments, which is central to a long-lasting debate on how numerical information is extracted, represented, and manipulated and how it relates to more advanced symbolic numerical abilities. We approached this issue from three main different viewpoints.

In Chapters 3 and 4, we tried to better characterize, in the healthy adult population, the effect of temporal magnitudes on numerosity judgments, a topic that has been largely neglected in the past literature. To this aim, we adapted the framework introduced by DeWind and colleagues (2015) to the temporal domain, through the orthogonal manipulation of numerosity and two mathematical variables summarizing the information related to the duration of events and their spacing in time within a given sequence. In all our studies, both comparison and estimation of numerosities presented as sequences of visual or auditory events did not rely on the temporal characteristics of the sequences, in support of theoretical accounts suggesting a direct extraction of numerical information from the environment (Anobile, Cicchini, et al., 2016). Nonetheless, we could detect significant biases from task-irrelevant temporal features, particularly related to the duration of the sequences or the rate of presentation of the events, with similar influence in visual and auditory modalities. More importantly, temporal cues played a role not only in discrimination but also in the estimation task, where individuals were asked to report the number of visual or auditory events using a symbolic notation, suggesting that cross-magnitude interplay cannot be entirely ascribed to response-selection conflicts (Yates et al., 2012). However, further investigations are required to clarify contradictory results regarding the direction of the bias, possibly emerging from the use of stimuli with a different spatial nature (Lambrechts et al., 2013; Martin et al., 2017).

The method introduced in this work to manipulate the temporal features of the sequences and analyze responses is complementary to what has already been adopted to investigate the contribution of spatial extent in numerosity responses, both at the behavioral and neural levels (Park et al., 2016; Tomlinson et al., 2020). In this sense, our variation can represent a common ground to further explore the interplay between numerosity, space, and time across presentation modes and sensory modalities (e.g., visual and haptic). The parallel results with visual and auditory sequences described in the presented studies can be taken as preliminary evidence of similarities in how temporal magnitudes and numerosity interact in different sensory modalities, at least under the same mode of presentation. However, the between-subject design of the experiments prevents a within-subject correlation and stronger claims in this direction.

Although the current method allows evaluating to a certain extent alternative strategies to perform numerosity decisions based on the consistent reliance on other magnitudes or a simple combination of multiple features, the adopted models might not suffice to rule out a dynamic complex integration of cues since they do not consider interactions beyond the intrinsic non-linearity in case of the probit model. Starting from the results in the estimation task presented in chapter four, future investigations could more directly investigate if and how the interaction between discrete and continuous quantities might vary at different levels of numerical and non-numerical magnitude. Such finer-grained analysis is prevented here by the relatively low number of trials, which was also constrained by the online nature of the study. In addition, future investigations could benefit from the introduced method to test the spontaneous saliency of the different features or to explore the possible processing stage of interaction between magnitudes more directly, with investigations at the neural level.

In Chapter 5 we moved our focus to the role of the interaction between numerical and continuous magnitudes in the development of basic numerical abilities in typical and atypical development. In particular, we assessed the influence of continuous spatial magnitudes during a parallel numerosity comparison task in a group of children (between 8 and 14 years of age) with dyscalculia and children with average mathematical skills but similar age, IQ, and visuospatial memory abilities. To investigate the spontaneous saliency of numerical and spatial information, we also administered a spontaneous categorization task where the numerosity and total surface area of visual arrays of items were pitted against each other. In all tasks, we detected a performance primarily based on the numerical information of the stimuli, in both groups of children. Moreover, both groups showed to be significantly influenced by spatial cues in the numerosity discrimination task, while they showed to not attend to the surface area of the stimuli in the spontaneous categorization task. Moreover, while no differences emerged between groups in the strength of non-numerical influences, children with dyscalculia showed lower precision in numerosity comparison and a weaker number-based strategy in the implicit categorization task. Overall, the results suggest that a reduced numerical acuity in developmental dyscalculia is not necessarily related to reduced filtering abilities, especially from the perspective of a cross-magnitude interference at the response selection level (Gilmore et al., 2013; Szucs et al., 2013). Associating the similar non-numerical bias between groups to the stringent matching procedures based on standardized tests of general intelligence and visuospatial memory abilities, the reduced numerical acuity in children with dyscalculia compared to matched controls is instead compatible with a less precise numerosity representation that is not related to increased interference effects. However, although we tried to consider several domain-general abilities potentially impairing numerical-related responses, future studies could benefit from more direct testing of additional abilities such as inhibitory control, to corroborate the present results.

Moreover, the lack of increased reliance on non-numerical information conflicts also with proposals of domain-specific filtering deficits or compensatory mechanisms in this learning disorder (Castaldi et al., 2018; Piazza et al., 2018). Additional work is thus necessary to clarify the potential role played by the saliency of numerical and non-numerical magnitudes to explain this result. Indeed, a critical limit of all the presented studies is the lack of calibration of the saliency of temporal and spatial dimensions compared to the changes in numerosity. Although similar ratios have been used for the different features in the third chapter, and similar ranges of variation have been considered in the estimation and categorization tasks in the fourth and fifth chapters, we did not perform an individualized calibration to equate the perceptual salience of changes in all magnitudes. This is particularly relevant for the spontaneous categorization task, given the complete disregard towards the dimension of the objects in the entire sample of children, compared to previous reports (Starr et al., 2017).

Finally, in the work presented in Chapter 6, we tried to address one of the methodological issues in the field, namely the manipulation of spatial features in visual arrays of items. We developed a new program to help researchers with different backgrounds in creating experimental stimuli according to their specific needs. The MATLAB app, based on a graphical user interface, can be used without any familiarity with programming languages or rules. Instead, it aims to help users concentrate on a more careful consideration of the features defining the experimental sets, beyond numerosity. In this context, we emphasize that CUSTOM GUIde is intended as a general-purpose tool, and it is not linked with any specific manipulation or with any “control” method. We are aware that the organization of the app was shaped by the most diffused manipulations in the field, reflected also in the documentation and tutorial of the program, providing examples on how to generate stimuli similar to what has been used in past literature. However, the software leaves to the user the utmost freedom in how to define the non-numerical parameters of their stimuli, which should tightly depend on the research question, the experimental paradigm, and the intended analysis. In this sense, it must be noted that, in its current form, CUSTOM GUIde allows the direct manipulation of common relevant spatial magnitudes such as surface area or convex hull, but not to vary in an equally explicit manner other basic visual properties such as contrast, brightness or spatial frequency (Mix et al., 2016). Similarly, it does not allow users to generate visual stimuli manipulating the appearance of complex visual objects. However, we underline that the program structure facilitates its expansion with further functionalities, to incorporate manipulations of features that might reveal crucial following future developments and advancements in the research field.

In conclusion, the different studies presented in the thesis offer an overview of the intriguing relationship between numerical and non-numerical magnitude and its pervasive ramification in all research areas related to numerosity processing. The experimental works described in the thesis provide evidence in favor of a significant interference of temporal and spatial magnitudes on numerosity decisions both in development and adulthood, but it reconsiders the role of filtering abilities or deficits in mathematical learning impairments. Further investigations are necessary to clarify the specific nature of the interaction between magnitudes, but even in the context of a marginal role of continuous quantity on numerosity representation, a better characterization of such interaction remains worth pursuing to improve the comparability of measures and tasks used in the investigation of non-symbolic number processing.

References

Abalo-Rodríguez, I., De Marco, D., & Cutini, S. (2022). An undeniable interplay: Both numerosity and visual features affect estimation of non-symbolic stimuli. *Cognition*, *222*, 104944. https://doi.org/10.1016/j.cognition.2021.104944

Adriano, A., Rinaldi, L., & Girelli, L. (2021). Visual illusions as a tool to hijack numerical perception: Disentangling nonsymbolic number from its continuous visual properties. *Journal of Experimental Psychology: Human Perception and Performance*, 47(3), 423. https://doi.org/10.1037/xhp0000844

Agrillo, C., Dadda, M., Serena, G., & Bisazza, A. (2008). Do fish count? Spontaneous discrimination of quantity in female mosquitofish. *Animal Cognition*, *11*(3), 495–503. https://doi.org/10.1007/s10071-008-0140-9

Agrillo, C., Piffer, L., Bisazza, A., & Butterworth, B. (2012). Evidence for two numerical systems that are similar in humans and guppies. *PLoS ONE*, *7*(2). https://doi.org/10.1371/journal.pone.0031923

Agrillo, C., Ranpura, A., & Butterworth, B. (2010). Time and numerosity estimation are independent: Behavioral evidence for two different systems using a conflict paradigm. *Cognitive Neuroscience*, *1*(2), 96–101. https://doi.org/10.1080/17588921003632537

American Psychiatric Association. (2013). *Diagnostic and statistical manual of mental disorders* (5th ed.)

Andres, M., Davare, M., Pesenti, M., Olivier, E., & Seron, X. (2004). Number magnitude and grip aperture interaction. *NeuroReport*, *15*(18), 2773–2777.

Anobile, G., Arrighi, R., Castaldi, E., & Burr, D. C. (2021). A Sensorimotor Numerosity System. *Trends in Cognitive Sciences*, *25*(1), 24–36. https://doi.org/10.1016/j.tics.2020.10.009

Anobile, G., Arrighi, R., Castaldi, E., Grassi, E., Pedonese, L., Moscoso, P. A. M., & Burr, D. C. (2018). Spatial but not temporal numerosity thresholds correlate with formal math skills in children. *Developmental Psychology*, *54*(3), 458–473. https://doi.org/10.1037/dev0000448

Anobile, G., Arrighi, R., Togoli, I., & Burr, D. C. (2016). A shared numerical representation for action and perception. *ELife*, *5*, 1–14. https://doi.org/10.7554/elife.16161

Anobile, G., Cicchini, G. M., & Burr, D. C. (2014). Separate Mechanisms for Perception of Numerosity and Density. *Psychological Science*, *25*(1), 265–270. https://doi.org/10.1177/0956797613501520

Anobile, G., Cicchini, G. M., & Burr, D. C. (2016). Number As a Primary Perceptual Attribute: A Review. *Perception 45*(1-2), 5-31. https://doi.org/10.1177/0301006615602599

Anobile, G., Domenici, N., Togoli, I., Burr, D., & Arrighi, R. (2020). Distortions Of Visual Time Induced By Motor Adaptation. *Journal of Experimental Psychology: General*, *149*(7), 1333–1343. https://doi.org/10.1037/xge0000709

Anobile, G., Tomaiuolo, F., Campana, S., & Cicchini, G. M. (2020). Three-systems for visual numerosity: A single case study. *Neuropsychologia*, *136*, 107259. https://doi.org/10.1016/j.neuropsychologia.2019.107259

Anobile, G., Turi, M., Cicchini, G. M., & Burr, D. C. (2015). Mechanisms for perception of numerosity or texture-density are governed by crowding-like effects. *Journal of Vision*, *15*(5), 1–12. https://doi.org/10.1167/15.5.4

Arrighi, R., Togoli, I., & Burr, D. C. (2014). A generalized sense of number. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1797), 1–7. https://doi.org/10.1098/rspb.2014.1791

Ashkenazi, S., Rosenberg-Lee, M., Metcalfe, A. W. S., Swigart, A. G., & Menon, V. (2013). Visuo-spatial working memory is an important source of domain-general vulnerability in the development of arithmetic cognition. *Neuropsychologia*, *51*(11), 2305–2317. https://doi.org/10.1016/j.neuropsychologia.2013.06.031

Aulet, L. S., & Lourenco, S. F. (2021). The relative salience of numerical and non-numerical dimensions shifts over development: A re-analysis of Tomlinson, DeWind, and Brannon (2020). *Cognition*, *210*, 104610. https://doi.org/10.1016/j.cognition.2021.104610

Badets, A., Bouquet, C. A., Ric, F., & Pesenti, M. (2012). Number generation bias after action observation. *Experimental Brain Research*, *221*(1), 43–49. https://doi.org/10.1007/s00221-012-3145-1

Bartelet, D., Ansari, D., Vaessen, A., & Blomert, L. (2014). Cognitive subtypes of mathematics learning difficulties in primary education. *Research in Developmental Disabilities*, *35*(3), 657–670. https://doi.org/10.1016/j.ridd.2013.12.010

Barth, H., Kanwisher, N., & Spelke, E. (2003). The construction of large number representations in adults. *Cognition*, *86*(3), 201–221. https://doi.org/10.1016/S0010-0277(02)00178-6

Barth, H., La Mont, K., Lipton, J., & Spelke, E. S. (2005). Abstract number and arithmetic in preschool children. *Proceedings of the National Academy of Sciences*, *102*(39), 14116–14121. https://doi.org/10.1073/pnas.0505512102

Benson-Amram, S., Heinen, V. K., Dryer, S. L., & Holekamp, K. E. (2011). Numerical assessment and individual call discrimination by wild spotted hyaenas, Crocuta crocuta. *Animal Behaviour*, *82*(4), 743–752. https://doi.org/10.1016/j.anbehav.2011.07.004

Biancardi, A., Nicoletti, C., & Bachmann, C. (2016). *BDE 2-Batteria discalculia evolutiva: Test per la diagnosi dei disturbi dell'elaborazione numerica e del calcolo in età evolutiva–8-13 anni.* Edizioni Centro Studi Erickson

Bisazza, A., Piffer, L., Serena, G., & Agrillo, C. (2010). Ontogeny of numerical abilities in fish. *PLoS ONE*, *5*(11). https://doi.org/10.1371/journal.pone.0015516

Blini, E., Romeo, Z., Spironelli, C., Pitteri, M., Meneghello, F., Bonato, M., & Zorzi, M. (2016). Multi-tasking uncovers right spatial neglect and extinction in chronic left-hemisphere stroke patients. *Neuropsychologia*, *92*, 147–157. https://doi.org/10.1016/j.neuropsychologia.2016.02.028

Bortot, M., Agrillo, C., Avarguès-Weber, A., Bisazza, A., Petrazzini, M. E. M., & Giurfa, M. (2019). Honeybees use absolute rather than relative numerosity in number discrimination. *Biology Letters*, *15*(6), 5–9. https://doi.org/10.1098/rsbl.2019.0138

Brannon, E. M., Lutz, D., & Cordes, S. (2006). The development of area discrimination and its implications for number representation in infancy. *Developmental Science*, *9*(6). https://doi.org/10.1111/j.1467-7687.2006.00530.x

Bridges, D., Pitiot, A., Macaskill, M. R., & Peirce, J. W. (2020). The timing mega-study: comparing a range of experiment generators, both lab-based and online. *PeerJ, 8*, e9414.

Bueti, D., & Walsh, V. (2009). The parietal cortex and the representation of time, space, number and other magnitudes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1525), 1831–1840. https://doi.org/10.1098/rstb.2009.0028

Bugden, S., & Ansari, D. (2016). Probing the nature of deficits in the "Approximate Number System" in children with persistent Developmental Dyscalculia. *Developmental Science*, *19*(5), 817–833. https://doi.org/10.1111/desc.12324

Bugden, S., Woldorff, M. G., & Brannon, E. M. (2019). Shared and distinct neural circuitry for nonsymbolic and symbolic double-digit addition. *Human Brain Mapping*, *40*(4), 1328–1343. https://doi.org/10.1002/hbm.24452

Bulthé, J., De Smedt, B., & Op de Beeck, H. P. (2014). Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. *NeuroImage*, *87*, 311–322. https://doi.org/10.1016/j.neuroimage.2013.10.049

Bulthé, J., Prinsen, J., Vanderauwera, J., Duyck, S., Daniels, N., Gillebert, C. R., Mantini, D., Op de Beeck, H. P., & De Smedt, B. (2019). Multi-method brain imaging reveals impaired representations of number as well as altered connectivity in adults with dyscalculia. *NeuroImage*, *190*, 289–302. https://doi.org/10.1016/j.neuroimage.2018.06.012

Burr, D. C., Turi, M., & Anobile, G. (2010). Subitizing but not estimation of numerosity requires attentional resources. *Journal of Vision*, *10*(6), 1–10. https://doi.org/10.1167/10.6.20

Burr, D., & Ross, J. (2008). A Visual Sense of Number. *Current Biology*, *18*(6), 425–428. https://doi.org/10.1016/j.cub.2008.02.052

Cai, Z. G., Wang, R., Shen, M., & Speekenbrink, M. (2018). Cross-dimensional magnitude interactions arise from memory interference. *Cognitive Psychology*, *106*, 21–42. https://doi.org/10.1016/j.cogpsych.2018.08.001

Cantlon, J. F., & Brannon, E. M. (2007). Basic math in monkeys and college students. *PLoS Biology*, *5*(12), 2912–2919. https://doi.org/10.1371/journal.pbio.0050328

Cappelletti, M., Didino, D., Stoianov, I., & Zorzi, M. (2014). Number skills are maintained in healthy ageing. *Cognitive Psychology*, *69*, 25–45. https://doi.org/10.1016/j.cogpsych.2013.11.004

Cappelletti, M., Freeman, E. D., & Cipolotti, L. (2009). Dissociations and interactions between time, numerosity and space processing. *Neuropsychologia*, *47*(13), 2732–2748. https://doi.org/10.1016/j.neuropsychologia.2009.05.024

Castaldi, E., Mirassou, A., Dehaene, S., Piazza, M., & Eger, E. (2018). Asymmetrical interference between number and item size perception provide evidence for a domain specific impairment in dyscalculia. *PLoS ONE*. *13*(12), e0209256. https://doi.org/10.1101/332155

Castaldi, E., Piazza, M., Dehaene, S., Vignaud, A., & Eger, E. (2019). Attentional amplification of neural codes for number independent of other quantities along the dorsal visual stream. *ELife*, *8*, 1–26. https://doi.org/10.7554/eLife.45160

Castaldi, E., Vignaud, A., & Eger, E. (2020). NeuroImage Mapping subcomponents of numerical cognition in relation to functional and anatomical landmarks of human parietal cortex. *NeuroImage*, *221*, 117210. https://doi.org/10.1016/j.neuroimage.2020.117210

Castelli, F., Glaser, D. E., & Butterworth, B. (2006). Discrete and analogue quantity processing in the parietal lobe: A functional MRI study. *Proceedings of the National Academy of Sciences*, *103*(12), 4693–4698. https://doi.org/10.1073/pnas.0600444103

Castronovo, J., & Göbel, S. M. (2012). Impact of high mathematics education on the number sense. *PloS One*, *7*(4), 24–25. https://doi.org/10.1371/journal.pone.0033832

Cavdaroglu, S., Katz, C., & Knops, A. (2015). Dissociating estimation from comparison and response eliminates parietal involvement in sequential numerosity perception. *NeuroImage*, *116*, 135–148. https://doi.org/10.1016/j.neuroimage.2015.04.019

Cavdaroglu, S., & Knops, A. (2019). Evidence for a Posterior Parietal Cortex Contribution to Spatial but not Temporal Numerosity Perception. *Cerebral Cortex*, *29*(7), 2965–2977. https://doi.org/10.1093/cercor/bhy163

Chen, Q., & Li, J. (2014). Association between individual differences in non-symbolic number acuity and math performance: A meta-analysis. *Acta Psychologica*, *148*, 163–172. https://doi.org/10.1016/j.actpsy.2014.01.016

Cheyette, S. J., & Piantadosi, S. T. (2020). A unified account of numerosity perception. *Nature Human Behaviour*, *4*(12), 1265–1272. https://doi.org/10.1038/s41562-020-00946-0

Choo, H., & Franconeri, S. L. (2014). Enumeration of small collections violates Weber's law. *Psychonomic Bulletin and Review*, *21*(1), 93–99. https://doi.org/10.3758/s13423-013-0474-4

Cicchini, G. M., Anobile, G., & Burr, D. C. (2019). Spontaneous representation of numerosity in typical and dyscalculic development. *Cortex*, *114*, 151–163. https://doi.org/10.1016/j.cortex.2018.11.019

Cirino, P. T., Fuchs, L. S., Elias, J. T., Powell, S. R., & Schumacher, R. F. (2015). Cognitive and Mathematical Profiles for Different Forms of Learning Difficulties. *Journal of Learning Disabilities*, *48*(2), 156–175. https://doi.org/10.1177/0022219413494239

Clayton, S., & Gilmore, C. (2015). Inhibition in dot comparison tasks. *ZDM - Mathematics Education*, *47*(5), 759–770. https://doi.org/10.1007/s11858-014-0655-2

Clayton, S., Gilmore, C., & Inglis, M. (2015). Dot comparison stimuli are not all alike: The effect of different visual controls on ANS measurement. *Acta Psychologica*, *161*, 177–184. https://doi.org/10.1016/j.actpsy.2015.09.007

Cohen Kadosh, R., Cohen Kadosh, K., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-Dependent and -Independent Representations of Numbers in the Parietal Lobes. *Neuron*, *53*(2), 307–314. https://doi.org/10.1016/j.neuron.2006.12.025

Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., Van De Ven, V., Zorzi, M., Hendler, T., Goebel, R., & Linden, D. E. J. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, *43*(9), 1238–1248. https://doi.org/10.1016/j.neuropsychologia.2004.12.017

Cohen Kadosh, R., & Walsh, V. (2009). Numerical Representation in the Parietal Lobes: Abstract or not Abstract? *Behavioral and Brain Sciences*, *32*(3–4), 313–328.

Coubart, A., Izard, V., Spelke, E. S., Marie, J., & Streri, A. (2014). Dissociation between small and large numerosities in newborn infants. *Developmental Science*, *17*(1), 11–22. https://doi.org/10.1111/desc.12108

Crollen, V., Castronovo, J., & Seron, X. (2011). Under- and over-estimation: A bi-directional mapping process between symbolic and non-symbolic representations of number? Experimental Psychology, *58*(1), 39–49. https://doi.org/10.1027/1618-3169/a000064

Cragg, L., & Gilmore, C. (2014). Skills underlying mathematics: The role of executive function in the development of mathematics proficiency. *Trends in Neuroscience and Education*, *3*(2), 63–68. https://doi.org/10.1016/j.tine.2013.12.001

Dakin, S. C., Tibber, M. S., Greenwood, J. A., Kingdom, F. A. A., & Morgan, M. J. (2011). A common visual metric for approximate number and density. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(49), 19552–19557. https://doi.org/10.1073/pnas.1113195108

Dantzig, T., & Mazur, J. (2007). *Number: The language of science*. Penguin.

De Hevia, M. D., Izard, V., Coubart, A., Spelke, E. S., & Streri, A. (2014). Representations of space, time, and number n neonates. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(13), 4809–4813. https://doi.org/10.1073/pnas.1323628111

De Marco, D., & Cutini, S. (2020). Introducing CUSTOM: A customized, ultraprecise, standardization-oriented, multipurpose algorithm for generating nonsymbolic number stimuli. *Behavior Research Methods*, *52*(4), 1528–1537. https://doi.org/10.3758/s13428-019-01332-z

De Smedt, B., & Gilmore, C. K. (2011). Defective number module or impaired access? Numerical magnitude processing in first graders with mathematical difficulties. *Journal of Experimental Child Psychology*, *108*(2), 278–292. https://doi.org/10.1016/j.jecp.2010.09.003

De Smedt, B., Noël, M. P., Gilmore, C., & Ansari, D. (2013). How do symbolic and non-symbolic numerical magnitude processing skills relate to individual differences in children's mathematical skills? A review of evidence from brain and behavior. *Trends in Neuroscience and Education*, *2*(2), 48–55. https://doi.org/10.1016/j.tine.2013.06.001

Decarli, G., Paris, E., Tencati, C., Nardelli, C., Vescovi, M., Surian, L., & Piazza, M. (2020). Impaired large numerosity estimation and intact subitizing in developmental dyscalculia. *PLoS ONE*, *15*(12), 1–19. https://doi.org/10.1371/journal.pone.0244578

Decarli, G., Sella, F., Lanfranchi, S., Gerotto, G., Gerola, S., Cossu, G., & Zorzi, M. (2022). Severe Developmental Dyscalculia Is Characterized by Core Deficits in Both Symbolic and Nonsymbolic Number Sense. *Psychological Science*, *34*(1), 8-21. https://doi.org/10.1177/09567976221097947

Decarli, G., Veggiotti, L., & de Hevia, M. D. (2022). The link between number and action in human infants. *Scientific Reports*, *12*(1), 1–8. https://doi.org/10.1038/s41598-022-07389-9

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition, 44*(1-2), 1-42.

Dehaene, S. (1997) *The Number Sense*, Oxford University Press

Dehaene, S. (2003). The neural basis of the Weber-Fechner law: A logarithmic mental number line. *Trends in Cognitive Sciences*, *7*(4), 145–147. https://doi.org/10.1016/S1364-6613(03)00055-X

Dehaene, S. (2007). Symbols and quantities in parietal cortex: Elements of a mathematical theory of number representation and manipulation. *Sensorimotor foundations of higher cognition*, *22*, 527-574.

Dehaene, S., & Changeux, J. P. (1993). Development of elementary numerical abilities: A neuronal model. *Journal of Cognitive Neuroscience*, *5*(4), 390–407. https://doi.org/10.1162/jocn.1993.5.4.390

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences*, *21*(8), 355–361. https://doi.org/10.1016/S0166-2236(98)01263-6

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital? Analogical and symbolic effects in two-digit number comparison. *Journal of Experimental Psychology: Human Perception and Performance, 16*(3), 626–641. https://doi.org/10.1037/0096-1523.16.3.626

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*(3–6), 487–506. https://doi.org/10.1080/02643290244000239

DeWind, N. K., Adams, G. K., Platt, M. L., & Brannon, E. M. (2015). Modeling the approximate number system to quantify the contribution of visual stimulus features. *Cognition*, *142*, 247–265. https://doi.org/10.1016/j.cognition.2015.05.016

DeWind, N. K., & Brannon, E. M. (2012). Malleability of the approximate number system: Effects of feedback and training. *Frontiers in Human Neuroscience*, *6*, 1–10. https://doi.org/10.3389/fnhum.2012.00068

DeWind, N. K., & Brannon, E. M. (2016). Significant inter-test reliability across approximate number system assessments. *Frontiers in Psychology*, *7*, 1–10. https://doi.org/10.3389/fpsyg.2016.00310

DeWind, N. K., Park, J., Woldorff, M. G., & Brannon, E. M. (2018). Numerical encoding in early visual cortex. *Cortex*, *114*, 76-89. https://doi.org/10.1016/j.cortex.2018.03.027

Dormal, V., Andres, M., Dormal, G., & Pesenti, M. (2010). Mode-dependent and mode-independent representations of numerosity in the right intraparietal sulcus. *NeuroImage*, *52*(4), 1677–1686. https://doi.org/10.1016/j.neuroimage.2010.04.254

Dormal, V., Andres, M., & Pesenti, M. (2008). Dissociation of numerosity and duration processing in the left intraparietal sulcus: A transcranial magnetic stimulation study. *Cortex*, *44*(4), 462–469. https://doi.org/10.1016/j.cortex.2007.08.011

Dormal, V., Andres, M., & Pesenti, M. (2012). Contribution of the right intraparietal sulcus to numerosity and length processing: An fMRI-guided TMS study. *Cortex*, *48*(5), 623–629. https://doi.org/10.1016/j.cortex.2011.05.019

Dormal, V., Larigaldie, N., Lefèvre, N., Pesenti, M., & Andres, M. (2018). Effect of perceived length on numerosity estimation: Evidence from the Müller-Lyer illusion. *Quarterly Journal of Experimental Psychology*, *71*(10), 2142–2151. https://doi.org/10.1177/1747021817738720

Dormal, V., & Pesenti, M. (2013). Processing numerosity, length and duration in a three-dimensional Stroop-like task: Towards a gradient of processing automaticity? *Psychological Research*, *77*(2), 116–127. https://doi.org/10.1007/s00426-012-0414-3

Dormal, V., Seron, X., & Pesenti, M. (2006). Numerosity-duration interference: A Stroop experiment. *Acta Psychologica*, *121*(2), 109–124. https://doi.org/10.1016/j.actpsy.2005.06.003

Dramkin, D., Bonn, C. D., Baer, C., & Odic, D. (2022). The malleable impact of non-numeric features in visual number perception. *Acta Psychologica*, *230*, 103737. https://doi.org/10.1016/j.actpsy.2022.103737

Droit-Volet, S., Clement, A., & Fayol, M. (2008). Time, number and length: Similarities and differences in discrimination in adults and children. *Quarterly Journal of Experimental Psychology*, *61*(12), 1827–1846. https://doi.org/10.1080/17470210701743643

Droit-Volet, S., Clément, A., & Fayol, M. (2003). Time and number discrimination in a bisection task with a sequence of stimuli: A developmental approach. *Journal of Experimental Child Psychology*, *84*(1), 63–76. https://doi.org/10.1016/S0022-0965(02)00180-7

Dumontheil, I., & Klingberg, T. (2012). Brain activity during a visuospatial working memory task predicts arithmetical performance 2 years later. *Cerebral Cortex*, *22*(5), 1078–1085. https://doi.org/10.1093/cercor/bhr175

Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., & Kleinschmidt, A. (2009). Deciphering Cortical Number Coding from Human Brain Activity Patterns. *Current Biology*, *19*(19), 1608–1615. https://doi.org/10.1016/j.cub.2009.08.047

Eger, E., Pinel, P., Dehaene, S., & Kleinschmidt, A. (2015). Spatially invariant coding of numerical information in functionally defined subregions of human parietal cortex. *Cerebral Cortex*, *25*(5), 1319–1329. https://doi.org/10.1093/cercor/bht323

Eger, E., Sterzer, P., Russ, M. O., Giraud, A. L., & Kleinschmidt, A. (2003). A supramodal number representation in human intraparietal cortex. *Neuron*, *37*(4), 719–726. https://doi.org/10.1016/S0896-6273(03)00036-9

Elliott, L., Feigenson, L., Halberda, J., & Libertus, M. E. (2019). Bidirectional, Longitudinal Associations Between Math Ability and Approximate Number System Precision in Childhood. *Journal of Cognition and Development*, *20*(1), 56–74. https://doi.org/10.1080/15248372.2018.1551218

Fazio, L. K., Bailey, D. H., Thompson, C. A., & Siegler, R. S. (2014). Relations of different types of numerical magnitude representations to each other and to mathematics achievement. *Journal of Experimental Child Psychology*, *123*(1), 53–72. https://doi.org/10.1016/j.jecp.2014.01.013

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences*, *8*(7), 307–314. https://doi.org/10.1016/j.tics.2004.05.002

Ferrigno, S., Jara-Ettinger, J., Piantadosi, S. T., & Cantlon, J. F. (2017). Universal and uniquely human factors in spontaneous number perception. *Nature Communications*, *8*(1), 13968. https://doi.org/10.1038/ncomms13968

Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., & Orban, G. A. (2003). Parietal representation of symbolic and nonsymbolic magnitude. *Journal of Cognitive Neuroscience*, *15*(1), 47–56. https://doi.org/10.1162/089892903321107819

Fias, W., Menon, V., & Szucs, D. (2013). Multiple components of developmental dyscalculia. *Trends in Neuroscience and Education*, *2*(2), 43–47. https://doi.org/10.1016/j.tine.2013.06.006

Fornaciai, M., Brannon, E. M., Woldorff, M. G., & Park, J. (2017). Numerosity processing in early visual cortex. *NeuroImage*, *157*, 429–438. https://doi.org/10.1016/j.neuroimage.2017.05.069

Franconeri, S. L., Bemis, D. K., & Alvarez, G. A. (2009). Number estimation relies on a set of segmented objects. *Cognition*, *113*(1), 1–13. https://doi.org/10.1016/j.cognition.2009.07.002

Fuhs, M. W., & Mcneil, N. M. (2013). ANS acuity and mathematics ability in preschoolers from low-income homes: Contributions of inhibitory control. *Developmental Science*, *16*(1), 136–148. https://doi.org/10.1111/desc.12013

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition*, *44*(1–2), 43–74. https://doi.org/10.1016/0010-0277(92)90050-R

Gebuis, T., Cohen Kadosh, R., & Gevers, W. (2016). Sensory-integration system rather than approximate number system underlies numerosity processing: A critical review. *Acta Psychologica*, *171*, 17–35. https://doi.org/10.1016/j.actpsy.2016.09.003

Gebuis, T., & Reynvoet, B. (2012a). The interplay between nonsymbolic number and its continuous visual properties. *Journal of Experimental Psychology: General*, *141*(4), 642–648. https://doi.org/10.1037/a0026218

Gebuis, T., & Reynvoet, B. (2012b). The role of visual information in numerosity estimation. *PLoS ONE*, *7*(5). https://doi.org/10.1371/journal.pone.0037426

Gevers, W., Kadosh, R. C., & Gebuis, T. (2016). Sensory Integration Theory: An Alternative to the Approximate Number System. *Continuous Issues in Numerical Cognition: How Many or How Much*, 405–418. https://doi.org/10.1016/B978-0-12-801637-4.00018-4

Gilmore, C., Attridge, N., Clayton, S., Cragg, L., Johnson, S., Simms, V., & Inglis, M. (2013). *Individual Differences in Inhibitory Control, Not Non-Verbal Number Acuity, Correlate with Mathematics Achievement*. *8*(6), 1–9. https://doi.org/10.1371/journal.pone.0067374

Gilmore, C., Cragg, L., Hogan, G., & Inglis, M. (2016). Congruency effects in dot comparison tasks: convex hull is more important than dot area. *Journal of Cognitive Psychology*, *28*(8), 923–931. https://doi.org/10.1080/20445911.2016.1221828

Gilmore, C. K., McCarthy, S. E., & Spelke, E. S. (2010). Non-symbolic arithmetic abilities and mathematics achievement in the first year of formal schooling. *Cognition*, *115*(3), 394–406. https://doi.org/10.1016/j.cognition.2010.02.002

Giurfa, M. (2019). Honeybees foraging for numbers. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *205*(3), 439–450. https://doi.org/10.1007/s00359-019-01344-2

Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature*, *423*(6939), 534–537. https://doi.org/10.1038/nature01647

Göbel, S. M., Johansen-Berg, H., Behrens, T., & Rushworth, M. F. (2004). Response-selection-related parietal activation during number comparison. *Journal of Cognitive Neuroscience, 16*(9), 1536-1551.

Guillaume, M., Nys, J., Mussolin, C., & Content, A. (2013). Differences in the acuity of the Approximate Number System in adults: The effect of mathematical ability. *Acta Psychologica*, *144*(3), 506–512. https://doi.org/10.1016/j.actpsy.2013.09.001

Guillaume, M., Schiltz, C., & Van Rinsveld, A. (2020). NASCO: A new method and program to generate dot arrays for non-symbolic number comparison tasks. *Journal of Numerical Cognition*, *6*(1), 129–147. https://doi.org/10.5964/jnc.v6i1.231

Halberda, J., & Feigenson, L. (2008). Developmental Change in the Acuity of the "Number Sense": The Approximate Number System in 3-, 4-, 5-, and 6-Year-Olds and Adults. *Developmental Psychology*, *44*(5), 1457–1465. https://doi.org/10.1037/a0012682

Halberda, J., Ly, R., Wilmer, J. B., Naiman, D. Q., & Germine, L. (2012). Number sense across the lifespan as revealed by a massive Internet-based sample. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(28), 11116–11120. https://doi.org/10.1073/pnas.1200196109

Halberda, J., Mazzocco, M. M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, *455*(7213), 665–668. https://doi.org/10.1038/nature07246

Halberda, J., & Odic, D. (2015). The precision and internal confidence of our approximate number thoughts. In *Mathematical cognition and learning* (Vol. 1, pp. 305-333). Elsevier.

Hamamouche, K., & Cordes, S. (2019). Number, time, and space are not singularly represented: Evidence against a common magnitude system beyond early childhood. *Psychonomic Bulletin and Review*, *26*(3), 833–854. https://doi.org/10.3758/s13423-018-1561-3

Harvey, B. M., & Dumoulin, S. O. (2017a). A network of topographic numerosity maps in human association cortex. *Nature Human Behaviour*, *1*(2). https://doi.org/10.1038/s41562-016-0036

Harvey, B. M., & Dumoulin, S. O. (2017b). Can responses to basic non-numerical visual features explain neural numerosity responses? *NeuroImage*, *149*, 200–209. https://doi.org/10.1016/j.neuroimage.2017.02.012

Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic Representation of Numerosity in the Human Parietal Cortex. *Science*, *341*, 201–217. https://doi.org/10.4159/harvard.9780674333987.c22

Hasuo, E., Nakajima, Y., Osawa, S., & Fujishima, H. (2012). Effects of temporal shapes of sound markers on the perception of interonset time intervals. *Attention, Perception, and Psychophysics*, *74*(2), 430–445. https://doi.org/10.3758/s13414-011-0236-1

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1445), 829–833. https://doi.org/10.1098/rspb.2000.1078

Hayashi, M. J., Kanai, R., Tanabe, H. C., Yoshida, Y., Carlson, S., Walsh, V., & Sadato, N. (2013). Interaction of numerosity and time in prefrontal and parietal cortex. *Journal of Neuroscience*, *33*(3), 883–893. https://doi.org/10.1523/JNEUROSCI.6257-11.2013

He, L., Zhang, J., Zhou, T., & Chen, L. (2009). Connectedness affects dot numerosity judgment: Implications for configural processing. *Psychonomic Bulletin and Review*, *16*(3), 509–517. https://doi.org/10.3758/PBR.16.3.509

He, L., Zhou, K., Zhou, T., He, S., & Chen, L. (2015). Topology-defined units in numerosity perception. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(41), E5647–E5655. https://doi.org/10.1073/pnas.1512408112

Hofstetter, S., Cai, Y., Harvey, B. M., & Dumoulin, S. O. (2021). Topographic maps representing haptic numerosity reveals distinct sensory representations in supramodal networks. *Nature Communications*, *12*(1), 1–13. https://doi.org/10.1038/s41467-020-20567-5

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, *6*(6), 435–448. https://doi.org/10.1038/nrn1684

Hyde, D. C., Khanum, S., & Spelke, E. S. (2014). Brief non-symbolic, approximate number practice enhances subsequent exact symbolic arithmetic in children. *Cognition*, *131*(1), 92–107. https://doi.org/10.1016/j.cognition.2013.12.007

Inglis, M., Attridge, N., Batchelor, S., & Gilmore, C. (2011). Non-verbal number acuity correlates with symbolic mathematics achievement: But only in children. *Psychonomic Bulletin and Review*, *18*(6), 1222–1229. https://doi.org/10.3758/s13423-011-0154-1

Inglis, M., & Gilmore, C. (2013). Sampling from the mental number line: How are approximate number system representations formed? *Cognition*, *129*(1), 63–69. https://doi.org/10.1016/j.cognition.2013.06.003

Iuculano, T., Tang, J., Hall, C. W. B., & Butterworth, B. (2008). Core information processing deficits in developmental dyscalculia and low numeracy. *Developmental Science*, *11*(5), 669–680. https://doi.org/10.1111/j.1467-7687.2008.00716.x

Izard, V., & Dehaene, S. (2008). Calibrating the mental number line. *Cognition*, *106*(3), 1221–1247. https://doi.org/10.1016/j.cognition.2007.06.004

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences*, *106*(25), 10382–10385. https://doi.org/10.1073/pnas.0812142106

Javadi, A. H., & Aichelburg, C. (2012). When time and numerosity interfere: The longer the more, and the more the longer. *PLoS ONE*, *7*(7), e41496. https://doi.org/10.1371/journal.pone.0041496

Jevons, W. S. (1871). The power of numerical discrimination. *Nature, 3*, 281–282.

Jordan, K. E., & Brannon, E. M. (2006). The multisensory representation of number in infancy. *Proceedings of the National Academy of Sciences*, *103*(9), 3486–3489. https://doi.org/10.1073/pnas.0508107103

Jordan, K. E., Brannon, E. M., Logothetis, N. K., & Ghazanfar, A. A. (2005). Monkeys match the number of voices they hear to the number of faces they see. *Current Biology*, *15*(11), 1034–1038. https://doi.org/10.1016/j.cub.2005.04.056

Jordan, K. E., MacLean, E. L., & Brannon, E. M. (2008). Monkeys match and tally quantities across senses. *Cognition*, *108*(3), 617–625. https://doi.org/10.1016/j.cognition.2008.05.006

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association, 90*(430), 773–795.

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The discrimination of visual number. *The American Journal of Psychology, 62*, 498–525. https://doi.org/10.2307/1418556

Kaufmann, L., Mazzocco, M. M., Dowker, A., von Aster, M., Göbel, S. M., Grabner, R. H., Henik, A., Jordan, N. C., Karmiloff-Smith, A. D., Kucian, K., Rubinsten, O., Szucs, D., Shalev, R., & Nuerk, H. C. (2013). Dyscalculia from a developmental and differential perspective. *Frontiers in Psychology*, *4*, 1–5. https://doi.org/10.3389/fpsyg.2013.00516

Khanum, S., Hanif, R., Spelke, E. S., Berteletti, I., & Hyde, D. C. (2016). Effects of non-symbolic approximate number practice on symbolic numerical abilities in Pakistani children. *PLoS ONE*, *11*(10), 1–21. https://doi.org/10.1371/journal.pone.0164436

Kirjakovski, A., & Matsumoto, E. (2016). Numerosity underestimation in sets with illusory contours. *Vision Research*, *122*, 34–42. https://doi.org/10.1016/j.visres.2016.03.005

Kirschhock, M. E., & Nieder, A. (2022). Number selective sensorimotor neurons in the crow translate perceived numerosity into number of actions. *Nature Communications*, *13*(1), 35–37. https://doi.org/10.1038/s41467-022-34457-5

Korkman, M., Kirk, U., & Kemp, S. (2007). *NEPSY-II: A developmental neuropsychological assessment.* The Psychological Corporation.

Lambrechts, A., Walsh, V., & Van Wassenhove, V. (2013). Evidence accumulation in the magnitude system. *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0082122

Ledesma, J. M., & McRobert, S. P. (2008). Shoaling in juvenile guppies: The effects of body size and shoal size. *Behavioural Processes*, *77*(3), 384–388. https://doi.org/10.1016/j.beproc.2007.10.006

Leibovich, T., & Ansari, D. (2016). The Symbol-Grounding Problem in Numerical Cognition: A Review of Theory, Evidence, and Outstanding Questions. *Canadian Journal of Experimental Psychology*, *70*(1), 12–23. https://doi.org/10.1037/cep0000070

Leibovich, T., & Henik, A. (2014). Comparing performance in discrete and continuous comparison tasks. *Quarterly Journal of Experimental Psychology*, *67*(5), 899–917. https://doi.org/10.1080/17470218.2013.837940

Leibovich, T., Katzin, N., Harel, M., & Henik, A. (2017). From "sense of number" to "sense of magnitude": The role of continuous magnitudes in numerical cognition. *Behavioral and Brain Sciences*, *40*. https://doi.org/10.1017/S0140525X16000960

Levinson, J. Z. (1968). Flicker Fusion Phenomena: Rapid flicker is attenuated many times over by repeated temporal summation before it is "seen". *Science, 160*(3823), 21-28.

Libertus, M. E., & Brannon, E. M. (2010). Stable individual differences in number discrimination in infancy. *Developmental Science*, *13*(6), 900–906. https://doi.org/10.1111/j.1467-7687.2009.00948.x

Libertus, M. E., Feigenson, L., & Halberda, J. (2011). Preschool acuity of the approximate number system correlates with school math ability. *Developmental Science*, *14*(6), 1292–1300. https://doi.org/10.1111/j.1467-7687.2011.01080.x

Libertus, M. E., Feigenson, L., & Halberda, J. (2013). Is approximate number precision a stable predictor of math ability? *Learning and Individual Differences*, *25*(410), 126–133. https://doi.org/10.1016/j.lindif.2013.02.001

Lipton, J. S., & Spelke, E. S. (2003). Origins of Number Sense. *Psychological Science*, *14*(5), 396–401. https://doi.org/10.1111/1467-9280.01453

Lourenco, S. F., & Aulet, L. S. (2019). Cross-magnitude interactions across development: Longitudinal evidence for a general magnitude system. *Developmental Science*, *22*(1), 1–10. https://doi.org/10.1111/desc.12707

Lourenco, S. F., & Longo, M. R. (2010). General magnitude representation in human infants. *Psychological Science: A Journal of the American Psychological Society / APS*, *21*(6), 873–881. https://doi.org/10.1177/0956797610370158

Lyons, I. M., Ansari, D., & Beilock, S. L. (2012). Symbolic estrangement: Evidence against a strong association between numerical symbols and the quantities they represent. *Journal of Experimental Psychology: General, 141*(4), 635–641. https://doi.org/10.1037/a0027248

Lyons, I. M., Ansari, D., & Beilock, S. L. (2015). Qualitatively different coding of symbolic and nonsymbolic numbers in the human brain. *Human Brain Mapping*, *36*(2), 475–488. https://doi.org/10.1002/hbm.22641

Maldonado Moscoso, P. A., Cicchini, G. M., Arrighi, R., & Burr, D. C. (2020). Adaptation to hand-tapping affects sensory processing of numerosity directly: Evidence from reaction times and confidence: Motor adaptation affects numerosity. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1927). https://doi.org/10.1098/rspb.2020.0801

Mammarella, I. C., Caviola, S., Giofrè, D., & Szűcs, D. (2018). The underlying structure of visuospatial working memory in children with mathematical learning disability. *British Journal of Developmental Psychology*, *36*(2), 220–235. https://doi.org/10.1111/bjdp.12202

Mammarella, I. C., Toffalini, E., Caviola, S., Colling, L., & Szűcs, D. (2021). No evidence for a core deficit in developmental dyscalculia or mathematical learning disabilities. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *62*(6), 704–714. https://doi.org/10.1111/jcpp.13397

Marinova, M., Sasanguie, D., & Reynvoet, B. (2020). Numerals do not need numerosities: robust evidence for distinct numerical representations for symbolic and non-symbolic numbers. *Psychological Research*, *85*(2), 764-776. https://doi.org/10.1007/s00426-019-01286-z

Martin, B., Wiener, M., & Van Wassenhove, V. (2017). A Bayesian Perspective on Accumulation in the Magnitude System. *Scientific Reports*, *7*(1), 1–14. https://doi.org/10.1038/s41598-017-00680-0

Mazzocco, M. M. M., Feigenson, L., & Halberda, J. (2011a). Impaired acuity of the approximate number system underlies mathematical learning disability (dyscalculia). *Child Development*, *82*(4), 1224–1237. https://doi.org/10.1111/j.1467-8624.2011.01608.x

Mazzocco, M. M. M., Feigenson, L., & Halberda, J. (2011b). Preschoolers' precision of the approximate number system predicts later school mathematics performance. *PLoS ONE*, *6*(9), 1–8. https://doi.org/10.1371/journal.pone.0023749

McCrink, K., & Wynn, K. (2004). Large-Number Addition and Subtraction by 9-Month-Old Infants. *Psychological Science*, *15*(11), 776–781.

Mejias, S., Grégoire, J., & Noël, M. P. (2012). Numerical estimation in adults with and without developmental dyscalculia. *Learning and Individual Differences*, *22*(1), 164–170. https://doi.org/10.1016/j.lindif.2011.09.013

Mejias, S., Mussolin, C., Rousselle, L., Grégoire, J., & Nol, M. P. (2012). Numerical and nonnumerical estimation in children with and without mathematical learning disabilities. *Child Neuropsychology*, *18*(6), 550–575. https://doi.org/10.1080/09297049.2011.625355

Mejias, S., & Schiltz, C. (2013). Estimation abilities of large numerosities in Kindergartners. *Frontiers in Psychology*, *4*, 1–12. https://doi.org/10.3389/fpsyg.2013.00518

Mix, K. S., Levine, S. C., & Newcombe, N. S. (2016). Development of quantitative thinking across correlated dimensions. In *Continuous issues in numerical cognition* (pp. 1-33). Academic Press.

Moyer, R. S., & Landauer, T. K. (1967). Time required for judgment of numerical inequality. *Nature*, *215*, 1519–1520.

Mussolin, C., De Volder, A., Grandin, C., Schlögel, X., Nassogne, M. C., & Noël, M. P. (2010). Neural correlates of symbolic number comparison in developmental dyscalculia. *Journal of Cognitive Neuroscience*, *22*(5), 860–874. https://doi.org/10.1162/jocn.2009.21237

Mussolin, C., Mejias, S., & Noël, M. P. (2010). Symbolic and nonsymbolic number comparison in children with and without dyscalculia. *Cognition*, *115*(1), 10–25. https://doi.org/10.1016/j.cognition.2009.10.006

Namdar, G., Tzelgov, J., Algom, D., & Ganel, T. (2014). Grasping numbers: Evidence for automatic influence of numerical magnitude on grip aperture. *Psychonomic Bulletin and Review*, *21*(3), 830–835. https://doi.org/10.3758/s13423-013-0550-9

Nieder, A. (2005). Counting on neurons: The neurobiology of numerical competence. *Nature Reviews Neuroscience*, *6*(3), 177–190. https://doi.org/10.1038/nrn1626

Nieder, A. (2016). The neuronal code for number. *Nature Reviews Neuroscience*, *17*(6), 366–382. https://doi.org/10.1038/nrn.2016.40

Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annual Review of Neuroscience*, *32*, 185–208. https://doi.org/10.1146/annurev.neuro.051508.135550

Nieder, A., Diester, I., & Tudusciuc, O. (2006). Temporal and spatial enumeration processes in the primate parietal cortex. *Science*, *313*(5792), 1431–1435. https://doi.org/10.1126/science.1130308

Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences*, *101*(19), 7457–7462. https://doi.org/10.1073/pnas.0402239101

Nys, J., & Content, A. (2012). Judgement of discrete and continuous quantity in adults: Number counts! *Quarterly Journal of Experimental Psychology*, *65*(4), 675–690. https://doi.org/10.1080/17470218.2011.619661

Odic, D. (2018). Children's intuitive sense of number develops independently of their perception of area, density, length, and time. *Developmental Science*, *21*(2), 1–15. https://doi.org/10.1111/desc.12533

Odic, D., Libertus, M. E., Feigenson, L., & Halberda, J. (2013). Developmental change in the acuity of approximate number and area representations. *Developmental Psychology*, *49*(6), 1103–1112. https://doi.org/10.1037/a0029472

Odic, D., & Starr, A. (2018). An Introduction to the Approximate Number System. *Child Development Perspectives*, *12*(4), 223–229. https://doi.org/10.1111/cdep.12288

Park, J. (2018). A neural basis for the visual sense of number and its development: A steady-state visual evoked potential study in children and adults. *Developmental Cognitive Neuroscience*, *30*, 333–343. https://doi.org/10.1016/j.dcn.2017.02.011

Park, J. (2021). Flawed stimulus design in additive-area heuristic studies. *Cognition*, *229*, 104919. https://doi.org/10.1016/j.cognition.2021.104919

Park, J., Dewind, N. K., Woldorff, M. G., & Brannon, E. M. (2016). Rapid and Direct Encoding of Numerosity in the Visual Stream. *Cerebral Cortex*, *26*(2), 748–763. https://doi.org/10.1093/cercor/bhv017

Passolunghi, M. C., & Siegel, L. S. (2004). Working memory and access to numerical information in children with disability in mathematics. *Journal of Experimental Child Psychology*, *88*(4), 348–367. https://doi.org/10.1016/j.jecp.2004.04.002

Paul, J. M., van Ackooij, M., ten Cate, T. C., & Harvey, B. M. (2022). Numerosity tuning in human association cortices and local image contrast representations in early visual cortex. *Nature Communications*, *13*(1), 1–15. https://doi.org/10.1038/s41467-022-29030-z

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., & Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods*, *51*(1), 195–203. https://doi.org/10.3758/s13428-018-01193-y

Pekár, J., & Kinder, A. (2020). The interplay between non-symbolic number and its continuous visual properties revisited: Effects of mixing trials of different types. *Quarterly Journal of Experimental Psychology*, *73*(5), 698–710. https://doi.org/10.1177/1747021819891068

Peng, P., Wang, C., & Namkung, J. (2018). Understanding the Cognition Related to Mathematics Difficulties: A Meta-Analysis on the Cognitive Deficit Profiles and the Bottleneck Theory. *Review of Educational Research*, *88*(3), 434–476. https://doi.org/10.3102/0034654317753350

Peters, L., & Ansari, D. (2019). Are specific learning disorders truly specific, and are they disorders? *Trends in Neuroscience and Education*, *17*. https://doi.org/10.1016/j.tine.2019.100115

Petrizzo, I., Anobile, G., & Arrighi, R. (2020). Motor adaptation distorts visual space. *Vision Research*, *171*, 31–35. https://doi.org/10.1016/j.visres.2020.04.007

Philippi, T. G., van Erp, J. B. F., & Werkhoven, P. J. (2008). Multisensory temporal numerosity judgment. *Brain Research*, *1242*, 116–125. https://doi.org/10.1016/j.brainres.2008.05.056

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Sciences*, *14*(12), 542–551. https://doi.org/10.1016/j.tics.2010.09.008

Piazza, M., De Feo, V., Panzeri, S., & Dehaene, S. (2018). Learning to focus on number. *Cognition*, *181*, 35–45. https://doi.org/10.1016/j.cognition.2018.07.011

Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., Dehaene, S., & Zorzi, M. (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition*, *116*(1), 33–41. https://doi.org/10.1016/j.cognition.2010.03.012

Piazza, M., Fumarola, A., Chinello, A., & Melcher, D. (2011). Subitizing reflects visuo-spatial object individuation capacity. *Cognition*, *121*(1), 147–153. https://doi.org/10.1016/j.cognition.2011.05.007

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, *44*(3), 547–555. https://doi.org/10.1016/j.neuron.2004.10.014

Piazza, M., Mechelli, A., Price, C. J., & Butterworth, B. (2006). Exact and approximate judgements of visual and auditory numerosity: An fMRI study. *Brain Research*, *1106*(1), 177–188. https://doi.org/10.1016/j.brainres.2006.05.104

Piazza, M., Pica, P., Izard, V., Spelke, E. S., & Dehaene, S. (2013). Education Enhances the Acuity of the Nonverbal Approximate Number System. *Psychological Science*, *24*(6), 1037–1043. https://doi.org/10.1177/0956797612464057

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A Magnitude Code Common to Numerosities and Number Symbols in Human Intraparietal Cortex. *Neuron*, *53*(2), 293–305. https://doi.org/10.1016/j.neuron.2006.11.022

Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and approximate arithmetic in an Amazonian indigene group. *Science*, *306*(5695), 499–503. https://doi.org/10.1126/science.1102085

Picon, E., Dramkin, D., & Odic, D. (2019). *Visual illusions help reveal the primitives of number perception*. *148(10),*1675. https://doi.org/http://dx.doi.org/10.1037/xge0000553

Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron*, *41*(6), 983–993. https://doi.org/10.1016/S0896-6273(04)00107-2

Pomè, A., Anobile, G., Cicchini, G. M., & Burr, D. C. (2019). Different reaction-times for subitizing, estimation, and texture. *Journal of Vision*, *19*(6), 1–9. https://doi.org/10.1167/19.6.14

Pomè, A., Anobile, G., Cicchini, G. M., Scabia, A., & Burr, D. C. (2019). Higher attentional costs for numerosity estimation at high densities. *Attention, Perception, and Psychophysics*, *81*(8), 2604–2611. https://doi.org/10.3758/s13414-019-01831-3

Price, G. R., Holloway, I., Räsänen, P., Vesterinen, M., & Ansari, D. (2007). Impaired parietal magnitude processing in developmental dyscalculia. *Current Biology*, *17*(24), 1042–1043. https://doi.org/10.1016/j.cub.2007.10.013

Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does subitizing reflect numerical estimation? *Psychological Science*, *19*(6), 607–614. https://doi.org/10.1111/j.1467-9280.2008.02130.x

Ritchie, S. J., & Bates, T. C. (2013). Enduring Links From Childhood Mathematics and Reading Achievement to Adult Socioeconomic Status. *Psychological Science*, *24*(7), 1301–1308. https://doi.org/10.1177/0956797612466268

Roitman, J. D., Brannon, E. M., Andrews, J. R., & Platt, M. L. (2007). Nonverbal representation of time and number in adults. *Acta Psychologica*, *124*(3), 296–318. https://doi.org/10.1016/j.actpsy.2006.03.008

Roquet, A., & Lemaire, P. (2019). Strategy variability in numerosity comparison task: a study in young and older adults. *Open Psychology*, *1*(1), 152–167. https://doi.org/10.1515/psych-2018-0011

Rotzer, S., Kucian, K., Martin, E., Aster, M. von, Klaver, P., & Loenneker, T. (2008). Optimized voxel-based morphometry in children with developmental dyscalculia. *NeuroImage*, *39*(1), 417–422. https://doi.org/10.1016/j.neuroimage.2007.08.045

Rousselle, L., & Noël, M. P. (2007). Basic numerical skills in children with mathematics learning disabilities: A comparison of symbolic vs non-symbolic number magnitude processing. *Cognition*, *102*(3), 361–395. https://doi.org/10.1016/j.cognition.2006.01.005

Rousselle, L., & Noël, M.-P. (2008). The development of automatic numerosity processing in preschoolers: Evidence for numerosity-perceptual interference. *Developmental Psychology, 44*(2), 544–560. https://doi.org/10.1037/0012-1649.44.2.544

Salti, M., Katzin, N., Katzin, D., Leibovich, T., & Henik, A. (2017). One tamed at a time: A new approach for controlling continuous magnitudes in numerical comparison tasks. *Behavior Research Methods*, *49*(3), 1120–1127. https://doi.org/10.3758/s13428-016-0772-7

Sasanguie, D., De Smedt, B., & Reynvoet, B. (2017). Evidence for distinct magnitude systems for symbolic and non-symbolic number. *Psychological Research*, *81*(1), 231–242. https://doi.org/10.1007/s00426-015-0734-1

Schneider, M., Beeres, K., Coban, L., Merz, S., Susan Schmidt, S., Stricker, J., & De Smedt, B. (2017). Associations of non-symbolic and symbolic numerical magnitude processing with mathematical competence: a meta-analysis. *Developmental Science*, *20*(3). https://doi.org/10.1111/desc.12372

Sella, F., Berteletti, I., Lucangeli, D., & Zorzi, M. (2016). Spontaneous non-verbal counting in toddlers. *Developmental Science*, *19*(2), 329–337. https://doi.org/10.1111/desc.12299

Sella, F., Onnivello, S., Lunardon, M., Lanfranchi, S., & Zorzi, M. (2021). Training basic numerical skills in children with Down syndrome using the computerized game “The Number Race.” *Scientific Reports*, *11*(1), 1–14. https://doi.org/10.1038/s41598-020-78801-5

Sella, F., Tressoldi, P., Lucangeli, D., & Zorzi, M. (2016). Training numerical skills with the adaptive videogame “The Number Race”: A randomized controlled trial on preschoolers. *Trends in Neuroscience and Education*, *5*(1), 20–29. https://doi.org/10.1016/j.tine.2016.02.002

Sengupta, R., Bapiraju, S., & Melcher, D. (2017). Big and small numbers: Empirical support for a single, flexible mechanism for numerosity perception. *Attention, Perception, and Psychophysics*, *79*(1), 253–266. https://doi.org/10.3758/s13414-016-1221-5

Skagerlund, K., & Träff, U. (2016). Number Processing and Heterogeneity of Developmental Dyscalculia: Subtypes With Different Cognitive Profiles and Deficits. *Journal of Learning Disabilities*, *49*(1), 36–50. https://doi.org/10.1177/0022219414522707

Smets, K., Sasanguie, D., Szücs, D., & Reynvoet, B. (2015). The effect of different methods to construct non-symbolic stimuli in numerosity estimation and comparison. *Journal of Cognitive Psychology*, *27*(3), 310–325. https://doi.org/10.1080/20445911.2014.996568

Sokolowski, H. M., Fias, W., Bosah Ononye, C., & Ansari, D. (2017). Are numbers grounded in a general magnitude processing system? A functional neuroimaging meta-analysis. *Neuropsychologia*, *105*, 50–69. https://doi.org/10.1016/j.neuropsychologia.2017.01.019

Sokolowski, H. M., Fias, W., Mousa, A., & Ansari, D. (2017). Common and distinct brain regions in both parietal and frontal cortex support symbolic and nonsymbolic number processing in humans: A functional neuroimaging meta-analysis. *NeuroImage*, *146*, 376–394. https://doi.org/10.1016/j.neuroimage.2016.10.028

Starr, A., DeWind, N. K., & Brannon, E. M. (2017). The contributions of numerical acuity and non-numerical stimulus features to the development of the number sense and symbolic math achievement. *Cognition*, *168*, 222–233. https://doi.org/10.1016/j.cognition.2017.07.004

Starr, A., Libertus, M. E., & Brannon, E. M. (2013). Number sense in infancy predicts mathematical abilities in childhood. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(45), 18116–18120. https://doi.org/10.1073/pnas.1302751110

Stoianov, I., & Zorzi, M. (2012). Emergence of a “visual number sense” in hierarchical generative models. *Nature Neuroscience*, *15*(2), 194–196. https://doi.org/10.1038/nn.2996

Szkudlarek, E., Park, J., & Brannon, E. M. (2021). Failure to replicate the benefit of approximate arithmetic training for symbolic arithmetic fluency in adults. *Cognition*, *207*, 104521. https://doi.org/10.1016/j.cognition.2020.104521

Szucs, D., Devine, A., Soltesz, F., Nobes, A., & Gabriel, F. (2013). Developmental dyscalculia is related to visuo-spatial memory and inhibition impairment. *Cortex*, *49*(10), 2674–2688. https://doi.org/10.1016/j.cortex.2013.06.007

Testolin, A., Dolfi, S., Rochus, M., & Zorzi, M. (2020). Visual sense of number vs. sense of magnitude in humans and machines. *Scientific Reports*, *10*(1), 1–13. https://doi.org/10.1038/s41598-020-66838-5

Testolin, A., & McClelland, J. L. (2020). Do estimates of numerosity really adhere to Weber’s law? A reexamination of two case studies. *Psychonomic Bulletin and Review, 28,* 158-168. https://doi.org/10.3758/s13423-020-01801-z

Thomas, E. C., & Brown, I. (1974). Time perception and the filled-duration illusion. *Perception & Psychophysics*, *16*(3), 449–458. https://doi.org/10.3758/BF03198571

Tibber, M. S., Greenwood, J. A., & Dakin, S. C. (2012). Number and density discrimination rely on a common metric: Similar psychophysical effects of size, contrast, and divided attention. *Journal of Vision*, *12*(6), 1–19. https://doi.org/10.1167/12.6.8

Togoli, I., Crollen, V., Arrighi, R., & Collignon, O. (2020). The shared numerical representation for action and perception develops independently from vision. *Cortex*, *129*, 436–445. https://doi.org/10.1016/j.cortex.2020.05.004

Togoli, I., Fedele, M., Fornaciai, M., & Bueti, D. (2021). Serial dependence in time and numerosity perception is dimension-specific. *Journal of Vision*, *21*(5), 1–15. https://doi.org/10.1167/jov.21.5.6

Togoli, I., Fornaciai, M., & Bueti, D. (2021). The specious interaction of time and numerosity perception. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1959). https://doi.org/10.1098/rspb.2021.1577

Tokita, M., Ashitani, Y., & Ishiguchi, A. (2013). Is approximate numerical judgment truly modality-independent? Visual, auditory, and cross-modal comparisons. *Attention, Perception, and Psychophysics*, *75*(8), 1852–1861. https://doi.org/10.3758/s13414-013-0526-x

Tokita, M., & Ishiguchi, A. (2011). Temporal information affects the performance of numerosity discrimination: Behavioral evidence for a shared system for numerosity and temporal processing. *Psychonomic Bulletin and Review*, *18*(3), 550–556. https://doi.org/10.3758/s13423-011-0072-2

Tokita, M., & Ishiguchi, A. (2012). Behavioral evidence for format-dependent processes in approximate numerosity representation. *Psychonomic Bulletin and Review*, *19*(2), 285–293. https://doi.org/10.3758/s13423-011-0206-6

Tokita, M., & Ishiguchi, A. (2016). Precision and Bias in Approximate Numerical Judgment in Auditory, Tactile, and Cross-modal Presentation. *Perception*, *45*(1–2), 56–70. https://doi.org/10.1177/0301006615596888

Tomlinson, R. C., DeWind, N. K., & Brannon, E. M. (2020). Number sense biases children's area judgments. *Cognition*, *204*, 104352. https://doi.org/10.1016/j.cognition.2020.104352

Trick, L. M., and Pylyshyn, Z. W. (1994). Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychological review, 101*(1), 80.

Tsouli, A., Dumoulin, S. O., te Pas, S. F., & van der Smagt, M. J. (2019). Adaptation reveals unbalanced interaction between numerosity and time. *Cortex*, *114*, 5–16. https://doi.org/10.1016/j.cortex.2018.02.013

Tsouli, A., van der Smagt, M. J., Dumoulin, S. O., & te Pas, S. F. (2019). Distinct temporal mechanisms modulate numerosity perception. *Journal of Vision*, *19*(6), 1–22. https://doi.org/10.1167/19.6.19

Tudusciuc, O., & Nieder, A. (2007). Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proceedings of the National Academy of Sciences*, *104*(36), 14513–14518. https://doi.org/10.1073/pnas.0705495104

Tudusciuc, O., & Nieder, A. (2009). Contributions of primate prefrontal and posterior parietal cortices to length and numerosity representation. *Journal of Neurophysiology*, *101*(6), 2984–2994. https://doi.org/10.1152/jn.90713.2008

van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., Etz, A., Evans, N. J., Gronau, Q. F., Haaf, J. M., Hinne, M., Kucharský, Š., Ly, A., Marsman, M., Matzke, D., Gupta, A. R. K. N., Sarafoglou, A., Stefan, A., Voelkel, J. G., & Wagenmakers, E. J. (2020). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychonomic Bulletin and Review*, 813–826. https://doi.org/10.3758/s13423-020-01798-5

van Marle, K., Chu, F. W., Li, Y., & Geary, D. C. (2014). Acuity of the approximate number system and preschoolers' quantitative development. *Developmental Science*, *17*(4), 492–505. https://doi.org/10.1111/desc.12143

van Rinsveld, A., Guillaume, M., Kohler, P. J., Schiltz, C., Gevers, W., & Content, A. (2020). The neural signature of numerosity by separating numerical and continuous magnitude extraction in visual cortex with frequency-tagged EEG. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(11), 5726–5732. https://doi.org/10.1073/pnas.1917849117

Vanbinst, K., Ghesquière, P., & De Smedt, B. (2014). Arithmetic strategy development and its domain-specific and domain-general cognitive correlates: A longitudinal study in children with persistent mathematical learning difficulties. *Research in Developmental Disabilities*, *35*(11), 3001–3013. https://doi.org/10.1016/j.ridd.2014.06.023

Vanmarle, K., & Wynn, K. (2006). Six-month-old infants use analog magnitudes to represent duration. *Developmental Science*, *9*(5). https://doi.org/10.1111/j.1467-7687.2006.00508.x

Viswanathan, P., & Nieder, A. (2013). Neuronal correlates of a visual "sense of number" in primate parietal and prefrontal cortices. *Proceedings of the National Academy of Sciences*, *110*(27), 11187–11192. https://doi.org/10.1073/pnas.1308141110

Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483–488. https://doi.org/10.1016/j.tics.2003.09.002

Wang, J., & Feigenson, L. (2021). Dynamic changes in numerical acuity in 4-month-old infants. *Infancy*, *26*(1), 47–62. https://doi.org/10.1111/infa.12373

Ward, C., & Smuts, B. B. (2007). Quantity-based judgments in the domestic dog (Canis lupus familiaris). *Animal Cognition*, *10*(1), 71–80. https://doi.org/10.1007/s10071-006-0042-7

Wechsler, D. (2003). *Wechsler intelligence scale for children (4th ed.).* The Psychological Corporation.

Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal Counting in Humans: The Psychophysics of Number Representation. *Psychological Science*, *10*(2), 130–137. https://doi.org/10.1111/1467-9280.00120

Wilkey, E. D., Barone, J. C., Mazzocco, M. M. M., Vogel, S. E., & Price, G. R. (2017). The effect of visual parameters on neural activation during nonsymbolic number comparison and its relation to math competency. *NeuroImage*, *159*, 430–442. https://doi.org/10.1016/j.neuroimage.2017.08.023

Wilkey, E. D., Men, V., Shanley, L., Heller, N. A., Sabb, F., Clarke, B., Ansari, D., & Cohen, J. C. (2021). Sharpening, focusing, and developing: A study of change in nonsymbolic number comparison skills and math achievement in 1st grade. *Developmental Science, 25*(3), e13194. https://doi.org/10.1111/desc.13194

Wilson, A. J., Revkin, S. K., Cohen, D., Cohen, L., & Dehaene, S. (2006). An open trial assessment of “the number race”, an adaptive computer game for remediation of dyscalculia. *Behavioral and Brain Functions*, *2*, 1–16. https://doi.org/10.1186/1744-9081-2-20

Xu, F., & Spelke, E. (2000). Large number discrimination in 6-month-old infants: Evidence for the accumulator model. *Cognition*, *74*, B1–B11. https://doi.org/10.1016/s0163-6383(98)91983-x

Yates, M. J., Loetscher, T., & Nicholls, M. E. R. (2012). A generalized magnitude system for space, time, and quantity? A cautionary note. *Journal of Vision*, *12*(7), 1–7. https://doi.org/10.1167/12.7.9

Yousif, S. R., & Keil, F. C. (2020). Area, not number, dominates estimates of visual quantities. *Scientific Reports*, *10*(1), 1–13. https://doi.org/10.1038/s41598-020-68593-z

Zanon, M., Potrich, D., Bortot, M., & Vallortigara, G. (2022). Towards a standardization of non-symbolic numerical experiments: GeNEsIS, a flexible and user-friendly tool to generate controlled stimuli. *Behavior Research Methods*, *54*(1), 146–157. https://doi.org/10.3758/s13428-021-01580-y

Zimmermann, E., & Fink, G. R. (2016). Numerosity perception after size adaptation. *Scientific Reports*, *6*, 1–7. https://doi.org/10.1038/srep32810

Zorzi, M., & Testolin, A. (2018). An emergentist perspective on the origin of number sense. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1740). https://doi.org/10.1098/rstb.2017.0043

Appendix

I - Supplementary description of methods used in Chapter 3-4

In temporal sequences of events, we can consider as intrinsic features mean event duration as the average duration of the individual events (MED) and mean event period as the total stimulus duration divided by the number of events (MEP). Extrinsic temporal features are total event duration as the sum of length of all pulses (TED) and total stimulus duration as the time from the beginning of the first pulse to the end of the last pulse, intervals included (TSD). Following the reasoning of DeWind and colleagues (2015) we can then define two variables independent from numerosity, as:

- $Duration = TED \times IED$
  or
  $log_2(Duration) = \ log_2(\ TED) + log_2(\ MED)$

- $Temporal\ Spacing = TSD \times MEP$
  or
  $log_2(Temporal\ Spacing) = \ log_2(\ TSD) + log_2(\text{MEP})$

Where:

$$log_2(n) = \ log_2\left(\frac{TED}{MED}\right) = \ log_2\left(\frac{TSD}{MEP}\right)$$

Therefore, we can mathematically describe the individual temporal features in terms of the three cardinal dimensions Numerosity (n), *Duration* (Dur) and *Temporal Spacing* (TmSp):

- $TED = \sqrt{Duration\ \times n}$
- $MED = \sqrt{\frac{Duration}{n}}$
- $TSD = \sqrt{Temporal\ spacing\ \times n}$
- $MEP = \sqrt{\frac{Temporal\ spacing}{n}}$
- $Coverage = \sqrt{\frac{Duration}{Temporal\ spacing}}$

Note that when we log scale the axes, the relationship between the cardinal dimensions to the other temporal features becomes linear. Moreover, in log space, the distance between stimulus points becomes proportional to the ratios of their features.

Table A.1. Algebraic relationship between several temporal features and cardinal features in log space

	Log of feature in terms of log of three orthogonal dimensions	**Log of feature ratio in terms of log of three orthogonal ratios**
Total event duration (TED)	$\log(TED) = \frac{1}{2}\log(Dur) + \frac{1}{2}\log(n)$	$\log(r_{TED}) = \frac{1}{2}\log(r_{Dur}) + \frac{1}{2}\log(r_n)$
Mean event duration (MED)	$\log(MED) = \frac{1}{2}\log(Dur) - \frac{1}{2}\log(n)$	$\log(r_{MED}) = \frac{1}{2}\log(r_{Dur}) - \frac{1}{2}\log(r_n)$
Total stimulus duration (TSD)	$\log(TSD) = \frac{1}{2}\log(TmSp) + \frac{1}{2}\log(n)$	$\log(r_{TSD}) = \frac{1}{2}\log\left(r_{TmSp}\right) + \frac{1}{2}\log(r_n)$
Mean event period (MEP)	$\log(MEP) = \frac{1}{2}\log(TmSp) - \frac{1}{2}\log(n)$	$\log(r_{MEP}) = \frac{1}{2}\log\left(r_{TmSp}\right) - \frac{1}{2}\log(r_n)$
Coverage (Cov)	$\log(Cov) = \frac{1}{2}\log(Dur) - \frac{1}{2}\log(TmSp)$	$\log(r_{Cov}) = \frac{1}{2}\log(r_{Dur}) - \frac{1}{2}\log(r_{TmSp})$

II - Supplementary description of methods used in Chapter 5

As described by DeWind and colleagues (2015) and Park (2021), when creating visual arrays of dots, we can consider various continuous magnitudes related to the single items and the entire arrays. We define item surface area (ISA) the individual area of the dots and total surface area the area of the entire set (TSA). We also define field area (FA) as the area where items are placed in the image (an approximation of convex hull), and sparsity (Spar) the inverse of density as n/FA. We can then compute two variables independent from numerosity, as:

- $Size = TSA \times ISA$

  or

  $log_2(Size) = \ log_2(\ TSA) + log_2(\ ISA)$

- $Spacing = FA \times Spar$

  or

  $log_2(Spacing) = \ log_2(\ FA) + log_2(Spar)$

Where:

$$log_2(n) = \ log_2\left(\frac{TSA}{ISA}\right) = \ log_2\left(\frac{FA}{Spar}\right)$$

Individual spatial magnitudes can be described in terms of the three cardinal dimensions Numerosity (n), *Size* (Sz) and *Spacing* (Sp):

- $TSA = \ \sqrt{Sz \ \times n}$
- $ISA = \ \sqrt{\frac{Sz}{n}}$
- $FA = \ \sqrt{Sp \ \times n}$
- $Spar = \ \sqrt{\frac{Sp}{n}}$
- $Total\ Perimeter\ (TP) = \ 2\sqrt{\pi} \times \ Sz^{\frac{1}{4}} \times \ n^{\frac{3}{4}}$
- $Item\ Perimeter\ (IP) = \ 2\sqrt{\pi} \times \ Sz^{\frac{1}{4}} \times \ n^{-\frac{1}{4}}$

- $Coverage\ (Cov) = \sqrt{\frac{Sz}{Sp}}$

- $Apparent\ Closeness\ (AC) = \sqrt{Sz \times Sp}$

Table A.2. Algebraic relationship between several spatial features and cardinal features in log space

	Log of feature in terms of log of three orthogonal dimensions	**Log of feature ratio in terms of log of three orthogonal ratios**
Total surface area (TSA)	$\log(TSA) = \frac{1}{2}\log(Sz) + \frac{1}{2}\log(n)$	$\log(r_{TSA}) = \frac{1}{2}\log(r_{Sz}) + \frac{1}{2}\log(r_n)$
Item surface area (ISA)	$\log(ISA) = \frac{1}{2}\log(Sz) - \frac{1}{2}\log(n)$	$\log(r_{ISA}) = \frac{1}{2}\log(r_{Sz}) - \frac{1}{2}\log(r_n)$
Field area (FA)	$\log(FA) = \frac{1}{2}\log(Sp) + \frac{1}{2}\log(n)$	$\log(r_{FA}) = \frac{1}{2}\log(r_{Sp}) + \frac{1}{2}\log(r_n)$
Sparsity (Spar)	$\log(Spar) = \frac{1}{2}\log(Sp) - \frac{1}{2}\log(n)$	$\log(r_{Spar}) = \frac{1}{2}\log(r_{Sp}) - \frac{1}{2}\log(r_n)$
Total perimeter (TP)	$\log(TP) = \log(2\sqrt{\pi}) + \frac{1}{4}\log(Sz) + \frac{3}{4}\log(n)$	$\log(r_{TP}) = \frac{1}{4}\log(r_{Sz}) + \frac{3}{4}\log(r_n)$
Item perimeter (IP)	$\log(IP) = \log(2\sqrt{\pi}) + \frac{1}{4}\log(Sz) - \frac{1}{4}\log(n)$	$\log(r_{IP}) = \frac{1}{4}\log(r_{Sz}) - \frac{1}{4}\log(r_n)$
Coverage (Cov)	$\log(Cov) = \frac{1}{2}\log(Sz) - \frac{1}{2}\log(Sp)$	$\log(r_{Cov}) = \frac{1}{2}\log(r_{Sz}) - \frac{1}{2}\log(r_{Sp})$
Apparent Closeness (AC)	$\log(AC) = \frac{1}{2}\log(Sz) + \frac{1}{2}\log(Sp)$	$\log(r_{AC}) = \frac{1}{2}\log(r_{Sz}) + \frac{1}{2}\log(r_{Sp})$